Habitat – Fishery Linkages and Implications for Habitat Repair

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Executive Summary

Concept

New South Wales Department of Primary Industries (NSW DPI) presents new information exploring the linkages between estuarine habitats and exploited species. Establishing linkages between fisheries and the habitats that support them is essential to the effective management and repair of marine and estuarine seascapes. A combination of novel chemical techniques, extensive field work, and numerical modelling was undertaken in several of New South Wales' most important estuarine fisheries between 2013-2016. This allowed the description of habitat-fishery linkages for penaeid prawn species, and other exploited fish and crab species. The findings demonstrate the extensive value of estuarine habitats that is realised through fisheries harvest, and this will support the business case for repair of these habitats in the years to come.

Background

Rapid development of communities, industry and agriculture around estuaries in the early 20th century showed little regard for the importance of estuarine habitats to productivity of aquatic ecosystems and the exploited species that rely on them. Reclamation and drying has led to the demise of extensive coastal saltmarsh and mangrove habitats (e.g. Evans and Williams, 2010), and the installation of floodgates has seen the widespread loss of connectivity between these wetlands and estuarine waters. This has contributed to a reduction of some 72% of prime fish habitat available to support estuarine fish species on the north coast of Australia (Rogers et al., 2015).

In recent years, the case for extensive estuarine habitat rehabilitation in Australia has been developing. A recent FRDC-funded business case suggested that relatively simple remediation activities (such as opening floodgates) can lead to substantial economic benefits (Creighton, 2013) through enhancement of the various ecosystem services derived from estuaries, especially fishery productivity. On the basis of this assessment, investment of the AUD350 million (Australia-wide) needed to undertake the necessary repair is expected to be recouped through these enhancements within 5 years (Creighton et al., 2015). To encourage investment in habitat repair, there is a need to prioritise and plan works to maximise benefits (Beck et al., 2001), and also to further develop the business case by refining estimates of associated economic benefits.

Given the large volume of harvest, high value of product, and general reliance on estuaries during their life history, it has been suggested that habitat repair should focus on areas of potential benefit to penaeid prawn species (Creighton et al., 2015). However, given the broad range of exploited species that use estuarine habitats, habitat repair will also benefit a broad cross-section of species and fisheries. Using Eastern King Prawn as a focal species, this project quantitatively defines habitat-fishery linkages, and shows how the nursery concept can support the prioritisation, planning, design and assessment of estuarine habitat repair projects in New South Wales. We also attribute potential economic value that can be derived from estuarine habitats from a broader fisheries perspective, and consider the potential benefits that may be realised from targeted repair.

Objectives

Specifically, the objectives of this project were to:

1) Determine to what extent young Eastern King Prawn are using natural, degraded or rehabilitated habitat in estuaries, and the contribution of these habitats to the fishery;

2) Determine the hydrographic conditions which provide for maximum growth and survival of Eastern King Prawn within nursery habitats;

3) Assess the extent of key Eastern King Prawn habitat lost and remaining in the Hunter and Clarence river estuaries;

4) Outline the potential improvements to the Eastern King Prawn fishery that could be achieved through targeted wetland rehabilitation;

5) Extend information on habitat-fishery linkages to commercial fisheries, landowners and other catchment stakeholders and incorporate recommendations into fisheries or water management;

While Eastern King Prawn were the focal species for this project, feedback from FRDC requested that where possible the project broaden its scope to account for other exploited species. Consequently, a further objective was addressed through the project:

6) Establish quantitative habitat-fishery linkages for the main exploited species in both the Hunter River and Clarence River systems.

Methodology

A combination of stable isotope composition, quantitative sampling of juvenile Eastern King Prawn, and historic habitat mapping, was used to determine factors contributing to recruitment of Eastern King Prawn to various juvenile habitats. A novel assignment method was developed to assess the contribution of juveniles sourced from those habitats to the adult or exploited stock. The study was conducted in three important but contrasting estuaries in New South Wales: Lake Macquarie; Hunter River and Clarence River; and School Prawn were also investigated in the Hunter River. Further, the role of physicochemical variation on Eastern King Prawn was assessed by simulating changes in estuarine physicochemistry that had been observed in the study estuaries, under laboratory conditions, and measuring prawn survival and the energetic costs of respiration associated with these changes. The current and historic extent of dominant estuarine habitats in the Hunter River and Clarence River was mapped from aerial imagery, and used to interpret the patterns observed from the field studies in the context of previous habitat repair, as well as make recommendations for targeted habitat repair in the future. Information on Eastern King Prawn biology, tagging, fisheries, and broadscale patterns in habitat loss, was integrated with a recent FRDC-funded bioeconomic model for the species (Courtney et al., 2014) to determine where habitat repair should be targeted (across latitudinal gradients), and the likely impact of targeted repair scenarios.

Stable isotopes were also used to examine the links between estuarine habitats and the broader assemblage of exploited species in the Hunter River and Clarence River. This allowed us to establish the contribution of different estuary habitats to the biomass of the exploited stock. These data were incorporated into a simple set of relationships that used fisheries catch data, market value, and recent FRDC-funded research on the economic impacts of commercial fisheries in New South Wales (Voyer et al., 2016), to assign an economic value to saltmarsh and mangrove habitats in these estuaries.

Project findings were extended to key stakeholders during and following the project, through a range of extension activities.

Key findings

The approaches employed allowed the compilation of a diverse and unique set of data that revealed intricate patterns of habitat – fishery linkages, the impact of current and future habitat repair, and the broadscale values of estuarine habitats which are derived through fisheries harvest.

Taken together, the stable isotope analysis and quantitative sampling of juvenile Eastern King Prawn revealed similar relationships among estuaries. The most important juvenile habitats were generally situated 6-15 km from the estuary mouth, were shallow but had good connectivity to adjacent channels which ensured adequate supply of ocean-spawned post-larvae. There was good agreement between the abundance of Eastern King Prawn supported in these habitats, and the contribution of juveniles from these habitats to the adult or exploited stock. Eastern King Prawn abundance tended to peak at salinities around the isosmotic salinity for the juveniles, and the recently restored Hexham wetland in the Hunter River was an important nursery for the species. In the Clarence River, the saltmarsh plant *Sporobolus virginicus* was the dominant source of nutrition for juvenile Eastern King Prawn, with marsh-derived productivity supporting 69-97% of juvenile biomass.

Eastern King Prawn experienced mortality when conditions that reflected moderate and high estuarine inflow events were simulated in the laboratory, but this also revealed a relatively low energetic cost of respiration at salinities greater than 10. Fifty-percent mortality occurred when salinity changed at a rate of ~8 % h^{-1}, and complete mortality was experienced when salinity changed at a rate of ~14 % h^{-1}. During the study, an extreme east coast low was observed, representing a real life scenario of the more acute salinity changes tested in the laboratory. Water quality was monitored continuously throughout this event; the implications of our findings were subsequently evident in commercial catches which saw a 60% drop in harvest in the area fed with recruits from the affected estuarine nurseries. These findings show that juvenile Eastern King Prawn are relatively resilient to press effects in estuarine nurseries, but pulse effects are likely to lead to significant mortality which has concomitant impacts on fisheries harvest.

Modelling of habitat repair scenarios suggested that repairing 200 ha of estuarine habitat would have differential effects along the NSW coast. The greatest benefit to the NSW Eastern King Prawn fishery would occur from repair targeted in Zone 3, for which 200 ha of repair would lead to an overall increase in annual Eastern King Prawn Ocean Trawl Fishery harvest of over 4% at a point 10 years after restoration. Increases of >2% would occur for 200 ha of repair in Zone 2 and 4, 0.5% for Zone 5, and negligible improvements for other zones. These are conservative estimates, as they do not include the (potentially considerable) value of prawns sourced from New South Wales estuaries that are harvested in Queensland waters.

For other exploited species in the Hunter River and Clarence River, stable isotope analysis indicated that saltmarsh habitats (i.e. *Sporobolous virginicus*) usually provided over 50% of nutrition for commercially sized individuals in these systems. Mangrove and other mangrove-associated producers provided the second greatest contribution of nutrition to the exploited biomass. Modelling incorporated these data alongside fishery catch histories and market values to estimate that the total economic output from fisheries harvest derived from productivity in these habitats ranged from AUD2,579- 25,741 ha^{-1} y^{-1} and AUD316- 5,297 ha^{-1} y^{-1} for saltmarsh and mangrove respectively. This suggests that restoration efforts directed at saltmarsh environments may be highly beneficial to commercial fisheries within estuarine systems.

Implications for relevant stakeholders

The key findings will provide commercial prawn fishers long-sought after answers to anomalies they have reported, such as reduced catch numbers and growth rates in years of heavy rain events, while also providing fishers with a better understanding of the key relationships between exploited species and estuarine habitats.

Furthermore, this information clearly demonstrates the impact of coastal land-use decisions such as historic drainage of wetlands on the productivity of fisheries. This information contributes to a greater appreciation of the implications of these decisions on the viability of coastal industries, businesses and the communities they support. Provision of initial estimates of habitat values will not only support this, but will assist in national efforts to better value natural assets.

Importantly this new information assists in building capacity in the industry and coastal communities to support better protection and preservation of key habitats. Better informed coastal communities will provide additional impetus for Natural Resource Managers and policy makers to drive change in the protection and management of these valuable resources through better targeted rehabilitation and protection efforts and stronger legislation. These resulting activities should help to increase the resilience of fisheries to future challenges including climate change.

The findings provide strong opportunities for Commercial (and Recreational) Fisheries Managers to consider and incorporate alternative measures, such as habitat management, into current and future management mechanisms that enhance fishery productivity. To ensure this opportunity is realised,

additional internal education activities are recommended. Increasing the fishery through habitat restoration provides a tangible means of increasing the economic contribution of the Eastern King Prawn fishery to the New South Wales economy. Similar research on other commercially and recreationally important species is recommended.

Keywords

Eastern king prawn, environmental accounting, repair, estuaries, rehabilitation, saltmarsh, mangrove, nursery, seagrass, provisioning, isotopes

Introduction

Estuaries are dynamic environments that are at the interface between freshwater, terrestrial and marine ecosystems. Estuarine systems form a key part of the coastal seascape, which are among the most productive of all aquatic ecosystems (Pauly and Christensen, 1995). Estuaries also provide a mosaic of different habitats that are important for both juvenile and adult fishes alike. The functional role of estuaries as nurseries for juveniles has received considerable attention (e.g. Beck et al., 2001, which has now been cited over 1600 times), and much of this literature identifies the role that estuarine vegetation within these habitats plays in various life stages of exploited fishes.

The vast majority of the world's population lives on or near estuarine environments (Lotze et al., 2006), and coastal catchments are often extensively utilised for agricultural purposes. In Australia, there is a heavy concentration of both human population and agriculture in coastal floodplains and a high degree of both urbanisation and agricultural development in coastal catchments. This has led to extensive anthropogenic modification of these environments. In urban areas, this often involves a complete transformation of the land-sea interface which includes land reclamation, shoreline modification, and sedimentation (McKinney, 2002). In rural areas, transformation also includes large-scale infilling of wetland and mangrove habitats (e.g. Evans and Williams, 2010), drying of wetland habitats (e.g. Rogers et al., 2015), and sedimentation arising from agricultural land-use practices. Over the last 200 years, the result has been considerable declines in the areal coverage of many different habitats, be they vegetated or otherwise, and also the modification of remaining habitats through altered physico-chemistry of the estuary.

Commercial and recreational fishing pressure in estuarine systems has generally increased alongside development and population growth. However, fisheries harvest has stagnated over the last 20 years which is likely due to constraints on productive capacity imposed by environmental changes across a range of scales (Taylor et al., 2017a), including those outlined above. Fisheries productivity is important for both the economy and food security; however, factors that are required to underpin this productivity do not always feature prominently in decision making surrounding development and land use. This is partially due to the fact that the relationship between such factors, fisheries production, and economic output, are poorly understood. Despite centuries of fishing activity in New South Wales, only recently have we gained a comprehensive understanding of the social and economic value of some of these fisheries to the local economy (Farber et al., 2006; O'Neill et al., 2014; Ives et al., 2013). At the state level, recent reports suggest that commercial fisheries and associated retail and processing in New South Wales are valued at over AUD500 million per annum (Voyer et al., 2016), while total economic output from recreational fisheries in New South Wales is estimated to be AUD3.65 billion (McIlgorm and Pepperell, 2013, converted to 2015 dollars). While these studies highlight the contribution that fisheries harvest and associated activities make to the New South Wales economy, there are few quantitative examples that extend such valuation to the factors that support healthy and productive fisheries (such as heathy habitat and good water quality).

The case for extensive estuarine habitat repair in Australia has been developing. A recent business case suggested that relatively simple remediation activities can lead to substantial economic benefits (Creighton, 2013) through enhancement of the various ecosystem services derived from estuaries, especially fishery productivity. On the basis of this assessment, investment of the AUD350 million (Australia-wide) needed to undertake the necessary repair is expected to be recouped through these enhancements within 5 years (Creighton et al., 2015). In New South Wales, a majority of the species that underpin fisheries productivity are thought to rely on estuaries for some or all of their life cycle. Consequently, improved knowledge of the linkages between habitats, recruitment, water quality, and fisheries harvest is required to link structural components of the ecosystem with the ecosystem services they support, and derive associated economic value. This is essential to encourage investment in habitat repair, prioritise and plan works to maximise benefits, and also to provide for analyses surrounding the economic value arising from these benefits, with which to compare with alternate land use strategies.

Historically, broad-scale links between productivity of estuarine habitats and the fisheries that rely on them have been used to build a case for habitat conservation and repair. Some of the best known examples of this rely heavily on the link between mangrove habitats and productivity of penaeid prawn fisheries (Turner, 1977; Rönnbäck, 1999), but consideration of even a small subset of the available literature demonstrates that there is substantial variation in such estimates. For example, Watson et al. (1993) estimated potential economic values of AUD72 –11,084 ha^{-1} y^{-1} (here and after, all values are converted to 2015 dollars) from prawn harvest derived from the standing stock of juveniles in seagrass in northern Australia; whereas Blandon and zu Ermgassen (2014) used a similar approach (across multiple species) and estimated the benefits of seagrass to commercial fisheries production to be as high as AUD31,650 ha^{-1} y^{-1}. Chong (2007) estimated the net fisheries contribution of mangrove forest (across multiple species) in Malaysia amounted to about USD967 ha^{-1} y^{-1}, and Bell (1997) calculated that coastal saltmarsh in the Gulf of Mexico supports recreational fisheries up to a value of about USD36,902 ha^{-1} y^{-1} (converted from value-per-acre). The different estimation approaches, species, habitats, fisheries and locations dealt with in this cross-section of studies likely contributes to the substantial variation in reported estimates. Nonetheless, with economic values spanning four orders of magnitude there is clearly scope to further refine our appreciation of the economic value of fishery-habitat linkages in estuarine ecosystems.

Penaeid prawn species are studied in the context of habitat repair for several reasons. They are generally highly fecund and fast growing, and their populations are thus likely to show benefits from any habitat repair efforts earlier than other species. Also, they generally have a high harvest volume coupled with a high market value, so habitat repair should lead to significant benefits. Finally, these species often have a general reliance on estuaries during their life history (Dall et al., 1990), so are most likely to benefit from estuarine habitat repair. Consequently, in Australia it has been suggested that habitat repair should focus on potential benefits to penaeid prawn species (Creighton et al., 2015), as this should demonstrate strong benefits “upfront”, which will support the justification of projects into the future. However, given the broad range of exploited species that also use estuarine habitats, there is no question that habitat repair will also benefit a broad cross-section of species and fisheries.

Using Eastern King Prawn as a focal species, this project quantitatively defines habitat-fishery linkages, and shows how the nursery concept can support the prioritisation, planning, design and assessment of estuarine habitat repair projects in New South Wales. We also attribute potential economic value that can be derived from estuarine habitats from a broader fisheries perspective, and consider the potential benefits that may be realised from targeted repair.

Eastern King Prawn

Eastern King Prawn (*Penaeus* [*Melicertus*] *plebejus*) (known hereafter as EKP) is an exploited species of penaeid prawn common to coastal regions of south-eastern Australia, between south-east Queensland and eastern Victoria. EKP is one of the most valuable species targeted in eastern Australia, and has a landed value in excess of AUD40 million (O'Neill et al., 2014). The species displays a type II penaeid life cycle, spawning off northern New South Wales and southern Queensland, with spawning intensity increases with decreasing latitude (Montgomery et al., 2007). Demersal eggs (Dakin, 1938; Dall et al., 1990) hatch into pelagic larvae, and disperse primarily in a southward direction in the East Australian Current, with spawning at higher latitudes leading to greater southward dispersal (Everett et al., 2017). Postlarvae migrate inshore (Rothlisberg et al., 1995) and into estuarine nurseries, where they settle and become demersal (Taylor and Ko, 2011). Prawns grow rapidly in the estuarine nursery during the summer months and emigrate to sea (Taylor et al., 2016), gradually moving offshore and northward to spawning grounds as they grow and mature (Montgomery, 1990). Consequently, there is a general gradient in prawn size (Gordon et al., 1995) and reproductive output (Montgomery et al., 2007) with decreasing latitude off the New South Wales coast.

EKP support a cross-jurisdictional oceanic demersal otter trawl fishery across New South Wales and Queensland (Prosser and Taylor, 2016), but small catches are also taken in the New South Wales Estuary General fishery (Taylor, 2016) and the inshore otter trawl fishery in Moreton Bay, Queensland (Wang et al., 2015). Catches in Victoria (at the far south of the species range) are small and do not occur every year (Suthers et al., 2016), and largely depend on optimal oceanic currents supplying recruits to waters in the far-south (Everett et al., 2017). The species is assessed as one biological stock (O'Neill et al., 2014), but managed under two adjacent management units from 22–28°S (Queensland), and 28–37.5°S (New South Wales, Prosser and Taylor, 2016). Due to the migratory nature and size structure of the species, in New South Wales the species is primarily targeted north of 33°S (O'Callaghan and Gordon, 2008), with the majority of harvest taken from waters north of 31°S.

Despite the significance of EKP fisheries in New South Wales and Queensland, there has been little targeted research of their early juvenile stages in New South Wales estuaries since the early 1970s. The estuaries of mid-north New South Wales are considered to be some of the most important recruitment areas for EKP, and fishers have provided many anecdotal reports of the extensive use of estuarine wetlands by young EKP prior to their degradation. Anecdotal information from fishers has also suggested adverse effects of freshwater inundation and lowering of salinities in estuarine nurseries on the growth and abundance of prawns. Quantitative knowledge on the use of estuarine nurseries by EKP, and their differential contribution of recruits to the exploited stock, is essential to address the information needs outlined in the previous section.

Other exploited species in New South Wales estuaries

While EKP was the focal species for this project, habitat-fishery linkages were also examined for several other important exploited fishes and crustaceans in New South Wales. The most significant of these is School Prawn (*Metapenaeus macleayi*) (known hereafter as SP), which is the second most valuable penaeid species harvested in New South Wales waters. Like EKP, SP display a Type-II penaeid life-cycle and share many common aspects of their life-history, but there are important differences in their biology and fishery. SP emigrate from estuarine systems but remain in the inshore area adjacent to the estuarine nursery to spawn, and do not undertake large migrations like the EKP. Also, harvest of SP is concentrated in estuaries and the inshore area, as opposed to EKP who are primarily harvested offshore.

Other exploited species that are dealt with in this study include Dusky Flathead (*Platycephalus fuscus*), Sea Mullet (*Mugil cephalus*), Yellowfin Bream (*Acanthopagrus australis*), Mulloway (*Argyrosomus japonicus*), Luderick (*Girella tricuspidata*), Giant Mud Crab (*Scylla serrata*), and Blue Swimmer Crab (*Portunus armatus*). Much of the background to Luderick and Yellowfin Bream is described in Curley et al. (2013), while other references provide background for Dusky Flathead (Gray and Barnes, 2008), Sea Mullet (Smith and Deguara, 2002), Mulloway (Silberschneider and Gray, 2008), Giant Mud Crab (Hill et al., 1982) and Blue Swimmer Crab (Kumar et al., 2000; Sumpton et al., 2003). Like EKP and SP, these species are known to rely upon estuarine habitats to varying degrees during their life cycle. Collectively, these species represent a large proportion of the commercial estuarine harvest in New South Wales, and also include some of the most common species targeted by recreational fishers (West et al., 2016).

Objectives

Specifically, the objectives of this project were to:

1) Determine to what extent young Eastern King Prawn are using natural, degraded or rehabilitated habitat in estuaries, and the contribution of these habitats to the fishery;

2) Determine the hydrographic conditions which provide for maximum growth and survival of Eastern King Prawn within nursery habitats;

3) Assess the extent of key Eastern King Prawn habitat lost and remaining in the Hunter and Clarence river estuaries;

4) Outline the potential improvements to the Eastern King Prawn fishery that could be achieved through targeted wetland rehabilitation;

5) Extend information on habitat-fishery linkages to commercial fisheries, landowners and other catchment stakeholders and incorporate recommendations into fisheries or water management;

While EKP were the focal species for this project, feedback from FRDC requested that where possible the project broaden its scope to account for other exploited species. Consequently, a further objective was addressed through the project:

6) Establish quantitative habitat-fishery linkages for the main exploited species in both the Hunter River and Clarence River systems.

Method

Study estuaries

The main estuaries studied in this project were the Hunter River estuary and the Clarence River estuary. Both these estuaries support significant fisheries dominated by the species outlined in the Introduction. Both these estuaries include wetland systems comprised of saltmarsh and mangrove habitats, but are seagrass limited, and have seen extensive habitat loss. An additional component of the project was conducted in Lake Macquarie. Unlike the Hunter River and Clarence River estuaries, aquatic vegetation in Lake Macquarie is dominated by various seagrass species. Lake Macquarie is closed to commercial fishing, but the estuary supports one of New South Wales' most important recreational fisheries. The estuary is an important nursery for EKP, and the recreational fishery encompasses a targeted, boutique EKP fishery, where prawns are harvested as they emigrate through the main channel during the third quarter of the lunar cycle.

Hunter River estuary

The Hunter River estuary is a wave-dominated barrier estuary located on the mid-northern coast of New South Wales, Australia (-32.91, 151.78). The estuary is fed by two major river systems, the Hunter River which drains the southern catchment, and the Williams River which drains the northern catchment. Both parts of the catchment are dominated by a combination of agriculture, coal mining, forest and national park. The lower estuary is heavily urbanised and includes the world's largest coal export port. Despite this, the lower estuary has abundant mangrove and saltmarsh habitats (Figure 1), which can be divided into three main areas: 1) Tomago wetland to the north; 2) Kooragang wetland, which is nested between the north and south arms of the lower estuary; and 3) Hexham wetland in the south. In addition, the estuary includes expansive shallow embayments located off the main channel in the north arm (Fullerton Cove and Fern Bay), and these are surrounded by extensive mangrove habitat (Figure 1). There is no seagrass present within the estuary.

The bifurcate channels in the lower estuary, and the off-channel embayments (Fullerton Cove and Fern Bay) make the Hunter River estuary a hydrologically complex system. The south arm of the estuary is heavily tidally dominated and characterised by an oceanic salinity regime. The upstream point of connection with the north arm represents a network of deltaic islands interspersed by very shallow channels, and consequently there is little influence of brackish water from the middle and upper estuary into south arm. Conversely, the north arm has a relatively contiguous channel from the mouth along the entire estuarine gradient. Consequently, there is a much greater influence of freshwater inflow from the upper estuary and a clear salinity gradient along the north arm under regular conditions (Figure 1). The estuary supports a substantial fishery, dominated by SP (Ruello, 1973), but also provides habitat for juvenile EKP who later recruit into the offshore trawl fishery (Ruello, 1971). There is also considerable harvest of various finfish and crab species (Taylor and Johnson, 2016), and while commercial fishing occurs from the ocean to Raymond Terrace (approximately 30 km from the ocean), the bulk (>75%) of commercial harvest (for both fish and crustaceans) occurs in or adjacent to the wetland systems and off-channel embayments in the north arm of the lower estuary

By the latter half of the 20th century the wetland systems in the lower Hunter River estuary had become severely degraded through development, grazing, and/or the installation of dykes and floodgates that removed connectivity between wetlands and the main estuary channels. Several rehabilitation projects have been carried out on these systems in recent decades, initially targeting the Kooragang wetland (undertaken from 1990-1996, Williams et al., 2000), followed by Tomago (undertaken from 2007-2011, Rayner and Glamore, 2010), and Hexham (from 2008-2013, Boys, 2016). These rehabilitation projects have largely involved restoring connectivity of these marsh and mangrove habitats to the estuary, thus allowing tidal flushing of the habitats. It is important to note that the repair of these locations (especially Tomago and Hexham) is relatively recent, and the systems are still undergoing changes which may have future implications for their productivity.

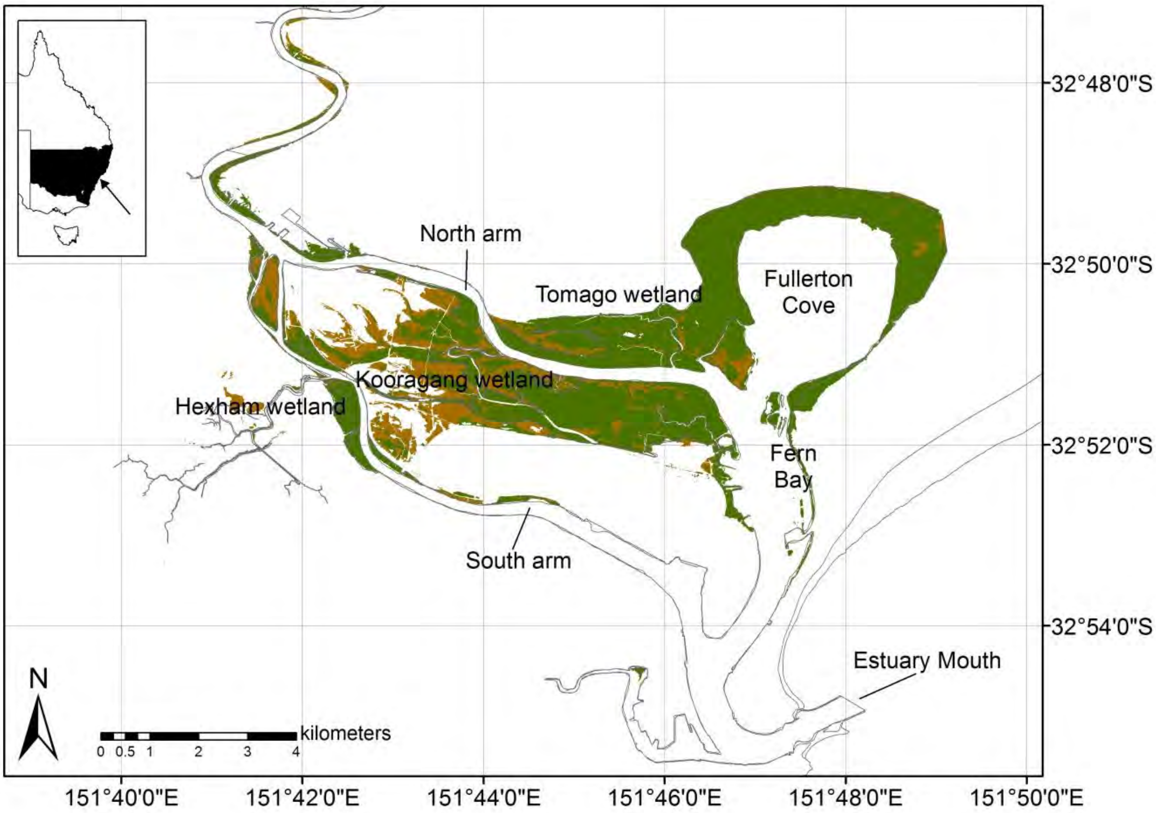

Figure 1 Map showing the lower Hunter River estuary and associated saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat. Main features of the estuary referred to in the text are labelled.

Clarence River estuary

The Clarence River estuary (-29.43, 153.37) is the largest estuarine system in New South Wales, and is classified as a mature, wave-dominated barrier estuary (Roy et al., 2001). The main river is fed by a large number of tributaries, mainly in the upper region of the floodplain, and the middle and lower estuary includes a number of islands to the north and south of the main river channel. Prominent features of the lower estuary include Lake Wooloweyah to the south and the North Arm to the north (Figure 2). Lake Wooloweyah is an expansive shallow lake connected to the river by a series of narrow channels, which intersperse deltaic islands that formerly comprised extensive saltmarsh and mangrove habitats, but much of which is now reclaimed or degraded. The lake represents important trawling grounds for SP, and in the early 20th century it contained large beds of seagrass (*Zostera* and *Halophila* sp.) which are now almost non-existent. The North Arm is fed directly from the main channel, and similarly contains a series of low-lying deltaic islands covered in saltmarsh and mangrove, interspersed with a network of shallow channels (Figure 2). The entrance morphology of the estuary is trained by extensive submerged rock walls that direct the bulk of tidal flow up the Main Channel and the North Arm of the estuary (Figure 2). Consequently, most of the tidal flow initially bypasses the downstream channel system connecting Lake Wooloweyah to the mouth, favouring the Main Channel and to a lesser extent the North Arm (Figure 2).

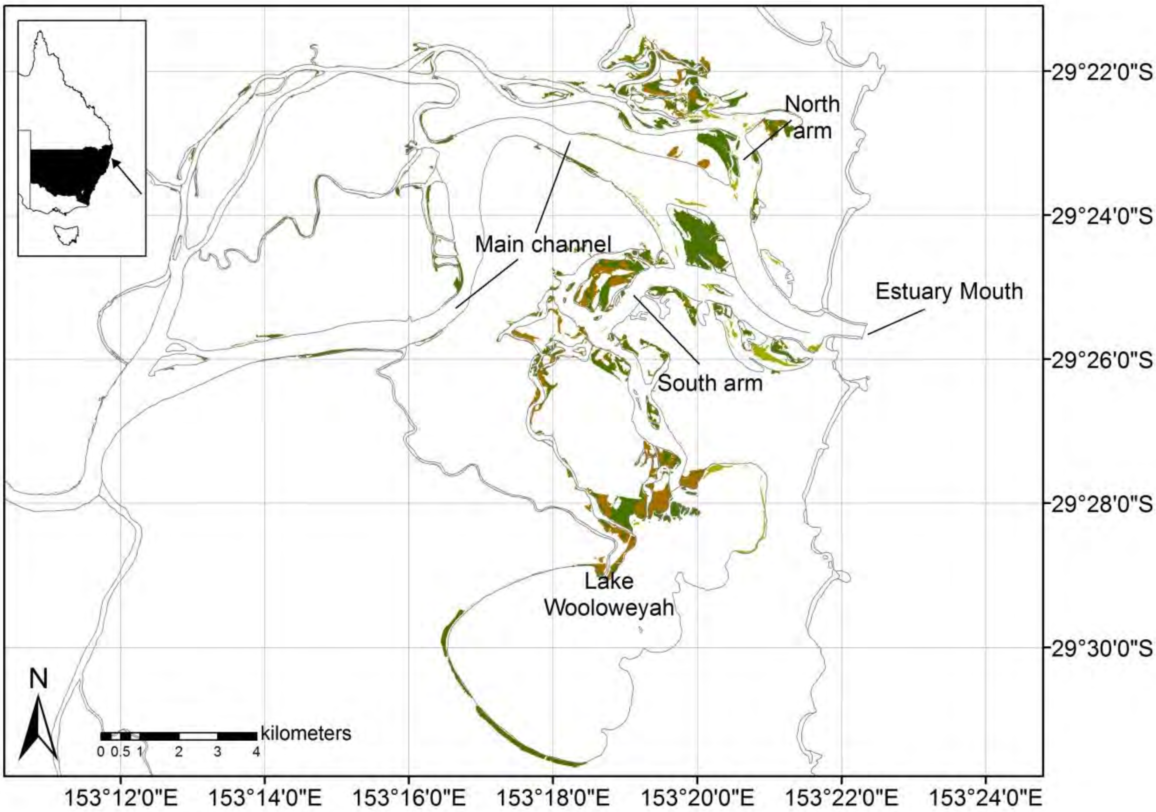

Figure 2 Map showing the lower Clarence River estuary and associated saltmarsh (shaded in brown), mangrove (shaded in dark green) and seagrass (shaded in light green) habitat. Main features of the estuary referred to in the text are labelled.

Lake Macquarie

Lake Macquarie (-33.09º, 151.66º) is a large, immature, wave-dominated barrier estuary (Roy et al., 2001), with a waterway area of 114 km^2. The lake contains extensive seagrass beds, dominated by *Zostera capricorni* and *Posidonia australis*, but minimal intertidal and submerged rocky reef area. The estuary catchment is moderately developed and two power stations draw lake water for their condenser cooling systems, discharging warm water back into the southern half of the lake. The lake has a fairly stable salinity regime; however the power stations can exert a considerable influence on water temperature (see Taylor et al., 2017c), which varies seasonally. The large lake exits to the sea through the Swansea Channel, a narrow channel of about 5 km in length, which is only 140 m wide at its narrowest point (Figure 3). Consequently, large volumes of water pass through this constriction on each tidal cycle, and emigrating EKP are intensively fished by recreational anglers in this channel over the summer using dip nets from boats (the most intensive fishing occurs during the months of January – March).

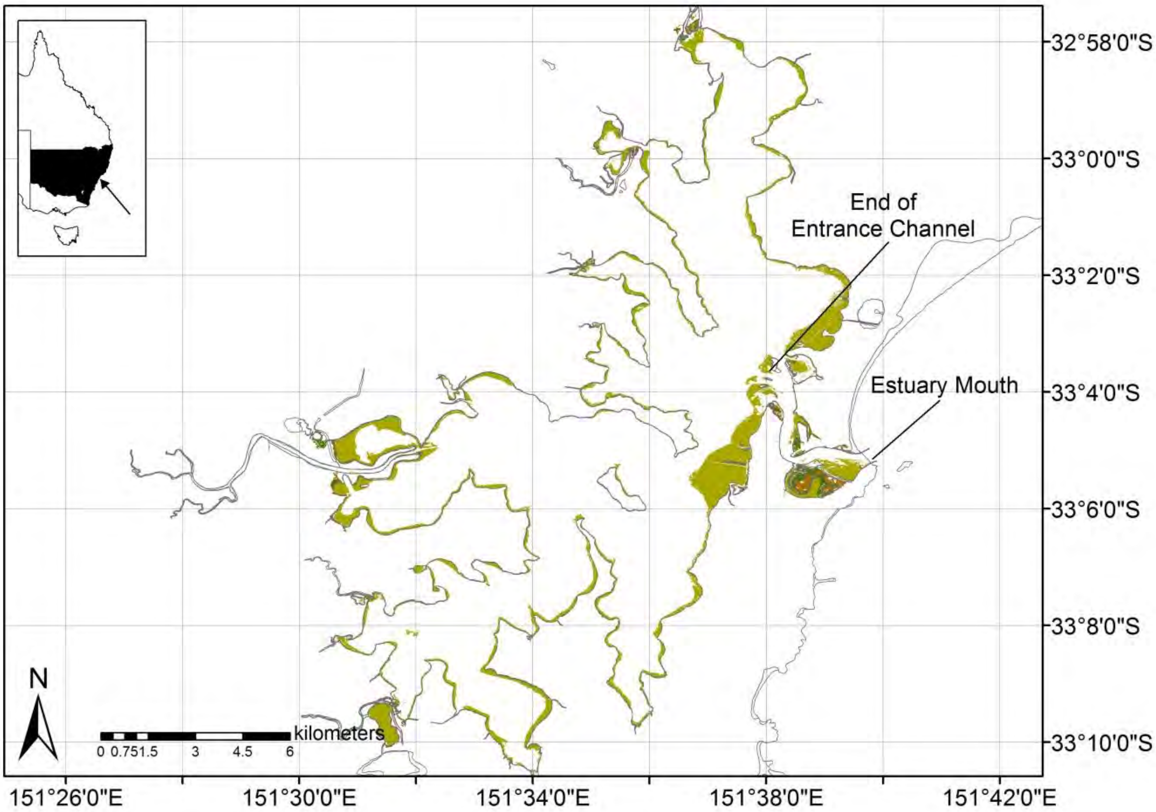

Figure 3 Map of Lake Macquarie and associated saltmarsh (shaded in brown), mangrove (shaded in dark green) and seagrass (shaded in light green) habitat. Main features of the estuary referred to in the text are labelled.

Objective 1 – Determine to what extent young Eastern King Prawn are using natural, degraded or rehabilitated habitat in estuaries, and the contribution of these habitats to the fishery

A combination of three approaches was used to investigate the direct usage of natural, degraded and rehabilitated habitats in the lower Hunter and Clarence River estuaries, and Lake Macquarie by EKP. These included the development and application of a stable isotope assignment approach (outlined below), which was supported by quantitative sampling in all three estuaries, and an investigation of prawn and fish interactions with the marsh surface and marsh edge in the Hunter River. In the Hunter River, the same methods were also applied to SP, and these results are reported as well.

Stable isotope-based assignment of emigrating prawns

As outlined in the Introduction, EKP and SP reside in various areas throughout the estuary as juveniles. Adolescent prawns of both species exhibit a predictable migration and "run" from the estuary out to the sea to join the adult and/or exploited component of the stock. This run is primarily synchronised with the period between the 7th and 17th day of the lunar cycle, and occurs in greatest intensity during the months of January to March (Racek, 1959). This behaviour underpinned the assumption that prawns sampled as they emigrated through the mouth of the estuary represented a useful proxy for prawns joining the adult population, and thus by determining the areas from which these emigrating prawns originated, we may assess the relative contribution of habitats within the estuary to adult stocks. Initially, a stable isotope assignment approach was developed and trialled for both EKP and SP with a small subset of putative nursery areas, which used isotopic similarity between emigrating prawns and putative nursery areas to infer the proportional contribution of individuals from different putative nursery areas within the estuary to the emigrating group. During this process, various assumptions of the technique were evaluated, and the analytical approach to assignment was developed. These are outlined in detail in Taylor et al. (2016), and Appendix 3 of this report.

Following methodological development and refinement, the approach was applied to the three study estuaries to evaluate the contribution of different putative nursery areas to emigrating prawns. This involved a 2-part sampling program, whereby 1) collection of prawn samples were targeted from up to 20 putative nursery areas within each estuary (concentrating on the lower estuary for the Hunter and Clarence River estuaries and littoral regions around the entire perimeter of Lake Macquarie) to characterise the stable isotope signature specific for those areas; and 2) a mixed sample of prawns were collected as they emigrated from the estuary on 3-6 nights during the last quarter of the lunar month between January and March. Emigrating prawns were used as a proxy for prawns joining the adult population, and thus the areas from which these emigrating prawns originated were used to assess the relative contribution of areas within the estuary to the adult component of the population. The origin of prawns captured as they emigrated from the estuary was assigned among those putative nursery areas sampled on the basis of the isotopic similarity between the groups, as described below. Samples were collected from putative nursery areas in the last quarter of the lunar month over the summer of 2013/14 (and 2014/15 in the Hunter River estuary) using tows of a sled net specifically designed to capture juvenile prawns from shallow estuarine habitats and narrow saltmarsh channels using a small shallow-draught boat (access to many of these areas is challenging). Sled samples were immediately placed on ice and then frozen for laboratory processing. Emigrating prawns were collected by trawler at the mouth of the estuary in the Hunter and Clarence River, and by dip net in Lake Macquarie.

In the laboratory, samples collected from putative nursery areas were thawed and the head and proventriculus dissected out of each animal to ensure the isotopic composition did not reflect that of recently consumed food items. Three composite samples (containing equal quantities of muscle tissue from six individual prawns) were prepared for stable isotope analysis from each area. This particular composite design (3 samples containing 6 individuals) was selected as a trade-off between precision error and the ability to produce average, area-specific signatures (see Taylor et al., 2016). All emigrating EKP and SP captured from the mouth of the estuary were prepared as individual samples (i.e. not composite samples).

Tissue samples (composite and individuals) were prepared for stable isotope analysis by first rinsing in distilled water for 10 min, followed by drying at 60°C for ~48 h. The isotopic composition (^{15}N and ^{13}C) was measured on a Sercon 20-20 isotope ratio mass spectrometer (IRMS, Cheshire, United Kingdom). Delta values were calculated relative to international standards using conventional methods (Fry, 2006). Measurement precision was determined through repeated measurements of internal standards, and were ±0.09 ‰ and ±0.05 ‰ for δ^{15}N and δ^{13}C respectively for samples collected in 2013/14, and ±0.11 ‰ and ±0.17 ‰ for δ^{15}N and δ^{13}C for samples collected in 2014/15.

Emigrating prawns were assigned to putative nursery habitat areas using a distance-based approach. The point-in-polygon technique (Smith et al., 2013) was initially applied to the dataset, to refine the set of emigrating prawns to be assigned based on the "completeness" of the isotopic map created from the putative nursery habitat areas. If an individual emigrating prawn fell outside of the simulated region, it was excluded from further analysis. Assignment was undertaken using the refined set of emigrating prawns. Firstly, the isotopic composition of each putative nursery habitat area was specified as a normal distribution, and each distribution was randomly sampled 1,000 times and used to calculate the Euclidian distance between the emigrating prawn and each putative nursery habitat area in bivariate isotopic space. The most likely putative nursery habitat area in each simulation was determined on the basis of the minimum distance between the emigrating prawn and the habitat area in isotopic space. For each emigrating prawn, the results from all simulations were then used to determine the binomial probability that each habitat area was the source area, and the habitat area with the greatest probability was selected as the source area for the emigrating prawn. All isotope modelling was undertaken using custom scripts in Matlab (Mathworks, Natick, MA, USA). Finally, the assignment data was used to determine whether each area may be considered an effective juvenile habitat (EJH), using the classification system of Dahlgren et al. (2006), which assigns an area as EJH if it has a greater than average contribution to the adult component of the population. In Lake Macquarie, assignment data was also used to determine whether each area may be considered a nursery habitat (NH) using the classification system of Beck et al. (2001). The key difference with this latter approach is that it assigns an area as a nursery habitat on the basis of a greater than average contribution per-unit-area of habitat, whereas the former approach relies only on a greater than average contribution from a particular area. The Nursery Habitat approach can exclude habitats that may have a small contribution-per-unit-area to adult populations, but may still be important for adult populations; the latter approach would include such habitats. For assignment of nursery habitats, the areas of the seagrass beds sampled were determined from the habitat shape files (from the NSW DPI Habitat Mapping Database) in ArcGIS. This approach was undertaken at Lake Macquarie as seagrass beds are simple to map and measure as discrete habitat units, whereas this approach is difficult when applied to the unvegetated subtidal habitats which dominate the Hunter and Clarence River estuaries.

Quantitative sampling

Following evaluation of the assignment data, up to 20 sampling locations were identified in each estuary that covered important source areas for emigrating EKP, and additional sampling surveys were targeted in these areas along with major rehabilitated marsh systems in the lower estuary. Each location was surveyed using nocturnal sled tows in last quarter of three lunar month between October 2014 and March 2015 (for Hunter River and Lake Macquarie) or two lunar months between November 2015 and February 2016 (for Clarence River). Four (Hunter River and Clarence River) or seven (Lake Macquarie) replicate tows were undertaken at each location during each sampling event. Tows were undertaken using a sled net, which had been specifically designed to capture juvenile prawns from soft sediments in shallow estuarine habitats and narrow saltmarsh channels using a small, shallow-draught boat (as noted above, access to many of these areas is challenging). A GPS waypoint was marked at the start and finish of each tow (to calculate tow-length), and depth and water quality (temperature, salinity, dissolved oxygen and turbidity) were recorded at each location. Bulk sled samples were immediately placed on ice and then frozen for later laboratory processing.

Sample processing involved sorting and identifying all penaeid prawns from the thawed bulk sample, and then enumerating the individuals from each species. The dimensions of the gear, the actual length of each tow (derived from GPS waypoints), and nocturnal gear efficiency estimates for sampling using this specific gear were used to standardise abundance estimates to number-per-hundred-square-metres (# EKP 100 m^{-2} for Eastern King Prawn, and # SP 100 m^{-2} for School Prawn). Quantitative survey data collected in the Hunter River and Lake Macquarie were evaluated using generalised additive models or generalised additive mixed models (using the mgcv package in R v. 3.2.0, R Core Team, 2016). Independent variables including distance-to-sea, depth, and turbidity were evaluated (full details are outlined in Appendix 4, 5 and 6).

Prawn and fish interactions with the marsh surface and marsh edge

A dedicated study was undertaken in the Hunter River to evaluate prawn and fish use of the surface of restored wetlands and sub-tidal creeks which drain these wetlands of this system. Fieldwork was carried out between January and April 2015, when EKP and SP are most abundant in estuaries (Racek, 1959). Sampling was conducted across the three restored marshes within the Hunter Estuary, Hexham wetland, Tomago wetland and Kooragang wetland (Figure 1), and all fieldwork was completed after sunset and within 5 days of the new moon. Sub-tidal creeks within the wetlands (n = 2 per wetland) were divided into *edge* and *middle* habitats, with edge habitats located within 3 m of the creek bank, and middle habitats located in the middle of the creek. Each habitat was sampled using a cast net (Superspreader, 2.4 m diameter, 4.8 mm mesh), and all nets were thrown by the same operator. Cast nets were chosen as they can provide precise placement of gear, which is especially necessary for targeting the creek edge habitats. Within each of the 6 creeks, 16 cast nets were thrown at each habitat along a length of at least 500 m (with 192 cast nets throws in total), during slack water. Cast net samples were discarded if the net spread less than 50% of its full capacity, or became entangled. A record of the percentage net spread for each throw was taken and this was used to standardise catches with varying net spread by dividing the catch with the percentage net spread. Depth readings were taken for each cast net sample.

Shallow intertidal ditches which drain the surface of the saltmarsh/mangrove habitat were sampled using small mesh double-wing fyke nets, which are effective in sampling this type of habitat (Mazumdar et al., 2005). The nets were constructed from 3 mm honeycomb mesh, had 5 m wings and a 60 cm mouth opening with two throats to prevent the escape of crustaceans and fish. Six fyke nets were set within each wetland during the sampling period. Nets were set just before dusk at low tide and retrieved following a tidal cycle and associated marsh inundation (full details given in Appendix 4). The nets were positioned so the wing spread covered the full width of the ditch and faced into the marsh so all nekton travelling down a ditch would be funnelled into the fyke. It is difficult to determine the exact area sampled by each fyke net, while every attempt was made to deploy these in similar locations, it is likely the exact area sampled varied slightly among nets. Fyke net sampling coincided with spring tides >1.7m, when the marsh becomes fully inundated. Within Hexham wetland, a Hobo U20 pressure logger (Onset Corporation, Cape Cod, Massachusetts) was positioned on the intertidal marsh so that the period of inundation could be determined. Basic water quality parameters in the sub-tidal creeks (salinity, pH, dissolved oxygen and temperature) were measured during each sampling trip.

All samples were frozen and later enumerated in laboratory facilities at the Port Stephens Fisheries Institute. Crustaceans and fish were identified under dissecting microscopes using published descriptions. Cast and fyke net data were used to calculate (separate) Bray-Curtis similarity matrices, and these were analysed separately. For cast nets, the abundance of EKP and SP, total fish abundance and total crustacean abundance was analysed using Permutational Analysis of Variance

(PERMANOVA) in the software package PRIMER v.6 (PRIMER E-Ltd, Plymouth, UK), and factors Wetland (fixed, 3 levels; Tomago, Kooragang, Hexham), Habitat, (fixed, 2-levels; Adjacent and Middle), and Creek (random and nested in 'Wetland) evaluated. Separate multivariate analyses were conducted on the whole community, the fish community and the crustacean community. Significant effects were further explored with post-hoc analyses using Monte-Carlo adjusted P-values where necessary due to low numbers of permutations (Anderson et al., 2008). For fyke nets, the total nekton community, the fish community and the crustacean community were compared among the three wetlands using PERMANOVA. The lengths of EKP and SP were also compared separately between habitats of creeks with ANOVA using R v. 3.2.0 (R Core Team, 2016).

Objective 2 – Determine the hydrographic conditions which provide for maximum growth and survival of Eastern King Prawn within nursery habitats

The effects of abiotic conditions on prawns, principally low salinity arising from freshwater inundation of estuaries, are relatively unknown. Professional fishers have observed and reported decreases in catch rates of EKP, and also slower growth, in years of high rainfall. EKP have been proposed as being relatively stenohaline when compared to other commercial prawn species in New South Wales (i.e. Greentail Prawn [*Metapenaeus bennettae*] and SP), however Dall (1981) demonstrates that that the species has the physiological capacity to deal with low salinity conditions through osmoregulation. Osmoregulation is an energetically expensive process, and extended hyper-regulation of serum osmolality may manifest in decreased growth rates, which provides some explanation of the observations from professional fishers. Thus, freshwater inflow to estuaries may have a direct impact on metabolism, appetite, availability of prey, availability of nursery habitats; and consequently the growth and survival within those habitats. These factors could have concomitant effects on associated yields of EKP.

In the field, reductions in salinity following rainfall occur through constant dilution and can last for extended periods (days to weeks), with limited potential for respite during the event. However, previous studies examining the effects of reduced salinity on prawns have generally undertaken stepwise reductions in salinity, over extended time periods (e.g. Dall, 1981; Dall and Smith, 1981). Consequently, we developed a novel experimental design to test the effects of simulated rapid salinity declines and physicochemical changes that have been directly observed in New South Wales estuaries (from logger data), and measured the survival and physiological responses of juvenile EKP. Specifically, this was achieved by measuring 1) overall survival; 2) oxygen consumption as a proxy for aerobic metabolic rate; and 3) water content of body tissue as an indicator of osmoregulatory capacity.

Prawn collection and husbandry

Juvenile EKP were collected from the North Arm of the Hunter River estuary in New South Wales (Figure 1) using short tows (3-5 minutes) of a sled net. EKP were immediately identified in the mixed catch of prawns and added to an on-board aerated holding tank. Prawns were transported to the Port Stephens Fisheries Institute and placed in ~5,000 L aerated, static water holding tanks containing ~5 cm of beach sand substrate. Water exchanges (25 - 50%) were conducted weekly with water of salinity ranging between 28 - 32. Prawns were fed *ad libitum* with a dry feed (sera® 'Shrimp Natural') each evening. Prawns were kept in holding tanks for up to eight weeks before exposure to experimental conditions, and animals of carapace length (CL) between 5 and 12 mm were used in the experiment.

Experimental procedures

Juvenile EKP were exposed to 24 different rates of salinity decline for 24 h, ranging between < 0.01% h^{-1} and 20% h^{-1}. Following the 24 h dilution, the respective endpoint salinity of each tank was maintained for five days. For logistic reasons, the 24 rates of salinity decline were carried out over four experimental runs. Each run tested six rates of salinity decline with each rate randomly assigned to a tank (full details given in Appendix 5). As the measurement of aerobic metabolism took up to eight hours, the initiation of the experimental treatment for each tank was separated by 24 h. Measures of aerobic metabolism were not taken for the fourth run and so these experimental treatments all commenced simultaneously. In total, 240 prawns were used, with 10 prawns randomly allocated to a tank for each rate of salinity decline. The 24 rates of decline began at a salinity of ~36 and resulted in endpoint salinities between 0.4 and 36.4.

The experimental setup consisted of six, 10 L Perspex tanks, each with an overflow and ~2 cm of washed beach sand substrate. With sand and overflows in place, each tank held 7.5 L of water. Water temperature and salinity data were recorded every 8 h using a water quality meter (Horiba U-5000, Horiba LTD; Japan). The tanks were individually aerated with 2 cm diameter stone diffusers, and the temperature was maintained at 24 °C (± 0.16 °C standard deviation) by standing tanks in water baths of circulating heated water. Each tank was allocated a dose pump (DMS-12-3A-PE/E/C-S, Grundfos Alldos; France) and a 200 L storage sump of aerated rainwater. Dose pumps were calibrated to supply an adequate flow of rainwater per unit time to the treatment tank to achieve the desired rate of decline in salinity.

Each day following the completion of the salinity decline, waste solids were removed from the tanks and 1 L of water was replaced with clean isosmotic water. Standard deviation in salinity associated with evaporation and water changes was ≤0.2. Prawns were fed 0.25 g dried food g^{-1} prawn dry weight each evening, except during the salinity decline and on the evening of the fifth day. Tanks were checked for dead prawns every 8 h, and those that appeared moribund (i.e. did not respond to physical stimuli) were removed and their CL (mm) and blotted wet weight (g) measured.

Aerobic metabolic rate was measured for all surviving prawns in the first three experimental runs, while surviving prawns from the fourth experimental run were sacrificed and CL and wet weight measurements were obtained as described above. Water composition of all prawns that survived the experiment was calculated by drying prawns at 70 °C for > 48 h and subtracting dry weights from wet weights.

Measurements of aerobic metabolic rate

A 10-channel Oxy-10 mini respirometer with fibre optic sensors (‘optodes’; PreSens, Regensburg, Germany) was used to measure oxygen concentration over time. The Oxy-10 mini was re-calibrated to the water of each treatment prior to each use due to the differing salinities. Respiration chambers (x10) were 70 mL LabServ® polypropylene specimen jars with cable-glands installed in the lid and Teflon tape wrapped around the thread of the jar. Up to nine prawns were randomly allocated individually to respiration chambers containing water from their experimental tank. Chambers were sealed within 5 min with care taken to ensure no air bubbles remained and that the chambers had not been pressurised. Optodes were installed to approximately mid-way within the chambers and the tenth chamber was filled with water only as a blank for background respiration. During measurements, all chambers were held in the dark in a Styrofoam box in a temperature-controlled room (24 °C). To account for potential circadian impacts on respiration, each run of oxygen consumption measurements was initiated at 0800 hrs (± 30 min). Data were recorded until either 20% air saturation or 8 h total run time was reached. On completion, prawns were removed, sacrificed and measured as described above.

To remove potential handling effects of the animals on estimates of metabolic rate, oxygen concentrations for the first hour were discarded. The slope of the linear relationship between oxygen concentration and time for the remaining data was used to calculate oxygen consumption rates using the following equation, created with reference to Deigweiher et al. (2008) and Parker et al. (2012):

$$O_{2_{Cons.}} = \frac{(V_C - WW) \times (\Delta C_E O_2 - \Delta C_B O_2)}{DW} \tag{1}$$

where $O_{2_{Cons.}}$ is the rate of oxygen consumption of each prawn per gram dry weight (mg O_2 g^{-1} h^{-1}), V_C is the volume of the respiration chamber, WW is the wet-weight of the prawn (in L, where 1 kg of wet prawn tissue is assumed to be equal to 1 L of water), $\Delta C_E O_2$ is the slope of oxygen concentration over time from the experimental chamber (mg O_2 h^{-1}), $\Delta C_B O_2$ is the slope of oxygen concentration over time from the blank chamber (mg O_2 h^{-1}) and DW is the dry-weight of the prawn (g).

Data analysis

Probit regression analyses were used to describe the relationship between the probability of death and the rate of salinity decline, which allowed an estimate of the rate of salinity decline at which 50% mortality would occur following 24 h of salinity decline, and 50% and 99% mortality, 120 h after the salinity decline ceased. These analyses were undertaken in IBM SPSS Statistics 22.

Generalised additive modelling (GAM) was used to identify and characterise the relationships between the response variables of prawn metabolic rates and water composition, and the explanatory variables of rate of salinity decline, final salinity and, for metabolic rates only, somatic condition. Exploratory models found that the final salinity was not as strong a predictor variable as the rate of salinity decline and so only models using rate of salinity decline are reported. Standardised residuals from the log CL – log dry weight data was used as a size-independent measure of the somatic condition of an individual at the whole animal level (e.g. Moltschaniwskyj and Semmens, 2000). The splines were based on thin plate smoothing terms with default settings (Wood, 2003) applied to each variable, using the *mgcv* package (Wood, 2011) in R v. 3.2.0 (R Core Team, 2016). Prior to accepting the validity of a GAM, assumptions of normality and homogeneity for the GAM were checked via observation of QQ-plots/histograms and plots of residuals vs predicted values, respectively.

Objective 3 – Assess the extent of key Eastern King Prawn habitat lost and remaining in the Hunter and Clarence river estuaries

Current and historic aerial imagery was compiled from a variety of sources and used to assess the changes in areal coverage of estuarine habitats over a multi-decadal time scale. This included imagery from the 1950s and 1990s for the Hunter River estuary, and the 1940s and 2000s for the Clarence River estuary. Aerial imagery was digitised and polygons drawn for saltmarsh, mangrove and seagrass habitat for each time period. In addition, perimeter of the river shoreline for which saltmarsh and mangrove habitats were adjacent to was also calculated. Mapping was concentrated in the lower estuary, which is the relevant nursery area for juvenile EKP. The data was extracted from spatial layers derived from the “early” and “late” maps for each estuary, and was compiled to reflect the changes that had occurred both in terms of areal coverage (hectares), and percent change between the two time periods.

Objective 4 – Outline the potential improvements to the Eastern King Prawn fishery that could be achieved through targeted wetland rehabilitation

Model structure

The north coast of New South Wales represents an important nursery area for EKP, but has seen some of the highest rates of habitat loss within this jurisdiction (Rogers et al., 2015). To evaluate the restoration of habitat in alternative areas, we compared predicted improvement in landings of EKP to the state of New South Wales using a quantitative model of the EKP fishery. This model represented the entire spatial range of the EKP population, thus including Victoria to the south and Queensland to the north, in addition to New South Wales. This allowed for realistic representation of the spatial dynamics of EKP life history and fishery in an equilibrium modeling framework, and followed recent publications (O'Neill et al., 2014) and stock assessment models (Courtney et al., 2014). An important component of this model was representing key, spatially explicit processes of EKP life history and fishery, including spatial distribution of fishing effort, the spatial dispersal of larvae to inshore recruitment areas from eggs spawned offshore (Everett et al., 2017), the spatial movement of post-recruit sub-adult and adult prawns from estuaries to offshore areas, and the habitat mediated, density-dependent recruitment process occurring in estuarine areas throughout the EKP range. Once parameterized appropriately, the model was used to examine what the effect of restoring a fixed amount of habitat in a specific management zone of New South Wales would be on the overall landing to New South Wales.

As the purpose of the model was to assess the expected effects of alternative restoration actions, we constructed a simulation model that represents the current state of the EKP stock. The model was designed to represent an age-structured, spatially explicit EKP stock and fishery in a deterministic fashion in discrete time. This permitted transparent predictions of expected outcomes at actual time intervals following restoration, while implicitly assuming an equilibrium state of the current fishery. To ensure the model represented the current fishery state reasonably well, the model was parameterized from recent fisheries data, stock assessments, and other studies (most notably O'Neill et al., 2014; Courtney et al., 2014). The model was tuned (via solving for the catchability parameter, q, Table 1 in Appendix 12) such that equilibrium, un-restored predictions from the model well match observations from the fishery. The most important components of the model are described below, and all parameters and equations referred to are presented in Appendix 12.

While the model represented the entire range EKP, from Victoria in the south to Queensland in the north, it focuses on New South Wales. The spatial structure was thus made up of 11 zones, including one each for Victoria and Queensland, and nine corresponding to management zones in New South Wales. In this model the greater detail provided for New South Wales was a function of the model objectives, while the inclusion of Victoria and Queensland are necessary to account for dispersal of larvae and movement of adult prawns to and from these states and New South Wales. Each zone occupies a single longitudinal area, such that the effects of offshore movement of prawns pertinent to the fishery is accounted for with the vulnerability to fishing gear (v_a^c).

Somatic growth of EKP was described in terms of carapace length, body weight and age following Courtney et al. (2014). Carapace length-at-age was described using a von Bertelanffy growth function, (L_a). Weight-at-age was assumed to be an allometric function of length (W_a). Survival of post-recruit EKP—i.e. sub adults and adults—was assumed to be age-specific as a function of length, using a Lorenzen-type mortality function (S_a). Fecundity at age was simply specified as a function of maturity and weight (f_a), with average weight at maturity (W_m) assumed to correspond to a carapace length of 42 mm following Glaister (1983). This specification of fecundity is relative in that it represents spawning biomass rather than absolute numbers of eggs, relying on the parameterization of the stock-recruit function (specifically the Beverton-Holt a parameter) to scale spawning biomass to appropriate numbers of recruits. Each of growth, survival and fecundity was assumed to be invariant among the spatial compartments represented in the model.

Current understanding of the EKP life history holds that animals aggregate offshore to reproduce, following which, eggs hatch as larvae and subsequently disperse to inshore estuarine areas as a function of active transportation via advective ocean currents. Dispersal processes dictate that zones within New South Wales have historically and continue to receive differing proportions of eggs spawned offshore. We account for dispersal using a matrix of probabilities giving the proportions of eggs spawned in each zone that disperse to all other zones, derived from recent modelling (Everett et al., 2017). It is critical to understand that the process of dispersal, as represented in this model, accounts only for the spatial allocation of larvae from eggs. Thus the total abundance of larvae in each year is exactly that of the eggs produced at the end of the previous year. All mortality associated with the multiple biological processes between eggs being spawned and juveniles exiting density dependent mortality is subsumed within the recruitment function, as is common in fisheries population models (Walters and Martell, 2004).

Recruitment was perhaps the most critical component of the model, as it needed to account for the habitat mediated density dependent mortality of juveniles. We assumed survival of larvae to post-recruit sub-adults were represented with a Beverton-Holt stock recruitment function following O'Neill et al. (2014). This parameterization of the Beverton-Holt implicitly converts relative biomass of eggs (described above) to numbers of recruits. The a parameter of the Beverton-Holt stock recruitment function, was calculated from the compensation ratio (Ω), and eggs-per-recruit (φ_{e}), and thus was initially identical across zones. The b parameter of the Beverton-Holt was also a function of recruitment at unfished conditions ($\bar{R}_k$), such that this parameter differs across zones (b_k). This implied that even in unfished and pre-degradation states, the individual zones would have naturally produced different numbers of recruits as a function of different absolute recruitment potential, presumably a function of a two-or-three dimensional spatial measurement of usable habitat. To account for zone-specific changes in habitat, both Beverton-Holt parameters were further modified by the zone-specific proportion of habitat remaining that is considered suitable for recruitment ($H_{t,k}$), and by the assumption that larvae can to some extent locate that habitat (c^*). This approach is based in Walters et al. (2007) and results in a matrix of Beverton-Holt parameters dimensioned by the time periods and zones considered in the simulation. Thus, following equilibration of the model (which must be attained via numerical simulation owing to non-random larval dispersal and zone-specific recruitment at unfished conditions) potential habitat restoration was represented by changing the $H_{t,k}$ matrix. This integration of assumptions regarding estuarine habitat to the EKP stock-recruit production function allowed reasonable representations of changes to the productivity in the EKP fishery following habitat restoration.

Previous studies have demonstrated that EKP move offshore and generally northward as they mature, eventually aggregating to reproduce, and concomitantly are targeted by commercial fisheries (Courtney et al., 2014; Montgomery, 1990; Taylor et al., 2016). Increasing vulnerability of EKP to the commercial fishery associated with offshore and northward movement was accounted for with age-specific vulnerability to capture, v_a^{c}, described as a function of carapace length. Latitudinal movement north or south was accounted for explicitly in the model, by considering both size- and age-based influences on probability of movement in either direction, as well as zone-specific differences in probability of sub-adult and adult prawns moving north or south. This ultimately resulted in age-specific probabilities of movement in each direction (north or south) dependent on the zone most recently occupied. These probabilities of movement were informed by recent empirical studies, including Courtney et al. (2014) and others. In the model the fishery was represented in a spatially explicit, zone-specific context. Spatial differences in harvest rate ($U_{t,k}$) were realized through spatial allocation of effort (E_k) that represent recent fisheries dependent data. This representation allowed for compatibility with effort and catch per unit effort metrics (presented in the same units) described in a recent bioeconomic assessment that estimated the boat hours which would be associated with maximum economic yield (O'Neill et al., 2014).

Model simulations

The model was run to unfished and then fished equilibrium prior to assessing the effect of restoration. The spatial structure, specifically with respect to dispersal, required that the model "spin up" to equilibrium and prevented the use of more traditional approaches for initializing at fished equilibrium (Walters and Martell, 2004). In this case, 10 years at monthly time steps was sufficient to accomplish this. The model was then run for an additional ten years to reach a fished equilibrium, following which restoration options were initiated as described below.

To address the primary objective of this work we evaluated the relative effect of restoring alternative New South Wales zones given the best available information regarding spatial dynamics of the stock and fishery. Accordingly, parameter values were used for this run as provided in Tables 1, 2 & 3 in Appendix 12, and this was achieved by running the model to fished equilibrium. Following fished equilibrium, percent habitat suitable for recruitment ($H_{t,k}$) was changed to represent a 200 hectare increase in habitat in each New South Wales management zone individually to represent restoration, and the model was run for an additional 10 years to describe equilibrium effects of restoration. Thus, the annual expected percent improvement in New South Wales EKP harvest was calculated as harvest in the tenth year following restoration relative to un-restored conditions.

Objective 5 – Extend information on habitat-fishery linkages to commercial fisheries, landowners and other catchment stakeholders and incorporate recommendations into fisheries or water management

Objective 5 was achieved through execution of a comprehensive Extension and Adoption Plan, which is included in its entirety in Appendix 13. The key methods employed to extend information to target audiences are outlined below

1. Information letter

The information letter provided details about the project outlining its purpose, objectives, personnel and ways to obtain more information and provide input.
Type: Printed publication
Audience: Commercial fishers and their co-ops
Phase: Project initiation
Frequency: Once

2. Project updates

Project updates provided a summary of research activities and results as well as engagement activities and feedback. These were provided throughout the project through both dedicated website and project partner newsletters.
Type: Printed and online publication
Audience: Commercial co-ops, relevant Local Land Services (former Catchment Management Authorities), relevant local councils
Phase: Throughout
Frequency: Annually (4 in total)

3. Research papers

Several research papers were completed and subjected to peer review. These are the main scientific outputs that documented the research results and the content of these papers was distilled and synthesised to support other extension activities.

Type: Printed and online publications
Audience: Fisheries researchers and managers
Phase: On completion of research components
Frequency: Dependent on results

4. Dedicated website

A project website was hosted at http://www.dpi.nsw.gov.au/fishing/habitat/rehabilitating/ekp.The website provided:

- project information and updates (six-monthly)
- plain English summaries of the research results
- resources developed on the habitat use and ecosystem requirements of EKP
- links to other relevant resources and information
- contact details for project team

Type: Website
Audience: General
Phase: Throughout and ongoing
Frequency: N/A

5. Face-to-face discussions with commercial fishers

Project team members visited EKP fishers at the fishers' convenience. Several face-to-face interviews were completed, with discussions focusing on:

- obtaining fishers' perspectives on issues affecting king prawn and EKP habitat
- determining what fishers' want to know about EKP and EKP habitat
- determining where these fishers go for information, what sources they trust and their information preferences

Type: Face-to-face
Audience: Commercial EKP fishers
Phase: Project outset, then as requested
Frequency: At least once per co-op involved in the EKP fishery

6. Survey

A survey was designed and administered to gather information about where commercial EKP fishers go for information, what sources they trust and their information preferences. The survey is included in Appendix 14. The results informed the development of a Communication Plan and information resources for commercial fishers.
Type: Face-to-face and online
Audience: Commercial EKP fishers
Phase: Project outset and open for first 3 months
Frequency: Once

7. Communication plan

The results of the survey and face-to-face discussions were employed to produce a succinct plan that defined an effective way to communicate with commercial fishers and coastal habitat stakeholders about habitat use and ecosystem requirements of exploited species.
Type: Electronic publication
Audience: Open
Phase: 6 – 9 month stage
Frequency: Once

8. Workshops

The project implications and findings were discussed at several dedicated and opportunistic workshops which were attended by key stakeholders.
Type: Workshops
Audience: local council planning staff, catchment management authority staff, relevant Crown Lands management staff, Aboriginal Land Council representatives, regional Landcare / Coastcare / Dunecare coordinators and relevant State agency planning and regulatory staff (eg, Fisheries, Planning, Water, Environment,) Ports Authorities
Phase: Late
Frequency: Several

9. Presentations

Conferences were attended to communicate with professionals involved in managing land, assets and infrastructure, sustaining local / regional business and economies and developing cross-agency / disciplines approaches to addressing coastal issues. The underlying concept of integrating habitat improvement, fisheries productivity and multi-sectoral involvement was conveyed to these stakeholders (and this will be continued in the future).
Type: Conference presentation
Audience: Professionals involved in coastal management in Australia
Phase: Late
Frequency: Three

10. Information products

The project findings contributed to general information products issued by the NSW DPI.
Type: Electronic publications
Audience: Various
Phase: Throughout
Frequency: N/A

11. Media

Media elements targeted throughout the project included media releases, radio, and articles for specialist interest media.
Type: Various
Audience: Broad
Phase: Throughout
Frequency: Throughout

Objective 6 – Establish quantitative habitat-fishery linkages for the main exploited species in both the Hunter River and Clarence River systems

As highlighted above, the Clarence River and Hunter River represent two of the most important estuarine commercial fisheries in south-eastern Australia. Both these estuaries have in the past experienced significant habitat loss through the construction of drainage and flood mitigation works, and the Clarence River has also suffered extensive seagrass loss (Taylor et al., 2018). Stable isotopes were employed to examine the linkages between emergent primary producers and key exploited species that comprise the majority of fisheries productivity in these modified ecosystems. These linkages were then used to assess the economic value that is derived from saltmarsh and mangrove habitats through fisheries production in these systems.

Collection and analysis of stable isotope samples

In the Hunter River estuary, 3 sites were sampled in Fern Bay (Figure 1), and 5 sites were sampled from the Main channel and North arm in the Clarence River (Figure 2). Potential food sources, including mangrove, mangrove pneumatophore epiphyte, fine benthic organic matter (FBOM – analogous to microphytobenthos), *Sporobolus virginicus, Sarcocornia quinqueflora, Sueda australis* and particulate organic matter (POM), were collected from all sites (where present) in Summer 2015 in both estuaries and immediately placed on ice and then frozen until processing. Commercial species were sampled in both estuaries by commercial operators, during Summer 2016. Commercial contractors were commissioned to capture fish and crabs using standard commercial mesh nets and traps deployed in the regions where commercial effort was generally concentrated. Prawns were captured either through commercial or fishery-independent prawn trawling. Upon landing, animals were immediately placed on ice and then frozen until subsequent dissection and processing of muscle tissue.

Frozen samples were thawed for preparation. Each consumer was processed individually to isolate isotopic signatures. In fishes, equal amounts of dorsal muscle tissue were removed, while leg muscle was used for the two crab species. Tissues from potential sources and consumers were rinsed using distilled water to remove surface contaminants and placed in individual HCl-cleaned petri dishes and dried at 60°C for 24 hours. Dried samples were then ground into fine powder using a Retsch Mixer Mill MM 200 and placed into aluminium caps (6-8 mg for plants and 1-2 mg for animal tissues) for isotopic analysis. POM samples were filtered onto pre-combusted glass fibre filter (GF/C) paper under low vacuum and placed in a drying oven at 60°C for 24 hours, and then placed into glass vials for isotopic analysis. Stable isotope analysis was conducted at Griffith University, Queensland, using a Sercon Hydra 20-22 automated Isoprime Isotope Ratio Mass Spectrometer. The standard used to compare carbon isotope content was Pee Dee Belemnite Limestone Carbonate. Stable isotope composition was expressed in delta-notation using conventional formulae (Fry, 2006).

Nitrogen isotopes are frequently used in trophic assessments as they provide information on diet source as well as trophic level (Hussey et al., 2014; Choy et al., 2015) . However, in this study there is a high probability that $\delta^{15}N$ signatures would be affected by anthropogenic activities, which would increase the variability of the analyses and lower the likelihood of correctly attributing the proportions of source contributions to diets (Hadwen and Arthington, 2007). $\delta^{15}N$ signatures are also greatly affected by trophic enrichment factors (TEFs) that can vary inter- and intra-specifically (McMahon et al., 2015), and the TEFs for the consumers in this study are not well known. Consequently, this study did not use nitrogen isotopes and focused instead on $\delta^{13}C$ signatures, which have been used in similar conditions and are less impacted by both TEFs and anthropogenic activities (Hadwen et al., 2007).

Data analysis

Sources were not present at all sites and the habitat ranges of the consumers in this study are not well known; therefore, a generalized linear model (GLM) was initially used to determine whether there were significant differences in ^{13}C signatures between sources and sites across the two estuaries. Since the likelihood of producing accurate predictions of the contributions of sources in a Bayesian model decreases with higher numbers of sources (Parnell et al., 2010), the GLM was also used to determine whether it was possible to pool sources and sites that were not significantly different from each other, thereby lowering the total number of sources in the model. School Prawn and EKP were both caught concurrently in the Clarence River, feed on similar sources (Taylor et al., 2016), and have much smaller home ranges than commercial fishes (Taylor and Ko, 2011); therefore, the samples of these two prawn species were grouped under ‘Prawns’ at each Clarence River site.

Bayesian mixing models were used to determine the proportional contribution of the main food sources to each consumer species in the estuary, using SIMMR (Parnell et al., 2013, available at https://github.com/andrewcparnell/simmr), which has an updated Bayesian mixing model based off the SIAR package (Parnell et al., 2010). All analyses were conducted using R v. 3.3.3. The trophic enrichment factor (TEF) for $\delta^{13}C$ was set to 1‰ (McCutchan et al., 2003), and the standard error for the TEF was set to 1.5‰ (Miller et al., 2013; Caut et al., 2009; Abrantes et al., 2015). Concentration dependences were not set because elemental concentration values were unlikely to vary within species. SIMMR does not incorporate trophic levels in corrections for trophic enrichment, so the TEF for consumer ^{13}C signatures was multiplied by the trophic level above that of the sources, which are generally assumed to be at trophic level 1 (Feng et al., 2014). Trophic levels of Yellowfin Bream, Mulloway, Luderick, Dusky Flathead, Sea Mullet, Giant Mud Crab, Blue Swimmer Crab and School Prawn (or 'Prawns' in the Clarence River), and zooplankton were assumed to be 2.5, 3, 2, 2.5, 2, 2, 2, 2, and 1.5, respectively (following Melville and Connolly, 2005; Hadwen et al., 2007). Once the models were run, Gelman diagnostics were conducted to determine whether confidence intervals were close to 1 and below 1.1 and thus whether more simulations had to be included in the model.

Modelling approach

We applied proportional contributions of primary producers to the biomass of exploited species modelled from stable isotope composition for both estuaries, alongside commercial catch data available through the NSW DPI Commercial Catch and Effort Reporting System and economic data that is recorded in the NSW DPI Resource Assessment System (full details are provided in Appendix 11). We employed a simple set of relationships that essentially differentiated the biomass of commercial landings between the two dominant primary producers in the systems, on the basis of stable isotope modelling. We then applied a simple market value at first-point-of-sale to establish the Gross Value of Product, as well as an economic multiplier (calculated from the economic data presented in Voyer et al., 2016) to convert the Gross Value of Production to Total Economic Output (described below). Simulations were conducted within a Monte-Carlo Analysis of Uncertainty (MCAoU) framework, and model parameters were thus provided as distributions where possible. All economic values are expressed in Australian dollars (AUD).

Stable isotope data for dominant primary producers in the estuary was used to derive average source contributions to commercially sized individuals in the Hunter and Clarence River, and errors around these distributions. Economic value was derived using the formula:

$$GVP_{s,p} = C_{s,p} \cdot H_s \cdot M_s \cdot P_s$$

where $GVP_{s,p}$ is the Gross Value of Production ($GVP_{s,p}$; AUD y^{-1}) of species s derived from primary producer p within the model region (the lower estuary), $C_{s,p}$ is the proportional contribution of primary producer p for species s derived from stable isotope modelling, H_s is the annual harvest of species s (kg y^{-1}), M_s is the market value for species s (AUD kg^{-1}), and P_s is the spatial partitioning coefficient for species s (see below). Collectively $H_s \cdot M_s$ represent the total GVP for species s in the entire estuary (GVP_s, AUD y^{-1}), $C_{s,p}$ apportions that GVP among primary producers in the estuary, and P_s further refines GVP to account for the relevant section of the estuary. Annual harvest (mean and variance) was estimated on the basis of catch reporting for each estuary for the 10 years between 2005/06 and 2014/15, which included a range of both wet years (2008-13) and dry years (2005-08, and 2013-15). The panel of species modelled was limited to those for which stable isotope data were available, but these species represented approximately 85% of the commercial harvest in these estuaries. Market price was estimated from CPI-corrected (consumer price index) Sydney Fish Market values across the same time period.

Estuarine catch in New South Wales is reported by fishers at the estuary level only. Although the bulk of species biomass often tends to occur in the lower estuary (e.g. Sheaves et al., 2016), a spatial partitioning coefficient (P_s) was incorporated so as not to artificially inflate estimated values for species that may be harvested along a greater length of estuary than that encompassed by our data. This parameter was essentially an estimated proportion of total catch that is taken on average within the model regions delineated in Figure 1 and Figure 2. While it is possible that outwelling and transport of particulate material further up the estuary could occur, inclusion of this parameter ensures that our data are not over-extrapolated and that our estimates remain conservative. The parameter was informed by expert opinion, given knowledge gained through several major sampling programs in the estuary, the salinity gradient in the estuary and its effect of the distribution of the species under investigation, and consultation with local fishers and fishery compliance officers.

A subsequent set of simulations was also undertaken using the equation above, but extrapolating to include the expected flow-on economic values from product harvested, on the broader economy. The multiplier was expressed as a normal distribution (m; $N[\mu,\sigma]$) derived from the relationship between the statewide-GVP for New South Wales (P_{GV}; AUDm79.44), and the minimum (O_{min}; AUDm436.13) and maximum (O_{max}; AUDm501.24) estimate of Total Economic Output from commercial fishing (including GVP, and the value of retail and processing output) reported in Voyer et al. (2016), using the relationships $\sigma = \frac{\frac{O_{max}}{P_{GV}} - \frac{O_{min}}{P_{GV}}}{6}$ and $\mu = \frac{O_{max}}{P_{GV}} - 3\sigma$; thus m was estimated as $N(5.90,0.14)$. For these simulations, Total Economic Output for species s derived from primary producer p ($TO_{s,p}$) was estimated using $GVP_{s,p} \cdot m$. It should be noted that TO reported here only encompasses the value derived through wild harvest fisheries, and does not encompass broader ecosystem services derived from estuarine habitats which are sometimes reported against this term in the literature.

For each producer, the Gross Value of Production and Total Economic Output were summed across all species within an estuary, to give the cumulative economic value for each producer within the estuarine system (GVP_p and TO_p respectively). These values were then divided by the areal extent of habitat for producer p (ha) within the model region, to give the habitat-specific economic value on a per-hectare basis.

Results

Objective 1 – Determine to what extent young Eastern King Prawn are using natural, degraded or rehabilitated habitat in estuaries, and the contribution of these habitats to the fishery

Stable isotope-based assignment of emigrating prawns

The various assumptions associated with the stable isotope assignment approach were evaluated, and these are presented in Appendix 3. For the 2013/14 Hunter River dataset, 87.2 % of EKP and 93.5 % of SP could be assigned to putative nursery habitat areas given the isotopic data collected. In 2014/15, however, when only 13 putative nursery habitat areas were sampled, only 62.5 % and 72.8 % of EKP and SP respectively could be assigned (due to the reduced amount of isotopic data from putative nursery habitats that was available). Some insight into the potential origin of these individuals may be garnered from their isotopic composition relative to adjacent putative nursery areas that were sampled. The origin of these unassigned EKP was most likely to be the higher salinity areas between areas 1 and 3 (see Figure 4 for reference to areas). The origin of unassigned SP likely included the less saline areas upriver of area 12 and the marsh areas in the south arm of the river (see Figure 4 for reference to areas).

In both years, the majority (>90%) of emigrating EKP were assigned to the higher salinity areas near the lower end of the estuary, and within Fullerton Cove (Figure 4 and Figure 5), with very small relative contributions from marsh systems in the lower estuary (areas 6, 7, 8, 15 and 16). The relative contributions among these areas differed slightly, with the greatest contributing areas being area 3 and area 5 in 2013/14 and 2014/15 respectively. Applying the classification system of Dahlgren et al. (2006), indicated that on the basis of the isotopic data collected during the study, areas 3, 4, 5 and 21 represented EJH.

Assignment of SP was highly asymmetric in 2013/14, with the majority (~70 %) of emigrating individuals assigned to areas in the south arm of the river (Figure 6), and much smaller contributions from other areas across the lower estuary. Nine areas made no contribution whatsoever, including the productive SP trawling areas in and around Fullerton Cove (Figure 6). In 2014/15, emigrating SP were assigned to all putative nursery habitat areas that were sampled, with the greatest contributions from the rehabilitated marsh areas in Tomago, Kooragang and Hexham, and the furthest area from the sea (area 12; Figure 7). In both years, areas spanning the length of the lower estuary were classified as EJH. In 2013/14, this included the south arm (areas 20 and 21) and the areas furthest up the study area (areas 10 and 12), whereas in 2014/15 more EJH was identified in the north arm of the estuary (e.g. areas 5, 12 and 22) and also the three main rehabilitated saltmarsh areas (areas 6, 8 and 15).

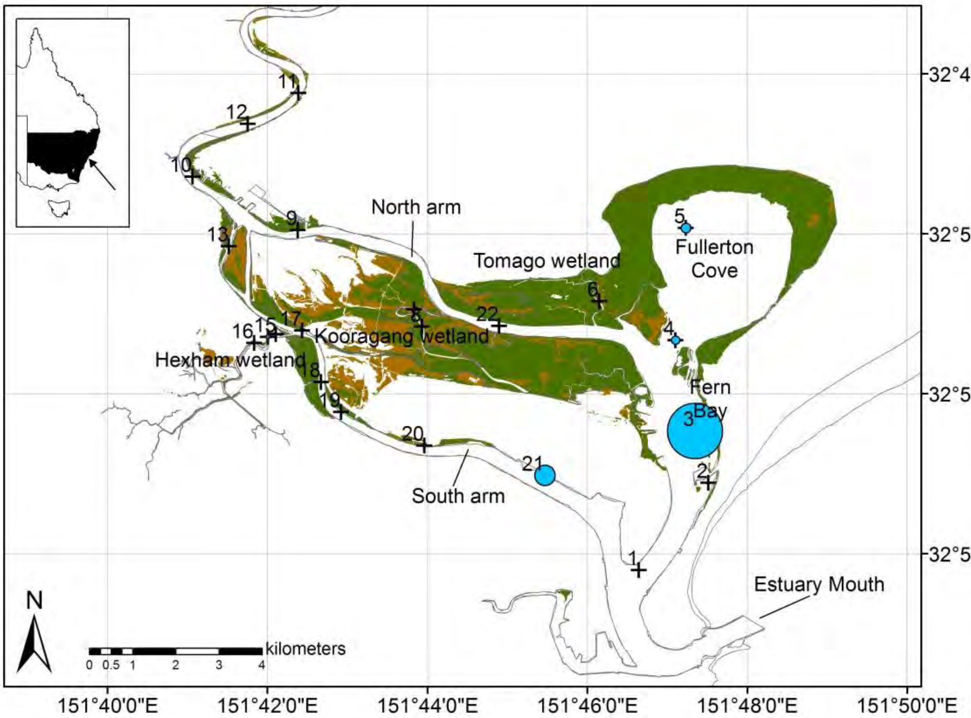

Figure 4 Proportional assignment of emigrating EKP to putative nursery areas across the lower Hunter River estuary in 2013/14 (numbered and shown by cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

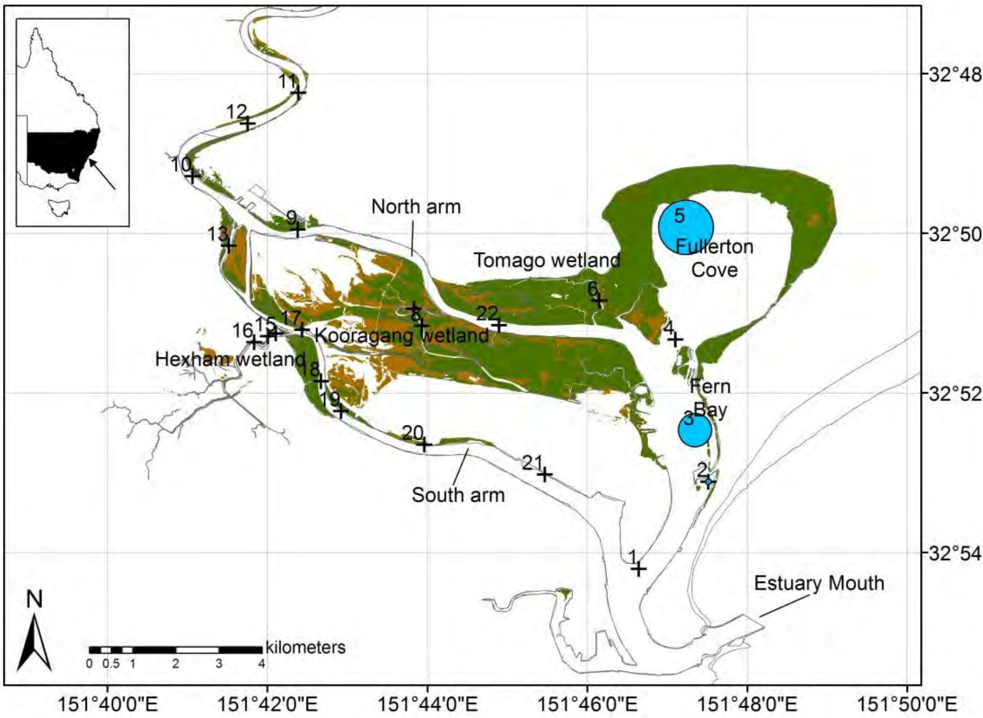

Figure 5 Proportional assignment of emigrating EKP to putative nursery areas across the lower Hunter River estuary in 2014/15 (numbered and shown by cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

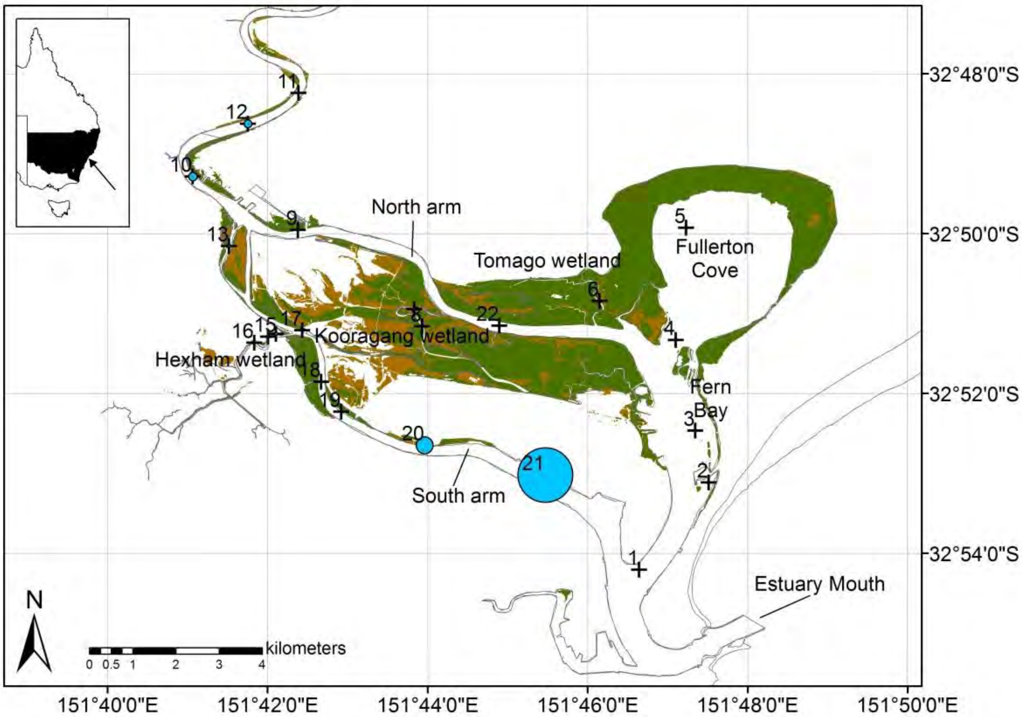

Figure 6 Proportional assignment of emigrating SP to putative nursery areas across the lower Hunter River estuary in 2013/14 (numbered and shown by cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

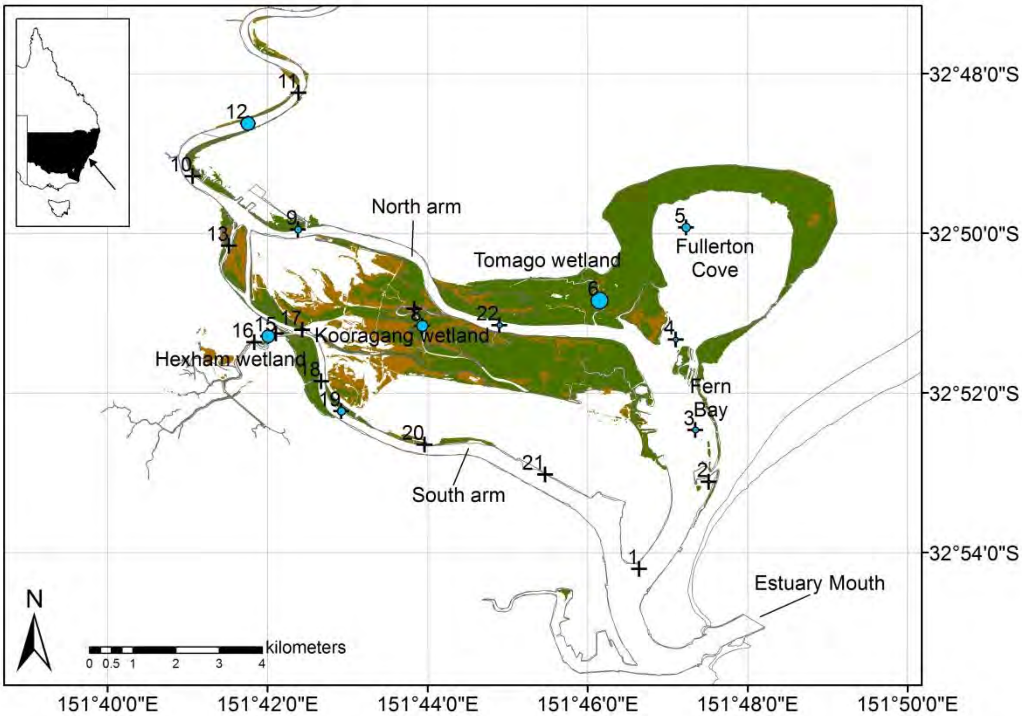

Figure 7 Proportional assignment of emigrating SP to putative nursery areas across the lower Hunter River estuary in 2014/15 (numbered and shown by cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

In the Clarence River estuary, 88% of EKP could be assigned to putative nursery habitat areas, given the isotopic data collected. EKP showed highly asymmetric patterns in assignment among putative nursery areas (Figure 8). Of the 12 areas sampled within the lower estuary, the vast majority of emigrating prawns were assigned to the North arm of the estuary in the vicinity of the main marsh/mangrove areas in this region of the estuary (area 8). The remaining prawns were assigned to areas in the main river channel (areas 10 and 11; Figure 8), and no prawns were assigned to areas in the south arm of the estuary or Lake Wooloweyah. Using the approach of Dahlgren et al. (2006), only areas 8 and 11 were designated as EJH.

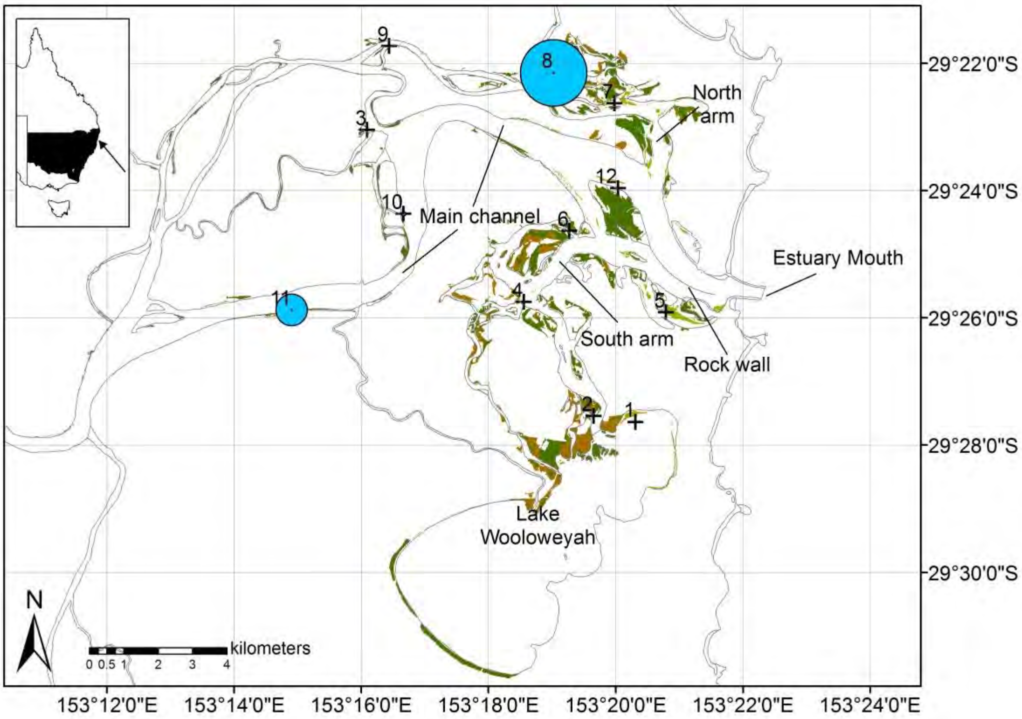

Figure 8 Proportional assignment of emigrating EKP to putative nursery areas across the lower Clarence River estuary in 2013/14 (numbered and shown by black cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown), mangrove (shaded in dark green), and seagrass (shaded in light green) habitat is indicated, as are the main features of the estuary referred to in the text.

In Lake Macquarie, EKP were only captured from 12 of the 20 sites surveyed, although other species of penaeid prawns were captured from other locations (mainly Greentail Prawn, *Metapenaeus bennettae*, data not presented here). Notwithstanding this, 84% of EKP could be assigned to putative nursery habitat areas, given the isotopic data collected. The proportional assignment of emigrating prawns to putative nursery areas on the basis of isotopic composition showed that most numerically important nursery areas were located in the northern and eastern regions of Lake Macquarie (Figure 9). The highest contributing areas were areas 2 and 4, followed by areas 1 and 8. With the exception of area 19, putative nursery sites in the southern and western regions of the estuary had negligible or nil contributions to emigrating prawns. In addition, the proportional contribution of area 11, a productive, off-lake lagoon, was negligible. Assignment of NH and EJH produced contrasting results. Sites 1, 2, 3, 4, 8, 10, 19, and 20 were all classified as EJH, whereas only a subset of these (sites 1, 2, 4, 8 and 10) were classified as NH.

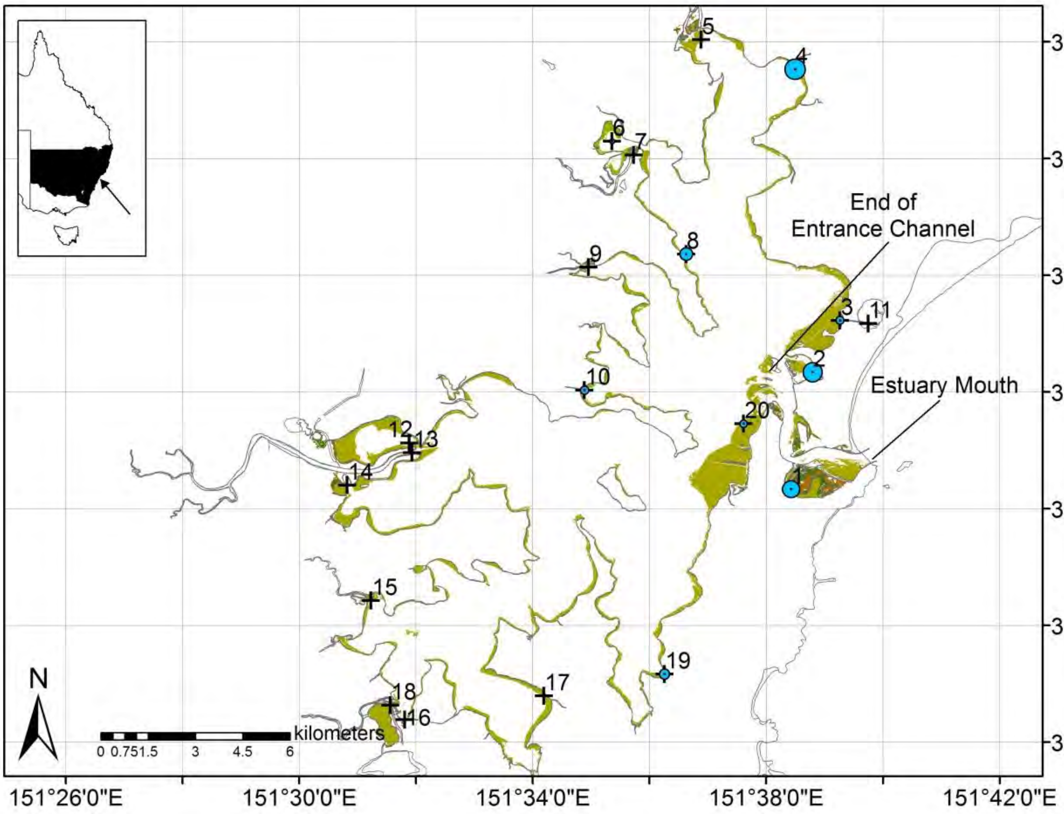

Figure 9 Proportional assignment of emigrating EKP to putative nursery areas across Lake Macquarie in 2013/14 (numbered and shown by black cross). Circles indicate the relative proportion of emigrating prawns assigned to each area. Saltmarsh (shaded in brown), mangrove (shaded in dark green), and seagrass (shaded in light green) habitat is indicated, as are the main features of the estuary referred to in the text.

Quantitative sampling

In the Hunter River, the abundance of EKP varied across the lower estuary (Figure 10). The average absolute abundance (averaged across all tows) estimated for EKP was 115 ± 8 EKP 100 m^{-2} (mean ± SE), and EKP were most abundant in the areas around Fern Bay, Fullerton Cove, and within the Hexham wetland (Figure 10). The generalised additive mixed model (GAMM) explained ~33% of the deviance in the data for EKP. In the north arm of the estuary, EKP abundance showed a distinctive peak between 8,000 and 10,000 m from the estuary mouth (F = 5.84, e.d.f. 4.81, P << 0.001, Figure 11a), whereas in the south arm abundance increased linearly with distance from the estuary mouth (F = 9.70, e.d.f. 1.00, P = 0.002, Figure 11b). Eastern King Prawn abundance peaked at a turbidity of 15 ntu (F = 6.81, e.d.f. 4.27, P << 0.001, Figure 11c), and showed a negative linear relationship with depth (F = 10.80, e.d.f. 1.00, P = 0.001, Figure 11d).

In the Clarence River, EKP were present at an average density of 76 ± 6 EKP 100 m^{-2} (mean ± SE), and were encountered at a maximum density of 499 EKP 100 m^{-2}. Distribution of prawns across the lower estuary indicated that juvenile EKP were present at the greatest densities 8-12 km from the mouth in the Main channel and North arm of the estuary (Figure 12). This included areas adjacent to the marsh/mangrove habitats in the North arm and the mangrove habitats in the main river channel.

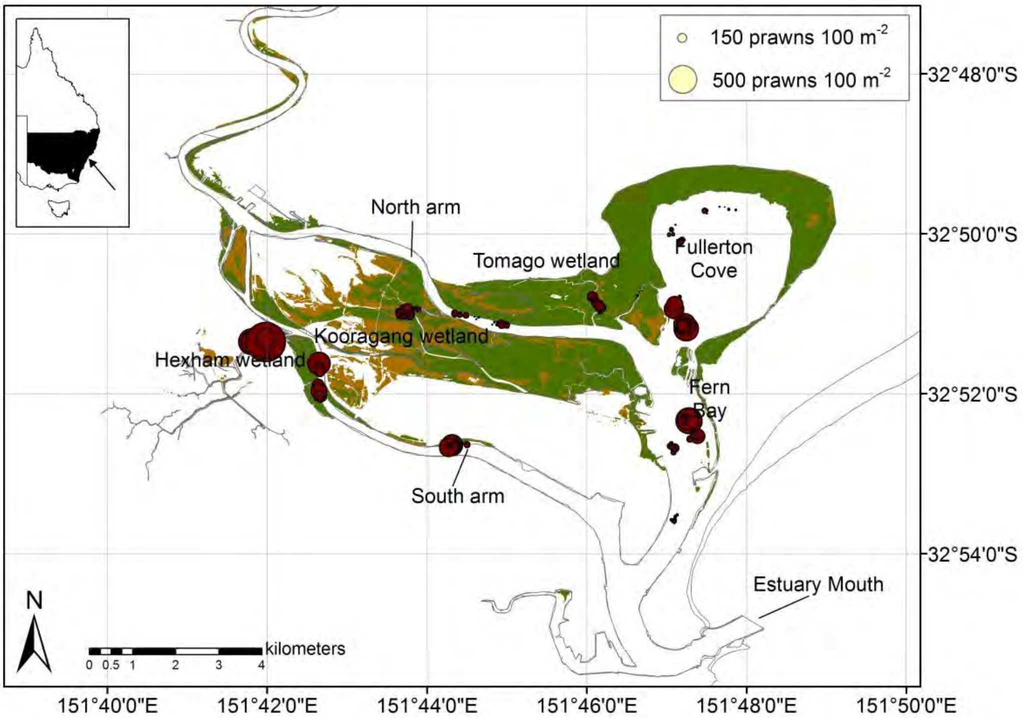

Figure 10 Density of EKP across the lower Hunter River estuary as sampled in 2014/15. Circles indicate the absolute density of prawns sampled, and sizes are indicated in the figure legend. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

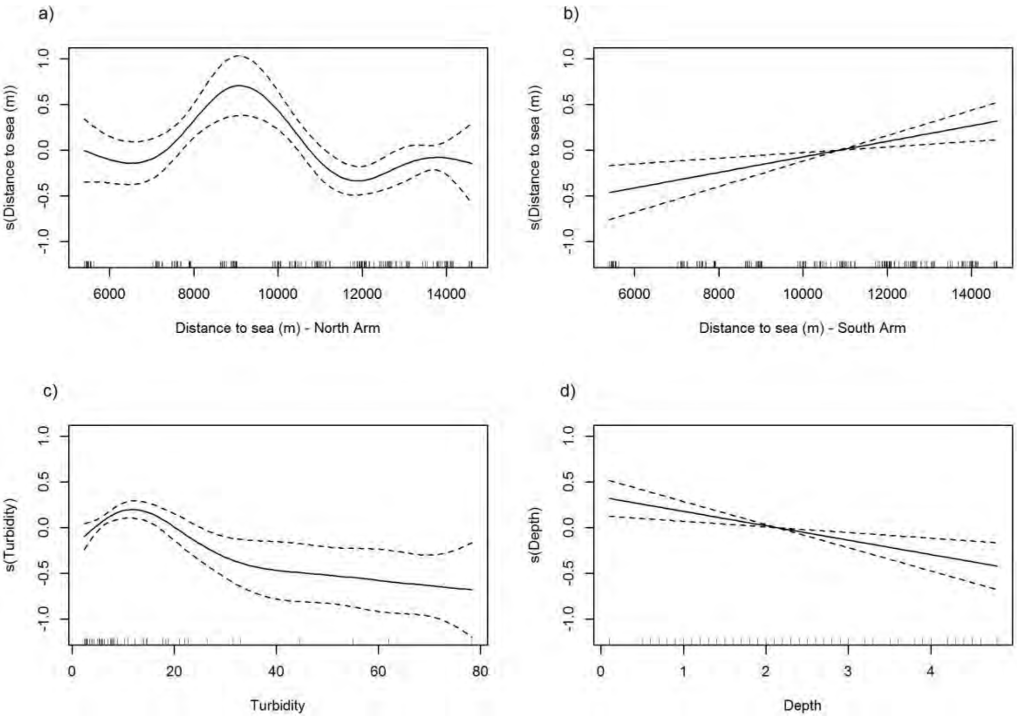

Figure 11 Plots of smoothed predictor variables (black lines) contributing to estimates of EKP abundance in the lower Hunter River estuary: a) the distance to sea (m) for the north arm; b) the distance to sea (m) for the south arm; c) turbidity (ntu); and, d) depth (m). The *y*-axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits.

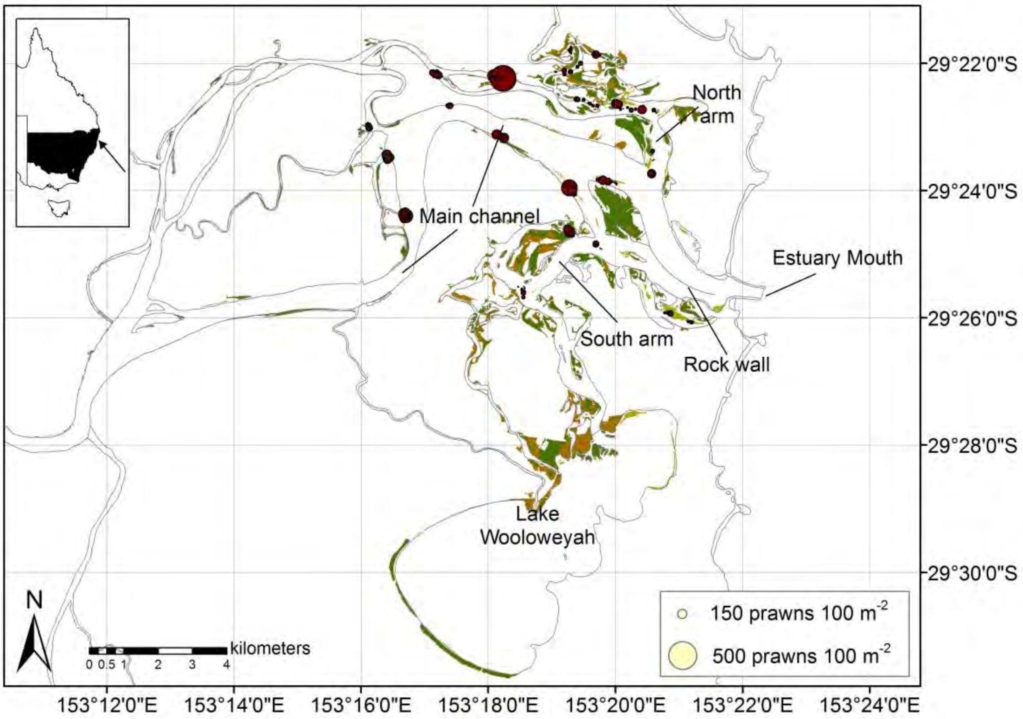

Figure 12 Density of EKP across the lower Clarence River estuary as sampled in 2015/16. Circles indicate the absolute density of prawns sampled, and sizes are indicated in the figure legend. Saltmarsh (shaded in brown) and mangrove (shaded in dark green) habitat is indicated, as are the main features of the estuary referred to in the text.

In Lake Macquarie, EKP were present at a global average density of 165 ± 11 EKP 100 m^{-2} (mean ± SE), and sizes ranged from 2.7 – 29.1 mm CL. The GAM explained ~30% of the deviance in the data, and indicated that prawn density had non-linear relationships with several variables (Figure 13). Prawn density peaked at an intermediate distance-to-mouth of around 6,000 – 9,000 m from the lakes entrance ($F = 4.27$, e.d.f. 5.00, P = 0.001, Figure 13a). Seagrass percent cover varied among sampling locations in the targeted quantitative survey, with means ranging between 25 and 98%. Prawn density did not change among locations where cover was <50%, however increasingly denser seagrass cover was correlated with declining numbers of prawns ($F = 7.86$, e.d.f. 2.09, P < 0.001, Figure 13b). Salinity did not vary greatly (31-37) across the locations or times sampled, and was not significantly correlated with prawn density ($F = 1.31$, e.d.f. 1.00, P = 0.253, Figure 13c). In contrast, prawn density peaked at a temperature of about 25°C ($F = 8.76$, e.d.f. = 3.84, P < 0.001, Figure 13d), with lower temperatures at lower densities.

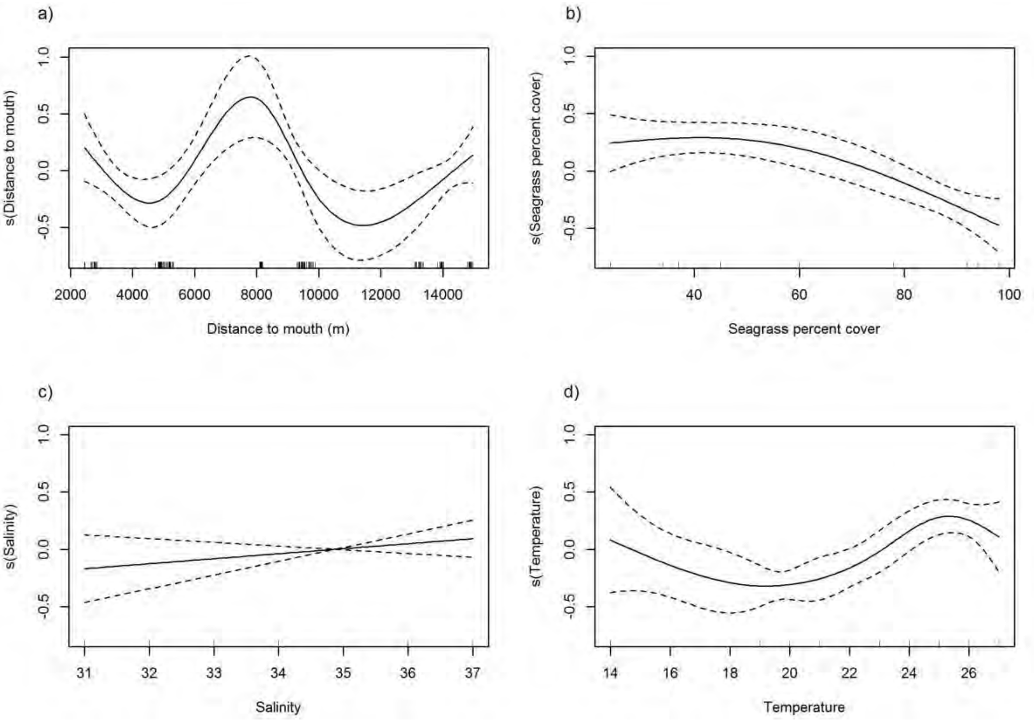

Figure 13 Plots of smoothed predictor variables (black lines) contributing to estimates of EKP density in Lake Macquarie: a) the distance to sea (m); b) estimated percent cover of seagrass (Seagrass); c) salinity and d) temperature (°C). The *y*-axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits.

Prawn and fish interactions with the marsh surface and marsh edge

Within sub-tidal creeks, a total of 31 species were collected in cast net samples including 22 species of fish and 9 of crustaceans (Table 1). The most abundant taxa was the pelagic shrimp *Acetes sibogae australis* and contributed to over 90% of the 'other crustaceans' (Figure 14), while the Castelnau's herring (*Herklotsichthys castelnaui*) was the most abundant fish (Table 1). The total abundance of EKP did not differ among habitats, but did differ among creeks ($F_{3,180} = 7.29$, $P < 0.001$, Fig. 14) as did the abundance of SP ($F_{3,180} = 5.11$, $P < 0.01$, Figure 14); as this was a random factor there was no further interpretation of the result. Total abundance of crustaceans was not found to differ among any of the factors examined. Fish abundance differed significantly among Habitats ($F_{1,3} = 12.61$, $P = 0.044$) with higher abundances found in *adjacent* habitats (Figure 14). Analysis of the community data within the creeks again showed there was only an effect for the random factor Creek ($F_{3,180} = 4.29$, $P < 0.001$). When the community was broken down into separate components, the fish community was found to significantly differ among the three wetlands ($F_{1,3} = 3.82$, $P < 0.01$). Pairwise comparisons among wetlands revealed a significant difference between Tomago and Hexham, but there were no differences between either of these wetlands and Kooragang. A SIMPER analysis revealed these community differences were primarily due to changes in the abundance of Castelnau's herring and Glassfish (*Ambassis jacksoniensis*). The crustacean community was found to differ among creeks ($F_{3,180} = 5.89$, $P < 0.001$), with no significant effects of higher level factors.

Table 1 Mean abundance of crustaceans and fish collected in fyke nets set within the intertidal marsh and cast nets (4.8 m^2) sampling sub-tidal creeks. Cast net data is pooled across the three wetlands. Commercial/recreationally important species are underlined, and standard error is shown in parentheses.

	Fyke Net Samples			Cast Nets Samples	
	Tomago	Kooragang	Hexham	Adjacent	Middle
Crustaceans					
Melicertus plebejus	0.33 (0.33)	0 (0)	1 (0.63)	0.13 (0.04)	0.26 (0.07)
Metapenaeus macleayi	4.33 (3.76)	3.83 (2.4)	6.83 (2.67)	0.47 (0.11)	0.33 (0.09)
Macrobrachium intermedium	331.16 (209.28)	407.83 (180.52)	359.16 (137.58)	0.44 (0.15)	0.17 (0.04)
Acetes sibogae australis	52.5 (45.32)	144.33 (91.92)	58.83 (37.29)	5.89 (1.22)	6.33 (0.75)
Neosarmatium trispinosum	0.83 (0.65)	2.66 (0.55)	3.16 (1.3)	0.04 (0.03)	0 (0)
Littorininae	0 (0)	0 (0)	2.66 (1.97)	0.04 (0.04)	0.12 (0.06)
Metapenaeus bennettae	0 (0)	0.66 (0.66)	1.33 (0.98)	0.16 (0.07)	0.06 (0.03)
Alpheidae	0 (0)	0 (0)	0 (0)	0.01 (0.01)	0.09 (0.04)
Buccinidae	0 (0)	0 (0)	0 (0)	0.11 (0.11)	0 (0)
Teleosts					
Gobiopterus semivestitus	152.5 (100.54)	79.33 (32.21)	126.16 (44.89)	0.22 (0.08)	0.21 (0.06)
Ambassis jacksoniensis	67.66 (46.82)	58 (43)	130.83 (92.36)	0.8 (0.22)	0.45 (0.13)
Liza argentea	15.5 (13.07)	20.16 (10.59)	1 (0.51)	0.29 (0.15)	0.02 (0.01)
Pseudogobius olorum	3.16 (2.19)	6.66 (6.06)	10.5 (5.25)	0.02 (0.01)	0 (0)
Favonigobius exquisitus	1.16 (1.16)	0 (0)	4 (2.14)	0.02 (0.01)	0.07 (0.03)
Acanthopagrus australis	0.83 (0.65)	0.66 (0.49)	1.16 (0.98)	0.08 (0.03)	0.02 (0.02)
Redigobius macrostoma	0.83 (0.83)	0 (0)	2.33 (1.22)	0 (0)	0 (0)
Tetractenos glaber	0.83 (0.65)	0 (0)	0 (0)	0.03 (0.02)	0 (0)
Hypseleotris galii	0.66 (0.66)	0 (0)	0.16 (0.16)	0 (0)	0.01 (0.01)
Myxus elongatus	0.66 (0.49)	5 (3.92)	1 (0.81)	0.06 (0.03)	0.1 (0.04)
Ambassis marianus	0.5 (0.34)	1.66 (0.76)	0 (0)	0.04 (0.02)	0.01 (0.01)
Philypnodon grandiceps	0.5 (0.5)	0.83 (0.83)	0.5 (0.34)	0.03 (0.02)	0.02 (0.02)

	Fyke Net Samples			Cast Nets Samples	
	Tomago	Kooragang	Hexham	Adjacent	Middle
Arenigobius bifrenatus	0.33 (0.33)	0 (0)	0.66 (0.42)	0 (0)	0.04 (0.02)
Mugilogobius platynotus	0.33 (0.21)	0 (0)	1 (0.44)	0 (0)	0 (0)
Gambusia holbrooki	0.33 (0.33)	0 (0)	2.66 (2.12)	0 (0)	0 (0)
Cryptocentroides gobioides	0.16 (0.16)	0 (0)	0 (0)	0 (0)	0 (0)
Gerres subfasciatus	0.16 (0.16)	1.5 (1.14)	0 (0)	0.08 (0.03)	0.1 (0.05)
Mugil cephalus	0.16 (0.16)	1.66 (1.28)	4.16 (4.16)	0.15 (0.1)	0.09 (0.03)
Anguilla reinhardii	0 (0)	0 (0)	0.33 (0.21)	0 (0)	0 (0)
Girella tricuspidata	0 (0)	0.33 (0.33)	0 (0)	0.01 (0.01)	0 (0)
Herklotsichthys castelnaui	0 (0)	0 (0)	0.16 (0.16)	1.73 (0.51)	0.88 (0.18)
Siphamia roseigaster	0 (0)	0.5 (0.5)	0 (0)	0 (0)	0.01 (0.01)
Platycephalus fuscus	0 (0)	0 (0)	0.5 (0.5)	0 (0)	0 (0)
Hyperlophus vittatus	0 (0)	0 (0)	0 (0)	0.22 (0.11)	0.36 (0.1)
Engraulis australis	0 (0)	0 (0)	0 (0)	0.11 (0.08)	0.02 (0.02)
Centropogon australis	0 (0)	0 (0)	0 (0)	0.07 (0.04)	0.06 (0.04)
Pomatomus saltrix	0 (0)	0 (0)	0 (0)	0.02 (0.02)	0.05 (0.02)
Favonigobius tamarensis	0 (0)	0 (0)	0 (0)	0.01 (0.01)	0.03 (0.03)
Hyporhampus australis	0 (0)	0 (0)	0 (0)	0 (0)	0.01 (0.01)

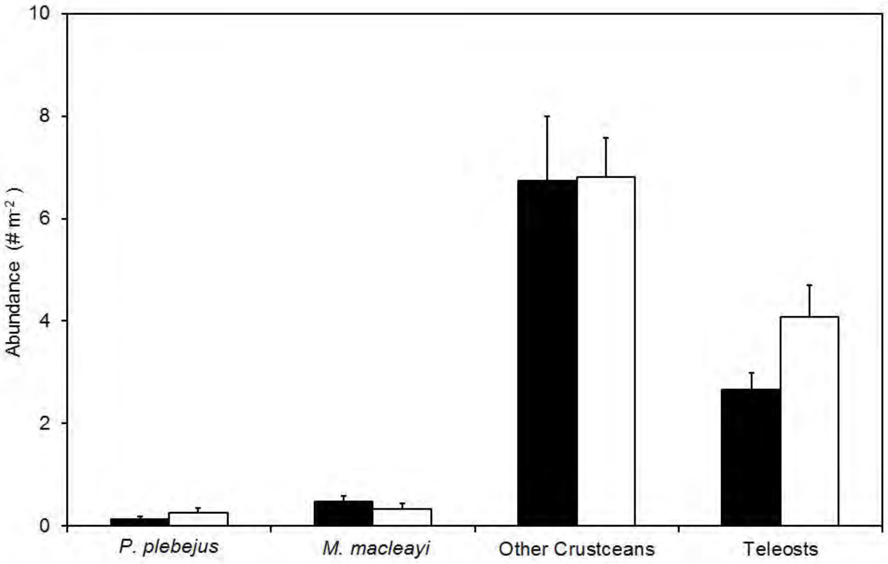

Figure 14 Mean abundance (± S.E.) of cast net samples (4.5 m^2) from the middle (filled bars) and adjacent (unfilled bars) habitat of sub-tidal creeks within the Hunter River estuary

Depth logger data indicated that the marsh only became inundated during spring high tides, with the marsh remaining exposed during the entire neap cycle, and that the marsh had a mean inundation period of only 30.3 h (± 3.5 S.E.) per month with each inundation lasting between 3 – 6 hours. Within intertidal marsh/mangrove habitats, fyke net catches were dominated by Striped River Prawn (*Macrobrachium intermedium*), which accounted for more than half of all nekton and 80% of all crustaceans (Table 1). The most abundant of the 20 species of fish was Glassgoby (*Gobiopterus semivestitus*) followed by Glassfish (*Ambassis jacksoniensis*), which collectively accounted for 85% of fish using the marsh habitat. The nekton community did not differ among the three wetlands when considered as a whole ($F_{2,15} = 1.173$, $P = 0.307$), or when broken into the crustacean community ($F_{2,15} = 1.20$, $P = 0.311$) or the fish community ($F_{2,15} = 1.02$, $P = 0.341$). Only 8 EKP were collected from the marsh surface in total, and none were collected at Kooragang.

Objective 2 – Determine the hydrographic conditions which provide for maximum growth and survival of Eastern King Prawn within nursery habitats

The rate of salinity decline explained the mortality rate at the end of the salinity decline (*z*-statistic = -6.971, sig. < 0.001), and predicted that the rate of decline resulting in 50% mortality was 15.545% h^{-1} (95% confidence limits 13.919 - 17.832% h^{-1}; Figure 15). This rate of salinity decline was estimated to result in a final salinity of 0.86, with the rates for the 95% confidence intervals estimated to result in salinities 1.28 and 0.50 respectively. The rate of salinity decline explained the mortality rate 120 h after the salinity decline ceased (z-statistic = -8.087, $P < 0.001$), with 8.033% h^{-1} decline predicted to result in 50% mortality (95% confidence limits 6.856- 9.733% h^{-1}; Figure 15b). This rate of salinity decline was estimated to result in a final salinity of 5.2, with the rates for the 95% confidence intervals estimated to result in salinities 6.95 and 3.48 respectively. The rate of salinity decline predicted to result in complete mortality 120 h after the salinity decline ceased was 15.741% h^{-1} (99% mortality; 95% confidence limits 13.019 - 21.461% h^{-1}; Figure 15b). This rate of salinity decline was estimated to result in a final salinity of 0.82, with the rates for the 95% confidence intervals estimated to result in salinities 1.58 and 0.21 respectively. It should be noted that the rate of salinity decline and the endpoint salinity were correlated (as this is what occurs in the natural environment), and the observed patterns may well be a function of both variables.

Aerobic metabolic rates of juvenile EKP ranged from 0.44 - 4.04 mg O_2 g^{-1} h^{-1} and showed a significant non-linear response to the rate of salinity decline ($F = 3.49$; edf 8.54; $P < 0.001$), with 25.6% of the observed deviance in metabolic rate explained. When the rate of salinity decline was close to zero, aerobic metabolic rates were close to the estimated intercept of 1.81 mg O_2 g^{-1} h^{-1}. Aerobic metabolic rates increased rapidly once the rate of salinity decline exceeded ~6% h^{-1}, with modelled values peaking at approximately 3.3 mg O_2 g^{-1} h^{-1} when the rate of salinity decline was 7.5% h^{-1} (Figure 16a). As rates of salinity decline increased, aerobic metabolic rates declined to less than the estimated intercept, with the slowest rates of 1.3 mg O_2 g^{-1} h^{-1} occurring for rates of salinity decline ≥ 9.5% h^{-1} (Fig. 16a). There was a negative linear relationship between somatic condition and metabolic rate ($F = 13.15$; edf 1; $P < 0.001$; Fig. 16b). The animals with the poorest somatic condition had the fastest aerobic metabolic rates, and the rate decreased at a rate of -0.12 mg O_2 g^{-1} h^{-1} per unit of somatic condition (Figure 16b).

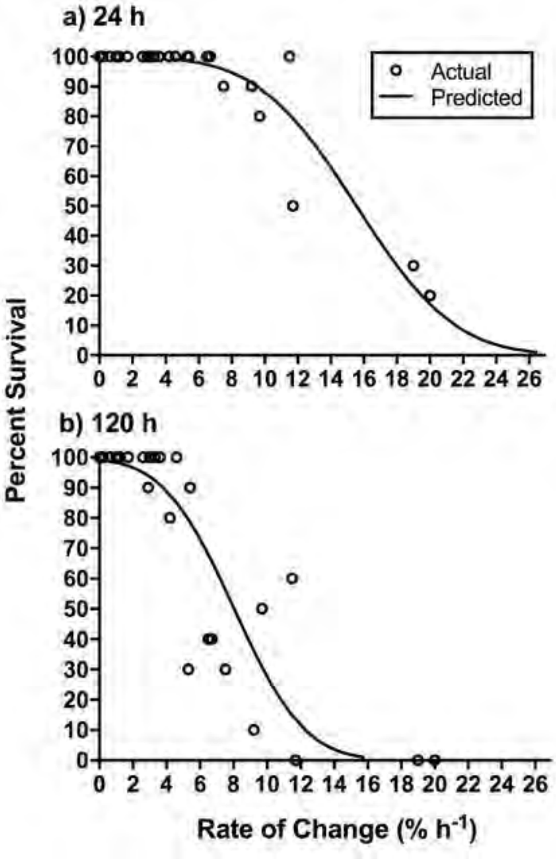

Figure 15 Percent survival of prawns in all salinity decline treatments (circles) with the predicted mortality from the Probit regression analysis (solid line) at a) the end of the 24 h salinity decline and b) 120 h after the end of the salinity decline.

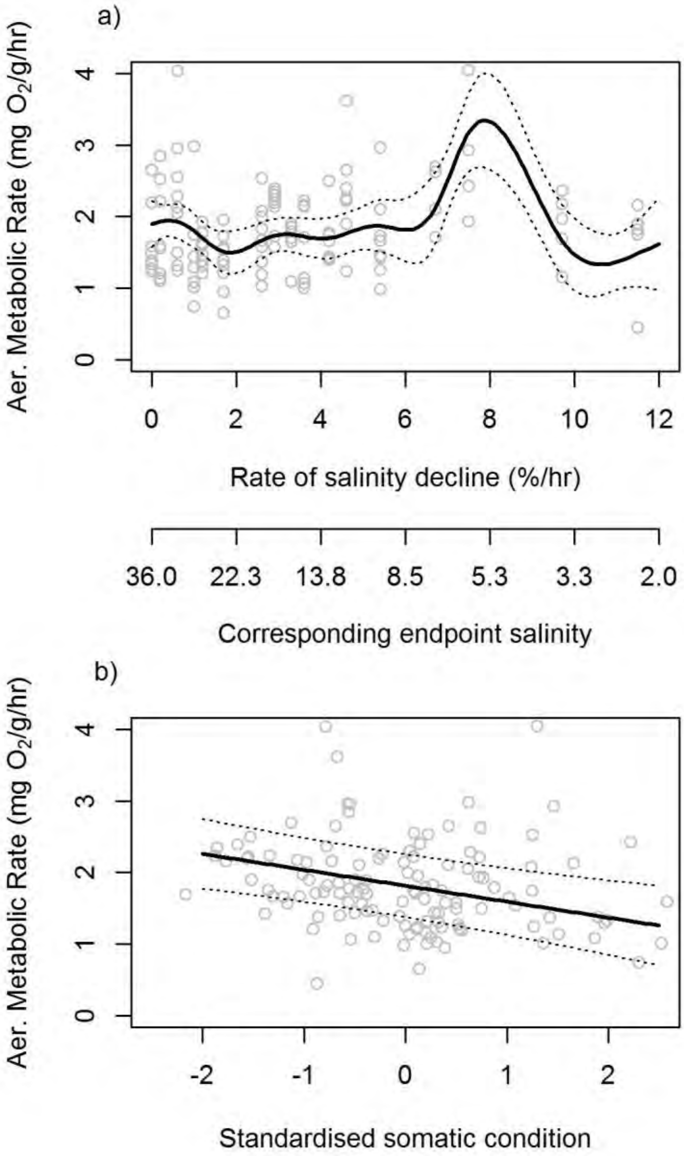

Figure 16 Fitted GAM reflecting the effect of the rate of salinity decline and somatic condition on metabolic rate for juvenile EKP. The solid line indicates the modelled aerobic (abbreviated as Aer.) metabolic rate across the range of salinity treatments (a), and across prawns of different somatic condition measured using standardised residuals from the carapace length – dry weight relationship (b). Dashed lines are 95% confidence intervals and grey circles are measured values.

The water content of prawns showed a significant non-linear response to the rate of salinity decline ($F = 11.9$; edf 5.39; $P < 0.001$), with 34.8% of the observed deviance in water content explained. The water content was highest in prawns that had experienced fast rates of decline in salinity, and was lowest in prawns that had experienced rates of salinity decline approaching zero. Prawns that had experienced the slowest rates of change contained ~79% water, but this increased to the estimated intercept value (estimated overall mean) of 80.3% as rates of salinity decline approached 2.5% h^{-1}. Water comprised 1% more of the body mass of prawns for rates of salinity decline that were faster than 2.5% h^{-1}, with water content then remaining similar for rates of decline approaching 7% h^{-1}; beyond which water content began to increase. Prawns that experienced rates of salinity decline faster than 9.2% h^{-1} had the greatest water content, with water comprising up to 5% more of their body mass than those that had experienced rates of salinity decline approaching zero.

Objective 3 – Assess the extent of key Eastern King Prawn habitat lost and remaining in the Hunter and Clarence river estuaries

There have been extensive changes in the areal coverage of habitat over the time scales examined, in both the Hunter (Figure 17) and Clarence (Figure 18) River estuaries. In the Hunter River estuary, almost three quarters of saltmarsh habitat present in the 1950s was lost by the 1990s (Table 2). Most of this habitat was lost from the Tomago wetland, the Hexham wetland, and the wetlands to the north of Fullerton Cove. The loss of habitat saw 100% of saltmarsh-lined shoreline lost from Fullerton Cove and almost 50% of all saltmarsh-lined shoreline lost from smaller tidal creeks across the system (Table 2). Over this time frame, mangrove coverage in the system increased by almost 20%, and this was coupled with an increase in the permitter of mangrove-lined shorelines across the system. The exception here was the main channel, which lost one quarter of its mangrove-lined shoreline mainly due to development and reclamation throughout the Kooragang wetland and along the South arm of the estuary. No seagrass was present in the Hunter River estuary in the 1950s.

Extensive changes in the coverage of saltmarsh habitat were also evident in the Clarence River estuary, with 64% of habitat lost between the 1940s and 2000s (Figure 18, Table 3). This led to a concomitant 40% change in the availability of saltmarsh-lined shoreline (Table 3). Most of the loss of saltmarsh occurred in the deltaic islands between Lake Wooloweyah and the Main channel, and also throughout the North arm (Figure 18). There was a moderate gain the mangrove habitat over this time frame, and a small change in the subtidal waterway area of creeks within the system.

It should be noted that it is likely that substantial habitat loss had already occurred prior to the availability of aerial photography from the 1940s onwards. Consequently, this analysis did not capture any of this pre-1940s habitat loss.

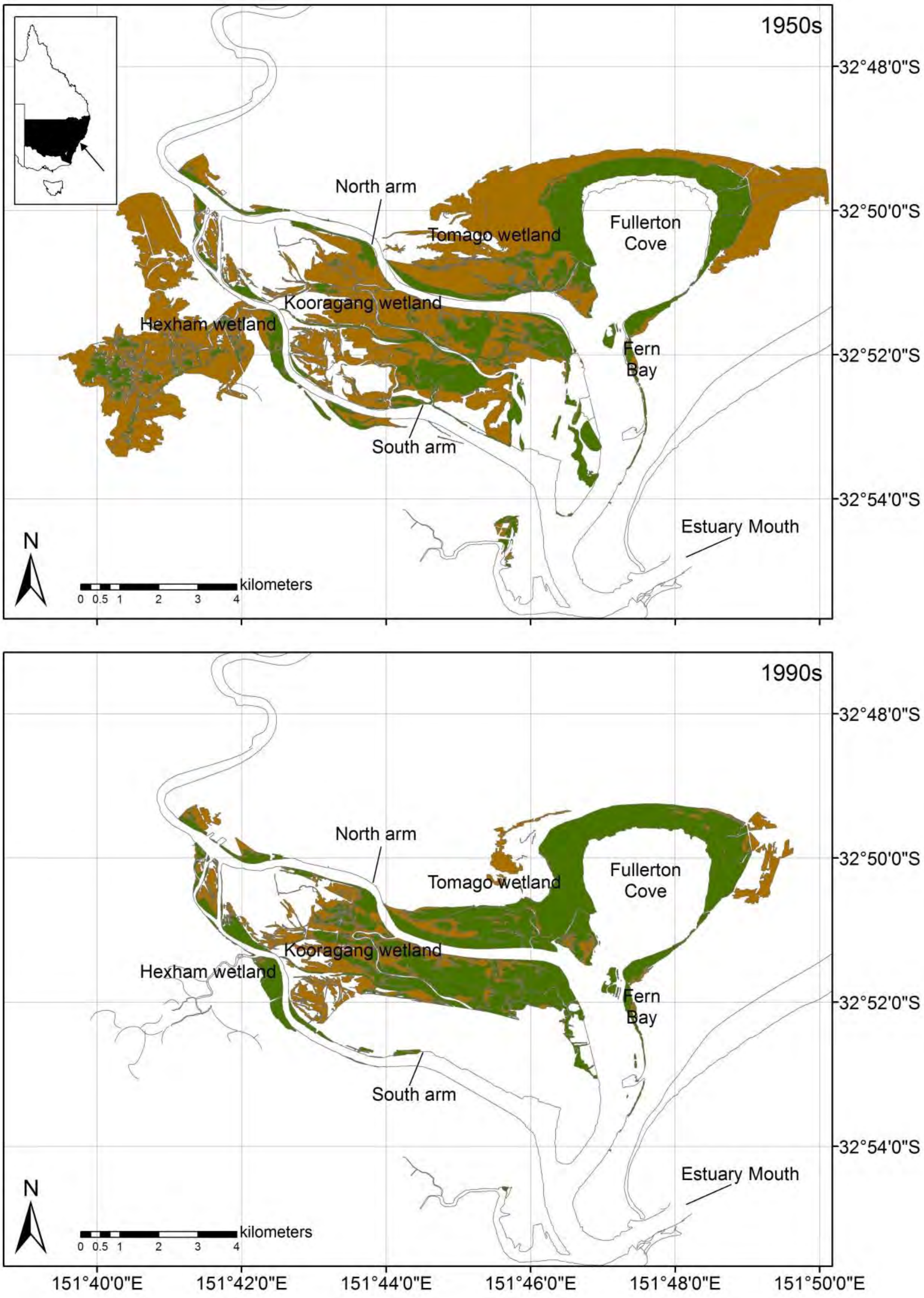

Figure 17 Habitat changes over decadal time periods in the lower Hunter River estuary. Areal habitat coverage in the 1950s is indicated the top panel, and coverage in the 1990s is indicated in the lower panel. Habitats shown include saltmarsh (shaded in brown), mangrove (shaded in dark green), and seagrass (shaded in light green) habitat is indicated, as are the main features of the estuary referred to in the text.

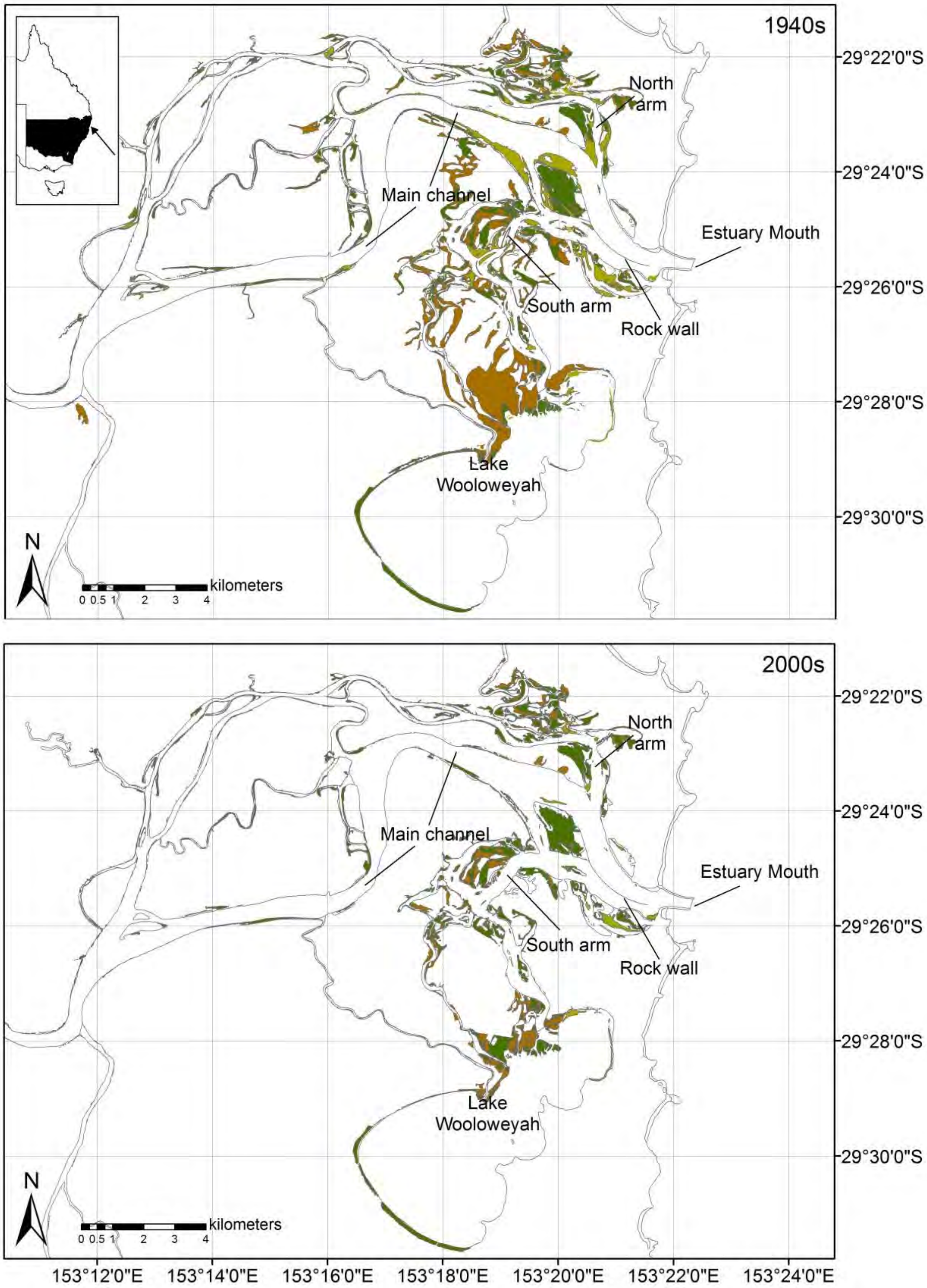

Figure 18 Habitat changes over decadal time periods in the lower Clarence River estuary. Areal habitat coverage in the 1940s is indicated the top panel, and coverage in the 2000s is indicated in the lower panel. Habitats shown include saltmarsh (shaded in brown), mangrove (shaded in dark green), and seagrass (shaded in light green) habitat is indicated, as are the main features of the estuary referred to in the text.

Table 2 Changes in habitat extent in the lower Hunter River estuary over decadal time scales. Habitat extent is shown for total waterway area (ha), shoreline perimeter (km, for saltmarsh and mangrove habitats, and shoreline not associated with these habitats [shown as “Other”]), and areal extent of the saltmarsh, mangrove and seagrass (ha).

	Waterway area (ha)	Shoreline Perimeter (km)			Overall macrophytes (ha)		
		Mangrove	Saltmarsh	Other	Mangrove	Saltmarsh	Seagrass
1950s							
Main channel	1396	39	5	33			
Small creeks (total)	191	25	37	17			
Embayment	790	12	0	0			
Total	2377	76	42	49	1456	2955	-
1990s							
Main channel	1375	29	2	46			
Small creeks (total)	179	40	20	19			
Embayment	790	12	0	0			
Total	2343	82	21	65	1733	766	-
Percent change							
Main channel	-1%	-25%	-62%	39%			
Small creeks (total)	-6%	58%	-47%	14%			
Embayment	0%	2%	-100%	-%			
Total	-1%	7%	-49%	-4%	19%	-74%	-

Table 3 Changes in habitat extent in the lower Clarence River estuary over decadal time scales. Habitat extent is shown for total waterway area (ha), shoreline perimeter (km, for saltmarsh and mangrove habitats, and shoreline not associated with these habitats [shown as "Other"]), and areal extent of the saltmarsh, mangrove and seagrass (ha).

	Waterway area (ha)	Shoreline Perimeter (km)			Overall macrophytes (ha)		
		Mangrove	Saltmarsh	Other	Mangrove	Saltmarsh	Seagrass
1940s							
Main channel	6523	76	15	277			
Small creeks (total)	1565	60	16	318			
Embayment	4533	27	7	33			
Total	12621	163	38	628	720	803	399
1990s							
Main channel	6523	96	9	270			
Small creeks (total)	1506	64	9	309			
Embayment	4533	33	4	26			
Total	12562	193	22	605	765	290	83
Percent Change							
Main channel	0%	27%	-40%	-2%			
Small creeks (total)	-4%	5%	-43%	-3%			
Embayment	0%	25%	-36%	-21%			
Total	0%	19%	-40%	-4%	6%	-64%	-79%

Objective 4 – Outline the potential improvements to the Eastern King Prawn fishery that could be achieved through targeted wetland rehabilitation

The most realistic parameterization off this model suggested that the greatest return from restoration would be realized by restoring 200 ha of habitat in zone 3 (Figure 19), with the equilibrium annual increase in harvest greater than 4% (Figure 20). Zones 2-4 would also provide relatively high returns. Alternatively, restoration in the most northern and southern zones is likely to have less of an effect on overall revenue from the fishery in New South Wales. In the north this is in part due to EKP migrating into Queensland waters, and so harvest was not recouped within the New South Wales fishery. In the southern zones (6-9), habitats are relatively un-degraded, but recruitment is low, so returns from restoration were similarly diminutive (Figure 20). Obviously the equilibrium annual increase in harvest does not account for the time stream of restoration benefits, which would be more modest immediately following restoration than at equilibrium. However, the relative return of alternative restoration zones would remain unchanged, thus this equilibrium metric is in keeping with the objectives of this work—to evaluate relative efficiency of alternative zones, rather than a full benefit cost analyses of the benefit of restoration to society.

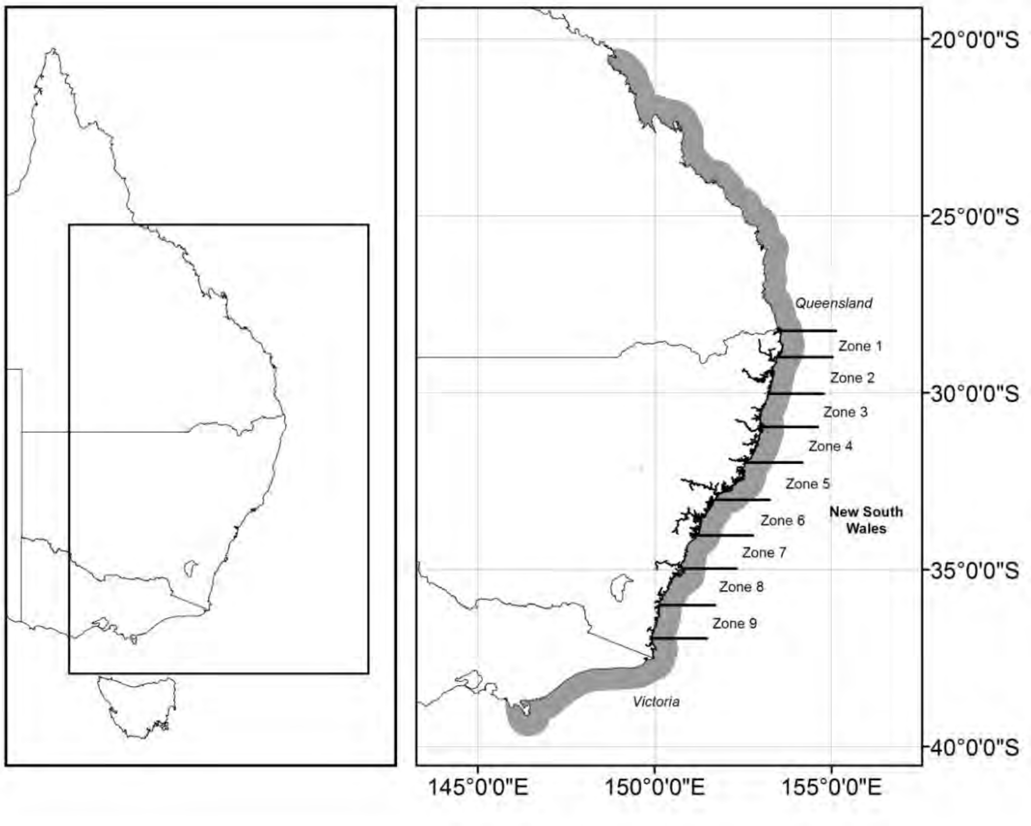

Figure 19 Spatial structure of the EKP model, showing the location of the model region on the Australian east coast (left panel), and the New South Wales zones employed in the model (which align with the reporting zones for the NSW Ocean Trawl Fishery). The additional spatial zones represented by the adjacent states (Queensland and Victoria) are also indicated. Grey shading reflects the latitudinal distribution of the species.

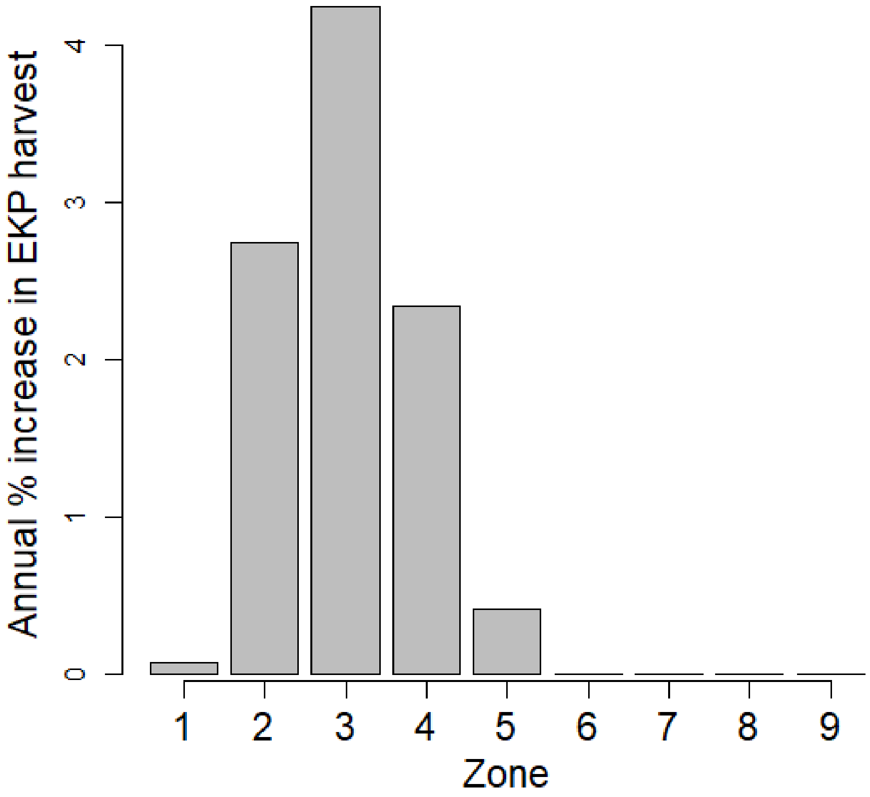

Figure 20 Expected outcomes from 200 hectares of habitat restoration in each alternative zone in New South Wales. Zones correspond to those in Figure 19.

Objective 5 – Extend information on habitat-fishery linkages to commercial fisheries, landowners and other catchment stakeholders and incorporate recommendations into fisheries or water management

Outcomes from Objective 5 are reported in detail in the *Extension and Adoption* section, below.

Objective 6 – Establish quantitative habitat-fishery linkages for the main exploited species in both the Hunter River and Clarence River systems

Trophic linkages

For other exploited species in the Hunter River, *S. virginicus* was the source that supported the largest mean proportion of the diet for all species of consumers (47-63%, Figure 21), except Yellowfin Bream and Luderick. The greatest contribution of *S. virginicus* was seen in Dusky Flathead (63%; Figure 21, Table 4), and for Yellowfin Bream and Luderick, the largest contribution to diet was FBOM (39% and 41%, respectively; Figure 21). Other sources had variable proportions of contributions and higher standard deviations, indicating that the model had difficulty separating those sources. Similar relationships were observed for species sampled in the Clarence River. Linear modelling supported some grouping among sites, and *S. virginicus* comprised the greatest contribution to diet in all consumers (40 – 95%) except Yellowfin Bream at site C4 which had a larger contribution of POM (30%; Figure 22). SP/EKP had the highest contribution of *S. virginicus* at all sites (95, 89 and 72 % for sites C4, C5 and Cgroup, respectively) and Dusky Flathead had the next highest contribution of *S. virginicus* at all sites (53, 65 and 69% for sites C4, C5 and Cgroup, respectively). For both estuaries, confidence intervals of Gelman diagnostics were < 1.02, suggesting that longer Bayesian simulation runs were not necessary.

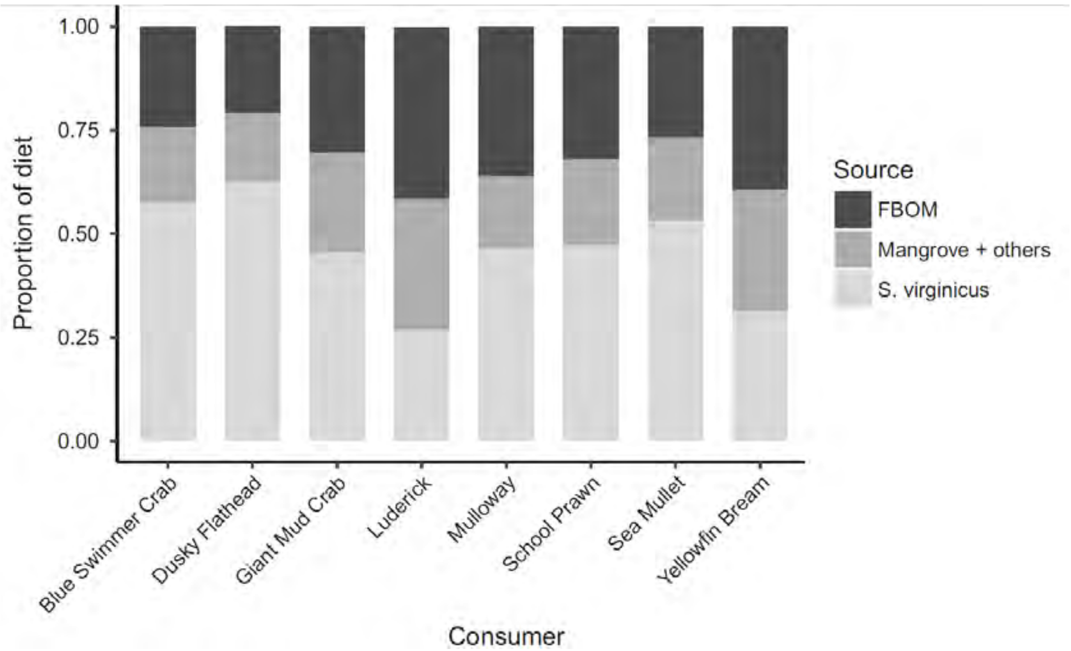

Figure 21 Mean proportion of contribution to diet of commercially-exploited consumers from each source in the Hunter River estuary, as calculated using Bayesian mixing models and $\delta^{13}C$. Note that FBOM refers to fine benthic organic matter.

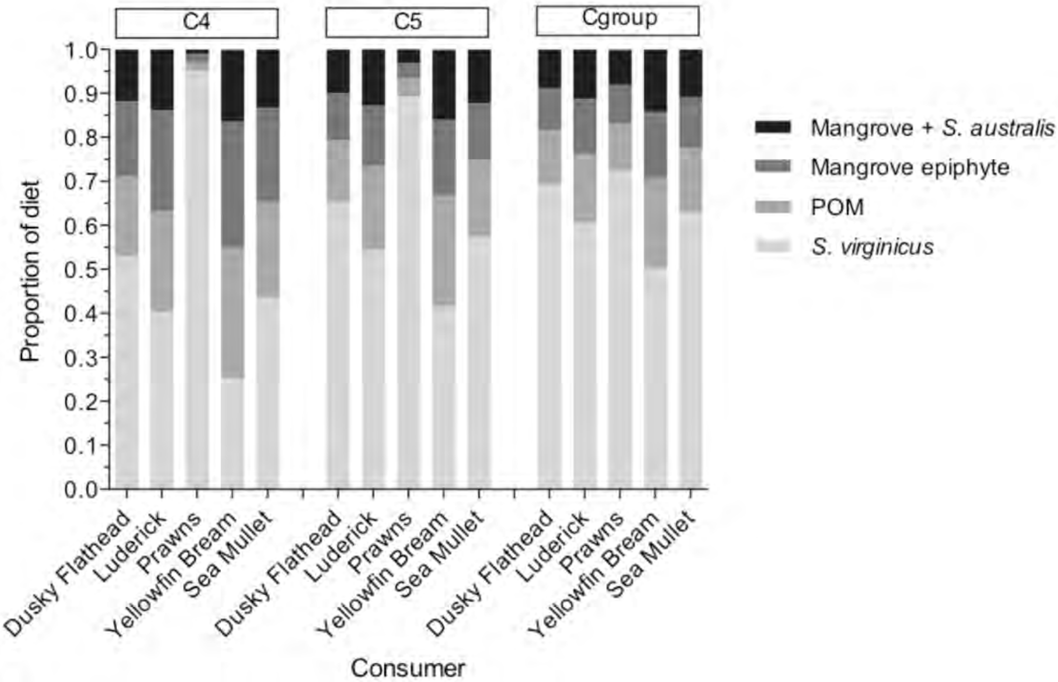

Figure 22 Stacked bar plot showing mean proportion of contribution to diet of each source for each commercially-exploited consumer in the Clarence River estuary at sites C4, C5, and grouped sites 1, 2, and 3, as calculated using Bayesian mixing models from $\delta^{13}C$. Note that POM refers to particulate organic matter.

Value of estuarine habitats

Parameter values for the Hunter River and Clarence River estuaries are outlined in Appendix 11. The distributions for potential economic values derived from saltmarsh and mangrove habitats are presented in Figure 23 and Figure 24 for the Hunter and Clarence Rivers respectively. All distributions were lognormal, which was primarily driven by the lognormal distributions of the total catches for species within each estuary (where very high catches can occur at a relatively low frequency). Higher overall catches in the Clarence River led to higher overall higher economic values (Figure 24), relative to the Hunter River (Figure 23), although the relative patterns in economic values among fish species were generally similar between estuaries. For fish species, the greatest overall value from each habitat was derived through Yellowfin Bream and Sea Mullet harvest, whereas the lowest value was derived through Luderick. Differences were largely driven by market value and catch levels. Yellowfin Bream, Mulloway and Dusky Flathead are all higher market value species, whereas Luderick and Sea Mullet have lower market values. The lower market value of Sea Mullet, however, was offset by much larger catches; and this was reflected in higher values derived from both saltmarsh and mangrove. For invertebrates, the patterns among species were also similar between estuaries (Figure 23 and Figure 24), with the greatest economic value from saltmarsh consistently derived through harvest of SP. The proportional contribution of saltmarsh to the diet of SP in the Clarence was more than double that of the Hunter River, which greatly increased the economic value derived from saltmarsh through harvest of this species.

Depending on the metric used (*GVP* or *TO*), total habitat values (summed across species) estimated within the model regions ranged from ~AUD100,000 y^{-1} to ~AUD7,200,000 y^{-1} (Table 4). As expected, the highest values derived were for Total Economic Output, which reflected the overall impact of harvest derived from the primary producers across the broader supply chain. Table 4 also shows the areal extent of each habitat in which the primary producers dominate, and when this is taken into account saltmarsh in the Clarence River had by far the greatest economic value per-unit-area, with an average estimated Total Economic Output (*TO*) of AUD25,741 ha^{-1} y^{-1}. The greatest economic value derived from mangrove habitats was also in the Clarence River with a *TO* of AUD5,297 ha^{-1} y^{-1}. Economic values in the Hunter River (*TO*) were AUD2,579 ha^{-1} y^{-1} and AUD316 ha^{-1} y^{-1} for saltmarsh and mangrove habitats respectively.

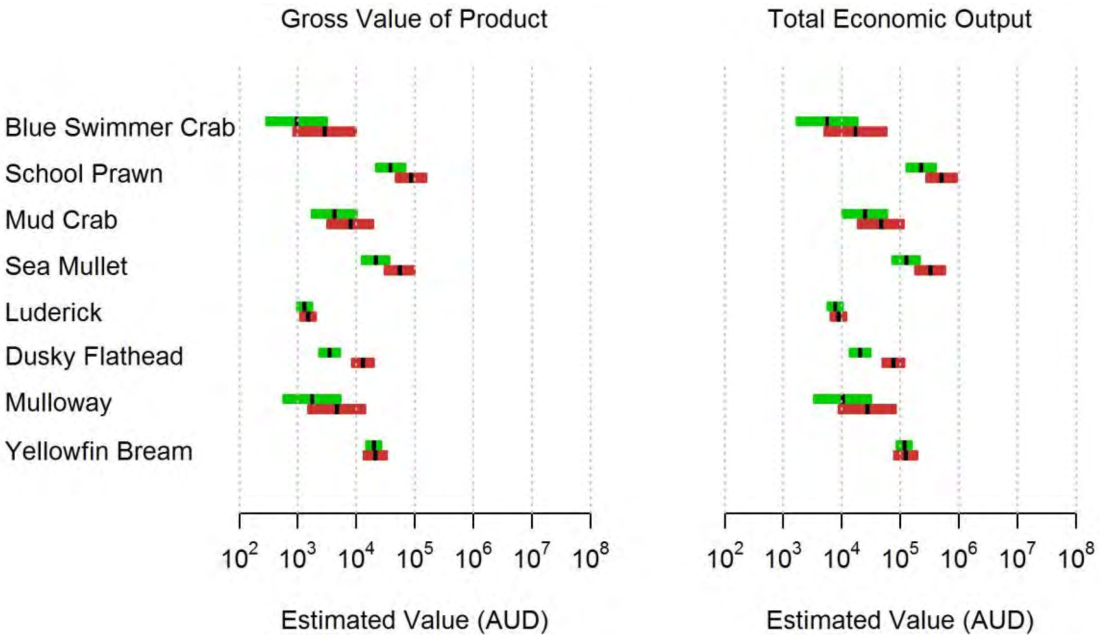

Figure 23 Output of model simulations for the Hunter River, New South Wales, showing Gross Value of Product (left panel) and Total Economic Output (right panel). Shaded horizontal bars indicate the 75% confidence intervals for the potential annual values (AUD) derived from emergent habitats for species harvested from within the model region. Bars are shaded brown for saltmarsh and green for mangrove, and horizontal black bars indicate the mean value for each species and habitat.

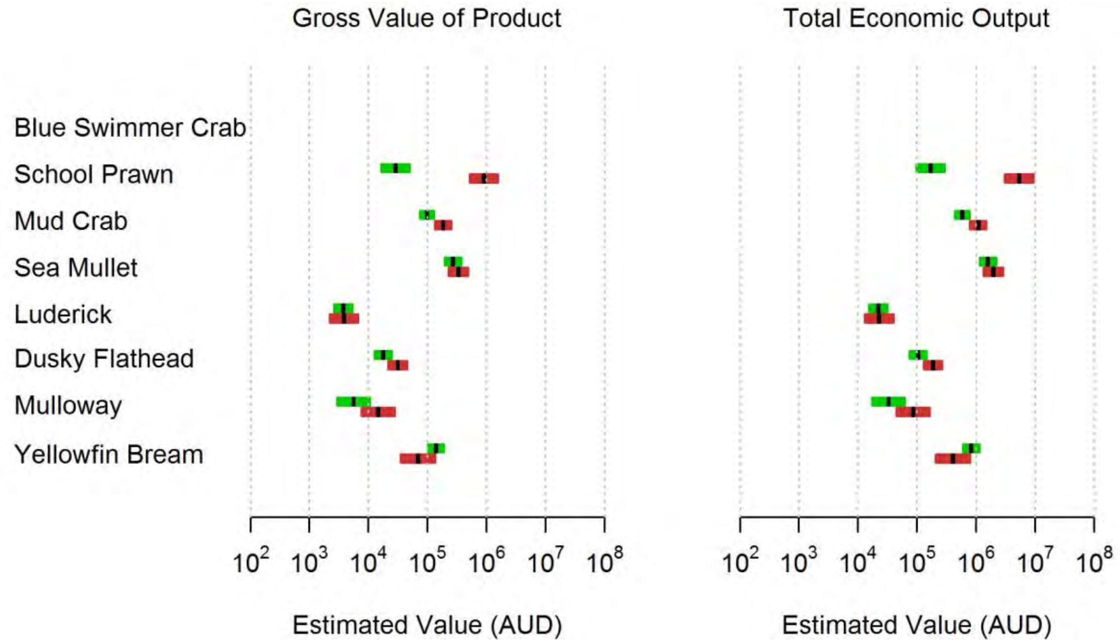

Figure 24 Output of model simulations for the Clarence River, New South Wales, showing Gross Value of Product (left panel) and Total Economic Output (right panel). Shaded horizontal bars indicate the 75% confidence intervals for the potential annual values (AUD) derived from emergent habitats for species harvested from within the model region. Bars are shaded brown for saltmarsh and green for mangrove, and horizontal black bars indicate the mean value for each species and habitat.

Table 4 Summary of average estimated values (AUD) for each species and primary producer across all simulations expressed in terms of Gross Value of Production (*GVP*) and Total Economic Output (*TO*).

Species		Hunter River				Clarence River			
		Saltmarsh		Mangrove		Saltmarsh		Mangrove	
		GVP	*TO*	*GVP*	*TO*	*GVP*	*TO*	*GVP*	*TO*
Acanthopagrus australis	Yellowfin Bream	21,903	129,160	20,537	121,108	83,815	494,738	147,699	872,003
Argyrosomus japonicus	Mulloway	8,707	51,374	3,298	19,459	17,800	104,948	6,696	39,479
Platycephalus fuscus	Dusky Flathead	14,210	83,753	3,760	22,164	33,451	197,281	18,727	110,441
Girella tricuspidata	Luderick	1,560	9,201	1,364	8,044	4,374	25,837	4,072	24,050
Mugil cephalus	Sea Mullet	62,580	369,591	22,994	135,806	349,015	2,061,717	279,328	1,650,066
Scylla serrata	Giant Mud Crab	11,381	67,214	6,017	35,537	197,777	1,167,145	104,856	618,770
Portunus armatus	Blue Swimmer Crab	5,174	30,498	1,634	9,635	-	-	-	-
Metapenaeus macleayi	School Prawn	96,934	571,703	42,774	252,259	618,770	3,650,691	34,271	202,196
Cumulative value across all species (y^{-1})		222,449	1,312,494	102,378	604,012	1,305,002	7,207,619	595,649	3,517,005
Areal extent of habitat within model region (ha)[1]		509		1,908		280		664	
Total value across region per unit habitat (ha^{-1} y^{-1})		437	2,579	54	316	4,661	25,741	897	5,297

[1] Measured from aerial photographs collected in 2001 (Hunter River) or 2004 (Clarence River)

Discussion

This report presents a synthesis of the outcomes of several extensive field programs, laboratory studies, and models as well as dedicated extension activities. Each of the former is dealt with in a series of stand-alone manuscripts, and these are presented in the appendices to this report and available in scientific literature. These manuscripts provide comprehensive details for each component of the study, including detailed discussion of assumptions, limitations, and interpretations. The discussion in this section is limited to synthesis and integration of the key findings to underpin the key recommendations arising from the work.

Juvenile prawn nurseries in New South Wales

The combination of approaches employed in this study provided a comprehensive picture of the potential nursery role of various habitats within the lower Hunter and Clarence River estuary, and Lake Macquarie. In the Hunter and Clarence River estuaries, important habitats for EKP were mostly confined to the lower part of the estuary and primarily included shallow unvegetated sedimentary habitat. However, other habitats were important, such as the Hexham wetland, which did support a high abundance of prawns in the lower regions due to strong connectivity and optimal salinity. Conversely, other habitats across the lower estuary were important for SP, especially the rehabilitated Kooragang and Tomago marshes, and lower salinity areas further up the estuary. In Lake Macquarie, which has a much more uniform salinity, distribution of EKP was not uniform across the system. Important juvenile nurseries were concentrated in certain parts within the system, as this was most likely driven by factors affecting supply of recruits.

Both the isotope and quantitative data presented here indicate a peak in abundance of juvenile EKP at 8,000-10,000 m from the estuary mouth in the riverine estuaries (where tidal flow is greater), and a peak at 6,000-8,000 m from the estuary mouth in Lake Macquarie (where tidal flow is much weaker). The patterns in hydrology, bathymetry, and physicochemical variation in the lower estuaries largely explain these patterns in EKP distribution. Firstly, both the current study and Young (1978) indicated that EKP abundance was maximised in littoral habitat of depth <2 m. In the Hunter River estuary, Fern Bay and Fullerton Cove contain the most expansive area of such habitat within the system. The fact that these are off-channel embayment's means these habitats have low water velocity that is probably ideal for juvenile prawns, but these are also directly adjacent to a higher velocity waters (the main river channel) that are important for the supply of recruits on the incoming tide. Similar patterns were observed in the Clarence River estuary, where the channels in the south of the estuary did not appear to support juvenile EKP despite appropriate habitat being available. This was likely due the diversion of tidal waters into the Main channel and North arm through tidal training walls, which essentially limits the ability of ocean-spawned EKP postlarvae to recruit to this part of the estuary. The salinity of areas that appeared most important as juvenile nurseries for EKP was generally 26-32, which reflects the isosmotic salinity for juvenile EKP (~28, Dall, 1981). Thus, these regions of the estuary also provide physicochemical habitats which align with the species physiological requirements, and this could provide some energetic advantage. Due to the general correlation between salinity and turbidity in estuaries (e.g. Loneragan and Bunn, 1999), it is likely the effect of turbidity observed in our data relates to the patterns outlined above for salinity.

For juvenile SP, we found that abundance generally increased with distance along the Hunter River estuary. It was apparent, however, that the lower estuary also supports early juveniles for the species. Similarly for EKP, juvenile SP appeared to be more abundant at shallower depths (<1 m), but abundance was greater in more turbid water. This probably reflected higher abundance in the more brackish, turbid waters of the Tomago and Kooragang wetlands. Unlike EKP, SP displayed asymmetric patterns in designation of EJH between the two years of sampling, with the majority of prawns contributed from the south arm of the estuary in 2013/14, compared to the designation of a greater number of areas dominated by the north arm in 2014/15 (which were also similar to the patterns presented in Taylor et al., 2016). Physicochemical conditions were similar between years and there were no major floods during the period that sampling took place; however, the commercial harvest was substantially different between years (~71 tonne in 2013/14, and ~36 tonne in 2014/15) and may well explain these differences. The majority of fishing effort in the Hunter River is concentrated in Fullerton Cove, the main north arm channel in the lower estuary, and to a lesser extent further upriver at Raymond Terrace (~30 km from mouth). Furthermore, a large portion of the south arm of the estuary is effectively closed to trawling, as low bridges mean this section of the estuary is not navigable by trawlers. Therefore, during the year when commercial harvest was highest, the bulk of emigrating SP were contributed from the south arm within and just downstream of the unfishable waters. When fishing effort and catch was lower in 2014/15, the contribution was much more evenly spread throughout the south arm and along the north arm and Fullerton Cove. This is further supported by the patterns in Taylor et al. (2016) which were similar to 2014/15. These samples were collected at the very beginning of the 2013/14 season (11-12/2013), and are thus indicative of patterns in 2013/14 prior to the extensive fishing mortality occurring throughout the season. While the above comparisons involve only three surveys, this evidence points to the potential role of fishing mortality in mediating the relative value of estuarine nurseries.

Within the juvenile nurseries of the Clarence River, the dominant source of carbon supporting nutrition of EKP was the saltmarsh grass *S. virginicus* (Appendix 8). While the areal coverage of saltmarsh is often somewhat lower that mangrove in both the Hunter and Clarence River estuaries, this plant supported between 45% and 97% of the nutrition supporting this species. Carbon fixed by saltmarsh vegetation has been shown to make an important contribution to the nutrition of other penaeid prawn species (Abrantes and Sheaves, 2008) and other invertebrates (Guest and Connolly, 2004). Since the saltmarsh surface spends little time inundated, and juvenile prawns are not observed directly utilising this habitat, it is likely that outwelling of both detritus and primary consumers (e.g. plankton and other small nekton) acts as a conduit between saltmarsh productivity and prawn productivity across these systems. For example, the Saltmarsh Crab *Parasesarma erythrodactyla* is a numerically abundant species that feeds on locally available autotrophic material (Saintilan and Mazumder, 2010), but their larvae are released to the water column and provide a link between the discrete saltmarsh habitat and the consumers that occupy the broader estuary (Mazumder et al., 2011). Eastern King Prawn have a varied diet typically comprised of plant material, crustaceans, microorganisms, small shellfish, and worms (Suthers, 1984; Moriarty, 1977; Racek, 1959), and it is likely that crab larvae form part of their diet when available. In addition, it is likely that transported particulate material also support the foodweb throughout the estuary (Simenstad et al., 2000)

While nursery habitats for EKP appear dependent on salinity, there is strong evidence that rapid salinity declines due to flooding could compromise the survival of juvenile EKP, potentially causing a subsequent reduction in recruitment to the fishery. Evidence of this is found in a severe east-coast low-pressure system that affected New South Wales in April 2015. Widespread flooding affected the Hunter River and logger data indicated that salinity in the main nursery area for this species declined from ~35 to 0 in less than 24 h. Our threshold for complete mortality was also exceeded, and thus it was conceivable that juvenile EKP would not have survived this event. Some evidence for mortality can be found in commercial catch statistics for the adjacent ocean fishery that is fed by recruits from the Hunter River (see Ruello, 1975). In this area, April and May usually yield the greatest catches of EKP compared to other months, however average catch in April/May 2015 saw a ~60% drop in catch to ~7.5 tonne, relative to the April/May average across 2011-2014 and 2016 (~18.5 tonne; NSW DPI – Fisheries Catch Statistics Database). By monitoring salinity within nursery habitats for EKP it may be possible to make rapid, real-time predictions on how changes in salinity may affect exploited populations. This could support more adaptive management of the fishery in response to flooding.

The findings presented here provide an integrated description of juvenile nurseries for EKP in the sub-tropical estuaries of New South Wales. EJH is generally found at intermediate distances along the lower estuary, and is largely a product of supply, connectivity, and physicochemical conditions. Pulse events that alter physicochemical conditions within these nurseries can ultimately have impacts on juvenile survival, and ultimately the components of the fishery that are supported by affected nurseries. Although saltmarsh and mangrove habitat were not found to be directly used by EKP, the subtidal channels draining these habitats in the recently repaired Hexham wetland was found to support some of the highest densities of juvenile EKP across the entire study. Similarly, juvenile SP were present at highest abundances in the other repaired wetland systems in the Hunter River. Finally, it is clear that primary productivity derived from the saltmarsh surface is extremely important in the support of juvenile prawns throughout the lower estuary. It is likely that healthy and productive saltmarsh systems support juvenile prawn productivity across a number of similar systems in mid-northern New South Wales.

Fishery value of saltmarsh and mangrove habitats

The stable isotope method applied here provided an effective means of apportioning fishery productivity among saltmarsh and mangrove habitats, as well as other sources of productivity. Similarly for EKP and SP, the saltmarsh grass *S. virginicus* provided a trophic subsidy for the major exploited species in the lower Hunter and Clarence River estuaries. These relationships supported the estimation of economic values derived from these habitats through fishery productivity. While the concept employed here has a basis in the theories of Odum et al. (1977) and the quantification of energy flows in order to value estuarine ecosystems, there is some novelty in combining stable isotopes with measures of economic output to assign values on the basis of this energy flow in a quantitative fashion. Examples of such estimations of saltmarsh and mangrove are rare for Australian estuaries, but the economic values reported here complement estimates already published that deal with habitat – fishery linkages. Bell (1997) presented a model estimating a (recreational) fishery value from saltmarsh which reported values of USD5,592 to USD36,902 ha^{-1} y^{-1} (all values converted to 2015 dollars), which span similar orders of magnitude to those reported here. Rönnbäck (1999) provided a synthesis of valuation studies of mangrove habitats through wild harvest fisheries, and reported values ranging from USD22 ha^{-1} y^{-1} to USD9,665 ha^{-1} y^{-1}, with the highest reported value derived from Moreton Bay (Morton, 1990). Thus, the range of economic values estimated for our study systems span the ranges published for other areas previously.

Our results suggested that restoring juvenile EKP habitat would be expected to have very different results on the extant fishery, depending on the zone of the restoration. Under the assumptions judged most realistic, zones 3 or 4 (Figure 19 and Figure 20) provided the greatest return to the fishery in terms of harvest. In terms of potential increases in revenue that might be derived from habitat repair through the harvest of EKP, a ~4% increase on annual landings of ~600 tonnes equates to an increase of ~24 tonnes. Assuming a market price of AUD17.00 kg^{-1}, the GVP arising from 200 ha of habitat repair in zone 3 would equate to ~AUD400,000 y^{-1} for the New South Wales fishery, or AUD2,040 ha^{-1} y^{-1}.

The key characteristics of zones that resulted in the greatest benefit included substantial habitat loss (Rogers et al., 2015), greater estimated recruitment at unfished conditions (O'Neill et al., 2014), greater settlement of EKP larvae (Everett et al., 2017), and greater or faster matriculation to the New South Wales fishery grounds. More northern zones were less attractive as restoration areas, given the likely northern movement of adult EKP out of New South Wales managed waters, whereas more southern areas generally were characterized by more pristine habitat, lesser larval settlement, and greater distances for EKP to migrate prior to reaching fishery grounds, thus higher potential for natural mortality between the nursery phase and harvest.

These values lay the foundation for further consideration of the costs and potential benefits that can be realised from habitat repair in Australian ecosystems (Creighton et al., 2015), and will support future economic evaluation of these efforts. However, linking such values to habitat rehabilitation requires additional consideration of ecological processes (such as recruitment at sufficient levels to utilize new habitat, Taylor et al., 2017b), as well as other economic factors (for examples see Leston and Milon, 2002; Rozas et al., 2005). At the very least, these estimates will be useful for comparison with the economic value derived from alternate land uses (e.g. Read and Sturgess, 1996).

Implications for management, recommendations, and future habitat rehabilitation

Losses of coastal fish habitat in New South Wales that have had an impact on the production of prawn and fish species have been occurring since the 1800's, with initial drainage of swamps to improve agricultural productivity. This work continued throughout the early 1900's and increased significantly after a period of floods in the 1950's, before ceasing on a large scale in the early 1970s. The level of loss of fish habitat has been significant with losses from the Manning to Tweed Rivers measured at 62,000 ha or 72% of the historical prime fish habitat (Rogers et al., 2015). In the Hunter River, the area of saltmarsh alone had fallen by approximately 74% from 2,955 ha in the 1950s to 766 ha in the 1990s. In addition over 1000 floodgates restricted fish passage to waterways and wetlands (Walsh et al., 2002). These losses and the consequent impacts on fisheries and other ecosystem services in estuaries and inshore marine areas have been reflected as priority threats (*Clearing riparian and adjacent habitat including wetland drainage*) in the state-wide New South Wales Marine Estate Threat and Risk Assessment Final Report (BMT WBM, 2017).

Initial projects aimed at repairing degraded fish habitat and reinstating connectivity to floodplain wetlands primarily for fish and crustacean species, had been guided by the general ideas that 1) fish habitat was principally important for fish; and, 2) that degraded fish habitat also led to poor water quality outcomes (particularly from oxidised acid sulfate soils), that in turn, can adversely affect fish populations. These projects focussed on restoration of natural hydrology by removing barriers and allowing tidal movement and fish access. Recent projects in New South Wales include the Kooragang Wetland Rehabilitation Project at Ash Island (780 ha), Tomago Rehabilitation Project (450 ha), Yarrahapinni Wetland Rehabilitation Project (806 ha), the Hexham Swamp Rehabilitation Project (see below), the North Coast Floodgate Project (57 barriers removed, Walsh and Copeland, 2004) and the Bringing Back the Fish project (86 barriers removed; http://www.dpi.nsw.gov.au/fishing/habitat/publications/pubs/bringing-back-the-fish-project-reports). Although now viewed as successful, the development and implementation of these projects provides a potential path for future habitat rehabilitation in the context of the information established in this research project.

The most recent large-scale example of habitat repair in coastal New South Wales is the Hexham Swamp Rehabilitation Project. This project reinstated connectivity between Hexham wetland and the lower Hunter River estuary for the first time since the early 1970s (Boys and Pease, 2017). This reinstated the potential for recruitment of economically important species to the wetland system, as well as the outwelling of marsh- and mangrove-derived productivity to other areas of the estuary. However, this wetland system had lost 763 ha (93 %) of saltmarsh and 124 ha (84 %) of mangrove, and this will take some time to recover. Sharp declines in commercial catches of SP were evident in the early 1970s and this may well have been caused by the removal of significant amounts of saltmarsh from the system. As the wetland system recovers, this may be reflected in an increase in SP landings, and given the patterns reported here, this could add considerable value to the fishery for this species (and other species as well).

Given the significant historic loss of fish habitat, the opportunities for repair are extensive and as with these previous projects will largely involve restoring natural hydrology. Some key sites have already been identified including major floodplain wetlands (e.g. Tuckean Swamp, Everlasting Swamp, the Collombatti-Clybucca) and the lower sections of most estuary floodplains areas (e.g. around Lake Wooloweyah, and the lower reaches of the Clarence; Macleay, Hastings and Shoalhaven Rivers). The bulk of the land in these areas is privately owned and managed in some form for low density cattle grazing. As a consequence any rehabilitation action will require landowner consent either through stewardship payments or land purchase. One of the key delays to both the Hexham and Yarrahapinni Projects was the time taken to purchase land given the case that needed to be made to secure funding from Federal, State and private sources. This can be overcome much more efficiently for future sites with the possibility of positive cost/benefit analyses, and business cases developed from the information from this research.

In addition to the potential for increased production evidenced here, the potential benefits for other exploited species (both commercial and recreational) can now also be assessed. In addition to these species-specific benefits, other ancillary benefits of fish habitat repair for estuary function will also be realised, including improvements to overall estuary health, tourism services, enhanced biodiversity such as birdlife, water quality, carbon sequestration and various other ecosystem service benefits. A recent project that commenced in 2017 led by The Nature Conservancy and Deakin University called Mapping Ocean Wealth is proposing to calculate these combined values for the New South Wales and Victorian coastal and estuarine environments, and a Draft Marine Estate Management Strategy in response to the priority threats identified in the Threat and Risk Assessment Final Report (BMT WBM, 2017) has been prepared. These combined activities are intended to result in the scaled-up restoration of these valuable fish habitats. The potential loss of intertidal habitats, saltmarsh in particular, resulting from sea level rise is of additional concern for the productivity of fisheries. Research carried out on impacts of sea level rise in the Hunter River estuary indicates that, without management interventions, estuarine wetlands will be largely lost under predicted sea level rise scenarios (Rogers et al., 2013) and with more recent research indicating accelerating sea level rise (Chen et al., 2017), pressure is mounting to secure paths for landward (upward) migration of these habitats in all New South Wales estuaries.

There are a number of activities in support of increased habitat rehabilitation that need to be pursued on the basis of the information provided by this research. Existing extension as part of this project which targeted commercial fishers and Local Land Services needs to take into account the broad applicability of these results across all species and be extended to recreational fishers and their respective organisations and to both recreational commercial fisheries managers in New South Wales and Queensland. The previous work of Rogers et al. (2013) needs to be expanded across all New South Wales estuaries to confirm likely impacts on saltmarsh and mangroves and the results of this new research incorporated with urgency into local and state planning instruments. Finally, the valuation of saltmarsh and mangrove habitats for fisheries production needs to be incorporated into current New South Wales Marine Estate Management activities, and other natural capital accounting endeavours, to provide impetus to the repair of degraded estuarine habitats across the State.

Extension and Adoption

Objective 5 of this project was to *Extend information on habitat-fishery linkages to commercial fishers, landowners and other catchment stakeholders and incorporate recommendations into fisheries or water management.* Following the projects commencement, letters were sent to 18 New South Wales Fishermen's Cooperatives and the six project partner organisations. The letters provided detail about the project's purpose, objectives, personnel as well as outlining ways for them to get more information and provide further input.

EKP fisher survey

In order to effectively deliver on Objective 5, we dedicated considerable effort to identifying the preferred means of accessing and receiving information by the key stakeholder group (commercial fishers), and what types of information were of particular interest. While this activity was principally aimed at identifying appropriate avenues of dissemination for the current project, this type of information is broadly applicable. Thus, the findings of this study will be used to guide engagement activities with commercial fishers on research and management relevant to habitat – fishery linkages into the future, as well as a broad cross-section of other projects relevant to commercial fishers which are undertaken by NSW DPI.

Approach

A survey of participants in fisheries that harvest EKP in New South Wales was undertaken in early 2014 through a combination of mail-out/return envelope surveys and face-to-face interviews (see Appendix 13). The survey was designed to achieve three objectives:

1. Establish some basic demographics about the respondents;
2. Fishers understanding of the links between estuarine habitats and EKP; and
3. Establish how those fishers preferred to access and receive information about EKP and what types of information were of particular interest.

In total, 174 fishers that were involved in fisheries relevant to the EKP were provided with the opportunity to complete the survey process. Twenty-five responses to the survey were received, giving the survey an overall response rate of 14%. The responses are summarised under each objective.

1. Demographics

The demographics of the respondents can be summarised as follows:

- Fishers were predominantly male (96%) with an average age of 57 (range 42 to 77 years);
- Collectively, they had 678 years of hands-on fishing experience (an average of 29 years each);
- Their home ports were spread fairly evenly between Tweed Heads and Shoalhaven Heads.

2. Fishers understanding of the links between estuarine habitats and Eastern King Prawn

Fishers recognised the importance of seagrass, mangrove and wetlands for EKP production.

Fishers attributed less value to saltmarsh and bare sediment habitat types.

Since they first started fishing, estuarine habitats were perceived to have declined (particularly wetlands, then seagrass, then mangrove, then saltmarsh).

They thought that the most important factors for EKP production (in order from most to least important) were wetlands, water quality, seagrass, mangrove, water temperature, saltmarsh, flood timing, flood level, harvest management and bare sediment.

Most fishers (83%) believed that more could be done to rehabilitate estuarine habitats.

3. Information needs and preferred avenues of communication

Fishers indicated that other fishers were their most trusted source of information. In order from most to least, the trusted sources of information were:

1. Other fishers (58%)
2. Scientists (18%)
3. Government (12%)
4. Newspapers/magazines (6%)
5. Internet (3%)
6. TV/radio (3%).

In terms of preferred methods of communication, fishers indicated that future information would preferably be received by (in order from most to least):

1. Face-to-face (23%)
2. Addressed letter (21%)
3. Industry conferences (13%)
4. Website (11.5%)
5. Email (11.5%)
6. Brochures (10%)
7. Scientific journals (6%)
8. Local paper (4%).

The information needs indicated in the survey responses included the following:

1. EKP fishers would like to receive more information about the relationships between EKP and estuarine habitats, and more detail about new research findings about EKP ecology and migrations;
2. While some Hunter-based fishers were aware of estuarine rehabilitation works underway in Hexham wetland, most fishers in other locations remained unaware of any similar rehabilitation works that had been or were being undertaken in their area;
3. In terms of participating in future rehabilitation projects, over half of the fishers would be prepared to be involved, either through letters of support (33%) or hands-on help (25%);

Eastern King Prawn Research and Communication Plan

The results of the survey directly informed the development of the EKP Research and Communication Plan, which is included in Appendix 14. The plan provided a framework to assist researchers and managers to effectively target communications in relation to habitat use and ecosystem requirements of EKP directly to key stakeholders in fisheries that harvest EKP. The content of this engagement plan is similarly relevant to engagement activities surrounding broader habitat – fishery linkages, as well as communicating information from other projects undertaken by NSW DPI to commercial fisheries stakeholders.

Communication and Extension outputs

Face-to-face presentations

Face-to-face dissemination of information was identified as the commercial fisher's most preferred method of information delivery. Six (6) informal face-to-face meetings have been conducted throughout the project at Fisherman's Co-ops in or near the areas investigated through the project. This included the Ballina, Maclean, Coffs Harbour, South West Rocks, Port Macquarie and Newcastle Fisherman's Co-operatives. Informal meetings were primarily held with the Co-op Manager, however when opportunities arose, discussions were also conducted with fisherman. In general all fishers received the concept and delivery of the project quite well. In contrast to many of the other issues facing the industry at present, this research was seen to be both important and positive, and well-geared to assisting the natural enhancement of prawn stocks.

In addition, the Principle Investigator has discussed the project findings with EKP fishers operating on the Hunter and Clarence Rivers, and out of the Ports of Newcastle and Yamba. This has involved face-to-face discussions at fishers' houses, on their boats, at boat yards and over the telephone. Fishers were engaged and interested in the distribution and dynamics of the prawn populations they harvest, particularly in relation to the estuarine habitats. Also of key interest were the findings from Objective 2, as many fishers across the state have long sought to understand why catches of EKP tend to be depressed in years where there is higher rainfall.

Two formal project partner meetings were conducted during the course of this project. These face-to-face presentations provided an opportunity to maintain relationships with project partners, discuss project aims, inform partners of the project's progress, and discuss any queries:

1. Project Inception Meeting, Newcastle Co-op, 11 November 2013.
    - Invitees included Hunter Water, Northern Rivers Catchment Management Authority, Hunter Central Rivers Catchment Management Authority, Griffith University,

Newcastle Ports Corporation, Origin Energy, Professional Fisherman's Association, the Newcastle Fishermen's Co-op, and OceanWatch Australia;

- A 35 minute presentation was delivered by the Principle Investigator, Dr. Matt Taylor.

2. Project update meeting, Newcastle Co-op, 30 July 2014

   - Invitees included Hunter Water, North Coast Local Land Services, Hunter Local Land Services, Griffith University, Newcastle Ports Corporation, Port of Newcastle Authority, Origin Energy, Professional Fishermen's Association, Newcastle Fishermans Co-op, and OceanWatch Australia;

   - Presentations included:

     a. Taylor, MD (2014) *The impact of habitat loss and rehabilitation on recruitment to the NSW eastern king prawn fishery*.

     b. Russell, K. (2014) *Why understanding Eastern King Prawn habitat is important*. Communicating the results.

     c. Boys, C. (2014) *Preliminary findings from recent Hexham Swamp restoration project site biological sampling.*

The final project workshop *Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop* was held on 12 October 2017, and attended by over 60 delegates who travelled from as far as Tasmania and Townsville. The diverse group of delegates included commercial fishers, project partners, habitat scientists from government and Universities, habitat, estuary and catchment managers (NSW Local Land Services, NSW DPI, NSW National Parks and Wildlife Service, NSW Office of Environment and Heritage, Hunter Water), and fishing co-op managers. Details of the workshop are summarised in Appendix 18. The following seminars were presented, followed by an afternoon workshop to build on the information presented titled *Growing the fishery! A planning session for coastal habitat restoration*:

1. The status of estuarine habitat in NSW. How the NSW Coast once looked. *Kylie Russell, NSW DPI*

2. Research overview and nursery basics. An introduction to the FRDC project. Understanding nursery habitats for exploited penaeid prawns in NSW estuaries. *Matthew Taylor, NSW DPI*

3. Saltmarsh secrets. Direct usage of saltmarsh habitats by exploited species in the Hunter River. Plus insights into DIDSON work on large-bodied species. *Alistair Becker, NSW DPI*

4. Saltmarsh surprises. Direct and indirect interactions between saltmarsh habitats and commercially important penaeid shrimp. *Troy Gaston, University of Newcastle*

5. What's for lunch? The contribution of estuarine habitats to the diets of commercially important fisheries species in the Hunter and Clarence Rivers. *Vincent Raoult, University of Newcastle*

6. Hexham Happenings. School Prawn (*Metapenaeus macleayi*) abundance and trophic relationships in the recovering Hexham wetland. *Craig Hart, University of Newcastle*

7. What's it worth? The economic value of saltmarsh to fisheries. *Matthew Taylor, NSW DPI*

Other strategic face-to-face presenting opportunities have also been identified and utilised to communicate the project's results with other interested parties and stakeholders including recreational fisheries stakeholders, Local Councils, natural resource managers, and other research colleagues and peers. This included being invited as a guest speaker to the 2017 Commercial Fisherman's Cooperative (Newcastle) Annual General Meeting, where project findings were presented to a diverse audience of commercial fishers from the NSW mid-north coast.

Additional presentations included:

1. Taylor MD (2013) Habitat – Fishery linkages in New South Wales. *Workshop on Agreed Future Directions in Fish Habitat Management in NSW*, Royal Botanic Gardens, 22nd August 2013 (attended by ALL major fisheries stakeholder groups in NSW);
2. Taylor MD (2013) Challenges and opportunities for fish habitat research: A NSW perspective. *Fish Use of Mangroves and Tidal Wetlands: Biological Drivers, Physical Constraints, Regional Variation*, Townsville, 1st October 2013;
3. Taylor, MD (2016) Identifying and understanding nursery habitats for exploited for exploited penaeid shrimp in NSW estuaries. *NSW Coastal Conference*, Coffs Harbour, 9-11 November 2016;
4. Walsh, S (2016) North Coast Local Land Services, Regional Managers workshop Grafton. Industry on Estuary. 15 attendees included Government Departments, cane growers, graziers, Local Council, aquaculture owners;
5. Taylor, MD, Becker, A, Fry, B, Moltschaniwskyj, NA, Tyler, K (2016) Identifying and understanding nursery habitats for exploited penaeid shrimp to inform habitat rehabilitation. *Restore America's Estuaries*, New Orleans, 11-14 December 2016;
6. Taylor, MD, Camp, E, Gaston, TF, Raoult, V (2017) Habitat-fishery linkages in New South Wales: Implications for restoration. *1st Australian Coastal Restoration Symposium*, Townsville, 31 August-1 September 2017;
7. Taylor, MD, Camp, E, Gaston, TF, Raoult, V (2017) Estimating potential economic value of estuarine habitat and benefits from its restoration. *NSW Coastal Conference*, Port Stephens, 8-10 November 2017
8. Taylor, MD (2017) Understanding Nursery Habitats for Exploited Penaeid Shrimp in NSW Estuaries: A synopsis of 3 years field and lab research. Commercial Fishermans Co-op Annual General Meeting, 27 October 2017.

Dedicated project website

Although the internet was identified as one of the least (3%) preferred sources of information, a project website was determined by a number of fishers (11.5%) to be a preferred means of receiving updates on the project. A dedicated project website was produced and provided a portal for regular project updates with results and key findings:

www.dpi.nsw.gov.au/fisheries/habitat/rehabilitating/ekp

Not only did fishers stay informed of the project's progress via this dedicated information space but other key stakeholder groups, project partners and the wider community could also access the information.

Fisher interviews

Commercial fishers are a key source of information about EKP, furthermore, information direct from their peers was clearly identified as the EKP fishers' most trusted source of information (58%). Therefore interviews with fishers were conducted to document this information and to establish:

1. their perspectives on issues affecting EKP habitat;
2. what fishers need to know about EKP and EKP habitat;
3. where fishers go to get information, which sources they trust and their information delivery preferences.

Several interviews were conducted, interviewees included: Jeff Hyde, John Hewitt (as recounted by Dennis Hirst), Dennis Hirst, Murray Ham and Reg Hyde. These interviews have produced some interesting oral histories and anecdotes, highlighting the historical abundance and use of estuarine wetlands by EKP.

Some comments from fishers in relation to Hexham wetland in the Hunter River are outlined below:

- *"Before the floodgates were constructed at Ironbark Creek in the early 1970s, Hexham swamp was considered to be the main nursery of EKP for the Hunter River. The results from tagging studies (which showed prawns migrated north as far afield as off Brisbane) led fishers to conclude that Hexham may have been the main nursery for an even larger area than just the Hunter"*;
- *"In the 1920s, a local fisherman saw a stream of king prawns 0.5 m wide by 0.5 m deep coming out of Ironbark Creek, out past the Heads and streaming out to sea for 7 - 8 miles towards the north. Then in the 1940s, the local BHP steelworks had ongoing issues with king prawns clogging up the screens on the water intake pipes. Enough prawns would be scraped off to fill a 44 gallon drum. Every two weeks over summer, the cast-off prawn shells would form drift piles on the side of the waterways that would crunch underfoot"*;
- *"One fisher caught enough prawns in nine days to pay off his new trawler. Another bought a new car with cash, just two weeks after he started prawning. Hexham also provided other resources for locals. The skies were black with ducks and swans. During the Depression in the early 1930s, Hexham supported 200 families that gathered prawns, fish, ducks and other waterfowl for consumption and sale. On Sundays, people hunting ducks with shotguns were so numerous that the booming shotguns made a continuous roar. This went on for years. On seeing an advert promoting tourism to Kakadu, one fisher said* "why would you go there? We've got it all here: ducks, magpie geese, jabiru, swans etc - just not the croc's!"

After construction of the floodgates on Ironbark Creek at the mouth of Hexham wetland, fishermen noticed a steady decline in their catch of prawns. This decline became increasingly obvious once the wetland really dried out. The numbers of EKP never recovered while the floodgates were in operation. Some fishermen agitated to return water to the wetland and have been engaged since the early 1970s to the present day, by sitting on various committees, lobbying politicians and seeking grant funds to actively restore tidal flows.

As a result, the floodgates on Ironbark Creek have been progressively opened during non-flood periods over the last few years. Each year there are increasing numbers of small EKP (<28 mm) being seen in Hexham. Landholders living next to the wetland have seen their first Jabiru's in years that were *"tossing back beakfuls of juvenile prawns"*. One fisherman was so confident of a revival of the EKP fishery that he bought a new trawler when he heard that the floodgates were being opened again.

Other Publications and products

Several other publications and/or communications have been prepared throughout the project in order to publish preliminary findings, provide research updates, build capacity in the wider community for the project, and maintain communication networks with project partners.

During the course of the project, project updates were periodically released. These were made available on the dedicated project website and have also been published in the Professional Fishing Association's Newsletter – PFA Update, see February 2014 http://www.nswpfa.com.au/wp-content/uploads/2014/02/PFA-Newsletter-14-February-2014.pdf, and October 2014 http://www.nswpfa.com.au/wp-content/uploads/2014/11/PFA-Newsletter-31-October-2014.pdf

Key findings of the project have been developed into stakeholder-targeted products (for land managers and commercial fishers in Appendices 17 and 18 respectively), and will continue to be conveyed to relevant parties where appropriate.

Project coverage

At the project's inception (December 2013) a media release was developed and provided to a number of news outlets and posted to social media to engage and inform the wider community (Table 5). The news release was picked up by the following outlets. An additional press release is planned to highlight the findings and key outcomes of the project.

Table 5 Summary of uptake of project media release.

Where	**Who**	**Distribution**
The Channel	Newcastle Ports Corporation Newsletter	Unknown
Clarence Floodplain Newsletter	http://www.clarence.nsw.gov.au/cp_content/resources/Clarence_Floodplain_Newsletter_December_2013.pdf	750
Twitter	https://twitter.com/nswdpi/status/411269255821135872/photo/1	2,844 followers
NSW DPI Facebook	https://www.facebook.com/pg/NSWDPIFisheries/photos/?tab=album&album_id=185575924972443	21,000 followers
ABC radio	ABC North Coast interview with Simon Walsh	unknown
Newcastle Herald	http://www.theherald.com.au/story/1982224/hunter-focus-for-prawn-research/	157,000
Northern Star	http://www.northernstar.com.au/news/future-of-king-prawns/2120098/	29,000
Sunshine Coast Daily	https://www.sunshinecoastdaily.com.au/news/future-of-king-prawns/2120098/	Unknown
WetlandLink newsletter	www.wetlandcare.com.au/index.php/download_file/view/1273/210/	Unknown
PFA magazine	Professional Fishing Association http://www.nswpfa.com.au/wp-	500 hard copies plus internet

Where	Who	Distribution
	content/uploads/2014/03/PFA_Magazine_Nov_2013_email_Spread.pdf	

Project materials developed

Project materials developed are described in detail in the Extension and Adoption Section (above). Other project materials can be found in Appendices 3-18

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Appendix 1 – Intellectual Property

The following manuscripts are included in the appendices and should be cited as papers rather than as part of the report.

- Appendix 3 – A rapid approach to evaluate putative nursery sites for penaeid prawns
- Appendix 4 – Nocturnal sampling reveals usage patterns of intertidal marsh and sub-tidal creeks by penaeid shrimp and other nekton in south-eastern Australia
- Appendix 5 – Rapid salinity changes affect the survival and physiology of a penaeid prawn: Implications of flood events on recruitment to the fishery
- Appendix 6 – Recruitment and connectivity influence the role of seagrass as a penaeid nursery habitat in a wave dominated estuary
- Appendix 7 – The role of connectivity and physicochemical conditions in effective habitat of two exploited penaeid species
- Appendix 8 – Direct and indirect interactions between lower estuarine mangrove and saltmarsh habitats and a commercially important penaeid shrimp
- Appendix 9 – Identifying and understanding nursery habitats for exploited penaeid shrimp in NSW estuaries
- Appendix 10 – Habitat-fishery linkages in two large estuarine fisheries: The role of saltmarsh in supporting fisheries productivity
- Appendix 11 – The economic value of fisheries harvest supported from saltmarsh and mangrove productivity in two temperate Australian estuaries
- Appendix 12 – Assessing the potential impact of habitat rehabilitation in a spatially complex penaeid fishery

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Appendix 3 – A rapid approach to evaluate putative nursery sites for penaeid prawns.

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A rapid approach to evaluate putative nursery sites for penaeid prawns

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ABSTRACT

Identifying nursery habitats for an aquatic species generally requires tracing adult individuals back through time and space to the area or habitat in which they developed as juveniles. We develop and trial a study design and analytical approach to evaluate the suitability of using stable isotopes to trace emigrating prawns to putative nursery sites, and evaluate assumptions inherent in the application of the approach using two penaeid species with Type-II life cycles: *Penaeus* (*Melicertus*) *plebejus* and *Metapenaeus macleayi*. Prawns were collected in putative nursery sites within the Hunter River, Australia, and analysed as composite samples of 6 individuals to provide habitat-specific isotopic signatures. Prawns emigrating from the mouth of the river were used as a proxy for individuals recruiting to the adult population, and assigned to putative nursery sites using a probabilistic mixing model and a simple, distance-based approach. Bivariate (δ^{15}N and δ^{13}C) isotopic data was sufficient to distinguish prawns from different putative nursery sites, and isotopic composition correlated closely with salinity. Approximately 90% of emigrating prawns collected could be assigned to these sites using bivariate isotopic data, and both analytical approaches gave similar results. The design developed here is broadly applicable to a suite of penaeid species, but its application will be most powerful when sampling is also aimed at understanding nursery function by simultaneous monitoring of size structure/growth, density, and trophic relationships within nursery habitats.

1. Introduction

For aquatic organisms, a juvenile nursery habitat is characterised as one that supports growth and survival, and thus contributes a disproportionately higher number of individuals to an adult population relative to other habitats (Beck et al., 2001). This means that increased abundance in a particular habitat in itself is not sufficient to imply nursery function, but rather the movement of individuals out of juvenile habitats and successful recruitment to the exploited or adult populations also needs to occur. Thus, identifying nursery habitats requires tracing older individuals back through time and space to the post-settlement habitat in which they developed as juveniles.

Penaeid prawns support some of the most economically important fisheries in the world (Dall et al., 1990a), and catches of these species reached a peak in the late 20th century. The Eastern King Prawn (*Penaeus* (*Melicertus*) *plebejus*; hereafter referred to as *Melicertus plebejus*) and the School Prawn (*Metapenaeus macleayi*) are two commercially exploited temperate penaeid species endemic to the east coast of Australia. Adults of both species spawn in oceanic waters (inshore in the vicinity of estuaries for School Prawn; and offshore for Eastern King Prawn, following a considerable northward migration), and postlarvae later recruit back into estuarine habitats for the duration of their juvenile phase.

There is no doubt that estuaries function as important nurseries for these two penaeids (Halliday, 1995; Racek, 1959; Young and Carpenter, 1977), and it has been established that adolescents of both species predictably emigrate in a synchronised manner from estuaries to join the exploited adult and spawning populations in oceanic waters (Montgomery, 1990; Racek, 1959). What remains unclear is whether certain habitats within estuaries contribute more to the exploited adult population than others and are therefore of greater nursery value. Knowing these habitats will assist in valuing their economic contribution to exploited fisheries and in doing so help prioritise their protection and rehabilitation. It will also help with identifying possible sites for fishery enhancement through targeted stocking activities (e.g. Ochwada-Doyle et al., 2011; Ochwada-Doyle et al., 2010). However, the identification of nursery habitats cannot be achieved by relying solely on the basis of existing datasets comparing relative prawn densities from different habitats (e.g. Haywood et al., 1995; Rönnbäck et al., 2002). Rather, it will require that individuals joining the adult population can also be traced back to the habitats they previously resided in. Once a subset of putative nursery sites is identified, further work on abundance, growth

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and survival will be warranted to provide a more complete picture of their nursery function.

For teleost species, relatively novel microchemical techniques have become available which can trace the distribution of an individual throughout its life using the elemental composition of the otolith (Edmonds et al., 1999). Depending on the environment and the migratory pathways used, this can provide an efficient means of assigning an adult to particular areas or habitats in which they have resided as juveniles (Elsdon and Gillanders, 2003). Applying such a technique to invertebrate species (such as penaeid prawns) is more problematic, since they lack permanent bony parts which can retain elemental signatures. Instead, the use of naturally occurring stable isotope tags in low-turnover tissues (such as muscle) has been proposed as a means of tracking the movement and connectivity of penaeid prawns (Fry et al., 2003; Gillanders et al., 2003), and has previously successfully been applied to describe penaeid prawn food webs (Loneragan et al., 1997; Newell et al., 1995). The underlying rationale of this approach is that penaeid prawns tend not to be dietary specialists in either their juvenile or adult phases (Dall, 1968; Dall et al., 1990b), so the isotopic composition of their muscle tissue may provide a useful signature for the particular habitat in which they have consumed food. This could be particularly true if water chemistry and basal nutrient sources differ between habitats (Fry, 2006).

In this paper, we test the suitability of using stable isotope tags in muscle tissue to trace emigrating prawns back to their nursery habitats. Such an approach will be useful in rapidly identifying important sites from a project outset, and using this information to target a more comprehensive sampling regime (particularly where there are a large number of putative nursery sites, or a large area to potentially cover). In doing so, some assumptions inherent in the application of the above design were tested. These assumptions include: 1) that bivariate (isotopes of carbon and nitrogen) prawn isotopic composition differs among different habitats and different areas within the estuary; 2) that there is no relationship between isotopic composition and prawn size; and 3) that the timing of emigration from the estuary is random within the lunar window, with respect to location of the nursery habitat in which an emigrating prawn resided (i.e. there is no correlation between the distance of a nursery habitat from the sea and the time within the lunar cycle in which an emigrating prawn was captured). Finally, this study compares the application of a probabilistic mixing model approach (Parnell et al., 2010) with a simple distance-based approach to assign the proportional contribution of emigrating prawns to nursery habitats.

2. Materials and methods

2.1. Sample collection and preparation

This study was conducted in the Hunter River estuary, New South Wales (−32.9054, 151.7749), during November and December 2013. The lower estuary is heavily urbanised and is the largest coal shipping port in the southern hemisphere, and also supports a substantial prawn trawl fishery (Ruello, 1973b). It contains extensive saltmarsh and mangrove habitats, with some recognised as significant under the RAMSAR Convention.

The sample design involved collecting juvenile School and Eastern King Prawn directly from eight habitat sites at a distance of between 8 and 20 km from the estuary mouth. Additionally, prawns of both species were collected as they emigrated from the estuary to sea. Adolescent prawns of both species exhibit a predictable migration and "run" from the estuary out to sea to join the adult exploited population, primarily synchronised with the period between the 7th and 17th day of the lunar cycle (Racek, 1959). This behaviour underpinned the assumption that prawns sampled emigrating through the mouth of the estuary represented a useful proxy for prawns joining the adult population, and thus by determining the areas from which these emigrating prawns originated we may assess the relative contribution of habitats within the estuary to adult stocks.

Juvenile prawns were sampled along the estuary during the night using three (≈100 m) tows of a benthic sled net (0.75 × 0.45 m mouth, 4 m length, 2 mm mesh body and 1 mm mesh cod-end) (modelled after Loneragan et al., 1995; Young, 1975). Bulk sled samples were immediately placed on ice and then frozen for later laboratory processing. Emigrating prawns ($n = 77$) were collected by a trawler as they exited the mouth of the estuary, from the 7th to the 16th day of the lunar cycle.

Prawn samples were thawed, identified to species, and carapace length measured to 1 decimal place. The head and proventriculus were dissected out of each prawn to prevent contamination of the isotopic composition by food items consumed in the most recent feeding event. Three composite samples for each site were prepared for stable isotope analysis, and each composite contained equal quantities of muscle tissue from six individual prawns. Three composite samples were used as it represented an optimal trade-off between precision error and the ability to produce average site-specific signatures (following Fry et al., 2008). Emigrating prawns were analysed as individual samples (i.e. not composite samples).

2.2. Sample analysis

All composite and individual samples were rinsed in distilled water for 10 min, dried (60 °C for 48 h), and completely homogenised using a ball mill. Isotopic composition (^{15}N and ^{13}C) was measured on a Sercon 20-20 isotope ratio mass spectrometer (IRMS, Cheshire, United Kingdom) with ANCA SL preparation unit. Delta values were calculated relative to international standards using standard methods (Fry, 2006). Measurement precision of ±0.09‰ and ±0.05‰ for δ^{15}N and δ^{13}C respectively was determined through repeated measurements of internal standards.

2.3. Data analysis

Where multiple isotopes are used, isotopic composition data of animal tissue essentially represents a multivariate data set. As the differences in the muscle isotopic composition (δ^{15}N *and* δ^{13}C) as a whole were of interest, comparisons were made using Permutational Multivariate Analysis of Variance (PERMANOVA in the PRIMER 6 + statistical package; Anderson et al., 2008; McArdle and Anderson, 2001) on the multivariate δ^{15}N and δ^{13}C dataset (following Novais et al., 2016; Selleslagh et al., 2015). Preliminary PERMANOVA on a Bray–Curtis resemblance matrix calculated from multivariate stable isotope data were used to evaluate differences in the stable isotope composition of composite samples, between species, and nursery sites. In addition, a composite isotope index was calculated by subtracting the average δ^{13}C from the δ^{15}N of the composites at each site, and the relationship between this composite index and salinity was evaluated using linear regression. Linear regression was also used to evaluate the relationship between isotopic composition and the size (total length) of individual emigrating prawns, and a one-way PERMANOVA used to test for differences in isotopic composition of emigrating prawns among collection nights.

The use of Bayesian mixing models to resolve relationships between organisms from stable isotope composition has recently been critiqued by Brett (2014). This study demonstrated that such models show a strong bias toward a null generalist hypothesis, particularly when source estimates are imprecise, or when consumers fall outside the resource polygon (Smith et al., 2013). Consequently, we sought to trial both the Bayesian mixing model (noting these limitations and the conceptual issues outlined below), alongside a simple distance-based approach, to resolve the assignment of emigrating prawns to putative nursery sites. For application of the mixing model (Parnell et al., 2010) to the assignment problem, composite samples from putative nursery sites were considered as "sources", and emigrating prawns (analysed as individuals) were considered "consumers". Probabilistic mixing models are tools developed for establishing the potential contribution of

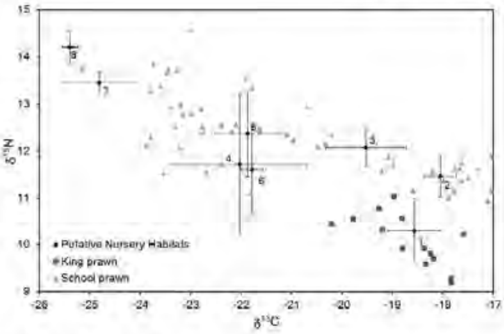

Fig. 1. Biplot showing isotopic composition (mean ± SE) for the composite samples of prawns captured from each putative nursery habitat along the length of the Hunter River estuary (indicated as "Habitats" in legend, numbers correspond to Table 1 and Fig. 3). Overlaid is the isotopic composition of emigrating individual School Prawn and Eastern King Prawn, which are representative of the emigrating stock captured at the mouth of the estuary (referred to as emigrating prawns in the text).

different sources to the diet of a consumer in the context of uncertainty in the data and fractionation factor. Recognising the recommendations in a recent paper by Phillips et al. (2014), their application to a problem of assignment of individuals to habitats creates some conceptual issues. The main issue is that a mixing model partitions a consumer's diet on the assumption that a consumer can feed on a number of different food sources. When applied to an assignment problem, the same mixing model must assume that an emigrating prawn can come from more than one habitat, which is unrealistic (i.e. 50% of an emigrating prawn cannot come from habitat *x*, and the other 50% from habitat *y*). This assumption is somewhat dealt with through the interpretation of the relationships, by considering the results to reflect a population average of the emigrating prawns tested, with no inference made at the individual level. No such assumption is necessary for the distance-based approach.

The point-in-polygon technique (Smith et al., 2013) was initially applied to the dataset, to determine which emigrating prawns had a solution for the mixing model, given the putative sources (a model solution was possible for 90% of the data set, and the remaining 10% were excluded from subsequent analyses). The first analytical (mixing model) method assigned emigrating prawns to putative nursery sites on the basis of probable sources derived using Stable Isotope Analysis in R (SIAR, Parnell et al., 2010), with the Trophic Enrichment Factor (TEF) set to zero. The second analytical (distance) method assigned an emigrating prawn to a putative nursery site on the basis of the minimum Euclidian distance between the emigrating prawn and the putative nursery site in bivariate isotopic space. Site-specific $\delta^{15}N$ and $\delta^{13}C$ values were specified as probability density functions [$N(\mu,\sigma)$], randomly sampled for each site, and distance calculated across 1000 simulations for each emigrating prawn, to account for uncertainty in source signatures. The smallest distance in each simulation was selected as the most likely source of the emigrating prawn.

3. Results

Bivariate stable isotope data for composite samples of prawns caught at putative nursery sites, and emigrating adults captured at the mouth of the estuary are shown in Fig. 1. There was no significant difference in the stable isotope composition of composite samples between School Prawn and Eastern King Prawn collected at the same putative nursery sites (PERMANOVA, pseudo-$F = 1.57$, $P = 0.28$). Significant differences were detected among composite samples from putative nursery sites (Table 1), and these differences had a strong negative correlation with salinity ($R^2 = 0.784$, Fig. 2). The stable isotope composition of emigrating prawns was tested against their length using linear regression, and was found to be independent of size for $\delta^{15}N$ ($F = 0.23$, $P = 0.63$) and $\delta^{13}C$ ($F = 0.63$, $P = 0.43$). There were also no significant differences between the stable isotope composition of prawns sampled on different nights, indicating that any correlation between the distance of the putative nursery site from the estuary mouth, and the night on which an emigrating prawn was sampled at the mouth of the estuary, was unlikely (PERMANOVA, pseudo-$F = 1.47$, $P = 0.20$).

The assignment of emigrating prawns to our 8 putative nursery sites (based on their similarity to composite prawn samples at those sites) for each analytical approach is visualised in Fig. 3. Both approaches show for School Prawn that the contributions of different putative nursery sites to emigrating adults were approximately equal (Fig. 3a, b); whereas for Eastern King Prawn the contributions of putative nursery sites were highly skewed to downstream areas (Fig. 3c, d). The output of the mixing model (using SIAR; Fig. 3a, c) indicated highly negative cross-correlations between posterior distributions for habitat sites 1 and 2 for both species (−0.38 and −0.87 for School and Eastern King Prawn respectively) and sites 7 and 8 for School Prawn (−0.53). Both these pairs of putative nursery sites were spatially adjacent, which indicated that the model could not effectively differentiate between these pairs of sites on the basis of the bivariate isotopic data provided.

The output from the distance model showed similar results (Fig. 3b, d) to those of the mixing model. Regression between the proportional assignments to putative nursery sites derived using each approach showed a slope ≈ 1 ($\beta = 0.930$ $F = 132.65$, $P \ll 0.001$; Fig. 4), indicating strong agreement between the two approaches. A chi-square test was also performed to evaluate whether the origin of emigrating prawns differed from the null model of equal probability-of-origin among all

Table 1
Comparisons between putative nursery sites for penaeid prawns, and pseudo-*t* values from pairwise comparisons showing significant differences in the isotopic composition of composite samples using $\delta^{15}N$ and $\delta^{13}C$ data.

Site	Distance to sea (km)	Pseudo t-values							Site and habitat description
		2	3	4	5	6	7	8	
1	8.35	0.9	1.5	1.9	2.9*	3.7*	11.2*	3.6*	Mangrove lined creek, lower estuary
2	9.65		1.8	2.8*	4.2*	5.5*	15.9*	5.2*	Shallow embayment, lower estuary
3	10.80			1.6	1.7	1.9	8.1*	4.0*	Shallow embayment, lower estuary
4	11.19				0.3	0.4	3.5*	1.9	Mangrove lined creek, lower estuary
5	14.10					0.4	5.7*	2.2	Mangrove lined creek, middle estuary
6	15.56						8.5*	2.5*	Mangrove lined creek, middle estuary
7	16.97							0.5	Mangrove lined main channel, middle estuary
8	20.00								Mangrove lined main channel, middle estuary

* Denotes significant difference at $\alpha = 0.05$.

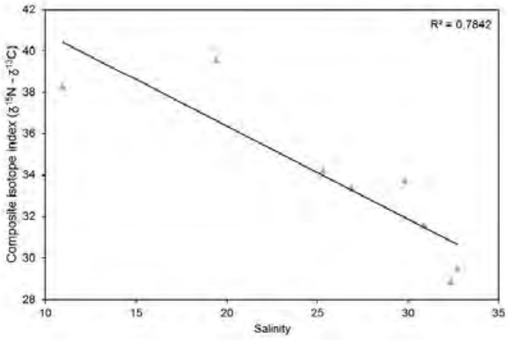

Fig. 2. Relationship between isotopic signatures of putative nursery sites, expressed as a composite variable ($\delta^{15}N$–$\delta^{13}C$), and salinity ($\beta = -0.45$ $F = 21.81$, $P = 0.003$).

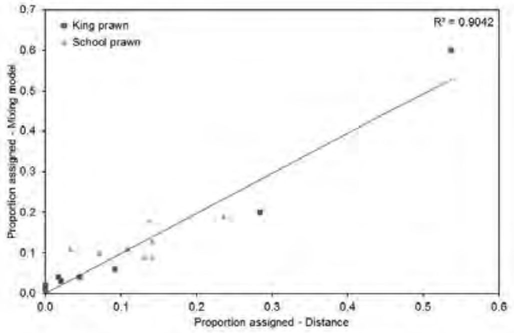

Fig. 4. Agreement between proportional assignment of emigrating School and Eastern King Prawn to putative nursery sites derived using the mixing model and distance approach.

putative nursery sites. The results largely confirmed the patterns observed in Fig. 3, with School Prawn showing no deviation of observed values from the null model ($P = 0.67$), and a significant departure from the null model for Eastern King Prawn ($P << 0.01$). Given that we could not model the specific area of each of habitat zone, and that composite isotopic composition varied more or less continuously with salinity, we were unable to use this data set to distinguish whether emigrating Eastern King Prawn are sourced more from certain sites

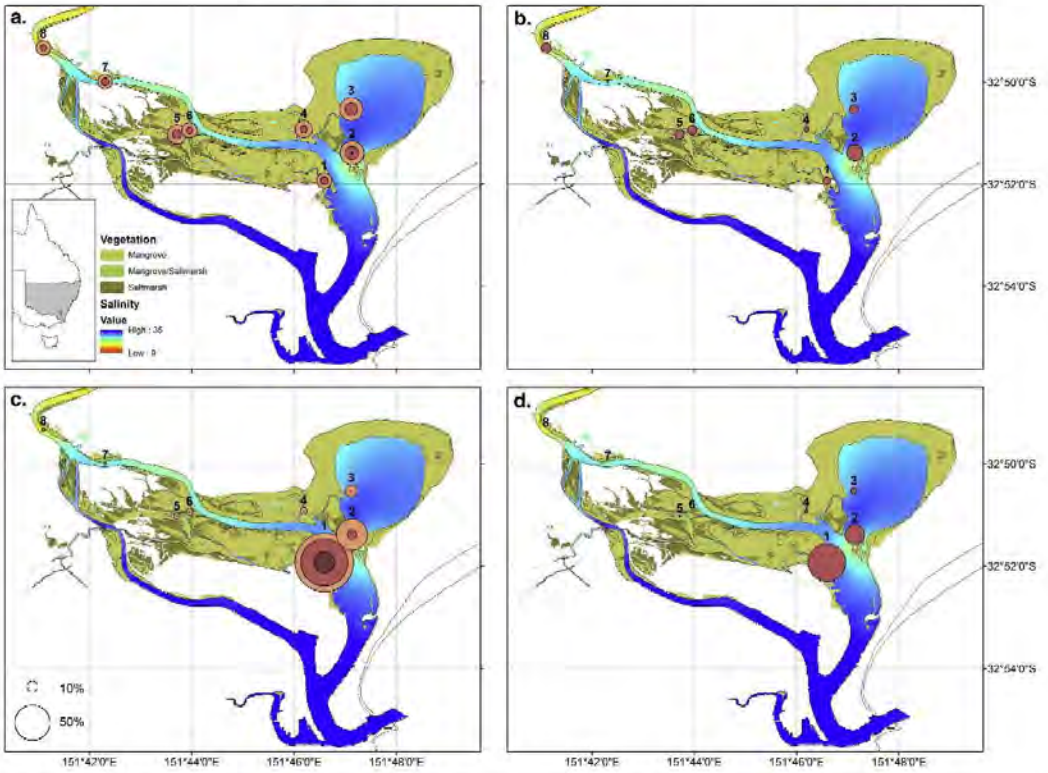

Fig. 3. Proportional assignment of emigrating prawns to putative nursery sites in the Hunter River for School Prawn (top row, a. and b.) and Eastern King Prawn (bottom row, c. and d.), using SIAR (left panels, a. and c.) and the distance (right panels, b. and d.) methods. Concentric circles on the left panels indicate 95% confidence interval (outermost), mean proportion (central), and 5% confidence interval (innermost, note that contour is not visible where 5% CI equalled zero), estimated by SIAR. An interpolated salinity surface and major aquatic habitat types are shown, and a scale is present in c. linking circle size to percent contribution. Site labels correspond to those in Table 1.

because those sites have better nursery habitat, or because those sites have a larger area of suitable nursery habitat.

4. Discussion

Both the mixing model and the minimum distance methods show promise for identifying important putative nursery sites, and the mixing model appeared to work well as an assignment model. The example presented here evaluated whether a solution to the underlying mixing model was possible given the isotopic data from putative nursery sites, and then conducted a population-level analysis to generate the most probable sources of emigrating prawns among the set of putative nursery sites. Although we sampled a relatively small subset of putative nursery sites in this study, ≈90% of emigrating prawns collected could be assigned to these areas using bivariate isotopic data. This sampling and analytical approach may be relevant to the broad suite of species which display a Type-I and Type-II lifecycle, which includes a large proportion of exploited *Penaeus* and *Metapenaeus* spp. (Dall et al., 1990c). Important nursery sites identified for Eastern King Prawn largely included shallow sedimentary habitats in areas of low current flow in the lower estuary. In contrast, important nursery sites for School Prawn extended much further along the estuary, which was expected based on prior knowledge for the species in this system (Ruello, 1973a) and the species broader salinity tolerance.

Both the minimum distance and the mixing-model method identified similar patterns of assignment to putative nursery sites. The minimum distance method is an analytically simpler approach to the problem, and while the simulations here were conducted in Matlab, similar calculations can easily be conducted in a spreadsheet if uncertainty in source signatures is not taken into account. Despite the conceptual issues outlined earlier in the manuscript, the mixing-model produced similar results to the minimum distance method. This approach also provided a measure of uncertainty in the model output; however, as Brett (2014) points out uncertainty in stable isotope analysis is strongly related to how distinct the sources (or in our case the putative nursery sites) are from each other. In our example, *most* sources were significantly different, and the model could not separate between those sources that were not (see below). As a final comment, application of the point-in-polygon evaluation (Smith et al., 2013) is an important initial step in the process outlined here, as it allows samples for which there is a low probability of a model solution using the source data to be excluded from further analysis. This minimises the chance that individuals will be assigned to habitats on the basis of unlikely model solutions.

The isotopic signature of estuarine water varies with the salinity gradient due to the fluctuating influence of freshwater, and the associated differences in dissolved inorganic carbon and nitrogen inputs. The mixing of freshwater and seawater along the length of the estuary creates an isotope imprint that is recorded in producers at the bottom of the food chain, and this signature is in turn transferred to consumers via trophic linkages (Fry, 2002). Consequently, the isotopic composition of prawns captured in different putative nursery sites reflects this mixing, and provides a good reflection of location along the estuary, but spatially adjacent putative nursery sites were not well differentiated. This was evident in the SIAR analysis, where some correlation coefficients derived indicated that the mixing model could not effectively differentiate between putative nursery sites (and these same pairs of sites were not significantly different in their bivariate isotopic signature, Table 1, Fig. 1). For example, Site 1 was a mangrove-lined tidal creek while Site 2 was the mouth to a large unvegetated mangrove-lined embayment; but both sites were a similar distance to the sea. Similarly, Sites 4, 5 and 6 represented mangrove-lined tidal creeks draining saltmarsh habitats further up the estuary. The salinity gradient also explains the divergent patterns observed for School and Eastern King Prawn, as the latter are far more stenohaline and halophilic (Ruello, 1973b), whereas the former tend to prefer more brackish water.

It is important to note that this study was done to evaluate the feasibility of applying stable isotopes as a tool to assign mobile animals to habitat, and compare analytical approaches to the problem. Either of the assignment approaches (SIAR, distance method) was feasible, and shows promise as a tool to generate a broad understanding of the relative importance of potential estuarine nursery habitats with a relatively rapid and straightforward sampling design. We wish to point out, however, that the patterns in stable isotope composition are potentially estuary- and seasonally-specific, influenced by catchment use, water chemistry, nutrient sources and dominant primary producers. We make several recommendations for applying a mixing model approach to habitat assignment. Firstly, the inclusion of an additional isotope (e.g. ^{34}S) may add power to assist in the differentiation of putative nursery sites at similar locations along the estuary where differentiation based on $\delta^{15}N$ and $\delta^{13}C$ alone are poor (e.g., see Fry, 2008). Secondly, when employing a mixing-model to assign individuals to nursery sites, the study design should target an appropriate number of putative nursery sites for the system under investigation, and the suspected distribution of the species within the system. The authors note that this involves a trade-off along similar lines to the "too many sources" problem (e.g. Phillips and Gregg, 2003). Although our approach incorporates the probabilistic method of Parnell et al. (2010) which is useful when the number of "sources" (or putative nursery sites) exceeds the number of isotopes, the overall number of putative "sources" used should be carefully balanced given the estuary under investigation, the diversity of habitat types therein, and the isotopes being used.

As a final point, while this approach is useful in evaluating putative nursery sites for a species, its application will be most powerful when supplemented by monitoring of size structure/growth, density, and trophic relationships within these sites. This may also help overcome issues surrounding the separation of adjacent putative nursery habitats or sites.

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Appendix 4 – Nocturnal sampling reveals usage patterns of intertidal marsh and sub-tidal creeks by penaeid shrimp and other nekton in south-eastern Australia.

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Nocturnal sampling reveals usage patterns of intertidal marsh and subtidal creeks by penaeid shrimp and other nekton in south-eastern Australia

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Abstract. The life cycle of most penaeid prawns includes a juvenile phase in protected coastal environments such as estuaries and embayments. In the tropics, some penaeids are known to utilise intertidal habitats, yet in temperate regions of Australia the use of marshes has not been investigated. We focused on determining the extent to which *Melicertus plebejus* and *Metapenaeus macleayi* directly utilise intertidal marsh habitat using fyke nets. Using cast nets, we also assessed the abundance of the two focal species in middle and edge habitat of adjacent subtidal creeks. Despite collecting 8300 crustaceans and 4259 teleosts, only 8 *M. plebejus* were sampled on the marsh. Abundances of *M. macleayi* were greater with 90 individuals collected. Within the subtidal creeks larger *M. macleayi* were collected in the middle habitat and the abundance of both penaeids varied among different creeks. The nekton community as a whole also differed among creeks within marshes. This study has demonstrated that juvenile *M. plebejus* and *M. macleayi* do not directly utilise intertidal marsh habitats. Despite this, marshes may provide important resources for prawns through the export of carbon. Future isotope studies would provide valuable information in this regard, providing a broader understanding of penaeids and specific estuarine habitats.

Additional keywords: estuary, fish, habitat, nursery, penaeid.

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Introduction

Eastern king prawn (*Melicertus plebejus*) and school prawn (*Metapenaeus macleayi*) are important commercial and recreational penaeid species in eastern Australia (Montgomery *et al.* 2007). Like many penaeids, these species exhibit a type-II life cycle including a juvenile estuarine phase and an adult marine phase. Although the general movement patterns, reproductive biology and stock structure of adults in the marine phase of their life cycle are well known (Montgomery 1990; Courtney *et al.* 1996; Montgomery *et al.* 2007; Braccini *et al.* 2012), the use of temperate estuarine habitats such as intertidal marshes remain poorly understood.

Broadly, mangrove creeks and intertidal marsh habitats are understood to be important habitats for juvenile penaeid prawns (Minello and Zimmerman 1985; Baran and Hambrey 1999), yet numerous studies have shown their distribution and abundance can differ among microhabitats within these areas. For example, the edges of creeks have been found to harbour more juvenile *Penaeus merguiensis* than intertidal forested areas (Rönnbäck *et al.* 2002; Meager *et al.* 2003), and *Penaeus aztecus* abundance was higher in dense marsh vegetation compared to non-vegetated areas (Minello and Zimmerman 1985). The habitat provided by marshes may extend beyond the marsh itself to the edges of subtidal creeks, which are generally shallow and contain structures such as mangrove roots, whereas the middle sections are often barren. It is possible this may also influence the distribution patterns of penaeids (Fry 2008). As a result of the mosaic of habitats that are located in estuaries, direct links between mangrove forests, intertidal marshes, the edges of marshes and fisheries productivity remain ambiguous (Sheaves *et al.* 2012).

The spatial variability of penaeid abundance among microhabitats leads to the hypothesis that some estuarine habitats may disproportionally support juvenile prawns relative to others. The identification of these areas is important, as it allows for resources for habitat restoration to be directed towards habitats where conservation outcomes could provide maximum ecosystem services (Beck *et al.* 2001). Although potentially important microhabitats have been identified for some penaeid species in some areas, most of this work has been conducted on tropical and subtropical species and none have dealt with the importance of temperate intertidal marshes for *M. plebejus* (Ruello 1975). In addition, few Australian studies have sampled these habitats nocturnally when organisms such as *M. plebejus* are more active (Wassenberg and Hill 1994; Griffiths 1999). A comprehensive understanding of prawn distribution of temperate marshes requires data collected at night. Such information is essential for the management, enhancement and restoration of juvenile habitats for fishery outcomes. It is important to clarify that although some recent literature (Flegel 2007, 2008) indicates that that the Eastern king prawn should retain the genus *Penaeus*, we use nomenclature consistent with that specified in the Australian Fish Names Standard (*Melicertus plebejus*). This study aimed to address a knowledge gap by nocturnally sampling intertidal mangrove and marsh habitats, and adjacent subtidal creeks, to examine the distribution and use of these habitats by *M. plebejus*, *M. macleayi* and other nekton.

Materials and methods

Site description

Fieldwork was conducted in the Hunter River Estuary located on the coastline of temperate New South Wales (32°52′S; 151°45′E). This system contains large intertidal wetlands, notably at Hexham Swamp, Tomago and Kooragang, which collectively contain the second largest area of mangroves (*Avicennia marina* and *Aegiceras corniculatum*) in New South Wales. Mangroves are generally located in the lower intertidal region of the wetlands, whereas the higher marsh consists of herbaceous species (e.g. *Sarcocornia*, *Zoysia macrantha*), *Juncus* sp. and stands of *Meleleuca*. The marsh is drained by a complex network of natural and man-made intertidal ditches, which flow into larger and deeper (>1 m) subtidal creeks that meander through the marsh and branch from the main channel of the estuary. The downstream sections of the estuary, where the majority of wetlands are located, are subject to semi-diurnal tides (0.1–2.0 m), and inundation of the marsh occurs only during the highest spring tides (>1.5 m) with the ditches fully draining at low tide. In general, the tidal creeks that drain these habitats have near vertical banks that drop steeply to the maximum depth of the creek bed.

Sampling

Fieldwork was carried out between 20 January and 18 April 2015 when *M. plebejus* and *M. macleayi* are most abundant in estuaries (Racek 1959). Sampling was conducted across three distinct marshes within the Hunter Estuary, which included Hexham Swamp, Tomago Wetland and Kooragang Wetland (Fig. 1). All fieldwork was completed after sunset and within 5 days of the new moon. Sampling was focused around the new moon period when prawns are most active (Young 1975; Griffiths 1999; Guest *et al.* 2003) and only undertaken during the night, as this is the period when both species are known to leave their burrows, becoming vulnerable to sampling gear. Subtidal creeks ($n = 2$ per marsh) were divided into *edge* and *middle* habitats, with edge habitats located within 3 m of the creek bank and middle habitats located in the middle of the creek. The width of most subtidal creeks was ~40 m (Fig. 1*b*), thereby providing clear spatial segregation between the edge and middle habitats. Each habitat was sampled using cast nets (Superspreader, Fitec Group, Memphis, TN, USA), 4.8-m^2 area at full spread, 4.8-mm mesh) by the same operator. Cast nets were chosen as they can provide precise placement of gear, which is especially necessary for targeting the creek edge habitats (Johnston and Sheaves 2007, 2008). Within each of the 6 creeks, 16 cast nets were thrown at each habitat along a length of at least 500 m (with 192 cast nets throws in total) during slack water. Cast net samples were discarded if the net spread less than 50% of its full capacity, or became entangled. A record of the percentage net spread for each throw was taken and this was used to standardise catches with varying net spread by dividing the catch with the percentage net spread. Depth readings were taken for each cast net sample. Comparisons in depth were made between the two habitats for each subtidal creek, but no differences were ever recorded because of the vertical nature of the banks and flat bottom of creeks.

The shallow intertidal ditches that drain the mangrove and marsh were sampled using double-wing fyke nets, which are effective in sampling this type of habitat (Mazumder *et al.* 2005). The nets were constructed from 3-mm honeycomb mesh and had 5-m wings and a 60-cm mouth opening with two throats to prevent the escape of crustaceans and fish. Six fyke nets were set within each marsh (Hexham, Tomago, Kooragang) during the sampling period. Nets were set just before dusk at low tide and retrieved the following morning after a single tidal cycle and marsh inundation. The nets were positioned so the wing spread covered the full width of the ditch and faced into the marsh so all nekton travelling down a ditch would be funnelled into the fyke. Fyke net sampling coincided with spring tides >1.7 m, when the marsh was fully inundated. Adjacent to the nets at Hexham Swamp a Hobo U20 pressure logger (Onset Corporation, Cape Cod, MA) was deployed. This logger showed water depth on the marshes near the ditches where the fykes were deployed exceeded 30 cm, thereby fully inundating the marsh and linking all intertidal ditches along the creeks. Although the fyke nets may have prevented nekton moving up a particular ditch during the flood tide, adjacent ditches were never more than 30 m away with recorded water depths allowing nekton to move freely around the marsh and return to the creeks via another ditch. In this way the fykes sampled nekton that entered the marsh via a nearby ditch. It is difficult to determine the exact area sampled by each fyke net. Despite every attempt being made to deploy these in similar locations, it is likely the exact area sampled varied slightly among nets. Basic water quality parameters in the subtidal creeks (salinity, pH, dissolved oxygen and temperature) were measured during each sampling trip using a Horiba (model U-50, Horiba Ltd, Kyoto, Japan) water quality meter.

All samples were preserved in 70% ethanol and enumerated in laboratory facilities at the Port Stephens Fisheries Institute. Crustaceans and fish were identified under dissecting microscopes using published descriptions (e.g. Kuiter 2000), the carapace length of all penaeids and total length of fish was measured to the nearest millimetre.

Analysis

Cast and fyke net data were analysed separately. For cast nets, the abundance of *M. plebejus*, *M. macleayi*, total fish abundance and total crustacean abundance was analysed using Permutational Analysis of Variance (PERMANOVA) in the software package PRIMER v.6 (PRIMER E-Ltd, Plymouth, UK). The sum-of-squares and *F*-ratios produced are analogous to Fisher's univariate *F*-statistic from traditional ANOVA when Euclidian distance measures are used (Anderson *et al.* 2008). Three factors were included in the design, consisting of Wetland (fixed, 3 levels; Tomago, Kooragang, Hexham), Habitat (fixed, 2 levels; Adjacent and Middle) and Creek (random and nested

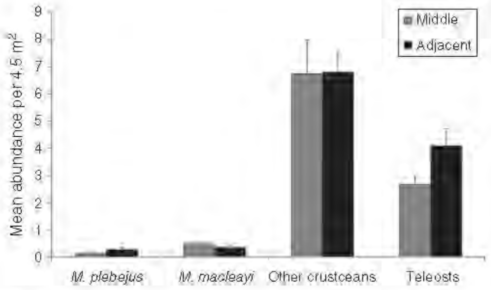

Fig. 2. Mean abundance (±s.e.) of cast net samples (4.5 m^2) from the middle and adjacent habitat of subtidal creeks within the Hunter River Estuary.

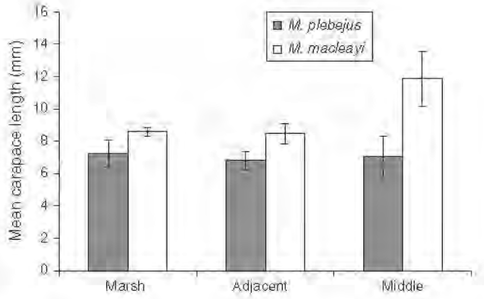

Fig. 3. Mean carapace length (±s.e.) of *M. plebejus* and *M. macleayi* collected from subtidal creek habitats (Adjacent and Middle), and Marsh habitat within the Hunter River Estuary.

H. castelnaui and *Ambassis jacksoniensis*. The crustacean community was found to differ among creeks ($F_{3,180} = 5.89$, $P < 0.001$), with no significant effects of higher level factors.

Use of intertidal marsh habitat

As expected, the marsh only became inundated during spring high tides, with the marsh remaining exposed during the entire neap cycle. Logger data indicated that during the sampling period, for each lunar month, the marsh had a mean inundation period of only 30.3 h (±3.5 s.e.) with each inundation lasting between 3 and 6 h. Within intertidal marsh and mangrove habitats, fyke net catches collected 12 575 individual nekton, but were dominated by *Macrobrachium intermedium*, which accounted for more than half of all nekton and 80% of all crustaceans (Table 1). The most abundant of the 20 species of fish was *Gobiopterus semivestitus* followed by *A. jacksoniensis*, which collectively accounted for 85% of fish using the marsh habitat. The nekton community did not differ among the three wetlands when considered as a whole ($F_{2,15} = 1.173$, $P = 0.307$), or when broken into the crustacean community ($F_{2,15} = 1.20$, $P = 0.311$) or the fish community ($F_{2,15} = 1.02$, $P = 0.341$). Interestingly, only eight *M. plebejus* were collected from the marsh, and none collected at Kooragang.

Prawn size

Carapace length of *M. plebejus* ranged between 3.5 and 14.0 mm with a mean of 7.3 mm ± 0.4 s.e. No difference was found in the carapace lengths of *M. plebejus* between the adjacent and middle habitats of creeks ($F_{1,19} = 0.084$, $P = 0.775$); however, carapace lengths of *M. macleayi* were significantly greater in middle as opposed to edge habitats ($F_{1,34} = 7.96$, $P = 0.008$; Fig. 3). Length data collected from the intertidal marsh habitat with the fyke nets were not compared statistically with data from the creeks due to differences in gear; however, these sizes were similar to both adjacent and middle habitats for *M. plebejus*, but only similar to *M. macleayi* size within the *adjacent* habitat (Fig. 3).

Discussion

Fyke net sampling across three wetlands indicated few *M. plebejus* directly move into intertidal marsh habitat. Although another commercial penaeid (*M. macleayi*) was sampled in higher numbers on the marsh surface, these numbers were still low compared to penaeid samples collected in other marsh habitats across Australia and the world (Zimmerman *et al.* 1984; Zimmerman and Minello 1984). During spring high tides, large portions of intertidal wetland consisting of a complex mosaic of mangroves and high marshes became inundated. Studies that sample these habitats nocturnally are rare in Australia, and to our knowledge this is the first published investigation of the nocturnal assemblage utilising high marsh habitats in temperate New South Wales. Generally, juvenile penaeids are known to use a variety of intertidal habitats on flooding tides including mangroves (Vance *et al.* 1996; Primavera 1998; Vance *et al.* 2002) and marsh (Zimmerman *et al.* 1984; Minello *et al.* 2003) across tropical and temperate zones. The lack of many observations of *M. plebejus* on the inundated marsh was very surprising, given the consistent pattern observed across wetlands for similar species. An explanation might be that there are simply few *M. plebejus* within the Hunter, but our catches are consistent with studies in other large New South Wales estuaries (Boys *et al.* 2012). Flooding duration and depth are important factors that can govern the numbers and types of species that move laterally into intertidal habitats (Connolly 1999; Minello *et al.* 2012; Baker *et al.* 2015). The short flooding duration of intertidal wetlands undoubtedly restricts access to these habitats for nekton and may explain our divergent findings regarding the abundance of penaeids. Reduced access, and therefore abundance of penaeids in intertidal wetlands, raises an important consideration about the differences in direct use of intertidal habitats by penaeids in temperate Australia. Penaeids are also regularly found in many intermittently closed and open lakes or lagoons (ICOLLs) that are common in temperate south-east Australia and that generally lack large intertidal habitats (Pollard 1994). High abundance of prawns both in systems with large intertidal wetlands but limited inundation, and ICOLLs with only small intertidal habitats may suggest penaeids in temperate systems are less reliant on such areas. Although the physical structure provided by marshes and mangroves is often cited to reduce predation on estuarine nekton (Primavera 1997), it is likely that in temperate estuaries, juvenile *M. plebejus* rely on burying within the substrate to avoid predators, a behaviour observed for several penaeid species (Ruello 1973).

Abundances of penaeids were similar in both the adjacent and middle habitats of the subtidal creeks. The littoral habitat or many estuaries is shallow and this is often cited as an important characteristic for juvenile habitat (Rozas and Minello 1997). Although littoral zones in the Hunter Estuary contained structure, a lack of shallow water may explain the similar numbers sampled in both habitats. Larger *M. macleayi* were found in the middle of creeks compared to adjacent habitat, and similarly sized individuals were also sampled with the fyke nets on the marsh. This may indicate a potential ontogenetic shift in the distribution of *M. macleayi*, with larger, older prawns moving away from the marsh onto the non-vegetated substrate of the creeks. Ontogenetic habitat shifts by estuarine nekton is well documented and is usually a response to changing diets and predation risk (Baltz *et al.* 1993; Beck *et al.* 2001). Changes in feeding or predation rates, however, are unlikely to explain these differences as prawns across these sizes consume similar food items (Ruello 1973), and even the largest *M. macleayi* sampled (27 mm CL) could be preyed upon by numerous fish species regularly encountered within east coast estuaries (Gray *et al.* 2011). Increased swimming ability of larger individuals is another potential explanation for these patterns, with the edges of the creeks and intertidal habitats providing refuge from tidal flow for smaller individuals compared to the middle of the channel.

Although we found little evidence to suggest *M. plebejus* directly occupy intertidal marsh habitats, these areas could still support prawn populations within estuaries through the export of carbon resources. Tidal transport of both dissolved and particulate organic carbon and the feeding migration of small nekton shift carbon resources from vegetated intertidal habitat into nearby estuarine waters (Hyndes *et al.* 2014). Future isotope studies would help identify any trophic links between *M. plebejus* and these vegetative habitats. This could help unravel indirect interactions among estuarine habitats and the nekton they support, moving beyond the scope of this and other studies that often view particular habitats as discreet spatial units (Sheaves *et al.* 2015).

Variation in the abundances of both penaeid species differed among creeks points to a degree of spatial variability within marsh habitats. Acoustic telemetry studies of juvenile *M. plebejus* showed that most movements are concentrated in small discrete areas (Taylor and Ko 2011). Penaeids can have specific sedimentary and epibenthic food requirements (Ruello 1973; Wassenberg and Hill 1987), this combined with limited movement patterns may explain variation at the spatial scale observed in our study. In contrast, the fish community varied at larger spatial scales with differences identified among wetlands. This was primarily due to changes in the abundances of some species, rather than a shift in the composition of the community itself. Higher abundances of the abundant species *H. castelnaui* and *A. jacksoniensis* were found at Hexham Swamp compared to Tomago. Hexham marsh lies on the south arm of the Hunter River and receives probably the greatest flushing with tidal water. *H. castelnaui* undergo a spawning migration from coastal waters into upper reaches of estuaries during summer–autumn (Neira *et al.* 1998), so it may be that this particular marsh receives improved recruitment of this species during this time of year.

The morphology of the creeks included steep, near vertical banks and deep (>1 m) water in the mid-channel region. Even though the fish community as a whole did not differ between middle and adjacent habitats of creeks, we did observe higher abundances of fish at adjacent sites. Johnston and Sheaves (2008) sampled 13 estuaries and developed conceptual models predicting the cross profile distribution of fish in relation to creek morphology. Our results partially conform to their broad model for deep creeks with steep banks, where higher abundances of benthivores were located along the banks. Many of the fish collected in our samples, however, were planktivores (e.g. *A. jacksoniensis* and *H. castelnaui*). In contrast to our findings, Johnston and Sheaves (2008) predicted higher abundances of this group in the centre of the channel. Diel cycles are known to alter the distribution of many estuarine fish (e.g. Becker *et al.* 2011; Becker and Suthers 2014), and this may explain these divergent findings.

This study demonstrated minimal direct interaction between *M. plebejus and M. macleayi* and the marsh surface. This is an important component in identifying potential nursery function for commercial species in temperate Australia, and also highlights the variability among penaeid species in their lateral movements into intertidal estuarine habitat. Future studies should expand this work to examinations of multiple estuaries, particularly those with intertidal habitat that undergo longer inundation periods. More importantly, evaluation of the supply of energy using isotopes could build upon the findings of this research and further unravel links among the various habitats and vegetation that may support juvenile prawn populations.

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Appendix 5 – Rapid salinity changes impact the survival and physiology of a penaeid prawn: Implications of flood events on recruitment to the fishery

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ORIGINAL ARTICLE

WILEY Fisheries Management and Ecology

Rapid salinity changes affect the survival and physiology of a penaeid prawn: Implications of flood events on recruitment to the fishery

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Abstract

Estuaries act as nurseries for many penaeid prawns, but these habitats are highly susceptible to salinity decline through flooding. The rate of salinity decline and duration of exposure to non-optimal salinity may affect survival and subsequent recruitment of prawns to the fishery. This study aimed to determine the effect of salinity fluctuations observed in local estuaries during flood events using a novel dilution approach. Mortality of juvenile *Melicertus plebejus* (Hess) was assessed after 24 hr exposure to 24 rates of salinity decline ranging from 0.01% to 20% per hr. After the salinity decline, prawns were held at the final salinities for five days before again assessing mortality as well as aerobic metabolic rate and prawn water content. Salinity decline from 36 to ~0.8 led to 50% mortality, but continued exposure to low salinity for five days increased mortality at this salinity to 99% and shifted the 50% mortality point to salinity ~5. Aerobic metabolic rate and water content data suggested the cause of mortality due to exposure to salinities < 5 was osmoregulatory failure. Rapid salinity declines over 24 hr and sustained low salinity due to flooding could compromise the survival of juvenile prawns, potentially reducing recruitment to the fishery.

KEYWORDS
eastern king prawn, estuary, osmoregulation, rainfall, respiration, shrimp

1 | INTRODUCTION

Stochastic environmental events, such as extreme changes in temperature or high rainfall, can cause dramatic physiochemical changes in estuaries that may affect aquatic organisms (e.g. Boesch, Diaz & Virnstein, 1976; Owen & Forbes, 1997; Payne et al., 2013; Preen, Lee Long & Coles, 1995; Taylor et al., 2014). Large rainfall events can dramatically reduce water salinity within 24 hr (Blöschl & Sivapalan, 1997; Robinson & Sivapalan, 1997) and salinity may remain low for weeks afterwards (Taylor et al., 2014). The frequency and intensity of large rainfall events are predicted to increase in the future (Pachauri et al., 2014); therefore, the potential impacts of these events on aquatic species will need to be considered by natural resource managers (e.g. Badjeck, Allison, Halls & Dulvy, 2010; Ives, Scandol, Montgomery & Suthers, 2009; Klyashtorin, 1998, 2001; Murawski, 1993).

The impacts of high rainfall and increased freshwater flow into estuaries on commercially valuable prawn species are not always predictable and are a function of species and life-history stage. Although studies correlating long-term fisheries catch data with rainfall or freshwater flow have found positive correlations (Glaister, 1978; Gunter & Hildebrand, 1954; Loneragan & Bunn, 1999; Penn & Caputi, 1986; Vance, Staples & Kerr, 1985), negative correlations have also been observed (Möller, Castello & Vaz, 2009; Piazza, La Peyre & Keim, 2010). Some increases in catch could potentially be driven by rainfall and freshwater flow stimulating juvenile emigration from the river or estuary (Ruello, 1973; Staples, 1980; Staples & Vance, 1986), but the mechanisms for initiating the migration are not clear. Freshwater flow into estuaries may also have lethal or sublethal effects over shorter time scales (i.e. days) and non-optimal salinity conditions can lead to negative effects on growth and survival of many penaeid prawn species (e.g. Antony et al., 2015; Chen, Lin, Chen & Lin, 1996; Rozas & Minello, 2011; Staples & Heales, 1991; Tantulo & Fotedar, 2006). The direction and intensity of such effects within estuarine systems are poorly understood due to logistical difficulties associated with directly studying estuaries during times of high rainfall and flooding. Aquarium experiments that directly simulate environmental variability observed in natural systems represent a useful approach to quantify the mechanistic processes by which environmental variability could affect fishery harvest.

Eastern king prawn (EKP; *Melicertus plebejus*, Hess) is the most valuable penaeid prawn species harvested in south-eastern Australia with fisheries valued at around AU$30 million annually (Lloyd-Jones et al., 2012). Stock assessments in 2011 suggest that substantial rainfall was potentially responsible for a significant reduction in EKP catch (Prosser & Doyle, 2014). Such a reduction could potentially have occurred through reduced growth, resulting from decreased food availability or quality after prolonged rain, increased energy allocation to osmoregulation at lower salinities, increased mortality or premature emigration from the estuarine nursery to avoid adverse physicochemical conditions (Ruello, 1975; Thomson, 1959). Previous studies revealed that adult EKP are less able to cope with low salinity compared to other penaeid species, but this difference is less prominent for juveniles (Dall, 1981; Dall & Smith, 1981). However, these studies used stepwise reductions in salinity over a protracted duration of time (≤ 8 days), which ultimately does not reflect the changes observed in natural systems. Reductions in salinity following rainfall occur through constant dilution with limited potential for respite during the event. Therefore, the effect of declining salinity on EKP requires further investigation. This study simulated the salinity declines and physicochemical changes observed in natural systems within the species range and measured the survival and physiological responses of juvenile EKP. Specifically, this was achieved by measuring (1) survival, (2) oxygen consumption as a proxy for aerobic metabolic rate and (3) water content of body tissue as an indicator of osmoregulatory capacity.

2 | METHODS

2.1 | Prawn collection and pre-experiment husbandry

Juvenile EKP were collected from the North Arm of the Hunter River estuary in New South Wales (NSW), Australia (between −32.853, 151.765 and −32.905, 151.778) using a small sled net (1 × 0.4 m mouth, 4 m length, 26 mm diamond mesh body and 6 mm octagonal mesh cod-end). Prawns were collected over five trips between the 22 January and 15 July 2015 with salinity ranging between 22 and 26 at the time of collection. Short tows (3-5 min) were used and EKP were immediately identified in the mixed catch of prawns and transferred to an on-board aerated holding tank. Prawns were transported to the Port Stephens Fisheries Institute and released into ~5,000 L aerated, static water-holding tanks containing ~5 cm of beach sand substrate. Prawns were kept in these holding tanks (salinity ~36) for up to eight weeks before exposure to experimental conditions. Water in the holding tanks was exchanged (≤ 50%) weekly to reduce waste load and replacement water salinity ranged from 28 to 32 to account for evaporation-driven salinity increases. Prawns in holding tanks were fed *ad libitum* with dry feed (sera® "Shrimp Natural") each evening.

2.2 | Experimental procedures

The experiments were designed to expose juvenile EKP to salinity conditions experienced during mild to extreme rainfall events within this species' distribution, which can potentially involve a rapid salinity decline followed by low salinity for days afterwards. Prawns were exposed to 24 different salinity decline treatments, with the rates of salinity decline chosen to provide an even spread of endpoint salinities between 36 and 0 after 24 hr of decline. Prawns were held at a salinity of 36 ± 0.4 (standard deviation; SD) for a minimum of 12 hr before being exposed to salinity declines. The rates of salinity decline that were achieved ranged from 0.01 to 20%/hr, which resulted in a

TABLE 1 Rates of salinity decline (sorted in ascending order) for the 24 hr dilution phase of the experiment

Rate of Salinity Decline (%/hr)	Endpoint Salinity	Experimental Run
0.0	36.4	1
0.2	35.7	2
0.6	32.5	1
1.0	30.1	1
1.2	28.7	2
1.7	24.8	2
2.6	19.9	1
2.9	18.7	3
3.0	17.5	4
3.3	17.2	2
3.6	15.6	3
4.2	13.4	3
4.6	12.3	3
5.3	10.1	4
5.4	10.4	3
6.5	7.2	4
6.7	7.6	2
7.5	6.4	1
9.2	4.0	4
9.7	3.7	3
11.5	2.4	2
11.7	2.2	4
19.0	0.4	1
20.0	0.3	4

The starting salinity was 36.2 ± 0.4 (mean ± SD). The corresponding endpoint salinity following the 24 h dilution phase is indicated, as is the experimental run in which it was conducted.

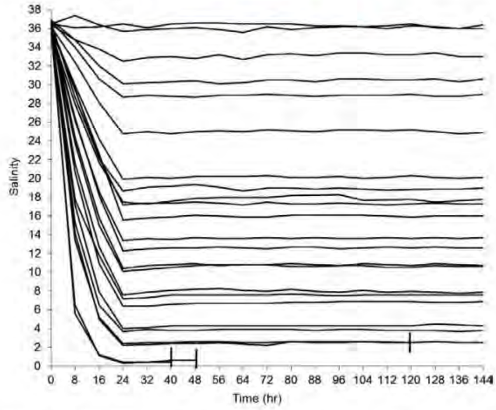

FIGURE 1 Salinity levels over time for each of the 24 treatments over the initial 24 hr of salinity decline and during the subsequent five days (120 hr) of maintained exposure. Treatments started at a mean salinity of 36.2 (± 0.08 SD). Measurements of salinity were taken at 8 h intervals. Standard deviation in salinity after the decline was ≤ 0.2 for all tanks. Rates of salinity change that did not run for the full five days (indicated by vertical bars) were due to 100% mortality of the prawns

range of endpoint salinities from 36.4 to 0.4, respectively (Table 1 and Figure 1). After the 24 h salinity decline, prawns were held at their respective final salinities (SD in salinity ≤ 0.2) for 5 days. For logistical reasons, the 24 rates of salinity decline were carried out over four experimental runs. Each run tested six (randomly assigned) rates of salinity decline and respective endpoint salinities. Each rate of salinity decline within each run was randomly assigned to one of six experimental tanks. Each tank was randomly allocated 10 prawns with carapace lengths (CL) between 5 and 12 mm (7.22 ± 1.24 mm, mean ± SD).

2.3 | Experimental equipment and husbandry

Each experimental tank (constructed of Perspex) was fitted with an overflow and contained ~2 cm of washed beach sand substrate. With sand and overflows in place, each tank held 7.5 L of water (10 L initial tank volume). The tanks were individually aerated with 2-cm diameter stone diffusers and the temperature was maintained at 24 °C ± 0.16 °C (standard deviation) by standing tanks in water baths of circulating heated water. Each tank was allocated a dose pump (DMS-12-3A-PE/E/C-S, Grundfos Alldos; France) and a 200 L storage sump of aerated rainwater. Dose pumps were calibrated to supply an adequate flow of rainwater per-unit-time to the treatment tank to achieve the desired rate of salinity decline. On completion of the 24 hr salinity decline, and every 24 hr thereafter, waste solids were removed from the tanks and 1 L of water was replaced with clean isosmotic water. Prawns were fed ~0.25 g dried feed g^{-1} prawn dry weight each evening, except during the salinity decline and on the evening of the fifth day.

2.4 | Data collection

Water temperature and salinity data of each tank were recorded every 8 h using a water quality meter (Horiba U-5,000, Horiba LTD, Japan). Mortality was determined by checking tanks for dead prawns every 8 h and those that appeared moribund (i.e. did not respond to physical stimuli) were removed and their CL (mm) and blotted wet weight (g) measured.

Measures of aerobic metabolism were taken for prawns that survived the entire six-day experiment. A 10-channel Oxy-10 mini-respirometer with fibre-optic sensors (optodes; PreSens, Regensburg, Germany) was used to measure oxygen concentration over time. The Oxy-10 mini was recalibrated to the water of each treatment prior to each use due to the differing salinities. Respiration chambers (x10) were 70 mL LabServ® polypropylene specimen jars with cable-glands installed in the lid and Teflon tape wrapped around the thread of the jar. Up to nine prawns were randomly allocated individually to respiration chambers containing water from their experimental tank. Chambers were sealed within 5 min with care taken to ensure no air bubbles remained and that the chambers had not been pressurised. Optodes were installed to approximately mid-way within the chambers. The tenth chamber was filled with water only as a blank for background respiration. During measurements, all chambers were held in the dark within a Styrofoam box in a temperature-controlled room (24 °C).

Each run of oxygen consumption measurements was initiated at 08:00 h (± 30 min) to account for potential circadian impacts on respiration. Pilot studies into the characteristics of the oxygen consumption over time curves produced by juvenile EKP indicated that a useable oxygen concentration over time curve was attained in ≤ 8 h and that there was no apparent switching in the mode of oxygen consumption from oxygen concentration independency to dependency when concentration levels remained above 20% air saturation. Therefore, oxygen concentration data were recorded until either 20% air saturation or 8 h total run time was reached. All prawns that survived the entire experiment were euthanised and measured (as described earlier) before their water content was calculated by drying at 70 °C for > 48 hr and subtracting dry weights from blotted wet weights.

2.5 | Data analysis

Our approach sought to measure mortality responses across as many rates of salinity decline as possible and to model the relationship between mortality and treatments. This was done because the range in rates of salinity decline where significant mortality was likely to occur was unknown. This is a common approach used in median lethal concentration (LC50) experiments (e.g. McLeese, Metcalfe & Zitko, 1980; Milani & Della Vedova, 1996; Praskova et al., 2011), as is the use of Probit regression analysis of data of this type (see review by Hoekstra, 1991). Probit regression analyses were used to describe the relationship between the probability of death and the rate of salinity decline using IBM SPSS Statistics 22. These analyses allowed an estimation of

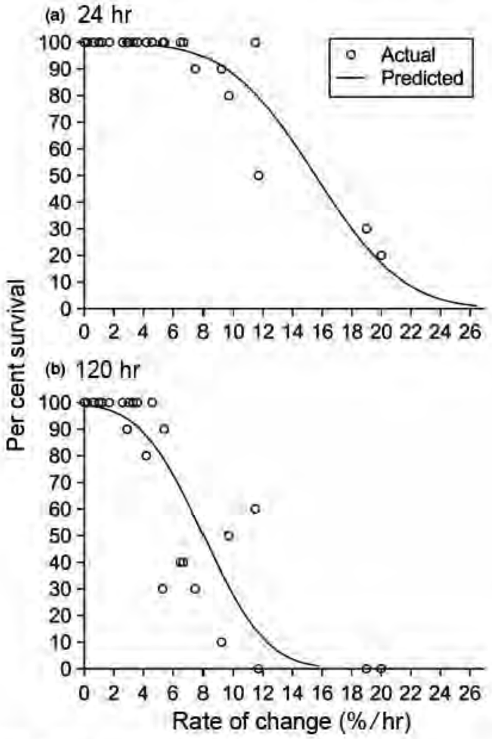

FIGURE 2 Percent survival of prawns in all salinity decline treatments (circles) with the predicted mortality from the Probit regression analysis (solid line) at (a) the end of the 24 h salinity decline and (b) 120 (5 days) after the end of the salinity decline

the rate of salinity decline at which 50% mortality would occur following 24 hr of salinity decline. In addition, these analyses were also used to estimate the rates of salinity decline that would cause 50% and 99% mortality, which were due to the combined effects of exposure to 5 days (120 h) of low salinity and to the respective rate of salinity decline for 24 hr.

To account for potential handling effects on measurements of prawn aerobic metabolic rate, the first hour of measurements was discarded. The slope of the linear relationship between oxygen concentration and time for the remaining data was used to calculate oxygen consumption rates using the following equation, modified from Deigweiher, Koschnick, Pörtner and Lucassen (2008) and Parker et al. (2012):

$$O_{2_{\mathrm{Cons.}}} = \frac{(V_C - WW) \times (\Delta C_E O_2 - \Delta C_B O_2)}{DW} \quad (1)$$

where $O_{2_{\mathrm{Cons.}}}$ is the rate of oxygen consumption of each prawn per gram dry weight (mg O_2/g/hr), V_c is the volume of the respiration chamber, WW is the wet weight of the prawn (in L, where 1 kg of wet prawn tissue is assumed to be equal to 1 L of water), $\Delta C_E O_2$ is the slope of oxygen concentration over time from the experimental chamber (mg O_2/hr), $\Delta C_B O_2$ is the slope of oxygen concentration over time from the blank chamber (mg O_2/hr), and *DW* is the dry weight of the prawn (g).

Generalised additive modelling (GAM) was used to identify and characterise the relationships between each of the response variables of prawn aerobic metabolic rates and water composition and the explanatory variables of rate of salinity decline, final salinity and, for aerobic metabolic rates only, somatic condition (see Wood [2006] and Zuur, Ieno, Walker, Saveliev and Smith [2009] for more information on GAM and interpretation of outputs). Exploratory models showed that the final salinity data were not as strong a predictor variable as the rate of salinity decline and so only models using the rate of salinity decline are reported. Standardised residuals from the log CL-log dry-weight data were used as a size-independent measure of the somatic condition of an individual at the whole animal level (e.g. Moltschaniwskyj & Semmens, 2000). The splines were based on thin plate smoothing terms with default settings (Wood, 2003) applied to each variable using the *mgcv* package (Wood, 2011) in R v.3.2.0 (R Core Team, 2015). Prior to accepting the validity of a GAM, assumptions of normality and homogeneity for the GAM were checked via observation of QQ plots/histograms and plots of residuals versus predicted values, respectively.

It should be noted that the rate of salinity decline and the endpoint salinity were correlated. Therefore, the patterns observed in data that were obtained at the end of the experiment may well be a function of both variables. In recognition of this, we report the endpoint salinity (ES) whenever a rate of salinity decline is reported. All ESs reported have been calculated using the following equation;

$$ES = S_s^{-R \times T} \quad (2)$$

where *ES* is the endpoint salinity, S_s is the starting salinity, *R* is the rate of salinity decline, and *T* is time (hr). Equation (2) describes the relationship of salinity with time that occurred during the 24 hr salinity decline phase of our experiments. Our experimental starting salinity of 36 was used for these calculations.

3 | RESULTS

3.1 | Mortality

The rate of salinity decline was a significant predictor of mortality after the initial 24 hr salinity decline in the Probit regression model (z-statistic =−6.971, p <.001) and the model predicted that the rate of decline resulting in 50% mortality was 15.6%/hr (95% confidence limits 13.9-17.8%/hr; Figure 2a). This rate of salinity decline was calculated to result in an ES of 0.86 with the rates for the 95% confidence intervals estimated to result in salinities 1.28 and 0.50 respectively. The rate of salinity decline was also a significant predictor of mortality (z-statistic =−8.087, p <.001) for the combined treatment (24 hr of salinity decline and 5 days of exposure to low salinity) with an 8.0%/hr decline predicted to result in 50% mortality (95% confidence limits 6.9-9.7%/hr; Figure 2b). This rate of salinity decline was calculated to result in an ES of 5.2 with the rates for the 95% confidence intervals calculated to result in salinities of 6.95 and 3.48 respectively. The rate of salinity decline predicted to result in 99% mortality due to the effects of the combined treatment was 15.7%/hr (95% confidence limits 13.0-21.5%/hr; Figure 2b). This rate of salinity decline was estimated to result in an ES of 0.82 with the rates for the 95% confidence intervals estimated to result in salinities 1.58 and 0.21 respectively.

3.2 | Aerobic metabolic rate

Aerobic metabolic rates of juvenile EKP ranged from 0.44 to 4.04 mg and showed a significant nonlinear response (Figure 3a) to the rate of salinity decline ($F = 3.49$; equivalent degrees of freedom (edf) 8.54; $p < .001$), with 25.6% of the observed deviance (as a measure of goodness of fit) in metabolic rate explained by the rate of salinity decline. For rates of salinity decline < 6%/hr (ES. > 8.5), the modelled aerobic metabolic rate was close to the estimated intercept of 1.81 mg O_2/g/hr (Figure 3a). The modelled aerobic metabolic rate increased rapidly once the rate of salinity decline exceeded ~6%/hr (ES < 8.5) and peaked at ~3.3 mg O_2/g/hr when the rate of salinity decline was ~7.5%/hr (ES ~6; Figure 3a). As rates of salinity decline increased beyond 7.5%/hr, the modelled aerobic metabolic rate declined to less than the estimated intercept with the slowest modelled rate of 1.3 mg occurring for rates of salinity decline ≥9.5%/hr (ES < 3.6; Figure 3a). There was a negative linear relationship between somatic condition and metabolic rate ($F = 13.15$; edf 1; $p < .001$; Figure 3b). The animals with the poorest somatic condition had the fastest aerobic metabolic rates (Figure 3b) and the slope of the line (Figure 3b) indicated that the metabolic rate of prawns decreased at a rate of −0.12 mg O_2/g/hr per unit of decrease in somatic condition.

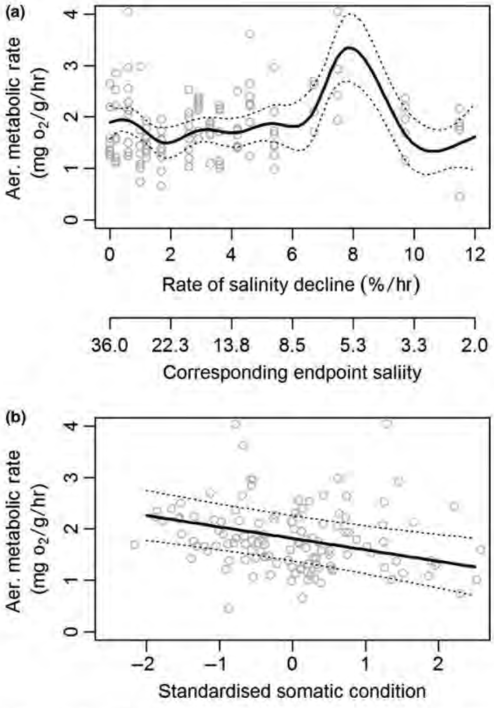

FIGURE 3 Fitted GAM reflecting the effect of the rate of salinity decline and somatic condition on metabolic rate for juvenile EKP. The solid line indicates the modelled aerobic (abbreviated as Aer.) metabolic rate across the range of salinity treatments (a), and across prawns of different somatic condition measured using standardised residuals from the carapace length – dry weight relationship (b). Dashed lines are 95% confidence intervals and grey circles are measured values

3.3 | Water content

The water content of prawns showed a significant nonlinear response (Figure 4) to the rate of salinity decline ($F = 11.90$; edf 5.39; $p < .001$), with 34.8% of the observed deviance (as a measure of goodness of fit) in prawn water content explained by the rate of salinity decline. Prawn water content generally increased alongside the rate of salinity decline, resulting in a negative relationship with the ES (Figure 4). As rates of salinity decline increased from ~2%/hr (ES ~22.3) to ~3%/hr (ES ~17.5), prawn water content increased from ~79% to ~81% (Figure 4). Prawn water content remained close to 81% until rates of salinity decline approached 7%/hr (ES ~6.7), beyond which water content began to increase. Prawns that experienced rates of salinity decline faster than 9%/hr (ES < 4.2) had the greatest water content, with water comprising ~4% more of their body mass than prawns that had experienced rates of salinity decline < 2%/hr (ES > 22.3; Figure 4).

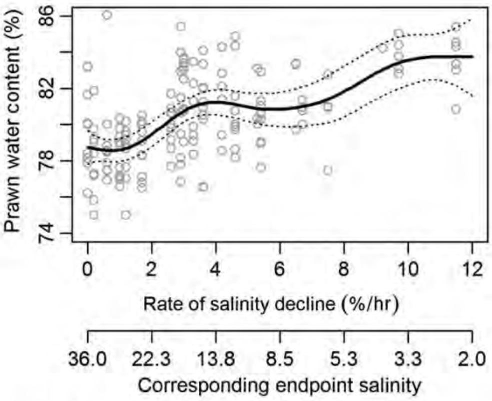

FIGURE 4 Fitted GAM reflecting the effect of the rate of salinity decline on the water content (%) of surviving prawns. The solid line indicates the modelled per cent water content across the range of salinity treatments, dashed lines represent 95% confidence intervals and grey circles are measured values

4 | DISCUSSION

Juvenile EKP responded differently throughout the range of salinity treatments tested. Low rates of mortality, uniform aerobic metabolism and a largely constant water content of prawns that had been exposed to a salinity decline < 6%/hr (ES > 8.5) suggest that EKP have some physiological plasticity to deal with both the rate of change in salinity and the depressed endpoint salinities. This agrees with the work of Dall (1981), who found a near-constant blood osmotic concentration of juvenile EKP kept within this same salinity range.

Aerobic metabolism did not increase for prawns exposed to salinity declines < 7%/hr (ES > 7), which suggests that osmoregulation did not require a measurable increase in energy expenditure, despite the prawns being in water salinities below their isosmotic point of 28 (Dall, 1981). It is possible that increased energetic costs of osmoregulation may have occurred, but the energy required was reallocated from another process instead of increasing the total rate of aerobic metabolism (see review by Guderley & Pörtner, 2010). Alternatively, the prawns may have altered the permeability of their boundary structures (i.e. gill membranes) and were using a near-passive form of osmoregulation (Péqueux, 1995) before aerobic metabolism was measured. Another potential explanation for the observed stability of aerobic metabolic rate could be the cell volume regulatory response (CVR; see reviews by Strange, 1993; Henry, 1995; Henry, Lucu, Onken & Weihrauch, 2012), as use of the CVR response needs not be accompanied by increases in metabolic rate (Emerson, 1969). In this process, cells undertake extensive nitrogen metabolism and cell osmolarity is then maintained through excretion of small nitrogenous species along with the obligated water that accompanies it (Henry, 1995; Henry et al., 2012; Strange, 1993).

Aerobic metabolic rate increased by up to ~50% and prawn water content by up to 4% for prawns from rates of salinity decline >7%/hr (ES < 6.7), which indicated they were potentially experiencing osmotic stress (see review by Romano & Zeng, 2012). This aligns with results of increased aerobic metabolic rates (Dalla Via, 1986; Pillai & Diwan, 2002; Shinji, Okutsu, Jayasankar, Jasmani & Wilder, 2012) and increases in body water (Chen & Lin, 1994, 1998; Chen, Lin, Ting & Lin, 1995) for other penaeid species upon exposure to lowered salinity. The increase in aerobic metabolic rate may be associated with osmoregulatory functions such as higher activity of ion pumps within the gills and other organs (Lucu & Pavičić, 1995; Piller, Henry, Doeller & Kraus, 1995; Siebers, Leweck, Markus & Winkler, 1982) and/or increased activity of the CVR response (Born, 1968; Denne, 1968; Kamemoto & Tullis, 1972; Lockwood, 1961; Pillai & Diwan, 2002; Spaargaren, Richard & Ceccaldi, 1982). Increased metabolic rate in association with a greater osmoregulatory response or utilisation of the CVR response may incur considerable energetic costs and rapid depletion of stored energy pools within the animals if the resupply of energy is not adequate (Dalla Via, 1986; Deaton, Hilbish & Koehn, 1984). Prawns that had the fastest metabolic rates had the lowest somatic condition, which suggests a depletion of energy stores. Observations of food consumption revealed that prawns that had been exposed to rates of salinity decline > 7%/hr (ES < 6.7) ate approximately 50% less than individuals from less severe salinity treatments, which suggests that the lowered salinity may have been affected their appetite or digestive system. Decreases in food consumption have been observed for other penaeid species when exposed to low salinity (Prangnell & Fotedar, 2005; Wang, Ma, Dong & Cao, 2004). If prawns were to survive such a period of low salinity, then the low food intake and high metabolic costs during this time could potentially have implications for their growth.

Osmoregulatory failure and associated osmotic stress during the additional 5 days of exposure to low salinity after experiencing rates of salinity decline > 8%/hr (ES < 5) is the likely cause for the high rates of mortality (> 50%) observed. Prawns that survived exposure to these rates of salinity decline and corresponding ES' had water comprising up to an additional 4% of their body mass and the slowest aerobic metabolic rates of all prawns in this study. The prawns with depressed rates of aerobic metabolism may have been at a point of metabolic preservation only and were attempting to survive until the return of more favourable conditions by only expending the minimum amount of energy required for somatic maintenance, placing them in the pessimism or lethal ranges of the energy-limiting stress tolerance limits concept (Sokolova, Frederich, Bagwe, Lannig & Sukhotin, 2012). Alternatively, they may have been experiencing metabolic arrest, where metabolic rates were depressed even lower than that which is required for somatic maintenance as a mechanism to stretch out available energy resources even further (Marshall, Dong, McQuaid & Williams, 2011; Sokolova, Bock & Pörtner, 2000; Sokolova & Pörtner, 2001; Sokolova et al., 2012).

A salinity decline of 15.6%/hr (ES < 0.8) over 24 hr was predicted to cause 50% mortality in the model; however, a similar decline was predicted to cause 99% mortality due to the combined effects of salinity decline and exposure to low salinity for 5 days. The estimate of salinity at complete mortality (~0.8) is close to the estimate of Dall (1981) who suggested the lower threshold for juvenile EKP was a salinity of ~3. This minor difference may be due to differing methodology between the two studies, as Dall (1981) used a series of daily stepwise reductions in salinity over up to 7 days, resulting in an extended time period that the juvenile EKP were exposed to low salinity compared to this study. However, Dall (1981) did not report the length of exposure that resulted in total mortality, which complicates direct comparison between the two studies. At any rate, both studies suggest that juvenile EKP can osmoregulate across a fairly broad range of salinities, although it appears this ability may be lost as prawns mature (Dall, 1981).

4.1 | Implications for the population and fishery

Within many estuaries, a reduction in salinity from near full marine levels to near fresh water (salinity ≤ 1) would likely only occur because of an extreme flood. In such a situation, a reduced salinity environment would be expected to continue until the catchment is sufficiently drained and a regular tidal hydrological regime can return (Blöschl & Sivapalan, 1997; Robinson & Sivapalan, 1997). Such an occurrence could explain the reduced EKP catch observed following the widespread flooding of south-eastern QLD in 2011 (Prosser & Doyle, 2014). Events that cause large-scale flooding have occurred numerous times in recent years (e.g. BoM., 2007, 2015) and in 2015 an example of the type and magnitude of event that exceeded the critical values presented in this study occurred.

In April 2015, a severe east-coast low-pressure system affected New South Wales, Australia. Large volumes of rain fell (436 mm fell at Belmore Bridge, Maitland; recorded over 21 and 22 April 2015), which resulted in widespread flooding, particularly in the catchment of the Hunter River (−32.904898, 151.777886); an important nursery for EKP (Taylor, Fry, Becker & Moltschaniwskyj, 2017; Taylor, Smith, Boys & Whitney, 2016). Floodwaters caused a rapid reduction in salinity from ~35 to 0 in less than 24 hr at the location where prawns used in this study were collected (Figures 5 and 6; M.D. Taylor, unpublished data). The change in salinity relative to time had a negative exponential relationship (Figure 6) which matched the dilution curves for the salinity treatments used in this study, validating the methodology as a realistic simulation of what can occur in an estuary subjected to prolonged, heavy rainfall. The rate of salinity decline within the Hunter River estuary in this event equated to a decline of 44.5%/hr (ES of 0 in < 24 hr; Figure 6), which far exceeded the rate at which immediate 50% mortality was predicted to occur (15.6%/hr; ES 0.8). The threshold for 99% mortality was also exceeded, both in terms of the rate of salinity decline (15.7%/hr) and in the duration of exposure to low salinity (5 days of exposure to salinity ~0.8) as the downstream flow of floodwaters maintained freshwater conditions for 8 days before any increase in salinity was recorded (Fig. 5). Therefore, it is conceivable that juvenile EKP within the estuary may not have survived this event and it appears possible that large magnitude floods could adversely affect cohorts of juvenile EKP. An indication that mortality may have been caused by this event can be found in commercial catch statistics for the adjacent ocean fishery for EKP that is fed by recruits from the Hunter River (see Ruello, 1975). In this area, April and May usually yield the greatest catches of EKP compared to other months, but average catch in April/May 2015 saw a ~60% drop in catch to ~7.5 t, relative to the April/May average across 2011-2014 and 2016 (~18.5 t; New South Wales Department of Primary Industries—Fisheries Catch Statistics Database).

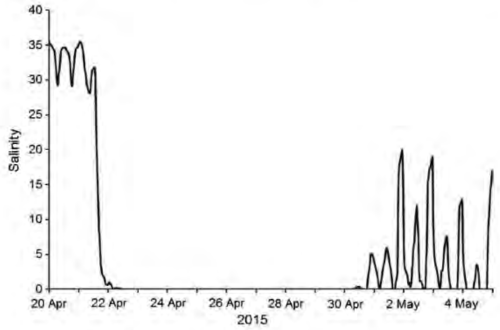

FIGURE 5 Salinity data collected from the benthos (approximately 4.5 m deep) of the main channel of the Hunter River estuary (−32.904898, 151.777886), near the Hexham Bridge (M.D. Taylor, unpublished data), for the days surrounding a severe low-pressure system that affected the catchment area between the 21 and 22 April 2015. Data were recorded continuously, with readings taken at half-hourly intervals

It is possible that EKP could alter its behaviour during reduced salinity events to escape unfavourable conditions. Renaud (1986) demonstrated that both brown shrimp *Penaeus aztecus* (Ives) and white shrimp *Penaeus setiferus* (L.) actively avoided low dissolved oxygen water and it is conceivable that all Penaeidae display a similar response to salinity. If this led to early emigration from the estuarine nursery (i.e. at a smaller size than when emigration would usually occur), it could potentially have consequences for growth, survival and harvest of the species (e.g. Witzell & Allen, 1982). Another consideration is that during minor to moderate flows, a lens of denser, more saline water may remain at depth and provide a refuge for prawns from the lower salinity water at the top of the water column. There is little published evidence to support these points, but they pose additional questions that could be examined in the future.

4.2 | Conclusion

This study provides evidence that rapid salinity declines over 24 hr due to flooding could compromise the survival of juvenile EKP, potentially causing a subsequent reduction in recruitment to the fishery. As both the frequency and intensity of large-scale flood events is predicted to increase within the geographical range of EKP due to the changing climate (Pachauri et al., 2014), the interannual variability of the EKP fishery may also increase as a result. By monitoring salinity within nursery habitats for EKP, it may be possible to make rapid, real-time predictions on how changes in salinity may affect EKP populations. This offers the potential for more adaptive management of the fishery in response to flooding. To our knowledge, this study is the first salinity tolerance experiment that produced a dilution curve that is directly comparable to that which occurs during flooding of the environment

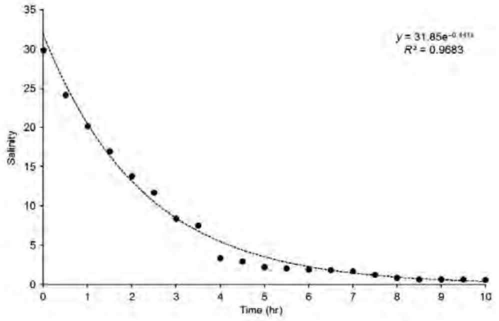

FIGURE 6 Salinity relative to time (hr) measured at the logger station described in Figure 5, following the onset of the salinity decline at ≈12:43 on 21 April 2015 until the salinity approached zero at 22:40 (10 hr later) on the same day

of the focal species. This approach is particularly useful because direct measurement of an organism's response to environmental change during severe flood events is often logistically difficult.

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Appendix 6 – Recruitment and connectivity influence the role of seagrass as a penaeid nursery habitat in a wave dominated estuary.

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Recruitment and connectivity influence the role of seagrass as a penaeid nursery habitat in a wave dominated estuary

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HIGHLIGHTS

- Abundance of prawns was affected by distance to the mouth, seagrass percent cover and temperature.
- Abundance depended on wind-driven currents during the recruitment season.
- Abiotic processes driving abundance ultimately determined the nursery role of habitat.

GRAPHICAL ABSTRACT

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ABSTRACT

Estuaries provide a diverse mosaic of habitats which support both juveniles and adults of exploited species. In particular, estuaries play an important role in the early life history of many penaeid prawn species. This study used a combination of stable isotope ecology and quantitative sampling to examine recruitment and the nursery function of seagrass habitats for Eastern King Prawn (*Penaeus* [*Melicertus*] *plebejus*), and the processes that contributed to this nursery role. Stable isotopes were used to assign prawns joining the adult stock to putative nursery habitat areas within the estuary. Emigrating prawns originated from only 11 of the 20 sites surveyed. Of these, 8 sites were designated as Effective Juvenile Habitat (EJH), and 5 sites designated as Nursery Habitat (NH). The contribution of individuals from different nursery areas to the adult stock was related to both the abundance of prawns within an area and the distance to the mouth of the estuary, and with the exception of 1 site all EJH and NH were located in the northern section of the estuary. Quantitative sampling in this area indicated that prawns were present at an average density of 165 ± 11 per 100 m^2, and density formed non-linear relationships with the distance to the mouth of the estuary, seagrass cover and temperature. Prawn size also formed non-linear relationships with prawn density and seagrass cover. Spatial patterns in abundance were consistent with wind-driven recruitment patterns, which in turn affected the nursery role of particular areas within the system. These findings have implications for targeted fishery restoration efforts for both Eastern King Prawn and other ocean spawned species in wave dominated estuaries where circulation is primarily wind-driven.

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1. Introduction

Successful recruitment depends on an adequate supply of eggs and larvae, availability of important habitats that maximise growth and minimise mortality, and connectivity between important habitats used across an organism's life history. Identifying important juvenile habitats is a key element of describing the recruitment cycle and has been the subject of a concerted research effort over previous decades. Estuaries are important nursery grounds and in more recent years research has sought to classify estuarine habitat as *nursery habitat* (habitat that makes a greater than average contribution-per-unit-area to the adult population, Beck et al., 2001), and *effective juvenile habitat* (habitat that makes a greater than average contribution to the adult population, Dahlgren et al., 2006). Consequently, determining whether a particular estuarine habitat functions as a nursery or effective juvenile habitat for a particular species involves quantifying this contribution. This can be achieved for fish by assigning adults to putative juvenile habitats on the basis of otolith elemental composition (Gillanders and Kingsford, 2000). Recently, progress has also been made using the stable isotope composition of muscle tissue to allow assignment of migratory species which lack permanent hard parts (e.g. crustaceans) to putative nursery habitats (Taylor et al., 2016b). Such research should ultimately improve how we manage habitats for exploited crustacean species, and the fisheries that depend on them.

Estuaries offer a variety of productive habitats to support juveniles of both estuary and ocean-spawned species. Ford et al. (2010) recently introduced the concept of settlement 'hotspots' in estuaries, and the impact that a greater supply of recruits can have in shaping which habitats are of high nursery value. This is particularly important for coastally spawned species, which often rely on favourable hydrographic conditions for advection to an appropriate settlement site (Forward et al., 2004; Hannan and Williams, 1998). Consequently, connectivity and supply-side ecology (Lewin, 1986) are fundamentally important in the role and function of estuarine habitats as nurseries (this is further reviewed in Sheaves et al., 2015).

There has been a substantial loss of estuarine fish habitats, including many potential fish nursery habitats in the last two centuries. Barbier et al. (2011) report a worldwide reduction in seagrass, saltmarsh and mangrove of 29%, 50% and 35% respectively. In Australia this may be as much as 45,000 ha of seagrass (Walker and McComb, 1992), and in New South Wales ~72% of the 'prime fish habitat' (62,000 ha, including saltmarsh and mangrove) that was present prior to European settlement has been lost (Rogers et al., 2015). Recent work in Australia and elsewhere has identified habitat restoration and rehabilitation as one of the few avenues of management whereby large gains in fisheries productivity can still be made (Sheaves et al., 2014). With such significant areas of habitat which can potentially be restored, prioritisation on the basis of fisheries outcomes is one approach to targeting restoration. In Australia, case studies indicate that restoration efforts targeted at enhancing valuable penaeid prawn species are likely to yield substantial economic benefits (Creighton et al., 2015). Effective targeting, however, relies on a comprehensive understanding of how aquatic organisms use estuaries, which habitats serve an effective nursery function, and where such habitats are located.

Penaeid species are valued for aquaculture and wild harvest across the world (Turner, 1977), usually representing high-value product. These species display a range of life-history strategies, but many commercially important species have Type-I or Type-II life cycles which include an estuarine nursery phase (Dall et al., 1990). Eastern King Prawn (*Penaeus* [*Melicertus*] *plebejus*) is one of the most valuable prawn species exploited off eastern Australia, harvested primarily from offshore trawl fisheries operating in northern New South Wales and southern Queensland. The species also spawns in this region (Montgomery et al., 2007), the larvae are subsequently transported south in the East Australian Current, and postlarvae are transported into estuaries (Rothlisberg et al., 1995). The species appears to be highly reliant on shallow littoral habitats in estuaries as nurseries (Halliday, 1995; Young, 1978), especially over summer, and can use different estuarine habitats to varying degrees (Ochwada et al., 2009). Following the nursery phase, prawns undergo a predictable emigration from the estuary during the last quarter of the lunar cycle (Racek, 1959), followed by a northward migration back to the spawning grounds (Braccini et al., 2012).

While the estuarine nursery phase of Eastern King Prawn is well described in its northern distribution, little is known about recruitment and the nursery function of different habitats in the southern estuaries which supply a large portion of the exploited stock (Montgomery, 1990). Using the largest coastal lake on the eastern Australian coast as a study system, we aimed to quantify the nursery role of different areas within the estuary by:

1. Conducting an estuary-wide survey of putative nursery habitat areas using a stable isotope-based assignment approach, and using this information to identify key nursery and effective juvenile habitats;
2. Comparing the nursery value with juvenile density and connectivity attributes of those areas;
3. Using targeted quantitative surveys to further resolve patterns of distribution observed in the broad-scale analysis, and factors driving this distribution.

2. Materials and methods

2.1. Study area

This study was conducted in Lake Macquarie, New South Wales (−33.09°, 151.66°), a large, immature, wave dominated barrier estuary (Roy et al., 2001), with a waterway area of 114 km^2. There are extensive seagrass beds, dominated by *Zostera capricorni* and *Posidonia australis*, but minimal intertidal and submerged rocky reef area. The estuary catchment is moderately developed and two power stations draw lake water for their condenser cooling systems, discharging warm water back in the southern half of the lake. The lake has a fairly stable salinity regime; however the power stations can exert a considerable influence water temperature (see Taylor et al., 2016a), which varies seasonally. The large lake exits to the sea through the Swansea Channel, a narrow channel of about 5 km in length, which is only 140 m wide at its narrowest point. Consequently, large volumes of water pass through this constriction on each tidal cycle, and emigrating Eastern King Prawn are intensively fished by recreational anglers in this channel over the summer using dip nets from boats (the most intensive fishing occurs during the months of January–March).

2.2. Sampling design and collection

Sampling was done from January 2014 to March 2015. The study design had two components: an estuary-wide survey (corresponding with Objectives 1 and 2), which was followed by a targeted quantitative survey, informed by the results of the estuary-wide survey (corresponding with Objective 3).

2.3. Estuary-wide survey of putative nursery habitats

The first component occurred during the first season of project (January–March 2014) and primarily focussed on using stable isotope composition to identify the source of adults emigrating from the estuary. Twenty putative nursery habitat areas were sampled around the lake system for juvenile Eastern King Prawn (EKP, Fig. 1). At each area, during the last quarter of the January and March lunar months, four ~100 m tows were done with a 26B-6C sled net (0.75 × 0.45 m mouth, 4 m length, 26 mm diamond mesh body and 6 mm octagonal mesh codend). A GPS waypoint was marked at the start and finish of each tow (to calculate tow-length), and water quality (temperature, salinity, dissolved oxygen and turbidity) was recorded at each site. Sled samples were immediately placed on ice and frozen for laboratory processing

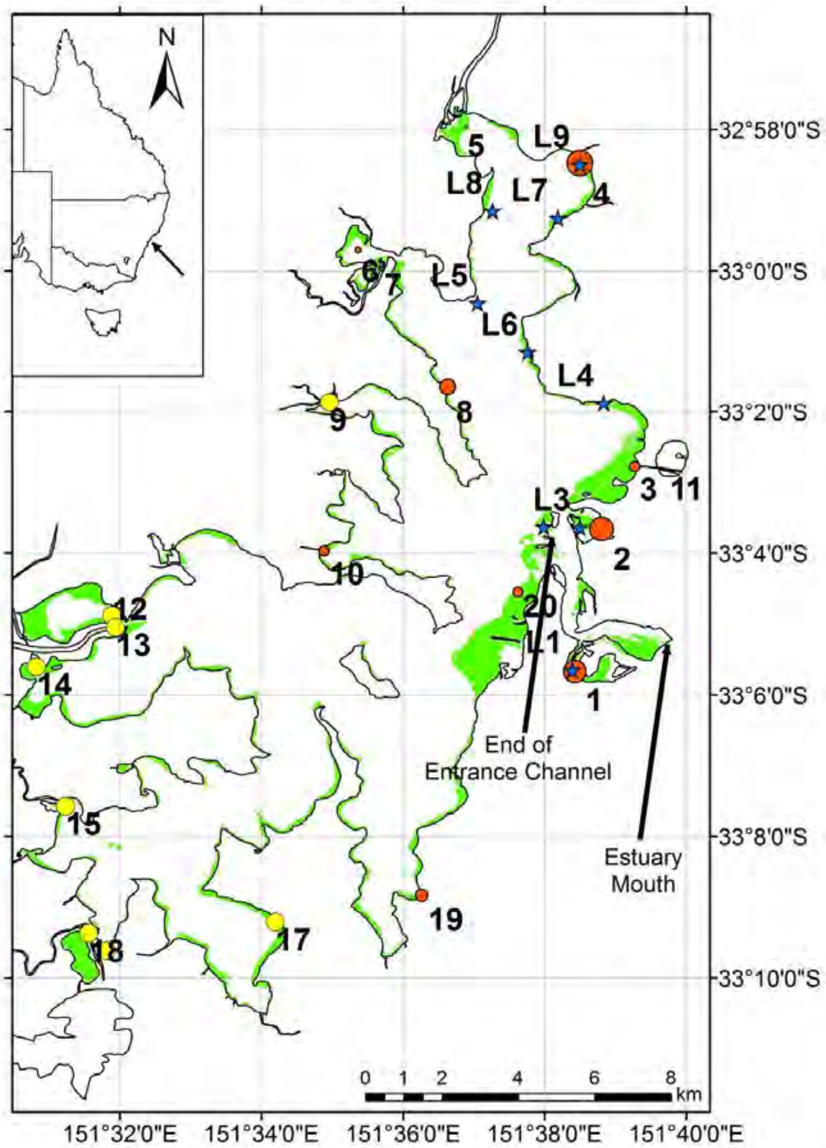

Fig. 1. Map of Lake Macquarie showing seagrass habitat (shaded in green), sites sampled for the estuary-wide survey (labelled by number), and locations sampled for the targeted quantitative survey are shown (indicated by stars, and numbered with an L prefix). Red circles provide a relative indication of the proportional contribution of a site to emigrating prawns captured at the mouth of the estuary, where larger red circles indicate a higher contribution (Table 1, note that the circles for sites 7 and 11 are vanishingly small). Yellow circles indicate sites at which no Eastern King Prawn were captured during the estuary-wide survey. The mouth of the estuary is to the east where indicated. Sites 11, 12 and 18 were inside small, shallow lagoons that were linked to the main lake by culverts or channels, and sites 7 and 13 were inside tributaries to the main lake.

(described below). In addition, Eastern King Prawn were collected using dip nets at the mouth of the estuary (Fig. 1) as they emigrated to the sea on 3–6 nights in each lunar month between the 7th and 17th day of the lunar cycle (Racek, 1959). Following the design of Taylor et al. (2016b), these samples were used as a proxy for prawns joining the adult population, and thus the habitats from which these emigrating prawns originated was used to assess the relative contribution of habitats within the estuary to the offshore adult stocks.

Prawn samples were identified to species, and the head and proventriculus dissected out of each animal to prevent contamination of the isotopic composition by recently consumed food items. Three composite samples for each site were prepared for stable isotope analysis, and each composite contained equal quantities of muscle tissue from six individual prawns. This combination (3 samples containing 6 individuals) provided an optimal trade-off between precision error and the ability to produce average site-specific signatures (Fry et al., 2008). All emigrating Eastern King Prawn were prepared as individual samples (i.e. not composite samples). Samples (composite and individuals) were rinsed in distilled water for 10 min, dried at 60 °C for ~48 h, and the isotopic composition (^{15}N and ^{13}C) measured on a Sercon 20–20 isotope ratio mass spectrometer (IRMS, Cheshire, United Kingdom). Delta values were calculated relative to international standards using standard methods (Fry, 2006). Measurement precision of ± 0.09‰ and ± 0.05‰ for $\delta^{15}N$ and $\delta^{13}C$ respectively was determined through repeated measurements of internal standards.

The composite isotopic composition was used to calculate a Bray-Curtis similarity matrix between sites, and was analysed using a single factor PERMANOVA (PRIMER-E, Anderson, 2001). Emigrating prawns were assigned to putative nursery habitat areas using the distance-based approach outlined in Taylor et al. (2016b). Briefly, the point-in-polygon technique of Smith et al. (2013b) was applied to the dataset, to refine the set of emigrating prawns which were to be tested on the basis of the completeness of the isotopic map used for assignment. If an individual emigrating prawn fell outside of the simulated region, it was excluded from further analysis. Subsequently, emigrating prawns which fell inside the polygon were assigned to a putative nursery habitat area on the basis of the minimum Euclidian distance between the emigrating prawn and the closest site in bivariate isotopic space (i.e. in each simulation the closest "site" in isotopic space was assigned as the "most likely" point of origin for the emigrating prawn). All isotope modelling was undertaken in Matlab (Mathworks).

The assignment data was used to determine whether each site may be considered a nursery habitat (NH) or effective juvenile habitat (EJH), using the classification system of Beck et al. (2001) and Dahlgren et al. (2006) respectively. The key difference between these two approaches is that the former assigns a nursery role on the basis of a greater than average contribution per-unit-area of habitat, whereas the latter approach relies only on a greater than average contribution from a particular area. The Nursery Habitat approach can exclude habitats that may have a small contribution-per-unit-area to adult populations, but may still be important for adult populations; the latter approach would include such habitats. For this reason we have included both approaches. The areas of the seagrass beds sampled were determined from the habitat shape files (from the NSW Department of Primary Industries habitat mapping database) in ArcGIS.

To address Objective 2, an index was calculated using the formula $AD_j = log_{10}\left(\frac{Abund_j}{Dist_j}\right)$, where AD_j is the index for putative nursery habitat area j, $Abund_j$ is the average standardised EKP abundance (# 100^{-2}, calculated from the gear dimensions, gear efficiency, and the actual distance sampled by the sled) for site j, and $Dist_j$ is the distance of site j to the mouth of the estuary (m). AD_j was regressed against the proportional contribution for each site using simple linear regression. A positive correlation between this index and the proportional contribution of a site was taken to imply that a higher abundance site closer to the mouth will contribute more than a higher abundance site further away from the mouth.

2.4. Targeted quantitative survey

To avoid confusion, areas sampled in the estuary-wide survey continue to be referred to as "sites", whereas areas sampled in the targeted quantitative survey are referred to throughout this manuscript as "locations". The targeted quantitative survey built on the results obtained in the estuary-wide survey, which indicated that the most important nursery sites were concentrated in the northern and eastern parts of the lake (see Results). Consequently, more intensive sampling was undertaken in seagrass beds in this area, targeting nine locations extending from the mouth to the north-eastern corner of the lake (Fig. 1).

An analysis of standard error as a proportion of the mean $(\frac{\sigma^2/\sqrt{n}}{\mu})$ was undertaken using means and variances estimated in the estuary-wide survey (Kingsford and Battershill, 2000). Seven replicates reduced proportional standard error from 0.9 to 0.35 of the mean for a scenario of average variance and this level of replication was logistically feasible, so $n = 7$, 70–100 m tows were used at each location. Each location was sampled during October, December and February, representing the main recruitment season for EKP in the estuaries of New South Wales (Racek, 1959). As for the estuary-wide survey, water quality was recorded, and waypoints were marked at the start and finish of each tow to calculate tow length. In addition, ~200 m video transects were used to determine the percent cover of seagrass at each location. A GoPro Hero 3 camera was mounted on an extendable pole and immersed until it was just above the seagrass. The boat slowly traversed the transect at a speed of ~0.5 knots. Percentage cover was determined by playing the video and pausing it at 40 randomly determined frames throughout each clip (pilot studies indicated that analysis of 40 frames accounted for the majority of variation encountered during a transect). The percent coverage of vegetation of each species was measured in each frame. All sampling was conducted in *Zostera* beds, except sites 12, 15 and 20 (Table 1).

As for the estuary-wide survey, following capture the bulk sled samples were immediately placed on ice and later frozen. In the laboratory, EKP were identified and sorted from the bulk sample, measured for carapace length using digital callipers. Gear dimensions, tow length and gear efficiency estimates (M.D. Taylor, unpublished data) were used to standardise abundance estimates to number-EKP-per-hundred-square-metres (EKP 100 m^{-2}).

Data collected during the targeted quantitative survey was evaluated using two analyses. A $\log_{10}$ transformation was used to normalise abundance data, and all analyses were undertaken in R v. 3.2.0 (R Development Core Team, 2016). A generalised additive model (using the gam function) was used to evaluate spatial patterns in recruitment over the main recruitment season as a function of abiotic factors:

$$log_{10}Abund_i = \beta + s_i(Dist_i) + s_i(Seagrass_i) + s_i(Salinity_i) + s_i(Temp_i) + \varepsilon_i$$

$$\varepsilon_i \sim N(0, \sigma^2)$$

where $Abund_i$ is the standardised EKP abundance (# 100^{-2}) for sample i, $Dist_i$ is the distance to the mouth of the estuary (m), $Seagrass_i$ is the estimated percent cover of seagrass, and $Salinity_i$ and $Temp_i$ are abiotic measurements (salinity and temperature respectively) potentially affecting EKP abundance (Tyler, 2015), β is a constant, and ε_i is the normally distributed residual error. The potential factors driving prawn size were investigated using the model:

$$MedianL_i = \beta + s_i(Abund_i) + s_i(Seagrass_i) + s_i(Temp_i) + \varepsilon_i$$

$$\varepsilon_i \sim N(0, \sigma^2)$$

where $MedianL_i$ is the median carapace length of animals in sample i, and the other variables are as outlined above.

3. Results

3.1. Estuary-wide survey of putative nursery habitats

In the estuary-wide survey, Eastern King Prawn were captured from 12 of the 20 sites surveyed (Fig. 1), although other species of penaeid prawns were captured from other locations (mainly Greentail Prawn,

Table 1
Designation of Effective Juvenile Habitat (EJH) and Nursery Habitat (NH) on the basis of the contribution of sampled seagrass beds to Eastern King Prawn captured emigrating from the estuary, using the criteria specified in Dahlgren et al. (2006) and Beck et al. (2001). Contribution area^{-1} is a standardised measure of contribution by the area (ha) of the seagrass bed at each site, multiplied by 10^4. Also shown is the mean isotopic composition of each site ($n = 3$ composites), and water quality measurements taken during the estuary-wide survey (standard deviations included in brackets).

Site	Contribution*	Avg. $\delta^{13}C$	Avg. $\delta^{15}N$	Habitat	Area (ha^{-1})	EJH	Contribution area^{-1}	NH	Salinity	Turbidity (ntu)	Temp (°C)	DO (mg L^{-1})
1	0.151	13.9 (0.3)	9.0 (0.5)	*Zostera* sp.	28	YES*	53.82	YES*	36.6 (0.1)	2.0 (1.9)	24.3 (0.5)	7.8 (0.5)
2	0.164	13.1 (0.1)	9.0 (0.3)	*Zostera* sp.	14	YES*	121.17	YES*	35.9 (1.2)	7.1 (14.2)	23.9 (0.9)	6.3 (1.1)
3	0.069	12.3 (0.5)	6.2 (0.1)	*Zostera* sp.	64	YES	10.70	NO	37.4 (2.1)	3.2 (2.7)	24.6 (1.7)	7.0 (0.8)
4	0.178	16.1 (0.1)	8.3 (0.3)	*Zostera* sp.	29	YES*	61.38	YES*	35.3 (1.3)	12.1 (5.2)	25.9 (1.2)	5.8 (0.7)
5	0.014	20.2 (0.2)	9.3 (0.4)	*Zostera* sp.	42	NO	3.26	NO	32.1 (3.8)	17.3 (4.8)	26.8 (1.2)	6.4 (1.3)
6	0.041	18.1 (0.2)	7.6 (0.2)	*Zostera* sp.	17	NO	16.40	NO	34.3 (1.0)	10.1 (2.4)	26.1 (0.9)	6.3 (1.2)
7	0.000	18.0 (0.1)	6.8 (0.1)	*Zostera* sp.	15	NO	0.00	NO	34.6 (1.4)	10.5 (4.0)	25.8 (1.0)	5.7 (0.4)
8	0.110	14.9 (0.1)	8.6 (0.2)	*Zostera* sp.	37	YES*	29.62	YES	36.2 (0.4)	1.4 (1.5)	25.0 (1.0)	6.4 (0.8)
9	0.000	–	–	*Zostera* sp.	27	NO	0.00	NO	36.0 (0.2)	2.7 (2.7)	26.4 (1.3)	6.7 (0.2)
10	0.068	15.1 (0.3)	10.8 (0.5)	*Zostera* sp.	25	YES	27.36	YES	36.0 (0.3)	0.8 (1.7)	25.7 (1.6)	6.9 (0.2)
11	0.014	14.3 (0.1)	5.3 (0.1)	Macroalgae	65	NO	2.09	NO	38.0 (0.0)	5.2 (0.0)	27.0 (0.0)	7.0 (0.4)
12	0.000	–	–	*Halophila* sp.	7	NO	0.00	NO	35.5 (3.5)	10.9 (4.1)	27.6 (1.4)	6.2 (0.5)
13	0.000	–	–	*Zostera* sp.	19	NO	0.00	NO	34.8 (2.5)	3.2 (3.6)	27.9 (1.7)	6.5 (1.0)
14	0.000	–	–	*Zostera* sp.	8	NO	0.00	NO	36.3 (1.8)	4.8 (7.2)	27.0 (1.3)	7.5 (0.5)
15	0.000	–	–	*Halophila* sp.	1	NO	0.00	NO	35.6 (2.1)	4.2 (6.7)	27.4 (0.4)	6.2 (1) 0.0
16	0.000	–	–	*Zostera* sp.	96	NO	0.00	NO	35.5 (1.2)	2.2 (3.9)	30.9 (0.7)	5.8 (0.4)
17	0.000	–	–	*Zostera* sp.	102	NO	0.00	NO	35.9 (1.2)	3.1 (2.6)	25.3 (0.7)	6.4 (0.1)
18	0.000	–	–	*Zostera* sp.	160	NO	0.00	NO	36.9 (0.0)	17.1 (0.0)	23.9 (0.0)	6.5 (0.0)
19	0.087	15.1 (0.1)	7.7 (0.1)	*Zostera* sp.	52	YES	16.77	NO	35.3 (0.8)	6.5 (2.9)	24.8 (0.5)	5.6 (1.1)
20	0.065	14.0 (0.3)	6.7 (0.2)	*Halophila* sp.	58	YES	11.24	NO	35.7 (1)	0.9 (2.5)	24.3 (0.2)	6.7 (0.6)
Mean	0.048					Mean	17.69					

*Contribution is analogous to the proportion of emigrating adults assigned to sites on the basis of the estuary-wide analysis, but assumes that sites where no Eastern King Prawn were captured (sites 9, and 12–18) made a contribution of zero to the emigrating population. If this assumption is not made, these sites do not contribute to calculation of the mean, raising the mean Contribution and Contribution area^{-1} to 0.087 and 32.17 respectively. For comparison, those sites which remain designated as EJH or NH against these elevated means are indicated (*).

Metapenaeus bennettae, data not presented here). The composite isotopic composition of EKP showed separation between sites (Fig. 2), and all sites were significantly different from each other. The point-in-polygon analysis indicated that the origin of 84% of emigrating prawns captured at the mouth of the estuary could be described by the isotope map (Fig. 2). The remaining 16% of emigrating prawns were excluded from subsequent analyses. Overall, water quality did not differ substantially among sites (Table 1), however turbidity varied, with elevated readings from sites near the mouths of tributaries.

The proportional assignment of emigrating prawns to putative nursery habitat areas on the basis of isotopic composition showed that most numerically important nursery areas were located in the northern and eastern regions of Lake Macquarie (Fig. 1, Table 1). The highest contributing areas were sites 2 and 4, followed by sites 1 and 8. With the exception of site 19, putative nursery sites in the southern and western regions of the estuary had negligible or nil contributions to emigrating prawns (the magnitude of the differences are evident in Fig. 1 and Table 1). In addition, the proportional contribution of site 11, a productive, off-lake lagoon, was negligible (Table 1). The proportional contribution of emigrating prawns had a significant relationship with AD_i in the estuary-wide survey ($R^2 = 0.33$, $F_{1,10} = 4.98$, $P = 0.049$, Fig. 3). Assignment of nursery habitats (NH) and effective juvenile habitats (EJH) produced contrasting results. Sites 1, 2, 3, 4, 8, 10, 19, and 20 were all classified as EJH, whereas only a subset of these (sites 1, 2, 4, 8 and 10) were classified as NH (Table 1).

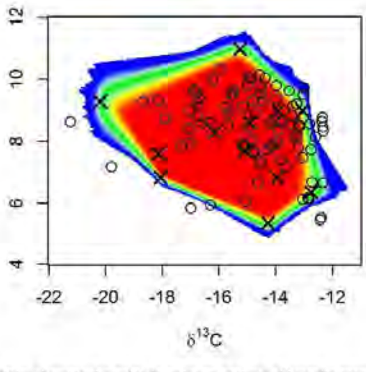

Fig. 2. Isotope biplot showing the point-in polygon analysis of juvenile prawns from putative nursery habitat areas, and emigrating prawn isotopic data. Isotopic composition of putative nursery habitat areas and emigrating prawns is indicated by crosses and open circles respectively.

3.2. Targeted quantitative survey

In the targeted quantitative survey, Eastern King Prawn (EKP) were present at a global average density of 165 ± 11 EKP 100 m^{-2} (mean ± SE), and sizes ranged from 2.7–29.1 mm carapace length (CL). The generalised additive model (GAM) explained ~30% of the deviance in the

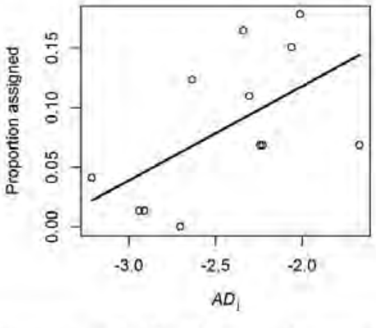

Fig. 3. Relationship between the AD_i and the proportional contribution of sites to emigrating Eastern King Prawn, for the estuary-wide survey.

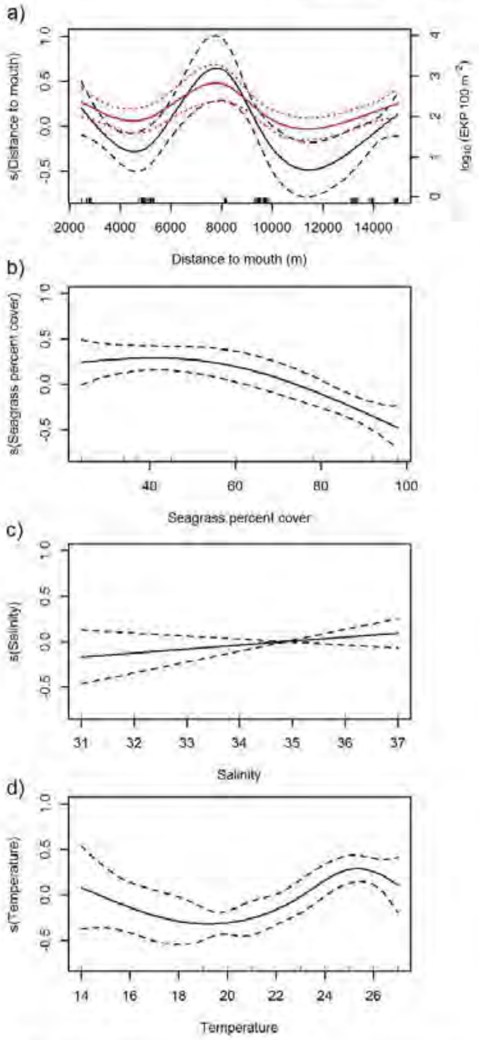

Fig. 4. Plots of smoothed predictor variables (solid lines) contributing to estimates of Eastern King Prawn abundance (*Abund*) in the northern section of Lake Macquarie, during the targeted quantitative survey: a) the distance to the mouth of the estuary (*Dist*. m); b) estimated percent cover of seagrass (*Seagrass*); c) salinity and d) temperature (°C). The *y*-axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits. Overlaid on panel a) is the actual effect of the distance to the mouth of the estuary on $\log_{10}$*Abund* (EKP 100 m^{-2}, solid red line) at a temperature of 25 °C, salinity of 35, and 80% cover of seagrass (values are shown on the secondary y-axis).

data, and indicated that prawn density had non-linear relationships with several variables (Fig. 3). Prawn density peaked at an intermediate distance-to-mouth of around 6000–9000 m from the lakes entrance (e.d.f. = 5.00, $F = 4.27$, P = 0.001, Fig. 4a). Seagrass percent cover varied among sampling locations in the targeted quantitative survey, with means ranging between 25 and 98%. Prawn density did not change among locations where cover was <50%, however increasingly denser seagrass cover was correlated with declining numbers of prawns (e.d.f. = 2.09, $F = 7.86$, P < 0.001, Fig. 4b). Salinity did not vary greatly (31–37) across the locations or times sampled, and was not significantly correlated with prawn density (e.d.f. = 1.00, $F = 1.31$, P = 0.253, Fig. 4c). In contrast, prawn density peaked at a temperature of about 25 °C (e.d.f. = 3.84, $F = 8.76$, P < 0.001, Fig. 4d), with lower temperatures at lower densities.

The GAM explained ~32% of the deviance in *MedianL*$_t$, used as a proxy for prawn size, which decreased with increasing prawn density (e.d.f. = 2.34, $F = 7.44$, P < 0.001, Fig. 5a) to densities of up to around 400 EKP 100 m^{-2}, although prawn size did not change at densities greater than this. Seagrass percent cover, however, positively correlated with prawn size (e.d.f. = 1.99, $F = 15.43$, P ≪ 0.001, Fig. 5b), indicating that the assemblage in denser seagrass beds tended to contain larger prawns. Temperature did not have a significant relationship with prawn size (e.d.f. = 1.00, $F = 3.22$, P = 0.075, Fig. 5c).

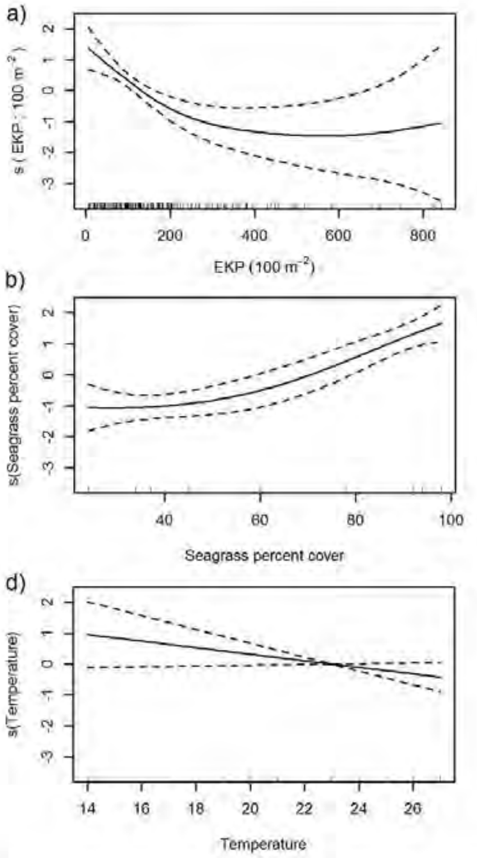

Fig. 5. Plots of smoothed predictor variables contributing to estimates of Eastern King Prawn size (*MedianL*) in the northern section of Lake Macquarie, during the targeted quantitative survey: a) the abundance of Eastern King Prawn (*Abund*, 100 m^{-2}); b) estimated percent cover of seagrass (*Seagrass*) and *c*) temperature (°C). The *y* axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits.

4. Discussion

In this focussed study on recruitment of Eastern King Prawn to juvenile nurseries, clear, asymmetric patterns in recruitment and emigration of Eastern King Prawn were evident. Seagrass beds in the northern basin of the estuary received greater numbers of recruits and there was a concentration of effective juvenile habitats and nursery habitats in this region. The supply of emigrating prawns from this area was generally related to an index reflecting abundance within the habitat (supply) and the distance from the mouth (connectivity), similarly to the relationships shown for penaeid shrimps in Blanco-Martínez and Pérez-Castañeda (2016). With the exception of one site, there was little evidence that seagrass beds in the southern basin of the lake received recruits or supplied individuals to the emigrating population, meaning it is unlikely that this region contains important nurseries for the species. Within the northern basin of the lake, the supply of recruits was greatest at intermediate distances from the estuary mouth, particularly in an area which includes several shallow seagrass covered embayments on the eastern edge of the estuary 2000–3000 m past the end of the entrance channel. A greater abundance of prawns was also associated with less seagrass, but conversely prawns sampled in denser seagrass tended to be larger. Finally, the effect of temperature on prawn abundance was likely a seasonal one, as the peak in abundance at 25 °C reflected the temperature in December (during the austral summer), which generally experiences high recruitment in New South Wales (Racek, 1959).

The findings are particularly relevant for three reasons. Firstly, the study applied a novel combination of stable isotopes and quantitative surveys to understand the nursery role of particular habitats across a broad spatial scale, which will be useful in exploring these concepts across other estuaries and species. Secondly, it explores the nexus between location and nursery function, and the importance of connectivity in driving recruitment outcomes for dispersive and migratory species (Sheaves et al., 2015). Finally, it provides several clear findings which should aid in the prioritisation of habitat rehabilitation and restoration for exploited penaeid prawns displaying Type-II life-cycles, for which restoration outcomes are high priority (Creighton et al., 2015).

While this is the first targeted survey of early juvenile Eastern King Prawn recruitment to seagrass habitats in south-eastern Australian estuaries, several other surveys have sampled the species in seagrass beds across the broader eastern seaboard. The most comprehensive work on the species was undertaken several decades ago in the Moreton Bay area as the commercial fishery for the species developed (Coles and Greenwood, 1983; Halliday, 1995; Young, 1975, 1978; Young and Carpenter, 1977), and this has been complemented with some more general studies of recruitment to seagrass in New South Wales that have measured the species (Bell et al., 1988; Worthington et al., 1992; Worthington et al., 1995). Multiple studies of different life stages have detected negative correlations between Eastern King Prawn abundance and distance-to-sea (Bell et al., 1988, working on juveniles; Coles and Greenwood, 1983, working on postlarvae and early juveniles; Young and Carpenter, 1977, working on newly settled postlarvae). In contrast, this study detected greatest abundance at intermediate distances from the mouth of the estuary. The negative relationship detected between juvenile abundance and seagrass percent cover has some support in the work of Halliday (1995) which suggested that juvenile Eastern King Prawn preferentially settled at greater densities in sparse seagrass habitat. A similar relationship has been found for Brown Shrimp (*Farfantepenaeus aztecus*) in *Zostera marina* beds (McCloskey and Unsworth, 2015), however Worthington et al. (1992) found no such relationship.

Placing the positive correlation between seagrass cover and the size of Eastern King Prawn in the context of the lower abundance measured in denser beds, points to the potential for density dependence occurring. This cannot be confirmed, however, without accounting for competing species which are occurring in the same habitats. Growth in *Farfantepenaeus* spp. was negatively related to density, whereby a fourfold increase in density led to a reduction in growth rate of about 25% (Pérez-Castañeda and Defeo, 2005). Loneragan et al. (2001) also showed a decrease in *Penaeus esculentus* growth at densities >8 individuals m^{-2}, alongside higher overall growth in higher biomass seagrass beds. An alternative explanation is a potential ontogenetic preference for denser beds as prawns grow. The experimental model of Smith et al. (2013a) provides a useful framework to further tease out the relationships between growth, density, space and food, to further understand the relationships observed here.

4.1. A conceptual model for wind-driven recruitment, and relationship to other studies

The observed patterns in Eastern King Prawn abundance among potential nursery habitat sites within Lake Macquarie, and the factors forcing water movements in this system, point to a conceptual model of hydrologically driven recruitment. Lake Macquarie is a tidal system with a permanently open mouth, and experiences rapid tidal currents up to 1.6 m s^{-1} along the entrance channel of the system (Fig. 1, Cox, 1995). However, at the western point of the entrance channel where it exits into the main lake, the tidal influence rapidly dissipates resulting in a tidal range of approximately ± 3–5 cm within the lake (Cox, 1995). In the lake body, winds from the south and south-east produce strong northward flowing currents (Cox, 1995), enhancing flow of oceanic water toward the north eastern edge of the lake (locations L3, L4 and L6), whereas wind from the north and west tends move water toward the entrance channel (Cox, 1995). Seasonal variation in wind conditions for Lake Macquarie across the study period is presented in Fig. 6, and shows that for the austral summer when recruitment occurs, the lake experiences predominantly easterly and south-easterly wind (direction 90–180°), and the wind is generally at its strongest.

As with many other systems, postlarvae initially enter the system on the flood tide, and are carried along the entrance channel by the strong tidal currents. At the end of the entrance channel, the wind conditions during the recruitment season (described above), are conducive to the transport of prawns from the end of the entrance channel into the northern section of the lake. This conceptual model of post larval transport mediated by both the tide and wind forcing largely describes the abundance patterns observed, and the concentration of recruits in the northern basins of the lake. Wind-forcing has similarly been recently implicated in recruitment patterns of Blue Crab *Callinectes sapidus* in Chesapeake Bay, USA (Biermann et al., 2016). It is quite likely that recruitment patterns form close temporal links with sporadic variation in wind patterns in wind-dominated systems like Lake Macquarie. The

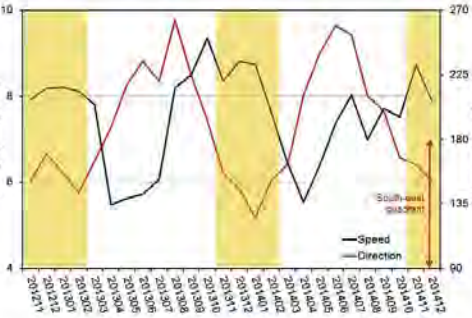

Fig. 6. Wind speed (primary y-axis) and direction (secondary y-axis) for Lake Macquarie over the course of the study period (data provided by the Australian Government, Bureau of Meteorology). The recruitment season for Eastern King Prawn is also indicated (shaded).

extent of this coupling could be further explored with sampling across finer temporal scales during the summer.

The concentrations of Eastern King Prawn in the northern basin of the lake are broadly similar to the distribution of coastally spawned larvae in Lake Macquarie reported in Hannan and Williams (1998), which showed substantially greater numbers of coastally spawned fish larvae *Acanthopagrus australis*, *Rhabdosargus sarba*, *Girella tricuspidata*, *Myxus elongatus*, (among other species) in the northern basin. A recruitment hotspot for coastally spawned fish larvae also occurs at a location corresponding to I.3 in the current study (Ford et al., 2010), and it was hypothesised that exceptional recruitment of coastally spawned species at this location was principally related to its vicinity to the high volume tidal channel. The most significant peak in abundance in Ford et al. (2010), however, was recorded in August when prevailing winds tend to be westerly (Fig. 6), and are above average strength. It may well be that this exceptional recruitment event resulted from depressed overall current velocity at this location created by the opposing forces of incoming tidal flow and wind currents. A limitation of the work of Ford et al. (2010) was that it was restricted to the entrance channel of Lake Macquarie; the current study indicates that complementary wind and tidal forcing may well enhance supply of recruitment hotspots further into the estuary. It would be of interest to develop the tidally-driven particle dispersal model used in Ford et al. (2010) to account for different wind-forcing scenarios.

4.2. Other potential contributing factors

In spite of the above conceptual model of wind-driven recruitment contributing to the observed patterns in abundance of Eastern King Prawn, it is important to mention other potential factors that could also have contributed to the overall patterns observed. Firstly, the southern basin of Lake Macquarie has a larger catchment and more significant tributaries the northern basin. Consequently, the influence of rainfall on surface salinity in this area may be more severe than experienced in the northern basin. This is potentially relevant, since Eastern King Prawn are a relatively stenohaline species and may experience mortality at lower salinities (Tyler, 2015). Having said that, Lake Macquarie is a marine dominated system (Hannan and Williams, 1998) and a significant rainfall event is required to alter the salinity of the lake. The salinity measured during the study was always in the optimal range for juvenile Eastern King Prawn (22–37, Tyler, 2015). Secondly, the temperature in the south-western basin of the lake can be highly influenced by thermal plumes radiating from two power station cooling water discharge points located adjacent to site 13 and 16, however, temperatures between 19 and 34 °C appears to have little effect on postlarval survival (Preston, 1985). The range of temperatures encountered in the estuary-wide survey was 21–32 °C, so assuming this relationship is similar for juvenile Eastern King Prawn, this is unlikely to be of any consequence.

4.3. Implications for management

Bell et al. (1988) suggests it is important that settlement habitats are distributed so as to capture the maximum number of settlement stage larvae or post-larvae, and where this does not occur populations of fish and decapods are susceptible to limitation through an inadequate supply of recruits. This has the potential to greatly affect the success of habitat rehabilitation efforts, but drivers of connectivity like seasonal wind forcing are not often taken into account (Sheaves et al., 2015). This study highlights the importance of understanding hydrographic characteristics of an estuary and its influence on the supply of recruits when planning targeted fisheries enhancements like habitat rehabilitation. For the Eastern King Prawn, seagrass rehabilitation efforts (such as replacement of swing moorings with seagrass friendly moorings, Demers et al., 2013) could prioritise areas between 6 and 9 km from the estuary mouth. This should maximise the supply of ocean spawned Eastern King Prawn recruits to the rehabilitated habitats over the main recruitment season. Considering the findings of Hannan and Williams (1998), this would likely lead to concomitant optimal impacts for other coastally spawned fishes. Conversely, such information is also important for identifying recruitment limitation to target stock enhancement efforts, particularly in coastal lakes. For example, in Lake Macquarie it is likely that while suitable habitats for coastally spawned prawns exist in the south-western portion of the lake, these areas are probably unlikely to receive recruits under most hydrographic scenarios. Similarly, the northern section of lake may remain recruitment limited in years where prevailing southerly winds do not occur over the recruitment season, so are unable to drive recruits further into the lake.

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Appendix 7 – The role of connectivity and physicochemical conditions in effective habitat of two exploited penaeid species

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Research paper

The role of connectivity and physicochemical conditions in effective habitat of two exploited penaeid species

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ABSTRACT

The value of estuarine habitats is often measured by their contribution to the adult component of the population, but a broader suite of attributes can also contribute to nursery function. Identifying and quantifying these elements allows habitat repair to be effectively targeted toward improving ecosystem function for desirable species. We present a study that incorporates stable isotopes and quantitative sampling to investigate the relative importance of different estuarine areas for juveniles of exploited prawn species within the context of habitat rehabilitation, and the potential drivers of these relationships. Eastern King Prawn (*Penaeus* [*Melicertus*] *plebejus*) and School Prawn (*Metapenaeus macleayi*) were studied for two years in the lower Hunter River estuary, on the temperate east coast of Australia. The higher salinity areas near the lower end of the estuary were most important for Eastern King Prawn, and marsh systems in the lower estuary were only important for the species where there was good connectivity with oceanic water. Areas along the estuary were important for juvenile School Prawn, especially marsh habitats, and relative abundance tended to increase with increasing distance along the estuary. Designation of effective juvenile habitat for School Prawn may have been affected by high fishing mortality in fished areas, but this requires further investigation. Salinity, depth, turbidity and distance along the estuary were all important indicators of prawn distribution. The implications of these patterns for current and future habitat rehabilitation in temperate Australia are discussed.

1. Introduction

Continued reliance on ecosystem services derived from estuaries has led to a new era of habitat protection, rehabilitation and restoration efforts in recent decades (Rogers et al., 2015). However, the relatively high cost of repair (e.g. Bayraktarov et al., 2016) gives impetus to the need to effectively target these efforts toward areas that are likely to produce the greatest benefits (for example, increases to fisheries productivity). Notwithstanding the role of habitat repair in managing coastal retreat (e.g. in North America, Scyphers et al., 2011), in some cases the most important ecosystem services derived from habitat repair are the increased productivity of high value exploited species (Creighton et al., 2015), but the greatest benefits will only be possible where repair is appropriately targeted based on species life-history patterns and recruitment dynamics. Consequently, estuarine habitat repair should take into account the relative nursery value of different areas within the estuary for species of interest.

The value of estuarine habitats is often measured by the contribution of recruits from these habitats to adult or exploited stocks (e.g. Beck et al., 2001; Dahlgren et al., 2006). This is a well-researched paradigm, but the mechanistic aspects contributing to habitat value needs greater attention. Sheaves et al. (2015) outline a set of attributes which contribute to the value of habitats, and discusses how combining various experimental and survey approaches can improve our assessment and ability to appreciate the interactions among the broader suite of attributes that can contribute to nursery function. A few of these attributes include the supply of natural recruits to a particular habitat (e.g. Taylor et al., 2017), physicochemical variation and the limitations imposed by an organisms physiology (e.g. Payne et al., 2015), structural habitat requirements of particular species (e.g. Ochwada et al., 2009), and connectivity between juvenile and adult or spawning habitats (e.g. Sheaves and Molony, 2001). Identifying and quantifying these elements will not only allow habitat repair to be effectively targeted, but will also help inform the structural requirements of repair necessary to improve or restore ecosystem function for desirable species.

Eastern King Prawn (*Melicertus plebejus*) and School Prawn (*Metapenaeus macleayi*) are two of the most valuable species of penaeid prawns exploited in eastern Australia. Both species display a penaeid

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Type-II lifecycle (see Dall et al., 1990), and rely on estuarine habitats during their juvenile phase. Adolescent prawns of both species display a predictable emigration from the estuary to the sea that is generally synchronised with the period around the last quarter of the lunar cycle, primarily during the months January – March (Racek, 1959; Ruello, 1971). Following emigration, School Prawn spawn in inshore areas usually adjacent to the mouth of the estuary from which they originated, or adjacent estuaries to the north (Ruello, 1977). In contrast, Eastern King Prawn move through the inshore area and migrate toward spawning areas further north (Montgomery, 1990). School Prawn are highly exploited in their estuarine and inshore phase (Glaister, 1978), whereas Eastern King Prawn are primarily exploited during their offshore migratory phase (Gordon et al., 1995). The abrupt and predictable emigration of prawns through the mouth of estuaries provides a useful bottleneck in space and time to concentrate sampling of adolescent prawns moving from estuarine nurseries to join the adult and/or exploited stock. Calculating the relative contribution of different areas or habitats within the estuary to these emigrating animals provides information useful for assessing nursery habitats within the estuary (Taylor et al., 2016), but as identified above this information will be most valuable when other attributes of the species-habitat relationship are also measured.

This manuscript presents a study on the relative importance of different juvenile habitats for exploited penaeid prawns within the context of habitat repair in temperate Australia, to better understand the outcomes of previous habitat rehabilitation efforts, and to inform future rehabilitation for the benefit of these species. Specifically, this study sought to:

- Evaluate putative effective juvenile habitats for penaeid prawns across the lower and mid-sections in the Hunter River estuary;
- Evaluate the distribution of juvenile penaeid prawns within the lower Hunter River estuary, and potential drivers of this distribution;
- Qualitatively evaluate the potential impact of habitat repair in the lower Hunter River estuary for exploited penaeid prawns.

2. Materials and methods

2.1. Study area

The Hunter River estuary is a wave-dominated barrier estuary located on the mid-northern coast of New South Wales, Australia (−32.9054, 151.7749). The estuary is fed by two major river systems, the Hunter River which drains the southern catchment, and the Williams River which drains the northern catchment. Both parts of the catchment are dominated by a combination of agriculture, forest and national park. The lower estuary is heavily urbanised and includes the world's largest coal export port. Despite this, the lower estuary has abundant mangrove and saltmarsh habitats (Fig. 1), which can be divided into three main areas: 1) Tomago wetland to the north; 2) Kooragang wetland, which is nested between the north and south arms of the lower estuary; and 3) Hexham wetland in the south. In addition, the estuary includes expansive shallow embayments located off the main channel in the north arm (Fullerton Cove and Fern Bay), and these are surrounded by extensive mangrove habitat (Fig. 1). There is no seagrass present within the estuary.

The bifurcate channels in the lower estuary, and the off-channel embayments (Fullerton Cove and Fern Bay) make the Hunter River estuary a hydrologically complex system. The south arm of the estuary is heavily tidally dominated and characterised by an oceanic salinity regime. The upstream point of connection with the north arm represents a network of deltaic islands interspersed by very shallow channels, and consequently there is little influence of brackish water from the middle and upper estuary into south arm. Conversely, the north arm has a relatively contiguous channel from the mouth along the entire estuarine gradient. Consequently, there is a much greater influence of freshwater inflow from the upper estuary and a clear salinity gradient along the north arm under regular conditions (Fig. 1). The estuary supports a substantial fishery, dominated by School Prawn (Ruello, 1973), but also provides habitat for juvenile Eastern King Prawn who later recruit into the offshore trawl fishery (Ruello, 1971). There is also considerable harvest of various finfish and crab species (Taylor and Johnson, 2016), with most fishing effort (for both fish and crustaceans) concentrated in the north arm of the estuary and the off-channel embayment's.

By the latter half of the 20th century the wetland systems in the lower Hunter River estuary had become severely degraded through development, grazing, and/or the installation of dykes and floodgates that removed connectivity between wetlands and the main estuary channels. Several rehabilitation projects have been carried out on these systems in recent decades, initially targeting the Kooragang wetland (undertaken from 1990 to 1996, Williams et al., 2000), followed by Tomago (undertaken from 2007 to 2011, Rayner and Glamore, 2010), and Hexham (from 2008 to 2013, Boys, 2016). These rehabilitation projects have largely involved restoring connectivity of these marsh and mangrove habitats to the estuary, thus allowing tidal flushing of the habitats. It is important to note that the repair of these locations (especially Tomago and Hexham) is relatively recent, and the systems are still undergoing changes which may have future implications for their productivity.

2.2. Sampling design and collection

Sampling for this study was conducted over the 2013/14 and 2014/15 austral summer and autumn. Sampling in both years included collection of material for stable isotope analysis (hereafter referred to as the stable isotope study), and in the second year sampling included a quantitative assessment of juvenile prawn abundance across the lower estuary. Noting the primary focus of this study was Eastern King Prawn, the rationale was to initially undertake a broader survey examining potential nursery value across the lower and middle sections of the estuary, and then use this information to conduct a more focussed quantitative survey in areas identified as important for this species. Consequently, the results from the first year stable isotope study were used to inform the quantitative assessment of prawn abundance in the second year, and thus sampling occurred across different spatial scales in 2014/15.

2.3. Stable isotope study on emigrating prawns

Stable isotopes were used to identify from which areas and repaired habitats in the lower estuary emigrating prawns originated (as per Taylor et al., 2016). This approach involved sampling prawns from putative nursery habitat areas to characterise the stable isotope signature of those areas, and assigning the origin of prawns captured as they emigrated from the estuary among those putative nursery habitat areas on the basis of their isotopic similarity. Eighteen putative nursery habitat areas were sampled across the lower estuary in 2013/14, and a subset of 13 of these nursery habitat areas were sampled in 2014/15 (Fig. 1). Samples for stable isotope analysis were collected from these putative nursery habitat areas in the last quarter of the January lunar month in the 2013/14 and 2014/15 season using ~100 m tows with a 26B-6C sled net (1 × 0.4 m mouth, 4 m length, 26 mm diamond mesh body and 6 mm octagonal mesh cod-end). Sled samples were immediately placed on ice and then frozen for laboratory processing. In addition, Eastern King Prawn and School Prawn were collected by trawler at the mouth of the estuary as they emigrated to the sea on 3–6 nights during the last quarter of the January and March lunar months. These samples were used as a proxy for prawns joining the adult population, and thus the areas from which these emigrating prawns originated were used to assess the relative contribution of areas

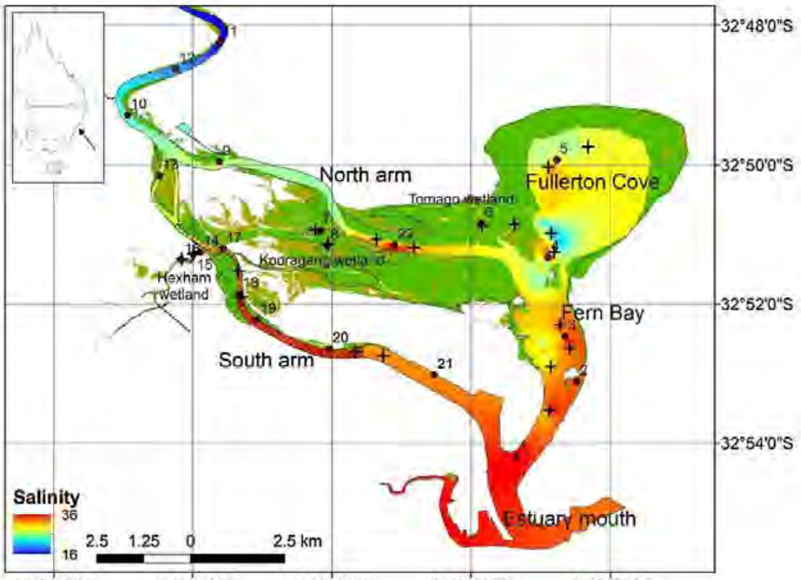

Fig. 1. Map of the Hunter River and associated saltmarsh (shaded in brown) and mangrove habitat (shaded in green). Putative nursery habitat areas sampled for isotope analysis across the estuary are indicated, and the numbers are cross-referenced with Table 1. Locations sampled for the quantitative study (in 2014/15) are indicated as crosses. A salinity surface interpolated from measurements collected throughout the study is also presented, and the colouring is described in the figure legend. Main features of the estuary referred to in the text are labelled, and the hatched area represents areas that are un-trawlable due the barriers to navigation for trawl vessels (low bridges). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

within the estuary to the adult component of the population.

In the laboratory, samples were thawed and the head and proventriculus dissected out of each animal to ensure the isotopic composition did not reflect that of recently consumed food items. Three composite samples (containing equal quantities of muscle tissue from six individual prawns) were prepared for stable isotope analysis from each area. This particular composite design (3 samples containing 6 individuals) was selected based on precision error and the ability to produce average area-specific signatures (see Taylor et al., 2016). All emigrating Eastern King Prawn and School Prawn captured from the mouth of the estuary were prepared as individual samples (i.e. not composite samples).

Tissue samples (composite and individuals) were prepared for stable isotope analysis by first rinsing in distilled water for 10 min, followed by drying at 60 °C for ~48 h. The isotopic composition (^{15}N and ^{13}C) was measured on a Sercon 20–20 isotope ratio mass spectrometer (IRMS, Cheshire, United Kingdom). Delta values were calculated relative to international standards using conventional methods (Fry, 2006). Measurement precision was determined through repeated measurements of internal standards, and were ± 0.09‰ and ± 0.05‰ for $\delta^{15}N$ and $\delta^{13}C$ respectively for samples collected in 2013/14, and ± 0.11‰ and ± 0.17‰ for $\delta^{15}N$ and $\delta^{13}C$ for samples collected in 2014/15.

Emigrating prawns were assigned to putative nursery habitat areas using a variation on the distance-based approach outlined in Taylor et al. (2016). The point-in-polygon technique (Smith et al., 2013) was initially applied to the dataset, to refine the set of emigrating prawns to be assigned based on the "completeness" of the isotopic map created from the putative nursery habitat areas. If an individual emigrating prawn fell outside of the simulated region, it was excluded from further analysis. Assignment was undertaken using the refined set of emigrating prawns. Firstly, the isotopic composition of each putative nursery habitat area was specified as a normal distribution, and each distribution was randomly sampled 1000 times and used to calculate the Euclidian distance between the emigrating prawn and each putative nursery habitat area in bivariate isotopic space. The most likely putative nursery habitat area in each simulation was determined on the basis of the minimum distance between the emigrating prawn and the habitat area in isotopic space. For each emigrating prawn, the results from all simulations were then used to determine the binomial probability that each habitat area was the source area, and the habitat area with the greatest probability was selected as the source area for the emigrating prawn. All isotope modelling was undertaken in Matlab (Mathworks, Natick, MA, USA). Finally, the assignment data was used to determine whether each area may be considered an effective juvenile habitat (EJH), using the classification system of Dahlgren et al. (2006) which assigns an area as EJH if it has a greater than average contribution to the adult component of the population.

2.4. Quantitative sampling of prawns across the lower estuary

Following evaluation of the assignment data from 2013/14 (described above), 20 sampling locations were identified that covered important source areas for emigrating Eastern King Prawn along with the three major rehabilitated marsh systems in the lower estuary were conducted, and additional sampling surveys that covered these areas was conducted. Each location was surveyed using nocturnal sled tows in last quarter of the November, January, and March lunar months over 2014/15, and four tows were undertaken at each location during each sampling event. Tows were undertaken using a 26B-6C sled net, with a GPS waypoint marked at the start and finish of each tow (to calculate tow-length). Depth and water quality (temperature, salinity, dissolved oxygen and turbidity) were recorded at each location during each sampling period. Bulk sled samples were immediately placed on ice and then frozen for later laboratory processing. Sample processing involved sorting and identifying all penaeid prawns from the thawed bulk sample, and then enumerating the individuals from each species. The dimensions of the gear, the actual length of each tow (derived from GPS waypoints), and nocturnal gear efficiency estimates for sampling on unvegetated habitats (0.48; M.D. Taylor, unpublished data) were used to standardise abundance estimates to number-per-hundred-square-metres (# EKP 100 m^{-2} for Eastern King Prawn; # SP 100 m^{-2} for School Prawn). It should be noted, however, that School Prawn are best sampled diurnally, and there may be some variation in catchability across the diel period. Consequently, School Prawn abundance estimates should only be considered as a relative measure (as opposed to an absolute estimate of abundance), as they likely represent an underestimation of the actual abundance.

To address Objective 2, quantitative survey data was evaluated using a generalised additive model (using the gam package). A log$_{10}$ transformation was used to normalise abundance data, and a number of variables evaluated:

$$\log_{10} Abund_i = \beta + s_{ik}(Dist_i) + s_i(Turbidity_i) + s_i(Depth_i) + \varepsilon_i$$

where $Abund_i$ was the standardised Eastern King Prawn or School Prawn abundance (# EKP 100 m^{-2} or # SP 100 m^{-2}) for sample i (each tow reflects a single sample). $Dist_i$ was the distance of the sample location to the sea (metres from the mouth of the estuary), and due to the differing relationship between various factors (such as salinity, Fig. 1) and the distance to the sea for the north and south arms of the estuary, splines were fitted to $Dist_i$ for the north arm and the south arm (denoted by k; North or South) separately. $Turbidity_i$ was the turbidity measured at the location during each sample, $Depth_i$ was the water depth at which the sample took place, β is a constant, and ε_i is the residual error. All analyses were undertaken in R v. 3.2.0 (R Development Core Team, 2016).

3. Results

3.1. Stable isotope study on emigrating prawns

Both sampling periods encompassed regular physicochemical conditions (i.e. the estuary did not receive excessive freshwater inflows during the sampling windows in either year). In both years, ^{13}C was depleted and ^{15}N was enriched as the distance to sea increased (similarly to patterns presented in Taylor et al., 2016; Fig. 2a and b). For the 2013/14 dataset, 87.2% of Eastern King Prawn and 93.5% of School Prawn could be assigned to putative nursery habitat areas given the isotopic data collected (Fig. 2a). In 2014/15, however, when only 13 putative nursery habitat areas were sampled, only 62.5% and 72.8% of Eastern King Prawn and School Prawn respectively could be assigned (due to the reduced amount of isotopic data from putative nursery habitats that was available, Fig. 2b). Some insight into the potential origin of these individuals may be garnered from their position on the isotope biplot relative to adjacent putative nursery habitat areas that were sampled (see Fig. 2b). Using these relationships, the origin of unassigned Eastern King Prawn was likely to be the higher salinity areas between areas 1 and 3 (see Fig. 1). Conversely, the origin of unassigned School Prawn with enriched δ^{15}N (Fig. 2b, crosses in the upper left) likely included the less saline areas upriver of area 12, whereas the origin of unassigned School Prawn with depleted δ^{15}N (Fig. 2b, crosses in the lower left) probably included the marsh areas in the south arm of the river.

In both years, the majority (> 90%) of emigrating Eastern King Prawn were assigned to the higher salinity areas near the lower end of the estuary, and within Fullerton Cove (Fig. 3a and b), with very small relative contributions from marsh systems in the lower estuary (Table 1, areas 6, 7, 8, 15 and 16). The relative contributions among these areas differed slightly, with the greatest contributing areas being area 3 and area 5 in 2013/14 and 2014/15 respectively. Applying the classification system of Dahlgren et al. (2006), indicated that on the basis of the isotopic data collected during the study, areas 3, 4, 5 and 21 represented effective juvenile habitat (Table 1).

Assignment of School Prawn was highly asymmetric in 2013/14, with the majority (~70%) of emigrating individuals assigned to areas in the south arm of the river (Fig. 3c), and much smaller contributions from other areas across the lower estuary. Nine areas made no contribution whatsoever (Table 1), including the productive School Prawn trawling areas in and around Fullerton Cove. In 2014/15, emigrating School Prawn were assigned to all putative nursery habitat areas that were sampled (Table 1), with the greatest contributions from the rehabilitated marsh areas in Tomago, Kooragang and Hexham, and the furthest area from the sea (area 12; Fig. 3d). In both years, areas spanning the length of the lower estuary were classified as effective juvenile habitat (EJH, Table 1). In 2013/14, this included the south arm (areas 20 and 21) and the areas furthest up the study area (areas 10 and 12; Table 1), whereas in 2014/15 more EJH was identified in the north arm of the estuary (e.g. areas 5, 12 and 22; Table 1) and also the three main rehabilitated saltmarsh areas (areas 6, 8 and 15; Table 1).

3.2. Quantitative sampling of prawns across the lower estuary

The abundance of both Eastern King Prawn (EKP) and School Prawn (SP) varied across the lower estuary (Fig. 4a and b). Eastern King Prawn (Fig. 4a) juveniles were generally more abundant than School Prawn (Fig. 4b) in this region of the estuary, but this may be an artefact of nocturnal sampling. Eastern King Prawn were most abundant in the areas around Fern Bay, Fullerton Cove, and within the Hexham wetland (Fig. 4a). School Prawn juveniles were only abundant in the Kooragang wetland and Fullerton Cove (Fig. 4b). The average absolute abundance (averaged across all tows) estimated for Eastern King Prawn was 115 ± 8 EKP 100 m^{-2} (mean ± SE), whereas the average relative abundance for School Prawn was estimated to be 16 ± 4 SP 100 m^{-2} (School Prawn abundance should only be considered a relative estimate as catchability may be lower during nocturnal periods).

The generalised additive model (GAM) explained ~33% and 37% of the deviance in the data for Eastern King Prawn and School Prawn respectively. In the north arm of the estuary, Eastern King Prawn abundance showed a distinctive peak between 8000 and 10,000 m from the estuary mouth (e.d.f. = 4.81, F = 5.84, $P \ll 0.001$, Fig. 5a), whereas in the south arm abundance increased linearly with distance from the estuary mouth (e.d.f. = 1.00, F = 9.70, P = 0.002, Fig. 5b). Eastern King Prawn abundance peaked at a turbidity of 15 ntu (e.d.f. = 4.27, F = 6.81, $P \ll 0.001$, Fig. 5c), and showed a negative linear relationship with depth (e.d.f. = 1.00, F = 10.80, P = 0.001, Fig. 5d).

Generalised additive modelling indicated that School Prawn abundance was non-linear in the north arm of the estuary (e.d.f. = 4.96, F = 6.29, $P \ll 0.001$, Fig. 6a). While abundance generally increased with increasing distance from the estuary mouth, abundance dropped between 8000 and 10,000 m, which is the same distance at which Eastern King Prawn abundance peaked in the north arm. Abundance was almost negligible in the south arm of the estuary, but did gradually increase with the distance from the estuary mouth (e.d.f. = 2.08, F = 3.89, P = 0.015, Fig. 6b). In contrast to Eastern King Prawn, School Prawn abundance appeared to increase with turbidity (e.d.f. = 4.25, F = 4.30, P = 0.001, Fig. 6c), but did not significantly vary with depth (e.d.f. = 3.44, F = 2.26, P = 0.062, Fig. 6d).

4. Discussion

The combination of approaches employed in this study provided a comprehensive picture of the potential nursery role of various habitats within the lower Hunter River estuary, and some of the factors that contributed to these patterns. Important habitats for Eastern King Prawn were mostly confined to the lower part of the estuary and primarily included shallow unvegetated sedimentary habitat. However, the Hexham wetland did support a high abundance of prawns which was likely due to strong connectivity and appropriate salinity at this location. Conversely, different habitats across the lower estuary were important for School Prawn, especially the rehabilitated Kooragang and

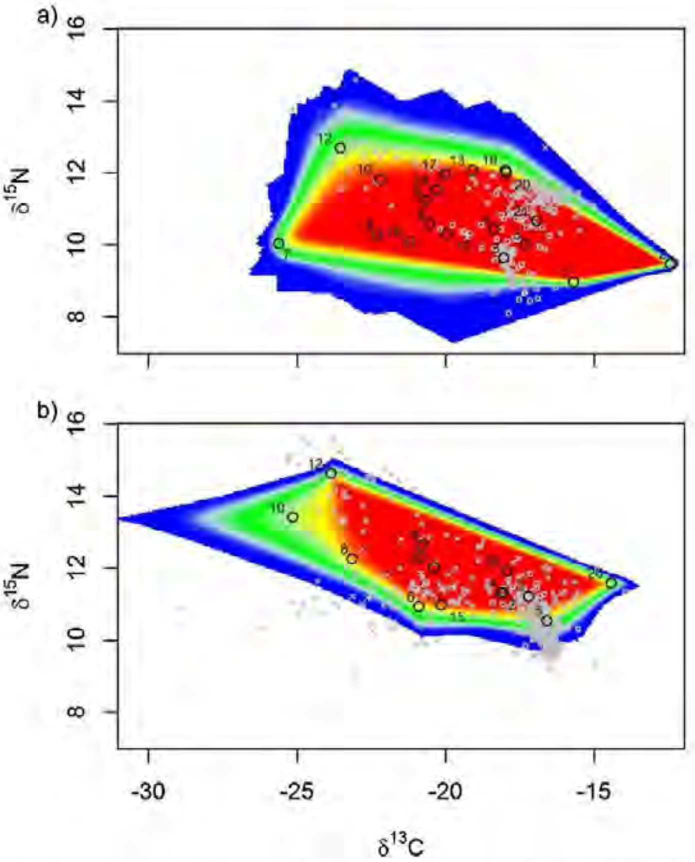

Fig. 2. Isotope biplot showing the completeness of the stable isotope map for determining the origin of emigrating prawns on the basis of their isotopic composition data for 2013/14 (a) and 2014/15 (b) seasons. Isotopic composition of putative nursery habitat areas is indicated by open circles, which are numbered to correspond with Fig. 1 and Table 1. Emigrating Eastern King Prawn and School Prawn are indicated by grey squares and crosses respectively. Red reflects the highest probability that the origin of an emigrating prawn lies within the sampled isotope map, and blue the lowest probability. Emigrating prawns falling outside the simulated region (see Smith et al., 2013 and; Taylor et al., 2016 for details) were excluded from the assignment analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Tomago marshes, and lower salinity areas further up the estuary.

The afore mentioned characteristics of the north and south arm and off-channel embayments, produced various bathymetric, hydrographic and physicochemical conditions that likely influenced the observed patterns in penaeid abundance and distribution. This in turn contributed to differences in nursery value for areas compared across the estuary. Quantifying these relationships improves our appreciation of the complex interactions that determine recruitment of penaeid prawns into estuarine habitats (Sheaves et al., 2015), and also the implications of these relationships for habitat repair.

4.1. Abundance of juvenile penaeid prawns in estuaries

Several studies have evaluated recruitment of early juvenile penaeid prawns to estuarine systems in New South Wales (e.g. Bell et al., 1988; Worthington et al., 1995). Earlier targeted surveys in Queensland principally focused on the role of Moreton Bay and associated riverine estuaries as a nursery. Young and Carpenter (1977) found that within the deltaic islands at the south of Moreton Bay, postlarval (2.1–3.0 mm CL) Eastern King Prawn abundance was inversely proportional to the distance from sea, with the greatest abundance on the exposed riverine banks at the mouth of the Nerang River. Within Moreton Bay itself, juvenile recruits were concentrated in oceanic influenced littoral habitats < 2 m depth (Young, 1978). While our data also show that juvenile Eastern King Prawn are concentrated in the lower estuary, both the isotope and quantitative data indicated a peak in prawn abundance 8000–10,000 m from the estuary mouth. Similar relationships were also recently found for this species in Lake Macquarie (Taylor et al., 2017).

The patterns in hydrology, bathymetry, and physicochemical variation in the lower estuary largely explain the patterns observed in Eastern King Prawn distribution. Firstly, both the current study and Young (1978) indicate that Eastern King Prawn abundance is maximised in habitat of depth < 2 m. Fern Bay and Fullerton Cove contain the most expansive area of such habitat within the system. The fact that these are off-channel embayment's means these habitats have low water velocity that is ideal for juvenile prawns, but these are directly adjacent to a higher velocity waters (the main river channel) that are important for the supply of recruits on the incoming tide. Secondly, the isosmotic salinity for juvenile Eastern King Prawn is approximately 28 (Dall, 1981), and the salinity in this area generally ranges from 26 to 32 (as these habitats are exposed to the influence on freshwater inflow on the salinity in the north arm). Thus, this region of the estuary also provides physicochemical habitats which align with the species physiological requirements, which could provide an energetic advantage through

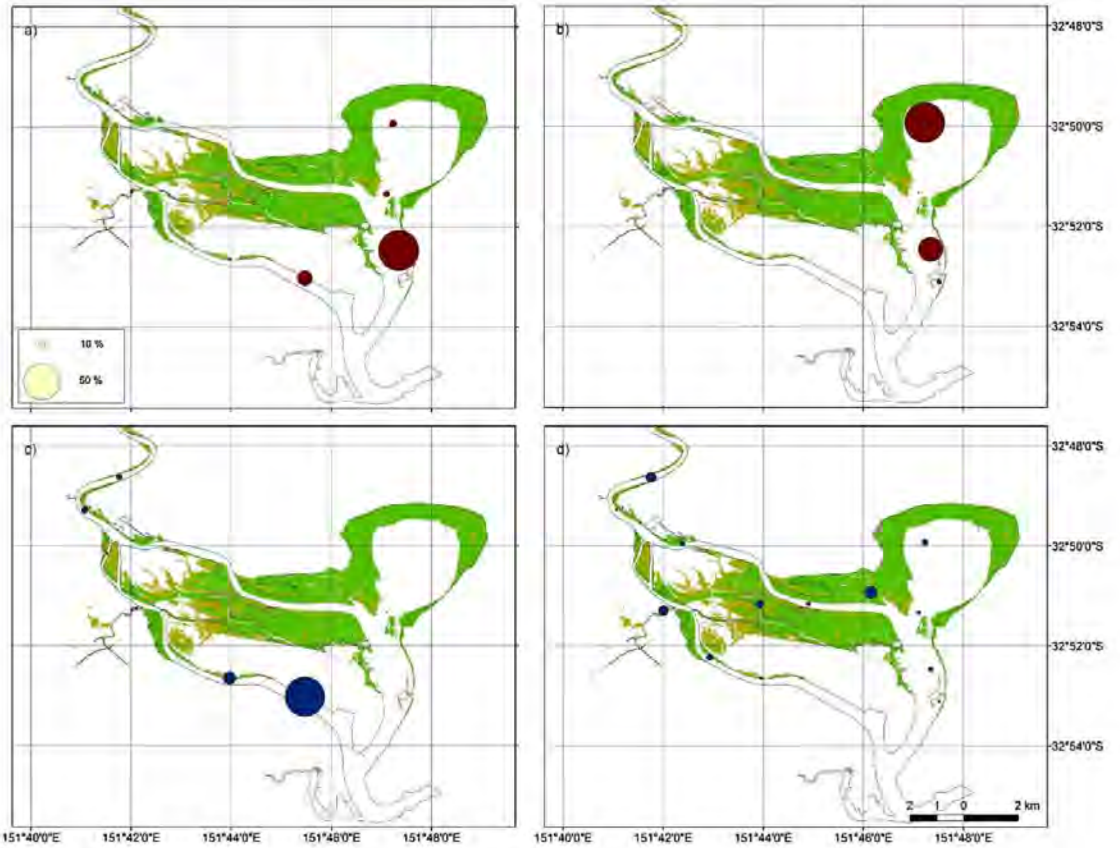

Fig. 3. Proportional assignment of emigrating prawns to putative nursery habitat areas in the Hunter River for Eastern King Prawn (top panels, a. and b., red circles) and School Prawn (bottom panels, c. and d., blue circles), in the 2013/14 season (left panels, a. and c.) and the 2014/15 season (right panels, b. and d.). Circles indicate the proportion of emigrating prawns assigned to each area, and the key for circle size is shown in panel a. Actual proportions are presented in Table 1, and habitat polygons are as described for Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduced osmoregulation. This could either represent a preferred habitat for juvenile Eastern King Prawn, or conversely the higher abundance observed under these conditions may reflect enhanced growth or survival arising from improved energetic efficiency at optimal salinity (Tyler, 2015). Reduced interspecific competition is another possibility, however we did not collect any data with which to assess this. Due to the general correlation between salinity and turbidity in estuaries (Loneragan and Bunn, 1999), it is likely the effect of turbidity observed in our data relates to the patterns outlined above for salinity.

Post-larval and juvenile School Prawn have previously been shown to recruit much farther up the estuary than Eastern King Prawn (Ruello, 1971). Despite the distribution measured through his field sampling, Ruello (1971) found that juvenile School Prawn actively selected higher salinity water over lower salinity water. While we found that abundance generally increased with distance to sea, it was apparent that the lower estuary also supports early juveniles for the species. The isosmotic salinity for School Prawn has not yet been reported, so cannot be compared to the salinity ranges in our study.

Similarly for Eastern King Prawn, juvenile School Prawn appeared to be more abundant at shallower depths (< 1 m), but abundance appears to have an opposing relationship with turbidity between the two species (with School Prawn at higher abundance in more turbid water). Although this corresponds with the findings of Ruello (1973) for adult School Prawn in inshore waters, in our case this probably reflects higher abundance in the more brackish, turbid waters of the Tomago and Kooragang wetlands. Further, Ruello (1973) found sediment characteristics played a role in the distribution of School Prawn, with juveniles having a clear preference for fine sandy substratum. Roy (1980) indicated that Fullerton Cove is dominated by estuary mud with < 10% sand and sandy substratum being more common to the river channels in this system; thus it is unlikely that this was a strong driving factor for distribution in the lower estuary. A final observation is that data collected during the current study point to a potential inverse relationship between juvenile Eastern King Prawn and School Prawn abundance. While this requires additional monitoring, it is possible that the abundance of Eastern King Prawn in a particular area also contributed to the patterns outlined above.

4.2. *Critical factors determining effective juvenile habitat*

The isotope approach employed here allowed the designation of effective juvenile habitat (EJH) in the lower estuary for both species. For Eastern King Prawn, the contributions from different areas to the emigrating portion of the population was fairly similar between years, with the expansive shallow sedimentary habitats in Fern Bay and Fullerton Cove being most important. These areas were identified as EJH for the species, as was the shallow habitat in the lower south arm in 2013/14. These patterns are similar to those detected in the pilot study

Table 1
Proportional contribution of sampled putative nursery areas (numbers correspond with those labelled in Figs. 1 and 2) to Eastern King Prawn and School Prawn captured emigrating from the estuary. Values in bold indicate that an area was designated as effective juvenile habitat using the criteria specified in Dahlgren et al. (2006, see text). Also shown are main water quality parameters measured for each area during the sampling program (SE included in brackets).

Area	Eastern King Prawn		School Prawn		Salinity	Temp (°C)	Turb (ntu)	DO (mg L^{-1})
	2014	2015	2014	2015				
1	0.000	–	0.007	–	35.7(0.9)	22.5(0.6)	4.5(0.5)	7.6(0.4)
2	0.000	0.061	0.000	0.030	31.3(0.6)	23.3(0.4)	8.7(0.9)	3.6(0.6)
3	**0.547**	**0.330**	0.000	0.060	33.2(0.4)	22.7(0.3)	10.3(1.4)	4.8(0.6)
4	0.080	0.017	0.014	0.045	26.1(0.7)	22.6(0.1)	25.1(2.9)	3.2(0.6)
5	**0.093**	**0.539**	0.000	**0.082**	28.7(0.4)	23.5(0.3)	48.7(6.8)	3.1(1.3)
6	0.000	0.017	0.000	**0.164**	31.1(0.7)	23.5(0.2)	23.8(4.2)	2.7(0.6)
7	0.000	–	0.000	–	23.9(0.7)	23.9(0.4)	14.1(2.2)	2.7(0.7)
8	0.000	0.000	0.000	**0.104**	24.1(0.9)	24.6(0.2)	8.6(1.7)	2.9(0.8)
9	0.000	0.009	0.000	**0.067**	27.2(2.1)	26.2(0.4)	8.8(1.6)	7.8(1.6)
10	0.000	0.000	**0.084**	0.030	24.0(1.4)	26.5(0.7)	6.0(2.9)	8.5(2.2)
11	[a]	–	[a]	–	16.1(2.3)	27.4(1.4)	6.5(2.1)	8.1(1.7)
12	0.000	0.000	**0.077**	**0.134**	20.8(2.5)	26.8(0.8)	6.0(1.4)	7.5(1.8)
13	0.000	–	0.028	–	29.5(0.8)	26.3(1.1)	4.5(0.8)	8.0(2.9)
14	0.000	–	0.035	–	32.5(2.3)	26.2(0.6)	6.5(2.6)	8.7(2.1)
15	0.040	0.009	0.021	**0.127**	31.6(0.7)	24.9(0.2)	6.4(0.2)	7.4(1.0)
16	0.013	–	0.000	–	25.5(1.8)	26.6(0.4)	9.1(0.6)	4.0(0.8)
17	0.000	–	0.014	–	33.1(0.6)	23.4(0.5)	6.4(0.8)	3.8(0.7)
18	[b]	–	[b]	–	34.1(0.4)	22.9(0.4)	6.2(0.7)	4.0(0.8)
19	0.000	0.009	0.000	**0.075**	34.9(2.3)	23.8(1.6)	6.4(1.9)	6.8(1.3)
20	0.027	0.000	**0.168**	0.030	35.1(0.4)	23.2(0.2)	6.0(0.8)	6.8(0.5)
21	**0.200**	–	**0.538**	–	35.3(1.6)	23.2(0.5)	6.1(0.5)	6.7(1.0)
22	–	0.009	–	**0.052**	30.3(0.6)	23.2(0.1)	9.3(1.1)	3.5(0.6)
Mean	0.052	0.083	0.052	0.079				

[a] No prawns were captured at this location.

[b] Isotope data were not available for this location due to technical issues.

presented in Taylor et al. (2016), and the factors contributing to the patterns in abundance described above likely contributed to importance of these habitats. It is important to note, however, that some of the highest estimates of juvenile abundance were detected in the Hexham wetland, and while this area did contribute some individuals to the emigrating stock, none of these areas were designated as EJH. This is likely an artefact of the EJH algorithm, and a standardised metric such as contribution per unit area (i.e. designation of Nursery Habitat, Beck et al., 2001) would probably have identified this as a nursery habitat due to the relatively small waterway area in this wetland. Nursery habitat was not calculated in this study due to the difficulty in precisely delineating discrete regions or areas represented by stable isotope composition, which is largely a function of salinity coupled with the influence of different primary producer assemblages along the estuarine gradient (Fry, 2002; Taylor et al., 2016). Regardless of the designation of EJH, consideration of Eastern King Prawn abundance implies some nursery value of the Hexham wetland for the species (Sheaves et al., 2015).

School Prawn displayed asymmetric patterns in EJH between the two years of the study. In 2013/14, the majority of emigrating prawns were contributed from the south arm of the estuary (areas 20 and 21), but areas 10 and 12 were also designated as EJH. In 2014/15, the contribution was spread much more evenly among areas, and were similar to the patterns presented in Taylor et al. (2016). Physicochemical conditions were similar between years and there were no major floods during the period that sampling took place; however, the commercial harvest was substantially different between years (~71 t in 2013/14, and ~36 t in 2014/15) and may well explain the differences in contribution and EJH. As mentioned earlier, the majority of fishing effort in the Hunter River is concentrated in Fullerton Cove, the main north arm channel in the lower estuary, and to a lesser extent further upriver at Raymond Terrace (~30 km from mouth). Furthermore, a large portion of the south arm of the estuary is effectively closed to trawling, as low bridges mean this section of the estuary is not navigable by trawlers (Fig. 1). While 2013/14 was an exceptional year for commercial School Prawn catch from the estuary (~71 t), the 2014/15 catch was half that (~36 t), due among other things to an infestation of weed that made trawling difficult in important fishing areas of the lower estuary. Thus, during the year when commercial harvest was highest, the bulk of emigrating School Prawn were contributed from the south arm within and just downstream of the unfishable waters. When fishing effort and catch was lower in 2014/15, the contribution was much more evenly spread throughout the south arm and along the north arm and Fullerton Cove. This is further supported by the patterns in Taylor et al. (2016) which were similar to 2014/15. These samples were collected at the very beginning of the 2013/14 season (11–12/2013), and are thus indicative of patterns in 2013/14 prior to the extensive fishing mortality occurring throughout the season. While the above comparisons involve only three surveys, this evidence points to the potential role of fishing mortality in mediating the relative value of estuarine nurseries.

4.3. Limitations of the study

For both species a reduction in the number of putative habitat areas for which isotope data was collected in 2014/15 meant that a smaller proportion of emigrating individuals could be assigned. The isotopic composition of these individuals provided some indication of their likely origin, and in the case of School Prawn some of the unassigned individuals may well represent prawns originating from the upper reaches of the recently rehabilitated Hexham wetland on the south arm of the estuary (Boys and Pease, 2016). The group of unassigned individuals in 2014/15 could have been greatly reduced with isotopic data for an additional 2 or 3 putative nursery habitat areas. This highlights the importance of carefully planning the spatial extent of sampling when employing the isotopic assignment approach.

While sampling in this study was relatively comprehensive, samples were only collected over two years and the sampling windows reflected regular estuarine conditions. Irregular perturbations such as moderate and high freshwater inflows to the estuary will alter flow velocities and water physico-chemistry, and this will alter the distribution and abundance of both species (Glaister, 1978; Racek, 1959). Targeted

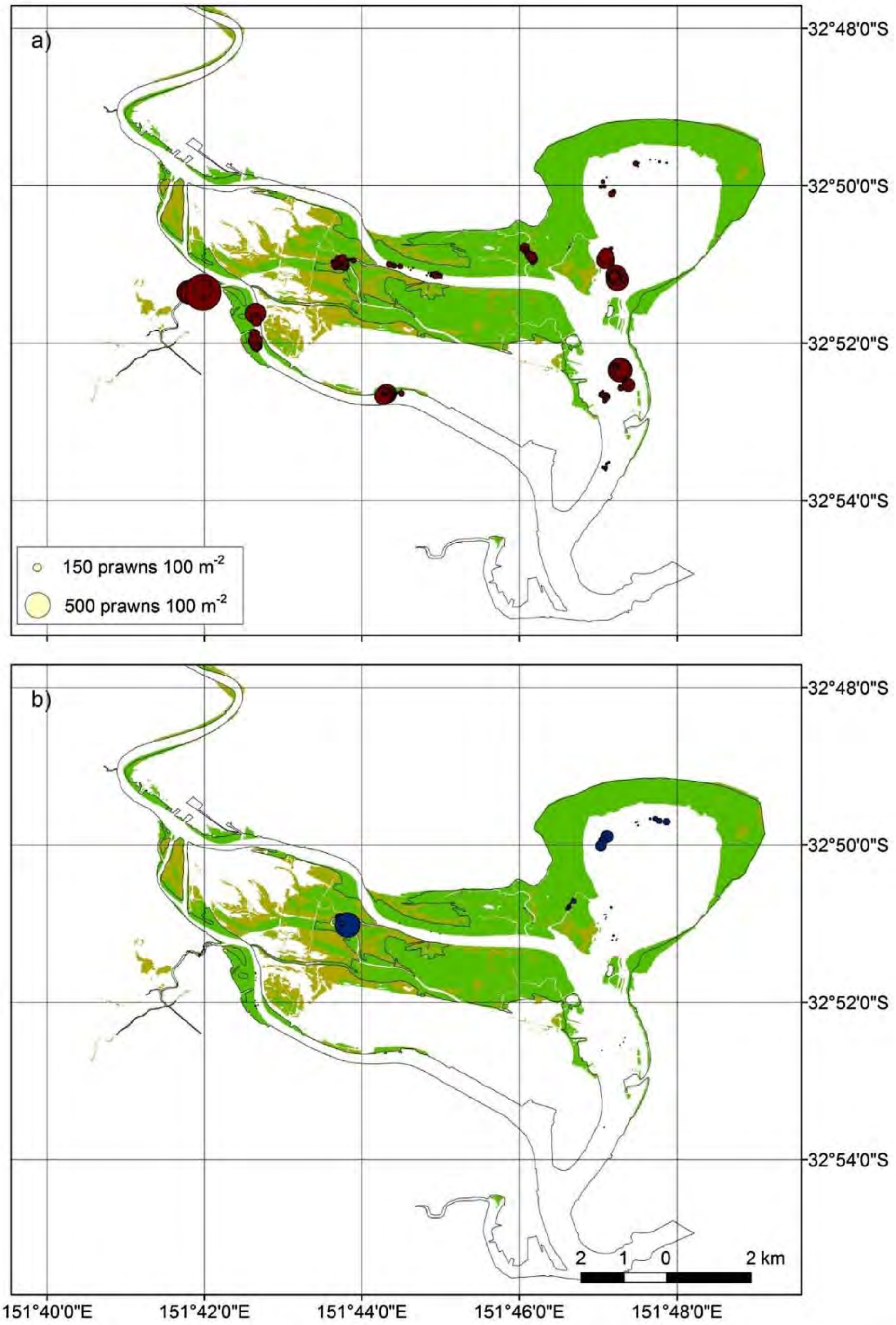

Fig. 4. Abundance estimates for Eastern King Prawn (a, red circles) and School Prawn (b, blue circles) captured in the lower Hunter River estuary in 2014/15. Circle size is proportional to prawn abundance, and a legend is provided in the bottom left of panel a. Habitat polygons are as described for Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

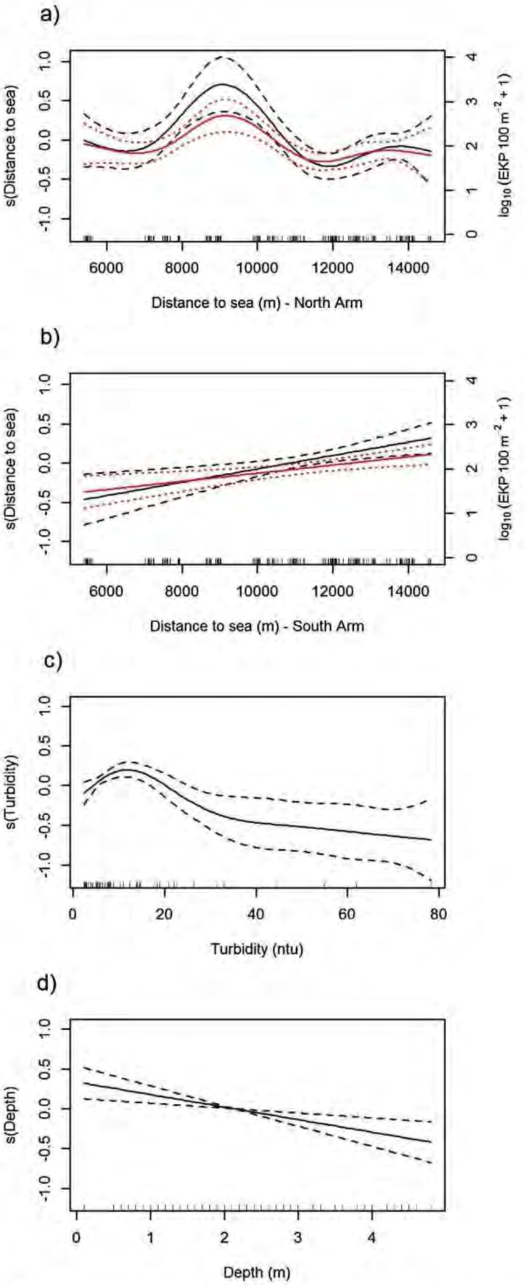

Fig. 5. Plots of smoothed predictor variables (black lines) contributing to estimates of Eastern King Prawn abundance in the lower Hunter River estuary: a) the distance to sea (m) for the north arm; b) the distance to sea (m) for the south arm; c) turbidity (ntu); and, d) depth (m). The *y*-axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits. Red lines overlaid on panel a) and b) represent the actual effect of the distance to sea on $\log_{10}$ transformed abundance (EKP 100 m^{-2}, solid red line) at turbidity of 14 ntu, and a depth of 2.1 m (values are shown on the secondary *y*-axis). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

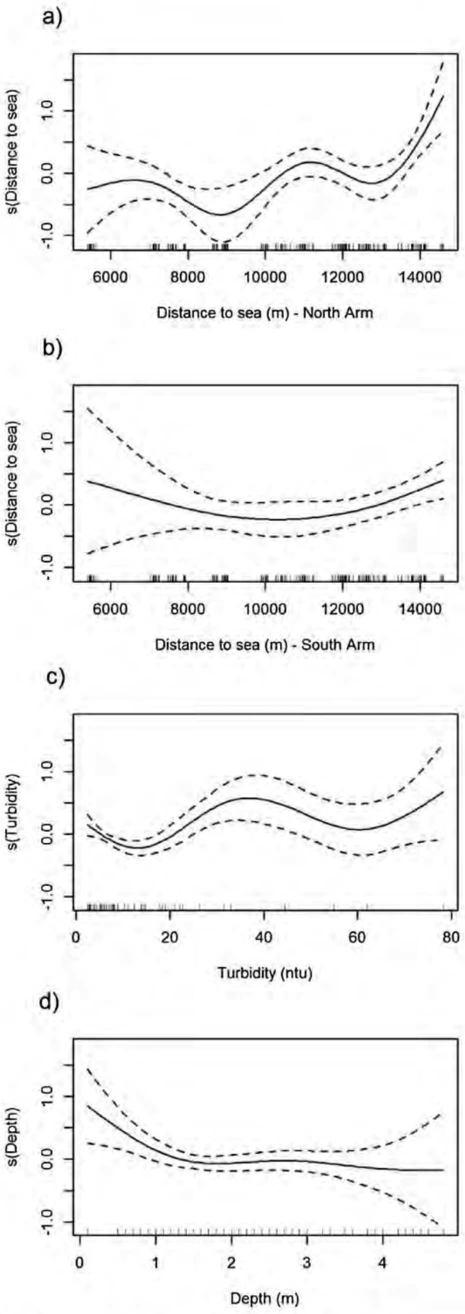

Fig. 6. Plots of smoothed predictor variables (black lines) contributing to estimates of School Prawn abundance in the lower Hunter River estuary: a) the distance to sea (m) for the north arm; b) the distance to sea (m) for the south arm; c) turbidity (ntu); and, d) depth (m). The *y*-axis values represent a relative measure of the contribution of the predictor variable to the model's fitted values, and dotted lines represent 95% confidence limits.

sampling of early juvenile Eastern King and School Prawn following these events would further reveal how juveniles respond to these conditions, and how abundance changes as conditions return to normal. At any rate, similar surveys in this and other riverine estuaries in the future should confirm the relationships described here.

4.4. Conclusions and implications for habitat rehabilitation

The key motivation for conducting the current study was to better understand the nursery role of different estuarine areas and habitats in south-eastern Australia (primarily for Eastern King Prawn, and to a lesser extent School Prawn), to evaluate current and inform future habitat rehabilitation efforts. Becker and Taylor (2017) show that direct use of the intertidal rehabilitated saltmarsh/mangrove habitats in the Hunter River estuary is minimal. However, we did find exceptional abundance of Eastern King Prawn in the subtidal channels within the Hexham wetland, and that elevated abundance of School Prawn were present in the Kooragang and Tomago wetlands. The Hexham wetland appears to be optimal for Eastern King Prawn as it receives good recruitment (has good connectivity with ocean waters), and contains good habitat (suitable salinity range and shallow littoral habitat). Our study reinforces that a range of factors will determine the value of different estuarine areas (Sheaves and Johnston, 2008; Sheaves et al., 2012), especially connectivity and salinity in the case of Eastern King Prawn. Although the Hexham wetland was not designated as EJH for Eastern King Prawn, it was for School Prawn, and has nursery value for both species. Given the inter-annual variability observed, however, sampling across additional years could help to further tease apart the patterns discussed here.

A great deal of research demonstrating the impact of habitat repair for prawns has been undertaken in the USA, but this has only recently been investigated in temperate Australia (Boys, 2016; Boys and Pease, 2016; Boys and Williams, 2012a; Boys and Williams, 2012b). Rozas et al. (2005) present a contemporary example outlining the significant value of rehabilitated marshes in the Gulf of Mexico for exploited penaeids and crabs, however they found that restored sites did not support as high abundance as adjacent undisturbed marsh systems. Boys and Pease (2016) show that following reinstatement of full connectivity to the Hexham wetland, School Prawn increased in abundance over 15 times in the upper reaches of the wetland. The study demonstrates that a combination of different approaches can improve our knowledge of potential nursery value for penaeid prawns, which is important in targeting future habitat repair efforts such that the fisheries outcomes for prawns are maximised. In the Hunter River estuary, restoring some tidal connectivity from the south arm of the estuary into the channels draining the Kooragang marsh system (i.e. near area 19, Fig. 1, see Williams et al., 2000 for historic network of tidal channels) will likely lead to increased value of the channels in this wetland for Eastern King Prawn. Finally, the potential role of fishing effort in moderating the nursery value of particular habitats is a novel finding which ultimately requires further investigation. If such patterns hold true, it highlights the benefits of having unfished areas within estuarine systems to provide a population subsidy in years of high fishing effort.

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Appendix 8 – Direct and indirect interactions between lower estuarine mangrove and saltmarsh habitats and a commercially important penaeid shrimp

Direct and Indirect Interactions Between Lower Estuarine Mangrove and Saltmarsh Habitats and a Commercially Important Penaeid Shrimp

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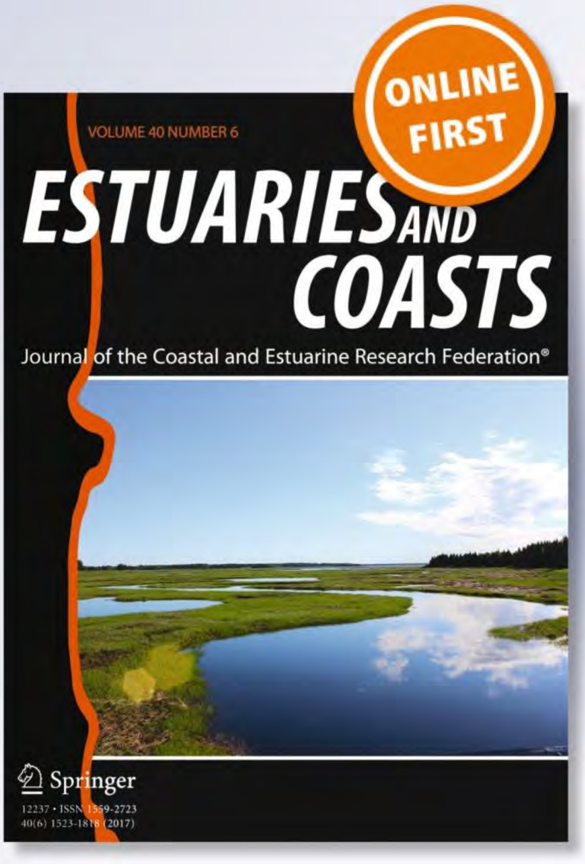

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Direct and Indirect Interactions Between Lower Estuarine Mangrove and Saltmarsh Habitats and a Commercially Important Penaeid Shrimp

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Abstract Vegetated habitats in estuaries may provide a structural refuge and food supply in the same place, but benefits are also derived where a productive food source and suitable habitat are adjacent to each other. Quantifying these relationships is fundamental to understanding the structural and functional characteristics of estuarine ecosystems and for informing management actions. Effective juvenile habitat (habitat that contributes greater-than-average numbers of recruits to the adult population), recruitment patterns and trophic relationships were studied for Eastern King Prawn (*Penaeus plebejus*) in the lower Clarence River estuary, New South Wales, between 2014 and 2016. Effective juvenile habitat was identified in both the north arm and main river channel of the estuary, and these areas also supported a higher abundance of juvenile prawns. There was minimal recruitment to the southern channels of the estuary, possibly due to reduced connectivity with the incoming tide arising from a rock wall. Trophic relationships in parts of the lower estuary were evaluated using stable isotopes, and saltmarsh grass (*Sporobolus virginicus*) was the dominant primary producer supporting juvenile Eastern King Prawn productivity across the area. Mangroves were of minimal importance, and seagrass cover was minimal in the area studied. The patterns observed indicate that nursery function of different areas within the lower estuary is a product of connectivity, recruitment and nutrition derived from primary productivity of vascular plants. Habitats within the lower Clarence River estuary have seen substantial degradation over decadal time scales, and the implications of our findings for targeting future habitat repair are discussed.

Keywords Nursery habitat · Effective juvenile habitat · Fisheries productivity · Stable isotope · Penaeidae · *Penaeus plebejus* · Clarence River

Introduction

Estuaries represent some of the most productive environments in the world and support a range of ecosystem services (Costanza et al. 1997). A large proportion of the value derived from estuarine systems occurs through the support of exploited aquatic species, through some or all of their life history stages (especially juveniles, Lenanton and Potter 1987; Elliott et al. 2007). The role of estuarine habitats during these early life history stages has led to the development of the nursery habitat paradigm (Beck et al. 2001), and diverse studies have compared and contrasted the relative values of different estuarine habitats for numerous aquatic species.

Food and refuge are two of the most important attributes that estuaries provide for the early life history stages of aquatic animals. Vegetated habitats in estuaries may provide a structural refuge and food supply in the same place (Ochwada et al. 2009; Becker et al. 2010), but benefits are also derived where a productive food source and suitable habitats are adjacent (Ahrens et al. 2012). Saltmarsh habitats are a good example of this, potentially providing protection from predation alongside a productive food web (Boesch and Turner 1984), and this ultimately supports rapid growth and higher survival through vulnerable early life history stages (Haas et al.

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2004). The net impact of such habitats, resulting in improved survival and productivity of exploited species that rely on them (such as penaeid shrimp) can be rather compelling (e.g. Turner 1977). Because estuaries typically contain a mosaic of habitats, establishing the relative importance of different areas or habitats within an estuary is fundamental to identifying the structural and functional characteristics of estuarine ecosystems, and also to effectively target management measures among estuarine habitats to achieve the best fisheries outcomes.

Penaeid prawns (shrimp) support some of the world's most economically valuable fisheries. Many penaeids have a biphasic life cycle, which includes an estuarine (juvenile) phase and an oceanic (adult) phase (Dall et al. 1990). During the estuarine phase, saltmarsh habitats, especially the subtidal channels and pools within them, support high abundances of juvenile penaeid shrimp (e.g. Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello et al. 2003; Minello and Caldwell 2006). The advent of stable isotope ecology has enabled quantitative studies of trophic linkages among saltmarsh, mangrove and exploited species. Recent work shows that food webs in or near saltmarshes and mangroves are supported by many primary producers (e.g. Melville and Connolly 2005; Sheaves et al. 2007). A combined focus on both habitat (i.e. quantitative measurements of abundance) and food webs within a seascape framework (e.g. Nagelkerken et al. 2015) can lead to powerful conclusions regarding relative nursery value (Fry and Ewel 2003).

Eastern King Prawn (*Penaeus plebejus*, EKP) is a valuable penaeid species occurring along the eastern Australian coast. Postlarval prawns recruit to estuarine nursery habitats from early summer, where they grow rapidly through their juvenile phase and undertake a synchronous emigration from estuarine nursery habitats during the last quarter of the lunar phase (most commonly during the January to March lunar months, Dakin 1938; Racek 1959; Taylor et al. 2016). Most prawns have left the estuary by mid-autumn and, as they mature, migrate north across several degrees of latitude toward the spawning grounds (Ruello 1975; Montgomery 1990). Larger estuaries in New South Wales (Australia) which contribute to fisheries productivity, often have significant areas of mangrove and intertidal saltmarsh (Saintilan and Wen 2012). The high value of Eastern King Prawn (and other penaeids) has led to recommendations for estuarine habitat repair targeted to benefit these species (see Creighton et al. 2015; Taylor 2016). There is, however, a need to better quantify the nursery role of different habitats for this species, to prioritise and target areas for rehabilitation. This study aimed to assess the importance and contribution of different habitats in the lower Clarence River estuary for Eastern King Prawn. This included the following:

1. A broad-scale assessment of the contribution of several areas across the lower estuary to the adult Eastern King Prawn stock
2. Estimation of Eastern King Prawn abundance in and around saltmarsh, mangrove and other habitats, in the lower estuary
3. Determination of the contribution of primary productivity from saltmarsh and mangrove habitats to Eastern King Prawn in the lower estuary

Materials and Methods

Study Area

The Clarence River estuary (−29.43, 153.37) is the largest estuarine system in New South Wales and is classified as a mature wave-dominated barrier estuary (Roy et al. 2001). The river is fed by a number of tributaries mainly in the upper floodplain, and the middle and lower estuary includes numerous islands north and south of the main river channel (Fig. 1). Prominent features of the lower estuary include Lake Wooloweyah in the south and North Arm in the north (Fig. 1). Lake Wooloweyah is an expansive shallow lake connected to the river by a series of narrow channels between deltaic islands that formerly comprised extensive saltmarsh (dominated by Salt Couch, *Sporobolus virginicus*) and mangrove (dominated by Grey Mangrove, *Avicennia marina*) habitats, but much of which is now reclaimed or degraded. The lake itself represents important commercial trawling grounds for School Prawn (*Metapenaeus macleayi*), and in the early twentieth century, it contained large beds of seagrass (*Zostera* sp. and *Halophila* sp.) which are now almost non-existent. North Arm is fed directly from Main Channel near the mouth and similarly contains a series of low-lying deltaic islands covered in saltmarsh and mangrove, interspersed with a network of shallow channels (Fig. 1). Just inside the entrance of the estuary, a rock wall has been constructed which directs the bulk of tidal flow up Main Channel and North Arm (Fig. 1; two small breaks in the wall allow for navigation by small vessels). Consequently, most of the tidal flow initially bypasses the downstream channel system connecting Lake Wooloweyah to the mouth, favouring Main Channel and to a lesser extent North Arm (Fig. 1).

Broad-Scale Assessment of Putative Nursery Habitat Areas

Spatial variation in stable isotope composition was used in a broad-scale assessment of the relative contribution of different areas within the lower estuary to the adult component of the Eastern King Prawn population, following Taylor et al.

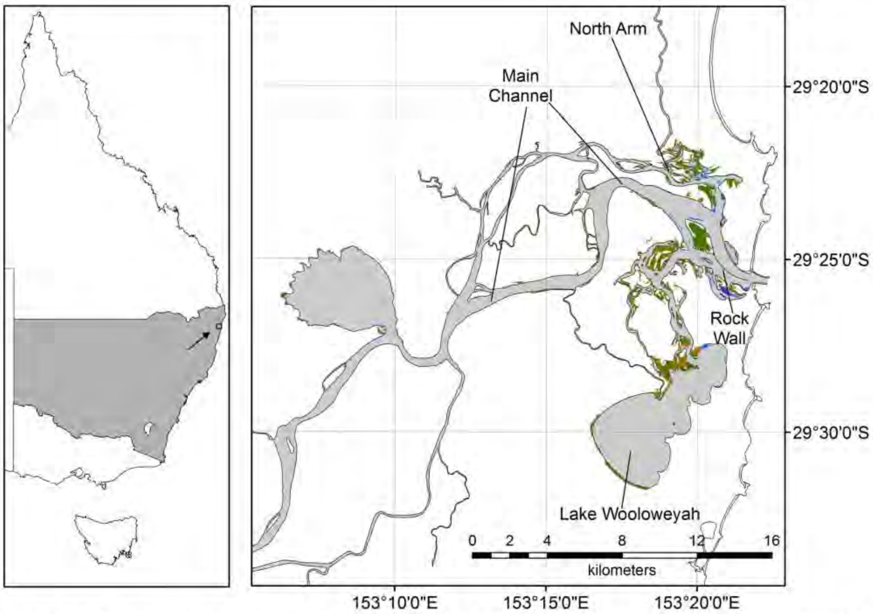


Fig. 1 Map of lower Clarence River estuary region with main features labelled. Waterway area (grey), mangrove (green), saltmarsh (brown) and seagrass (dark blue) habitats indicated

(2016). This approach exploits the species' abrupt migrations from nursery habitats within the estuary to the ocean (which coincide with the last quarter of the lunar phase, Racek 1959) and thus uses prawns emigrating from the estuary as a proxy for individuals moving from the estuarine nursery to the adult component of the population. Prawns are first captured from putative nursery areas throughout the estuary to characterise the isotopic composition specific to that area. Emigrating prawns come from nursery areas throughout the estuary and are captured near the mouth as they run to sea and matched back to putative nursery areas on the basis of isotopic similarity (Taylor et al. 2016). This allows contributions of various putative nursery areas to be estimated.

To determine the isotopic composition of different areas across the estuary, juvenile Eastern King Prawn were sampled across 12 putative nursery areas in the lower estuary during early February 2014, using up to four ~ 100-m tows of a sled net (see description of gear below). Emigrating Eastern King Prawn were collected by commercial trawler as they exited the mouth of the estuary, with sampling conducted over six nights during the last quarter of the lunar phase in the January and February lunar months, when emigration is greatest, in 2014. For prawns captured in putative nursery areas, three composite samples containing equal quantities of muscle tissue from six individual prawns were prepared for stable isotope analysis. All prawns captured from the mouth of the estuary were prepared as individual samples for analysis (i.e. not composite samples). Muscle tissue was rinsed in distilled water for 10 min, dried at 60 °C for ~ 48 h and isotopic composition (^{15}N and ^{13}C) measured on a Sercon 20-20 isotope ratio mass spectrometer (IRMS, Cheshire, UK). Measurement precision was determined through repeated measurements of internal standards and was ±0.11 and ±0.17‰ for δ^{15}N and δ^{13}C, respectively. Isotopic composition was expressed as a delta value relative to international standards using conventional methods (Fry 2006).

A distance-based approach was used to assign emigrating Eastern King Prawn to putative nursery habitat areas across the lower Clarence River estuary. The specific isotopic turnover rate for Eastern King Prawn has not yet been determined; however, 8–10 weeks is a likely time range for a new isotopic signature to be reflected in prawn muscle. To avoid making unlikely assignments, a point-in-polygon simulation (Smith et al. 2013) was applied to the dataset. This assessed the completeness of isotopic data from putative nursery habitat areas for assigning the set of emigrating prawns and used to exclude emigrating prawns from assignment (i.e. assignment was not attempted) whose source area was not reflected in the isotope map. Non-excluded emigrating prawns were assigned to putative nursery habitat areas as follows. The isotopic composition of each putative nursery habitat area was specified as a normal distribution, based upon the composite samples of juvenile Eastern King Prawn analysed from each area. In each simulation, the distribution of values from each putative nursery habitat area was randomly sampled and used to calculate the Euclidian distance between the emigrating prawn and the putative nursery habitat areas in bivariate (i.e. C and N) isotopic space. For each emigrating prawn in each simulation, a binomial response was returned: "1" for the putative nursery habitat area that was closest to the emigrating prawn in bivariate isotopic space and "0" for all other putative nursery habitat areas. One thousand simulations were conducted for each emigrating prawn and the associated binomial probability calculated for each habitat. The putative nursery habitat area with the greatest probability was selected as the most likely source habitat for that emigrating prawn. The assignment data were also used to determine whether each area could be considered an effective juvenile habitat (EJH), using the classification approach of Dahlgren et al. (2006). This approach designates EJH as areas that contribute more to the adult population than the average of contributions across all areas. All isotope modelling was undertaken using a custom script written in Matlab (Mathworks, Natick, MA, USA).

Determination of Prawn Abundance Across the Lower Estuary

We then sought to determine patterns in Eastern King Prawn abundance across important areas identified from the broad-scale analysis described above. Twenty sites within these important areas in the lower estuary (some corresponding with the putative nursery habitats described above) were sampled in December 2015 and February 2016 (these time points span the period where juvenile Eastern King Prawn are most abundant within estuarine nurseries). Each site was sampled after dusk using a sled net (0.75 × 0.45-m mouth, 4-m length, 26-mm diamond mesh body and 6-mm octagonal mesh cod-end, see Taylor et al. 2017) in last quarter of the moon. Four ~ 100-m tows were undertaken at each site on each sampling date, with a GPS waypoint marked at the start and finish of each tow (to calculate tow length). Water depth, temperature, salinity, dissolved oxygen and turbidity were recorded at each site during each sampling time. Samples were immediately placed on ice and then later frozen. Each sample was sorted, and all penaeid prawns were identified and counted. The dimensions of the gear, the actual length of each tow and gear efficiency estimates (0.48; M.D. Taylor, unpublished data) were used to standardise abundance estimates to number-EKP-per-hundred-square-metres (no. EKP 100 m^{-2}). Abundance data were analysed using Geostatistical Analyst in ArcMap v. 10.2.2 (Environmental Science Research Institute, California, USA). A predicted surface showing relative juvenile Eastern King Prawn abundance across the survey areas was computed from standardised point abundance data (derived from sled tows) with a fifth-order global polynomial interpolation (GPI).

Contribution of Potential Food Sources to Eastern King Prawn Diet

Several potential basal sources (referred to as "sources" below) were identified for Eastern King Prawn and collected from areas 6, 7, 8 and 10 (from the broad-scale assessment) in December 2015 and March 2016. These included *S. virginicus* (Saltwater Couch), *Suaeda australis* (Austral Seablite), *Avicennia marina* (Grey Mangrove) and mangrove pneumatophore epiphytes, microphytobenthos and fine benthic organic matter (MPB/FBOM) and particulate organic matter (POM). MPB/FBOM, which includes detritus, microphytobenthos, sediment and other biological material, was separated from bulk sediment by sieving following the method of Saintilan and Mazumder (2010) and then sent for stable isotope analysis. POM samples were obtained by filtering 1 L of water onto a pre-combusted (450 °C for 24 h) glass fibre filter paper (GF/C) under low vacuum and then dried at 60 °C for 24 h before being placed in a glass vial for stable isotope analysis. For Eastern King Prawn, muscle tissue was excised from the tail for stable isotope analysis. All plant and animal samples were rinsed with deionised water and placed in individual HCl-rinsed glass petri dishes, dried at 60 °C for 24 h and then ground to a fine powder using a Retsch Mixer Mill MM200. Ground samples were placed in aluminium capsules (6–8 mg for plant material and 1–2 mg for animal tissue) and sent to Griffith University, Queensland, for stable isotope analysis using a Sercon Hydra 20-22 automated Isoprime Isotope Ratio Mass Spectrometer. The standard used to compare carbon isotope content was Pee Dee Belemnite Limestone Carbonate, and stable isotope composition was expressed in delta-notation using conventional formulae (Fry 2006).

Mean $\delta^{13}C$ values ($n \geq 3$) were calculated for Eastern King Prawn and all food sources at each site. These mean values were used in the IsoSource model of Phillips and Gregg (2003) to calculate feasible food source combinations that could explain the prawn stable isotope signatures. The IsoSource model examines all possible combinations of each food source (0–100%) in 1% increments and reports the feasible solutions for each taxon as a distribution, mean, maximum, minimum and 1 and 99 percentiles. Although samples were also analysed for $\delta^{15}N$, only $\delta^{13}C$ was used in the IsoSource modelling. Mean isotope values of consumers need to be corrected for trophic fractionation prior to running the IsoSource model. Trophic fractionation is much larger and uncertain for $\delta^{15}N$ than $\delta^{13}C$ (e.g. Peterson and Fry 1987), and the fractionation value for $\delta^{15}N$ is known to vary considerably with animal age, growth rates and food quality (Vander Zanden and Rasmussen 2001). For this reason, the potential contribution of food sources to consumer diet was calculated only using $\delta^{13}C$ (with a 1‰ correction) following earlier studies in Australian systems that used a similar design (see Melville and Connolly 2005; Connolly and Waltham 2015).

Results

Broad-Scale Assessment of Putative Nursery Habitat Areas

Average carbon isotopic composition was correlated with the location of putative nursery habitat areas along the estuary (Fig. 2, $F_{1,\ 11} = 19.98$, $P = 0.001$, $R^2 = 0.67$). In Lake Wooloweyah (areas 1 and 2), putative nursery habitat areas were depleted in ^{15}N relative to other areas that were a similar distance from the sea (e.g. area 9; Fig. 2), but in general, ^{15}N was enriched and ^{13}C was depleted with increasing distance from the mouth. The point-in-polygon simulation indicated that nine of the 77 emigrating Eastern King Prawn which were analysed for stable isotope composition should be excluded from assignment (Fig. 2). The remaining emigrating Eastern King Prawn showed highly asymmetric patterns in assignment among putative nursery habitat areas. Of the 12 areas sampled, the vast majority of emigrating prawns were assigned to the main marsh/mangrove areas in the North Arm (area 8; Fig. 3 and Table 1). The remaining prawns were assigned to areas within the main river channel (areas 10 and 11; Fig. 3 and Table 1), and no prawns were assigned to areas within the south arm of the estuary or Lake Wooloweyah. Using the approach of Dahlgren et al. (2006), only areas 8 and 11 were designated as EJH (Table 1).

Abundance of Eastern King Prawn Across the Lower Estuary

Eastern King Prawn were generally the most abundant epibenthic species across the lower estuary, except in the southern channels and Lake Wooloweyah. Eastern King Prawn mean (± SE) abundance was 76 ± 6 EKP 100 m^{-2} (size range 3–20 mm carapace length), with a maximum abundance of 499 EKP 100 m^{-2}. The interpolated surface across the lower estuary (bounded by the sampling area) indicated that juvenile Eastern King Prawn were most abundant 8–12 km from the mouth in the Main Channel and North Arm (Fig. 4). This included areas adjacent to the marsh/mangrove habitats in North Arm and the mangrove habitats in Main Channel (see Fig. 1).

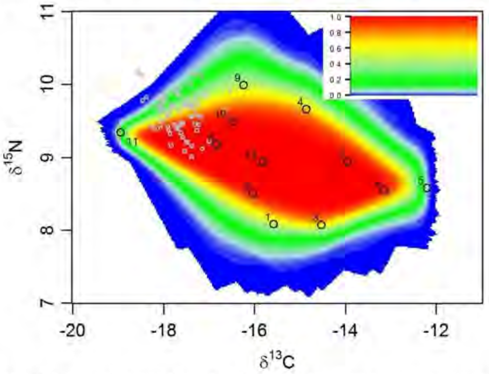


Fig. 2 Isotope biplot and simulated contours indicating completeness of putative nursery habitat area isotopic data (open circles; numbers correspond to Fig. 3 and Table 1) for assigning emigrating Eastern King Prawn (squares). Colouring indicates simulated probability (see scale bar) that habitat isotopic data reflects emigrating prawns origin. Emigrating prawns were excluded from assignment if outside the 5% (green) contour, as habitat isotopic data did not encompass the likely source

Contribution of Basal Sources of Nutrition to Eastern King Prawn

At all areas sampled, potential trophic sources were well separated in isotopic space (Fig. 5). The saltmarsh plant *S. australis* had the lowest $\delta^{13}C$ in area 10 (−28.5 ± 0.1‰) and area 6 (−28.5 ± 0.1‰), mangrove was lowest in area 8 (−30.3 ± 0.4‰) and area 7 (−29.7 ± 0.3‰) and the saltmarsh grass *S. virginicus* was most enriched in ^{13}C across all areas (−15.1 to −14.5‰, Fig. 5). For $\delta^{15}N$, *S. virginicus* had the lowest values (0.2 to 1.9‰) in all areas and POM had the highest values in area 10 (4.9 ± 1.0‰) and area 8 (4.0 ± 1.8‰), MPB/FBOM in area 7 (3.5 ± 0.4‰) and mangrove/MPE in area 6 (5.1 ± 0.5‰, Fig. 5). For Eastern King Prawn ($n = 58$), $\delta^{13}C$ ranged over 7.2‰ and $\delta^{15}N$ ranged over 1.6‰. Area 10 was the only location sampled in both December 2015 ($n = 5$) and March 2016 ($n = 14$), and at this location, there was a significant increase in $\delta^{13}C$ from −19.4 ± 1.5 to −16.3 ± 0.2‰ ($F_{1,\ 19} = 20.215$, $P < 0.001$) and $\delta^{15}N$ from 7.8 ± 0.6 to 9.6 ± 0.2‰ ($F_{1,\ 19} = 11.543$, $P = 0.001$) over that time (Fig. 5a). In March 2016, when all areas were sampled, Eastern King Prawn in area 8 had the lowest $\delta^{13}C$ (−17.2 ± 0.2‰) and $\delta^{15}N$ (8.2 ± 0.1‰; Fig. 5b) and the highest $\delta^{13}C$ (−14.4 ± 0.1‰) and $\delta^{15}N$ (9.8 ± 0.2‰) were in area 6 (Fig. 5d).

The contributions of potential food sources to Eastern King Prawn were calculated for each area on the basis of $\delta^{13}C$. The saltmarsh plant *S. virginicus* was the dominant source of nutrition across all sites (47–97%; Fig. 6). MPB/FBOM was the second most important nutrition source (2–11%; Fig. 6). The relative proportion of each potential food source at area 10 changed slightly between December 2015 to March 2016, with *S. virginicus* making a greater proportional contribution to the diet during March 2016 (47 vs. 75%; Fig. 6).

Discussion

General Comments

The observed distribution patterns indicated that the lower estuary was important for Eastern King Prawn, with the areas

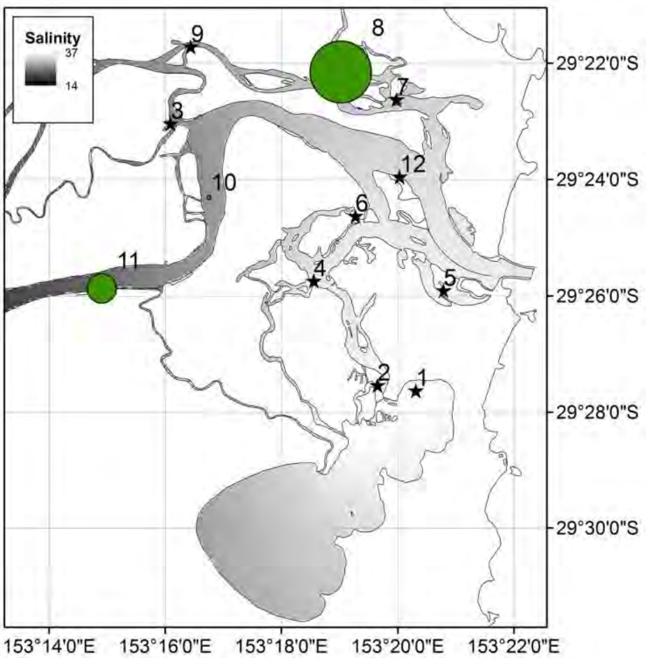


Fig. 3 Relative contribution of emigrating Eastern King Prawn among putative nursery habitat areas (actual contributions listed in Table 1), indicated by circle size. Areas that did not contribute shown as stars (note small contribution only from area 10). An interpolated salinity surface is shown (scale indicated in figure legend). Numbers correspond to Fig. 2 and Table 1

of greatest contribution (from the broad-scale assessment) or abundance (from the quantitative survey) occurring 8–12 km from the mouth. When considered alongside the trophic relationships described for Eastern King Prawn, these various lines of evidence suggest that nursery function of different areas within the lower estuary is a product of connectivity, recruitment and nutrition derived from primary productivity of vascular plants. The relationships observed have implications for the repair of habitats within the estuary, which have seen substantial degradation over decadal time scales (Fig. 7).

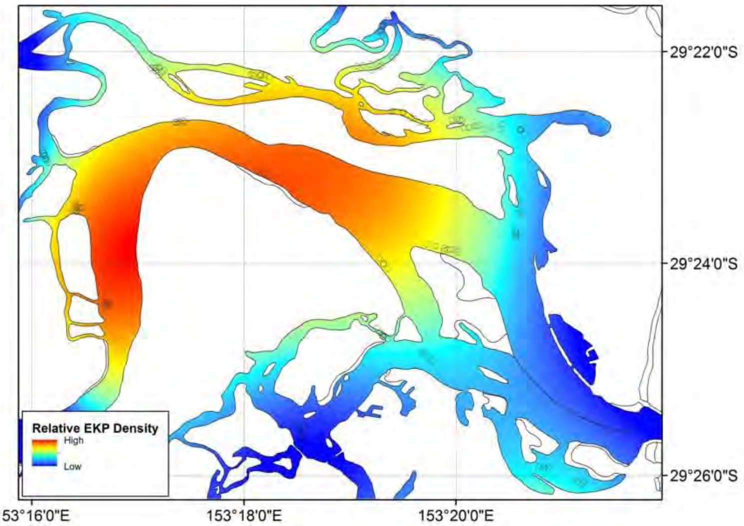
Table 1 Average isotopic composition (SE), n = 3, for 12 areas in Clarence River estuary and designation of effective juvenile habitat (bold) on the basis of contribution of sampled putative nursery habitat areas to Eastern King Prawn (n = 68) captured emigrating through mouth of estuary

Area	$\delta^{15}N$	$\delta^{13}C$	Contribution
1	8.08 (0.19)	−15.58 (0.36)	0.00
2	8.50 (0.14)	−16.04 (0.19)	0.00
3	8.07 (0.09)	−14.53 (0.09)	0.00
4	9.66 (0.18)	−14.86 (0.04)	0.00
5	8.58 (0.14)	−12.20 (0.05)	0.00
6	8.54 (0.06)	−13.15 (0.11)	0.00
7	8.93 (0.33)	−13.95 (0.23)	0.00
8	9.17 (0.35)	−16.83 (0.10)	**0.65**
9	9.99 (0.25)	−16.24 (0.17)	0.00
10	9.49 (0.12)	−16.49 (0.04)	0.04
11	9.34 (0.05)	−18.95 (0.14)	**0.31**
12	8.93 (0.07)	−15.82 (0.13)	0.00
Mean			0.08

Patterns in Effective Juvenile Habitat and Abundance of Eastern King Prawn

The broad-scale assessment indicated that the majority of the Eastern King Prawn emigrating from the estuary originated from the network of subtidal channels and deltaic islands within the North Arm of the lower estuary. This habitat is primarily shallow, unvegetated, subtidal soft sediment with limited seagrass cover but is surrounded by extensive intertidal mangrove and saltmarsh habitat. Similar habitats are also present in the network of deltaic islands connecting Lake Wooloweyah to Main Channel; however, these areas did not appear to contribute to the emigrating prawns. These findings were somewhat confirmed by the quantitative sampling program which found few Eastern King Prawns inhabiting this area. Quantitative sampling indicated the greatest abundance of prawns in 2015/16 was in Main Channel and also in North Arm 8–12 km from the estuary mouth.

Fig. 4 Heat map showing global polynomial interpolation of relative Eastern King Prawn abundance across lower Clarence River estuary from quantitative sampling (scale indicated in figure legend). Unfilled circles indicate locations sampled (tows). The rock wall directing tidal flow toward main channel and North Arm is evident just inside estuary mouth



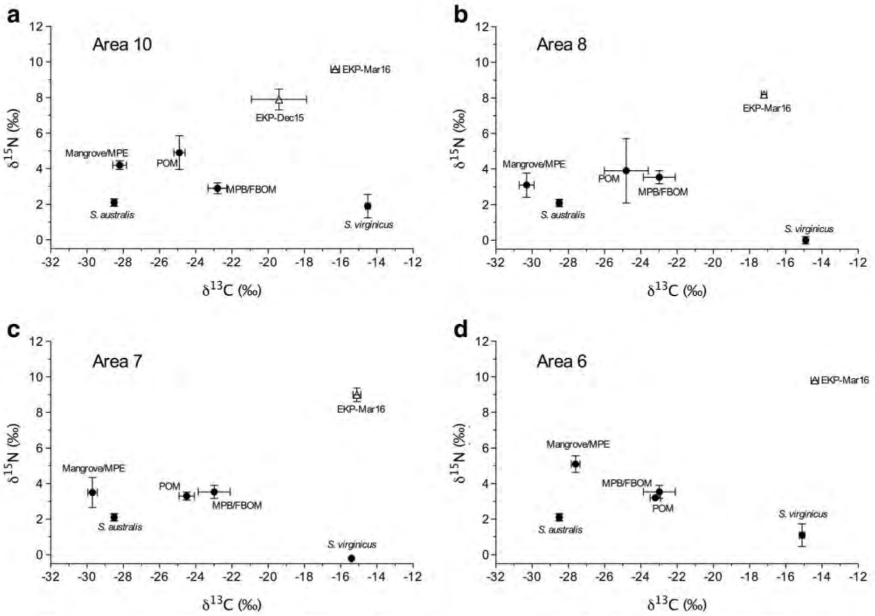


Fig. 5 Carbon and nitrogen stable isotope ratios for Eastern King Prawn (EKP; open triangles) and potential basal sources (closed circles) across lower Clarence River estuary for **a** area 10 ($n = 19$), **b** area 8 ($n = 16$), **c** area 7 ($n = 7$) and **d** area 6 ($n = 16$) (mean ± SE; area names correspond to Table 1 and Fig. 3). Mangrove/MPE, mangrove leaves and mangrove pneumatophore epiphyte; MPB/FBOM, microphytobenthos and fine benthic organic matter, POM, particulate organic matter; *S. virginicus*, *Sporobolus virginicus*; *S. australis*, *Suaeda australis*. EKP caught in December 2015 and March 2016 are shown for area 10 (panel **a**)

Fig. 6 Mean feasible contributions of five potential food sources for Eastern King Prawn (EKP) at areas 6, 7, 8 and 10 sampled in March 2016 (and area 10 December 2015). Area names correspond to Table 1, Fig. 3 and Fig. 5. Proportions calculated after correction for ^{13}C trophic level fractionation (described in the text). Only ^{13}C values were included in IsoSource modelling

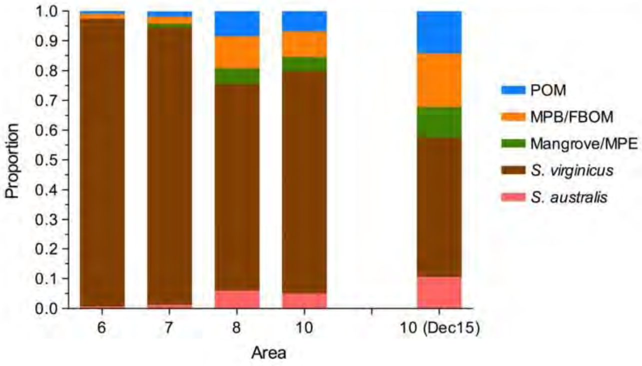
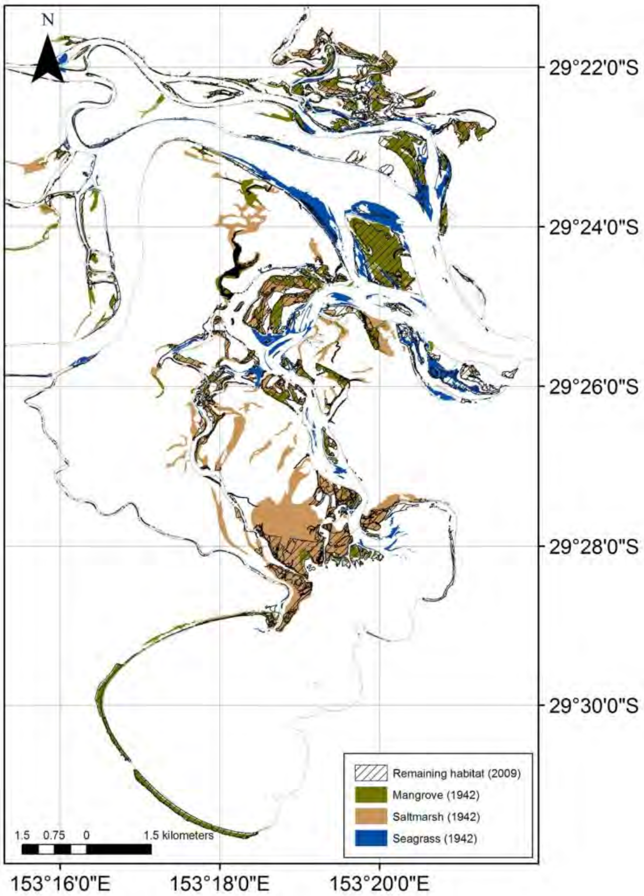


Fig. 7 Extent of habitat loss in lower Clarence River estuary between 1942 and 2009. Figure legend indicates main habitat classes present in 1942. Areal extent of habitat classes in 2009 indicated with overlaid diagonal hatching. Historic (1942) and current habitat data obtained from NSW Department of Primary Industries–Fisheries, Habitat Mapping Database (courtesy of G. West)



The observed patterns in abundance and contribution to the adult stock in our study are not so surprising when the morphology of the estuary is taken into account. Recent studies highlight the effect of circulation and connectivity on recruitment of penaeid prawns, as well as the designation of Nursery Habitat or Effective Juvenile Habitat for these species. In a study of the Laguna Madre estuary in Mexico, Blanco-Martínez and Pérez-Castañeda (2017) found that *Farfantepenaeus* spp. were most abundant in seagrass beds near the estuary mouth. Taylor et al. (2017) explored distribution patterns for Eastern King Prawn in Lake Macquarie, another wave-dominated estuary in south-eastern Australia, and found that abundance peaked in seagrass beds at intermediate distances from the estuary mouth, due to a combination of both tidal forcing and wind-driven circulation.

In the Clarence River, a rock wall forms a prominent feature of the morphology of the estuary mouth, ultimately directing the bulk of tidal flow up Main Channel and toward North Arm. This may affect the ability of ocean-spawned Eastern King Prawn postlarvae to recruit into the south arm of the estuary and Lake Wooloweyah, providing one explanation for the low abundance of Eastern King Prawn in this area and the lack of any detectable contribution of this part of the estuary to the adult population. Consequently, despite there being abundant macrophyte habitat and appropriate salinity to support juvenile Eastern King Prawn, limited connectivity may contribute to recruitment limitation for this species in the southern part of the lower estuary.

Contribution of Basal Sources of Nutrition to Eastern King Prawn

At the time of sampling, the dominant sources of carbon had reasonably similar isotope values in each area and these values were similar to those reported elsewhere in Australia for saltmarsh, mangrove and MPB (Melville and Connolly 2003; Melville and Connolly 2005; Abrantes and Sheaves 2008; Mazumder and Saintilan 2010; Connolly and Waltham 2015). The saltmarsh grass, *S. virginicus*, was the dominant nutritional source for Eastern King Prawn in all areas, ranging from 47 to 97%. Eastern King Prawn have a varied diet, typically comprised of plant material, detritus, crustaceans, microorganisms, small shellfish and worms (Racek 1959; Moriarty 1977; Suthers 1984). Carbon fixed by saltmarsh vegetation makes an important contribution to the nutrition of other penaeids (Abrantes and Sheaves 2008) and other invertebrates (Guest and Connolly 2004). If a buffer of radius 750 m (chosen to avoid overlap between adjoining sites) is placed around sampling areas, *S. virginicus* represents a maximum of 35% of the vegetated area. In contrast, mangrove habitat represents up to 100% of the available vegetated habitat, but mangroves only support a maximum of 8% of Eastern King Prawn diet. Throughout the entire Clarence River estuary, saltmarsh represents 26% of the vegetated habitat, whereas mangroves represent 67%.

The movement of carbon within an estuary can range from a few meters (Guest and Connolly 2004) to adjacent habitats (Connolly et al. 2005; Melville and Connolly 2005) and even kilometres (Gaston et al. 2006). As a consequence, organisms do not always derive nutrition from primary production in their immediate area and can be supported by other sources. In subtropical Australia (Moreton Bay), shorecrabs (*Parasesarma erythrodactyla* and *Australoplax tridentata*) in mangroves have stable isotope signatures that reflect incorporation of saltmarsh grass and microphytobenthos but not mangrove material (Guest and Connolly 2004; Guest et al. 2006). Similarly, in a tropical Australian estuary (Ross River), the Banana Prawn *Penaeus merguiensis* has relatively high $\delta^{13}C$ values consistent with the incorporation of *S. virginicus*, even in areas with extensive mangrove habitat (Abrantes and Sheaves 2008). While transport of organic matter throughout estuaries is clearly important, the apparent contribution of saltmarsh grass to estuarine food webs can sometimes be uncertain, as it shares a similar isotope value to seagrass (Melville and Connolly 2005). In the Clarence River estuary, there is a much greater areal extent of saltmarsh than seagrass, particularly in the areas that are important to Eastern King Prawn (see Figs. 1 and 7). In addition, recent work by Connolly and Waltham (2015) shows that the role of seagrass as a nutrient source for consumers declines exponentially over distances < 100 m from seagrass beds, indicating that any influence of seagrass would be highly localised. This was in contrast to saltmarsh grass, which showed no such decline with distance (Connolly and Waltham 2015). These factors provide further support for our conclusion that saltmarsh grass is the dominant nutritional source for Eastern King Prawn productivity in the Clarence River.

Our analysis also indicated that the importance of saltmarsh to Eastern King Prawn diet showed some temporal variation, with the mean proportion of *S. virginicus* increasing from 47% in December to 75% the following March for area 10. This may be explained by the environmental conditions influencing the estuary earlier in the season. Substantial (up to 45 ML day^{-1}) freshwater inflows to the Clarence River were observed from October to December 2015, whereas negligible inflow was observed from mid-January to April 2016 (NSW Office of Water Pineena Database, station 204055). The greater freshwater inflow in late 2015 potentially displaced the saltmarsh material accumulated in the estuary and replaced it with organic material (POM) from the upper catchment which has a more depleted $\delta^{13}C$ signature. This could explain the greater proportion of POM in the diet in December relative to March.

Interpretation of trophic relationships determined using IsoSource is not without limitations. The contribution of each basal resource to a particular consumer is usually not known exactly, because the number of major basal source pools may exceed the number of stable isotope ratios available for analysis (Layman 2007). In addition, IsoSource results do not actually correspond to an exact solution for the diet of a species, but to a distribution of possible solutions, given a set of possible basal sources (Abrantes and Sheaves 2008). In this study, the IsoSource results are reported with reasonable confidence because there is minimal variation in the isotopic composition of basal resources among sampling areas, and the 1st and 99th percentile were within a narrow range of the mean value. Furthermore, *S. virginicus* was the only likely basal resource with an enriched δ^{13}C value relative to Eastern King Prawn, and the isotopic difference between Eastern King Prawn and the major basal resource was similar among sampling areas.

Management Implications

The Clarence River is the largest estuarine system in New South Wales and supports the state's largest estuarine commercial fishery. The lower catchment is dominated by agriculture (primarily cane farming), and the installation of flood gates and historic reclamation for agriculture and development has led to substantial habitat loss. Comparison between the areal extent of habitat in 1942 and 2009 (calculated from the NSW Department of Primary Industries–Fisheries, Habitat Mapping Database) indicates that 63% of saltmarsh habitat (512 ha) and 79% of seagrass habitat (316 ha) have been lost, with most of this loss concentrated in the lower estuary (Fig. 7). Conversely, areal coverage of mangrove habitat has increased by ~ 6% during this time. In addition, > 60 ha of waterway area has been lost during this period.

The data presented here indicate that saltmarsh is an important habitat supporting productivity of juvenile Eastern King Prawn within the estuary. Much of the lost saltmarsh habitat is around the mouth of Lake Wooloweyah, where high numbers of Eastern King Prawn recruits are unlikely to occur. However, outwelling of saltmarsh material from this area to other areas of the estuary is likely, so the impacts of this loss may be relevant across the estuary. Also, substantial losses of saltmarsh habitat have also occurred along Main Channel in the lower estuary, and it is likely that the loss of this habitat has had consequences for the productivity of Eastern King Prawn, as well as other species that feed in food webs supported by saltmarsh productivity.

While we have demonstrated the importance of saltmarsh to Eastern King Prawn in terms of direct occupation and trophic subsidy, we did not directly address the benefits different estuarine habitats provide as a refuge from predation. Evidence from other systems highlight the dual role provided by these habitats (i.e. food and refuge, Boesch and Turner 1984); however, recent work suggests direct occupation of these habitats may not be as prevalent for commercial species as previously thought (Becker and Taylor 2017; Sheaves 2017). Eastern King Prawn certainly occur in subtidal channels draining saltmarsh, but there is a lack of data on the use of these habitats by predatory species in south-eastern Australia to evaluate whether these habitats offer a reduced risk of predation. At this stage, additional benefits of saltmarsh and mangrove habitats as refugia remain a possibility and a topic for future research.

Repair of estuarine habitat through the reinstatement of tidal flow is a potential management action which would both re-establish key estuarine habitat and most probably support increased productivity of nektonic species (Boys et al. 2012; Boys and Williams 2012). For example, in the Hunter River, the removal of culverts and the return of tidal flow to a series of creeks which fed a complex intertidal wetland system resulted in immediate changes to the fish and crustacean communities, whereby they began to reflect communities in unimpacted reference locations (Boys and Williams 2012). Furthermore, research in the Clarence River itself has showed that floodgate remediation enhanced the passage and connectivity of crustaceans and fish, including exploited species (Boys et al. 2012). These examples highlight how management actions such as reinstatement of connectivity within the estuary can result in beneficial ecological outcomes for commercially important species. As wetland systems recover, it is likely that they will also provide a trophic subsidy to other areas of the estuary.

Conclusions

Stable isotope ratios have routinely been used to determine the relative importance of mangrove material to the estuarine food web (Melville and Connolly 2003; Melville and Connolly 2005; Layman 2007; Abrantes and Sheaves 2008). Here, we show the importance of saltmarsh-derived material in providing nutritional support for juveniles of a commercially important penaeid species. Fry and Ewel (2003) suggest that a broader focus that examines patterns in habitat usage alongside trophic relationships resolved through isotopic composition contributes to a clearer evaluation of the importance of habitat for exploited species. The combination of connectivity modelling (based on isotope data), quantitative sampling and food web analysis employed here has provided a holistic snapshot of nursery habitat function within the lower Clarence River estuary. There is a clear link between Eastern King Prawn and saltmarsh habitat, both in the direct occupation of subtidal channels by juvenile prawns, and also in support of productivity from saltmarsh-synthesised primary production. This demonstrates the importance of these habitats for Eastern King Prawn, and it is likely that other exploited species in these habitats are similarly supported by marsh-derived productivity. These findings indicate that repair of the extensive habitats lost to the system are likely to yield significant benefits for Eastern King Prawn. Our appreciation of the importance of saltmarsh in the lower reaches of estuarine systems, and the potential outcomes from habitat repair will be further improved by examining these relationships for other species.

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Appendix 9 – Identifying and understanding nursery habitats for exploited penaeid shrimp in NSW estuaries

IDENTIFYING AND UNDERSTANDING NURSERY HABITATS FOR EXPLOITED PENAEID SHRIMP IN NSW ESTUARIES

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The need for estuarine habitat rehabilitation

The vast majority of Australia's population lives on the coastal fringes (Birch, 2000). Given the geographic isolation of Australia, access to ocean waters from sheltered ports for trade has been a key factor in the location and development of larger communities. This, coupled with the aesthetic benefits and desirability of living close to the sea, has meant that most of our major cities, and many of our major regional centres, are concentrated around estuaries.

Rapid development of communities, industry and agriculture around estuaries in the early 20th century showed little regard for the importance of estuarine habitats to species exploited for food or the health of ecosystems as a whole. Reclamation through infilling has seen the demise of extensive coastal wetland and mangrove habitats (e.g. Evans and Williams, 2010), and the installation of flood gates has seen the widespread loss of connectivity between coastal wetlands and estuarine waters. This has contributed to a reduction of some 72% of prime fish habitat available to support estuarine fish species (Rogers et al., 2015). In the estuarine waters themselves, various anthropogenic pressures have seen the degradation and loss of about 45,000 hectares of seagrass (Walker and McComb, 1992).

Recently, the case for extensive estuarine habitat rehabilitation in Australia has been developing. A recent business case suggested that relatively simple remediation activities can lead to substantial economic benefits (Creighton, 2013) through enhancement of the various ecosystem services derived from estuaries, especially fishery productivity. On this basis of this assessment, investment of the AUD350 million (Australia-wide) needed to undertake the necessary repair is expected to be recouped through these enhancements within 5 years (Creighton et al., 2015). To encourage investment in habitat repair, there is a need to prioritise and plan works to maximise benefits, and also to employ reliable analyses to place a financial value on these benefits.

Given the large volume of harvest, high value of product, and general reliance on estuaries during their life history, it has been suggested that habitat rehabilitation should focus on areas of potential benefit to penaeid prawn species (Creighton et al., 2015). This manuscript summarises some very recent data collected for penaeid prawns in NSW, and uses these patterns to show how the nursery concept can support the prioritisation, planning, design and assessment of estuarine habitat rehabilitation projects in New South Wales.

Establishing nursery value and use in the planning habitat rehabilitation

The estuarine nursery concept is a long-standing paradigm in marine ecology (Boesch and Turner, 1984), and suggests that the structural complexity and productivity of estuaries plays a significant role in the growth and survival of early stages of marine organisms. This in turn affects the abundance at later stages when these organisms reproduce, and can be exploited for human consumption. A large proportion of exploited species in south-eastern Australian estuaries utilise estuaries for some component of their lives, with levels of usage ranging from a few short months during an organisms early life history (i.e. the nursery stage) to the entire life cycle of an organism.

Penaeid prawns are among the most heavily exploited benthic crustaceans in the world. Many penaeid species display a Type-II life cycle, whereby spawning occurs in oceanic areas, young prawns recruit into estuaries for their juvenile stage, and migrate back to the ocean as they mature (Dall et al., 1990). During this period, young prawns are thought to be reliant on both the overall productivity for food, and the various habitats available in estuarine systems for shelter, but this varies between species. The overall dependence of these taxa on estuaries is however highlighted by Turner (1977), whose meta-analysis shows a strong positive correlation between estuarine habitats (intertidal vegetation) and landings of penaeid prawns, which transcends species and geographic areas.

Along the length of the NSW coast, the two major species of penaeid prawns that use estuaries are Eastern King Prawn (*Penaeus plebejus*) and School Prawn (*Metapenaeus macleayi*). Both species display a penaeid Type-II life-cycle, but display different levels of estuarine usage. Eastern King Prawn spawn off northern NSW and southern Queensland, and their larvae develop as they drift south in the Eastern Australian Current (Everett et al., in review). As they reach their postlaval stage, they emigrate inshore and into estuaries, where they settle out across a range of different habitats. They remain in the estuary for 2-3 months, before emigrating to inshore areas and commencing an extensive migration toward the spawning areas further north (Braccini et al., 2012). School Prawn spawn in inshore areas, usually adjacent to the mouth of an estuary, recruit into the estuary as postlarvae, and rely on estuarine habitats during their juvenile phase (Racek, 1959). Maturing prawns emigrate from the estuary usually within the months of December – March, and spawn around the mouth of the estuary from which they emigrated, or adjacent estuaries to the north (usually within about 70 km, Ruello, 1977). School Prawn are highly exploited in their estuarine and inshore phase (Glaister, 1978), whereas Eastern King Prawn are primarily exploited in their offshore migratory phase (Gordon et al., 1995).

While these species both use estuaries, they are not ubiquitous and are present in different numbers at different places, and in different habitats. If estuarine habitat rehabilitation is to be targeted at the enhancement of these valuable species, understanding the nursery *value* of different areas within the estuary, and the processes that might be driving these patterns, will allow managers to: 1) prioritise areas for rehabilitation that are likely to result in the greatest benefits for these species; 2) give regard to factors that may increase nursery value when engineering rehabilitation works; and 3) estimate the potential outcomes of different rehabilitation scenarios for different species.

Nursery habitats for exploited penaeid shrimp in NSW estuaries

Defining nursery value is most commonly approached through the designation of different areas within the estuary as *nursery habitats*. The general definition of a nursery habitat is one that contributes a disproportionate number of recruits to the exploited or reproducing components of the population (Beck et al., 2001). This usually involves tracing individual animals captured in the exploited or adult components of the population, back through space and time, to the location where they grew up, and using the contribution of different putative areas or habitats to derive a standardised contribution (i.e. contribution-per-unit-area of habitat). Habitats or areas that have a greater than average contribution-per-unit-area, are generally designated as *nursery habitats*. The spatial extent of the habitat or area from which an animal originates, however, may not always be explicitly defined. In these cases, a simpler method is used to assess nursery value, which only considers total contribution of a habitat or area regardless of its spatial extent (Dahlgren et al., 2006), and defines areas that have a greater than average contribution as *effective juvenile habitat*. While these two approaches provide suitable methods for assessing nursery value, Sheaves et al. (2015) highlight that a broader suite of variables need to be considered, including the supply of natural recruits to a particular habitat, limitations imposed by an organisms physiology, requirements for refuge habitat, and connectivity between juvenile and adult habitats.

Considering the information above, tracing older animals back to their juvenile habitat is an important component of understanding nursery value. For fish, this is often achieved by using the concentrations of certain elements laid down in the fishes otolith (Elsdon and Gillanders, 2003), but this is most often used to classify individuals among different estuaries. Similar approaches have been trialled for crustaceans, but similarly only work at broader spatial scales (Courtney et al., 1994). Taylor et al. (2016) recently developed a method for assigning penaeid prawns to particular areas within an estuary, using the stable isotope signature of muscle tissue. This two part process involves firstly collecting animals from across the estuary (i.e. in putative nursery habitat areas) to develop a library to which animals of “unknown origin” can be assigned. The second part of the process involves collecting animals as they emigrate from the estuary to join the adult or exploited component of the population, and matching the muscle stable isotope signature from these individuals to putative nursery habitat areas to derive the most likely area from which they originated. This novel approach was used in conjunction with traditional trawl sampling to define nursery habitats and effective juvenile habitats for Eastern King Prawn and School Prawn across a number of estuaries in NSW, and quantify how completed rehabilitation projects were benefiting these species.

Lake Macquarie is a large, immature, wave dominated barrier estuary, and NSW’s largest coastal lake with a waterway area of 114 km^2. The lake has a small tidal range, a relatively stable salinity regime, and extensive seagrass beds dominated by *Zostera* and *Posidonia*. Using the approach described above, Taylor et al. (in review) assigned Eastern King Prawn that were emigrating from the estuary among 20 putative nursery habitat areas (School Prawn do not occur in the estuary in large numbers). Over 80% of the emigrating prawns could be assigned among these areas, although they were only assigned to 11 of the areas surveyed. The level of contribution from these areas was significantly related to both the abundance of prawns within an area and the distance of that area to the mouth of the estuary. Given the definitions outlined above, 8 areas were designated as effective juvenile habitat (EJH), and 5 areas were designated as nursery habitat (NH). All of the EJH and NH were located in the northern section of the estuary. The isotope sampling was followed up in the following year by quantitative sampling aimed at evaluating the absolute densities of prawns present in each area. These results supported the patterns observed from the isotope analysis conducted in the previous season. Prawn densities were significantly related to distance to sea, and densities were greatest at a distance of 6-9 km from the estuary mouth.

Examination of circulation and wind patterns led to the conclusion that tidal transport of incoming postlarvae could not explain the recruitment patterns. Rather, the spatial patterns in abundance were consistent with transport from the end of the lakes entrance channel being driven by predominantly southerly winds during the recruitment season. Ultimately, the supply of recruits through wind-driven transport, and the density of seagrass in a particular habitat, was most important in determining whether a habitat was a nursery habitat or effective juvenile habitat. Other ocean-spawned species also recruited at greatest densities to these areas (Hannan and Williams, 1998).

The second estuary examined was the Hunter River Taylor et al. (in preparation), a mature, wave-dominated barrier estuary located just to the north of Lake Macquarie. While the lower estuary is heavily urbanised, it has abundant mangrove and saltmarsh habitats, and includes 4 main features: 1) an expansive mangrove lined system of shallow embayment's (Fullerton Cove and Fern Bay); 2) Tomago wetland to the north; 3) Kooragang wetland, which is nested between the north and south arms of the lower estuary; and 4) Hexham wetland in the south. The historic installation of dykes and floodgates removed connectivity of three wetland systems and the main estuary, however several recent rehabilitation projects have reinstated this connectivity, initially to Kooragang wetland (Williams et al., 2000) followed by Tomago (Rayner and Glamore, 2010) and most recently the Hexham wetland was rehabilitated (Boys and Pease, 2016).

Using the approach employed by (Taylor et al., 2016), up to 93.5 % of prawns could be assigned to putative nursery habitat areas. Emigrating Eastern King Prawn were primarily assigned to the higher salinity areas of the lower estuary, with most originating from the shallow, unvegetated habitats of Fullerton Cove and Fern Bay, and sites in these are were all designated as effective juvenile habitat (designation of nursery habitat was performed with this data). The wetland systems mentioned above made only minor contributions to the emigrating component of the population. The relationship between distance to sea and abundance was not linear, however, and quantitative sampling revealed a distinctive peak in between 8 and 10 km from the estuary mouth, and also that prawns were more abundant in shallower water. This area corresponded with a salinity primarily in the range 26-32. The isosmotic salinity for juvenile EKP is 28 (Dall, 1981), and recent physiological experiments have shown that energetic efficiency is greatest at this salinity (Tyler et al., in review), allowing for optimal somatic growth. Bathymetry, salinity, and connectivity ultimately affected the nursery value of different areas for Eastern King Prawn in the Hunter River.

For School Prawn in the Hunter River, the contribution of different areas to emigrating prawns was spread much more evenly across the lower estuary, and the three main wetland areas described above were designated as effective juvenile habitat for this species. Abundance of School Prawn was also positively related with distance to the mouth of the estuary, and preliminary examination of the patterns indicated that fishing effort may affect the contribution of different areas to the emigrating component of the population.

Applying knowledge of penaeid nursery value to habitat rehabilitation

The information above presents some clear patterns which highlight areas of particular nursery value in two contrasting estuaries, and the factors that influence this value. This information is extremely useful in evaluating existing habitat rehabilitation efforts, and informing future efforts.

The patterns resolved for Eastern King Prawn in Lake Macquarie have implications for targeted fishery restoration efforts, both for Eastern King Prawn as well as other ocean spawned species in wave dominated estuaries. It is clear that under natural recruitment conditions, those habitat rehabilitation strategies targeting seagrass (such as replacement of traditional moorings with seagrass friendly moorings) should have the greatest positive impact on this species when efforts are targeted toward locations where hydrographic patterns provide the greatest number of recruits, which in the case of Lake Macquarie is 6 – 9 km inside the estuary mouth.

In the Hunter River, the patterns presented indicate that a number of factors combine to determine the nursery value of different areas within an estuary. For Eastern King Prawn, these were bathymetry, connectivity and salinity. The importance of shallow estuarine areas in the lower estuary highlight the potential impact that extensive loss of high nursery value habitat through land reclamation throughout the lower Kooragang Island may have had on the species (Williams et al., 2000). It also shows that improving tidal connectivity from the south arm into the lower Kooragang wetland could lead to increased value of this habitat for Eastern King Prawn. Due to its small relative waterway area, the Hexham wetland was not designated as an effective juvenile habitat for Eastern King Prawn, however, the highest abundances encountered during the research were present in the subtidal channels of this recently rehabilitated wetland system. The Hexham wetland certainly appears to be of high nursery value for Eastern King Prawn as it receives good recruitment, suitable salinity and a shallow sub-tidal channel system. For School Prawn, all rehabilitated wetland systems were of high nursery value.

These points represent preliminary recommendations and conclusions as field research is being finalised and published. An important use of this data will be application of the abundance information through a fishery model to predict the economic benefits that may be derived from different habitat rehabilitation scenarios for these species. In recent years, examples of such modelling have emerged for Australia (e.g. Blandon and zu Ermgassen, 2014), although there has not yet been a dedicated study in NSW. Future work may also apply the approach described above to other valuable taxa, such as Mud Crab and Blue Swimmer Crab, to identify critical factors affecting nursery value and provide data to model the potential outcomes from habitat rehabilitation.

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Appendix 10 – Habitat-fishery linkages in two large estuarine fisheries: The role of saltmarsh in supporting fisheries productivity

Hydrobiologia
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PRIMARY RESEARCH PAPER

Habitat–fishery linkages in two major south-eastern Australian estuaries show that the C4 saltmarsh plant *Sporobolus virginicus* is a significant contributor to fisheries productivity

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Abstract Estuarine fisheries productivity is dependent upon numerous factors, including the productivity of primary producers supporting the food web and the transport of organic matter derived from those primary producers. In this study, we use stable isotope ratios in a Bayesian mixing model to estimate the contribution of primary producers to fully recruited commercial species in two important estuarine commercial fisheries in south-eastern Australia; the Hunter and Clarence estuaries. The C4 saltmarsh plant *Sporobolus virginicus* had the greatest contribution to consumer diet among almost all sites and times (25–95%), though for prawns the presence of seagrass may be exerting some influence on this calculated contribution in the Clarence estuary. Particulate organic matter (POM; 30%) and fine benthic organic matter (FBOM; 39–41%) also contributed significantly to consumer diet. Mangroves and other C3 sources generally had the lowest contribution to consumers (1–31%). While the exact contributions of each source are uncertain within our Bayesian framework, these results highlight the relatively large role of saltmarsh habitat as a contributor to fishery productivity, especially in estuaries with no seagrasses. Given the anthropogenic threats to saltmarsh habitat, there is potential for loss of fishery productivity with further loss of saltmarsh areal extent.

Keywords Habitat rehabilitation · Habitat restoration · Provisioning · Carbon isotopes · Mangroves · SIMMR · Bayesian mixing model

Introduction

Evidence from a broad suite of ecosystems indicates that fisheries productivity is largely dependent on appropriate physico-chemical conditions (e.g., Sundby, 2000), effective advection (e.g., Werner et al., 1996) and recruitment (e.g., Hjort, 1914) of early life history stages, and sufficient trophic productivity. Primary production forms the basis for most aquatic food webs on which exploited species depend (Pauly & Christensen, 1995), and the resultant trophic productivity is important throughout all life history

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stages. This includes ensuring that larvae can rapidly grow and escape vulnerable stages (e.g., Cushing, 1971), but also in ensuring rapid growth to a reproductive size (Roff, 1983), and overall somatic (Golet et al., 2007) and reproductive (Tyler & Dunn, 1976) condition. Consequently, productivity of exploited species is inextricably linked to the basal productivity of autotrophs at the bottom of the food chain.

Estuaries are dynamic environments that represent some of the most productive aquatic ecosystems on Earth (Schelske & Odum, 1961). This productivity is largely a result of dissolved and particulate autochthonous and allochthonous matter derived from the adjacent catchment. Within estuaries, aquatic macrophytes such as seagrass play a large role in the synthesis of organic material, both through their own growth and as a substrate for the epiphytes that grow on them (Sand-Jensen & Borum, 1991). Vascular plants growing in intertidal habitats, such as mangroves and saltmarsh, may also represent an important supply of allochthonous detrital material to support aquatic consumers (Josselyn & Mathieson, 1980). Despite their importance, these habitats have suffered extensive losses over the last 100–200 years (Creighton et al., 2015; Rogers et al., 2015; Taylor et al. in review), and it is hard to imagine that this has not led to concomitant effects on the overall productivity of exploited fishes.

Recent efforts to build a business case in support of the repair of estuarine habitats are reliant on demonstrable habitat–fishery linkages (Sheaves et al., 2014; Creighton et al., 2015; Taylor, 2016). Historically, such studies have sought to demonstrate this by broad-scale associations (e.g., Turner 1977), but in recent years other methods have been used to elucidate both direct (e.g., Sheaves et al., 2016; Becker & Taylor, 2017) and indirect (e.g., Fry & Ewel, 2003; Taylor et al. in review) interactions between such habitats and fisheries that depend on them. Stable isotopes are a powerful tool for quantifying trophic linkages between primary producers and exploited species (Fry, 2006), and provide an efficient means to characterize linkages between lower estuarine habitats and the exploited species that depend on those environments (Quan et al., 2007; Lebreton et al., 2011). Currently, the evidence for habitat–fishery linkages is conflicting, with some studies indicating dominant saltmarsh provisioning in lower estuaries (Deegan et al., 2002; Bergamino & Richoux, 2015; Eberhardt et al., 2015; Baker et al., 2016) and others suggesting a greater role of seagrass or benthic matter (Claudino et al., 2013; Connolly & Waltham, 2015; Garcia et al., 2017). Microphytobenthos can also be an important food source for estuary fishes (Ortega-Cisneros et al., 2016). It is possible that the conflicting results of previous studies were due to analyses conducted in single estuaries or on too few exploited species: exploring habitat–fishery links on a latitudinal scale and on a wide range of exploited taxa may help to address this issue. Defining habitat–fishery relationships in a quantitative fashion is essential to establish the potential economic outcomes that can result from habitat repair through trophic support of commercial and recreational fisheries productivity.

The Clarence and Hunter estuaries represent two of the most important estuarine commercial fisheries in south-eastern Australia, with a combined catch value of ~ AUD 20 million. Both these estuaries have in the past experienced significant habitat loss through the construction of drainage and flood mitigation works (Williams et al., 2000; Boys et al., 2012), and the Clarence estuary has also suffered extensive seagrass loss (Taylor et al. in review). This study employed stable isotopes to examine the linkages between emergent primary producers and key exploited species that comprise the majority of fisheries productivity in these modified ecosystems. Specifically, our objectives were to: (1) Characterize the isotopic composition of the main primary producers available in the lower estuarine ecosystem; (2) Apply a Bayesian mixing model to estimate the contribution of these various primary producers to fully recruited commercial species within the estuaries, and quantify the variation therein.

Materials and methods

Study systems

The Hunter estuary (− 32.90 S, 151.78 W) is a mature, wave-dominated barrier estuary (Roy et al., 2001) on the mid-north coast of New South Wales, Australia (Fig. 1). The catchment of the lower estuary includes a diverse range of urban, industrial, and agricultural land uses, with extensive modification to habitats in some areas. Fullerton Cove and Fern Bay are two off-channel embayment's which are important

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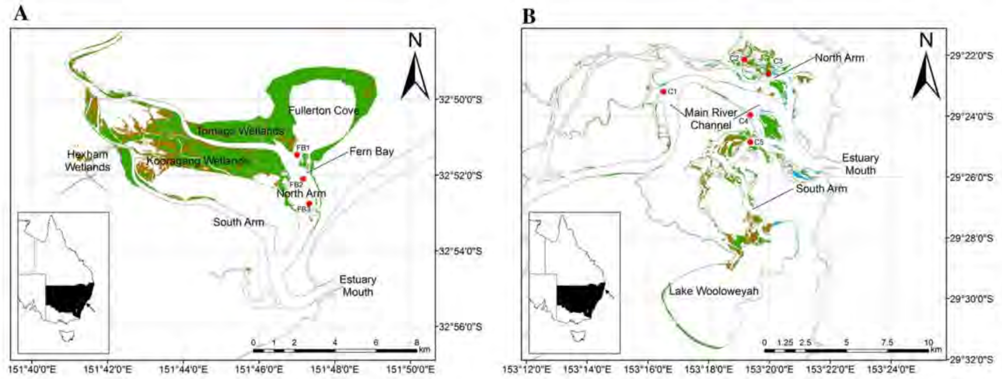

Fig. 1 Maps of the lower Hunter (**A**) and Clarence (**B**) estuaries, New South Wales, showing saltmarsh (shaded in brown), mangrove habitat (shaded in green), and remnant seagrasses (shaded in blue). Key features of the estuary referred to in the text are shown, and sampling locations are indicated by the red circles

features of the lower estuary. These areas are shallow, sedimentary habitats, and comprise over 70% of the fishable area within the entire estuary (Fig. 1), and are immediately adjacent are the rehabilitated Kooragang (Williams et al., 2000) and Tomago (Rayner & Glamore, 2010) wetlands. Collectively, this area of the lower estuary contains some of the most extensive wetland habitats of any estuary in New South Wales. While commercial fishing occurs from the ocean to Raymond Terrace (approximately 30 km from the ocean), the bulk of commercial harvest occurs in or adjacent to these habitats in the north arm of the lower estuary. The estuary supports a significant commercial fishery dominated by harvest of School Prawn *Metapenaeus macleayi* (Haswell, 1879), Mud Crab *Scylla serrata* (Forsskål, 1755), Luderick *Girella tricuspidata* (Quoy & Gaimard, 1824), Yellowfin Bream *Acanthopagrus australis* (Günther, 1859), Sea Mullet *Mugil cephalus* (Linnaeus, 1758), Dusky Flathead *Platycephalus fuscus* (Cuvier, 1829), Blue Swimmer Crab *Portunus armatus* (A. Milne Edwards, 1861) and Mulloway *Argyrosomus japonicus* (Temminck & Schlegel, 1844), and is an important nursery for Eastern King Prawn *Penaeus plebejus* (Hess, 1865). These species all have larval, juvenile and adult stages that persist within estuarine environments, although some species temporarily move to sea to spawn (Montgomery, 1990; Gray & Miskiewicz, 2000; Griffiths, 2001; Silberschneider & Gray, 2008; Gray et al., 2010). Consequently, the species assemblage examined in this study accumulates most of its biomass within estuarine systems, thus relying heavily on estuarine productivity.

The Clarence estuary (− 29.43 S, 153.37 W) is the largest estuarine system in New South Wales, and is also classified as a mature wave-dominated barrier estuary (Roy et al., 2001, Fig. 2). The upper and lower catchment is a mix of forested and agricultural land use (including aquaculture in the lower catchment), with several small townships along the estuary. The middle and lower estuary include a number of islands to the north and south of the main river channel, and Lake Wooloweyah (to the south) and the North Arm (to the north) are key off-channel features of the estuary. The lower estuary supports commercial harvest of a similar suite of species to the Hunter estuary, and formerly contained expansive seagrass beds which have now almost completely vanished (Taylor et al. in review, Fig. 2). The majority of the remaining saltmarsh habitat in the Clarence estuary is in the North Arm, and the deltaic islands between the main river channel and Lake Wooloweyah, whereas mangroves are present throughout the lower estuary.

Sample collection

All samples were collected in December 2015. In the Hunter estuary, 3 sites were sampled in Fern Bay (FB1–FB3; Fig. 1). This area has significant areal extent of mangrove habitat (562 ha, total catchment 12,586 ha), some saltmarsh habitat (41 ha; total catchment 7259 ha) and is adjacent to areas of

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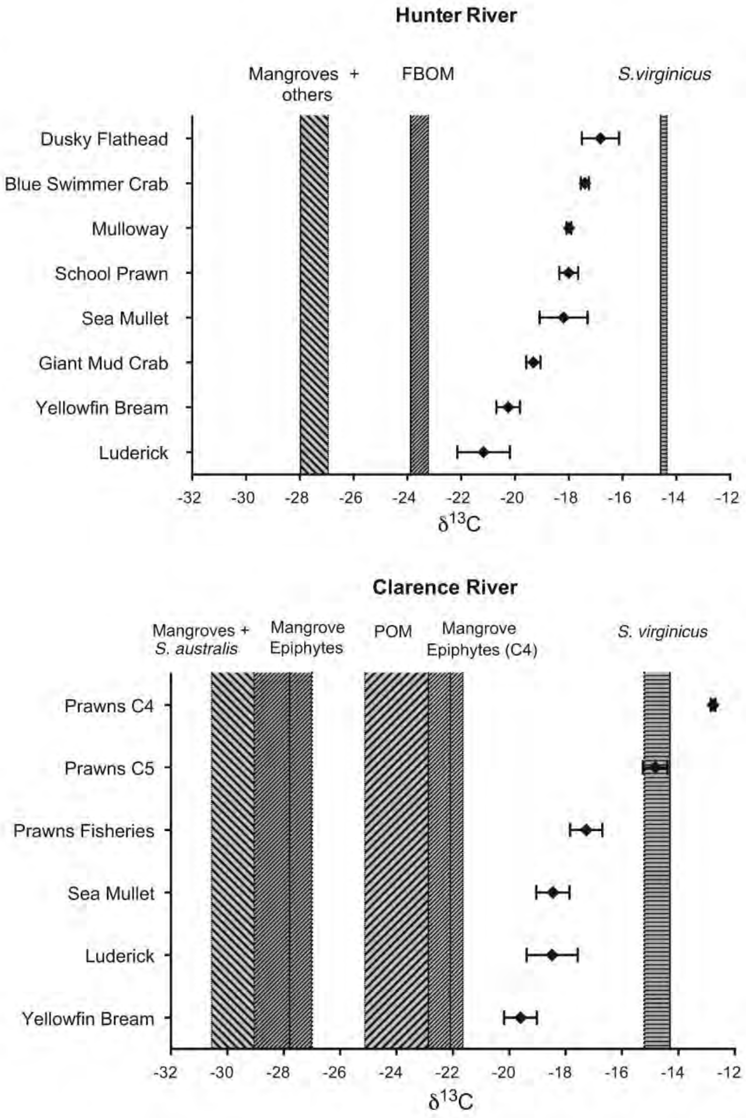
Fig. 2 Mean ± S.E. $\delta^{13}C$ signatures for each potential source and consumer in the Hunter and Clarence estuaries, New South Wales. These are raw values and do not account for isotopic fractionation. In the Hunter, 'mangrove and others' includes mangroves, mangrove epiphyte, *S. australis* and *S. quinqueflora*. In the Clarence, there were significant difference between signatures of sources across various sites, which is why there is more than one 'mangrove epiphyte' source



commercial harvest (see above). In the Clarence estuary, 5 sites were sampled from the northern arm (C1–C5; Fig. 2). The northern arm has comparable areal extent of mangrove (513 ha; total catchment 765 ha) to the Hunter estuary, but a greater areal extent of saltmarsh habitat (124 ha; total catchment 290 ha). Potential food sources for commercially important consumers, including mangrove, mangrove pneumatophore epiphyte, fine benthic organic matter (FBOM—analogous to microphytobenthos), *Sporobolus virginicus* (Salt Couch, (L.) Kunth), *Sarcocornia quinqueflora* (Beaded Samphire, Bunge ex Ung.-

Sternb.), *Sueda australis* (Austral Seablite, Thompson, 2003) and particulate organic matter (POM), were collected from all sites (where present) in both estuaries and immediately placed on ice and then frozen until processing. Plants and mangrove epiphytes were collected by hand. FBOM was separated from sediment by sieving using a method similar to Saintilan and Mazumder (2010), while POM was filtered from 1 l samples of seawater onto pre-combusted glass fiber filter paper. Seagrasses, which are often seen as an important nutrient source in estuaries (Melville & Connolly, 2005), do not occur in the Hunter estuary, and there are only remnant seagrass beds in the Clarence estuary mostly adjacent to the mouth of the estuary where no consumers were sampled. Consequently, seagrasses were not sampled for inclusion in the mixing models.

Commercial species were sampled in both estuaries by commercial operators, during the Austral summer 2016. Commercial contractors were commissioned to capture fish and crabs using standard commercial mesh nets and traps deployed in the regions where commercial effort was generally concentrated. Prawns were captured either through commercial or fishery-independent prawn trawling. Upon landing, animals were immediately placed on ice and then frozen until subsequent dissection and processing of muscle tissue.

Laboratory analysis

Frozen samples were thawed for preparation. Each consumer was processed individually to isolate isotopic signatures. In fishes, equal amounts of dorsal white muscle tissue were removed, while leg muscle was used for the two crab species, and muscle from the abdomen was used for the species of prawn. Tissues from potential sources and consumers were rinsed using distilled water to remove surface contaminants and placed in individual HCl-cleaned petri dishes and dried at 60°C for 24 h. Dried samples were then ground into fine powder using a Retsch Mixer Mill MM 200 and placed into aluminum caps (6–8 mg for plants and 1–2 mg for animal tissues) for isotopic analysis. Sieved FBOM material was analyzed similarly to other plant matter. POM samples were filtered onto pre-combusted glass fiber filter (GF/C) paper under low vacuum and placed in a drying oven for 60°C for 24 h, and then placed into glass vials for isotopic analysis. Stable isotope analysis was conducted at Griffith University, Queensland, using a Sercon Hydra 20–22 automated Isoprime Isotope Ratio Mass Spectrometer. The standard used to compare carbon isotope content was Pee Dee Belemnite Limestone Carbonate. Stable isotope composition was expressed in delta-notation using conventional formulae (Fry, 2006).

Nitrogen isotopes are frequently used in trophic assessments as they provide information on diet source as well as trophic level (Hussey et al., 2014; Choy et al., 2015). However, in this study, there is a high probability that δ^{15}N signatures would be affected by anthropogenic activities, which would increase the variability of the analyses and lower the likelihood of correctly attributing the proportions of source contributions to diets (Hadwen & Arthington, 2007). This is supported by the fact that generalized linear models run on our data suggested significant inter-site variation in δ^{15}N signatures of sources in both estuaries, indicative of anthropogenic impacts. δ^{15}N signatures are also greatly affected by large trophic enrichment factors (TEFs) that can vary inter- and intra-specifically from 2 to 7.6‰ (Hoen et al., 2014; McMahon et al., 2015); the TEFs for the consumers in this study are not well known. Preliminary analyses found that even when including a large standard deviation for the TEF of the species in this study (1.5‰) into Bayesian models, changes of 0.5 from the commonly accepted value of 3.4 could result in consumer distributions outside the bounds of the mixing region; this would result in unresolvable mixing models. The range of δ^{13}C values for autotrophic sources is much wider than for δ^{15}N (− 30 to − 10 vs 0.5–6), which means that even if δ^{15}N is included in analyses, the results will be primarily driven by δ^{13}C signatures. Considering that numerous other studies have encountered these issues and resolved to exclude δ^{15}N signatures from studies as a conservative measure (Melville & Connolly, 2005; Hadwen et al., 2007; Abrantes et al., 2015), this study did not use nitrogen isotopes and focused instead on δ^{13}C signatures, which have been used in similar conditions and are far less impacted by both TEFs and anthropogenic activities (Hadwen et al., 2007).

Data analyses

Sources were not present at all sites and the habitat ranges of the consumers in this study are not well known; therefore, a generalized linear model (GLM)

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was initially used to determine whether there were significant differences in δ^{13}C signatures between sources and sites across the two estuaries, with δ^{13}C values as the response variable and site and source as determinants. A GLM was deemed appropriate here, as the range of sample isotope values were highly variable between sources (i.e., POM and FBOM compared to mangroves) and numbers of source samples were low (= 3) at each site. While many studies do not statistically separate potential sources and sites (e.g., Melville & Connolly (2005)), our approach ensures that stable isotope data are used optimally within a Bayesian model framework. Since the likelihood of producing accurate predictions of the contributions of sources in a Bayesian model decreases with higher numbers of sources (Parnell et al., 2010), the GLM was also used to determine whether it was possible to pool sources and sites that were not significantly different from each other, thereby lowering the total number of sources in the model. *Metapenaeus macleayi* and *P. plebejus* were both were caught concurrently in the Clarence estuary, feed on similar sources (Taylor et al., 2016), and display minimal intra-estuarine movement (excluding spawning migrations) relative to commercial fishes (Taylor & Ko, 2011). Therefore, the samples of these two species of prawn were grouped under 'Prawns' at each Clarence estuary site.

Bayesian mixing models were used to determine the proportional contribution of the main food sources to each consumer species in the estuary, using SIMMR (Parnell et al., 2013, available at https://github.com/andrewcparnell/simmr) which has an updated Bayesian mixing model based off the SIAR package (Parnell et al., 2010). All analyses were conducted using R statistical package version 3.3.3 and RStudio version 1.0.136 (Team, 2013). Bayesian isotope mixing models make two primary assumptions: that all dietary sources are included in the analyses, and that there is complete mixing (Phillips et al., 2014). To meet the criteria for the former assumption, we attempted to sample all known dominant primary producers in each of these systems dominated by mangrove and saltmarsh habitats (Roy et al., 2001), and the species we sampled within those habitats were the known dominant saltmarsh and mangrove species (Saintilan et al., 2013). It is difficult to assess whether we included all potential sources in such open systems, however, we sampled all the known carbon sources typically used in research in this area (Melville & Connolly, 2003; Guest et al., 2006; Alderson et al., 2013; Connolly & Waltham, 2015), and all the isotope values of consumers were within the bounds of the isoscape set by our sources (with the exception of prawns at site C4 in the Clarence). While this cannot exclude the possibility of missing sources, it does suggest that we obtained an isotope 'range' of sources that is solvable by the model. To control for temporal variation that may affect results, the use of muscle tissue for our consumers is a relatively long-term indicator of diet preference, and this reduces the possible temporal variability in source availability. Finally, since we only measure the isotope values within muscle tissue, our model cannot explicitly determine the proportions of sources consumed, rather the proportion of sources absorbed into tissues.

Within the SIMMR framework, the trophic enrichment factor (TEF) for δ^{13}C was set to 1‰ (McCutchan et al., 2003; Abrantes et al., 2015). The standard deviation for the TEF was set to 1.5‰ as a conservative measure to reflect uncertainties around trophic levels and enrichment factors which are known to strongly affect Bayesian models (Caut et al., 2009; Bond & Diamond, 2011; Galván et al., 2012; Miller et al., 2013; Abrantes et al., 2015). Concentration dependencies were not incorporated because elemental concentration values of FBOM and POM were extremely diluted due to the presence of inorganic matter in FBOM and the use of filter paper (which does not affect isotopic analysis) for POM filtration. Organic proportions of FBOM and POM were likely ~ 3% of total weight: using concentration dependencies would have unrealistically increased the contribution of these sources by a factor of ~ 40. SIMMR does not directly incorporate trophic levels in corrections for trophic enrichment; so the TEF for consumer δ^{13}C signatures was multiplied by the trophic level above that of the sources, which are generally assumed to be at trophic level 1 (Feng et al., 2014). Trophic levels of *A. australis, A. japonicus, G. tricuspidata, P. fuscus, M. cephalus, S. serrata, P. armatus,* and *M. macleayi* (or 'Prawns' in the Clarence estuary) were assumed to be 2.5, 3, 2, 2.5, 2, 2, 2, and 2, respectively (following Melville & Connolly, 2005; Hadwen et al., 2007). Once the models were run, Gelman diagnostics were conducted to determine whether confidence intervals were close to 1 and below 1.1 and thus whether more simulations had to be included in the model. Only providing the mean contributions of each source with standard deviations may hide multimodality or the extent of variations in dietary preference within consumer populations (Semmens et al., 2013), and consequently probability densities were calculated using the density plot function in SIMMR.

Results

Source signatures

In the Hunter estuary mean source δ^{13}C signatures were generally depleted relative to consumers, except for *Sporobolus virginicus* which has a mean δ^{13}C signature more enriched (− 14.5 ± 0.1‰) than all producers in the data set (Table 1, Fig. 2). Generalized linear models for the Hunter estuary dataset indicated that δ^{13}C signatures of FBOM ($t = 2.26$, $P = 0.03$) and *S. virginicus* ($t = 7.65$, $P < 0.001$) were significantly different from all other producers, but there were no significant differences among mangrove (*Avicennia marina* (Forssk.) Vierh.), mangrove epiphyte, *S. australis* or *S. quinqueflora* δ^{13}C signatures. As a result, since Bayesian models would not be able to separate these sources due to their similar signatures (Parnell et al., 2013), these four sources were grouped into a single source for the following analyses (mean − 27.5 ± 0.5‰, Table 1, Fig. 2).

Mean source δ^{13}C signatures in the Clarence estuary followed similar patterns to those in the Hunter estuary, except for mangrove epiphyte that had a high standard deviation. For example, *S. virginicus* was the most enriched source (− 14.4 ± 0.1‰ at Site C4, Table 1, Fig. 2) and mangrove + *S. australis* was the most depleted (− 30.3 ± 0.2‰ at Clarence estuary Group, Table 1, Fig. 2). Mangrove epiphyte δ^{13}C signatures were highly variable, ranging from − 29 to − 22 across sites (Table 1, Fig. 2). Generalized linear models suggested that δ^{13}C signatures in sites C4 and C5 were significantly enriched compared to sites C1, C2, and C3 ($t = 2.42$, $P < 0.05$; $t = 3.58$, $P < 0.001$, respectively; see Supplementary Material 1). Mangrove epiphyte, POM, and *S. virginicus* had significantly higher δ^{13}C signatures than mangroves and other C3 saltmarsh plants ($t = 4.91$, $P < 0.001$; $t = 29.19$, $P < 0.001$, respectively). There were no significant differences between mangrove and *S. australis* δ^{13}C signatures ($t = 0.38$, $P = 0.70$); therefore, these two sources were grouped and data from

Table 1 Mean ± SE δ^{13}C signatures for grouped sources collected from Hunter estuary and different sites in the Clarence estuary, New South Wales

Estuary	Species	N	Mean δ^{13}C	S.E.	C:N
Hunter	FBOM	9	− 23.51	0.30	13.7
	Mangrove + Mangrove Epiphyte + *Sueda australis* + *Sarcocornia quinqueflora*	24	− 27.46	0.51	19.3
	Sporobulus virginicus	3	− 14.47	0.12	43.2
Clarence C4	POM	3	− 22.1	0	
	Mangrove + *Sueda australis*	6	− 28.56	0.17	23.5
	Mangrove Epiphyte	3	− 22.26	0.62	11.6
	Sporobulus virginicus	3	− 14.39	0.07	32.6
Clarence C5	POM	3	− 23.16	0.29	
	Mangrove + *Sueda australis*	3	− 28.03	0.24	29
	Mangrove Epiphyte	3	− 27.23	0.23	15.9
	Sporobulus virginicus	3	− 15.07	0.14	33.4
Clarence Cgroup (C1–C3)	POM	9	− 24.73	0.39	
	Mangrove + *Sueda australis*	9	− 30.34	0.21	61.2
	Mangrove Epiphyte	9	− 28.66	0.38	18.4
	Sporobulus virginicus	9	− 14.95	0.14	32.4

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sites C1, C2, and C3 were grouped into *Cgroup* (Table 1). Consumers had in some cases low variability in δ^{13}C signatures (e.g., Mulloway; Table 2), which is indicative of a constrained dietary preference, or high variability (e.g., Yellowfin Bream, Dusky Flathead and Luderick) that suggests a degree of omnivory.

Contribution to commercial species: Hunter estuary

In all species of consumers, except Yellowfin Bream and Luderick, the saltmarsh grass *S. virginicus* was estimated to be the source that supported the largest mean proportion of the diet (47–63%, Fig. 3) and had the lowest standard deviation (Table 2). Dusky Flathead had the greatest contribution of *S. virginicus* of all commercial species (63%; Fig. 3, Table 2). For Yellowfin Bream and Luderick, the largest contribution to diet was FBOM (39 and 41%, respectively). Other sources of diet had variable proportions of contributions and higher standard deviations, indicating that the model had difficulty separating those sources. However, confidence intervals of all Gelman diagnostics were < 1.02, suggesting that longer Bayesian simulation runs were not necessary. Across all species, *S. virginicus* probability densities had proportions of contribution within a narrow range of 0.4 (Supplemental Fig. 1). Probability densities of FBOM were more variable; however, the range of proportion of contributions varied from 0 to 1, indicating high variability of contribution across consumers. Mangrove and others had the lowest proportion, and a variable range of proportions, in addition to showing some bimodality towards the extremes of the range.

Contribution to commercial species: Clarence estuary

Sporobolous virginicus made up the largest proportion of contribution to diet in all consumers (40–95%), except Yellowfin Bream at site C4 which had a larger contribution of POM (30%; Fig. 4, Table 3). Prawns (*M. macleayi* + *P. plebejus*) had the highest contribution of *S. virginicus* at all sites (95, 89 and 72% for sites C4, C5 and Cgroup, respectively). Dusky Flathead had the next highest contribution of *S. virginicus* at all sites (53, 65 and 69% for sites C4, C5 and Cgroup, respectively; Tables 3 and 4, 5). Confidence intervals of Gelman diagnostics were < 1.02, suggesting that longer Bayesian simulation runs were not necessary. Across all sites, probability distributions were generally left-skewed (high probability of low proportions) for all sources except *S. virginicus*, which was generally right-skewed (high probability of higher proportion; Supplemental Figs. 2, 3 and 4). POM and mangrove epiphytes had the widest range of

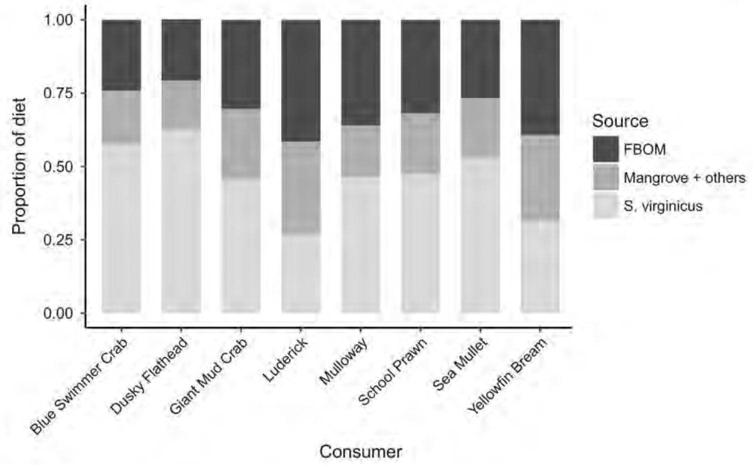
Table 2 Mean proportion (and standard deviation in brackets) of contribution to diet for commercially exploited consumers in the Hunter estuary, as predicted by Bayesian mixing models from δ^{13}C

Consumer	*n*	FBOM	Mangrove + others	*S. virginicus*	SD ^{13}C
Acanthopagrus australis					
Yellowfin Bream	26	**0.392 (0.222)**	0.292 (0.154)	0.316 (0.080)	1.873
Argyrosomus japonicas					
Mulloway	12	0.360 (0.113)	0.175 (0.078)	**0.465 (0.047)**	0.315
Platycephalus fuscus					
Dusky Flathead	10	0.208 (0.188)	0.166 (0.083)	**0.627 (0.083)**	2.183
Girella tricuspidata					
Luderick	6	**0.414 (0.238)**	0.315 (0.174)	0.270 (0.119)	2.542
Mugil cephalus					
Sea Mullet	10	0.267 (0.151)	0.200 (0.106)	**0.533 (0.108)**	3.046
Scylla serrata					
Giant Mud Crab	47	0.303 (0.169)	0.241 (0.118)	**0.456 (0.057)**	1.371
Portunus armatus					
Blue Swimmer Crab	3	0.241 (0.147)	0.183 (0.113)	**0.576 (0.143)**	2.275
Metapenaeus macleayi					
School Prawn	11	0.318 (0.144)	0.208 (0.100)	0.474 (0.060)	0.656

Values in bold are the greatest contribution for that consumer

Mangrove + others: mangrove, mangrove epiphyte, *S. australis* and *S. quiqueflora*

Fig. 3 Stacked bar plot showing mean proportion of contribution to diet from each source for commercially exploited consumers in the Hunter estuary, as calculated using Bayesian mixing models and δ^{13}C. In the Hunter, 'mangrove and others' includes mangroves (Avicennia marina), mangrove epiphyte, *S. australis* and *S. quinqueflora*



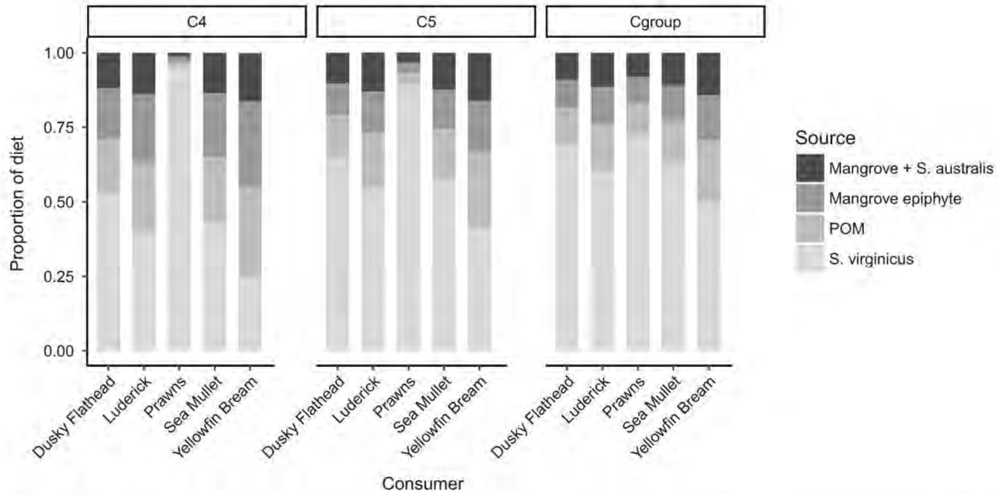


Fig. 4 Stacked bar plot showing mean proportion of contribution to diet of each source for each commercially exploited consumer in the Clarence estuary at sites C4, C5, and grouped sites 1, 2, and 3, as calculated using Bayesian mixing models from δ13C. 'Prawns' indicate School Prawns and Eastern King Prawns.'Mangrove' was exclusively the dominant Avicennia marina

proportions, in some cases ranging to 100%. Unlike the Hunter estuary, no bimodality was evident across any source or site.

Discussion

This study presents data from two estuaries separated by over 3 degrees of latitude (525 km) that point to similar conclusions regarding habitat–fishery linkages for key exploited species in eastern Australia. Saltmarsh-derived carbon was usually a large source of

Table 3 Mean proportion (and standard deviation) of contribution to diet for commercially exploited consumers in the Clarence estuary site C4, as predicted by Bayesian mixing models from $\delta^{13}C$

Consumer	*n*	POM	Mangrove + *S. australis*	Mangrove epiphyte	*S. virginicus*	SD ^{13}C
Acanthopagrus australis						
Yellowfin Bream	14	**0.296 (0.206)**	0.162 (0.104)	0.289 (0.204)	0.252 (0.108)	2.150
Platycephalus fuscus						
Dusky Flathead	14	0.179 (0.117)	0.118 (0.065)	0.172 (0.112)	**0.531 (0.065)**	0.808
Girella tricuspidata						
Luderick	13	0.230 (0.161)	0.138 (0.085)	0.229 (0.160)	**0.403 (0.131)**	3.572
Mugil cephalus						
Sea Mullet	14	0.217 (0.108)	0.134 (0.151)	0.213 (0.106)	**0.436 (0.071)**	2.245
Metapenaeus macleayi + *Penaeus plebejus*						
Prawns	17	0.018 (0.013)	0.012 (0.008)	0.018 (0.013)	**0.952 (0.021)**	0.465

Values in bold are the greatest contribution for that consumer

Table 4 Mean proportion (and standard deviation) of contribution to diet for commercially exploited consumers in the Clarence estuary site C5, as predicted by Bayesian mixing models from $\delta^{13}C$

Consumer	*n*	POM	Mangrove + *S. australis*	Mangrove epiphyte	*S. virginicus*	SD ^{13}C
Acanthopagrus australis						
Yellowfin Bream	14	0.251 (0.169)	0.159 (0.099)	0.172 (0.109)	**0.417 (0.087)**	2.230
Platycephalus fuscus						
Dusky Flathead	14	0.139 (0.090)	0.101 (0.057)	0.107 (0.062)	**0.653 (0.046)**	0.708
Girella tricuspidata						
Luderick	13	0.191 (0.134)	0.130 (0.081)	0.136 (0.087)	**0.544 (0.109)**	3.544
Mugil cephalus						
Sea Mullet	14	0.172 (0.115)	0.123 (0.073)	0.130 (0.077)	**0.575 (0.074)**	2.206
Metapenaeus macleayi + *Penaeus plebejus*						
Prawns	20	0.042 (0.029)	0.033 (0.020)	0.034 (0.022)	**0.892 (0.038)**	1.559

Values in bold are the greatest contribution for that consumer

nutrition for most species in both the Hunter and Clarence estuaries, ranging from 25 to 95% of diet contribution. For each of the exceptions, fine benthic organic material (Luderick and Yellowfin Bream in the Hunter estuary) or particulate organic matter (Yellowfin Bream at site C4) was the dominant producer source. The extreme contribution of *S. virginicus* to prawns at sites C4 and C5 of the Clarence estuary suggests some contribution of seagrass. While there is some uncertainty around the exact proportions contributed by these dominant sources, this study suggests that, in all cases, the saltmarsh plant *S. virginicus* is an important source of carbon for many estuarine species. These findings are significant as they highlight a clear link between estuarine habitats of conservation concern, and exploited species that underpin important estuarine fisheries.

Habitat–fishery linkages

Elucidating the autotrophic sources of estuarine food webs provides an additional means of assessing the relative value of vegetated habitats, particularly where consumers are spatially separated from the sources providing their nutritional base (Hindell & Warry, 2010). The importance of saltmarsh-derived material

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Table 5 Mean proportion (and standard deviation) of contribution to diet for commercially exploited consumers in the Clarence estuary site Cgroup, as predicted by Bayesian mixing models from $\delta^{13}C$

Consumer	*n*	POM	Mangrove + *S. australis*	Mangrove epiphyte	*S. virginicus*	SD ^{13}C
Acanthopagrus australis						
Yellowfin Bream	14	0.205 (0.135)	0.142 (0.085)	0.152 (0.093)	**0.501 (0.069)**	2.159
Platycephalus fuscus						
Dusky Flathead	14	0.121 (0.074)	0.089 (0.049)	0.096 (0.053)	**0.694 (0.038)**	0.648
Girella tricuspidata						
Luderick	13	0.157 (0.109)	0.113 (0.069)	0.124 (0.079)	**0.606 (0.093)**	3.533
Mugil cephalus						
Sea Mullet	14	0.144 (0.095)	0.109 (0.062)	0.116 (0.070)	**0.631 (0.061)**	2.160
Metapenaeus macleayi + *Penaeus plebejus*						
Prawns	48	0.108 (0.069)	0.080 (0.047)	0.087 (0.051)	**0.724 (0.050)**	3.894

Values in bold are the greatest contribution for that consumer

to the estuarine foodwebs, and in particular for such a broad cross section of exploited fish and crustaceans, was surprising. Here, we found that the probability distributions of source contributions were narrower for *S. virginicus* and wider for other sources: this suggests that *S. virginicus* is consistently a large carbon source for consumers, but that other sources have varied levels of contributions across consumers. Studies that have examined the contribution of saltmarsh to fish diet generally found that saltmarsh had smaller confidence intervals compared to other sources, but did not provide the largest contribution (Melville & Connolly, 2003; Connolly et al., 2005; Garcia et al., 2017). Those same studies also generally had lower feasible contributions from FBOM, which was usually the second largest contributor in our study. For example, Melville and Connolly (2003) estimated saltmarsh to contribute 0–21%, mangroves 0–20%, POM 0–42%, and seagrass 1–64% of Yellowfin Bream diets. For Giant Mud Crab, previous research had estimated that mangroves contribute 0–40% and seagrass/saltmarsh 40–80% (Connolly & Waltham, 2015). Part of this discrepancy can be explained by the differences in source isotope signatures recorded in previous studies, which may be indicative of C_3 rather than C_4 plants (e.g., saltmarsh signatures of $-$ 26.5‰, Connolly et al., 2005; Melville & Connolly, 2005), as well as having a large number of sources with similar isotopic signatures that could not be distinguished (Connolly & Waltham, 2015). By a smaller number of sources with distinct isotopic signatures, our analyses provide relatively strong evidence that saltmarsh habitats contribute substantially to commercial species of fish and crustaceans in temperate estuaries.

Although saltmarsh has been shown to make an important contribution to the nutrition of penaeid prawns (Abrantes & Sheaves, 2009; Taylor et al. in review), there is little evidence that saltmarsh supports other commercial species in temperate marshes (Abrantes et al., 2015). In fact, evidence suggests there is little impact of saltmarsh beyond their borders (Hyndes et al., 2014), which is potentially a consequence of Australian saltmarsh systems being located high in the intertidal zone and infrequently inundated (Hollingsworth & Connolly, 2006; Becker & Taylor, 2017). Furthermore, due to the low nutritional status of mangrove leaves (Connolly & Waltham, 2015), many studies have found little impact of mangroves to adjacent systems beyond the forest boundary (Loneragan et al., 1997; Bouillon et al., 2008). Despite this, movement of carbon can occur at multiple spatial scales within estuarine systems (Melville & Connolly, 2005; Gaston et al., 2006; Guest et al., 2006), and organisms can derive nutrition from both their immediate area of occupation, and from adjacent habitats. In the Hunter and Clarence estuaries, the distribution of saltmarsh is not continuous, but there is substantial water movement (both flow and tidal exchange) which facilitates mixing and transport of organic matter throughout these systems. In addition, while the relative proportions of the cover of saltmarsh plants in these estuaries is not known, the $\delta^{13}C$ signature of saltmarsh (*S. virginicus*) is relatively consistent within and between estuaries, and is significantly enriched in ^{13}C relative to other basal saltmarsh and mangrove resources (Melville & Connolly, 2003). Both the Clarence and Hunter estuary are seagrass limited systems, and saltmarsh is the only enriched ^{13}C basal resource in the Hunter estuary. In the Clarence the areal extent of saltmarsh is much greater than seagrass and seagrass is concentrated near the mouth of the estuary. Together, these points give confidence in the finding that saltmarsh is a significant nutritional source for commercially important fish and crustaceans.

The mechanism through which saltmarsh productivity contributes significantly to the diets of commercial fishes and crustaceans is not well understood, especially since the saltmarsh surface is not often directly used by commercial species in Australian estuaries (Connolly et al., 1997; Becker & Taylor, 2017). Primary production in saltmarshes (1.38 kg C m^{-2} year^{-1}) is known to be much higher than other estuary habitats and nearly three times that of seagrasses (0.46 kg C m^{-2} year^{-1}, see Hyndes et al. (2014)). Also, the productivity of *S. virginicus,* the dominant saltmarsh plant examined in our study, is higher than other saltmarsh species and has been estimated at 1.50 kg C m^{-2} year^{-1} (Linthurst & Reimold, 1978). Previous work suggests that 3–63% of this productivity is exported out of these saltmarsh habitats in the form of dissolved organic carbon (DOC) through tidal transport (Rozas, 1995; Taylor & Allanson, 1995) before being processed by benthic and epibenthic biota (Svensson et al., 2007) and transferred through the food web. Another potential avenue for carbon export is through intensive feeding by consumers on saltmarsh-associated invertebrates during inundation (Whitfield, 2017), where saltmarshes have been shown to be an important source for transient fish (West & Zedler, 2000; Laffaille et al., 2001). Finally, saltmarsh wrack is likely to be transported during tidal events, where particulate organic carbon can be processed by benthic and epibenthic consumers, such as mysids (Fockedey & Mees, 1999) and amphipods (Zagursky & Feller, 1985). A majority of the species in our study that display a high contribution of saltmarsh have a high contribution of these pericarid crustaceans in their diet (Pease et al., 1981). Thus, the high productivity and high export rates of saltmarshes provides a plausible mechanism through which these habitats can indirectly support a broad range of commercially important species of fish and crustaceans.

The three dominant species of saltmarsh plant were examined here, yet only one (*S. virginicus*) appeared to be contributing to the diets of exploited estuary species. The difference in contribution to diets of these closely associated C3 and C4 saltmarsh plants may explain the discrepancies between our study and other studies that generally consider saltmarsh contribution to be low (e.g. Connolly et al., 2005; Selleslagh et al., 2015): if only a single saltmarsh species (or only C3 species) is sampled, contributors to diets of estuary species may not be detected. While there is currently no information on the relative areal coverage of each saltmarsh plant in these regions, it is commonly thought that *S. virginicus* is the most common plant. However, differences in areal extent alone are unlikely to explain the differences in source contributions. Unlike the other species, *S. virginicus* is a C4 pathway plant (Marcum & Murdoch, 1992) generally perceived to have lower digestibility (Wilson & Hacker, 1987; Wilson & Hattersley, 1989) though they may be more palatable to fishes than C3 plants (McMahon et al., 2005). In saltmarshes, C4 plants are thought to decompose at a faster rate than C3 plants (Haines, 1976), and *S. virginicus* growth rates are generally higher than sympatric C3 plants (Linthurst & Reimold, 1978). Thus, *S. virginicus* may disproportionally contribute to the diets of exploited species relative to other saltmarsh plants because it is more biologically available to consumers. It is possible that in saltmarshes which have few or no C4 plants, the contributions of saltmarsh to fisheries productivity are lower.

Fine benthic organic matter (FBOM) and particular organic matter (POM) were consistently the second-most important contributor, and for some species (e.g., *A. australis*), they were the dominant source. Previous studies have suggested that microphytobenthos could be the most important primary producer in estuary and coastal lagoon systems (Webster et al., 2002), and that carbon produced by microphytobenthos was rapidly absorbed by various organisms within aquatic environments (Middelburg et al., 2000), especially benthic and epibenthic invertebrates (Kanaya et al., 2008). In some cases, it has been suggested that high contributions of microphytobenthos could be related to losses of saltmarsh (Svensson et al., 2007). While both the Hunter and Clarence estuaries have lost significant amounts of saltmarsh habitat, the area available to microphytobenthos (read: sedimentary environment) has remained relatively constant, although both systems are relatively turbid which may constrain productivity. While our results highlight the importance of microphytobenthos for fisheries productivity, it is possible that habitat rehabilitation and recolonization of saltmarsh may reduce the proportional contribution of FBOM and POM measured here.

Some examples have suggested that mangroves are a dominant autotrophic carbon source in estuarine environments (e.g., Islam & Haque, 2004); yet in this study, mangroves consistently provided the smallest proportion of carbon to commercial species of fish. It could even be suggested that mangroves made no contribution to the diets of consumers assessed here, and that mangroves should be removed from our analyses because the isotope signatures of most consumers were above more enriched sources already included in the Bayesian models. Nevertheless, here we chose to include mangroves in our analyses because mangroves were isotopically indistinguishable from other, less well-understood sources, and because some consumers had isotope signatures that require the presence of a more depleted source to not violate Bayesian model assumptions. While the nursery role of mangroves is reasonably well accepted (Kimirei et al., 2013) with some exceptions (Sheaves, 2017), global assessments have found that fish associated with mangroves are often supported by food from adjacent habitats (Igulu et al., 2013). The relatively low productivity of mangroves compared to saltmarsh plants or macrophytes (White et al., 1978; Komiyama et al., 2008) may contribute to a lower proportion of mangrove-derived carbon in our study. Furthermore, the 'toughness' of leaf litter is inversely correlated with consumption by grazers (Motomori et al., 2001), and mangrove trees produce tough leaves with waxy cuticles (Choong et al., 1992) that may make it more difficult to access nutrient than saltmarsh leaves. Consequently, the bioavailability of carbon produced by saltmarsh plants is likely to be higher, and may explain the relative differences in contribution of these two producers.

Technical considerations and assumptions

The determination of the exact contribution of each basal resource to a particular consumer is usually not feasible because the number of major basal resource pools often exceeds the number of stable isotope ratios (Layman et al., 2007), or there is overlap in the stable isotope ratio of basal resources. For example, seagrasses and C_4 saltmarsh plants share a similar stable carbon isotope ratio, although seagrass $\delta^{13}C$ isotope signatures (− 9 to − 12.5‰) are generally enriched relative to saltmarsh (− 15.9‰; Connolly & Waltham, 2015), and was measured at ~ − 14.8‰ in this study. Other studies have found that in seagrass-dominated communities, seagrass can represent the dominant source of carbon for consumers (Loneragan et al., 1997; Connolly & Waltham, 2015). However, neither the Hunter nor the Clarence estuaries are seagrass-dominated systems, as there are no seagrasses in the Hunter, and the areal extent of seagrasses in the Clarence estuary is approximately 7% of the total vegetated area (Industries 2017). While we cannot exclude the possibility of seagrass wrack being transported throughout the estuary by tidal movements (Whitfield, 1988), increasing distance to seagrass has been negatively correlated with $\delta^{13}C$ isotope signatures (Connolly & Waltham, 2015).The distances to seagrass meadows in our study are in some instances greater than 5 km; therefore, it is unlikely that the highly enriched signatures measured here are related to seagrass provisioning, except for prawns at sites C4 and C5 in the Clarence which are enriched above that of *S. virginicus*. We stress that there is a degree of uncertainty associated with the exact contributions of each source to consumer diet, and that we cannot exclude seagrass from affecting the calculated contribution of *S. virginicus* with the dataset presented.

In estuarine systems where seagrasses are not present either due to anthropogenic activities or natural variability, it is possible that saltmarshes fill the productivity niche that an absence of seagrasses may create (Ricklefs, 2010). If seagrasses were more abundant in the Clarence estuary and represented a larger contribution to consumer diet, consumer signatures would be further enriched above that of saltmarsh $\delta^{13}C$ signatures after correction for trophic fractionation. This prediction is generally not in accordance with the consumer isotope signatures measured in this study, which when considered with the limited areal extent (see above) and position of seagrass within the estuary, suggest that seagrass is probably not a major source of carbon in the Clarence

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estuary. Furthermore, if seagrasses were a significant contributor to consumer diet, the close proximity of saltmarsh signatures may make it difficult for Bayesian models to separate the contributions of these two carbon sources. Similar difficulties separating seagrass signatures from other sources were encountered by Connolly and Waltham (2015) and Melville and Connolly (2005), and both of those studies decided to amalgamate seagrasses and saltmarshes into one source. In our study, since all consumers in the Clarence estuary have δ^{13}C signatures that are equal or depleted relative to saltmarshes after accounting for trophic fractionation (bar prawns at sites C4 and C5), even the addition of a significantly different and less depleted seagrass source (obtained from Lake Macquarie, NSW) would still attribute a greater contribution by the saltmarsh than the seagrass (see Supplementary Material 2). While our study does not account for a seagrass source, it is important to note that a portion of the contribution attributed to saltmarshes could potentially be derived from seagrasses in the Clarence estuary, but the limited coverage of seagrass in the Clarence estuary makes this less likely for the species analyzed. Using additional isotope markers such as sulfur, which is known to further distinguish autotrophs and have low levels of fractionation (Connolly et al., 2004) would add another dimension for models to analyze and assist in the separation of these two sources to determine the respective roles of saltmarsh and seagrasses in estuarine trophic ecology.

Concluding comments

These findings are significant in that they quantitatively demonstrate an indirect link between intertidal estuarine habitats and fishery productivity. As highlighted in the Introduction, loss of such habitats is a pervasive problem, and may lead to a reduction in overall primary productivity, which could have concomitant impacts on the secondary consumers and higher trophic levels that support fishery output. Quantifying links between estuarine habitats and productivity is a fundamental step in building a case for repair of degraded habitats, and such links can even underpin assessments of the economic value of habitats that are derived through fishery productivity. The results presented here indicate that saltmarsh habitats are particularly important for most of our study species across both systems; but this habitat has experienced some of the most substantial losses in temperate Australian estuaries (Rogers et al., 2015; Taylor et al. in review; Taylor et al., 2017). For example, in the Hawkesbury estuary (just south of Newcastle), losses of saltmarsh cover were estimated to range up to 96% since the 1960s (Williams & Thiebaud, 2007), and losses in the Koorang wetland in the Hunter estuary were similar (Williams et al., 2000). These habitat–fishery linkages highlight that fisheries are likely to be one of the key beneficiaries of enhanced ecosystem services arising from future habitat repair (Creighton et al., 2015).

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Appendix 11 – The economic value of fisheries harvest supported from saltmarsh and mangrove productivity in two temperate Australian estuaries

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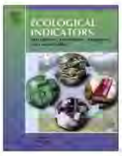

Research paper

The economic value of fisheries harvest supported by saltmarsh and mangrove productivity in two Australian estuaries

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ABSTRACT

Broad-scale links between productivity of estuarine habitats (such as saltmarsh and mangrove) and the exploited species that rely on them have often been used to build a case for habitat conservation and repair. Stable isotope composition can provide a temporally and spatially integrated measure of trophic connectivity with which to quantify habitat-fishery linkages, allowing primary producers that comprise these habitats to be linked with harvested biomass with relatively few assumptions. We present a novel model that applies this approach to estimate the economic value of fisheries harvest derived from dominant estuarine habitats, in two eastern Australian estuaries. Estimated values of fisheries harvest supported by habitats within the model regions ranged from ~AUD100,000 y^{-1} to ~AUD7,200,000 y^{-1}. Saltmarsh in the Clarence River had by far the greatest economic value per-unit-area, with an average estimated Total Economic Output (from fisheries harvest) of AUD25,741 ha^{-1} y^{-1}, whereas mangrove was estimated to be AUD5,297 ha^{-1} y^{-1}. Average Total Economic Output in the Hunter River was AUD2,579 ha^{-1} y^{-1} and AUD316 ha^{-1} y^{-1} for saltmarsh and mangrove habitats respectively. Estuarine habitats are key ecological indicators of fisheries productivity, and the framework presented here will be broadly useful in estimating the potential economic impacts associated with changes in these indicators.

1. Introduction

Estuaries represent the interface between land and sea, and while these ecosystems provide a highly productive environment, they can also be subject to substantial anthropogenic modification (such as habitat loss). Many exploited species rely on the various resources available in estuarine systems for one or more life-history stages (Abrantes et al., 2015), such as favorable physico-chemical conditions conducive to optimal juvenile growth, structural habitats that provide a refuge from predation, and productive trophic resources (Beck et al., 2001). Consequently, habitat loss and concomitant effects on these resources can adversely affect ecosystem services such as fisheries production, either through effects on mortality and growth of early life-history stages, or through impacts on the productivity of exploited size-classes that rely on food webs supported by vascular primary producers. Any decline in ecosystem services has an economic cost, but estimating this cost ultimately relies on quantifying the monetary value of the services and linking back to the habitats that support them (Barbier et al., 2011).

The valuation of ecosystem services is increasingly being employed to support an economic case for habitat conservation and repair. Such valuation also supports national environmental accounting (e.g. the System of Environmental-Economic Accounting [SEEA], Bureau of Meteorology, 2013), where expenditures for protection or costs of degradation of environmental assets (such as fish habitat) are quantified relative to production gains or losses (Food and Agriculture Organization of the United Nations, 2004). Valuation of ecosystem services derived from fish habitat is essential for considering environmental assets in monetary terms, but examples of this are rare as it requires a quantitative measure of the linkages between estuarine habitats, the fish stocks they support, and the value of those fish stocks (i.e. quantifying habitat-fishery linkages). Such valuations are usually system-specific (Grabowski et al., 2012), and even a small subset of the available literature demonstrates that there is substantial variation in such estimates across species, systems and habitats, and across different valuation approaches. For example, Watson et al. (1993) estimated potential economic values of AUD72–AUD11,084 ha^{-1} y^{-1} (here and after, all values are converted to 2015 dollars) from prawn harvest derived from the standing stock of juveniles in seagrass in northern Australia; whereas Blandon and zu Ermgassen (2014a) used a similar

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approach across multiple species in south-eastern Australia, and estimated the benefits of seagrass to commercial fisheries production was around AUD31,650 $\text{ha}^{-1}\,\text{y}^{-1}$ (Blandon and zu Ermgassen, 2014b). Chong (2007) estimated the net fisheries contribution of mangrove forest (across multiple species) in Malaysia amounted to about USD967 $\text{ha}^{-1}\,\text{y}^{-1}$, and Bell (1997) calculated that coastal saltmarsh in the Gulf of Mexico supported recreational fisheries up to a value of USD36,902 $\text{ha}^{-1}\,\text{y}^{-1}$ (converted from value-per-acre). This variation highlights a need to further refine estimation of economic values across multiple habitats and estuarine ecosystems. Although many methods exist to achieve this, using trophic relationships as a basis for these linkages may represent an efficient method that can be applied in a similar fashion across multiple systems.

Both physical and biological connectivity mediate the transfer of resources from productive intertidal estuarine habitats (such as mangrove and saltmarsh) to adjacent sub-tidal habitats. Mangrove habitats are inundated relatively frequently, and although recent work has questioned the extent to which fish directly interact with these habitats (Sheaves, 2017), there is evidence of broader exchange of mangrove-derived productivity and other areas in the estuary (Bouillon et al., 2008). In southern Australian estuaries, high elevation of saltmarsh habitats mean there are lower rates of inundation during which larger nekton can directly access the marsh surface (Becker and Taylor, 2017; Connolly et al., 1997). However, the movement of carbon synthesized on the marsh surface, either through the transport of particulate material (e.g. Abrantes and Sheaves, 2009; Melville and Connolly, 2005) or the movement of primary consumers and other nekton (e.g. Guest and Connolly, 2004, albeit over small scales), has been shown to link saltmarsh productivity with adjacent areas. Consequently, the transport of carbon from intertidal habitats can provide an important trophic resource for animals in other parts of the estuary (Abrantes et al., 2015).

While there is a long history of research that deals with the trophic linkages between various primary producers and exploited species in estuaries (e.g. Dittel et al., 2006; Hadwen et al., 2007; Loneragan et al., 1997; Selleslagh et al., 2015), these studies are rarely extended to estimate the actual fisheries impact of these primary producers. Modelling source contributions from stable isotope composition is ideal for establishing the trophic resources underpinning fisheries productivity. Stable isotopes can provide a temporally and spatially integrated measure of this contribution in fish of harvestable size that can be directly linked to the harvested biomass with relatively few assumptions. This manuscript provides two case studies that demonstrate a novel model to establish habitat-fishery linkages and derive associated economic value using trophic relationships established through stable isotopes.

2. Materials and methods

2.1. Description of the study systems

The Hunter River estuary (−32.90, 151.78) is a mature wave-dominated barrier estuary and important fishery on the mid-north coast of New South Wales, Australia (Fig. 1), particularly for crustacean species. Wave dominated barrier estuaries are often characterized by high coverage of mangrove and saltmarsh habitat, and generally support high productivity of important commercial species such as *Metapenaeus macleayi* (School Prawn; the species supporting the highest prawn harvest by biomass in New South Wales), *Mugil cephalus* (Sea Mullet; the species supporting the highest fish harvest by biomass in New South Wales), *Girella tricuspidata* (Luderick) and *Scylla serrata* (Mud Crab, Pease, 1999; Saintilan, 2004). The Clarence River estuary (−29.43, 153.37) is the largest estuarine system in New South Wales, and supports the state's largest estuarine fishery similarly dominated by harvest of School Prawn and Sea Mullet. Overall, the catchment is a mix of forested and agricultural land use, and areas adjacent to the lower watershed are dominated by agriculture and aquaculture. The Clarence River estuary shares similar geomorphological attributes and a similar species assemblage to the Hunter River estuary. In both estuaries, a model region was specified that dealt with the areas between the mouth of the estuary and ~20 km from the mouth, since this is where much of the commercial harvest takes place (Fig. 1).

2.2. Overview of framework

A summary of the biology of exploited species examined in this study is provided in Table 1; all species investigated were estuarine-dependent or -resident, and primarily harvested within estuarine systems. We used the contributions of saltmarsh and mangrove plants to the biomass of these exploited species as modelled from stable isotope composition (Tables 2 and 3; and see Supplementary information) for the Hunter and Clarence Rivers, to apportion the commercial harvest biomass that was derived from these habitats. We then applied a simple market value at first-point-of-sale to establish the Gross Value of Production, as well as an economic multiplier (calculated from the economic data presented in Voyer et al., 2016) to convert the Gross Value of Production to Total Economic Output (described below). Simulations were conducted within a Monte-Carlo Analysis of Uncertainty (MCAoU) framework, and model parameters were thus provided as distributions where possible (see Tables 2 and 3). While this framework represents the union of a simple set of relationships to link habitats with species harvested in an estuary and the value of that harvest, it is important to highlight there are two main assumptions associated with the approach: 1) that modelling of stable isotopes effectively describes trophic relationships; and 2) that the fishery and market price data are accurate. The effects of these assumptions on model estimates are elaborated in the Discussion.

2.3. Parameterisation and modelling

Stable isotope data for dominant primary producers in the estuary (see Supplementary information) was used to derive average source contributions for commercially sized individuals in the Hunter and Clarence River, and errors around these contributions (Tables 2 and 3). Economic value was derived using the formula:

$$GVP_{s,p} = C_{s,p} \cdot H_s \cdot M_s \cdot P_s$$

where $GVP_{s,p}$ is the Gross Value of Production (AUD y^{-1}) of species s derived from primary producer p within the model region (the lower estuary; Fig. 1), $C_{s,p}$ is the proportional contribution of primary producer p for species s derived from stable isotope measurements and associated modelling, H_s is the annual harvest of species s (kg y^{-1}), M_s is the market value for species s (AUD kg^{-1}), and P_s is the spatial partitioning coefficient for species s (see below). Collectively $H_s \cdot M_s$ represent the total GVP for species s in the entire estuary (GVP_s, AUD y^{-1}), $C_{s,p}$ apportions that GVP among primary producers in the estuary, and P_s further refines GVP to account for the relevant section of the estuary. Commercial catch data was extracted from the NSW DPI Commercial Catch and Effort Reporting System (see http://www.dpi.nsw.gov.au/fishing/commercial/catch-effort), and annual harvest (mean and variance, Tables 2 and 3) was estimated on the basis of catch reporting for each estuary for the 10 years between 2005/06 and 2014/15. This period included a range of both wet years (2008–13) and dry years (2005–08, and 2013–15). The panel of species modelled (Table 1) represented approximately 85% of the commercial harvest biomass in these estuaries. Market price was estimated from CPI-corrected (consumer price index) Sydney Fish Market values across the same time period (extracted from records compiled in the NSW DPI Resource Assessment System).

Estuarine catch in New South Wales is reported by fishers at the estuary level only. Although the bulk of species biomass often tends to

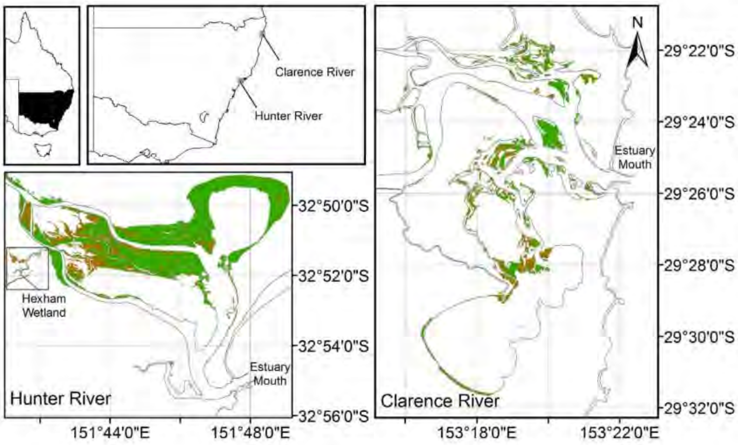

Fig. 1. Map of the model regions (defined by the spatial extent of the inset panels) in the lower Hunter River estuary, and the lower Clarence River estuary, New South Wales. The map shows saltmarsh (shaded in brown) and mangrove habitat (shaded in green) present within the model region in each system. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of life history and fishery characteristics for species modelled in this study, including the minimum size at which each species can be legally retained, and references summarizing aspects of the species life history.

Species name	Common name	Min. size (cm)	Life history and fishery[b]	Relevant references[e]
Acanthopagrus australis	Yellowfin Bream	25[d]	● Estuary-dependent species ● Recruit to estuaries by 13 mm TL ● Migrate down the estuary to spawn ● Aggregations observed outside estuaries ● Primarily harvested using mesh nets	Curley et al. (2013)
Argyrosomus japonicus	Mulloway	70[c,d]	● Estuary-dependent species ● Recruit to estuaries by 30 mm TL ● More common on unvegetated habitats ● Tagging data indicates most animals recaptured with tag estuary ● Migrate down the estuary to spawn ● Primarily harvested using mesh nets	Silberschneider and Gray (2008)
Platycephalus fuscus	Dusky Flathead	36[d]	● Primarily estuary-resident species ● Settles in estuaries within two months of spawning ● Common across multiple estuarine habitats ● Primarily harvested using mesh nets	Gray and Barnes (2008)
Girella tricuspidata	Luderick	27[d]	● Estuary-dependent species ● Recruit to estuaries by 15 mm TL ● Tagging data indicates some adults migrate from estuary and along the coast, while most remain in the estuary ● Primarily harvested using mesh nets	Curley et al. (2013)
Mugil cephalus	Sea Mullet	30	● Estuary-dependent species ● Recruit to estuaries by 30 mm TL ● Migrates to sea to spawn, although majority of catch is estuarine ● Primarily harvested using mesh and haul net	Smith and Deguara (2002)
Scylla serrata	Mud Crab	8.5[a,d]	● Estuary-dependent species ● Recruit to estuary as megalopae ● Associated with saltmarsh and mangrove habitats ● Migrates to sea to spawn ● Primarily harvested using traps	Alberts-Hubatsch et al. (2016)
Portunus armatus	Blue Swimmer Crab	6[a,d]	● Estuary-dependent species ● Recruit to estuary as megalopae ● Associated with seagrass and unvegetated sediments ● Migrate down estuary to spawn ● Primarily harvested using traps	Kangas (2000) and Sumpton et al. (2003)
Metapenaeus macleayi	School Prawn	NA	● Estuary-dependent species ● Recruit to estuary as postlarvae ● Migrate to sea to spawn ● Primarily harvested in estuaries using trawl net	Taylor et al. (2016) and Taylor et al. (2017b)

Updated information and regulations can be found at www.dpi.nsw.gov.au/fishing.
[a] Carapace width (cm).
[b] Fishery information refers to estuarine fishery (the majority of catch for all species occurs within estuaries).
[c] Limited bycatch above 45 cm can be retained by commercial fishers.
[d] Important recreational species.
[e] Kailola et al. (1992) also provide a good description of the biology, ecology and fishery of all species listed here.

Table 2

Parameter values for the Hunter River estuary for the species modelled in the current study (full descriptions of parameters are given in the text, and parameter distributions are indicated where applicable). Distributions are specified by the shape (either normal [*N*] or lognormal [*LN*]), and the mean and standard deviation for the distribution. P_s refers to the estimated spatial partitioning coefficient. Annual landings are estuary landings only.

Species	Mangrove contribution ($C_{s,mangrove}$)	Saltmarsh contribution ($C_{s,saltmarsh}$)	Annual landings (H_s, '000 kg)	Market price (M_s, AUD)	P_s
Yellowfin Bream	0.292	*N*(0.316, 0.080)	*LN*(8.5, 2.3)	*N*(11.93, 0.69)	0.80
Mulloway	0.175	*N*(0.465, 0.047)	*LN*(5.1, 2.5)	*N*(10.00, 0.82)	0.85
Dusky Flathead	0.166	*N*(0.627, 0.083)	*LN*(4.9, 1.7)	*N*(9.27, 0.90)	0.80
Luderick	0.350	*N*(0.400, 0.010)	*LN*(4.0, 0.8)	*N*(1.95, 0.28)	0.90
Sea Mullet	0.200	*N*(0.533, 0.108)	*LN*(69.5, 31.7)	*N*(3.37, 0.20)	0.50
Mud Crab	0.241	*N*(0.456, 0.057)	*LN*(12.1, 0.8)	*N*(26.40, 2.45)	0.80
Blue Swimmer Crab	0.183	*N*(0.576, 0.143)	*LN*(1.6, 2.0)	*N*(9.60, 1.05)	1.00
School Prawn	0.208	*N*(0.474, 0.060)	*LN*(54.5, 24.3)	*N*(9.27, 0.90)	0.70

Table 3

Parameter values for the Clarence River estuary for the species modelled in the current study (full descriptions of parameters are given in the text, and parameter distributions are indicated where applicable). Distributions are specified by the shape (either normal [*N*] or lognormal [*LN*]), and the mean and standard deviation for the distribution. P_s refers to the estimated spatial partitioning coefficient. Annual landings are estuary landings only.

Species	Mangrove contribution ($C_{s,mangrove}$)	Saltmarsh contribution ($C_{s,saltmarsh}$)	Annual landings (H_s, '000 kg)	Market price (M_s, AUD)	P_s
Yellowfin Bream	0.451	*N*(0.252, 0.108)	*LN*(38.6,9.9)	*N*(11.93, 0.69)	0.70
Mulloway	0.175*	*N*(0.465, 0.047)*	*LN*(7.3,3.3)	*N*(10.00, 0.82)	0.50
Dusky Flathead	0.297	*N*(0.531, 0.065)	*LN*(13.5,3.7)	*N*(9.27, 0.90)	0.50
Luderick	0.367	*N*(0.403, 0.131)	*LN*(11.4,3.0)	*N*(1.95, 0.28)	0.50
Sea Mullet	0.347	*N*(0.436, 0.071)	*LN*(479.9,136.1)	*N*(3.37, 0.20)	0.70
Mud Crab	0.241*	*N*(0.456, 0.057)*	*LN*(20.4,52)	*N*(26.40, 2.45)	0.75
School Prawn	0.030*	*N*(0.952, 0.021)*	*LN*(292.3,115.2)	*N*(9.27, 0.90)	0.40

*Contributions derived from isotope values from the Hunter River were used for Mulloway and Mud Crab, as no isotope data was available for these species in the Clarence River. Also, due to low sample sizes, stable isotope data from a pooled sample of School Prawn and Eastern King Prawn captured in the Clarence River was used to estimate source contributions for School Prawn (see Supplementary information).

occur in the lower estuary (e.g. Sheaves et al., 2016), particularly in New South Wales, a spatial partitioning coefficient (P_s) was incorporated so as not to artificially inflate estimated values for species that may be harvested along a greater length of estuary than that encompassed by the stable isotope data used to model the source contributions. This parameter was essentially a subjective estimate of the proportion of total estuarine catch that is taken on average within the model regions delineated in Fig. 1. While it is possible that outwelling and transport of particulate material further up the estuary could occur, inclusion of this parameter ensures that our data are not over-extrapolated and that our estimates remain conservative. This parameter was estimated for each species in each estuary, and was informed by expert opinion, including knowledge gained through several major sampling programs in the estuaries, the salinity gradient in the estuary and its effect of the distribution of the species under investigation, and one-on-one consultation with fishers in each estuary or fishery compliance officers regarding where particular species are most often targeted and captured. The values estimated for each species are largely supported by unpublished tag recapture and acoustic telemetry data that have been collected for these species in New South Wales.

The proportional contribution of primary producers (including saltmarsh and mangrove plants) to the biomass of exploited species ($C_{s,p}$) was modelled from stable isotope composition (see Supplementary information). The saltmarsh grass *Sporobolous virginicus* was a major contributor to the biomass of commercial species in both the Hunter River and Clarence River; and these contributions were remarkably similar between most species sampled in the different estuaries. Consequently, proportional contribution of the producer *S. virginicus* was used to specify $C_{s,saltmarsh}$. In this dataset, however, the isotopic composition of Grey Mangrove (*Avicennia marina*) was not significantly different from the epiphytic algae that grew on the mangrove pneumatophores, and consequently these producers were pooled in the analysis and both considered "mangrove" habitat. Mangroves were a lower contributor, and there was moderate uncertainty surrounding these estimates. To avoid inflating variation in our model estimates, $C_{s,mangrove}$ were specified as mean values in both systems, rather than distributions (Tables 2 and 3).

A subsequent set of simulations was also undertaken using the equation above, but extrapolating to include the expected flow-on economic values from product harvested, on the broader economy. The multiplier was expressed as a normal distribution (m; $N[\mu,\sigma]$) derived from the relationship between the statewide-GVP for New South Wales (P_{GV}; AUDm79.44), and the minimum ($O_{\min}$; AUDm436.13) and maximum ($O_{\max}$; AUDm501.24) estimate of Total Economic Output from commercial fishing (including GVP, and the value of retail and processing output etc.) reported in Voyer et al. (2016), using the relationships $\sigma = \frac{\frac{O_{max}}{P_{GV}} - \frac{O_{min}}{P_{GV}}}{6}$ and $\mu = \frac{O_{max}}{P_{GV}} - 3\sigma$; thus m was estimated as $N(5.90,0.14)$. For these simulations, Total Economic Output for species s derived from primary producer p ($TO_{s,p}$) was estimated using $GVP_{s,p} \cdot m$. It should be noted that TO reported here only encompasses the value derived through wild harvest fisheries, and does not encompass other ecosystem services derived from estuarine habitats which are sometimes reported against this term in the literature.

For each producer, the Gross Value of Production and Total Economic Output were summed across all species within an estuary, to give the cumulative economic value for each producer within the estuarine system (GVP_p and TO_p respectively). These values were then divided by the areal extent of the habitat represented by producer p (ha) within the model region, to give the habitat-specific economic value on a per-hectare basis.

3. Results

The results of the MCAoU are presented in Fig. 2 (for the Hunter River) and Fig. 3 (for the Clarence River). The distributions for potential economic values were lognormal, which was primarily driven by the lognormal distributions of the total catches for species within each estuary (where very high catches can occur at a relatively low frequency).

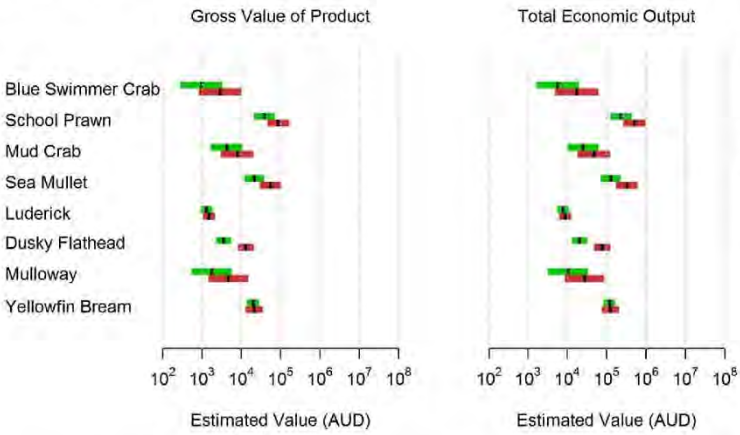

Fig. 2. Output of model simulations for the Hunter River, New South Wales, showing Gross Value of Production (left panel) and Total Economic Output (right panel). Shaded horizontal bars indicate the 75% confidence intervals for the estimated annual values (AUD y^{-1}) derived from the primary producers dominating emergent habitats for species harvested within the model region. Bars are shaded brown for saltmarsh and green for mangrove, and vertical black bars indicate the mean value for each species and habitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Between estuaries, the higher overall catches in the Clarence River (Table 3) relative to the Hunter River (Table 2) drove higher overall economic values derived from the two habitats in this estuary. The relative patterns in economic values among fish species were generally similar between estuaries (Figs. 2 and 3). For fish, the greatest overall value from each habitat was derived through Yellowfin Bream and Sea Mullet harvest, and the lowest value derived through Luderick. These differences were largely driven by differences in market value and catch volume. Yellowfin Bream, Mulloway and Dusky Flathead are all higher market value species, whereas Luderick and Sea Mullet have lower market values (Tables 2 and 3). The lower market value of Sea Mullet, however, was offset by much larger catches; and this was reflected in higher values derived from both saltmarsh and mangrove.

For invertebrates, the patterns among species were also similar between estuaries (Figs. 2 and 3), with the greatest economic value from saltmarsh consistently derived through harvest of School Prawn. School Prawn harvest from the model region in the Clarence River was still ~3 times that of the Hunter River even after accounting for the lower spatial partitioning coefficient. However, the proportional contribution of saltmarsh to the diet of School Prawn in the Clarence was also double that of the Hunter River, which greatly increased the economic value derived from saltmarsh through harvest of this species. Blue Swimmer Crab harvest in the Clarence River is negligible, and consequently no values were modelled for this species (Table 4).

Depending on the metric used (*GVP* or *TO*), total habitat values (summed across species) estimated within the model regions ranged from ~AUD100,000 y^{-1} to ~AUD7,200,000 y^{-1} (Table 4). As expected, the highest values derived were for Total Economic Output, which reflected the broader impact of harvest derived from the primary producers across the broader supply chain. Table 4 also shows the areal extent of each habitat in which the primary producers dominate, and when this is taken into account saltmarsh in the Clarence River had by far the greatest economic value per-unit-area, with an average estimated Total Economic Output (*TO*) of AUD25,741 ha^{-1} y^{-1}. The greatest economic value derived from mangrove habitats was also in the Clarence River with a *TO* of AUD5,297 ha^{-1} y^{-1}. Average economic values in the Hunter River (*TO*) were AUD2,579 ha^{-1} y^{-1} and AUD316 ha^{-1} y^{-1} for saltmarsh and mangrove habitats respectively.

4. Discussion

4.1. General comments and implications for management

The use of stable isotopes bears some conceptual similarity to the

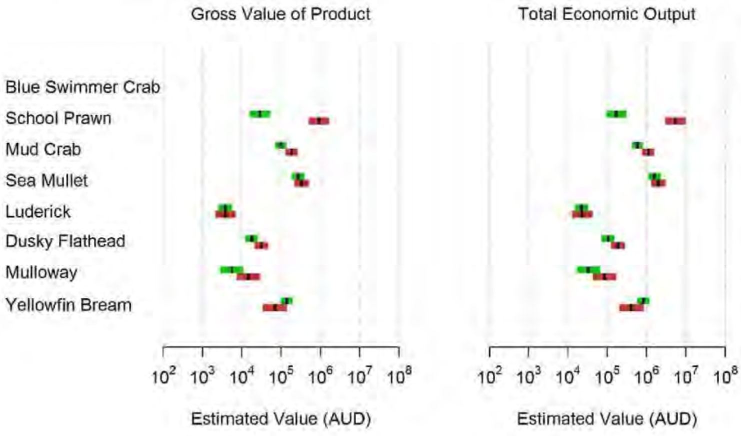

Fig. 3. Output of model simulations for the Clarence River, New South Wales, showing Gross Value of Production (left panel) and Total Economic Output (right panel). Shaded horizontal bars indicate the 75% confidence intervals for the estimated annual values (AUD y^{-1}) derived from the primary producers dominating emergent habitats for species harvested within the model region. Bars are shaded brown for saltmarsh and green for mangrove, and vertical black bars indicate the mean value for each species and habitat. Note that Blue Swimmer Crab harvest in the Clarence River is negligible, and consequently no values were modelled for this species. Also, see footnotes to Table 3 regarding stable isotope data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Summary of average estimated values (AUD) for each species and primary producer across all simulations expressed in terms of Gross Value of Production (*GVP*) and Total Economic Output (*TO*).

Species	Hunter River				Clarence River			
	Saltmarsh		Mangrove		Saltmarsh		Mangrove	
	GVP	*TO*	*GVP*	*TO*	*GVP*	*TO*	*GVP*	*TO*
Yellowfin Bream	21,903	129,160	20,537	121,108	83,815	494,738	147,699	872,003
Mulloway	8707	51,374	3298	19,459	17,800	104,948	6696	39,479
Dusky Flathead	14,210	83,753	3760	22,164	33,451	197,281	18,727	110,441
Luderick	1560	9201	1364	8044	4374	25,837	4072	24,050
Sea Mullet	62,580	369,591	22,994	135,806	349,015	2,061,717	279,328	1,650,066
Mud Crab	11,381	67,214	6017	35,537	197,777	1,167,145	104,856	618,770
Blue Swimmer Crab	5174	30,498	1634	9635	–	–	–	–
School Prawn	96,934	571,703	42,774	252,259	618,770	3,650,691	34,271	202,196
Cumulative value across all species (y^{-1})	222,449	1,312,494	102,378	604,012	1,305,002	7,207,619	595,649	3,517,005
Areal extent of habitat within model region (ha)	509		1908		280		664	
Total value across region per unit habitat ($ha^{-1}\ y^{-1}$)	437	2579	54	316	4661	25,741	897	5297

use of a seagrass residency index to apportion commercial and recreational fishery landings to seagrass habitats (Jackson et al., 2015). Such a method may not be effective for saltmarsh (and less effective for mangrove) habitats, as commercial species do not necessarily use these habitats directly (e.g. Becker and Taylor, 2017; Connolly et al., 1997). While provisioning is assumed implicit through association with habitats in Jackson et al. (2015, and the references therein), our method directly apportions harvest and value on the basis of quantifiable provisioning, but the combination of these approaches may further improve estimates (as detailed below).

While the concept employed here has a basis in the theories of Odum et al. (1977) and the quantification of energy flows in order to derive monetary value from estuarine ecosystems, there is some novelty in combining stable isotopes with measures of economic output to assign values on the basis of this energy flow in a quantitative fashion. Examples of valuations for saltmarsh and mangrove are rare for Australian estuaries, and in a recent review Wegscheidl et al. (2017) reported only 9 Australian studies that included quantitative information appropriate for use in economic valuation. Nonetheless, the economic values reported here complement several previously published estimates that deal with habitat-fishery linkages. Bell (1997) presented a model estimating a (recreational) fishery value from saltmarsh that reported values of USD5,592 to USD36,902 $ha^{-1}\ y^{-1}$ (all values converted to 2015 dollars), which span similar orders of magnitude to those reported here. Rönnbäck (1999) provided a synthesis of valuation studies of mangrove habitats through wild harvest fisheries, and reported values ranging from USD22 $ha^{-1}\ y^{-1}$ to USD9,665 $ha^{-1}\ y^{-1}$, with the highest reported value derived from Moreton Bay (Queensland, Australia, Morton, 1990). Thus, the range of economic values estimated for our study systems span the ranges published for other areas previously.

Environmental accounting is receiving increasing attention internationally (e.g. Food and Agriculture Organization of the United Nations, 2004), as governments and other organisations endeavor to increase accountability and stimulate investment in environmental management activities (Bureau of Meteorology, 2013). Our approach to establishing habitat-fishery linkages in support of economic evaluation may prove useful in future efforts in this area, but the actual values estimated here also lay the foundation for further consideration of the costs and potential benefits that can be realised from habitat repair in Australian ecosystems (Creighton et al., 2015). It is important to note, however, that linking fisheries values to habitat rehabilitation does require additional consideration of other ecological processes (such as adequate recruitment, Taylor et al., 2017a), the value of these habitats as a refuge, as well as other economic factors (for examples see Leston and Milon, 2002; Rozas et al., 2005) which are not captured here. At the very least, our estimates will be useful for comparison with the economic values derived from alternate uses of these environmental assets (e.g. cattle grazing on drained saltmarsh habitat, Read and Sturgess, 1996).

In the Hunter River, connectivity between Hexham wetland (Fig. 1) and the lower estuary was recently reinstated for the first time since the early 1970s (Boys and Pease, 2017). This reinstated the potential for recruitment of economically important species to the wetland system, as well as the outwelling of saltmarsh- and mangrove-derived productivity to other areas of the estuary. However, this wetland had lost 763 ha (93%) of saltmarsh and 124 ha (84%) of mangrove during this period, and this will take some time to recover. As recovery progresses, concomitant increases in landings of School Prawn and other species could occur, and when the patterns presented here are considered, this may add considerable value to the fishery.

4.2. Assumptions and limitations

To our knowledge, there are no other studies that combine stable isotope-derived trophic linkages with fisheries catch and economic data for the purposes of habitat valuation. Thus, it is prudent to highlight the various assumptions and areas of uncertainty inherent in the approach, both to properly understand factors that detract from confidence in estimates, and also to provide some target areas for future investigations to improve confidence.

As a minimum, any model is only as good as the data from which it is parameterized, so it is necessary to consider the various attributes of model parameters in the context of the estimates produced. The market value estimates used in these simulations were probably accurate (as it is obtained directly from the auction floor at the state's largest fish market), but taking the value from a single market essentially ignores the potentially enhanced values that might be achieved through other niche markets. Failing to account for these means that our estimates may be on the conservative side. Furthermore, there is also the possibility that harvest levels and market prices are correlated for some species. This is less of a concern when working at the estuary level, but it could be addressed from a technical perspective by defining a bivariate distribution for these parameters if appropriate data were available. The main effect of failing to account for this correlation is likely to be the inflation of variability in model outputs.

The proportional contribution of primary producers to the biomass of exploited species ($C_{s,p}$) used in this model was determined through stable isotope analysis. This parameter was determined using data directly collected from the study systems, and employed widely accepted Bayesian modelling of consumer source contributions (Escalas et al., 2015) based on the isotopic composition of sources and consumers within the two estuaries (see Supplementary information). The sources used were taken from sites throughout the lower estuary, and the proportion of diet supported by saltmarsh consistently had the lowest variability, suggesting that it was a relatively accurate estimate (Parnell et al., 2010, evident in relatively low standard deviations in Tables 2 and 3). Mangrove sources were pooled with other primary producers (such as mangrove pneumatophore epiphytes), as isotope signatures of those sources were not significantly different, and this led to the possibility of incorrectly attributing *GVP* or *TO* value to mangrove habitats. However, while the area covered by mangrove is significantly greater than the other pooled sources, a small proportion of those values could be attributed to the other pooled sources in this grouping (such as pneumatophore epiphytes). The principle way to improve the confidence in these source contributions (and to avoid pooling sources) is to use additional isotope markers that are unlikely to be affected by anthropogenic activities, such as sulfur (Lamontagne et al., 2016).

The spatial partitioning coefficient essentially used expert opinion to partition out the variability in species distribution along the estuary and its effect on catch, and is intended to reflect the average spatial distribution of harvest in relation to our model region. This parameter was derived from expert opinion, and is also intended to ensure that our estimates are conservative and not extrapolated to include harvest in areas of the estuary that are not reflected in the stable isotope data used to parameterise the model. While the proportional distribution of catch that we estimated generally reflects the findings of Sheaves et al. (2016) that most biomass is concentrated in the lower estuary, a more quantitative basis for this parameter could be derived from either collecting spatial data alongside catch data from estuary commercial fishers, or analysis of fish distribution patterns through methods such as acoustic telemetry (Payne et al., 2013; Taylor et al., 2014). There are an expanding number of such movement studies for major commercial species in eastern Australia which could be useful for predicting the spatial distribution of harvest, but these patterns generally support the coefficients estimated in our study. For example, Taylor et al. (2014) showed that acoustically-tagged Mulloway spent the majority of their time in the lower 15 km of the Shoalhaven River estuary (New South Wales). Also, unpublished acoustic telemetry data on commercially sized animals in the Parramatta River estuary (New South Wales) indicates similar patterns for Mulloway, and found Sea Mullet were mainly distributed 10 to 24 km from the mouth of the estuary, and Luderick distributed in the lower 10 km of the estuary (Taylor et al., 2017c). Using such data to establish linear kernel density distributions reflecting animal distribution along the estuary should help refine estimates of the spatial partitioning coefficient, but fishing effort may not always target species across their entire distribution.

4.3. *Patterns across systems*

Our estimates of the economic value of saltmarsh were consistently greater in the Clarence River. Although previous studies have found variation in the contribution of primary producers between systems (e.g. Sheaves et al., 2016), the magnitude by which the value of habitats in the Clarence River exceeded that of the Hunter River was surprising. Greater harvest levels in the Clarence River clearly play a role here, but the value-per-hectare was also considerably greater in the Clarence River. Saintilan (2004) describes broad patterns that link estuarine geomorphology to the areal extent of primary producers in a system, and associated fish harvest. Although separated by 3.4° of latitude, our study estuaries are geomorphologically similar, so this is unlikely to be the main driver of the observed variation.

There are several other factors which may underpin both the increased catch and the greater economic values derived per unit habitat in the Clarence River estuary. Firstly, average temperatures in the Clarence River (26 °C) are warmer than the Hunter River (23 °C), and this may explain improved fisheries productivity through faster growth and concomitant effects on survival (e.g. Munday et al., 2008; Russell et al., 1996). Secondly, the Clarence River has a much larger waterway area (89 km^2 compared with 29 km^2 in the Hunter River), meaning there is greater subtidal habitat available (i.e. more space) to support fishes. Thirdly, the Clarence River also experiences greater freshwater flows and a lower level of flow regulation (Gillson et al., 2009), which also contributes to increased recruitment and/or catch of many of the species examined here (e.g. Gillson, 2011; Gillson et al., 2012; Loneragan and Bunn, 1999; Robins et al., 2005; Ruello, 1973; Taylor et al., 2014). Finally, species in the Hunter River are exposed to various contaminants not found in the Clarence River catchment (e.g. perfluoroalkyl substances, Taylor and Johnson, 2016), which could have an adverse affect on growth or reproduction. Consequently, it is likely that habitat value depends on a number of these other factors which may contribute to fisheries productivity, in addition to the areal extent of habitat, and these additional factors may have contributed to the inter-estuarine variation observed here.

4.4. *Areas for improvement*

There are several other factors that might be useful to consider in future applications of this approach. In our model, interspecific interactions are ignored as there are little data available to quantify them, but it is unlikely that high catches of all species will occur at the same time. This is dealt with here by considering the mean of the model outputs, but again there are emerging studies describing such interactions and how this links to fish harvest in the acoustic telemetry literature (e.g. Mulloway and Sand Whiting, Payne et al., 2015). In its current form, this approach is only appropriate for species that grow and are caught in the estuary. Attributing fish captured from areas away from the estuary to specific estuarine primary producers requires a more complex set of relationships, and an isotope-based approach is unlikely to be appropriate for all species given tissue turnover once animals move from the estuary. Also, our data does not include recreational harvest. This is a major shortcoming potentially representing significant value (for some species) that has not been accounted for. The net impact again means that our valuation is conservative, however such data could easily be incorporated should it be available for the estuaries being studied.

The samples from which source contributions were derived in this study were collected over a single season (see Supplementary information). It would be useful to further refine the stable isotope data and associated modelling by incorporating stable isotope data from additional samples collected across multiple years. Also, given the importance of both School Prawn and Sea Mullet in driving economic values for both estuaries, an important objective for future work should be to refine these estimates by bolstering sample sizes for these species (especially for School Prawn in the Clarence River), and examining the potential for variation in source contributions further along the length of the estuary. Incorporation of additional stable isotope data will ultimately improve confidence in model estimates.

As a final point, our simulations are based solely on the trophic subsidy provided by some primary producers. It is clear that habitats such as saltmarsh and mangrove may also provide a refuge for many commercial species (Boesch and Turner, 1984), particularly as juveniles. While it is likely that these fish also feed in these habitats (which is captured in our patterns), non-trophic benefits are not explicitly captured in our simulations. The integration of our approach with that of Jackson et al. (2015, as discussed above) could help to address this.

5. Conclusion

The approach presented here represents a synthesis of existing techniques to derive estimates of the economic value of estuarine mangrove and saltmarsh habitats through the support of harvested biomass. The approach should be broadly useful in situations where direct usage (occupation) of the habitat may not be the primary conduit through which species benefit from the habitat (e.g. Becker and Taylor, 2017; Connolly et al., 1997). We also present the first such estimates of economic value of these habitats derived through fisheries harvest in south-eastern Australian ecosystems, and our estimates generally reflect the magnitude and variability estimated for similar habitats elsewhere. Given the inherent variability in our model parameters, as well as variation in other factors across spatial and temporal scales, it is unlikely that an "actual" value will ever be known, and consequently we have expressed our model outputs as distributions so the range of potential values and the level of uncertainty in these estimates can be considered. These estimates deal with commercial fisheries outputs only; consideration of recreational harvest and other ecosystem services will ultimately lead a more holistic valuation, but such estimates will increase the number of underlying assumptions and may rely on relationships that are more difficult to quantify.

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Appendix A. Supplementary information

Supplementary information associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.08.044.

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Appendix 12 – Impacts of habitat repair on a spatially complex fishery

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Impacts of habitat repair on a spatially complex fishery

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ABSTRACT

Restoring juvenile habitat remains a key fisheries management action, but a persistent challenge is identifying the areas likely to most efficiently improve fishery outcomes. A spatial simulation model is presented that estimates the anticipated improvement in harvest of the Eastern King Prawn fishery in New South Wales, Australia, following potential restoration. By integrating environmental, biological and fisheries information gleaned from previous studies, this model suggests zones with ample larval settlement but greatly diminished habitat for juvenile life stages (recruitment), and that are in close proximity to the main fishery grounds, are likely to provide the greatest anticipated improvements in harvest. Uncertainty analyses demonstrated the particular sensitivity of these outcomes to assumptions of larval dispersal, and zone-specific recruitment at unfished conditions. The work emphasizes the utility of spatial models for restoration planning, but also the dependence of these models on information provided from empirical studies. This work also highlights the implications of input-controlled fisheries in which total effort is regulated, as this will determine the form of, and to whom, benefits of potential restoration actions will accrue.

1. Introduction

The loss of estuarine fish habitat is a pervasive problem, and good evidence suggests substantial losses (> 65%) of coastal seagrass and wetland habitats have occurred from development and poor water quality over the last 100 years (Lotze et al., 2006). While the magnitude of effects from such large scale habitat loss are largely unknown, this likely affects recruitment and survival for a large number of species which require estuarine nurseries (Beck et al., 2001). At a broad scale, incorporation of habitat repair with other fisheries management measures will likely lead to considerable gains in fisheries productivity (Taylor et al., 2017a; Worm et al., 2009). It is clear, however, that for habitat and catchment repair to be supported as a means to improve the productivity of fisheries, policymakers need to be convinced of the benefits that rehabilitation will provide for populations of exploited species (Done and Reichelt, 1998).

Australia has experienced similar rates of habitat loss as other areas across the world. For example, about 72% of prime fish habitat has been lost from estuaries on the north coast of New South Wales, mainly due to transformation of coastal drainage and land reclamation (Rogers et al., 2015). Also, 60% of estuarine habitat has been lost from one of Australia's largest coastal embayments, Moreton Bay, since colonial development (Lotze et al., 2006). Over three quarters of the exploited fish species in Australia, including both fish and crustaceans, spend at least some part of their life cycle within estuaries and inshore wetlands (Creighton et al., 2015). Given the important role of estuarine habitats in these species life histories (Beck et al., 2001), it is likely that the observed habitat losses have contributed to concomitant decreases in fisheries productivity.

Many species of penaeid prawn (= shrimp) are reliant on estuarine habitats during their life history (Haas et al., 2004; Loneragan et al., 2013a). This includes species that live in the estuary throughout their entire life (Type-1 species), and species that are reliant on the estuary as a nursery for early life-history stages before emigrating to sea as adults or sub-adults (Type-2 species, Dall et al., 1990). When residing in the estuary, juvenile prawns use a variety of different habitats for both feeding and shelter from predation (e.g. Minello et al., 1989; Taylor et al., 2017b, c), and can experience rapid growth during this estuarine phase (Taylor, 2017). Some penaeid species display relatively specific habitat requirements (e.g. marsh edge habitats; Browder et al., 1989, or segrass beds adjacent to mangrove habitats; Skilleter et al., 2005; Staples et al., 1985), and decreases in productivity of prawn species have been attributed to loss of estuarine habitats (e.g. Loneragan et al., 2013b; Loneragan et al., 2006). These habitat dependencies, coupled

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with high growth, high fecundity and the high value of wild-caught penaeid prawns mean these species will be one of the main beneficiaries of estuarine habitat repair, and fisheries that depend on them may experience the greatest economic impact. This is exemplified in the Gulf of Mexico, where the benefits to shrimp fisheries alone can be large enough to offset the costs of habitat repair (see Rozas et al., 2005).

This study presents a spatial simulation model to explore and compare anticipated improvements in harvest arising from competing restoration scenarios. Specifically, a novel approach which assesses the relative expected return from restoring estuarine nursery habitats in different spatial areas is presented, and the approach demonstrated using the Eastern King Prawn (*Penaeus [Melicertus] plebejus*, EKP) fishery as a case study. The utility of this simulation approach in habitat management and its application to other species is discussed, as well as important factors that affect the expected return, inter-jurisdictional considerations for habitat repair, and the role of repair in improving fishery management.

2. Methods

2.1. Background to the study species and fishery

Eastern King Prawn is one of the most valuable species targeted off the east-coast of Australia, and has a landed value in excess of AUD40 million (O'Neill et al., 2014). The species spawns off northern New South Wales and southern Queensland, and spawning intensity increases with decreasing latitude (Montgomery et al., 2007). Demersal eggs hatch into pelagic larvae (Dakin, 1938), and disperse primarily in a southward direction in the East Australian Current, with spawning at higher latitudes leading to greater southward dispersal (Everett et al., 2017). Post-larvae migrate inshore (Rothlisberg et al., 1995) and into estuarine nurseries, where they settle and become demersal (Taylor and Ko, 2011). Prawns grow rapidly in the estuarine nursery during the summer months and then emigrate to sea (Taylor et al., 2016), gradually moving offshore and northward toward to spawning grounds as they grow and mature (Montgomery, 1990). Consequently, there is a general gradient in prawn size with decreasing latitude off the New South Wales coast (Gordon et al., 1995).

Eastern King Prawn supports a cross-jurisdictional oceanic demersal otter trawl fishery across New South Wales and Queensland (Prosser and Taylor, 2016), but smaller catches are also taken in the New South Wales Estuary General fishery (Taylor, 2016) and the inshore otter trawl fishery in Moreton Bay, Queensland (Wang et al., 2015). Catches in Victoria (at the far south of the species range) are small and do not occur every year, and largely depend on optimal oceanic currents supplying recruits to waters in the far-south (Everett et al., 2017). The species is assessed as a single biological stock (O'Neill et al., 2014), but managed under two contiguous management units from 22 to 28°S (Queensland), and 28–37.5°S (New South Wales, Prosser and Taylor, 2016; Fig. 1). Due to the migratory nature and size structure of the species, in New South Wales the species is primarily targeted north of 33°S (O'Callaghan and Gordon, 2008), with the majority of harvest taken from waters north of 31°S. The north coast of New South Wales represents an important nursery area for EKP, but has seen some of the highest rates of estuarine habitat loss within New South Wales (Rogers et al., 2015). Estuarine habitat loss has involved loss of substantial areas of seagrass (e.g. Taylor et al., 2018) and floodgating and conversion of coastal wetlands for agriculture. This removes connectivity with the estuary, and thus prevents recruitment into coastal wetland systems (Taylor and Creighton, 2018), outwelling of saltmarsh-derived nutrition which supports fisheries productivity (Raoult et al., 2018), and can affect water quality over the entire estuary (Creighton et al., 2015). Coastal wetland habitats are important for Eastern King Prawn both in the provision of subtidal habitat for occupation (Taylor et al., 2017c), and trophic support of juveniles during their nursery phase (Taylor et al., 2018).

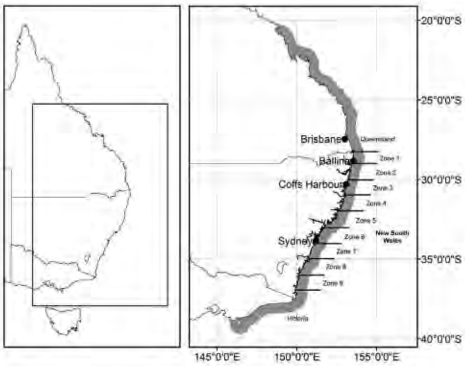

Fig. 1. Spatial structure of the EKP model, showing the location of the model region on the Australian east coast (left panel), and the New South Wales zones employed in the model (which align with the reporting zones for the New South Wales Ocean Trawl Fishery). The additional spatial zones represented by the adjacent states (Queensland and Victoria) are also indicated. Grey shading reflects the latitudinal distribution of the species.

2.2. Conceptual model

To evaluate the restoration of habitat in alternative areas, predicted improvement in landings of EKP to the state of New South Wales were compared using a quantitative model of the EKP fishery. This model represented the entire spatial range of the EKP population, thus including Victoria to the south and Queensland to the north, in addition to New South Wales (Fig. 1). This representation allowed for realistic representation of the spatial dynamics of EKP life history (Fig. 2) and fishery in an equilibrium modelling framework, and followed recent publications (O'Neill et al., 2014) and stock assessment models (Courtney et al., 2014). An important component of this model was representing key, spatially explicit processes of EKP life history and fishery, including spatial distribution of fishing effort, the spatial dispersal of larvae to inshore recruitment areas from eggs spawned offshore (Everett et al., 2017), the spatial movement of post-recruit subadult and adult shrimp from estuaries to offshore areas, and the habitat mediated, density dependent recruitment process occurring in estuarine areas throughout the EKP range (this process is conceptually described in Fig. 2). Once parameterized appropriately, the model was used to examine what the effect of restoring a fixed amount of habitat in a specific zone of New South Wales would be on the overall landings to New South Wales.

As the purpose of the model was to assess the expected effects of alternative restoration actions, a simulation model was constructed that represents the current state of the EKP stock. The model was designed to represent an age-structured, spatially explicit EKP stock and fishery in a deterministic fashion in discrete time. This permitted transparent predictions of expected outcomes at actual time intervals following restoration, while implicitly assuming an equilibrium state of the current fishery. To ensure the model represented the current fishery state reasonably well, the model was parameterized from recent fisheries data, stock assessments, and other studies (most notably Courtney et al., 2014; O'Neill et al., 2014). The model was tuned (via solving for the catchability parameter, q, Table 1) such that equilibrium, un-restored predictions from the model match observations from the fishery. All parameter values are provided in Tables 1–3, and equations used to construct the model provided in Table 4, while the most important components of the model are also described below.

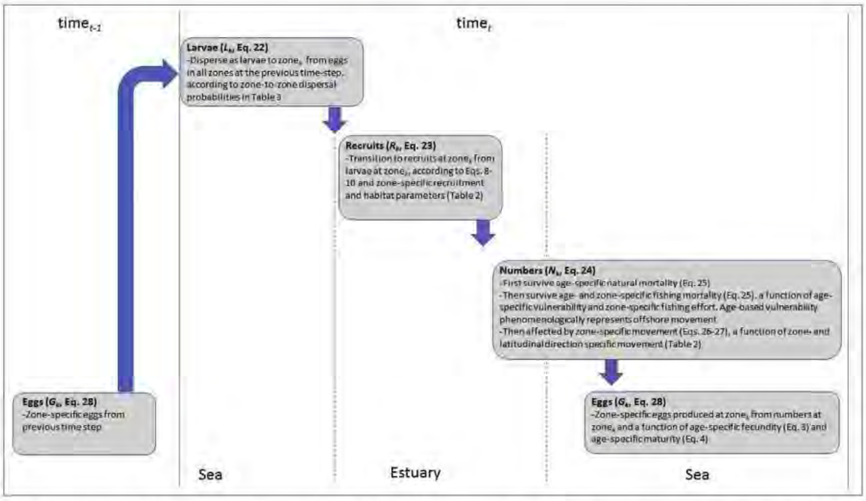

Fig. 2. Conceptual representation of the spatial and temporal population model of Eastern King Prawn that includes specific detail of modelling assumptions.

2.3. Spatial representation

The model represents the entire range of EKP, from Victoria in the south to Queensland in the north, but focuses on New South Wales, which is where the potential restoration would occur (Fig. 1). The spatial structure is made up of 11 zones, including one each for Victoria and Queensland, and nine corresponding to management reporting zones in New South Wales. In this model the greater detail provided for New South Wales is a function of the model objectives, while the inclusion of Victoria and Queensland are necessary to account for dispersal of larvae and movement of adult shrimp to and from these states and New South Wales. Each zone occupies a single longitudinal area, such that the effects of offshore movement of shrimp pertinent to the fishery is accounted for with the vulnerability to fishing gear (v_a^c, Eq. 28; Table 4).

2.4. Growth, survival and fecundity

Somatic growth of EKP was described in terms of carapace length and body weight and age following Courtney et al. (2014). Carapace length-at-age was described using a von Bertelanffy growth function, (L_a, Eq. 1, Table 4). Weight-at-age was assumed to be an allometric function of length (W_a, Eq. 2, Table 4). Survival of post-recruit EKP—i.e. sub adults and adults—was assumed to be age-specific as a function of length, using a Lorenzen-type mortality function (S_a, Eq. 4, Table 4). Fecundity at age was simply specified as a function of maturity and weight (f_a, Eq. 3, Table 4), with average weight at maturity (W_m, Table 1) assumed to correspond to a carapace length of 42 mm following Glaister (1983). This specification of fecundity is relative in that it represents spawning biomass rather than absolute numbers of eggs, relying on the parameterization of the stock-recruit function (specifically the Beverton-Holt *a* parameter, Eq. 8, Table 4) to scale spawning biomass to appropriate numbers of recruits. Each of growth, survival and fecundity was assumed to be invariant among the spatial compartments represented in the model.

2.5. Dispersal

Current understanding of the EKP life history holds that animals aggregate offshore to reproduce, following which eggs hatch as larvae and subsequently disperse to inshore, estuarine areas as a function of transportation via advective ocean currents (Fig. 2). Dispersal processes dictate that zones within New South Wales have historically and continue to receive differing proportions of eggs spawned offshore. Dispersal is incorporated using a matrix of probabilities reflecting the proportions of eggs spawned in each zone that disperse to all other zones (Table 3), derived from recent modelling (Everett et al., 2017). It is critical to understand that the process of dispersal, as represented in this model, accounts only for the spatial allocation of larvae from eggs (Eq. 20, Table 4). Thus, the total abundance of larvae in each year is exactly that of the eggs produced at the end of the previous year (first stage of Fig. 2). All mortality associated with the multiple biological processes between eggs being spawned and the conclusion of the density dependent juvenile mortality stage is subsumed within the recruitment function (Eq. 23, Table 4), as is common in fisheries population models (Walters and Martell, 2004).

2.6. Recruitment

Recruitment was perhaps the most critical component of this model, as it must account for the habitat mediated density dependent mortality of juveniles. Survival of larvae to post-recruit sub-adults was assumed to be represented with a Beverton-Holt stock recruitment function following O'Neill et al. (2014). This parameterization of the Beverton-Holt implicitly converts relative biomass of eggs or larvae (per section 2.4) to numbers of recruits (the "estuary" stage of Fig. 2). The *a* parameter of the Beverton-Holt stock recruitment function, (Eq. 8, Table 4), was calculated from the compensation ratio (Ω, Table 1), and eggs-per-recruit (φ_k, Eq. 7, Table 4), and thus is initially identical across zones. The *b* parameter of the Beverton-Holt is also a function of recruitment at unfished conditions ($\bar{R}_k$, Table 2), such that this parameter differs across zones (b_k, Eq. 9, Table 4). This implies that even in unfished and pre-degradation states, the individual zones would have naturally produced different numbers of recruits as a function of different absolute recruitment potential, presumably a function of a two-or-three dimensional spatial measurement of usable habitat. To account for zone-specific changes in habitat, both Beverton-Holt parameters are then further modified by the zone-specific proportion of habitat

Table 1
Description of parameters and parameter values in the spatial model to estimate impact of habitat restoration for the Eastern King Prawn fishery ("*" preceding parameter indicates value estimated). Symbols relate to the information presented in Table 2 and formulae outlined in Table 4 and the text.

Symbol	Description	Units	Value	Source
$\bar{R}_k$	Recruitment at unfished conditions at zone $_k$	fish	Variable, see Table 2	O'Neill et al. (2014)
L_∞	Asymptotic length, carapace	mm	55	Courtney et al. (2014)
K	Von Bertalanffy metabolic parameter	month^{-1}	0.20	Courtney et al. (2014)
t_0	Age at length = 0	month^{-1}	0.00	Expert opinion
w_a	Weight-length constant	g	0.0006	Courtney et al. (2014)
w_b	Weight-length exponent	g	3.09	Courtney et al. (2014)
α_f	Fecundity alpha parameter		0.199	O'Neill et al. (2014)
β_f	Fecundity beta parameter		4.753	O'Neill et al. (2014)
L^T	Length at 50% maturity	mm	39	O'Neill et al. (2014)
σ^T	Standard deviation of maturity		0.05	O'Neill et al. (2014)
M	Instantaneous mortality at L_m	month^{-1}	0.20	O'Neill et al. (2014)
L_m	Reference carapace length for mortality	mm	25	Expert opinion
C_1	Allometric exponent of length-mortality relationship	constant	1.0	Expert opinion
A_m	Maximum age	months	18	
Ω	Recruitment compensation parameter	ratio	6	Courtney et al. (2014)
L^c	Carapace length at 50% vulnerability to capture	mm	20	Courtney et al. (2014)
σ^c	Standard deviation of length-specific vulnerability to capture		$0.075 * L^c$,	Courtney et al. (2014)
A_1^m, A_2^m	Ages at 50% probability of moving	month	4, 11	Expert opinion
σ_1^m, σ_2^m	Standard deviation of age-specific movement probability		$0.18 * A_1^m$, $0.09 * A_2^m$	
$\bar{p}$	Maximum proportion of individual moving per time period for all time periods and zones	Numbers	0.5	Expert opinion
p_k	Zone-specific probability of moving per time period	Proportion	Variable, see Table 2	Expert opinion
p_k^N	Zone specific probability of moving north per time period	Proportion	Variable, see Table 2	Expert opinion
p_k^S	Zone-specific probability of moving south per time period	Proportion	Variable, see Table 2	Expert opinion
E	Total fishing effort	Days	1841.09	NSW Department of Primary Industries–Fisheries Commercial
E_k	Zone specific effort	month^{-1}	Variable, see Table 2	Catch and Effort Reporting System
*q	Catchability coefficient scaling parameter	rate	2.198e 05	Estimated
H_k	Zone-specific proportion of habitat suitable for recruitment	Proportion	Variable, see Table 2	Rogers et al. (2015)
$\bar{H}_k$	Zone-specific hectares suitable for recruitment	Hectares	Variable, see Table 2	NSW Department of Primary Industries (2017a)
α	Area restored per zone	Hectares	200	
c^*	Logical parameter for whether larval are assumed to be capable of locating recruitment habitat (1) or not (0)	Unitless	0	Walters et al. (2007)
$\Upsilon_{k,k}$	Matrix of probabilities of dispersal from zone k to zone k	Proportion	Variable, see Table 3	Everett et al. (2017)

remaining that is considered suitable for recruitment ($H_{t,k}$, Table 2), and by the assumption that larvae can to some extent locate that habitat (c^*, Table 1), per Eqs. 10–11 (Table 4). This approach is based in Walters et al. (2007) and results in a matrix of Beverton-Holt parameters dimensioned by the time periods and zones considered in the simulation. Thus, following equilibration of the model (which must be attained via numerical simulation owing to non-random larval dispersal and zone-specific recruitment at unfished conditions) potential habitat restoration can be represented by changing the $H_{t,k}$ matrix (Table 2). This integration of assumptions regarding estuarine habitat to the EKP stock-recruit production function is what allows reasonable representations of changes to the productivity in the EKP fishery following habitat restoration.

2.7. Migration

Previous studies have demonstrated that EKP move offshore and generally northward as they mature and eventually aggregate to reproduce, and concomitantly are targeted by commercial fisheries (Courtney et al., 2014; Montgomery, 1990; Taylor et al., 2016).

Table 2
Zone-specific (subscript k) parameter values. Here the values for proportion of habitat suitable for recruitment, $H_{t,k}$, represent initial conditions prior to restoration actions. Parameter symbols are defined in Table 1.

Symbol	Queensland	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8	Zone 9	Victoria
$\bar{R}_k$	5.884×10^8	0.044×10^8	1.097×10^8	2.150×10^8	0.668×10^8	0.668×10^8	0.001×10^8	0.001×10^8	0.001×10^8	0.001×10^8	0.001×10^8
E_k	1380.817	98.268	181.200	84.551	9.713	78.936	5.799	0.138	0.184	0.966	0.506
$H_{t,k}$	0.171	0.171	0.223	0.221	0.535	0.4	0.7	0.8	0.95	0.95	0.95
$\bar{H}_k$		1360	1498	1661	1987	7609	2228	1402	1204	806	
p_k^N	0	0.5	0.5	0.5	0.5	0.75	0.9	0.9	0.9	0.9	0.9
p_k^S	0	0	0	0	0	0	0	0	0	0	0
p_k	0	0.5	0.5	0.5	0.5	0.75	0.9	0.9	0.9	0.9	0.9

Table 3
Dispersal probability matrix, indicating the probability of eggs spawned in each zone dispersing throughout the entire area. For example, it is assumed that 20% of eggs spawned in Queensland disperse to Queensland, whereas 95% of eggs spawned in Victoria disperse to Victoria.

	Queensland	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 8	Zone 9	Victoria
Queensland	0.2	0	0	0	0	0	0	0	0	0	0
1	0.2	0.2	0	0.01	0.01	0	0	0	0	0	0
2	0.2	0.2	0.2	0.05	0.01	0.01	0	0	0	0	0
3	0.15	0.2	0.2	0.2	0.06	0.02	0.01	0	0	0	0
4	0.1	0.15	0.2	0.2	0.2	0.02	0.02	0.01	0	0	0
5	0.05	0.1	0.15	0.2	0.2	0.2	0.02	0.02	0.01	0	0
6	0.05	0.1	0.15	0.15	0.2	0.2	0.2	0.02	0.02	0.01	0
7	0.02	0.02	0.05	0.1	0.1	0.2	0.2	0.2	0.02	0.02	0.01
8	0.02	0.02	0.02	0.05	0.15	0.15	0.2	0.2	0.2	0.02	0.02
9	0.01	0.005	0.02	0.02	0.05	0.15	0.15	0.2	0.2	0.2	0.02
Victoria	0	0.005	0.01	0.02	0.02	0.05	0.2	0.35	0.55	0.75	0.95

Increasing vulnerability of EKP to the commercial fishery associated with offshore and northward movement is accounted for with age-specific vulnerability to capture, v_a^c, described as a function of carapace length (Eq. 29, Table 4; Fig. 2). Latitudinal movement north or south is accounted for explicitly in the model, by considering both size- and age-based influences on probability of movement in either direction, as well as zone-specific differences in probability of sub-adult and adult shrimp moving north or south (Eqs. 12–16, Table 4). This ultimately results in age-specific probabilities of movement in each direction (north or south) dependent on the zone most recently occupied. These probabilities of movement were informed by recent empirical studies, including Courtney et al. (2014) and others.

2.8. Fishery

In the model the fishery is represented in a spatially explicit, zone-specific context. Spatial differences in harvest rate ($U_{t,k}$, Eq. 21, Table 4) are realized through spatial allocation of effort (E_k, Table 2) that represent recent fisheries dependent data. This representation allows for compatibility with effort and catch per unit effort metrics (presented in the same units) described in a recent bioeconomic assessment that estimated the boat hours which would be associated with maximum economic yield (O'Neill et al., 2014).

2.9. Model simulations

In all cases, the model was run to unfished and then fished equilibrium prior to assessing the effect of restoration. The spatial structure, specifically with respect to dispersal, required that the model "spin up" to equilibrium and prevented the use of more traditional approaches for initializing at fished equilibrium (Walters and Martell, 2004). In this case, 10 years at monthly time steps was sufficient to accomplish this. The model was then run for an additional ten years to reach a fished equilibrium, following which restoration options were initiated as described below.

2.9.1. Expected parameterization

The primary objective of this work was evaluated by estimating the relative effect of restoring habitat in alternative New South Wales management reporting zones given the available information on spatial dynamics of the stock and fishery. Accordingly, parameter values were used for this run as provided in Tables 1–3, and this was achieved by running the model to fished equilibrium. Following fished equilibrium, restoration was represented by altering the percent habitat suitable for recruitment ($H_{t,k}$, Table 2) to reflect a 200 ha increase in habitat within each zone individually (Eq. 32, Table 4). A 200 ha restoration scenario was chosen following consultation with habitat managers, and generally reflects a moderate size wetland restoration program. Following restoration, the model was run for an additional 10 years to describe equilibrium effects of restoration. Thus, the annual expected percent improvement in New South Wales EKP harvest was calculated as harvest in the tenth year following restoration relative to un-restored conditions.

2.9.2. Zone-specific effect of increasing restoration

The functional relationship between the proportion of habitat restored and changes in EKP harvest, was also explored. This was expected to vary between zones, owing to zone-specific differences in initial carrying capacity, remaining habitat, influx of dispersing larvae, and proximity to fishing grounds, as EKP from more distal areas would suffer greater natural mortality prior to potential capture. To accomplish this, for each zone, the amount of habitat restored was varied across a range of absolute areas (0–1000 ha), per equation 32 (Table 4). Habitat was not allowed to be improved beyond initial conditions (e.g., $H_{t,k} < = 1$ in all cases), which would limit the changes made to less degraded zones (e.g. zones 8–9).

2.9.3. Sensitivity analyses

All models, and especially spatial models such as the one described here, obviously rely upon multiple assumptions. This particular fishery has been well studied and much of the information included in this model could be borrowed from previous empirical and statistical studies. Nonetheless, it is important to understand the effect that various spatial assumptions had on the model results. Specifically, it is critical to assess which suite of assumptions result in markedly different implications—for example, if changes in assumptions in dispersal result in dramatic changes to the relative returns of restoring different zones. We assessed this by sequentially changing individual elements of the spatial components of the model, and re-evaluating the relative returns of improving each zone. These alternative assumptions are provided in Table 5.

3. Results

3.1. Expected parameterization

The most realistic parameterization off this model suggested that the greatest return from restoration would be realized by restoring 200 ha of habitat in zone 3, with the equilibrium annual increase in harvest greater than 4% (Fig. 3). Zones 2–4 would also provide relatively high returns. Alternatively, restoration in the most northern and southern zones is likely to have less of an effect on overall harvest from the fishery in New South Wales. In the north this is in part due to EKP migrating into Queensland waters, and so harvest was not recouped within the New South Wales fishery. In the southern zones (6–9), habitats are relatively un-degraded, but carrying capacities are low, so returns from restoration were similarly diminutive (Fig. 3). Obviously the equilibrium annual increase in harvest does not account for the time stream of restoration benefits, which would be more modest immediately following restoration than at equilibrium. However, the

Table 4
Description of model components and equations used in the spatial model to estimate impact of habitat restoration for the Eastern King Prawn fishery. Parameter symbols are defined in Table 1.

Eqn.	Component	Equation
Life History Characteristics of Stock		
Eq. 1	Length (mm) L at age $_a$	$L_a = L_\infty(1 - e^{-K(a-t_0)})$
Eq. 2	Mass (kg) W at age $_a$	$W_a = w_a L_a^{w_b}$
Eq. 3	Fecundity f at age $_a$	$f_a = 10^{\left(a_f L_a + b_f\right)}$
Eq. 4	Maturity T at age $_a$	$T_a = \left(1 + e^{-(L_a - L^T)\sigma^T L^T}\right)^{-1}$
Eq. 5	Survival (year^{-1}) S at age $_a$	$S_a = e^{(-(M L_m L_a^{-1}))^{C}}$
Eq. 6	Survivorship l at age $_a$	$\begin{array}{l\|l} l_a = 1 & a = 1 \\ l_a = l_{a-1}S_{a-1} & a = 2{:}Amax \end{array}$
Eq. 7	Eggs per recruit φ_e	$\varphi_e = \sum_a f_a T_a l_a$
Eq. 8	General Beverton-Holt a parameter	$a = \Omega\varphi_e^{-1}$
Eq. 9	Zone-specific Beverton-Holt b_k parameter	$b_k = (\Omega - 1)(R_k\varphi_e)^{-1}$
Eq. 10	Beverton Holt a parameter modified by zone $_k$ and time $_t$ specific recruitment habitat $H_{t,k}$	$a_{t,k}^H = aH_{t,k}^{\varepsilon^a}$
Eq. 11	Beverton-Holt b parameter modified by zone $_k$ and time $_t$ specific recruitment habitat $H_{t,k}$	$b_{t,k}^H = H_{t,k}^{\varepsilon^b} b_k (H_{t,k})^{-1}$
Movement Characteristics of Stock		
Eq. 12	Age-specific probability p at age $_a$ to moving (^{m}) upper lower	$p_a^m = \|h_a^m - g_a^m\|$ where $g_a^{l} = \left(1 + e^{-(a-A_l^m)\sigma_l^{m-1}}\right)^{-1}, h_a^m = \left(1 + e^{-\left(a-A_u^m\right)\sigma_u^{m-1}}\right)^{-1}$
Eq. 13	Zone-specific probability of movement	$p_k^m = p_k P$
Eq. 14	Age $_a$ and zone $_k$ specific probabilities of movement	$p_{a,k}^m = p_a^m p_k^{mT}$
Eq. 15	Zone $_k$ and age $_a$ specific probabilities of moving North ^{N}	$p_{a,k}^{m^N} = p_a^m p_k^{NT}$
Eq. 16	Zone $_k$ and age $_a$ specific probabilities of moving South ^{S}	$p_{a,k}^{m^S} = p_a^m p_k^{ST}$
Initialization		
Eq. 17	Recruitment at unfished conditions per zone $_k$ in initial time period $_{(t=1)}$	$R_{t=1,k} = (a_{t=1,k}^H\varphi_e - 1)(b_{t=1,k}^H\varphi_e)^{-1}$
Eq. 18	Numbers at age $_a$, zone $_k$ in initial time period $(_{t=1})$	$N_{t=1,a,k} = R_{t=1,k} l_a$
Eq. 19	Eggs at zone $_k$ in initial time period $(_{t=1})$	$G_{t=1,k} = \sum_a f_a T_a N_{t=1,a,k}$
Eq. 20	Recruits at zone $_k$ in initial time period $(_{t=1})$	$G_{t=1,k} = R_{t=1,k}$
Time Dynamics		
Eq. 21	Exploitation rate U at time $_t$, zone $_k$	$U_{t,k} = 1 - e^{\varphi_{t,k}}$
Eq. 22	Larvae at zone $_k$ in time period $_t$	$L_{t,k} = \sum_k G_{t-1,k}\gamma_{k,1:k}$
Eq. 23	Recruits at zone $_k$ in time period $_t$	$R_{t,k} = aL_{t,k}(1 + bL_{t,k})^{-1}$
Eq. 24	Numbers at time $_t$, age $_a$ and zone $_k$	$N_{t,a,k} = N_{t,a,k}^S\left(1 - p_{a-1,k}^m\right) + N_{t,a,k}^{m^N} + N_{t,a,k}^{m^S}$
Eq. 25	Numbers at time $_t$, age $_a$, zone $_k$ that survive each time period	$N_{t,a,k}^S = N_{t-1,a-1,k}S_{a-1}(1 - v_{a-1}^c U_{t-1,k})$
Eq. 26	Numbers at time $_t$, age $_a$ that move North into zone $_k$	$N_{t,a,k}^{m^N} = p_{a,k}^{m^N} N_{t-1,a-1,k+1}S_{a-1}(1 - v_{a-1}^c U_{t-1,k+1})$
Eq. 27	Numbers at time $_t$, age $_a$ that move South into zone $_k$	$N_{t,a,k}^{m^S} = p_{a,k}^{m^N} N_{t-1,a-1,k-1}S_{a-1}(1 - v_{a-1}^c U_{t-1,k-1})$
Eq. 28	Eggs at zone $_k$ at time period t	$G_{t,k} = \sum_a f_a T_a N_{t,a,k}$
Fishery Characteristics		
Eq. 29	Vulnerability v at age $_a$ to capture (^{c})	$v_a^c = \left(1 + e^{-(L_a - L^c)\sigma^{c-1}}\right)^{-1}$
Eq. 30	Total catch C_t in year $_t$ at zone $_k$	$C_{t,k} = U_t v_a^c N_{t,a,k}$
Eq. 31	Catch per unit effort per time period $_t$ and zone $_k$	$y_{t,k} = C_{t,k}E_{t,k}^{-1}$
Restoration Representations		
Eq. 32	H_k value for restoring O hectares per zone	$O/\left(\frac{H_k}{H_k}\right)$

relative return of alternative restoration zones would remain unchanged, thus this equilibrium metric is in keeping with the objectives of this work—to evaluate relative efficiency of alternative zones, rather than a full benefit cost analyses of the benefit of restoration to society.

3.2. Zone-specific effect of increasing restoration

The functional response of New South Wales EKP harvest with increasing proportion of restored habitat differed across zones (Fig. 4). Zones 2–5 showed relatively steady improvements, although improvements were much lower in zone 5 than the other zones. The more northern and southern zones showed negligible improvement, for many of the reasons stated above. The roughly linear relationship in all zones is a function of the proportional increase in effective carrying capacity with restoring habitat. These results reinforce the idea that the most desirable zones for restoration would by zones 2–4, and especially zone 3.

Table 5

Description of parameter values used for sensitivity analyses. Number refers sequentially to each assumption scenario tested, and the outcomes of each scenario are presented in the corresponding figure panels on Fig. 5.

Number	Assumption	Fig. 5 panel
1	Symmetrical dispersal to zones north and south—e.g. for zone 5, 40% of larvae dispersed to zone 5, 20% to zones 4 and 6, and 10 percent to zones 4 and 7.	a
2	Identical effort, E_k, distributed to all zones, 130.5 days per month	b
3	Identical recruitment at unfished conditions, R_k, for all zones, 9.09×10^7	c
4	Identical habitat degradation among all zones ($H_{l,k} = 0.5532$, the arithmetic mean of all zones presented in Table 2), and also identical current habitat suitable for recruitment ($\hat{H}_k = 2195$ ha, the arithmetic mean of all zones) in all zones.	d
5	Assuming no movement between zones, $\hat{p} = 0$	e
6	Assumptions 1 & 3	f
7	Assumptions 1, 3, & 4	g
8	Assumptions 1-4	h
9	Assumptions 1-5	i

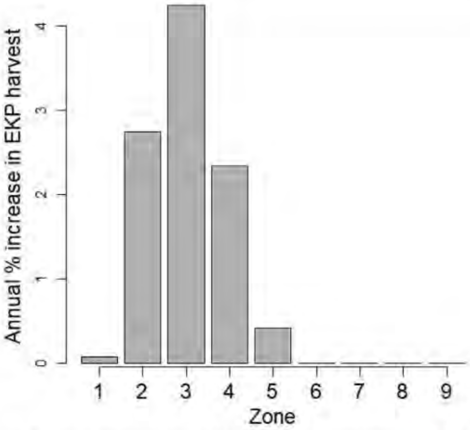

Fig. 3. Expected outcomes from 200 ha of habitat restoration in each alternative zone in New South Wales. Zones correspond to those in Fig. 1.

3.3. Sensitivity analyses

Sensitivity analyses generally demonstrated that the results of the model were relatively robust to changes in individual assumptions of spatial dynamics of the EKP population and life history, at least with respect to the selection of potential restoration zones. This is demonstrated by the fact that changing only a single parameter at a time (Fig. 5a through 5e) would mostly yield a similar pattern of the expected returns from restoring alternative zones, in that zone 3 would be preferred. There were some exceptions, however. Assuming that all zones had the same recruitment at unfished conditions (Fig. 5, panels c, f-i) had a substantial effect on results, causing greater improvements in harvest from restoring southern zones. A slight difference was also evident when there was no movement assumed between zones—which sharply contradicts current understanding of EKP life history—and in this case zone 2 had the greatest return from restoration (Table 5, Fig. 5 panel e). As multiple spatial parameters are simultaneously changed, the results become more dissimilar among the zones, eventually favoring southern zones (Fig. 5f–i). This culminates in the effective "null" model represented by panel i, in which all zones are assumed to be essentially identical in all respects, thus restoring them produced similar improvements in EKP harvest. Here the slight preference for more internal zones represents the fact that more northern and southern zones would be "losing" some potential animals via symmetrical dispersal.

4. Discussion

4.1. Application of spatial models to explore restoration scenarios

This research demonstrates the utility of spatial models for evaluating the fisheries impacts of different habitat restoration scenarios. Habitat restoration will likely remain a high priority for many fisheries agencies, particularly in coastal areas subject to a suite of potentially interacting stressors such as invasive species, coastal human development, and pollution (Ruiz et al., 1999; Schulte, 2007; Teichert et al., 2016). Further, past and ongoing habitat alteration from such stressors may be exacerbated by climate-change-related stressors (Lotze et al., 2006), whether gradual (e.g., sea level rise, changing pH) or episodic (e.g. harmful algal blooms, hypoxia events, increased frequency of intense storms, Delorenzo, 2015; Hughes et al., 2015; Paerl et al., 2014; Warwick et al., 2018). Thus, the causes of intensifying estuarine stressors, including but not limited to climate change, suggests such stressors are unlikely to soon subsist. Under such circumstances, it is likely that situations similar to those precipitating this case study will be increasingly common (Pastorok et al., 1997) – with multiple potential spatial locations (if not habitat types) to restore, agencies must select those providing the greatest benefit to society. In these situations, decision support tools are required to ensure efficient investment, and to foster greater stakeholder support for choices (Wyant et al., 1995). To this end, spatial simulation models that assess outcomes of alternative restoration plans can be useful (Walters et al., 2007). These models act as a template for describing multiple assumptions regarding environmental, ecological and socioeconomic attributes described from previous studies, while also identifying key uncertainties for future research. While habitat restoration is a common management action (Turner et al., 1999), and while nearly all such restoration activities must select suitable areas for restoration, remarkably few restoration programs use such models to support decisions (The National Academies of Sciences Engineering and Medicine, 2017). Thus, while this case study is specific for the EKP fishery, we believe this approach has much broader value and potential to be adapted to many other species and systems.

Linkages between habitats and exploited species are common throughout all coastal fisheries, and potential increases to fisheries productivity are often touted as a justification for habitat repair. Quantifying habitat-fishery linkages is central to estimating this impact. In the case study presented here, "habitat restoration" is referring to the reinstatement (or improvement) of connectivity between the estuary and former wetland habitats, allowing return toward natural functioning of the wetland systems and exchange with the estuary (e.g. Boys et al., 2012; Boys and Pease, 2017; Boys and Williams, 2012). Recent examples show that penaeid prawns, including EKP, return to utilize these wetlands within very short timeframes (Boys and Pease, 2017; Hart et al., 2018; Taylor et al., 2017c). Our approach is built around a

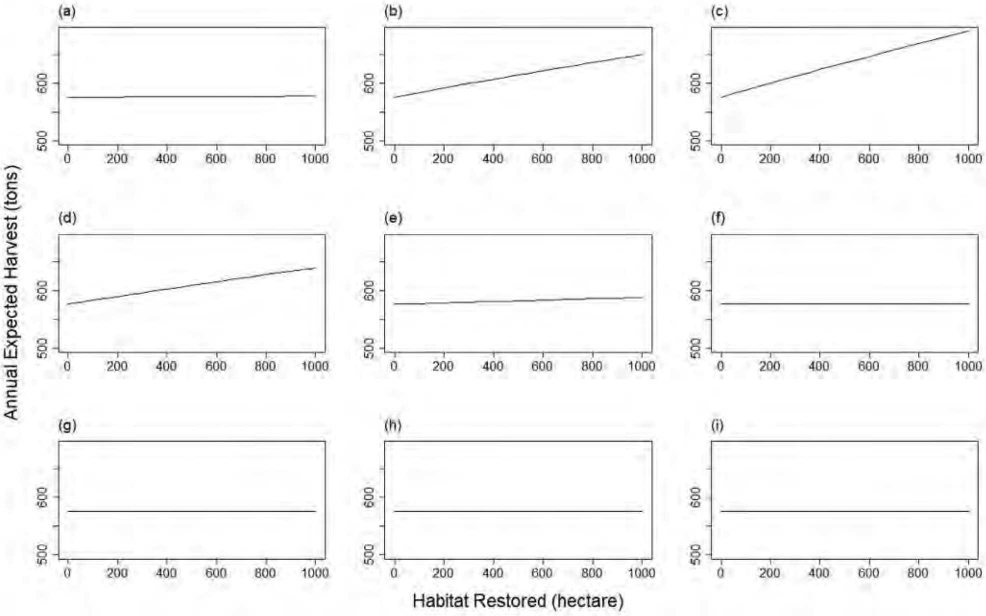

Fig. 4. Functional shape of the effect of habitat restoration on improved EKP harvest with New South Wales. Panels a–i represent zones 1–9 (Fig. 1), respectively.

generic foundation of stock-recruitment and density-dependence relationships, and while the spatial linkages incorporated within the model are species-, system- and fisheries-specific, these can be easily adapted. These two factors mean that this approach can lend itself to potentially any species with a known migration and advection pathway and known habitat linkages (e.g., linkages with mangrove, salt marsh, or seagrass habitats during early life stages), and any habitat repair scenario. Discussion of the assumptions of the model (below) should assist in the application of our approach to other species and ecosystems where habitat repair may be under investigation.

4.2. Impact of habitat restoration on Eastern King Prawn

Our results suggested that restoring juvenile EKP habitat would be expected to have very different results on the extant fishery, depending on the zone of the restoration. Under the assumptions judged most realistic, zones 3 or 4 provided the greatest return to the fishery in terms of harvest (and thus anticipated market revenue). The key characteristics of these zones included (1) substantial habitat loss (Rogers et al., 2015), greater estimated recruitment at unfished conditions (O'Neill et al., 2014), greater settlement of EKP larvae (Everett et al., 2017), and greater or faster recruitment to the main New South Wales ocean trawling grounds. More northern zones were less attractive as restoration areas, given the likely northern movement of adult EKP out of New South Wales managed waters, whereas more southern areas were generally characterized by more pristine habitat, lesser larval settlement, and greater distances for EKP to migrate prior to reaching fishery grounds (thus higher potential for natural mortality between the nursery phase and harvest). The importance of these assumptions were aptly demonstrated via the uncertainty analyses. While the magnitude of the effects of restoration varied from the outcomes assumed most realistic under any alternative assumptions, most single alternative assumptions suggested similar relative zone-specific effects. However, alternative assumptions regarding recruitment at unfished conditions had substantial effects on which zone might be seen to provide the greatest return on investment from restoration. This is notable since zone-specific recruitment at unfished conditions is not readily observable but rather must be estimated, generally (and in this case) from stock assessment methods (O'Neill et al., 2014).

4.3. The ecological impact of restoration

The ecological relationships connecting juvenile organisms to the habitat they use is a particularly important model assumption for habitat restoration (Walters and Juanes, 1993). In most cases, habitat considered important for recruitment processes subsumes multiple functions including predation refuge, foraging opportunities, and physical requirements (Beck et al., 2001; Peterson et al., 2000) – this has been specifically true for penaeids (e.g. Loneragan et al., 2013b). Thus "habitat" constitutes an interaction of physical structure and environmental conditions generally suitable for survival through the early life stages where mortality is assumed to be density dependent (Levin and Stunz, 2005; Walters and Juanes, 1993). Of particular influence for this work was the specific assumption of how habitat restoration effects on juvenile survival ought to be described in the representation of density dependent recruitment processes—in this case, the Beverton-Holt relationship. At least two options exist (Walters et al., 2007). It may be assumed that change in habitat actually affects the a parameter of the Beverton-Holt relationships, corresponding to the maximum survival rate under low densities. This is a strong assumption, since this maximum survival is related to the overall productivity (recruitment compensation ratio or steepness) of the stock. Thus, assuming restoration-dependent changes in this parameter would probably require altering scale parameters (e.g., recruitment at unfished conditions, catchability) which, in combination with recruitment compensation, define the population dynamics of a fishery. The alternative assumption is that changes in habitat effectively alters the $\boldsymbol{b}$ parameter of the Beverton-Holt, relating to the density-dependent effects of survival and at what

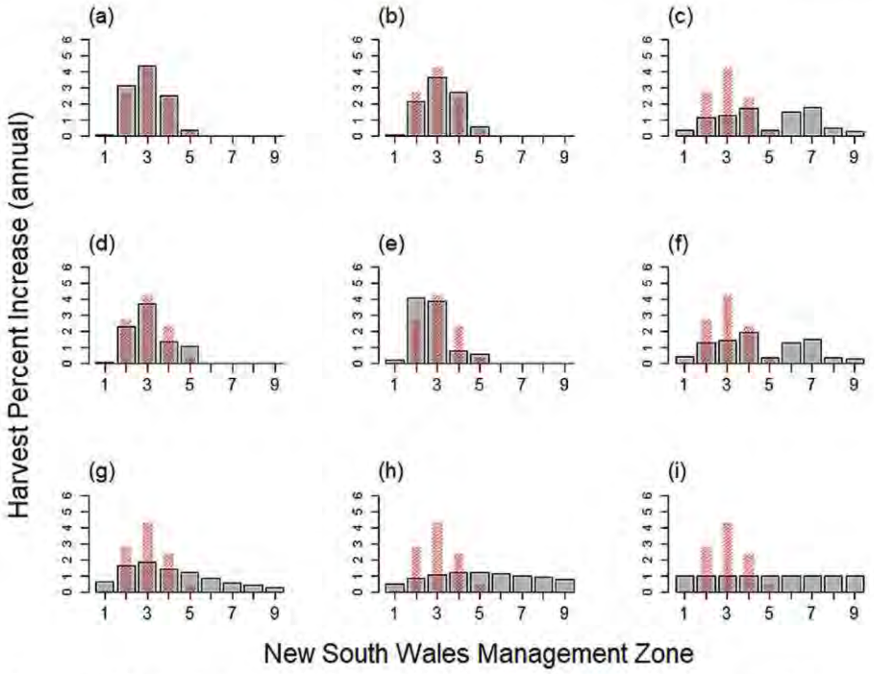

Fig. 5. Results of scenarios tested during sensitivity analysis. The details of each scenario are outlined in Table 5, and grey bars represent the improvement in average annual EKP revenue under these assumptions, across management reporting zones (see Fig. 1) within New South Wales. Red bars represent the expected outcomes under the base model for comparison. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

population levels these intensify (Walters et al., 2007). Making this assumption implies that restoration actions will increase the effective maximum recruitment of an area, which would correspond to an increase in the effective "carrying capacity" for an estuary. It should be noted that either assumption could result in the positive effects of structured habitat like seagrasses or algal beds on penaeid survival and growth (Haywood et al., 1995; Kenyon et al., 1995); consequently it may not be easy to infer which assumption is more likely from such studies alone.

The latter assumption (represented by c^*, Table 1) was incorporated in the model simulations presented here, implemented following methods described by Walters et al. (2007). This assumption ought to be considered conservative, in that it will substantially underestimate benefits of recruitment if in fact restoration actually affects overall productivity. Given the importance of assuming how restoration activities will enhance juvenile survival specifically, it is perhaps surprising that these issues have rarely been addressed empirically. An additional benefit of prefacing restoration actions with modelling is that, with appropriate monitoring, it may allow for inferences to be made about this or other similar assumptions.

4.4. *Fisheries management and jurisdictional considerations*

A major assumption of the model was that fishing effort remained unchanged following restoration, both in terms of absolute magnitude (number of trips) and spatial allocation. Management of the Ocean Trawl Fishery in the New South Wales is being altered to a share-linked effort quota system, which will prescribe a total allowable annual effort (TAE) that is to be distributed among shareholders in the limited-entry fishery (NSW Department of Primary Industries, 2017b). While it is reasonable to consider that, at least in the near term, TAE will be independent of any restoration actions that are implemented, the relationship between restoration actions and effort levels presents an interesting point for consideration. By continuing to limit effort following habitat restoration targeted at enhancing the fishery, the benefits will accrue to already licensed fishers simply from the increase in prawn abundance, which should result in greater catches per unit of effort (CPUE) and the benefits of restoration should manifest in a more profitable fishery. However, if habitat restoration was successful and led to increased prawn abundance, this may well be used to justify an increase in TAE, particularly if the resultant CPUE is well above the relevant reference point. Under both of these scenarios, total catch and market activity (economic impact) would increase, but economic value (i.e. profitability and rent) would likely only or most substantially increase under the first scenario. Thus, limiting effort effectively determines whether restoration improves economic value or economic impact.

This issue raises a potential area of future research. While many agencies might prefer to have a fishery operate at greatest efficiency (represented by maximum economic yield), it is often difficult to imagine socially acceptable scenarios for reducing effort to the extent that this can be achieved. However, the results of this work demonstrate the possibility that in some cases, habitat restoration may support an effort management regime to increase the efficiency of the fishery—essentially to move the fishery towards maximum economic yield without further reduction in fishing effort or other fishing capital (e.g. boats or licenses). Future work is needed to explore this as a potentially powerful tool to enhance fisheries economic value.

The core objective of this work was specifically related to the impact of habitat repair on the New South Wales EKP fishery, to help facilitate the investment of state funds in this activity. Consequently, this work does not consider the potential effects of restoration to areas beyond New South Wales, despite the migration of EKP from estuarine nurseries in the northern zones into Queensland waters where they are available to the Queensland fishery. Thus, the results of this work do not represent the relative, zone-specific effects of restoration to Australia as a whole. For example, while the results of this work suggest zone 3 is the most efficient area for restoration for New South Wales, zone 2 to the north also provides substantial improvements in harvest, but likely contributes more to Queensland fisheries. This raises the possibility of collaboration between the two states, such that if costs of repair were shared between jurisdictions then New South Wales may consider investing in the zone that provides the greatest benefit for both jurisdictions.

Such cross-jurisdictional collaboration would need to consider several factors. First, the benefits that could accrue to Queensland from New South Wales restoration depend on EKP migration patterns, but also on spatial patterns in fishing effort in New South Wales from which EKP would presumably have to escape before becoming available to Queensland fishers. Thus, cross-state collaboration might depend in part on New South Wales decisions regarding effort allocation. Further, it is possible that the financial contribution from Queensland for such activities might not be sufficient to incentivize New South Wales towards selecting an alternate, more northward zone. Given the general paucity of research on the cross-jurisdictional impacts of habitat repair, and the possibility that both states (and Australia as a whole) might benefit from the collaboration, future research on this issue is warranted.

4.5. Additional value of habitat repair

It is critical to understand the scope of this work, which focuses solely on identifying the areas for which repair efforts will accrue the greatest increase in value for the New South Wales EKP fishery. Thus this work falls far short of a benefit-cost analysis, as would be necessary to evaluate whether restoration represents a net positive for society, as well as what alternative actions (e.g. stock enhancement, marketing, effort changes) might or might not provide greater return on investment. It is highly likely that the restoration actions intended to improve the EKP fishery may have additional benefits for other ecosystem services, such as productivity of other exploited species (both recreational and commercial), imperiled species or habitats, restoration of hydrological function and improvements to physico-chemical conditions, and storm protection (Barbier et al., 2011; Spencer and Harvey, 2012). None of these potential benefits were considered in this evaluation, though they may well vary across zones, or even exceed the potential benefits expected for EKP. Similarly, it is implicitly assumed here that the per-capita costs of restoring habitat will be similar across the spatial areas (zones 1 through 9 of New South Wales) considered, though this may not be the case. Finally, while the results are presented in terms of future anticipated yield, the harvest has not been discounted and no time-streams of benefits are described. It is assumed that future harvest is inherently less valuable than current harvest, but that this will only change the absolute magnitude of benefits and not the relative differences among zones.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.02.007.

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Appendix 13 – Extension and Adoption Plan

The impact of habitat loss and rehabilitation on growth, survival and recruitment to the NSW eastern king prawn fishery

EXTENSION AND ADOPTION PLAN

E&A OBJECTIVES

1. To engage with commercial EKP fishers in order to
    a. Improve understanding of commercial fishers' knowledge about EKP habitat requirements and impacts
    b. To improve commercial EKP fishers' appreciation of the benefits of EKP habitat restoration.
2. To provide research results (relating to Project Objectives 1, 2 and 3) in forms appropriate to each of the target audiences
3. To develop as far as possible regionally specific information relating to potential improvements associated with targeted rehabilitation
4. To foster in-principle agreement from local and regional land managers to incorporate EKP habitat improvement into Estuary Management Plans, Catchment Action Plans and similar local and regional planning instruments.
5. To obtain in-principle agreement from fisheries managers and commercial EKP fishers to incorporate relevant habitat improvement into the EKP Fishery Management Plan when next reviewed.

TARGET AUDIENCE/S

1. Commercial EKP fishers in NSW and Queensland
2. Commercial fisheries managers
3. Commercial fishing sector more broadly
4. Catchment and land management agencies, local councils and landowners

END USERS

*Commercial EKP fishers in NSW and Queensland

*Commercial fisheries managers

*Commercial fishing sector more broadly

*Coastal land management and planning bodies, including catchment management agencies and councils

* Fish Habitat managers

* Private and public companies with estuary management responsibilities or concerns

*General public, including recreational fishers

KEY MESSAGE/S

Note: Specific message elements will be identified as a result of both on-ground research (project objectives 1, 2, 3) and desktop research (project objectives 3, 4).

Key message 1

A productive and sustainable EKP fishery depends on healthy habitat for juveniles

1a. The EKP productivity associated with different habitat types, complexes and states [as identified by the research]

1b. How juvenile EKP use different types of habitat [as identified by the research]

1c. Specifics of what is needed for survival and growth [as identified by the research]

1d: The factors and conditions that support optimal carrying capacity [as identified by the research]

Target audience:

- commercial EKP fishers
- commercial fisheries managers

Incidental audience:

- recreational fishers
- fisheries researchers

Key message 2

Habitat that supported the survival and growth of EKP has been lost

Target audience:

- commercial EKP fishers
- commercial fisheries managers

Incidental audience:

- recreational fishers
- fisheries researchers

Key message 3

Targeted habitat improvement will improve the potential productivity of the EKP fishery

3a. Specific rehabilitation options as identified by the research

3b. The local / regional social and economic value of a productive and sustainable EKP fishery

Target audience:

- commercial EKP fishers
- commercial fisheries managers
- local / regional land managers (incl local councils, county councils and catchment management authorities / Local Land Service agencies

Incidental audience:

- recreational fishers
- fisheries researchers

Key message 4

Improving the potential productivity of the EKP fishery through habitat improvement has social and economic benefits

3a. The local / regional social and economic value of a productive and sustainable EKP fishery

Target audience:

- commercial fisheries managers
- local / regional land managers (incl local councils, county councils and catchment management authorities / Local Land Service agencies

Incidental audience:

- recreational fishers
- coastal planning and policy professionals

Key message 5

Commercial fishers have a stake in improving the potential productivity of the EKP fishery

Target audience:

- commercial EKP fishers
- commercial fisheries managers

****

METHODS

1. Information letter

Information about the project outlining its purpose, objectives, personnel and ways to get more information and provide input.

Type: Printed publication

Audience: Commercial EKP fishers and their co-ops

Phase: Project initiation

Frequency: Once

Cost elements: salary, printing, postage (every EKP licencee and coop)

2. Project updates

Summary of research activities and results as well as engagement activities and feedback. Provided six-monthly, these reports will also be available online through both dedicated website (see Method 4) and partner organisations' websites.

Type: Printed and online publication

Audience: Commercial co-ops, relevant Catchment Management Authorities / Local Land Services, relevant local councils

Phase: Throughout

Frequency: Six monthly (6 in total)

Cost elements: salary, printing, postage (every EKP coop)

3. Research papers

Papers documenting research results will be prepared for peer-reviewed journals. Note: the dissemination of information / results to a more general audience will not be delayed until after publication. Internal review of results and their interpretation will take place prior to public dissemination.

Type: Printed and online publications

Audience: Fisheries researchers and managers

Phase: on completion of research components

Frequency: dependent on results

Cost elements:salary

4. Dedicated website

A project website will be hosted within www.dpi.nsw.gov.au/fisheries. Links to the websites of OceanWatch and other partner organisations and FRDC. The website will provide:

- project information and updates (six-monthly)
- plain English summaries of the research results
- resources developed on the habitat use and ecosystem requirements of EKP
- links to other relevant resources and information
- contact details for project team

Type: Website

Audience: General

Phase: Throughout and ongoing

Frequency: N/A

Cost elements: salary

5. Face-to-face discussions with commercial fishers

Project team members will visit EKP fishery participants, at the fishers' convenience. At least 25 face-to-face interviews from at least 6 sites, specifically: Tweed Heads, Ballina, Yamba, South West Rocks, Coffs Harbour and Newcastle.

The focus of these discussions with commercial fishers includes:

- obtaining fishers' perspectives on issues affecting king prawn and EKP habitat
- determining what fishers' want to know about EKP and EKP habitat
- determining where these fishers go for information, what sources they trust and their information preferences

Wherever possible, this activity will co-occur with other activities with which the commercial fishers are familiar or have reason to be interested in (eg, in concurrence with SEAnet officer visits, coop meetings, and similar). Every effort will be made to minimize inconvenience to the fishers and to maximize the value they get from their time.

Note: this method is linked with Method 6.

Type: Face-to-face

Audience: Commercial EKP fishers

Phase: Project outset, then as requested

Frequency: at least once per co-op involved in the EKP fishery

Cost elements: salary, travel, accommodation

6. Survey

A survey designed to be administered during face-to-face discussions as well as available online (download and return and web-based). This short survey will gather information about where commercial ERP fishers go for information, what sources they trust and their information preferences. The results will inform the development of a communication plan (see Method 7) and information resources for commercial fishers.

Type: Face-to-face and online

Audience: Commercial EKP fishers

Phase: Project outset and open for first 3 months

Frequency: Once and concurrent with #5

Cost elements: salary

7. Communication plan

A succinct (10 page maximum) plan using the results of the survey and the face-to-face discussions to define an effective way to communicate with commercial fishers and coastal habitat stakeholders about habitat use and ecosystem requirements of EKP. As well as informing the development of the information products, this plan is likely to have a broader application beyond the life of this project for individuals and organisations wishing to communicate effectively with commercial fishers.

Note: This is not a Project communication plan; it is a plan for effective communication of information in relation to habitat and the commercial EKP fishers.

Type: Electronic publication

Audience: Open

Phase: 6 – 9 month stage

Frequency: Once

Cost elements: salary

8. Regional land managers' workshops

A series of 3-hour workshops (one per region: Ballina, Kempsey and Newcastle) to discuss the implications of the project for local and regional planning and land management. Specific attention will be paid to opportunities for incorporating standard operating procedures and rehabilitation activities into estuary management plans, climate change adaption plans and catchment action plans. These workshops will be free to participants.

Type: Workshops

Audience: local council planning staff, catchment management authority staff, relevant Crown Lands management staff, Aboriginal Land Council representatives, regional Landcare / Coastcare / Dunecare coordinators and relevant State agency planning and regulatory staff (eg, Fisheries, Planning, Water, Environment,) Ports Authorities

Phase: Late

Frequency: Once per region

Cost elements: salary, staff travel and accommodation, venue hire, catering, printed materials for participants

9. Presentations

These conferences offer the opportunity to inform a variety of professionals involved in managing land, assets and infrastructure, sustaining local / regional business and economies and developing cross-agency / disciplines approaches to addressing coastal issues. The EKP and habitat information will be directly relevant to Queensland commercial fishers and fisheries managers. The underlying concept of integrating habitat improvement, fisheries productivity and multi-sectoral involvement will be of interest to a wider range of stakeholders.

Three conferences will be targeted:

- The 2014 or 2015 NSW Coastal Management Conference
- The 2014 or 2015 Coast to Coast National Conference
- Seafood Directions (2015 – Note, this conference is not held in 2014 or 2016)

The year in which these presentations will be provided, ie either 2014 or 2015, will depend on the progress and timing of research results, conference themes, time of year (early 2014 less suitable), and location (east coast venues preferred).

Type: Conference presentation

Audience: Professionals involved in coastal management in Australia

Phase: Late

Frequency: Three

Cost elements: salary, staff travel and accommodation, conference registration

10. Information products

(a) Products designed to inform commercial fishers about the habitat requirements of EKP. The format and style of these and how they are provided will be informed by the results of the survey (within budget limitations). At the least, information will be developed in an appropriate style and language into a web page and downloadable brochures. The budget does not cover printed materials.

(b) Products designed to inform and assist land managers. This information will be available as a web page and downloadable brochures. These products will be made available to other professional bodies, such as the Local Government and Shires Association and the Local Land Services, to facilitate dissemination.

(c) General information product designed to be accessible and available to a broad general audience and suitable for distribution at field days, boat and industry shows, school visits and similar.

Note: providing printed materials may be possible if additional corporate funding is secured over the course of the project.

Type: Electronic publications

Audience: Various

Phase: Throughout

Frequency: N/A

Cost elements: salary

11. Media

Three media elements will be targeted:

- Media releases on research findings and to promote workshops *(*At least 4 media releases)

- Articles for special interest media (eg. The Land, recreational fishing magazine, FRDC FISH magazine) building profile of land use issues and link to fisheries productivity to broad audience. At least 4 articles.

- Radio – at least one interview

Type: various

Audience: broad

Phase: throughout

Frequency: throughout

Cost elements: salary

12. Final Project Report

The Final Report provides an opportunity to consolidate all the project activities, results, and outputs.

Type: Print and electronic publication

Audience: FRDC

Phase: End

Frequency: Once

Cost elements: salary

13. Opportunistic

Several staff and organisations involved in the project are involved in extension activities that will provide other opportunities to provide information or talk with specific groups. Examples include the engagement work with recreational fishers that Fisheries NSW does through the Fish Habitat Network and the community engagement and schools work done by Oceanwatch.

Type: various

Audience: general public

Phase: throughout

Frequency: as opportunities arise

Cost elements: in-kind

ACTION PLAN

During Project

Method	**Responsibility**	**Completion date**
1. Information letter	Co-investigator Liz Baker	1 month after contract signed
2. Project updates	Co-investigator Liz Baker All others contributing information	Every 6 months
3. Research papers	Principle investigator Co-investigator Craig Boys Co-investigator Craig Copeland Co-investigator James Smith Co-investigator Greg West	As possible during project and ongoing after completion
4. Dedicated website	Co-investigator Liz Baker	1 month after contract signed with ongoing updates throughout
5. Face-to-face with commercial fishers	Principle investigator Co-investigator Liz Baker Co-investigator Craig Copeland	Throughout first 6 months after contract signed
6. Survey	Co-investigator Liz Baker	Data collection complete 6 months from contract signed
7. Communication plan	Co-investigator Liz Baker	9 months from contract signed
8. Regional land managers' workshops	Co-investigator Liz Baker Co-investigator Craig Boys	Final 6 mth period
9. Conference presentations	Principle investigator or Co-investigator	As appropriate – 2014 and 2015
10. Information products	Co-investigator Liz Baker	Throughout. Some products might be able to be produced (eg, habitat maps) within the first 3 months. The majority of products will be produced in the second half of the project (eg, Jan 2015 to May 2016)
11. Media	Principal investigator Co-investigators	Throughout
12. Final Project Report	Principal investigator	June 2016
13. Opportunistic	All	Throughout

After Project

It is likely that the preparation research papers for peer-reviewed journals will be ongoing or still in progress at the completion of the project.

EVALUATION PLAN

Project Title: The impact of habitat loss and rehabilitation on growth, survival and recruitment to the NSW eastern king prawn (EKP) fishery

Research Agency: NSW DPI

Client: Industry / Local government/ Catchment managers /Fisheries NSW / FRDC

Driver/instigator for the research?	Industry	Government	Researcher	Other:
Adoption potential	During	Immed. after	2-5 years after	Other: Will vary with target audience and the nature of adoption activities

Extension Target	Tools	Performance indicators	What would success look like?	Measurement	Adoption potential	Impact potential	Rating
Primary – NSW commercial EKP fishers	• One-on-one interactions • survey • website • regular updates • Audience-specific information products	• Meetings held • Survey developed and administered • Website developed and live • Updates delivered • Information products developed	• More information requested about habitat. • Industry support for investment in habitat improvement.	• Attendance at face-to-face discussions • Survey response rate • Feedback and communication from fishers or co-ops	Low end of likely	Significant	Medium - high
Primary – NSW coastal land managers	• Project website • Project updates • Regional workshops • Conference presentations	• Website developed and live • Updates delivered • Workshops held • Work presented at conferences	• Indication of specific actions to address EKP habitat-relevant issues in planning reviews • Improved incorporation of habitat considerations into coastal planning policies/ plans	• Attendance at workshops • Evaluation of each workshop • Incidental identification of adoption or feedback	Low end of likely	Major	High to extreme
Primary – NSW fishery managers	• Project updates • Research papers • Regional workshops	• Updates delivered • Workshops held • Research papers prepared and in review process	• Revision of EKP FMP includes consideration of habitat issues	• Attendance at workshops • workshop evaluation • Inclusion of habitat issues in FMP review (if occurs)	High end of Unlikely	Major	High to extreme
Secondary – Other Australian fisheries /coastal land managers	• FRDC final report. • Conference presentations	• Final report accepted • Work presented at conferences	• Understanding of implications for other EKP fisheries and other fisheries in general • Pick-up of information products	• Feedback from attendees • Requests for information access or products	High end of Unlikely	Minor	Low
Secondary – recreational fishers and general public	• FRDC final report. • Project updates and website	• Updates prepared • Website developed and live	• Understanding of factors affecting fisheries productivity • Reduced blame on commercial fishers for poor prawn catch	• Informal communication • Requests for information	Unlikely	Minor	low

Appendix 14 – Eastern King Prawn Fisher Survey

NSW GOVERNMENT | Department of Primary Industries

Eastern King Prawn habitat - commercial fisher survey

This survey has been designed by Fisheries NSW, as part of a three year project looking at the relationship of Eastern King Prawn (EKP) productivity to estuary habitats. This will inform land and estuary managers to make decisions that can directly benefit prawn production.

A key component of the project is to seek the views of commercial fishermen on your knowledge of estuary habitats, as well as finding out what other information you would like and how you would prefer to receive it.

Individual survey responses will be kept completely confidential and participant's names are not being stored.

Thank you for your interest and participation in this survey.

If you need any further information, please contact simon.walsh@dpi.nsw.gov.au or call

Simon on **6626 1256** or **0438 465 882.**

1. What is your gender:

☐ Male ☐ Female

2. What is your age?

………..years

3. How long have you been professionally fishing for prawns?

………..years

4. Where is your home port?

……………………………………………………………………

5. Please list the estuary(s) or general marine location(s) where you fish for EKP.

………..

6. Of the following estuary habitat types, which ONE do you think most benefits EKP numbers?

☐ Seagrass ☐ Mangroves ☐ Wetlands ☐ Saltmarsh ☐ Bare sediment

☐ Don't know

7. Since you began fishing, which habitat types have improved or declined in your area?

	Improved	No change	Declined	Not sure / don't know
Seagrass	☐	☐	☐	☐
Mangroves	☐	☐	☐	☐
Saltmarsh	☐	☐	☐	☐
Wetlands	☐	☐	☐	☐
Other ………………	☐	☐	☐	☐

8. On a scale of 1 (very important) to 4 (not important), how would you rate each of the following factors on EKP *production* (not catch-ability)?

	1 very important	2 important	3 some importance	4 not important	5 don't know
River flood level	☐	☐	☐	☐	☐
River flood timing	☐	☐	☐	☐	☐
Water temperature	☐	☐	☐	☐	☐
Water quality	☐	☐	☐	☐	☐
Availability of seagrass	☐	☐	☐	☐	☐
Availability of mangroves	☐	☐	☐	☐	☐
Availability of saltmarsh	☐	☐	☐	☐	☐
Availability of wetlands	☐	☐	☐	☐	☐
Availability of bare sediment	☐	☐	☐	☐	☐
Harvest management	☐	☐	☐	☐	☐
Other …………………………………	☐	☐	☐	☐	☐

9. How do you rate DPI's efforts to fix estuary habitats?

☐ Could do more ☐ About right ☐ Do too much ☐ Don't know

10. If too much or too little, what should they do more or less of?

………
………

11. Whose information on fishing (in general) do you have the most confidence in? (Multiple responses are OK)

☐ Government ☐ Other fishers ☐ Articles in magazines / newspapers ☐ Internet
☐ Info from TV, radio ☐ Scientists

Why……………………………………………………………………………………………………

12. Whose information on fishing (in general) do you have the least confidence in? (Multiple responses are OK)

☐ Government ☐ Other fishers ☐ Articles in magazines / newspapers ☐ Internet

☐ Info from TV, radio ☐ Scientists

Why……

13. How would you prefer to access future information about prawn research and habitat rehabilitation? (Multiple responses are OK)

☐ Website ☐ Email ☐ Printed brochures

☐ Local newspaper ☐ Radio ☐ Face to face

☐ Scientific Journals ☐ Industry conferences ☐ Addressed letter

14. What information would you like to know about EKP habitat?

☐ What types are most important ☐ What is happening to it ☐ How it could be improved

☐ Other……………………………………………………………………………………………

15. What sort of other information would you like to know about EKP?

………

16. Can you list any estuary habitat restoration works affecting locations where you fish?

………

17. Have you noticed a change in EKP catch since the rehabilitation works?

☐ Large Increase ☐ Slight Increase ☐ No change ☐ Slight Decrease

☐ Large Decrease ☐ Not Applicable

18. If an estuary habitat rehabilitation project was happening in your area, would you be able to help with:

☐ Cash ☐ Hands-on help ☐ Letter of support ☐ None of the above

☐ Other………………………………………………………………………………………

Thank you for your participation in this survey.

Appendix 15 – Eastern King Prawn Research: Communication Plan

Eastern King Prawn Research Communication Plan

November 2014

NSW GOVERNMENT

Department of Primary Industries

Background

The Eastern King Prawn (EKP) fishery is one of the most valuable fisheries in NSW. Despite this, little is known of the ecology of EKP during their estuarine juvenile stages in NSW or about how habitat change has affected productivity.

Our current research project was developed to improve the understanding of both the critical habitat factors affecting prawn recruitment in NSW estuaries, and the nursery habitats that support the EKP fishery. Understanding habitat use and the impact of habitat change is important for the future of the EKP fishery and it is critical that both commercial fishers and coastal land managers are well aware of this information. Such information will also assist with targeting restoration and rehabilitation activities to maximise fishery benefits.

This Communication Plan has been developed to assist in delivering key messages to EKP fishery stakeholders and the broader community. It is evidence-based, drawing from both the literature and a survey of EKP fishers conducted in 2014. It is designed to be a living document and retains sufficient flexibility to ensure that emerging information is provided in a timely and appropriate manner.

EKP fisher survey

A survey of all NSW EKP fishers was undertaken in early 2014 through a combination of mail-out / return envelope surveys and face-to-face interviews. It was designed to establish some basic demographics about the respondents and determine their understanding of the role played by estuarine habitat in EKP production. Its other intent was to find out how those fishers preferred to access their information about EKP and what types of information were of particular interest. The results of the survey have directly informed the development of this Communication Plan.

Results

In total, 174 fishers were provided with the opportunity to complete the survey process. The response rate was 14%. The chief findings include:

Demographics

- Fishers were predominantly male (96%) with an average age of 57 (range 42 to 77 years).
- Collectively, they had 678 years of hands-on fishing experience (an average of 29 years each).
- Their home ports were spread fairly evenly between Tweed Heads and Shoalhaven Heads.

Fishers understanding of EKP / estuarine habitat links

- Fishers recognised the importance of seagrass, mangrove and wetlands for EKP production.
- Fishers attributed less value to saltmarsh and bare sediment habitat types.
- Since they first started fishing, estuarine habitats were perceived to have declined (particularly wetlands, then seagrass, then mangrove, then saltmarsh).

- They thought that the most important factors for EKP production (in order from most to least important) were wetlands, water quality, seagrass, mangrove, water temperature, saltmarsh, flood timing, flood level, harvest management and bare sediment.
- Most fishers (83%) believed that more could be done to rehabilitate estuarine habitats.

Information needs

- Other fishers are clearly their most trusted source of information. In order from most to least, the trusted sources of information were other fishers (58%), scientists (18%), government (12%), newspapers/magazines (6%), internet (3%) and TV/radio (3%).
- Future information would preferably be received by (in the following order): face-to-face (23%), addressed letter (21%), industry conferences (13%), website (11.5%), email (11.5%), brochures (10%), scientific journals (6%) and the local paper (4%).
- EKP fishers would like to receive more information about EKP relationships with estuarine habitats and more detail about new research findings about EKP ecology and migrations.
- While some Hunter-based fishers were aware of estuarine rehabilitation works underway in Hexham swamp, most fishers in other locations remained unaware of any similar rehabilitation works that had been or are being undertaken in their area.
- In terms of participating in future rehabilitation projects, over half of the fishers would be prepared to be involved, either through letters of support (33%) or hands-on help (25%).

Communication Plan Objectives

This Communications Plan provides a framework to assist researchers and managers to effectively target communications in relation to habitat use and ecosystem requirements of EKP.

Specifically, the objectives of the plan are to:

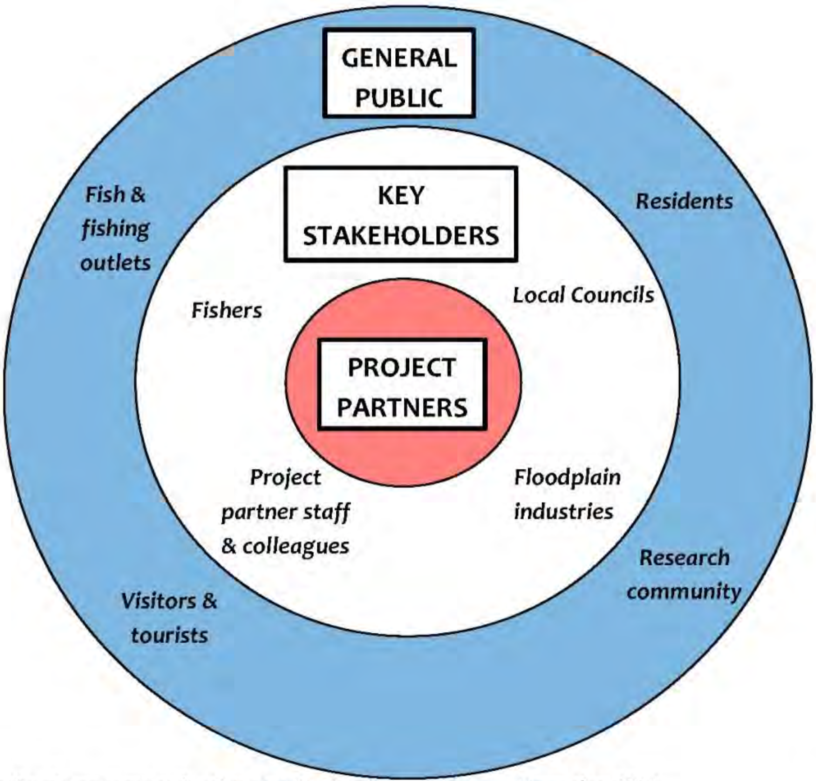
- Facilitate the development and promotion of consistent messages.
- Develop messages addressing specific information gaps.
- Identify the key target audiences in relation to specific messages and/or information.
- Improve the awareness of existing rehabilitation projects and what they are achieving.
- Identify specific roles and responsibilities and timelines for actions.
- Build and enhance communications between project partners, stakeholder groups and the general community.
- Enable adaptive communication approaches in response to new information, opportunities, and/or requests from stakeholders

Key messages

- NSW estuarine habitats provide critical nurseries for larval and juvenile EKP.
- Much of the important estuarine habitat has been historically degraded.
- Better EKP fishery production can be achieved with targeted habitat rehabilitation.
- Our understanding of the linkages between estuarine habitat and juvenile EKP are continually improving and these findings are important for the future of the EKP fishery.
- Research is helping target future rehabilitation works to the estuarine sites, habitats and activities that are best placed to enhance fishery production.
- Engaging all stakeholders in the rehabilitation of habitats important for EKP productivity is critical.

Target Audience

The following diagram identifies and prioritises our target audiences. The inner circle identifies the project partners as the priority and the areas where this communication strategy will initially concentrate its efforts. As achievements are made and objectives achieved, the strategy can then be increasingly implemented for the audiences identified in the outer circles. The diagram aims to assist in visualising the strategy's realm of influence and focus.



The messages and findings of the EKP project first need to be understood and digested by the project partners themselves. Once these are understood, the members are then responsible for communicating to their immediate stakeholder groups. For example, a Local Land Services (LLS) member would need to communicate findings to other LLS staff through their existing networks, meetings, phone calls and other communications media. These immediate stakeholders are then encouraged in turn, to communicate findings more widely amongst the broader community.

The full range of potential audience groups has been identified, and the following table lists those:

EKP Project Partners	NSW Department of Primary Industries Fisheries Research & Development Corporation Hunter Water North Coast Local Land Services Hunter Local Land Services Griffith University Newcastle Ports Corporation Origin Energy Professional Fishermen's Association OceanWatch Australia
Stakeholders	NSW Fishermen's Co-operatives Ocean Prawn Trawl fishers Estuary Prawn Trawl fishers Project partners' staff Local Councils Floodplain industries (e.g. cane farmers, graziers, dairy etc)
General Community	Residents Visitors & tourists Fishing & Boating industries

Communications Activities, Timing and Responsibilities

Achieving the objectives of the communication strategy is the collective responsibility of the EKP team (NSW DPI) and the project partners. The table below details the desired communication actions, timing and responsibilities for each of the three identified target audiences – project partners, key stakeholders and the wider community.

Target audience: Project partners

Aim	Actions / activities	Responsibility	Timing / frequency
Effective information exchange and understanding of the project progress and key findings	Project partner update meetings	All project partners physically attend meetings	Annual project update meetings at Newcastle Fishermen's Cooperative
	Review website updates	All project partners	Check website updates every 6 months following notification from NSW DPI staff. Respond with any queries on the information provided.

Target audience: Key stakeholders

Aim	Actions / activities	Responsibility	Timing / frequency
Effective understanding of the project progress and key findings	Develop EKP Communication Plan	NSW DPI	Complete by 2014
	Reports from project partners to their in-house colleagues	All project partners	Immediately after each 6 monthly update and annual meeting
	Update partner websites	All project partners with websites	Link to 6 monthly web-based update summaries
	Addressed letters to Coops and EKP fishers	NSW DPI	At the project outset, detailing the aims and intent of the research program.
	Face to face discussions with EKP commercial fishers	NSW DPI	Minimum one visit to each participating Coop (including Ballina, Maclean, Coffs Harbour, South West Rocks, Port Macquarie and Newcastle)
	Survey of EKP commercial fishers	NSW DPI	Commence at the project outset. Completed by 2014

Aim	Actions / activities	Responsibility	Timing / frequency
	Deliver 2 - 3 workshops	NSW DPI with project partner support	Towards end of project in 2015/16, targeting coastal land managers and planners
	Industry media articles in newsletters magazines etc.	NSW DPI and project partners	One article per annum minimum. Examples include FRDC FISH magazine, The Land, PFA Professional Fishing Association News etc.
	Electronic information products (e.g. Brochures)	NSW DPI	Two delivered based on research findings towards project completion in 2016

Target audience: Wider community

Aim	Actions / activities	Responsibility	Timing / frequency
Communicate the key messages.	Develop and update the EKP project website	NSW DPI	6 monthly updates with plain English summaries of the research results, extension activities and key findings
	Media outputs (TV, radio & print)	NSW DPI	Minimum 4 media articles (print or electronic) and one radio interview, completed by 2016
	Publish scientific papers	NSW DPI	Journal articles published by 2016, number dependent upon results
	Conference presentations	NSW DPI	Three Conferences targeted by 2016

Risk management

This communication plan helps to address some project risks associated with stakeholder engagement.

Risk	Management
Project partners not contributing to communication project information	- Providing regular project updates to partners - Single point of call for project information - Meeting face-to-face to address issues – e.g. information not in a form that partners can use; timing in relation to partner publications
EKP fishers not engaged	- Letters about the project and about the survey sent to all relevant Coops and individual fishers - Information provided in ways consistent with the trusted and preferred sources of information identified in the survey - Open access to contact primary project manager - DPI EKP Industry Manager well informed on project progress and results, and able to discuss it during routine interactions with industry - Information available to all via website
Research information not communicated in a timely manner	- Plain English results not held up by formal refereed publication process - DPI EKP Industry Manager well informed on project progress and results, and able to discuss it during routine interactions with industry

Appendix 16 – Flyer for Land Managers

Eastern King Prawn Habitat

Managing land to grow more prawns

Photo credits: left, Doug Beckers; middle, Scott Nichols; right, Matt Taylor.

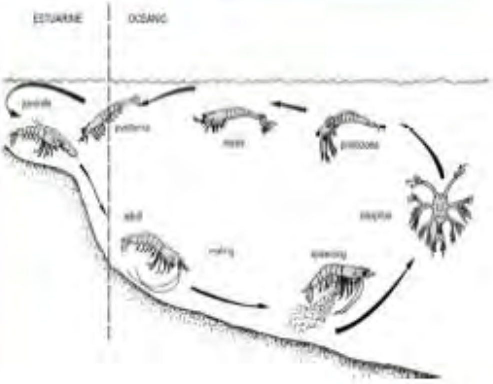
We now know more than ever about the ways in which healthy habitat and good quality water benefit Eastern King Prawn, helping them survive adversity and thrive in the good times. In NSW, the Clarence, Hunter and Lake Macquarie estuaries are particularly important for Eastern King Prawn. All of these estuaries have lost some of the essential habitat that helps sustain prawn populations, however, in recent years work has started to repair the damage and return important areas to a more natural state. Prawns are just starting to take advantage of these improved conditions, which is good news for the prawns, the commercial fishery and the local coastal communities they support.

The most important habitat for juvenile Eastern King Prawn (EKP) is the estuary. Juvenile prawns depend on nursery areas in estuaries to grow to adulthood, before moving out to sea to complete their life cycle. The healthier the mangrove and saltmarsh habitat the greater the carrying capacity of the estuary to support and grow more prawns. However, until now there has been little detail about which parts of the estuary are more important to young EKP. Researchers have spent several years using a combination of methods, including specialised research sled nets and chemical 'signatures', to identify where the prawns came from, what they had been eating and where their food was from. This is what they found out.

Good juvenile EKP habitat

- An estuary has different areas that are potential habitat for juvenile EKP. Where EKP are found depends on currents, salinity, and food availability.
- Ideal habitat areas have a supply of food, the salinity isn't too low, and the temperature isn't too cold.
- Shallow sand flats with low currents and marsh channels that are submerged across all tides are ideal. In some estuaries, the juveniles are more abundant along the littoral zone of shallow, muddy creeks near mangroves, while in others they were found mainly on seagrass beds.
- Stable temperature and salinity are best. Rapid declines in temperature and salinity levels, such as what can happen during flood events, can result in juveniles dying and any survivors generally don't grow well.
- Young EKP have a varied diet, eating plant material, crustaceans, microorganisms, small shellfish, and worms. Much of their nutrition is derived from saltmarsh habitats and is transported to the subtidal waters where the prawns live.
- Estuaries need to be connected to wetlands, saltmarsh areas and floodplains. Cutting-off tidal flows and draining wetlands reduces food availability and has had a significant impact on EKP populations. Restoration of more natural tidal flows is having a positive impact on EKP.

Eastern King Prawn (EKP) spawn at sea in waters off northern NSW and southern Queensland. The larvae develop as they drift south on the East Australian Current before moving into coastal estuaries. The tiny prawns spend 2 to 3 months over summer growing in the estuary, before heading back out to sea and swimming northwards; where they continue their growth to full maturity and complete the breeding cycle.



Supported by good land management

Understanding the nursery value of different areas within an estuary, and the processes that make some areas more valuable than others, allows managers to:

1) prioritise areas for rehabilitation that are likely to result in the greatest benefits for EKP

2) consider factors that may increase nursery value when engineering rehabilitation works

3) estimate the potential outcomes of different rehabilitation scenarios.

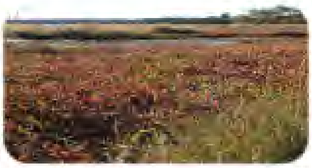
Keep it all connected

- **Hydrological connectivity** in estuaries needs to be maintained or restored. This includes both connections along creeks and rivers to the ocean, and connections to floodplain wetlands, both saltwater and freshwater.
- **Tidal flow** should be as natural as possible. Tidal flushing ensures food supply from saltmarsh and mangroves, helps maintain stable salinity, and enables prawns to move into and out of habitats as their suitability changes or as the prawns' needs change.

Protect Seagrass

- Reduce the impacts of **marine infrastructure** on seagrass beds. For example, replace traditional moorings with environmentally friendly designs to reduce scour.
- **Water quality** affects seagrass. Good quality water means less algal growth on the seagrass, higher productivity and greater resilience to flood and other adverse events.
- Turbidity and sedimentation can reduce the productivity of seagrass. Fencing waterways to better manage livestock access, controlling erosion and managing urban stormwater helps **reduce sedimentation** and nutrient loads to the estuary.

Give Saltmarsh room



- Saltmarsh **wetlands** are an important source of food for juvenile EKP. These areas also protect estuary foreshores by absorbing the energy of wind and wave action and providing a natural buffer that helps minimise erosion and play a major role in carbon sequestration.
- As sea level rises, **mangroves** and saltmarsh migrate landward. Areas where these plants can retreat, with sea level rise need to be identified and protected to allow mangroves and saltmarsh to adapt.

Saltmarsh has a significant economic value. For example, in the Clarence River, the fisheries harvest derived from saltmarsh productivity is around $25,000 per hectare per year.

Case study: The Hunter – rehabilitation in action

Shallow estuarine areas in the lower estuary are high value habitat for juvenile EKP, highlighting the likely impact of the extensive loss of this habitat through land reclamation. Before floodgates were installed in the early 1970s, Hexham swamp was considered to be the main EKP nursery for the Hunter River and as far as Brisbane. In the 1920s, locals saw a stream of EKP 50cm wide and 50cm deep coming past the Heads and out to sea for over 7 miles towards the north. Between the 1950s and 1990s, approximately 21 ha of channel habitat and 1426 ha of saltmarsh were lost in the lower Hunter. This could equate to a loss of 100,000 to 500,000 emigrating prawns each year.

Rehabilitation projects have been restoring hydrological connectivity of saltmarsh and mangrove habitats to the estuary, thus allowing tidal flushing and recruitment of important species.

Monitoring indicates that prawns are moving into the recently rehabilitated habitat around Hexham with the reopening of the floodgates on Ironbark Creek. When the floodgates were closed, the numbers of EKP were negligible. Commercial catches increased after the first gate was opened and have further increased now that all the floodgates are open.

EKP are being found much further into the tributary, with strong recruitment occurring. This provides the first clear demonstration of the impact of restoring connectivity with estuarine wetlands for commercial species of prawns in New South Wales.

Researchers used a combination of methods to understand where the prawns were in each of the estuaries, and what they had been eating. Specialised research sled nets were used to capture early juvenile prawns. Researchers were able to identify where in the estuary the prawns were sourcing their food by analysing isotopes from the prawns and comparing these against the unique isotope signatures of plants and algae that grow within the estuary.

About the project

Commercial fishers have provided many anecdotal reports of the extensive use of estuarine swamps by young EKP prior to wetland degradation, and of the adverse effects of freshwater inundation and lowering of salinity in estuarine nurseries on the growth and abundance of prawns. However there has been a lack of quantitative research on the early estuarine stages of EKP in NSW to support this. Quantitative knowledge on the use of estuarine nurseries by EKP is essential to accurately value coastal wetland habitats, and assess the benefits of rehabilitation.

This project is supported by funding from the Fisheries Research and Development Corporation on behalf of the Australian Government, with significant in-kind support from NSW Department of Primary Industries. Additional funding is being provided by the Hunter and the North Coast Local Land Services, as well as Hunter Water, the Newcastle Ports Corporation, and Origin Energy. The project is supported by the NSW Professional Fisherman's Association, the Newcastle Commercial Fishermen's Co-operative and OceanWatch.

The results of the research are summarised in the Project Updates and detailed methods and data have been published in scientific journals. Both the updates and details of the papers published are available on the project website, www.dpi.nsw.gov.au/fishing/habitat/rehabilitating/ekp, or contact Dr Matt Taylor, NSW DPI Fisheries.

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Appendix 17 – Flyer for Commercial Fishers

Eastern King Prawn Habitat

Growing your fishery, naturally

We now know more than ever about the ways in which healthy habitat and good quality water benefit Eastern King Prawn, help them survive adversity and thrive in the good times. This resilience will help sustain an important commercial fishing industry and provide consumers with a much-loved seafood.

The most important habitat for Eastern King Prawn (EKP) is the estuary. In recent years, work has started to repair estuaries and return them to a more natural state. Prawns are just starting to take advantage of these improved conditions, which is good news for the prawns, the commercial fishers and local towns involved in the prawn fishery. Researchers have spent several years using a combination of methods, including specialised research sled nets and chemical 'signatures', to identify where the prawns came from, what they had been eating and where their food was from. This is what they found out.

- *Food + not too much freshwater + warm water is ideal.*
- *Rapid declines in temperature and salinity are not good.*
- *An estuary is not one big habitat: prawns live in the patches where conditions are favourable.*
- *Much of the food eaten by juveniles is coming from saltmarsh habitats.*

Good juvenile EKP habitat

- Ideal habitat areas are places within estuaries where there is a supply of food, the salinity isn't too low, and the temperature isn't too cold. Shallow sand flats with low currents and marsh channels that are submerged across all tides are ideal, particularly in the lower estuary.

- Stable temperature and salinity are best. Juvenile EKP do not like rapid declines in temperature and salinity levels, such as what can happen during flood events. More tend to die and the survivors generally don't grow well. This helps explain why commercial fishers tend to notice fewer, and smaller, EKP in wetter years.

- An estuary has many different habitats. Where EKP are found seems to depend on currents, salinity, and food availability.

- In some estuaries, the juveniles are more abundant along the edges of shallow, muddy creeks near mangroves, while in others they were found mainly on seagrass beds.

- Young EKP have a varied diet, eating plant material, crustaceans, microorganisms, small shellfish, and worms. Much of their nutrition is derived from saltmarsh habitats and is transported to the subtidal waters where the prawns live.

- Estuaries need to be connected to wetlands, saltmarsh areas and floodplains. Cutting-off tidal flows and draining wetlands reduces food availability, which can impact on EKP populations. Restoration of more natural tidal flows is producing benefits for juvenile EKP.

The Hunter – rehabilitation in action

The contribution of the Hunter River estuary as a juvenile EKP nursery depends on the area of habitat available. Shallow estuarine areas in the lower estuary are of high value, highlighting the likely impact of the extensive loss of this habitat through land reclamation. In the lower Hunter, approximately 21 ha of channel habitat and 1426 ha of saltmarsh were lost between the 1950s and 1990s. This could equate to a loss of several hundred thousand emigrating prawns each year. Rehabilitation projects have been reconnecting marsh and mangrove habitats to the estuary, thus allowing tidal flushing, restoration of saltmarsh and recruitment of important species. Monitoring indicates that prawns are moving into rehabilitated habitat around Hexham with the reopening of the floodgates on Ironbark Creek. When the floodgates were closed, the numbers of EKP were negligible. Catches increased after the first gate was opened and have further increased now that all the floodgates are open.

EKP are now being found much further into the tributary, with strong recruitment occurring. This is significant because it provides the first clear demonstration of the impact of restoring connectivity with estuarine wetlands for commercial species of prawns in New South Wales.

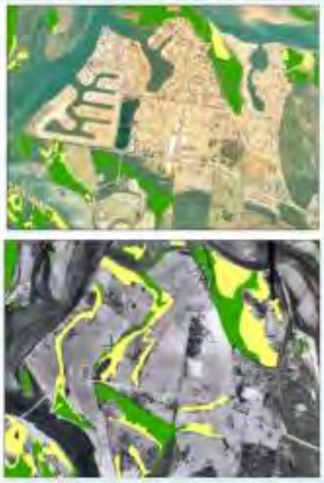
Before floodgates were installed in the early 1970s, Hexham swamp was considered to be the main EKP nursery for the Hunter River and beyond, even as far as Brisbane. In the 1920s, locals saw a stream of EKP 50cm wide and 50cm deep coming past the Heads and out to sea for over 7 miles towards the north.

The Clarence Estuary – the importance of Saltmarsh

Juvenile EKP were found 8-12 km from the mouth of the estuary in the main channel and north arm. Important areas were adjacent to saltmarsh and mangrove habitats in this region of the estuary. Saltmarsh grass was the dominant source of food supporting the growth of juvenile EKP, and mangroves were not as important for providing food. The areas of saltmarsh and seagrass in this estuary have both decreased substantially due to development. 64% of all saltmarsh has been lost - just 290 ha remain.

There were very few EKP found in the southern channels of the estuary, despite there being abundant habitat and appropriate salinity. This could be because these areas are not well connected to incoming tides due to a large training wall. There is suitable habitat and more natural tidal flow could boost the local EKP population.

Saltmarsh in the Clarence River has a significant economic value. The fisheries harvest coming from saltmarsh productivity yields around $25,000 per hectare per year.



The distribution of mangrove (green) and saltmarsh (yellow) in 2009 (top) compared to 1942 (bottom) near the mouth of the Clarence River.

Lake Macquarie – wind and seagrass

In Lake Macquarie, there is an abundance of seagrass important for juvenile EKP. However, seagrass beds in the northern basin received greater numbers of recruits than other areas. The supply of recruits was greatest in several shallow seagrass covered embayments on the eastern edge of the estuary, about 2 –3 km past the end of the entrance channel. EKP were largely absent from the south-western area of the lake. Very young EKP initially enter the system on the flood tide and are carried along the entrance channel by the strong tidal currents. At the end of the entrance channel, the wind conditions during the recruitment season transport the prawns from the end of the entrance channel into the northern basin. So, both wind and tide are important factors influencing which habitat areas in Lake Macquarie the prawns use. Habitat rehabilitation efforts do not usually take drivers of connectivity like seasonal wind into account. For the EKP, seagrass rehabilitation efforts (such as replacement of swing moorings with seagrass friendly moorings) could prioritise areas between 6 and 9 km from the estuary mouth to maximise any benefits for EKP.

Researchers used a combination of methods to understand where the prawns were in each of the estuaries, and what they had been eating. Specialised research sled nets were used to capture early juvenile prawns. Researchers were able to identify where in the estuary the prawns were sourcing their food by analysing isotopes from the prawns and comparing these against the unique isotope signatures of plants and algae that grow within the estuary.

About the project

Fishers have provided many anecdotal reports of the extensive use of estuarine swamps by young EKP prior to wetland degradation, and of the adverse effects of freshwater inundation and lowering of salinity in estuarine nurseries on the growth and abundance of prawns. However there has been a lack of quantitative research on the early estuarine stages of EKP in NSW to support this. Quantitative knowledge on the use of estuarine nurseries by EKP is essential to accurately value coastal wetland habitats, and assess the benefits of rehabilitation.

This project is supported by funding from the Fisheries Research and Development Corporation on behalf of the Australian Government, with significant in-kind support from NSW Department of Primary Industries. Additional funding is being provided by the Hunter and the North Coast Local Land Services, as well as Hunter Water, the Newcastle Ports Corporation, and Origin Energy. The project is supported by the NSW Professional Fisherman's Association, the Newcastle Commercial Fishermen's Co-operative and OceanWatch.

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Appendix 18 – Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop: A report for participants

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Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop

A report for participants

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Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop. A report for participants.

First published December 2017

More information

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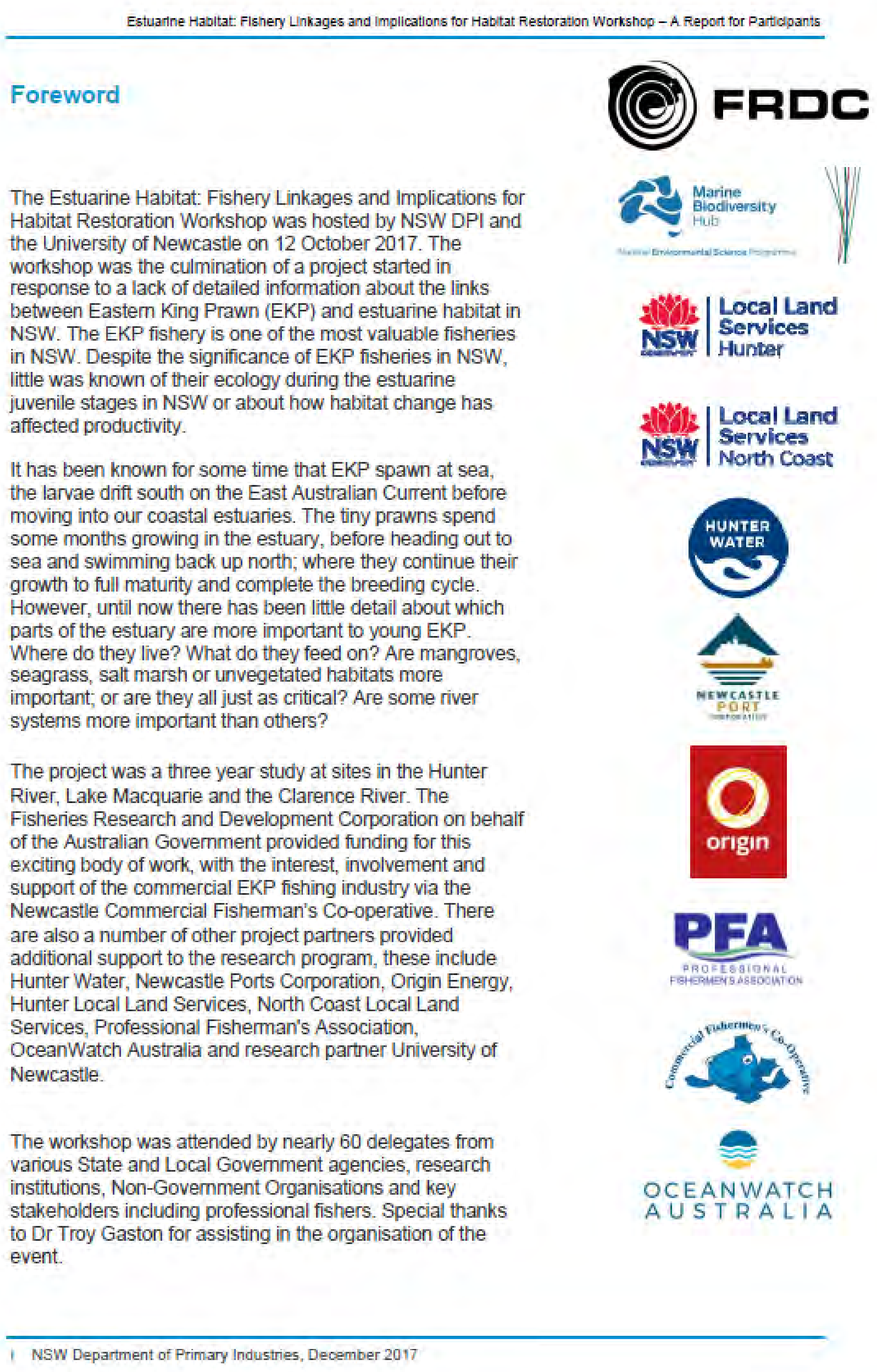
www.dpi.nsw.gov.au

Acknowledgments

This report summarises a workshop which presented the research findings of a NSW DPI and University of Newcastle (UoN) research team comprising Matthew Taylor, (NSW DPI), Alistair Becker (NSW DPI), Troy Gaston (UoN), Vincent Raoult (UoN) and Craig Hart (UoN). The workshop was coordinated by Charlotte Jenkins and Kylie Russell (NSW DPI) and chaired by Craig Copeland (NSW DPI).

[Cover image: Will MacBeth]



Foreword

The Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop was hosted by NSW DPI and the University of Newcastle on 12 October 2017. The workshop was the culmination of a project started in response to a lack of detailed information about the links between Eastern King Prawn (EKP) and estuarine habitat in NSW. The EKP fishery is one of the most valuable fisheries in NSW. Despite the significance of EKP fisheries in NSW, little was known of their ecology during the estuarine juvenile stages in NSW or about how habitat change has affected productivity.

It has been known for some time that EKP spawn at sea, the larvae drift south on the East Australian Current before moving into our coastal estuaries. The tiny prawns spend some months growing in the estuary, before heading out to sea and swimming back up north; where they continue their growth to full maturity and complete the breeding cycle. However, until now there has been little detail about which parts of the estuary are more important to young EKP. Where do they live? What do they feed on? Are mangroves, seagrass, salt marsh or unvegetated habitats more important; or are they all just as critical? Are some river systems more important than others?

The project was a three year study at sites in the Hunter River, Lake Macquarie and the Clarence River. The Fisheries Research and Development Corporation on behalf of the Australian Government provided funding for this exciting body of work, with the interest, involvement and support of the commercial EKP fishing industry via the Newcastle Commercial Fisherman's Co-operative. There are also a number of other project partners provided additional support to the research program, these include Hunter Water, Newcastle Ports Corporation, Origin Energy, Hunter Local Land Services, North Coast Local Land Services, Professional Fisherman's Association, OceanWatch Australia and research partner University of Newcastle.

The workshop was attended by nearly 60 delegates from various State and Local Government agencies, research institutions, Non-Government Organisations and key stakeholders including professional fishers. Special thanks to Dr Troy Gaston for assisting in the organisation of the event.

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Estuarine Habitat: Fishery Linkages and Implications for Habitat Restoration Workshop – A Report for Participants

Workshop Program

Workshop: Estuarine Habitat

Fishery linkages and implications for Habitat Restoration

Room X204, Newcastle University City Campus, Newcastle, 12 October 2017

Program

9.00 – 9.10	**Welcome, Workshop Introduction and Objectives** *Craig Copeland NSW DPI*
9.10 – 9.25	**The status of estuarine habitat in NSW** How the NSW coast once looked. *Kylie Russell NSW DPI*
9.25 – 9.45	**Research overview and nursery basics** An introduction to the FRDC project. Understanding nursery habitats for exploited penaeid prawns in NSW estuaries. *Matthew Taylor NSW DPI*
9.45 – 9.55	**Saltmarsh secrets** Direct usage of saltmarsh habitats by exploited species in the Hunter River. Plus insights into DIDSON work on large-bodied species. *Alistair Becker NSW DPI*
9.55 – 10.10	**Saltmarsh surprises** Direct and indirect interactions between saltmarsh habitats and commercially important penaeid shrimp. *Troy Gaston University of Newcastle*
10.10 – 10.25	**What's for lunch?** The contribution of estuarine habitats to the diets of commercially important fisheries species in the Hunter and Clarence Rivers. *Vincent Raoult University of Newcastle*
10.25 – 10.40	**Hexham Happenings** School Prawn (*Metapenaeus macleayi*) abundance and trophic relationships in the recovering Hexham wetland. *Craig Hart University of Newcastle*
10.40 – 10.55	**What's it worth?** The economic value of saltmarsh to fisheries. *Matthew Taylor NSW DPI*
10.55 – 11.00	**Finishing up** Wrapping up the workshop. Moving on from here *Craig Copeland NSW DPI*
11.00 – 11.20	**Refreshments** Followed by ***Growing the fishery! A planning session for coastal habitat restoration*** chaired by *Craig Copeland NSW DPI*

NSW Department of Primary Industries, December 2017

Growing the fishery!

A planning session for coastal habitat restoration

What is currently happening?

Existing programs, activities, management strategies, research

For example:

- Natural Infrastructure Business Case
- Marine Estate Strategy
- Global Ocean Wealth
- Hunter Flood Mitigation Scheme review
- Habitat Action Flagship Program
- Coastal Management – Coast and Estuary Grants Program

What needs to be happening?

In **Research** – what are the key emerging issues? Addressing knowledge gaps.

In **Policy** – how do we better manage the fishery/coastal resources of NSW? Is current policy adequate to face the challenge of sea level rise?

In **Management Action** – what activities are needed? On-ground and otherwise. How will they be funded?

In **Communication** – how do we foster support in the community? How do we get information out to where it matters?

The above points are for open discussion.
All session participants are invited to actively contribute to the session.

Presentation Summaries

The following is a plain English summary of each of the seven presentations delivered at the workshop. For further detail of the research and its findings please see the links to research papers published in peer reviewed journals provided where applicable. A summary of all the research findings is provided in the targeted education brochures, one for professional fishers and one for estuarine land managers, see Appendix A and B.

1: The status of estuarine habitat in NSW. How the NSW Coast once looked. *Kylie Russell, NSW DPI*

This presentation provided knowledge on the importance of healthy, connected estuarine systems to fish and other aquatic organisms and the current reality regarding the health and status of estuaries in NSW.

Healthy, intact estuarine habitats including seagrass beds, mangrove forests, saltmarsh, riparian zone vegetation, mud flats and floodplain wetlands which are connected to each other via the natural ebb and flow of the tide helps ensure the estuary can sustain a high carrying capacity of the aquatic organisms which it supports.

However, it is estimated that since 1950, most estuaries in southeast Australia have lost over a quarter of their saltmarsh with some estuaries losing up to 80 per cent from anthropogenic impacts such as draining and land reclamation. Up to 60% of coastal wetlands and floodplains were lost or highly impacted by 1970. Coastal urbanisation, declines in water quality and sedimentation from catchment runoff have resulted in an 85% loss of seagrass beds in some estuaries, thousands of man-made barriers impede fish the migration patterns of native fish and ongoing grazing and clearing of riverbanks have denuded riparian zones of tress and removed the river's vital buffer which protected it from overland flow.

The cumulative result of these impacts is a heavily impacted estuarine environment that can no longer sustain a high carrying capacity for aquatic organisms.

Habitat restoration and rehabilitation efforts are starting to make positive inroads to improve estuarine habitats and assist in the recovery of native fish populations.

Figure 1: *Slides showing left, an intact, healthy estuary supporting a high carrying capacity of fish versus, right, a heavily impacted estuary supporting a low carrying capacity of fish.*

2: Research overview and nursery basics. An introduction to the FRDC project. Understanding nursery habitats for exploited penaeid prawns in NSW estuaries. *Matthew Taylor, NSW DPI*

This presentation provided a synopsis of the 3 years of field and lab research. Many penaeid prawns (e.g. Eastern King Prawn, EKP) are the subject of iconic, valuable fisheries. Prawns are highly fertile and fast growing. The prawn's basic life cycle and the importance of estuaries to juvenile prawns is widely known however there has been little detail about which parts of the estuary are more important.

The broad research objectives were to quantify estuarine habitat-fishery linkages including identifying important prawn nurseries with a particular emphasis on EKP, to a lesser degree on School Prawn, and a strong focus on saltmarsh habitat. This information was then used to estimate the monetary value of a habitat type (primarily saltmarsh) in terms of fishery productivity. Using this data it is suggested that prawns, and the value of their fishery, can be used to stimulate investment for targeted habitat restoration and rehabilitation activities.

The identification of important habitat types was conducted through the analysis of stable isotopes based on the old adage – you are what you eat! Researchers were able to identify where in the estuary the prawns were sourcing their food by analysing isotopes from the prawns and comparing these against the unique isotopes signatures of estuarine plants and algae.

Further analysis was conducted to ascertain what factors such as distance of habitat from the estuary mouth, salinity levels and connectivity of habitat, were influencing habitat linkages.

Results for the Hunter estuary showed that:

- Recently rehabilitated marshes are important for school prawn.
- The connectivity of habitats supporting a supply of food plus salinity are key drivers for EKP, the optimal salinity for juvenile EKP was found to be between 25-28 ppt.
- Hexham Wetland was found to be particularly important for EKP.
- Expansive shallow unvegetated habitat and optimal salinity are important.
- EKP demonstrated minimal use of the Kooragang Island area, perhaps highlighting this areas lack of connectivity with the river's south arm
- Freshwater inflows, while good for School Prawn, is bad for EKP

Figure 2: *Extracts from the presentation*

Identify important habitats – stable isotopes *You are what you eat!*

Hunter River: Key drivers of patterns

Further reading: Taylor, M., Smith, J. A., Boys, C. A., Whitney, H. 2016. A rapid approach to evaluate putative nursery sites for penaeid prawns. Journal of Sea Research. 114. 26-31. http://dx.doi.org/10.1016/j.seares.2016.05.004

3: Saltmarsh secrets. Direct usage of saltmarsh habitats by exploited species in the Hunter River. Plus insights into DIDSON work on large-bodied species. *Alistair Becker, NSW DPI*

This presentation provided a synopsis on the study in the lower Hunter River estuary into the direct usage of intertidal marsh habitat by penaeids and the small sub-tidal creeks which meander through marshes. The variation in estuaries was highlighted, noting that most estuaries contain a mosaic of habitats and that not all these habitats are created equal. For example some habitats fulfil a nursery function for certain species better than others. The identification of key juvenile habitat will allow for better targeted management of estuarine habitats.

Nocturnal sampling was conducted in intertidal marsh - mangrove habitats in Tomago, Kooragang and Hexham wetlands using fyke nets and in sub-tidal creeks using cast nets. The key findings were explained: intertidal marshes which are only fully inundated during the Spring tide cycle (approximately 30 hours during a lunar month) discharged 12,575 nekton (actively swimming aquatic animals), 50 % of which were freshwater prawn (*Macrobrachium*). Only 8 EKP were captured and 90 School Prawn, providing minimal evidence to support the direct usage of intertidal marshes by these species. Results were consistent across all 3 wetlands.

In the subtidal creeks relatively similar abundances of EKP and school prawn were sampled at the edges compared to the middle of the creeks, with densities in a similar range to that previously described from other studies. Collectively there was a high abundance of crustaceans from these habitats. These findings show that although there are penaeids in the system they don't appear to be directly using these habitats in the Hunter estuary.

The researchers were unable to make a direct comparison between the numbers on the marsh to the numbers in the creek due to differences in the sampling methods used. However, the ratio of EKP to school prawns in the creeks was similar to that found in the intertidal marsh.

The presentation also described a future project which will utilise DIDSON (Dual frequency Identification SONar) technology to look at fish behaviour and movements. This underwater camera creates video using sound as opposed to light which allows video to be recorded from highly turbid waters (such as estuaries) or at night time with no loss in quality of the footage. The researchers will be placing the DIDSON at floodgates on wetland systems to directly observe and quantify the passage of fish into the wetlands during different stages of the tidal cycle. Recent research has demonstrated that the reinstatement of tidal flow has led to an increase in nekton abundance and diversity in these study wetlands, however no research has been conducted on larger bodied fish.

Figure 3: *Extracts from the presentation*

- Nocturnally sampled intertidal marsh/mangrove habitats and adjacent sub-tidal creeks in Tomago, Kooragang and Hexham Wetlands
- Fyke nets used in intertidal habitat, cast nets used in the creeks, sampling smaller nekton

- Reinstatement of tidal flow known to lead to increase nekton abundance/diversity
- No research on larger bodied fish
- Ideal location for DIDSON study
- Quantify numbers passing during tides and direction of travel
- Effect of tide direction, amplitude (spring/neap), diel period

Further reading: Becker, A & Taylor, M .D., 2017. Nocturnal sampling reveals usage patterns of intertidal marsh and subtidal creeks by penaeid shrimp and other nekton in south-eastern Australia. Mar and Freshwater Res. 68, 780-787

4: Saltmarsh surprises. Direct and indirect interactions between saltmarsh habitats and commercially important penaeid shrimp. *Troy Gaston, UoN*

This presentation described the work conducted in the Clarence River to quantify the direct and indirect interactions between penaeids and habitat in that river system, and answer questions such as where are these organisms living and what food are they relying on. The different habitat types within the Clarence River estuary were highlighted including saltmarsh, mangroves and seagrass, but also the importance of mud and the green 'slime' (Fine Benthic Organic Matter) present on this mud.

The project's aims and relevant methods were described:

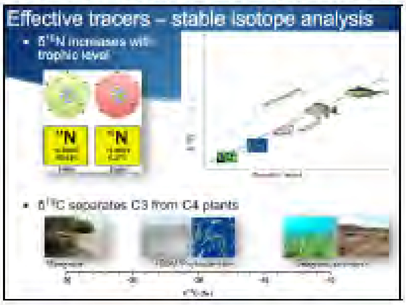
1. Undertake a broad-scale assessment of the contribution of several areas across the lower estuary to the adult EKP stock via stable isotope (chemical signature) analysis to identify what areas prawns were coming from.
2. Estimate EKP densities supported by different habitat types in the lower estuary via sled tow sampling at 20 sites across the estuary then mapping software to plot densities.
3. Determine the contribution of primary production to EKP in the lower estuary. Using the results from aim 1, four main areas in the estuary were sampled and the stable isotopes in all available food sources in these areas were analysed to identify what foods the prawns had taken nutrition from.

The key findings provided the following conclusions: EKP were the most abundant of benthic organisms sampled. The lower estuary was identified as the most important. Shallow unvegetated subtidal sediment is an important habitat type but mangrove and saltmarsh adjacent to these habitats and the connectivity between these are still important. The findings demonstrated that prawn recruitment is driven by where these habitats are located.

Saltmarsh featured highly in EKP diet (up to 97% in prawns sampled from certain areas) and was described as 'disproportionately' important to EKP. Carbon from saltmarsh is mobile in an estuarine system due to the daily influx and egress of the tide. Mangrove didn't show up as a strong nutritional source for prawns.

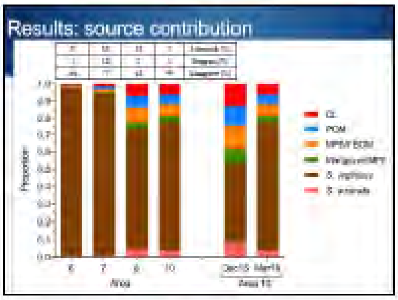
The presenter concluded that there are significant implications for these findings in the future management of estuarine habitat including the targeted protection and restoration of saltmarsh in the Clarence River estuary.

Figure 4: *Extracts from the presentation*



Effective tracers – stable isotope analysis

- $\delta^{15}N$ increases with trophic level
- $\delta^{13}C$ separates C3 from C4 plants



Results: source contribution

Further reading: Taylor, M .D., Becker, A., Moltschaniwskyj, N.A., Gaston, T. F. 2017. Direct and indirect interactions between lower estuarine mangrove and saltmarsh habitats and a commercially important Penaeid shrimp. Estuaries and Coasts. DOI 10.1007/s12237-017-0326-y

5: What's for lunch? The contribution of estuarine habitats to the diets of commercially important fisheries species in the Hunter and Clarence Rivers. *Vincent Raoult, UoN*

(At time of writing the findings from the Clarence River and some from the Hunter River are in preparation, therefore only a selection of those from the Hunter study are summarised here)

This presentation provided an insight into the contribution of estuarine habitats in the Hunter River estuary to other commercially important species including Sea Mullet and Yellowfin Bream in the context of energy provision through food availability.

The presenter highlighted that by understanding where a fish's energy is coming from then effectively, if you restore those habitats, you can increase food availability for those organisms and potentially increase productivity in response.

The project's aim was to determine the contribution of primary producers (mangroves, seagrass, saltmarsh, epiphytes and phytoplankton) to commercial fisheries in the Hunter River i.e. what habitat/plants do these fishes get the bulk of their energy from?

The method for addressing this aim was described, which included sampling commercially caught fish from around Fern Bay in the lower estuary, and analysing stable isotopes from the muscle tissue of these fishes and then comparing the analysis to that from primary producers. Using a model, the contribution of each primary producer to nutrition in each commercial species sampled was identified.

Key features of the Hunter River estuary were described: it has the largest wetland system in coastal NSW, it has a strong dominance of mangroves, it has some saltmarsh but there is no seagrass. There are also a large number of restoration efforts underway in this system.

The findings presented showed that although saltmarsh only represents a small amount of the aerial coverage of habitat in the Hunter estuary (12.1% compared to mangrove 87%), it provides a disproportionately large contribution of the energy absorbed by many commercially important fish species in the Hunter River.

These findings differ from other studies which largely reported seagrass provided the highest contribution to diet and generally found a low contribution from saltmarsh. It was explained that there is a potential overlap in the chemical signatures of seagrass and saltmarsh, however, with the Hunter lacking seagrass the researchers could confidently identify the chemical signatures reported in this study came from the saltmarsh.

The presenter concluded that saltmarsh is providing a significant amount of nutrients for fisheries species in the Hunter River. Further study is underway to identify if saltmarsh is providing a food substitute for seagrass in systems where seagrass beds are limited and to separate the isotopes signatures of these different plants. The implication of saltmarsh restoration having a positive flow on benefit for commercial fisheries production was highlighted.

Figure 5: *Extracts from the presentation*

Nutrition for Estuarine Fish: where does the energy that they absorb come from?

- Primary Producers
  - Mangroves
  - Seagrass
  - Epiphytes
  - Saltmarsh
  - Phytoplankton

Saltmarsh Compared to Other Habitats

- Saltmarsh represents 12.1 % of habitat in the North Arm
- Mangrove 87.9 % of habitat in the North Arm
- No Seagrass
- Disproportionate Contribution to Hunter River Fisheries

6: Hexham Happenings. School Prawn (*Metapenaeus macleayi*) abundance and trophic relationships in the recovering Hexham wetland. *Craig Hart, UoN*

This presentation provided a synopsis of a study to quantify School Prawn (*Metapenaeus macleayi*) abundance and the drivers of those abundance patterns within Ironbark Creek, Hexham wetland in the lower Hunter River estuary. The School Prawn (SP) fishery is the fifth largest catch in NSW however numbers have declined by 25% since the 1970s.

The presenter highlighted the importance of estuarine wetlands to commercial and recreational fisheries in Australia and specifically the key ecological role of saltmarsh habitat in the provision of nursery habitat for Penaeidae, such as SP. Human disturbance on coastal wetlands has been significant, demonstrated by a 50% decline in global saltmarshes. The installation of floodgates on Ironbark Creek as part of flood mitigation efforts during the 1970's led to the degradation of Hexham wetland and wetland habitat and the reduction in abundance and diversity of valuable commercial and recreational fish and crustacean species.

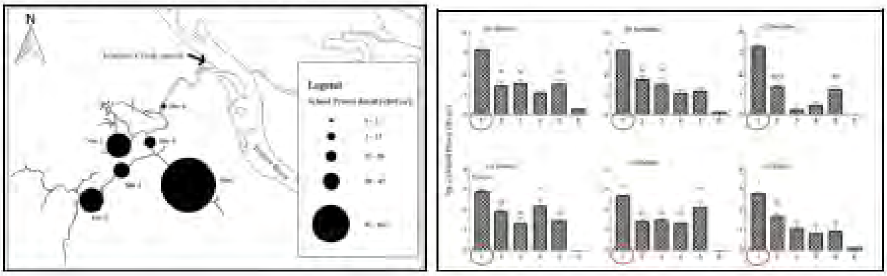
In 2008 the Hexham Swamp Rehabilitation Project was launched which included remediation of the Ironbark Creek floodgates to restore tidal flushing to the wetland. Previous studies have sampled juvenile fish and crustacean populations both up and downstream of the floodgates however, until now the quantification of fisheries value has not been conducted.

The study aimed to determine the spatial variability in density of commercially important SP populations within the Hexham wetland. If the restoration effort has been successful in increasing juvenile SP populations, then it was anticipated there should have been a high abundance in the tidal creeks throughout the wetland. The study's data could be used to provide industry and fisheries with estimates in population value, and managers with an assessment of wetland repair to support investment in further repair activities.

Sampling was conducted using a modified seine net at 6 sites in Ironbark Creek over a period of 6 months. The findings showed juvenile SP density levels greater than any previous study undertaken in the area. However, the results also showed a highly disproportionate abundance across sites, yet consistent across the monthly sampling events. For example, site 1 had the largest SP abundance, yet the lowest dietary proportion of the saltmarsh plant *Sporobolus virginicus*. Dietary sources including mangrove and *Phragmites australis* (a wetland grass) provided the major proportion of diet at this site. This difference may relate to the dominance of *P. australis*, and the scarcity of mangrove and saltmarsh plants at site 1 compared to other sites.

The presenter concluded that the study has shown the likelihood that Hexham wetland may be contributing strongly to annual SP recruitment within the Hunter River and demonstrates the importance of conservation and restoration effort to the wetland. As the recovery of Hexham wetland continues the benefits to estuarine species throughout the entire Hunter River is likely to increase. Ongoing sampling of the population was recommended and further investigations into water quality and hydrological flow to better understand associated impacts within the wetland.

Figure 6: *Extracts from the presentation*



7: What's it worth? The economic value of saltmarsh to fisheries. *Matthew Taylor, NSW DPI*

This presentation provided a synopsis of how the research outcomes were extended to estimate the potential economic value of estuarine habitat and benefits from its restoration.

The researcher's data on contributions of saltmarsh and mangrove to the biomass of penaeid shrimp (and other fish species) as modelled from stable isotope composition for the Hunter and Clarence estuaries, was used to apportion the commercial harvest biomass that was derived from each of these habitats. Using a complex equation they then used a simple market value for each species at first-point-of-sale to establish the Gross Value of Production. Using an economic multiplier, this Gross Value of Production could then be converted to Total Economic Output i.e. the potential economic value.

The model enabled the identification of quantifiable direct (recruitment) and indirect (trophic) linkages of different estuarine habitat types. Significantly, these results provided an avenue for the determination of estimates of the monetary value associated with estuarine habitats in NSW to be calculated for the first time.

Here's what they found:

- Saltmarsh in the Clarence River had by far the greatest economic value per unit-area, with an average estimated Total Economic Output (from fisheries harvest) of over $25,000 per hectare per year, whereas mangrove was estimated to be approximately $5,000 per hectare per year.
- The Average Total Economic Output in the Hunter River was approximately $2,500 per hectare per year for saltmarsh and just over $300 per hectare per year for mangrove habitats.
- The value of trophic subsidy appears to be greater than recruitment subsidy.
- Restoration and rehabilitation activities will enhance both trophic and recruitment subsidies. These activities have the potential to result in a commensurate revenue increase for the fishery of tens of thousands of dollars per hectare per year.

Figure 7: *Extracts from the presentation*

Indirect

- Trophic subsidy
  - Intertidal habitat

Trophic subsidy	Saltmarsh	Mangrove
GVP	$\$2{,}209\ \mathrm{ha^{-1}\ y^{-1}}$	$\$92\ \mathrm{ha^{-1}\ y^{-1}}$
TO	$\$13{,}038\ \mathrm{ha^{-1}\ y^{-1}}$	$\$304\ \mathrm{ha^{-1}\ y^{-1}}$

Indirect (other species)

- Trophic subsidy
  - Intertidal habitat

Trophic subsidy	Saltmarsh	Mangrove
TO Hunter R.	$\$2{,}579\ \mathrm{ha^{-1}\ y^{-1}}$	$\$316\ \mathrm{ha^{-1}\ y^{-1}}$
TO Clarence R.	$\$25{,}701\ \mathrm{ha^{-1}\ y^{-1}}$	$\$5{,}297\ \mathrm{ha^{-1}\ y^{-1}}$

Further reading: Taylor, M.D., Gaston, T and Raoult V. 2018. *The economic value of fisheries harvest supported from saltmarsh and mangrove productivity in two temperate Australian estuaries*. Ecological Indicators. 84. 701-709. http://dx.doi.org/10.1016/j.ecolind.2017.08.044

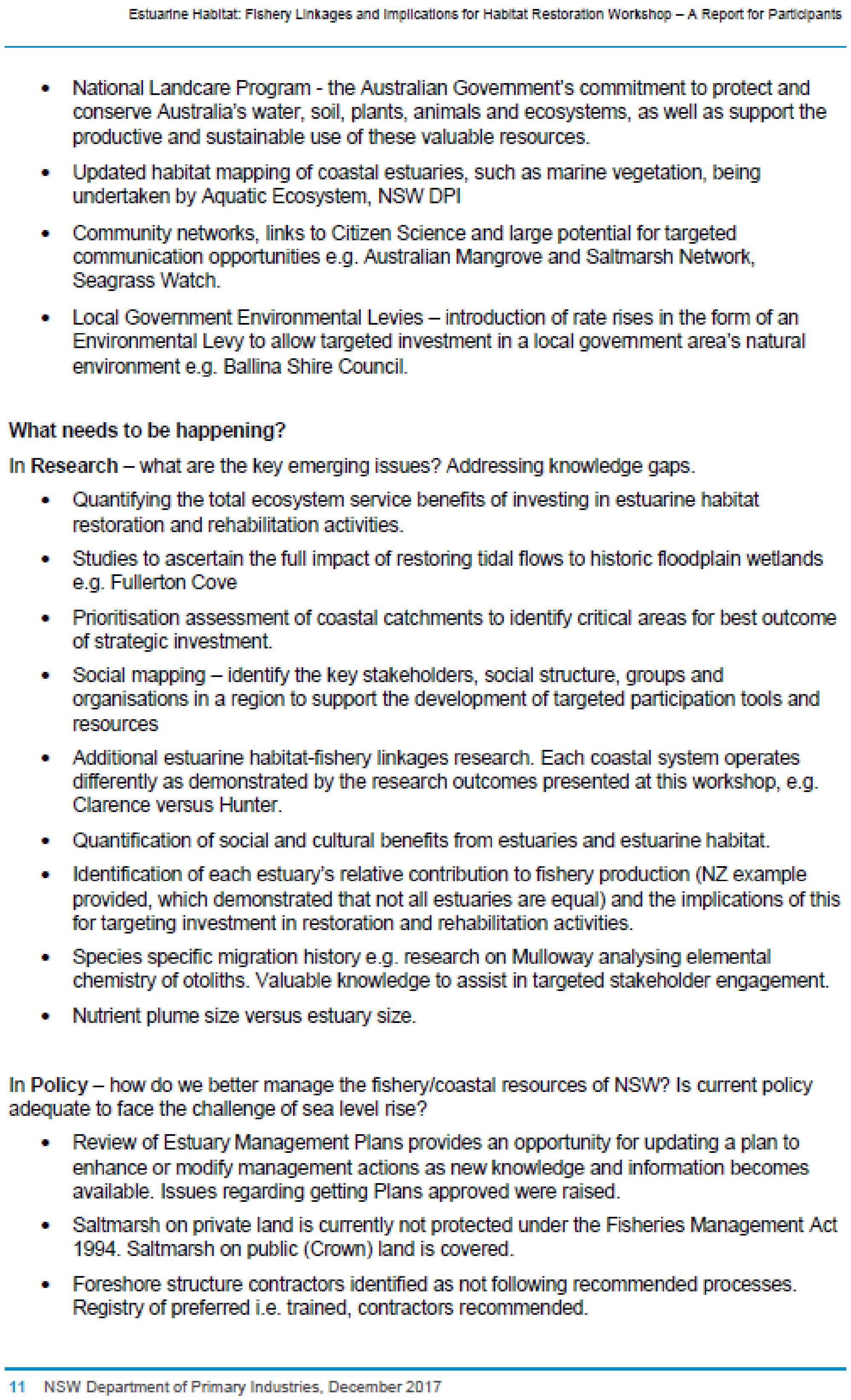
Feedback from the Growing the Fishery Planning Session for Coastal Habitat Restoration

As a direct consequence of the research project's significant findings, the project's extension staff recognized the potential opportunity the workshop presented to translate the findings into current and projected management actions for the NSW coast.

The following information is collated contributions provided by workshop participants based on a series of discussion points developed by the workshop coordinators.

What is currently happening? (Existing programs, activities, management strategies, research, and resources)

- Natural Infrastructure Business Case – NSW DPI led Business Case development with consultants KPMG. If successful the Business Case will support the delivery of significant on-ground investment in estuarine habitat restoration that would both benefit the Marine Estate but also the Government's Strategic Plan for addressing climate change.
- Marine Estate Management Strategy – a new approach to managing the marine estate in NSW as a single continuous system for the greatest well-being of the community. It aims to maximise current and future economic, social and environmental benefits of the Marine Estate.
- Global Mapping Ocean Wealth project – funded by the Nature Conservancy, seeks to out a value on marine habitats and gain an insight into the value people gain from the natural environment and improve management strategies.
- Lower Hunter Flood Mitigation Scheme (LHFMS) review – review of the scheme which was designed in direct response to the 1955 flood. The review will look at the costs and benefits of the current management of the LHFMS from a triple bottom-line perspective, including the environmental impacts.
- Habitat Action Flagship Program – investment from the NSW Recreational Fishing Trust administered by Aquatic Habitat Rehabilitation, NSW DPI
- Coastal Management – Coast and Estuary Grants Program, significant investment in improved management actions in NSW estuaries for local Councils with an approved Estuary/Coastal Zone Management Plan.
- Hunter focus workshop on Estuarine Vegetation Migration predictions in the Lower Hunter Estuary due to Climate Change and implications for restoration, land tenure, and RAMSAR values of the estuary.
- Water Research Laboratory research on estuarine salt plumes.
- Blue Carbon, provision of potential incentives to retire areas of land for saltmarsh accretion.
- Biodiversity Conservation Act and the implications for biodiversity offsets in State Significant Developments.
- Infrastructure Investment Program – significant investment from the Australian Government to boost economic growth and prosperity, increase productivity and support thousands of jobs.



- National Landcare Program - the Australian Government's commitment to protect and conserve Australia's water, soil, plants, animals and ecosystems, as well as support the productive and sustainable use of these valuable resources.
- Updated habitat mapping of coastal estuaries, such as marine vegetation, being undertaken by Aquatic Ecosystem, NSW DPI
- Community networks, links to Citizen Science and large potential for targeted communication opportunities e.g. Australian Mangrove and Saltmarsh Network, Seagrass Watch.
- Local Government Environmental Levies – introduction of rate rises in the form of an Environmental Levy to allow targeted investment in a local government area's natural environment e.g. Ballina Shire Council.

What needs to be happening?

In **Research** – what are the key emerging issues? Addressing knowledge gaps.

- Quantifying the total ecosystem service benefits of investing in estuarine habitat restoration and rehabilitation activities.
- Studies to ascertain the full impact of restoring tidal flows to historic floodplain wetlands e.g. Fullerton Cove
- Prioritisation assessment of coastal catchments to identify critical areas for best outcome of strategic investment.
- Social mapping – identify the key stakeholders, social structure, groups and organisations in a region to support the development of targeted participation tools and resources
- Additional estuarine habitat-fishery linkages research. Each coastal system operates differently as demonstrated by the research outcomes presented at this workshop, e.g. Clarence versus Hunter.
- Quantification of social and cultural benefits from estuaries and estuarine habitat.
- Identification of each estuary's relative contribution to fishery production (NZ example provided, which demonstrated that not all estuaries are equal) and the implications of this for targeting investment in restoration and rehabilitation activities.
- Species specific migration history e.g. research on Mulloway analysing elemental chemistry of otoliths. Valuable knowledge to assist in targeted stakeholder engagement.
- Nutrient plume size versus estuary size.

In **Policy** – how do we better manage the fishery/coastal resources of NSW? Is current policy adequate to face the challenge of sea level rise?

- Review of Estuary Management Plans provides an opportunity for updating a plan to enhance or modify management actions as new knowledge and information becomes available. Issues regarding getting Plans approved were raised.
- Saltmarsh on private land is currently not protected under the Fisheries Management Act 1994. Saltmarsh on public (Crown) land is covered.
- Foreshore structure contractors identified as not following recommended processes. Registry of preferred i.e. trained, contractors recommended.

- The objects of the Water Management Act 2000 are to provide for the sustainable and integrated management of the water sources of NSW. Chapter 2, Part 3, Division 4 of the Act provides for (in s26(c)) the development of Drainage Management Plans that must deal with the ecological impacts and impacts on water quality of drainage works however these parts of the Act are not 'turned on'.

In **Management Action** – what activities are needed, on-ground/other? How will they be funded?

- Whole-of-system approach to floodplain management based on the model recently employed in the Shoalhaven estuary. Identification of critical subcatchments coupled with strategic focus of rehabilitation efforts.
- Further improvements of tidal flow to the Hexham Swam complex e.g. removal of the earthen block bank dam at the historic Iron Bark Creek outlet.
- Acknowledgment of the cultural connectivity to landscapes and the adoption of inclusive consultation and working parties in management action initiatives. This was highlighted as having a positive flow-on effect in garnering support for ongoing maintenance of on-ground works.
- Enhanced engagement of industry in management action programs e.g. aquaculture and commercial fisheries. The Wallis Lake project working with local oyster farmers was highlighted as a good example.

In **Communication** – how do we foster support in the community? How do we get information out to where it matters?

- Improved capacity building in floodplain land managers e.g. farmers for the benefits of active floodgate management
- Enhanced knowledge of social structure in a community – translating social mapping data into improved communication with key stakeholders and the general public.
- Support for the commercial and recreational sectors to demonstrate shared benefits for both groups. The model of the NSW Fish Habitat Partnership was mentioned as a demonstration of the willingness of different parties to come together for shared beneficial outcomes.

Workshop images and feedback

Feedback from the Workshop included:

"Great gathering this morning! Very interesting and couldn't be more timely with the current emphasis on business cases. Thank you for all the effort getting the research results presented today and also for what would have been years of work getting this research designed, funded and completed. I look forward to seeing the story version suitable for reading by the executive!"

"This morning was fantastic – thanks again."

"I just wanted to send through my feedback on the workshop last week. The workshop was really well facilitated and was a great opportunity to gain insight to the current research by DPI and the University of Newcastle. It was also beneficial to collectively discuss industry challenges and opportunities in the planning session. Please pass on my thanks to those involved and providing the valuable opportunity. "

Attachments

Work shop handouts –

a) EKP Research Summary Product for Land Managers

b) EKP Research Summary Product for Commercial Fishers

Note:

These attachments are included in the main body of this Final Report as Appendices 16 and 17.