CROSS-SHELF DISTRIBUTION AND INTERANNUAL VARIABILITY IN THE ABUNDANCE OF COMMERCIALLY IMPORTANT ICHTHYOPLANKTON OFF TOWNSVILLE, QUEENSLAND

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DISCLAIMER

Cover

Pelagic juvenile of the common coral trout, Plectropomus leopardus, which is the single most valuable fish extracted from the Great Barrier Reef

CONTENTS

EXECUTIVE SUMMARY

An earlier FIRDC grant (87/046) was used to develop robust submersible light-traps as an alternative to conventional techniques (ie towed plankton nets) for sampling fish larvae. These automated devices were proven on the northern Great Barrier Reef (GBR) where they were found to catch a wide variety of ichthyoplankton including species with adults that are exploited by commercial and/or recreational fisheries. Since light attracts large pelagic juveniles that are poorly sampled by plankton nets, light-traps are superior research tools when it comes to identifying nursery areas and monitoring recruitment potential to valuable fish stocks.

This grant provided a demonstration project of the light-trap technique. Drifting traps were used for regular sampling of ichthyoplankton assemblages along a 160 km transect across the continental shelf off Townsville, which covered a wide range of fish habitats from turbid shallow waters near Magnetic Island to transparent deep waters of the Coral Sea. Simultaneous sampling was done with traps anchored downstream of four small coral reefs of similar size, but different cross-shelf position, to examine the use of near-reef habitats. In both circumstances, sampling was depth-stratified.

This sampling protocol was repeated on the new moon of four consecutive months (Oct-Jan), which covers most of the spawning season for tropical fishes, in two consecutive years (90/91, 91/92). Initially, I planned to sample each open water location three times during each cruise but this design was curtailed randomly by weather and systematically in response to the low catches extracted from the Coral Sea. Instead, increased sampling effort was devoted when possible to the GBR Lagoon, between the reef matrix and the coast, because of the high productivity of this area especially with respect to scombrids (tunas and mackerels). The relative importance of this area as a potential nursery ground was recognised by further sampling in 1992/93.

In total, the traps collected >150,000 pelagic juvenile fish from almost 4000 hr of effort. Preliminary results are given for six groups of interest to commercial and/or recreational fisheries (trevallys, baitfishes, emperors, snappers, mackerels & tuna, cods & gropers).

Although there were many species-specific patterns, some varying with size and age, one of the more interesting results was the persistent presence across years of a diverse larval assemblage in the middle of the GBR Lagoon. The location of this community is consistent with hypothesized velocity shear between shelf-water and a trapped coastal boundary layer. This zone is indicated as a strategic place for future monitoring that could be used to track recruitment variability into local stocks of the common mackerels.

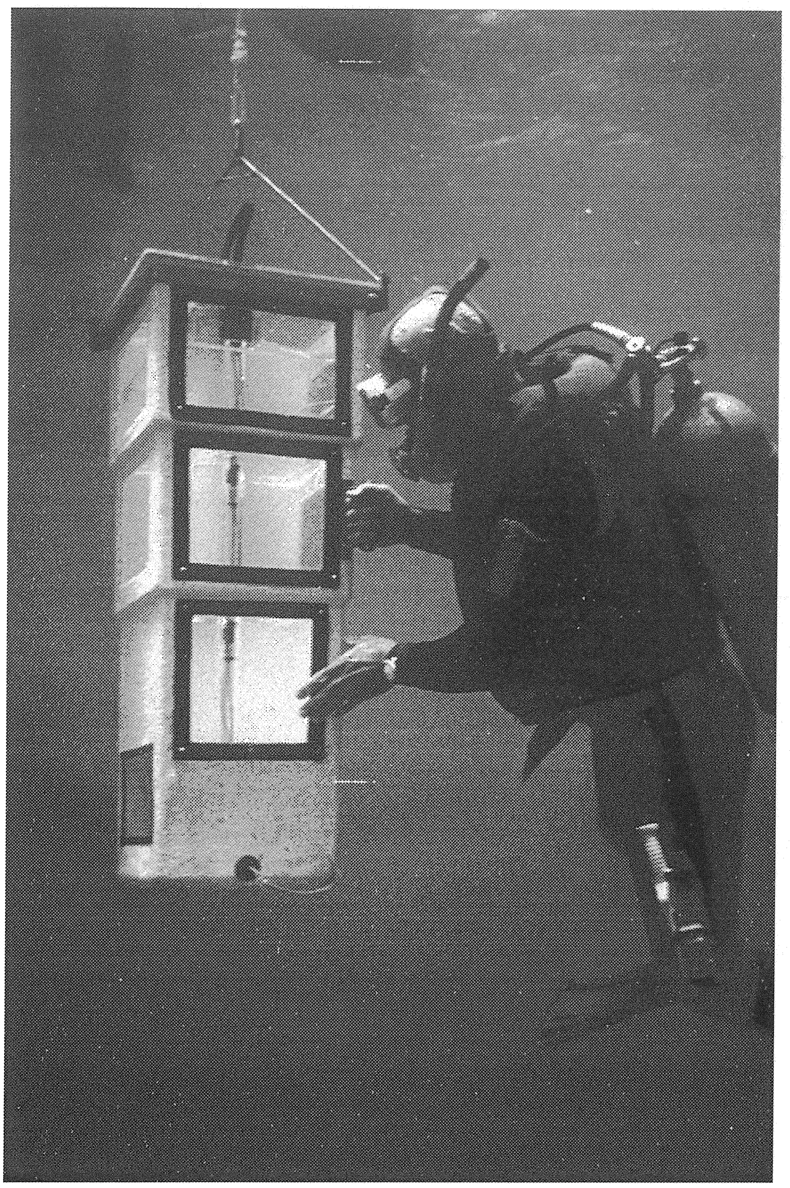


Figure 1. Sampling for this project was done exclusively with submersible light-traps, which target pelagic juveniles that are inaccessible to conventional gear types.

INTRODUCTION

JUSTIFICATION

Line fishing pressure in the GBR Marine Park is estimated to have doubled in the last decade to yield in excess of 12,000 tonnes wet weight of fish per annum (Brown *et al.* 1994). This industry is a multi-species fishery including both pelagic and demersal targets. For many of these species, basic life history information is lacking despite evidence that some have complex life cycles with different stages dependent on reef and coastal habitats. Almost nothing is known about the early life history stages of most of these fishes and no effort is currently being made to monitor recruitment to the resource. This is despite evidence that recruitment is a major force structuring the abundance of marine fish populations (Sissenwine 1984) including those of the tropics (Doherty *et al.* 1994).

Mackerels and a small number of demersal reef fishes contribute the bulk of commercial fin-fish landings from waters adjacent to the GBR. A total commercial catch of at least 3,000 tonnes live weight (worth >$15 million) has been estimated to support 150-200 full-time and 100 part-time fishermen (Brown *et al.* 1994). Total exploitation of these stocks is much higher than these figures suggest because an increasingly mobile recreational industry has been estimated to take a further 7,000 tonnes of reef fishes. On the best available figures, the recreational effort is increasing at about 10% per annum and it is expected that this annual catch will exceed 12,000 tonnes in the nineties. There is obviously considerable potential in this situation for conflict between the major user groups, especially given evidence of declining CPUE and mean size of fish (Craik 1981).

Sustainable development will be difficult without a better understanding of the basic resource. While population parameters like age, growth and longevity have begun to be collected (Williams and Russ 1991), information about dispersal and replenishment is needed given evidence that tropical fish stocks are just as prone as temperate ones to environmental forcing of stock size (Brown *et al.* 1994) and the potential threat from changing water quality to species dependent on coastal nurseries. For most species, however, it is premature to speak of collecting statistics on stock-recruitment relationships or population dynamics given the lack of knowledge about basic life histories. This project addresses this gap. Specifically, it was the first attempt to catalogue the pelagic juvenile fish fauna found in different coastal and marine habitats off Townsville, adjacent to the headquarters of the Australian Institute of Marine Science.

The technology forming the basis of this project was that of submersible light-traps (Fig.1) developed with the support of an earlier grant from FIRDC (Doherty 1995). These devices use light-attraction to sample large pelagic juveniles that are poorly sampled by conventional gear because of net avoidance (Choat *et al.* 1993). The mature state of this material aids precise identification (Fig.2) as well as providing the most appropriate index of recruitment potential to fish stocks.

The automation of the light-traps is a feature that makes them particularly suitable to the extended sampling required for monitoring larval supply, which is notoriously uneven over time (Milicich 1988). In addition, automation permits the deployment of multiple traps in numerous locations permitting simultaneous sampling and the reconstruction of synoptic patterns of distribution and abundance (Doherty 1987).

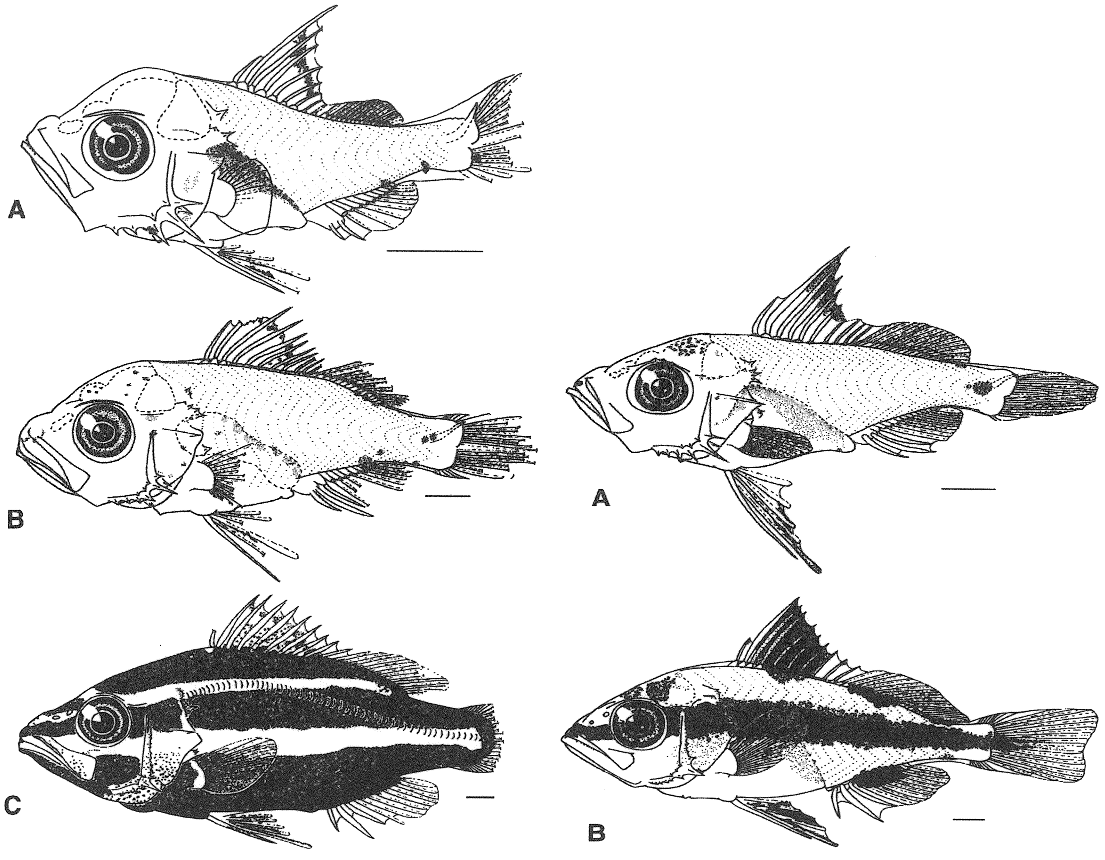


Figure 2. Pelagic juveniles of the Chinaman, *Symphorus nematophorus*, (bottom left) and the Sailfin Snapper, *Symphorichthys spilurus*, (bottom right) collected during this study were able to complete the developmental series for these two monotypic genera within the snapper family: Lutjanidae (Reproduced from Leis and Bray 1995).

BACKGROUND

During the summers of 88/89 and 89/90, Simon Thorrold, a graduate student enrolled at James Cook University and sponsored by AIMS, regularly sampled four localities (0, 10, 20 and 30 km) along two parallel cross-shelf transects in the GBR lagoon using a smaller version of the light-traps (Thorrold 1992, 1993). At two sites, 1 km apart within each locality, he allowed three traps to drift with the surface currents. After 1 hr of fishing, they were retrieved and redeployed to the next locality. The two transects, separated by 30 km, were sampled on alternative nights and there was no deep sampling.

The hierarchical design of Thorrold's sampling allowed him to partition the variance of his catches across three spatial scales (replicate, locality, station). Analysis of the data from the most abundant species showed that >95% of the spatial pattern was caused by patchiness at scales of >10 km (Thorrold and Williams in press). While the spatial pattern at each locality changed only slowly between consecutive samplings, substantial differences were detected between similar localities along the two transects. This suggests that larval abundance is patchy in both cross-shelf and long-shore directions. Although small reef fishes and loliginid squids dominated the catches in this study, some families of commercially-important food fishes (e.g. scombrids) were taken in numbers high enough for useful analysis (Thorrold 1993).On the basis of this preliminary study, I submitted a proposal to FIRDC for funds to sample a wider range of shelf habitats including those in deeper water, as well as near and far from reefs.

OBJECTIVES

(i) to map the distribution of fish larvae along a 160 km cross-shelf transect with a hierarchically-nested and depth-stratified sampling design

(ii) to compare distribution and abundance near and far from reefs

(iii) to measure the temporal variability in abundance of selected stocks of commercial interest at daily, monthly and annual scales

(iv) to determine the influence of water quality and coastal circulation on larval distribution and abundance.

METHODS

Full implementation of the sampling protocol was achieved in the 90/91 breeding season with four cross-shelf cruises (Oct, Nov, Dec, Jan) each lasting 10 days. Each cruise was scheduled between the third and first quarter of the moon when larval fish are most abundant (Milicich 1988). With the exception of December, when Cyclone Joy curtailed operations, samples were collected from the following stations.

Four light-traps, three at the surface and one at 20m, were anchored immediately downstream of four coral reefs (Keeper, Helix, Faraday, Myrmidon) and sampled daily. These reefs, chosen for their similar size, isolation and position on the southern side of the Magnetic passage, span the full width of the reef matrix off Townsville (Fig.3). Each daily sample taken from a trap represented the integrated catch from the standard operating protocol for anchored traps - three periods of fishing during the previous night: 2100-2200, 0000-0100, 0300-0400 EST.

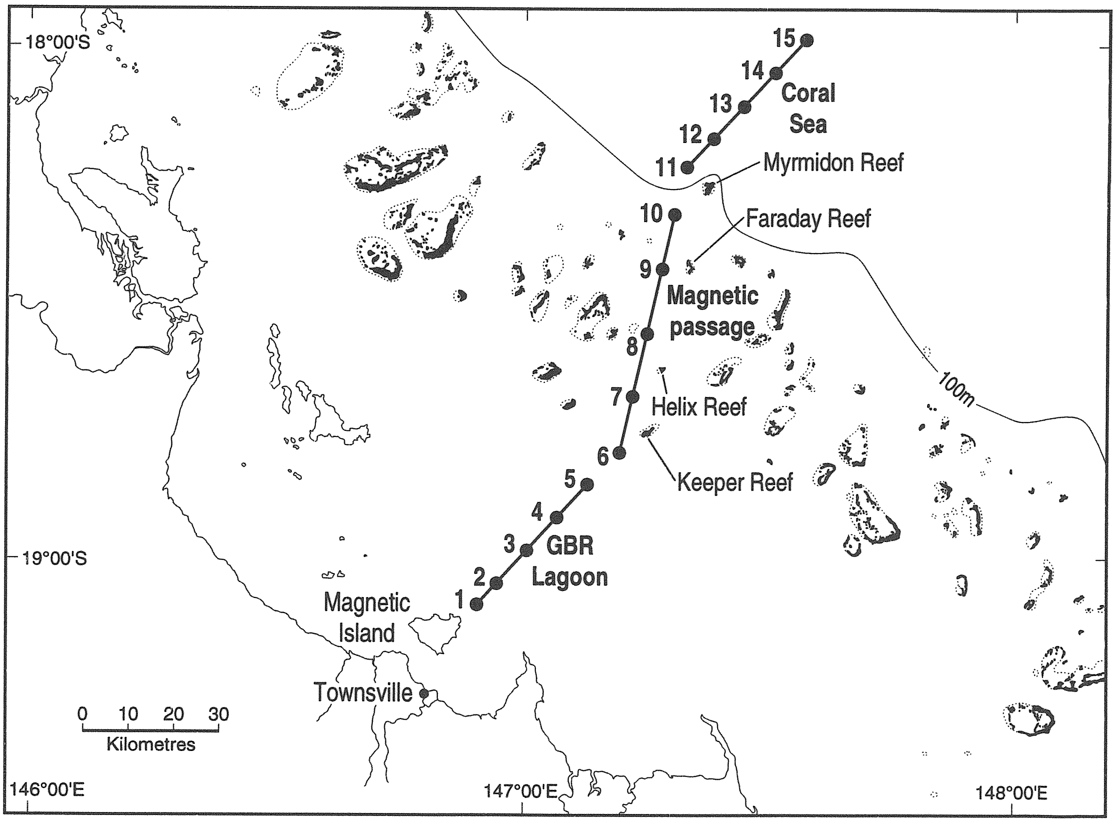


Figure 3. Locality map.

This sampling in the near-field was complemented by night operations in the far field which consisted of drifting light-traps at five open-water stations representing a mini-transect across either the GBR Lagoon (Stations 1-5), the Magnetic Passage (6-10) or the western Coral Sea (11-15). In perfect weather, each nightly transect (and hence the entire transect of 160 km) was completed three times in a cruise. At each of the 15 stations, two buoy strings were released 200-300m apart; each string supported one light-trap at the surface and another at 20m. All traps were recovered after one hour of fishing and their contents were processed as the ship steamed to the next station.

At Station 1, the water depth approached 20m so that the deep traps there fished very close to the bottom. Further offshore the bottom slopes gradually to 40 m at the inner edge of the reef matrix and 60-80 m at the shelf-break. Stations beyond Myrmidon Reef (11-15) were all in depths in excess of 1000 m.

The biological sampling was complemented by the collection of oceanographic data from a series of moored current meters. These instruments were located on both sides of the reef matrix with a third in the Magnetic Passage. This coverage was considered sufficient to model hydrodynamic flows through the matrix and around individual reefs.

In 91/92, the same protocol was repeated with a few significant differences. First, due to the availability of additional traps, the effort near each of the four reefs was boosted by an extra trap at 20 m. Second, due to the better sealing introduced by constant upgrading of the trap design (Doherty 1995), the depth of the deep drifting traps was increased so that they sampled within 5 m of the bottom, to a maximum of 100 m. Third, effort was reduced in the Coral Sea due to the extra difficulty of working off the continental shelf at night and the consistently low return from such sampling. As a result, sampling off the shelf was reduced to a single night per cruise but compensated whenever possible by additional effort at the inshore end of the transect, which was the most productive area. Finally, profiles of water temperature, salinity and frequently light-transmission (depending on availability of a transmissometer) were captured with a Seabird™ CTD at each of the open water stations.

In 92/93, detailed sampling was initiated at Bowden Reef to examine the effect of small-scale circulation on larval supply. Since this reef is not far south of Townsville, we took the opportunity to obtain another three nights of sampling in the GBR Lagoon on each of five cruises during that summer (new moons of Oct-Feb). For this part of the transect then (stations 1-5), three consecutive years of data were collected.

All samples were preserved in 70% alcohol to preserve the otoliths in the heads of these fishes, so that a portion of them could be extracted and measured for age and growth histories by interpreting daily growth rings in their microstructure. To date, one student project has accessed this archived material (Murdoch, MSc - James Cook University).

In summary, the project resulted in almost 4000 hours of sampling allocated to stations and depth strata as follows:

TABLE 1. TOTAL EFFORT- 3881 h

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	204	162	143	509
91/92	239	180	80	499
92/93	259			259

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
250	255	237	228	970
423	396	423	402	1644

TABLE 2. EFFORT (shallow traps) 2379 h - 61% of total effort

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	102	81	71	254
91/92	119	90	40	249
92/93	129			129

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
181	192	180	183	736
255	258	255	243	1011

TABLE 3. EFFORT (deep traps) 1502 h - 39% of total effort

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	102	81	72	255
91/92	120	90	40	250
92/93	130			130

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
69	63	57	45	234
168	138	168	159	633

RESULTS

SUMMARY STATISTICS

The following tables record the total catch of all fishes by station and depth stratum. Tables in Appendix 2 provide a breakdown of relative abundance by family of the catches from each of the reefs and each of the open-water transects.

TABLE 4. TOTAL FISH CAUGHT N=154278

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	4446	1186	393	6025
91/92	11821	2551	59	14431
92/93	20142			20142

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
11111	17541	6810	4463	39925
34898	7480	12179	19198	73755

TABLE 5. CATCH (shallow traps) n=124798 (81% of total catch)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	2082	663	352	3097
91/92	6665	1518	54	8237
92/93	7375			7375

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
10596	17226	6672	4357	38851
32603	7145	11569	15921	67238

TABLE 6. CATCH (deep traps) n=29480 (19% of total catch)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	2364	523	41	2928
91/92	5156	1033	5	6194
92/93	12767			12767

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
515	315	138	106	1074
2295	335	610	3277	6517

The data show the complex and dynamic nature of larval supply. The majority of all fish were collected from shallow traps but the proportion of the catch taken from the two depth strata varied between far- and near-field collections (Tables 5,6). Pooled across years, >100,000 fish were collected from shallow water near reefs and these reflect the concentrations of some common reef fishes, particularly sprats (*Spratelloides delicatulus* and *S. gracilis*) and a diverse range of small coral reef fishes (Appendices 2D-G). In contrast, a large number of fish were caught in deep water from the bottom of the GBR Lagoon, especially in the third year (Table 6).

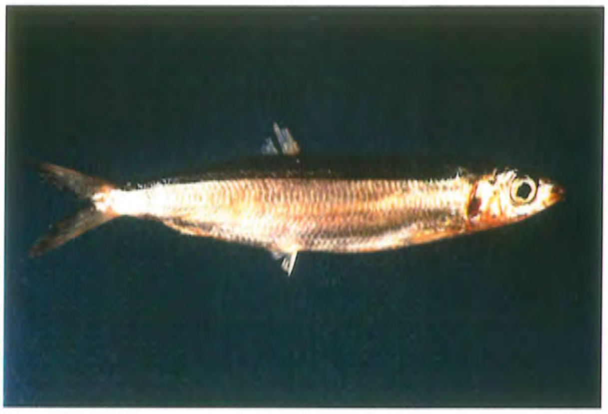
Catch composition on individual reefs showed both patterns of coherence and independence. For example, between the first two years, total catch per unit effort increased on two reefs (Keeper, Myrmidon), decreased on one (Helix) and remained stable on the fourth (Faraday). The pattern at Helix may have been influenced by its smaller size, which affects its efficiency as a larval attractor, but two taxa (leatherjackets and pelagic codlets) increased disproportionately over the same period (Appendix 2E). Furthermore, the decline in catches at Helix was shared with taxa that that do not disperse among coral reefs (sprats and hardyheads). Leaving aside Helix, most of the reefs recorded an increase in the relative abundance of common coral reef fishes between the two years indicating large-scale changes in larval supply. At the level of individual taxa, the number of significant changes between year-classes increased systematically across the shelf, which is consistent with the hypothesis that larval supply is more variable on outer shelf reefs as a result of hydrodynamic characteristics. For example, squirrelfishes declined between the years on both Faraday and Myrmidon, while damselfishes increased on both (Appendices 2F,G). These former are one of very few families adapted to truly oceanic habitats and the concentration of squirrelfishes recorded at open water stations off the shelf also declined over the same period (Appendix 2C). In contrast, damselfishes are characteristic of neritic habitats and the replacement of these two groups suggests a change in water quality, presumably as a result of the degree of intrusion of oceanic water over the edge of the shelf. When years were pooled, however, total catch did not vary greatly among reefs with the exception of highest catches at Keeper on the inner edge of the reef matrix, which appears to have more concentrated and reliable larval supply.

The pattern among the open water habitats was different. First, total catches declined consistently with distance from the coast (Appendices 2A-C). Catches from the Coral Sea were particularly low and it appears that few shallow-water taxa complete their early development off the continental shelf. In the most productive section of the transect, the five stations in the GBR Lagoon, deep habitats were no less important than shallow ones and arguably were more important during the third and final season. At both depths, there was a steady increase in mean CPUE among the years corresponding to change of almost an order of magnitude, especially among the fish caught near the bottom.

Because diversity tends to obscure pattern, the remaining analyses focus on the abundance of selected species of commercial interest (Fig.4). The groups chosen for this analysis were the Carangidae (jacks, trevallies); small pelagic baitfish including Clupeidae (herrings, sardines, sprats), Dussumieriinae (round herrings), Atherinidae (hardyheads) and Engraulidae (anchovies); Lethrinidae (emperors); Lutjanidae (snappers); Scombridae (mackerels and tunas); and the Serranidae (cods and gropers).

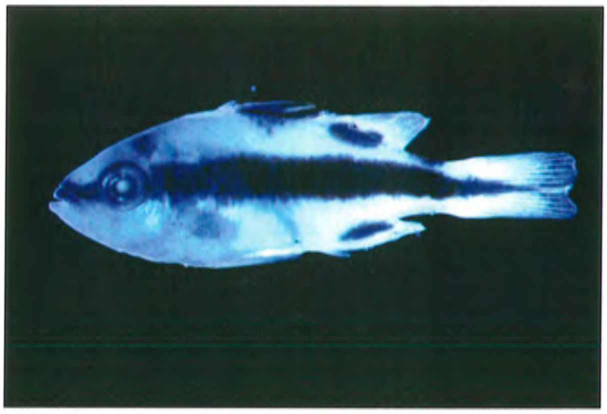
Figure 4. Examples of the selected families chosen for analysis (a) *Gnathanodon speciosus*, the Golden Trevally, (b) *Sardinella gibbosa*, a typical clupeid, (c) *Gymnocranius grandoculis*, the Big-eye Bream, (d) *Symphorichthys spilurus*, the Sailfin Snapper, (e) *Scomberomorus commerson*, the Spanish Mackerel, (f) *Plectropomus laevis*, the Footballer Coral Trout (cf *Plectropomus leopardus* on the front cover).

a. *Gnathanodon speciosus*



b. *Sardinella gibbosa*

c. *Gymnocranius grandoculis*



d. *Symphorichthys spilurus*

e. *Scomberomorus commerson*

f. *Plectropomus laevis*

TREVALLIES (CARANGIDAE)

This family consisted of two major groups. A diverse collection of species from the Tribe Carangini, including the large common trevallies in the genera *Caranx, Carangoides* and *Gnathanodon*, were collected from shallow water, especially near reefs. The opposite pattern was shown by several species of scad belonging to the genus *Decapterus*. These were more common near the bottom and far more important away from reefs, especially in the Magnetic Passage where large schools were sometimes encountered. Scads were more common in the second year, raising the total catches of carangids from the open water stations on the shelf, whereas catches around the reefs were quite stable.

TABLE 7. TOTAL CARANGIDAE. n=2281 (73% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	135	243	1	379
91/92	397	854	0	1251
92/93	182			182

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
164	25	26	6	221
120	79	38	11	248

TABLE 8. *Decapterus macrosoma* n=1265 (88% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	53	52	0	105
91/92	221	746	0	967
92/93	42			42

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
69	9	18	0	96
23	24	8	1	55

TABLE 9. *Decapterus russelli* n=407 (91% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	18	179	0	197
91/92	58	93	0	151
92/93	16			16

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
13	1	0	0	14
26	3	0	0	29

BAITFISHES (ATHERINIDAE, CLUPEIDAE, ENGRAULIDAE)

This is a mixed assemblage containing representatives of several families (hardyheads; herrings, sardines and sprats; anchovies). The aggregate statistics show that the largest proportion of these fish were found in shallow water near reefs (Table 10) but this is almost completely due to the dominance of two species of sprat (*Spratelloides delicatulus* and *S. gracilis*) in this habitat (Table 11). Both species are strongly reef-associated and the few records from elsewhere may represent larval forms of other clupeoids incorrectly assigned to this genus.

TABLE 10. TOTAL ATHERINIFORMS AND CLUPEIFORMS n=78581 (78% shallow)

	DRIFTING TRAPS				ANCHORED TRAPS				
	STN 1-5	STN 6-10	STN 11-15	Total	Keeper	Helix	Faraday	Myrmidon	Total
90/91	1891	63	10	1964	5055	13993	5249	2407	26704
91/92	6441	174	1	6616	11793	3462	3191	11774	30220
92/93	13077			13077					

TABLE 11. *SPRATELLOIDES* n=53294 (93% shallow)

	DRIFTING TRAPS				ANCHORED TRAPS				
	STN 1-5	STN 6-10	STN 11-15	Total	Keeper	Helix	Faraday	Myrmidon	Total
90/91	9	4	4	17	4891	13729	5130	2386	26136
91/92	12	23	1	36	11207	3367	2362	10150	27086
92/93	19			19					

The second most abundant family of baitfishes was the anchovies which showed the opposite habitat association to that of the sprats. Anchovies, mostly of the genus *Stolephorus*, were most common near the bottom of the GBR lagoon (Table 12). Standardised catches of this group increased disproportionately over the three years.

TABLE 12. ENGRAULIDAE n=12069 (94% deep)

	DRIFTING TRAPS				ANCHORED TRAPS				
	STN 1-5	STN 6-10	STN 11-15	Total	Keeper	Helix	Faraday	Myrmidon	Total
90/91	255	1	0	256	0	2	0	0	2
91/92	2104	8	0	2112	35	0	0	0	35
92/93	9664			9664					

A mixed group of herrings and sardines, (common genera: *Amblygaster, Herklotsichthys, Sardinella*) were also common in the GBR Lagoon but concentrated at the surface in contrast to the anchovies. These species include many coastal baitfishes that appear to have offshore spawnings and larval transport to shallow coastal nurseries (Williams and Cappo unpubl. data).

TABLE 13. CLUPEIDAE n=6556 (78% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	1273	1	0	1274
91/92	2584	0	0	2584
92/93	2682			2682

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
1	0	0	0	1
0	15	0	0	15

Like the sprats, hardyheads were found to be reef-associated fish, rarely taken in deep water.

TABLE 14. ATHERINIDAE n=1341 (100% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	6	0	0	6
91/92	3	1	0	4
92/93	7			7

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
162	240	117	15	534
116	67	287	317	787

Round herrings in the genus *Dussumieria* had spatial characteristics similar to those of anchovies and were often encountered with the latter as mixed schools in the bottom of the GBR Lagoon.

TABLE 15. DUSSUMIERIINAE n=990 (63% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	228	1	0	229
91/92	513	0	0	513
92/93	237			237

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
1	0	0	0	1
0	9	0	1	10

EMPERORS (LETHRINIDAE)

The emperors were one of the most difficult families to dissect because of their non-descript appearance before settlement (Fig.4). This is a diverse group and it is certain that the juveniles collected inshore from the GBR Lagoon were not the same species as those collected from the offshore reefs. Compared with catches of this family at other times and places (Milicich and Doherty 1994), the near-reef catches recorded in this study appear very impoverished. It is not clear whether regional factors are involved or whether this reflects the small size of the lagoonal habitats available on the Townsville reefs compared with other sampling locations. After standardising for changes in effort, the GBR Lagoon was more important than the reefs in all years and, in common with a number of other taxa, there was a large increase in the abundance of this family in year 3.

TABLE 16. TOTAL LETHRINIDAE. n=1003 (96% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	84	29	0	113
91/92	108	18	0	126
92/93	717			717

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
4	6	1	0	11
9	17	8	2	36

SNAPPERS (LUTJANIDAE)

Snappers were too rare to analyse and may not be well-sampled with light. The exception appears to be the common stripey, *Lutjanus carponotatus*, which provided the majority of observations from the reefs. Unlike the emperors, snappers were more common near the bottom.

TABLE 17. TOTAL LUTJANIDAE. n=26 (81% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	2	1	0	3
91/92	1	0	0	1
92/93	0			0

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
14	1	1	0	16
3	1	0	2	6

MACKERELS AND TUNA (SCOMBRIDAE)

This family of fishes contains a number of targets for the commercial troll-line fishery, particularly the Spanish mackerel, *Scomberomorus commerson,* and several of the smaller species are targeted by net fisheries in southern Queensland . With <10% of these fish caught near reefs, the GBR Lagoon is obviously the primary habitat for juvenile scombrids. The exception was the shark mackerel, *Grammatocynus bicarinatus*, which appears more site attached than its relatives. Among the rest, the small non-commercial long-jaw mackerel, *Rastrelliger,* was found almost exclusively near the bottom whereas most of the larger mackerels, *Scomberomorus,* were found in shallow water. A multivariate ordination shows this spatial segregation of the different genera (Fig.5a). The three stations nearest the coast were discriminated well from the collections taken further offshore and near the reefs. At the inshore end, the fauna was clearly segregated by depth and this difference disappeared with increasing distance from the coast. When the species contributing most to this pattern were identified (Fig.5b), three patterns emerged. First, as noted, *Grammatocynus* was different from all other scombrids in its clear association with shallow reef habitats. Second, there was a shallow inshore fauna characterised by three species of *Scomberomorus*. Finally, there was a deep inshore fauna dominated by *Rastrelliger* and *Euthynnus affinis* (the mackerel tuna).

Mackerel tuna was the most common scombrid and a breakdown of its abundance shows how mobile these fish can be even before reaching large size. Fig.6 is another multivariate ordination based on the monthly collections of this species, pooled across years but stratified by depth. In spring, there was little difference between samples of *Euthynnus affinis* from deep and shallow water but a progressive divergence was observed during summer. Analysis of the size structures of the various collections showed that average size increased with time, especially in the deep collections. Late spawning continued to deliver small fish into the surface layer which explains why the shallow collections remained in one part of the multivariate space. The divergence between the deep and shallow collections appears to have been caused by the ontogenetic migration of these small tunas into deeper water and their movement further offshore. The cross-over from shallow to deep lifestyles appears to happen around November at a size between 20-30 mm SL (Fig.6).

TABLE 18. TOTAL SCOMBRIDAE n=5905 (69% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	751	62	9	822
91/92	1906	82	0	1988
92/93	2579			2579

ANCHORED TRAPS

	Keeper	Helix	Faraday	Myrmidon	Total
90/91	51	58	71	9	189
91/92	52	131	129	15	327

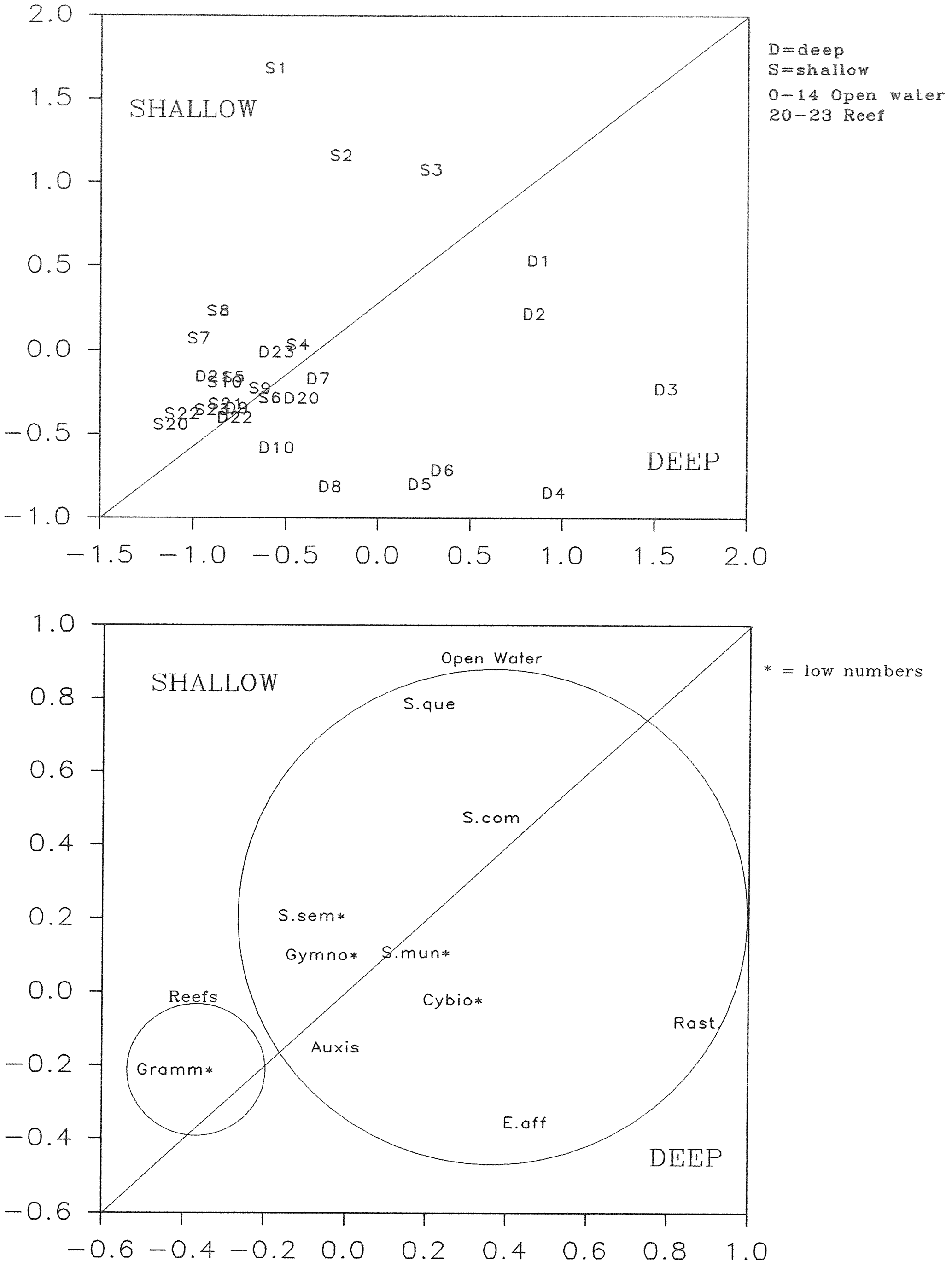


Figure 3 (a) Multivariate ordination of sampling stations based on all scombrids pooled over time. (b) Multivariate ordination of scombrid species pooled over time and space.

TABLE 19. *Rastrelliger sp.* n=1751 (94% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	396	17	0	413
91/92	381	2	0	383
92/93	926			926

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
2	1	0	0	3
3	17	2	4	26

TABLE 20. *Scomberomorus sp.* n=885 (65% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	195	6	1	202
91/92	220	2	0	222
92/93	455			455

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
2	1	0	0	3
0	2	0	1	3

TABLE 21. *Auxis sp.* n=478 (62% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	20	11	3	34
91/92	173	8	0	181
92/93	198			198

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
5	19	1	0	25
4	32	2	2	40

TABLE 22. *Grammatocynus sp.* n=67 (96% shallow)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	0	2	0	2
91/92	0	0	0	0
92/93	3			3

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
15	10	12	0	37
13	0	10	2	25

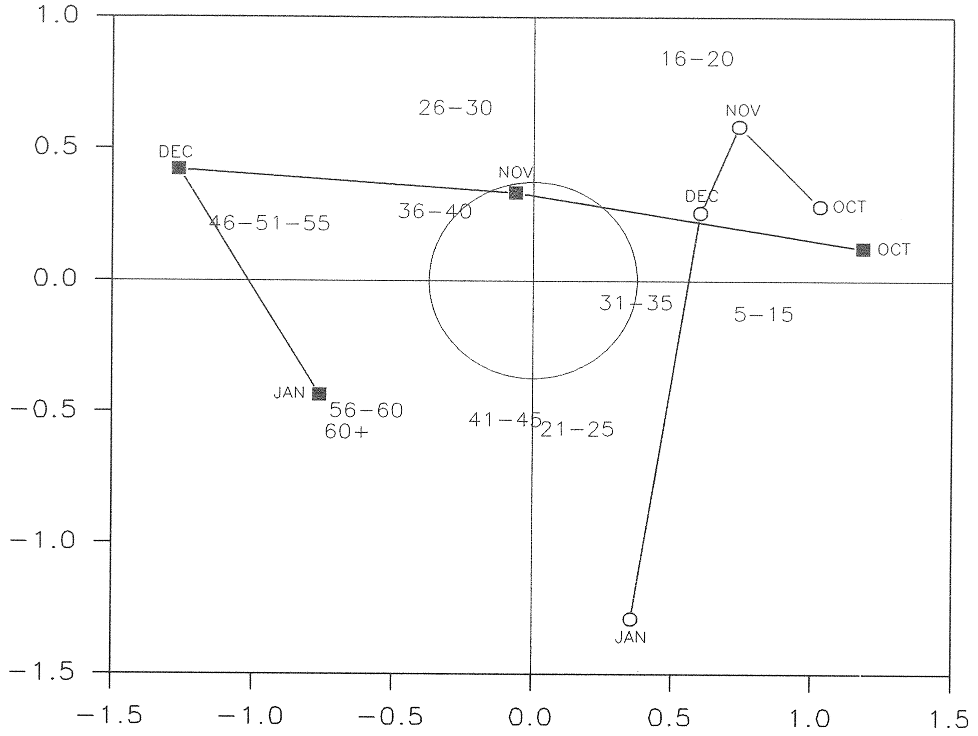


Figure 6. Multivariate ordination of samples from shallow (circles) and deep (squares) collections of *Euthynnus affinis* with mean size superimposed on the same space.

TABLE 23. *Euthynnus affinis* n=2301 (78% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	118	9	2	129
91/92	1096	63	0	1159
92/93	900			900

ANCHORED TRAPS

Keeper	Helix	Faraday	Myrmidon	Total
9	22	11	2	44
19	32	15	3	69

CODS AND GROPERS (SERRANIDAE)

As with the lutjanids, this group was too rare to analyse in detail although experience elsewhere has shown that some species can be caught in quite large numbers (Brown *et al.* 1994). Those places have all involved sampling behind large reefs which may act as more efficient concentrators of rare taxa.

TABLE 24. TOTAL SERRANIDAE n=82 (52% deep)

DRIFTING TRAPS

	STN 1-5	STN 6-10	STN 11-15	Total
90/91	9	0	0	9
91/92	22	1	0	22
92/93	27			27

ANCHORED TRAPS

	Keeper	Helix	Faraday	Myrmidon	Total
90/91	3	0	0	0	3
91/92	12	0	3	5	20

OTHER FAUNA

Apart from fish, this sampling program also yielded significant numbers of squid and octopods, which provided the ecological part of a recent doctoral thesis (Moltschaniwsky PhD - James Cook University) and two scientific publications (Moltschaniwsky and Doherty 1994, 1995). In addition, there appear to be sufficient phyllosoma larvae, presumably of scyllarid lobsters, in the collections to merit a separate publication.

PHYSICAL OCEANOGRAPHY OF THE GBR LAGOON

On most sampling occasions over the last two seasons, temperature and salinity profiles were determined for the water column at all open water sites. Moltschaniwsky and Doherty (1995) analysed the data from the sites in the GBR Lagoon given its apparent importance as a nursery for numerous species of invertebrate and fishes. This analysis was done by analysing the deviation of each variable at the five locations from the average for all stations in a particular month, thereby standardising for the seasonal cycles. The average deviations reveal a steep gradient across the lagoon with maximal change somewhere in the middle, consistent with a proposed shear zone and trapped coastal boundary layer at this point (Thorrold and McKinnon 1992). For a number of reef species common in the outer part of the GBR Lagoon, this area seems to form a barrier to further dispersal shorewards. It also appears that this region provides a suitable environment for many species of planktivore as indicated by the dense schools of engraulids and

Rastrelliger, which may indicate elevated secondary productivity. With high concentrations of zooplankton and small fish, it is not surprising that the fast-growing piscivores like the scombrids are attracted to this area. The location of known spawning grounds for the Spanish mackerel on some of the reefs on the inner edge of the reef matrix (e.g. Rib, Lodestone, and Keeper) is consistent with the hypothesized drift of eggs and small larvae into the central GBR Lagoon where they may find high food densities. Consequently, this zone would be an appropriate place to monitor local replenishment of these valuable stocks.

AGE AND GROWTH

One final outcome of this study was Murdoch's study of age and growth of three species of non-exploited damselfishes collected from the four coral reefs. These species were chosen for their abundance and certain identification in order to assess the extent to which possible gradients in food or environmental stress might influence the performance of a single species. Surprisingly, the study revealed no effect despite the obvious differences in particulate loadings across the shelf. Murdoch found that that larval growth was nearly linear and constant among locations in contrast to a previous study comparing different regions of the GBR (Thorrold and Milicich 1990). Fish on the outer shelf did settle at larger size but this is because they had spent slightly longer in the plankton. This is consistent with the lower chance of encountering a reef at the shelf break and may suggest that hydrodynamic explanations are more important than food limitation in this system. It is anticipated that other species will be examined as labour becomes available to test the generality of this hypothesis.

DISCUSSION

Regular depth-stratified sampling across the continental shelf off Townsville showed that most pelagic juvenile fishes congregate near the surface at night , with a few notable exceptions that remain near the bottom throughout life (e.g. *Rastrelliger* spp.). Others start high in the water column and move closer to the bottom as they make ontogenetic migrations across the shelf. This may be particularly true of species that make cross-shelf excursions in the absence of suitable transport mechanisms, where directional swimming is the only option. Among reef-associated species, the main groups occurring near the bottom are all large fish and capable swimmers (Stobutzki and Bellwood 1994).

The open-water sampling (Stations 1-15) revealed strong cross-shelf gradients in the distribution and abundance of all taxa; almost none were cosmopolitan. The Coral Sea was the most difficult environment to sample; it does not appear to be an important habitat for shelf taxa with the exception of a few non-commercial species (e.g. surgeonfishes, squirrelfishes). The Magnetic Passage was a transition zone with a gradation of larval abundance reflecting the distribution of spawning stocks on the adjacent reefs. Potential larval supply to the reef matrix as measured in the open water diminished across the shelf. As well as being more intense at the inshore end, larval assemblages were also more stable among years near the inner edge of the reef matrix. This pattern is consistent with the hypothesized onshore vector to longshore dispersal in this part of the GBR and the presumptive patterns of connectivity (i.e. larval exchanges) among reefs (Dight *et al.* 1990).

A substantial number of species were found to be concentrated at stations in the centre of the GBR Lagoon, potentially corresponding to velocity-sheared transition between shelf water and a trapped coastal wedge. This feature has been identified and sampled previously (Thorrold and McKinnon 1992). Its persistence over several years suggests that it would be a strategic location for sampling the replenishment of pelagic fish stocks in an environment that has few other internal features. Stations further inshore (1-3) had fewer fish larvae overall but appeared to define the larval habitat of several species including Grey Mackerel. These stations also returned large numbers of squid and phyllosoma larvae (probably of various slipper lobsters) near the bottom.

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OUTPUTS

SCIENTIFIC PUBLICATIONS

The following publications were a direct consequence of this grant from FIRDC. Additional information about the inshore end of the cross-shelf transect is given in publications arising from the doctoral research program of Simon Thorrold (see bibliography) who was supported by funds and vessel resources from AIMS.

Doherty, P.J. (1992) Spatial and temporal patterns in the abundance of pre-settlement fishes from the Great Barrier Reef. Pp. 89-93 In: D.A. Hancock (Ed.) Recruitment Processes. ASFB Workshop, Hobart, 21 August 1991. BRR Proc. 16, AGPS, Canberra

Moltschaniwskyj, N.A. and P.J. Doherty (1994) Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef Lagoon. Fish. Bull. 92: 302-312

Moltschaniwskyj, N.A. and P.J. Doherty (1995) Cross-shelf distributions of tropical juvenile cephalopods sampled by light-traps. Mar. Freshwater Res. 46: 707-714

STUDENT THESES

Natalie Moltschaniwskyj PhD (James Cook)
Julie Murdoch MSc (James Cook)
Christine Schmit BSc(Hons) (Munster)
Simon Thorrold PhD (James Cook)

SELECTED PRESENTATIONS

Boden Conference, Thredbo, February 1990
42nd Tuna Conference, Lake Arrowhead, California, May 1991
Oregon State University, Zoology Department, May 1991
ASFB Larval Biology Workshop, Hobart, August 1991
Sydney University, Zoology Department, October 1991
ICLARM Workshop on Reef Resource Management, Townsville, March 1992
Seventh International Coral Reef Symposium, Guam, July 1992
Universite dé Perpignan, France, June 1994
International Larval Fish Conference (3 talks), Sydney July 1995
GBRMPA Status of the GBR World Heritage Area, Townsville, November 1995

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Milicich, M.J. (1988) The distribution and abundance of presettlement fish in the nearshore waters of Lizard Island. Proc. 6th Inter. Coral Reef Symp. 2: 785-790

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Thorrold, S.R. and M.M. Milicich (1990) Comparison of the larval duration and pre- and post-settlement growth in two species of damselfish, *Chromis atripectoralis* and *Pomacentrus coelestis* (Pisces: Pomacentridae) from the Great Barrier Reef. Mar. Biol. 105: 375-384

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Williams, D.McB. and G.R. Russ (1991) Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Report to GBRMPA, Townsville

APPENDICES

APPENDIX 1

Moltschaniwskyj, N.A. and P.J. Doherty (1994) Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef Lagoon. Fish. Bull. 92: 302-312

Moltschaniwskyj, N.A. and P.J. Doherty (1995) Cross-shelf distribution patterns of tropical juvenile cephalopods sampled with light-traps. Mar. Freshwater Res. 46: 707-714

APPENDIX 2

Catch composition by season and location

- GBR Lagoon (Stations 1-5)
- Magnetic Passage (Stations (6-10)
- Coral Sea (Stations 11-15)
- Keeper Reef
- Helix Reef
- Faraday Reef
- Myrmidon Reef

Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef Lagoon

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Abstract.—This study quantified the temporal and spatial abundance of juveniles of two *Photololigo* species on the continental shelf off Townsville, Australia with the use of light-traps. The two *Photololigo* species (A and B) showed very distinct and separate spatial distribution patterns. *Photololigo* sp. A was found close to the coast and was the smaller and more abundant of the two species. This species was most abundant in surface waters, although larger individuals were generally caught deeper. There was no evidence of vertical movements during the night. The presence of small and large juvenile *Photololigo* sp. A during summer and winter months suggests spawning and recruitment occur throughout the year. In contrast, *Photololigo* sp. B was caught predominantly offshore. All sizes of *Photololigo* sp. B were caught both near the benthos and at the surface in the mid-lagoon, but farther offshore juveniles were deeper and larger. The presence of small juvenile squid of both species throughout the summer suggests that these species spawn for an extended period during the summer. This study demonstrates that light-traps are an effective way of sampling small cephalopods.

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The current poor state of knowledge about processes important in squid population dynamics is mainly due to limited information about the juvenile phase (Voss, 1983; Boyle, 1990). Life-history characteristics have largely been derived from information about the adult phase. Our limited information about young squid is demonstrated in attempting to define the life-history phases (Young and Harman, 1988). Jackson and Choat (1992) suggest, given the comparatively short life time of tropical squid (<250 days), that a proportionally long period of the life cycle is spent as small individuals. In the case of *Loligo chinensis,* with a summer life time of 120 days, individuals less than 60 days old (<50-mm mantle length) have not been studied. Hence, for almost half the life history of most squid there is not even the most basic information. Temporal and spatial abundance patterns of juvenile squid will provide a basis for understanding the processes of mortality, growth, and recruitment. However, such information has traditionally been difficult to obtain because of problems in capturing and identifying a sufficient size range of juvenile cephalopods (Vecchione, 1987).

To examine the ecology of juvenile squid it is necessary to use techniques that catch a size range of individuals, hatchlings to juveniles, in good condition. Pelagic squid produce either benthic or pelagic eggs and have a planktonic juvenile phase (Boletzky, 1977). Juvenile squid are alert, mobile organisms that easily avoid capture by towed nets (Vecchione, 1987). The use of a combination of different towed nets to sample an area enables the collection of a wider size range of juvenile squid (Rodhouse et al., 1992). However, it is difficult to obtain replicates needed to provide density estimates from towed nets. In this study we have employed an alternative technique based on light-attraction that is effective in sampling pelagic juvenile fishes. Automated light-traps (Doherty, 1987) can overcome the problems of net avoidance and enable sampling at discrete depths in the water column. The ability to sample concurrently within an area ensures that estimates of variability in abundance are not confounded by time. This technique also collects live material in good condition, which can facilitate taxonomic identification. However, sampling an unknown volume of water by individual traps requires cautious interpretation of abundance estimates (Choat et al., 1993).

There are four species of loliginid squid currently recognized in the Townsville region: *Sepioteuthis lessoniana, Loliolus noctiluca, Photololigo* sp. B, and *Photololigo* sp. A.[1] There are currently no morphological descriptions of the two *Photololigo* species, but they can be readily identified by using allozyme electrophoretic techniques (Yeatman and Benzie, in press). Previously both of these species have been referred to as *Photololigo* (*Loligo*) *chinensis* (Jackson and Choat, 1992; Yeatman and Benzie, in press), but neither correspond to *P. chinensis* from Thailand.[2] Electrophoretic analysis of a subset of juveniles collected during three months of the program found that all *Photololigo* sp. A were found less than 33 km offshore and 90% of the *Photololigo* sp. B were found 33 km or more offshore.[2] Because these species are morphologically identical as juveniles, we assumed that all individuals found at stations less than 33 km offshore were *Photololigo* sp. A and that *Photololigo* collected more than 33 km offshore were *Photololigo* sp. B. *Photololigo* sp. A (previously known as *Loligo chinensis*) has been the topic of recent growth studies using statolith aging techniques (Jackson and Choat, 1992). This species is a small short-lived neritic squid. Individuals are approximately 60 days old when they appear in the adult population and they can grow to 180 mm in 120 days. Little is known about the early life-history and juvenile distribution patterns of either *Photololigo* species. The objectives of this study were to describe the spatial and temporal distribution patterns of juvenile *Photololigo* species across the continental shelf in the Townsville region of the Great Barrier Reef.

Materials and methods

Sampling design

Two major habitat types are found on the continental shelf, off Townsville, Australia. The inshore habitat is a 56 km wide soft bottom coastal lagoon ranging in depth from 15 m to 40 m. The offshore habitat is a complex reef matrix of similar extent, dissected by channels ranging from 40 m to 75 m deep at the shelf break. To assess the cross-shelf distribution of juvenile squid, four automated light-traps (Doherty, 1987) were deployed at fifteen sampling stations spanning the continental shelf and the western Coral Sea (Fig. 1). Abundance along this transect was assessed over four months, October to January, during two austral summers, 1990/91 and 1991/92. At each station, the abundance of juvenile squid was determined at two depths by deploying two pairs of light-traps. In each pair, one light-trap was suspended immediately below the surface while the other light-trap was set deeper. In 1990/91, all deep light-traps were suspended 20 m below the surface. In 1991/92, the deep light-traps were suspended within 5 m of the bottom to a maximum of 100 m in the Coral Sea.

In all deployments, the two pairs of light-traps were released approximately 300 m apart and allowed to drift for one hour. Allowing the traps to drift in the water minimized potential problems with differential water movement among stations. The use of drifting light-traps has been shown to be a more effective way of catching pelagic organisms than anchored light-traps in open water (Thorrold, 1992). After one hour, the four light-traps were retrieved and the entire catch was fixed and preserved in 100% ethanol. Each evening the first light-trap was deployed after 1930 hours (Eastern Standard Time) and the last light-trap retrieved before 0430 hours. Travel time between each station allowed only five cross-shelf stations to be sampled per night. Thus, each night's activity concentrated on one of the two continental shelf habitats or the Coral Sea. Each monthly cruise consisted of nine nights during which time each of the 15 stations was sampled three times. However, sea conditions were not always favorable. Sampling effort at each station is shown in Table 1.

It was not logistically possible to sample all stations in each habitat simultaneously. Therefore, time of night is confounded with station position. Haphazard selection of the first station sampled each night ensured that no station was consistently sampled at the same time on all nights. Cruises were scheduled to include the new moon because this is the lunar phase when light attraction has proved most effective for fishes and various invertebrates (Milicich, 1992). Temperature and salinity profiles of the water column were collected at each station by using a Seabird Conductivity Temperature Device during the 1991/92 summer.

Concurrent with the summer cross-shelf sampling, light-traps were anchored within 100 m of the southeasterly side (weather-side) of four reefs; Keeper, Helix, Faraday, and Myrmidon, to sample near-reef water (Fig. 1). The use of drifting light-traps near the reefs was not possible. During the summer of 1990/91, four light-traps were anchored at each reef; three immediately below the surface

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[1] C. C. Lu, Museum of Victoria, Australia, pers. commun. 1990.

[2] J. Yeatman, James Cook Univ., Australia, unpubl. data 1993.

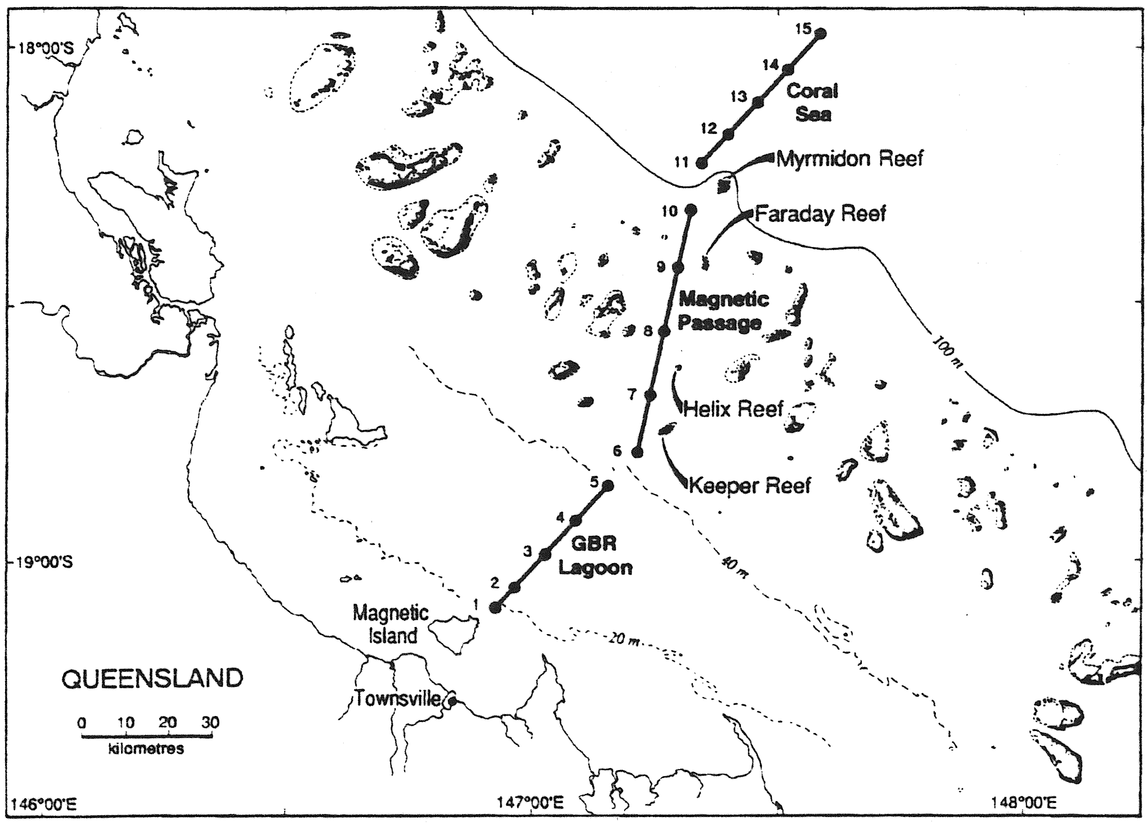

Figure 1

Map of the cross-shelf transect off Townsville, Australia, showing the position of each station along the transect. Station 1 = 19 km from Townsville, 2 = 24 km, 3 = 33 km, 4 = 43 km, 5 = 52 km, 6 = 61 km, 7 = 75 km, 8 = 92 km, 9 = 100 km, 10 = 115 km, 11 = 136 km, 12 = 145 km, 13 = 152 km, 14 = 163 km, and 15 = 172 km.

and one at 20 m below the surface. In 1991/92, an extra light-trap was added at 20 m. The anchored light-traps had an automatic timer, enabling the lights to be switched on and off automatically at predetermined periods during the night. Each light-trap on the reef fished for a total of three hours per night; lights came on for one hour at 2200 hours, 2400, and 0300 hours. Light-traps at all reefs were emptied the following day.

Squid were identified in the laboratory and the dorsal mantle length recorded for each individual. Individuals were measured within 14 days of preservation in 100% ethanol. A comparison of measurements of individuals (ranging in size from 5.3 mm to 29.5 mm) before and 14 days after preservation found that shrinkage was on average 0.5 mm.

Abundance patterns of the two *Photololigo* species during the two summers of sampling were examined by using ‘planned comparisons,’ where specific pregenerated hypotheses were examined (Day and Quinn, 1989). For each species we were interested in differences in abundance between years, locations, and depths.

To examine seasonality of juvenile *Photololigo* sp. A, the inshore station (19 km) was sampled during the austral winter months of May, June, July, and August 1991. Three sites at this station were sampled with four shallow and four deep (13-m) light-traps. Sites were sampled during the period of the new moon, on five nights in May and three nights in June, July, and August. Densities in summer and winter months were compared by using an unbalanced one-way analysis of variance (ANOVA), with month as the factor analyzed. Values in each light-trap for nights and sites within a month were treated as replicates.

To determine whether vertical migration might influence horizontal distribution patterns we examined the size structure of *Photololigo* sp. A at two depths during the night. On at least one occasion

Table 1

Total sampling effort for *Photololigo* spp. in each month in light-trap hours (and number of nights sampled) at each station during the two summers of sampling.

Year and month	Distance (km) from Townsville															Total no. sampled
	19	24	33	43	52	61	75	92	100	115	136	145	152	163	172	
1990																
Oct	8(2)	15(4)	16(4)	12(3)	16(4)	15(4)	4(1)	4(1)	4(1)	4(1)	12(3)	10(3)	10(3)	10(3)	10(3)	150(40)
Nov	12(3)	12(3)	12(3)	0(0)	16(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	4(1)	4(1)	144(35)
Dec	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	3(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	67(17)
1991																
Jan	12(3)	12(3)	12(2)	12(2)	12(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	4(2)	8(2)	8(2)	136(32)
Oct	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	124(31)
Nov	12(3)	12(3)	11(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	4(1)	4(1)	4(1)	4(1)	4(1)	139(35)
Dec	12(3)	10(3)	11(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	121(31)
1992																
Jan	12(3)	12(3)	12(3)	11(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	123(31)
Total	88(22)	93(24)	90(22)	75(18)	96(22)	87(22)	64(16)	63(16)	64(16)	64(16)	48(12)	46(12)	42(12)	42(11)	42(11)	1004(254)

in each month of the 1991/92 sampling period the 19- and 24-km stations were sampled both early and late in the night. The samples were separated into early (captured before 2400 hrs) and late (captured after 2400 hrs). By combining data from stations, across nights and months, it was possible to compare the size distributions between depths and time of night. A multiway-frequency analysis was used to determine the effect of time of night and depth on the size-frequency distribution.

Results

Distribution patterns

Juvenile *Photololigo* individuals were predominantly caught within 52 km of the mainland (Fig. 2). The few individuals found farther offshore were in the Magnetic Passage (five individuals) and on the reefs (six individuals). *Photololigo* species were not found in the Coral Sea. *Photololigo* sp. A was numerically the most abundant of the two species during both summers (Fig. 2); 856 individuals were caught in 181 hours of light-trapping (4.73 individuals caught per hour), compared with 379 *Photololigo* sp. B caught in 348 hours of light-trapping (1.09 individuals per hour). Catch per hour of light-trapping was greatest for *Photololigo* sp. A, especially at the 24-km station. The catch per unit of effort for *Photololigo* sp. B was greater at the 33-km station (Table 2). Overall, *Photololigo* sp. A juveniles were present in higher numbers at the 24-km station in the surface waters (Table 3). This pattern was consistent in both years, but higher numbers were caught in 1991/92 (Table 3), largely because of very high catches in December 1991 (Fig. 2). In comparison, highest numbers of *Photololigo* sp. B were consistently found at the 33-km station and abundance levels tended to decrease farther offshore (Fig. 2). Overall, *Photololigo* sp. B demonstrated no difference in abundance levels between the two years (Table 4). In contrast to *Photololigo* sp. A, juvenile *Photololigo* sp. B was more abundant deeper in the water column (Table 4). Farther offshore, *Photololigo* sp. B juveniles were present in very low numbers and were caught only in the deep light-traps (Fig. 2).

Photololigo sp. A ranged in size from 2.6 to 47.9 mm. The size-frequency distributions at the two depths were not significantly different between the 19-km and 24-km stations (χ^2=12.28; df=9; P=0.1979) (Fig. 3). There was no systematic change in the size-frequency distribution of *Photololigo* sp. A during either summer (Fig. 4). A modal shift in the size-frequency distribution in January 1992 suggested that fewer small individuals were available to be caught. However, catches were very low in this month.

Photololigo sp. B ranged in size from 3.6 to 61.6 mm (Fig. 3). From the size-frequency distributions it was clear that larger juveniles were found farther offshore and deeper in the water column (Fig. 3). No modal shift in the size-frequency distribution during the summers was apparent (Fig. 4). However, catches were low in most months.

The multiway-frequency analysis established that the size-frequency distribution of juvenile *Photololigo* sp. A at both depths changed as a function of time of night (Table 5). Small juveniles dominated in the surface waters, but larger individuals were generally found closer to the benthos (Fig. 5). During the night, the relative abundance of small individuals decreased at both depths. Close to the benthos an increase in large individuals was evident. There was no discernible pattern of vertical migration; however, combining data across months to increase the number of juveniles in the analysis removed the possibility of detecting vertical migration in any one month.

The number of *Photololigo* sp. A juveniles captured during the winter months was similar to most of the summer monthly catches (Fig. 6); although winter catches never reached levels such as those seen in December 1991 (Table 6). The large number of small juveniles captured over the winter (Fig. 6) indicates that *Photololigo* sp. A spawns and hatches in both seasons. A similar size range was captured at each sampling during the summer months (Fig. 7).

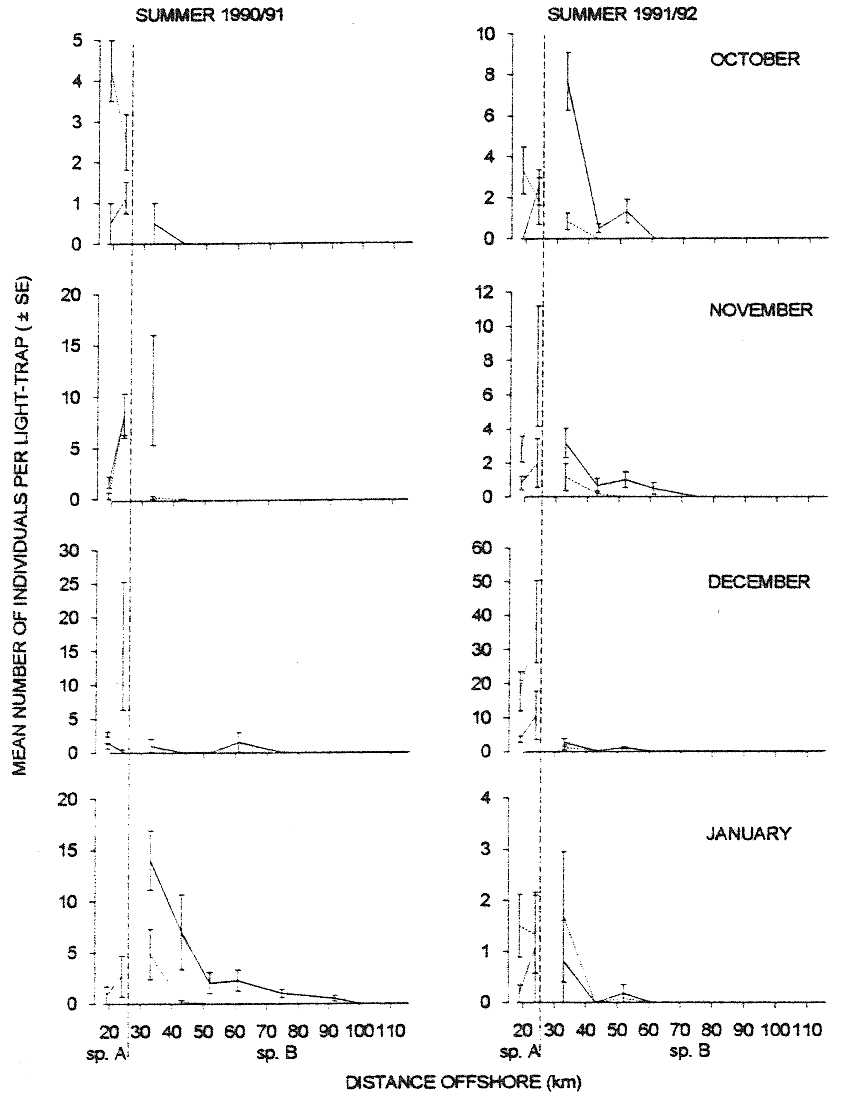

Figure 2

Catches of juvenile *Photololigo* sp. A (found at 19 and 24 km) and *Photololigo* sp. B (found at 33 km and greater) from Townsville, Australia. Most values are averages (± standard error) of six one-hour sets over three nights. See Table 1 for replicates at each station. (Solid lines, deep light-traps; dashed lines, shallow light-traps). Note the variable scale of the Y-axes.

Physical parameters

Both temperature and salinity decreased nonlinearly across the lagoon; discontinuities in both variables occurred midway across the Lagoon (Fig. 8). Temperature or salinity discontinuities were detected on at least six out of nine nights between the 33-km station and one or both of the neighbouring stations. This suggested that in the lagoon the water mass was heterogenous and may have influenced the distribution patterns of juvenile squid.

Salinity-temperature profiles of the water column at each station indicated thermoclines were present on some nights (Table 7). A thermocline was defined as a temperature change greater than 0.5°C between surface and bottom water; differences as great as 3°C were detected during January. However, these thermoclines were a temporally and spatially unstable feature of the water column, possibly due to variable wind conditions and the shallow body of water being sampled.

Discussion

Light-traps have provided a technique by which spatio-temporal distribution patterns of two *Pho-*

tololigo species can be described. Identification of *Photololigo* species using allozyme electrophoresis suggests that the two species are separated geographically across the Great Barrier Reef Lagoon (Yeatman and Benzie, in press). This separation occurs in a region of the coastal lagoon where temperature-salinity data indicate heterogeneity. High numbers of juvenile *Photololigo* sp. A at stations close to the mainland suggests that spawning grounds for this species may be close to the coast, a feature typical for loliginid squid (Mangold, 1987). Furthermore, the presence of small and large individuals during summer and winter months indicates that spawning, hatching, and recruitment are not seasonal events. This characteristic may be more common for tropical species that tend to have shorter lifespans than temperate species (Jackson and Choat, 1992). Large numbers of small juveniles collected during the winter may be a function of slower growth during the winter (Jackson and Choat, 1992). Little is known about *Photololigo* sp. B adults; however, the presence of juveniles in this region suggests that an adult population does occur in the Townsville region and that spawning occurs throughout the summer. The identification of juvenile *Photololigo* was confirmed on a subsample of specimens captured during the summer. Conclusions drawn from this study are based upon the assumption that the offshore distribution pattern of the two species was consistent in all other months of sampling.

Table 2

Catch per hour of light-trapping for each *Photololigo* species across the Great Barrier Reef Lagoon for eight months of summer sampling. *Photololigo* sp. A at stations 19 km and 24 km and *Photololigo* sp. B farther offshore.

	Species A		Species B				
Month	19km	24km	33km	43km	52km	61km	Total
1990							
Oct	2.38	1.81	0.25	0	0	0	0.62
Nov	0.75	8.25	5.42	—	0	0	2.88
Dec	1.88	8.00	0.50	0	0	0.75	2.63
1991							
Jan	0.42	1.33	9.42	3.58	1.00	1.13	2.91
Oct	1.67	2.17	4.25	0.25	0.67	0	1.50
Nov	1.83	4.83	2.17	0.42	0.50	0.25	1.67
Dec	10.67	24.42	1.92	0.17	0.50	0	6.28
1992							
Jan	0.83	1.75	1.67	0.17	0.08	0	0.75
Total	2.59	6.31	3.30	0.72	0.36	0.17	2.33

Table 3

Planned comparisons of juvenile *Photololigo* sp. A densities between depths, years, and sites.

Contrast	df	Contrast sums of squares	Mean squares	*F*-value	*P>F*
Depths	1	9.8165	9.8165	12.20	0.0006
Years	1	3.7565	3.7565	4.67	0.0320
Sites	1	8.6892	8.6892	10.80	0.0012
Residual	177	142.3838	0.8044		

Table 4

Planned comparisons of juvenile *Photololigo* sp. B densities between depths and years.

Contrast	df	Contrast sums of squares	Mean squares	*F*-value	*P>F*
Depths	1	17.0607	17.0607	37.85	0.0001
Years	1	0.0438	0.0438	0.10	0.7554
Residual	335	148.7448	0.4507		

Juvenile squid are not easily sampled with towed nets (Vecchione, 1979; Vecchione and Gaston, 1985; Holme, 1974). They have highly developed sensory and locomotor systems (Boletzky, 1974) and it is likely that these animals are often undersampled because of net avoidance. Choat et al. (1993) have shown that plankton nets select for small larval fish, but larger fish are captured from the same water column by using light attraction. Thorrold (1992), as well as this study, showed that light-traps are a useful technique for capturing juvenile squid. However, like most sampling techniques, the light-traps have biases. One problem is that light-traps sample an unknown volume of water. Nonetheless, they have

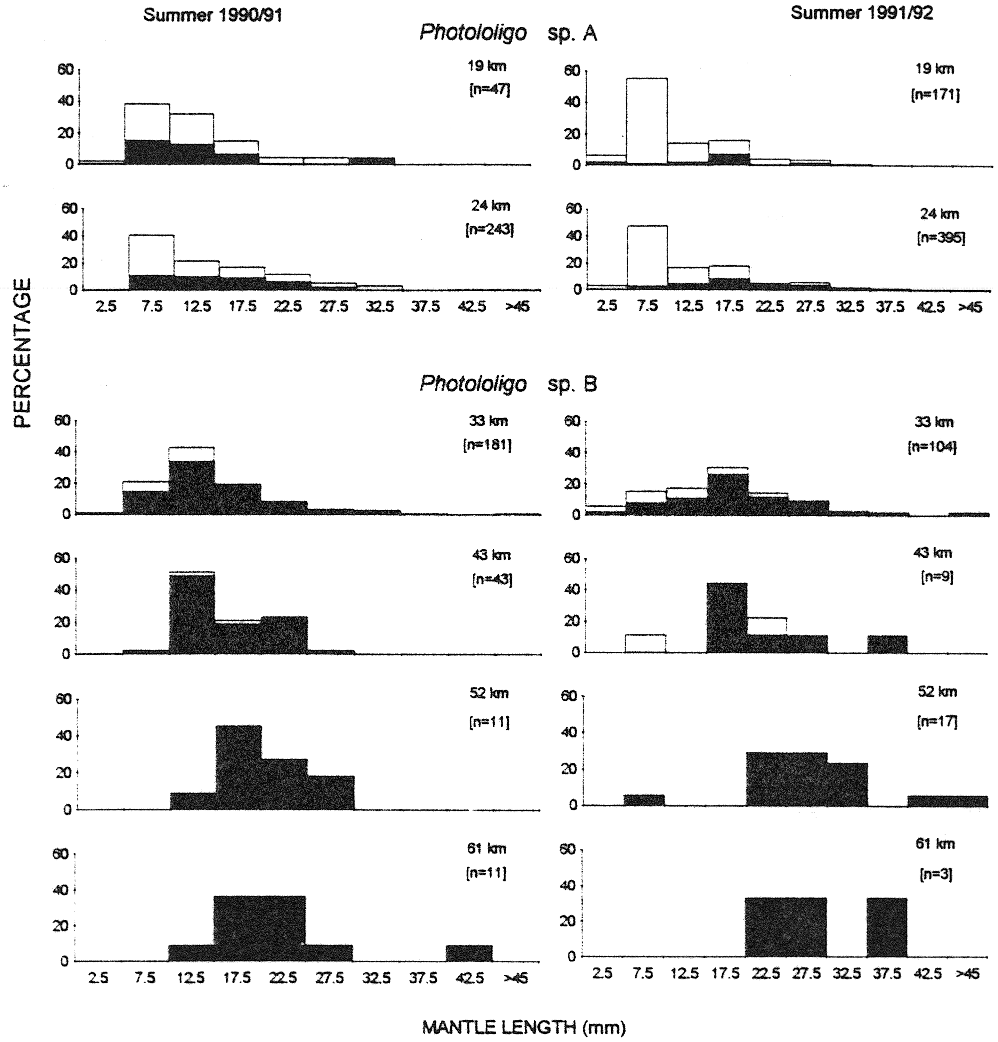

Figure 3

Size-frequency distribution of *Photololigo* sp. A and *Photololigo* sp. B caught at each station (pooled across months) in deep (shaded) and shallow (unshaded) light-traps. Total number of juveniles indicated in brackets.

Table 5

Results of the multiway frequency analysis to examine changes in the size distribution of *Photololigo* sp. A between time of night and depth.

Source	df	χ^2	*P*
Depth	1	92.8	0.00
Time	1	25.57	0.00
Depth × Time	1	0.19	0.66

been validated as useful devices for monitoring relative abundance patterns in larval supply of pelagic juvenile fish at fixed locations (Milicich et al., 1992). Great care needs to be exercised when interpreting catch rates from different locations because changes in water transparency can bias light-trap efficiency. Similarly, it is not possible to quantitatively compare catches from drifting and anchored light-traps (Thorrold, 1992). This is because the former act as lagrangian drifters and sample photopositive organisms from within a constant light pool. In contrast, the moored light-traps experience a variable water flow that may greatly increase the volume of water swept in an hour of sampling. Despite more intensive sampling on the reefs, catches of *Photololigo* were low and we conclude that spawning does not occur near the reefs and that juvenile *Photololigo* individuals are concentrated in the lagoon. In the

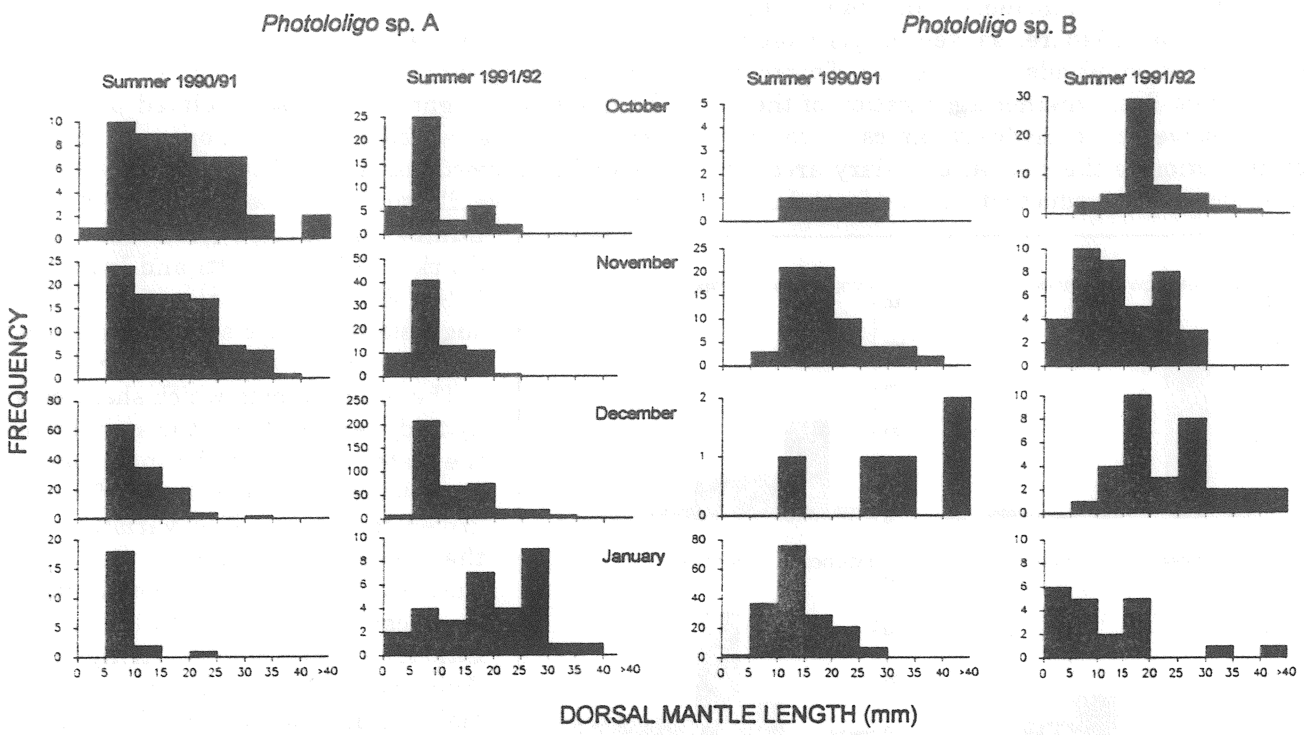

Figure 4

The size-frequency distribution of juvenile *Photololigo* sp. A and *Photololigo* sp. B during eight months of summer sampling. Size classes are mid-points of each class. Data are pooled across depths and stations.

Table 6

Analysis of variance examining differences between densities of *Photololigo* sp. A at the 19 km station between summer months of 1990/91 and 1991/92 and winter months of 1991.

Source	df	Contrast sums of squares	Mean squares	*F*-value	*P*>*F*
Month	11	1118.200	101.654	9.55	0.0001
Residual	214	2277.910	10.644		

present study, a gradient of turbidity across the shelf makes it possible that inshore catches would underestimate abundance if corrected for diminishing light-pools. However, if the error was significant, it would only exaggerate, not diminish, our observation that juvenile squid were more abundant within the coastal lagoon.

High catches of juvenile squid in the coastal lagoon were at locations where discontinuities were often observed in surface temperature and salinity. Hydrodynamic modelling of this region suggests that the coastal lagoon is often subject to velocity shear (King and Wolanski, 1992). Water in the lagoon typically flows southward under the influence of the poleward East Australian Current, which pushes water onto the outer shelf and through the reef matrix, especially through channels like the Magnetic Passage. Under typical south-easterly wind conditions the shallow body of water trapped against the coast moves in the opposite direction, northwards. The result is a velocity shear between the two water masses and a zone of low residual displacement. Modelling studies suggest that the cross-shelf location of this feature, referred to as a separation front (King and Wolanski, 1992), will shift seawards as the wind strength increases and vice versa. This mobility of the frontal region is consistent with the daily and monthly variability of salinity and temperature at the surface indicated by our physical monitoring during the second summer.

This low-shear zone is identified as a significant place for aggregation of planktonic organisms. Cross-shelf studies have shown highest abundances of larval reef fishes in a similar location near the center of the Great Barrier Reef Lagoon (Thorrold, in press). These catches included individuals taken from reefs farther offshore, as well as piscivorous larvae of various scombrids from inshore (Thorrold, 1993). It is not clear whether aggregation of these stages is passive, due to hydrodynamics, or the result of attraction to the coastal boundary area by enhanced secondary productivity in this frontal zone (Thorrold and McKinnon, 1992). This discontinuity may be a mechanism separating the two *Photololigo* species geographically. The separation of juvenile cephalopod species in the Gulf Stream east of New England is thought to be closely related to mesoscale hydrological features (Vecchione and Roper, 1986). The importance of hydrological features in aggregating juvenile squid has been identified in a number of species (Rodhouse and Clarke, 1985; Brunetti and Ivanovic, 1992; Rodhouse et al., 1992). This suggests that these areas are ecologically important for juvenile squid.

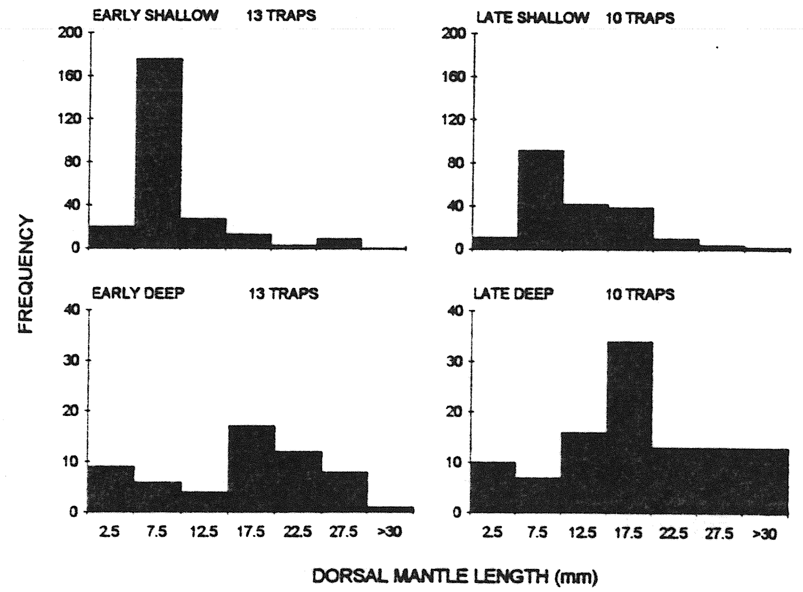

Figure 5

Size-frequency distributions of juvenile *Photololigo* sp. A from the two inshore stations at two sampling depths (pooled across the summer months 1991/92), captured early (before 2400 hr) and late (after 2400 hr) in the night.

The second way in which shelf-scale hydrodynamics affects the stability of the water column is the intrusion of upwelled waters from the shelf-break driven onto the shelf by variations in the speed and position of the East Australian Current. These cold intrusions can be tracked into the Great Barrier Reef Lagoon (King and Wolanski, 1992) and the strong thermal stratification observed in January 1992 was consistent with an intrusion at this time. A cold bottom layer at 33 km was evident on one night in November, but the inner stations were not stratified. The presence of juvenile *Photololigo* at most stations in all months, despite a range of physical conditions, suggests juvenile *Photololigo* can tolerate substantial environmental variation. This tolerance is consistent with a nonseasonal reproductive strategy, which is essential for a species that lives for only four months.

Figure 6

Catches of juvenile *Photololigo* sp. A at the 19-km station over twelve months: during summer 1990/91, winter 1991, and summer 1991/92. (Data pooled across depth and nights.)

During the night there was little evidence of a pronounced vertical migration such as the mass aggregations of juvenile *Loligo* spp. on the benthos (Vecchione and Gaston, 1985) or the general movement to the surface by juvenile *L. pealei* (Vecchione, 1981). The absence of vertical movement during the night suggests that the observed ontogenetic shift of *Photololigo* sp. B farther offshore and deeper is real and not a product of location confounded with time of night when sampling occurred. However, as was noticed in the catch-per-unit-of-effort values, both species are caught in relatively low numbers; hence, conclusions based on small differences that are not significantly different are limited. There was a problem with low numbers in all spatial and temporal trends described. However, this was a preliminary study with just two hours of sampling at each station per night. More intensive sampling in bound-

Table 7

Depth of the thermocline (m) at each station on each night of sampling during the three months of the 1991/92 summer.

Sampling period and situation	Depth of thermocline		
	Day 1	Day 2	Day 3
October 1991			
19 km	14	11	Absent
24 km	13	14	Absent
33 km	10	13	Absent
43 km	10	Absent	Absent
52 km	25	Absent	Absent
61 km	31	Absent	—
November 1991			
19 km	Absent	Absent	Absent
24 km	Absent	Absent	Absent
33 km	Absent	Absent	20
43 km	Absent	Absent	22
52 km	Absent	Absent	25
61 km	Absent	Absent	29
January 1992			
19 km	7	7	9
24 km	9	9	9
33 km	11	13	12
43 km	15	15	18
52 km	28	24	27
61 km	31	47	—

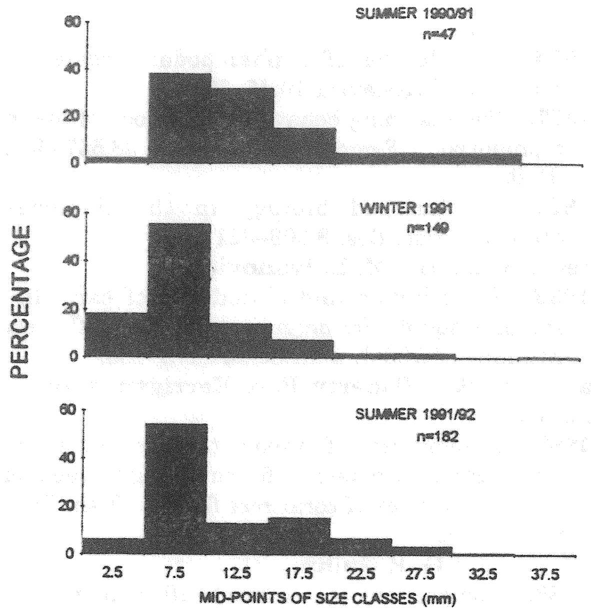

Figure 7

Size-frequency distributions of juvenile *Photololigo* sp. A at the 19-km station during the summer and winter months. (Numbers are pooled across months, depth, and nights.)

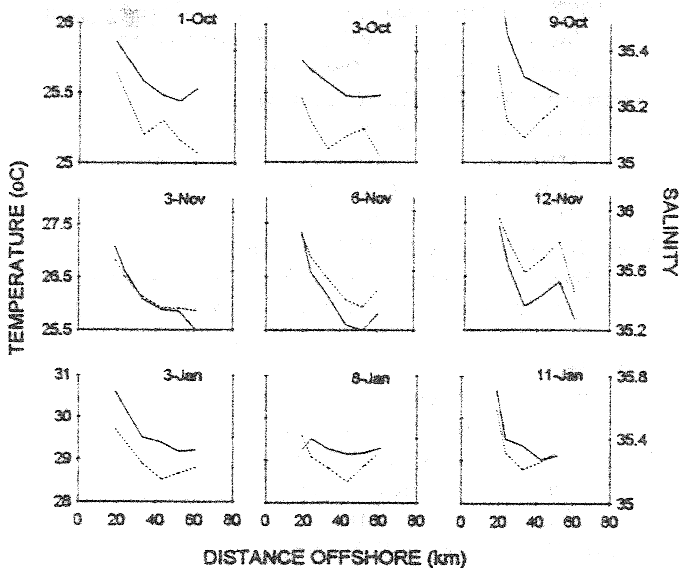

Figure 8

Surface temperature (dashed) and salinity (solid) profiles across the Great Barrier Reef Lagoon for each night of sampling in October and November 1991 and in January 1992. The Conductivity Temperature Device failed during the December cruise.

ary waters, both vertical and horizontal, is needed to understand how juvenile squid react to the physical environment. This study has shown that light-traps are useful devices for catching juvenile squid, providing a basis for a more intensive study of the early life-history of squid.

Acknowledgments

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Cross-shelf Distribution Patterns of Tropical Juvenile Cephalopods Sampled with Light-traps

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Abstract. This paper describes the cephalopod genera caught with light-traps at different locations and depths in the waters of the central Great Barrier Reef (GBR). Multiple stations were sampled in four locations: (*1*) the coastal GBR Lagoon, (*2*) inter-reef passages (Magnetic and Palm), (*3*) near-reef environments (Keeper, Helix, Faraday and Myrmidon) ranging from mid- to outer-shelf locations, and (*4*) the Coral Sea. A total of 13 cephalopod genera was caught from monthly cruises conducted from October to January of 1990–91 and 1991–92. *Octopus*, the most abundant juvenile cephalopod, was present in relatively high numbers at all shelf locations; few were caught in the Coral Sea. *Photololigo*, the most abundant squid, was rarely caught outside the GBR Lagoon. In contrast, *Sthenoteuthis*, the second most abundant squid, was caught at all locations. Deep samples from most locations were dominated by *Octopus*. *Abralia* was found only near the bottom of the GBR Lagoon; in contrast, *Euprymna*, the fourth most abundant genus, was collected only at the surface. Cephalopod communities from the GBR Lagoon had higher abundances of *Octopus*, *Photololigo* and *Abralia* compared with communities from the three other areas. Reef passages and reef locations shared similar communities, with the squid component dominated by *Sthenoteuthis*. Very low numbers of cephalopods were caught in the Coral Sea by light attraction. High concentrations of cephalopods detected in the middle of the GBR Lagoon are consistent with present knowledge about oceanographic processes over this shelf.

Introduction

Australian waters have a rich diversity of cephalopod species (Lu and Phillips 1985) that extends into the tropics (Roper and Hochberg 1987). Juveniles of these animals are a diverse and important component of the nektonic community, being both predators and prey within pelagic food chains. Despite this importance, early life histories of most cephalopods are poorly described and fundamental information is lacking.

However, juvenile cephalopods have received little attention because of difficulties in capturing and identifying many of these forms. Historically, sampling of very small cephalopods has been limited by the effectiveness of towed nets as sampling devices. Juvenile squid are agile and effective swimmers capable of evading towed nets (Vecchione 1987) and a size range of juveniles can be obtained only by using multiple net gears (Rodhouse *et al.* 1992). Logistically, it is difficult to sample more than one location at a time with towed nets and hence synoptic views of spatial distribution usually ignore the temporal component in the data collection. This is no problem when distribution and abundance patterns are static, but juvenile squid distributions are often determined by current systems (Dawe and Beck 1985). Furthermore, net-induced damage suffered by small soft-bodied specimens hinders identification of specimens (Vecchione 1987). Automated light-traps (Doherty 1987) provide an alternative solution to both of these problems and allow juvenile cephalopods in good condition to be sampled through time at multiple locations (Thorrold 1992). Thorrold (1992) used light-traps to sample significant numbers of lologinid [*sic*] squid from the inner half of the Great Barrier Reef (GBR) Lagoon adjacent to Townsville. This study, although based on similar technology, expanded the horizontal and vertical scale of the sampling, which resulted in a greater diversity of cephalopods being caught.

The aim of this study was to describe the distribution and relative abundance of genera in the juvenile cephalopod community sampled by light attraction. The programme was based on regular sampling of cross-shelf locations: from turbid coastal to clear oceanic environments, both close to and far from reefs to include maximum contrast. This study describes cross-shelf and vertical distribution patterns to provide the spatio-temporal framework for designing further work on the local dynamics or regional patterns of specific taxa.

Materials and Methods

Sampling was based on repeated sampling within four major cross-shelf locations near Townsville (Fig. 1) with the aid of light-traps of similar design to those of Doherty (1987). The four locations were:

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(1) GBR Lagoon. This is a 56-km-wide stretch of open water between the mainland and the offshore reef matrix. This location is shallow (15–40 m) with a gently sloping soft bottom habitat. The hydrodynamics of the GBR Lagoon are complex as a result of oceanic influences at its outer boundary and coastal influences at its inner boundary. The most prominent features relevant to this study are *(i)* vertical stratification arising from cold-water intrusions at the shelf break and *(ii)* horizontal velocity shear in the middle of the lagoon (Wolanski and Ridd 1990). Both features are unstable over time and their exact manifestation depends on the interaction of several driving forces, most notably the East Australian Current in the Coral Sea and wind stress on the shallowing water column near the coast (Wolanski 1994).

(2) Reef Passages. Two broad, relatively deep passages (Magnetic and Palm) dissect the reef matrix in the Townsville region of the GBR. Both provide major conduits for semi-diurnal tidal waves that oscillate perpendicular to the coast (Dight *et al.* 1990*b*). When the East Australian Current meanders close to the shelf break, upwelling can occur and cold intrusions can be forced along the bottom of the passages, occasionally extending well into the GBR Lagoon (Andrews and Gentien 1982).

(3) Coral Reefs. Four reefs (Keeper, Helix, Faraday and Myrmidon) of similar sizes but different cross-shelf locations were selected to represent shallow near-reef environments. All four are located on the southern side of the Magnetic Passage and are exposed to the same dominant flows between lagoon and ocean.

(4) Coral Sea. Waters beyond the shelf break, where depths exceed 1000 m, were sampled to determine which cephalopod taxa are associated with oceanic waters and to monitor exchange between coastal and oceanic habitats.

Each location needed to be sampled in a way appropriate to its physical nature. The open-water locations (GBR Lagoon, reef passages and Coral Sea) were sampled by drifting light-traps at five different stations, whereas waters near the coral reefs were sampled by anchored light-traps at three different stations within 100 m of the reef crest on the downstream side (Moltschaniwskyj and Doherty 1994). The importance of this difference is that water around anchored light-traps can be exchanged by local current patterns, leading to larger swept volumes per hour of operation compared with the drifting light-traps, which should fish the same body of water. Table 1 summarizes the sampling strategies used at each location. To determine the vertical distribution of juvenile cephalopods in the water column, light-traps were suspended at two depths: surface and subsurface. In 1990–91, the subsurface light-traps were deployed at 20 m at all stations. In 1991–92, the subsurface light-traps were deployed within 3 m of the bottom, except in the Coral Sea where the maximum depth of deployment was 100 m. In both years, subsurface light-traps anchored near reefs were set at 20 m.

All sampling was carried out during 10-day periods centred on the new moons of October, November, December and January of 1990–91 and 1991–92. Stations in the GBR Lagoon, passages and Coral Sea were sampled for a maximum of three nights during each period. Water masses near the reefs were sampled for a maximum of nine nights during each of those months. By the end of the first summer of sampling, it was clear that cephalopod catches in the Coral Sea were very low and that other locations justified more sampling effort. Hence, sampling effort was reduced offshore and increased elsewhere, notably by adding the Palm Passage (in 1991–92 only). Throughout the sampling, weather resulted in occasional abandonment of stations and/or locations, with greatest effect in December 1990 (Moltschaniwskyj and Doherty 1994). Table 2 shows the total fishing effort at each location and depth.

Replication at each open-water station was provided by simultaneously deploying two light-traps at each depth spaced several hundred metres

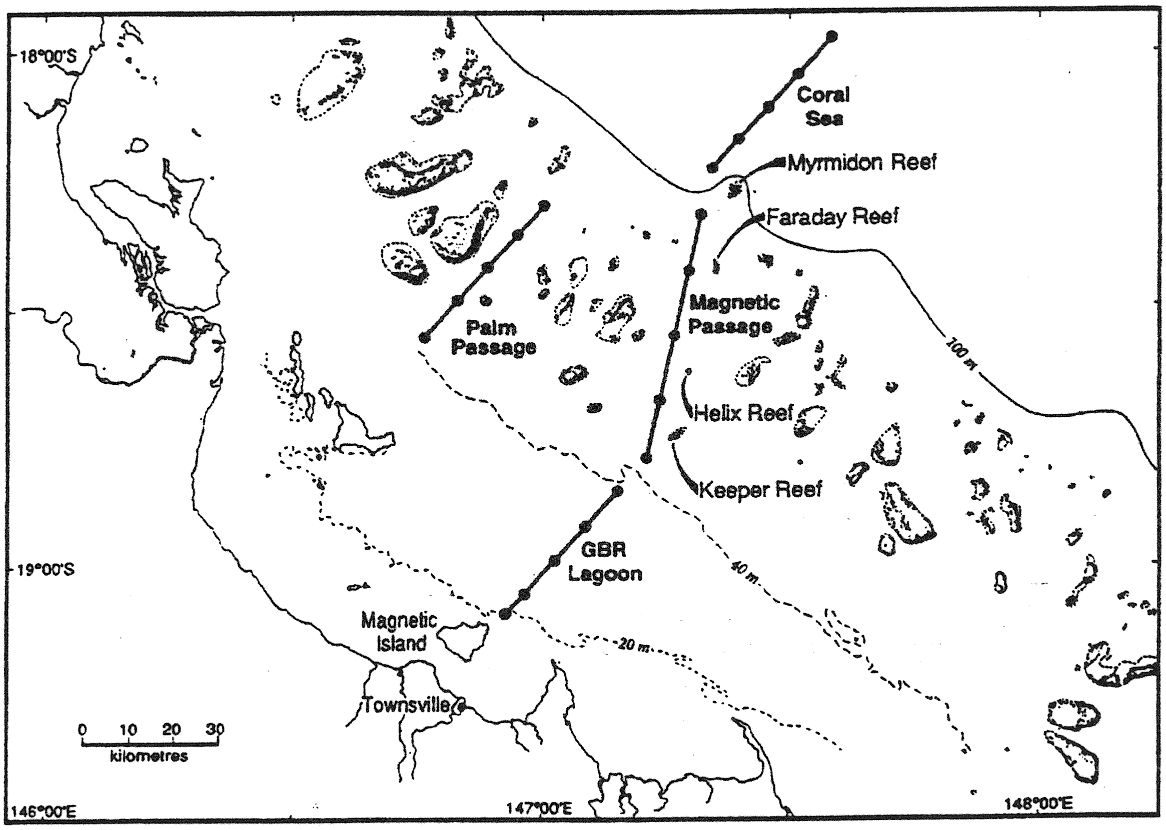

Fig. 1. Continental shelf off Townsville, showing the locations of samples collected with drifting light-traps (four open-water locations) and anchored light-traps (four named reefs).

Table 1. Sampling programme in each location

Location	No. of stations	Light-traps	1990–91		1991–92	
			Depth (m)	No. of traps	Depth (m)	No. of traps
GBR Lagoon	5	Drifting	0	2	0	2
			20	2	Near bottom	2
Passages	5^A (10^B)	Drifting	0	2	0	2
			20	2	Near bottom	2
Reefs	4	Anchored	0	2	0	3
			20	1	20	2
Coral Sea	5	Drifting	0	2	0	2
			20	2	100	2

[A] 1990–91.

[B] 1991–92 (Palm Passage was not sampled in 1990–91).

Table 2. Total fishing effort (in light-trap hours) at each location and depth, pooled across the two summers

Location	Subsurface	Surface
GBR Lagoon	220	219
Passages	225	226
Reefs	311	613
Coral Sea	114	113

apart. Each night, the light-traps were deployed by 1930 hours (Eastern Standard Time). Light-traps were retrieved after 1 h of fishing and the catch was processed while the ship was moving to the next station. The last light-trap had to be recovered by 0530 hours, which meant that it was only possible to sample five stations per night owing to the distances between the stations. Because stations in each location were sampled sequentially within nights, time of night is confounded with station within a location. Likewise, only one location could be sampled in a night, hence location is confounded with nights within cruises. These effects were minimized, to some degree, by haphazardly selecting the order of locations within cruises. The order in which the stations were sampled within locations could not be random because of the distances involved. Consequently, stations in each location were sampled consecutively either towards or away from the coast. The choice of directions was haphazard within cruises but balanced over the whole design. Replication in the near-reef waters consisted of surface and subsurface light-traps anchored on the southern reef slope to standardize position with respect to water flow. All anchored light-traps at each reef fished for a total of 3 h per night (between 2100 and 2200 hours, between 2400 and 0100 hours, and between 0300 and 0400 hours) to reduce the confounding effects of tide and time (Doherty 1987).

Temperature and salinity profiles at each station were obtained with a Seabird conductivity–temperature device during the cruises in October, November and January 1991–92. The temperature–salinity data were used to determine if a temperature and salinity gradient occurred across the GBR Lagoon. To allow the data to be combined across months, the data were standardized for monthly changes in these parameters. Deviations of temperature and salinity for each station were calculated from the pooled average for each month and the deviations averaged over time.

Specimens were fixed and preserved in 100% ethanol and identification of the cephalopods was undertaken in the laboratory. Given the taxonomic problems associated with juvenile cephalopods, specimens were identified to genus. Dr C.C. Lu (Victoria Museum, Australia) identified sample specimens for a reference collection that was used for all subsequent identifications. Terminology describing the pre-adult phase of cephalopods has recently been defined (Young and Harman 1989) and the term 'juvenile' is used here to describe the stage between hatching and sub-adult.

Multivariate techniques were used to analyse the relationships between cephalopod genera and locations. These techniques are useful when it is necessary to examine relative abundance patterns of assemblages rather than component taxa. Multivariate analysis of variance (MANOVA) determined the effects of location, depth and their interaction on the composition of the cephalopod communities. The data were examined for multivariate normality and homogeneity of variances (Multivariate Levene's Test). Raw values were transformed ($\log_{10}+1$) before analysis to emphasize the relative abundances of the different genera instead of their absolute numbers. The MANOVA was followed by a canonical discriminant analysis (CDA) to determine which cephalopod genera were associated with different locations and depths.

Results

In all, 3862 juvenile cephalopods representing 13 genera, including sepioids, myopsids, oegopsids and octopods, were caught with light-traps during the two summers of sampling. The two most abundant genera were *Octopus* and *Photololigo* (Table 3). Half of the genera were very rarely caught, especially *Sepia*, *Pyroteuthis*, *Abraliopsis*, *Argonauta*, *Pterygioteuthis* and *Onkyia*.

The diversity of juvenile cephalopods was similar in the GBR Lagoon, the passages and the reefs. In the Coral Sea, few juvenile cephalopods were captured and the diversity was low; *Sthenoteuthis* and *Octopus* were both caught off the shelf, but in very low numbers. An examination of the total number of juvenile cephalopods found that the pattern of catches from subsurface light-traps was consistent over the two years, despite different protocols. Consequently, data from the subsurface light-traps were pooled across years. Numbers of juvenile cephalopods varied as a function of an interaction between location and depth (Table 4). The interaction was detected because in the Coral Sea there was no difference in the catches between depths, but in the other locations higher numbers of cephalopods were caught at greater depths (Fig. 2). Highest catches of juveniles were taken in the GBR Lagoon, especially from subsurface

Table 3. CPUE (number of cephalopods caught per light-trap hour) at each depth–location combination
Data have been pooled across years. CPUE < 0.01 indicated by an asterisk. Zero catch indicated by a dash

Genus	Total number	GBR Lagoon		Reefs		Passages		Coral Sea	
		Surface	Subsurface	Surface	Subsurface	Surface	Subsurface	Surface	Subsurface
Octopus	2066	0.57	4.57	0.51	1.49	0.05	0.64	0.02	0.07
Sepiola	27	0.01	0.01	*	0.05	*	0.02	—	—
Euprymna	117	0.18	*	0.09	0.03	0.04	—	0.03	—
Photololigo	1314	3.16	2.69	*	0.01	—	0.10	—	—
Sepioteuthis	83	0.18	—	0.03	0.07	0.02	—	—	—
Abralia	57	—	0.12	*	0.07	*	0.02	—	—
Abraliopsis	2	—	—	—	0.01	—	—	—	—
Pyroteuthis	1	—	—	—	—	—	—	*	—
Pterygioteuthis	1	—	*	—	—	—	—	—	—
Sthenoteuthis	182	0.17	0.02	0.09	0.11	0.10	0.05	0.10	0.02
Onkyia	6	*	—	*	*	—	—	*	—
Sepia	1	—	—	*	—	—	—	—	—
Argonauta	5	—	—	*	—	—	—	—	—
Total	3862	936	1630	458	573	50	187	18	10

Table 4. Analysis of variance table, examining the catch of juvenile cephalopods as a function of depth and location
Data pooled across years

Source	d.f.	Sums of squares	Mean square estimates	*F*	*P* > *F*
Location	3	51.729	17.243	173.89	0.0001
Depth	1	1.703	1.703	17.17	0.0001
Location * Depth	3	1.237	0.412	4.16	0.0060
Error	2030	201.592	0.0992		

Table 5. Analysis of variance table, examining the number of juvenile cephalopods caught at the four different stations within the GBR Lagoon
Data pooled across years

Source	d.f.	Sums of squares	Mean square estimates	*F*	*P* > *F*
Distance	4	10.713	2.678	12.24	0.0001
Error	434	94.940	0.219		

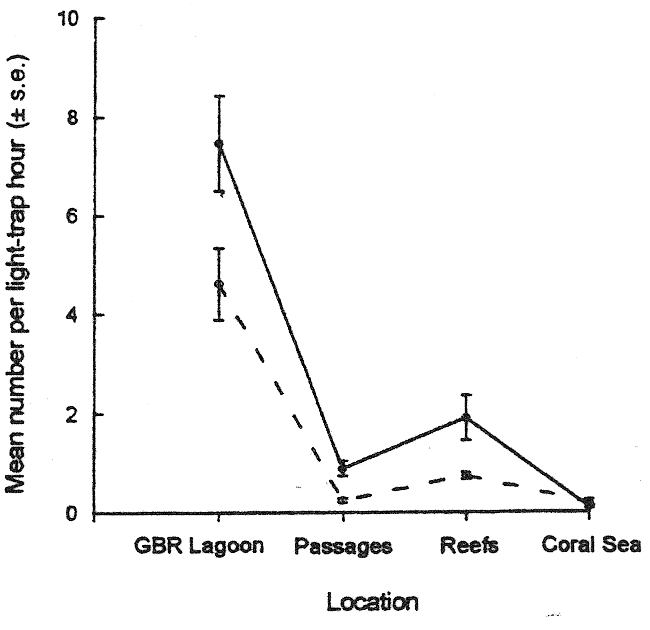

Fig. 2. CPUE (average number of cephalopods captured per light-trap hour) at four sampling locations and two depths. Solid line, subsurface; dashed line, surface.

light-traps (Fig. 2). Catches from the reefs and passages were lower than those in the GBR Lagoon, but the relative proportion of cephalopods between depths remained the same, with highest catches deeper in the water column (Fig. 2).

Catches among stations in the GBR Lagoon were significantly different (Table 5). Low numbers of cephalopods were caught on both edges of the GBR Lagoon, with elevated abundances at two stations (24 and 33 km) in the middle (Fig. 3). Clear temperature and salinity gradients were also evident across the GBR Lagoon (Fig. 4). Surface water temperature and salinity at the two stations closest to the coast were consistently higher than the average values for the GBR Lagoon. Further offshore, surface water parameters were lower than the average.

Octopus, the most abundant of all the juvenile cephalopods, was present at all locations, although rare in the Coral Sea. *Octopus* juveniles were considerably more abundant in subsurface light-traps within each location and highest catches were taken in the GBR Lagoon (Table 3). Owing to its numerical abundance, this genus greatly influenced patterns of total juvenile abundance between locations and depths. Among the squid, *Photololigo* was also very abundant in the GBR Lagoon, but low numbers were caught around the reefs and in the passages. In contrast to *Octopus*, *Photololigo* was more common in surface waters of the GBR Lagoon (Table 3). The other 11 genera were caught in relatively low numbers. *Sthenoteuthis*, the second most abundant squid, was ubiquitous throughout the areas sampled and was the only species caught with any consistency in the Coral Sea. The sepioid *Euprymna*, the fourth most abundant genus, was predominantly caught at the surface in the GBR Lagoon, passages and reefs.

Multivariate analyses were carried out for the most abundant genera: *Octopus*, *Photololigo*, *Sthenoteuthis*, *Euprymna*, *Sepioteuthis* and *Abralia*. It was evident that the distribution of juvenile cephalopods was specific to depth and location as indicated by a significant location–depth interaction (Pillai's Trace = 0.466; F = 24.4786; d.f. = 42, 12198; P = 0.0001). Most of the differences in juvenile cephalopod composition occurred between the GBR Lagoon and the other three locations (Fig. 5). In particular, the GBR Lagoon was clearly discriminated owing to high numbers of *Octopus* and *Photololigo*. The other locations appeared to be very similar (Fig. 5). A second factor that explained some of the variation among the location–depth combinations was depth (Fig. 5). In particular, the GBR Lagoon exhibited different communities of cephalopods at the two depths. This major difference was largely due to *Abralia* (Table 3). *Abralia* and *Octopus* were dominant in samples caught in the subsurface light-traps in the GBR Lagoon, passages and reefs. *Octopus* was also caught predominantly in subsurface light-traps, whereas the sepioid *Euprymna* was caught predominantly in the surface light-traps (Table 3). *Photololigo*, *Sepioteuthis* and *Sthenoteuthis* were more commonly found in surface light-traps, but these genera were also relatively abundant in catches from subsurface light-traps (Table 3). The depth distribution of *Sepioteuthis* was dependent upon the location; they were present in subsurface samples at the reefs and surface light-traps in the GBR Lagoon. The remaining variation in the data was

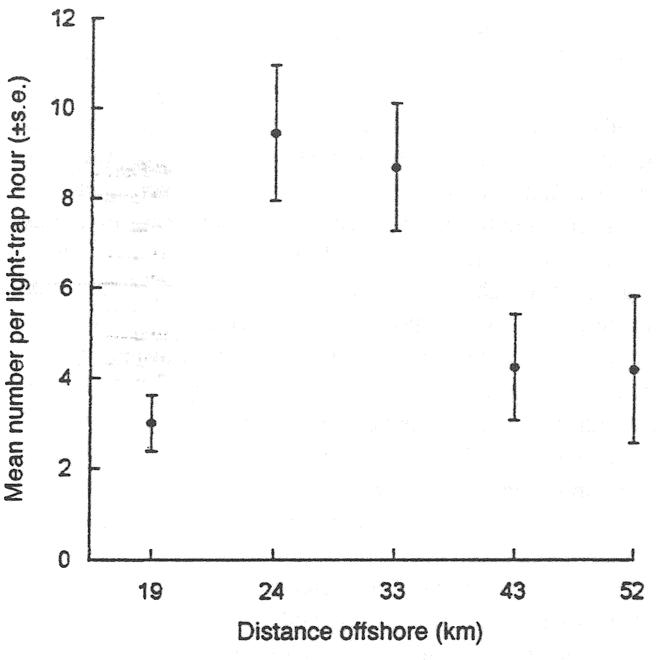

Fig. 3. CPUE of cephalopods within the five stations of the GBR Lagoon. Data pooled across depths.

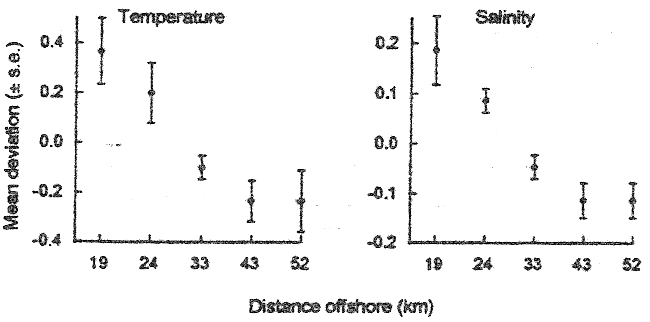

Fig. 4. Spatial patterns in physical parameters across the GBR Lagoon, standardized for monthly differences (see text for calculation method). Standard errors expressed across three months.

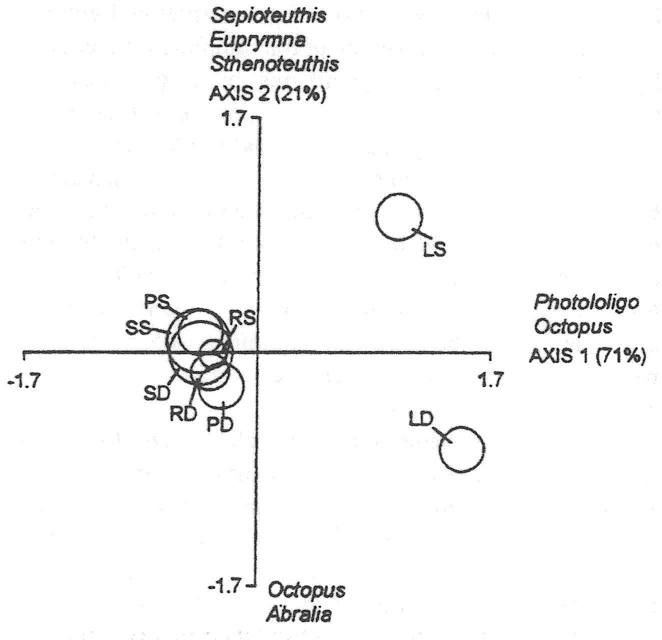

Fig. 5. Results of canonical discriminant analysis, showing the relationship of each area–depth combination on the first two discriminant axes. Values plotted are means and 95% confidence intervals of canonical scores for each location–depth combination. LS, GBR Lagoon surface; LD, GBR Lagoon subsurface; PS, passages surface; PD, passages subsurface; RS, reefs surface; RD, reefs subsurface; SS, Coral Sea surface; SD, Coral Sea subsurface.

described by a further four axes. Although the analysis indicated that Axes 3 and 4 explained statistically significant variation, it was decided that 4.4% and 2.3% (for Axes 3 and 4 respectively) of the variation was unlikely to be biologically important in this data set.

Discussion

This study demonstrates that submersible light-traps can be useful alternative sampling devices to assess the relative abundance of some cephalopod species. Juvenile cephalopods from 13 genera were caught by active attraction instead of passive collection. Although no independent assessment is available to show that all the available diversity was sampled, clearly a wide range of taxa show responses to light that can be exploited to determine their relative abundances. Both *Octopus* and *Photololigo* were caught in sufficient numbers to allow the examination of temporal and spatial distributions in more detail (Moltschaniwskyj and Doherty 1994). The live state of all material collected by this method also demonstrates the usefulness of light-traps to provide material for physiological and behavioural investigations not previously possible.

Deployment of light-traps in drifting and anchored modes made it possible to sample a wide a range of habitats from coastal to oceanic conditions, near and far from reefs. However, there must be caution when interpreting light-trap catch rates. Little is known about the sampling efficiency of light-traps. However, comparisons of catch rates can provide a useful index of relative abundance. Although this is adequate for many questions about recruitment and juvenile supply, such comparisons depend on unchanging efficiency. This is less of a problem when sampling the same place over time (e.g. Milicich *et al.* 1992), but it can become a problem when sampling a wide range of locations, as in this study. This assessment has not been tested for cephalopods, but the following arguments suggest that the patterns shown here were not caused by differential catching efficiency of the light-traps.

By including pelagic and near-reef habitats, this study deployed light-traps in water conditions ranging from shallow coastal turbid water to deep oceanic transparent water (Wolanski 1994). Therefore, biases in light-trap efficiency due to water clarity would predict better performance in clearer water. Thus, any species demonstrating increasing abundance away from the mainland could provide an ambiguous case. None of the species sampled in this study showed this pattern and highest catches were from lagoonal stations close to the coast. Although these may be biased estimates of abundance, it is likely that the inshore samples underestimated the true densities, therefore resulting in a greater difference between inshore and offshore patterns than was identified in this study. Accordingly, we do not believe that variable light-trap efficiency among different water masses contributed to the qualitative patterns of abundance observed.

Since different modes of deployment were necessary to sample habitats near and far from reefs, caution is needed when comparing catch rates from drifting and anchored light-traps. Thorrold (1992) showed that drifting light-traps catch higher numbers of fish in open water than do anchored ones, implying that current speed past the light-traps affected capture efficiency. However, data were not presented for squid and it is not clear if this result was due to the presence of small fish, which are typically poor swimmers. Even if this was true for squid, real abundances may have been underestimated in near-reef habitats when sampling was deliberately spread over three sampling periods of each night to include periods of tidal flow and slack. The extent to which this was offset by the longer period of sampling by light-traps each night in the near-reef habitat and the exposure to greater volumes of water is unknown and is unlikely to be simple. However, anchored light-traps have been very successful in capturing juveniles of reef fish (Milicich 1992; Milicich *et al.* 1992), which suggests that light-traps behave differently in open water and near-reef water, possibly as a function of current systems. To compare cephalopod communities in the different locations, we have emphasized relative abundances of cephalopod genera rather than absolute comparisons. In this respect, light-traps captured similar cephalopod genera on the reefs and in the adjacent passages; few differences were detected in the relative abundances of cephalopod genera.

The greatest differences detected by this study were those related to cross-shelf location and depth. The Coral Sea yielded sparse catches of cephalopods, with only the oceanic genus being caught with any consistency. In contrast, reasonably high numbers of juvenile ommastrephid squids have been caught in oceanic waters off the eastern Australian coast with towed nets (Dunning 1985). However, comparison between this study and Dunning's is difficult given the geographic difference. Therefore, apart from *Sthenoteuthis*, which was ubiquitous and able to tolerate a wide range of conditions, the Coral Sea appears not to provide suitable nursery conditions for any shelf taxa. This may be due to the oligotrophic status of the East Australian Current that dominates this habitat or the selective disadvantage imposed by rapid southward advection in this strong boundary current. Most genera sampled by this study complete their early life history on the continental shelf, where there was no evidence that the coral reef habitat or passages contained any unique assemblages.

Although highest diversity occurred in near-reef waters, the GBR Lagoon yielded the highest catch rates for the six most abundant genera. High numbers of juvenile cephalopods in the middle of the GBR Lagoon (24 to 33 km offshore) suggest that juveniles in this area either have better survivorship or are aggregating here, actively or passively. High numbers of juvenile cephalopods have also been caught in this area with towed nets (Jackson 1986) and light-traps (Thorrold 1992*a*). There is a shear zone in this region of the GBR Lagoon, produced by the interaction of a coastal boundary water mass and the East Australian current (Wolanski 1981; Wolanski and Ridd 1990). Differences in the surface water temperatures and salinities across the GBR Lagoon indicated that this interaction of the two water masses was occurring midway across the GBR Lagoon during this study. High secondary productivity (Sammarco and Crenshaw 1984; Thorrold and McKinnon 1992) and high densities of juvenile and larval fish (Thorrold 1992*b*) suggest that this area is important biologically and hydrodynamically. Given that juvenile squid are able to feed exogenously within hours of hatching (Boucher-Rodoni *et al.* 1987), the higher secondary production of the GBR Lagoon would provide feeding grounds suitable for rapidly growing predators. Boundary regions have been identified as areas in which juvenile cephalopods are an important component of the nektonic community (Reid *et al.* 1991; Rodhouse *et al.* 1992). The interactions of cephalopods in this community are not recognized and these areas may determine growth and survivorship of juvenile squid.

The presence of a juvenile cephalopod community characteristic of specific locations and depths has interesting implications for the dispersal of juveniles to and away from adult populations. The location and depth occupied by juveniles will modify the extent and rate of dispersal, thereby determining growth rates and recruitment patterns (O'Dor and Coelho 1993). During the summer, the longshore current is predominantly southward; however, closer to the coast in shallower water (<40 m), water movement is more restricted than it is on the outer shelf (Williams *et al.* 1984). Dispersal rates and extent will also be affected by the depth in the water column; closer to the bottom, dispersal will be more restricted than it is at the surface (Williams *et al.* 1984; Dight *et al.* 1990*a*). Given the complex nature of hydrology interacting with topography, it is difficult to speculate on the sources of juveniles. Generally, the trend is for movement southward and inshore according to modelling of the dispersion of passive particles (Dight *et al.* 1990*b*). Consequently, it is possible that juvenile cephalopods in the outer GBR Lagoon have come from adult populations offshore and to the north. Since water movement is restricted across the shelf, the dispersal of juvenile pelagic organisms across the shelf will be limited (Williams *et al.* 1984; Dight *et al.* 1990*b*). Therefore, the observed cross-shelf patterns of abundance of different genera may be a function of species-specific spawning areas across the shelf. Such distinct cross-shelf patterns of species have been described for larval flathead (Andrews 1982), juvenile *Photololigo* (Moltschaniwskyj and Doherty 1994) and zooplankton communities (Sammarco and Crenshaw 1984).

This is the first study that has used automated light-traps to examine communities of juvenile cephalopods from a wide range of taxa. The use of light-traps to describe spatial and temporal abundances of pelagic organisms is still relatively new (Doherty 1987). Ecological investigations of the juvenile phase of both pelagic and benthic cephalopods require the capture of juveniles over a variety of locations and in different water conditions. Catches of cephalopods were often very low, making generalizations about spatial patterns difficult. However, a sampling programme concentrating on regions of importance, such as the GBR Lagoon, is now possible in the future. Jackson (1986) did 161 h of net tows in the GBR Lagoon and captured a total of 969 individuals in seven taxonomic groups. In comparison, this study captured 936 individuals in seven genera in 219 h of sampling surface waters of the GBR Lagoon. The major difference in the individuals caught was that light-traps catch larger juveniles (Thorrold 1992; Moltschaniwskyj and Doherty 1994). Therefore, light-traps are a successful and useful technique to capture juvenile cephalopods that have eluded other methods used in this region (Jackson 1986). Furthermore, identification of areas where high densities of zooplankton, teleosts and cephalopods occur provides an exciting opportunity to investigate community interactions involving juvenile cephalopods, particularly from the perspective of squid predator–prey interactions.

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Appendix 2A. Relative abundance of the 20 most abundant families collected from the GBR Lagoon (Stations 1-5) in three consecutive years of sampling.

	1990/1991		1991/1992		1992/1993
1630	Clupeidae	4334	Clupeidae	9664	Engraulidae
884	Pomacentrinae	2104	Engraulidae	3406	Clupeidae
751	Scombridae	1906	Scombridae	2579	Scombridae
255	Engraulidae	1650	Pomacentrinae	1689	Pomacentrinae
135	Carangidae	397	Carangidae	776	Siganidae
134	Priacanthidae	355	Priacanthidae	717	Lethrinidae
114	Trichiuridae	263	Siganidae	449	Priacanthidae
113	Bregmacerotidae	164	Synodontidae	182	Carangidae
84	Lethrinidae	108	Lethrinidae	137	Synodontidae
67	Siganidae	65	Chrominae	98	Chrominae
56	Synodontidae	63	Bregmacerotidae	53	Mullidae
35	Mullidae	60	Mullidae	49	Bregmacerotidae
19	Chrominae	45	Trichiuridae	38	Caesionidae
19	Blennidae	33	Chaetodontidae	27	Serranidae
13	Monocanthinae	31	Blennidae	26	Trichiuridae
12	Syngnathidae	29	Apogonidae	23	Gerreidae
11	Caesionidae	23	Gobiidae	18	Blennidae
10	Apogonidae	22	Serranidae	14	Monocanthinae
10	Labridae	21	Holocentridae	13	Apogonidae
10	Dactylopteridae	17	Dactylopteridae	12	Chaetodontidae

Appendix 2B. Relative abundance of the 20 most abundant families collected from the Magnetic Passage (Stations 6-10) in two consecutive years of sampling.

1990/1991		1991/1992	
433	Pomacentrinae	854	Carangidae
243	Carangidae	681	Pomacentrinae
62	Clupeidae	327	Gobiidae
62	Scombridae	165	Clupeidae
41	Labridae	99	Chrominae
40	Apogonidae	82	Scombridae
40	Mullidae	73	Blennidae
38	Gobiidae	42	Labridae
33	Bregmacerotidae	27	Apogonidae
29	Lethrinidae	24	Caesionidae
28	Blennidae	20	Priacanthidae
28	Chrominae	18	Lethrinidae
20	Holocentridae	17	Synodontidae
13	Syngnathidae	16	Bregmacerotidae
10	Dactylopteridae	15	Mullidae
8	Pseudochromidae	15	Holocentridae
7	Myctophidae	8	Engraulidae
6	Nomeidae	8	Trichiuridae
5	Synodontidae	7	Siganidae
4	Plesiopidae	5	Scaridae

Appendix 2C. Relative abundance of the most abundant families collected from the Coral Sea (Stations 11-15) in two consecutive years of sampling

1990/1991		1991/1992	
313	Myctophidae	35	Myctophidae
36	Holocentridae	10	Pomacentrinae
10	Clupeidae	7	Holocentridae
9	Scombridae	1	Clupeidae
7	Pomacentrinae	1	Bregmacerotidae
3	Bregmacerotidae	1	Chrominae
3	Mullidae	1	Gobiidae
3	Synodontidae	1	Balistinae
1	Chaetodontidae		
1	Exocoetidae		
1	Chrominae		
1	Acanthuridae		
1	Muraenidae		
1	Bothidae		
1	Carangidae		

Appendix 2D. Relative abundance of the 20 most abundant families collected from Keeper Reef in two consecutive years of sampling.

	1990/1991		1991/1992
4889	Clupeidae	14256	Pomacentrinae
3252	Pomacentrinae	11783	Clupeidae
1077	Apogonidae	5131	Chrominae
508	Chrominae	1893	Apogonidae
390	Monocanthinae	369	Blennidae
175	Blennidae	274	Gobiidae
164	Carangidae	258	Monocanthinae
162	Atherinidae	198	Microdesmidae
75	Gobiidae	133	Synodontidae
47	Synodontidae	127	Bregmacerotidae
44	Caesionidae	121	Carangidae
38	Bregmacerotidae	117	Atherinidae
37	Nomeidae	77	Nomeidae
35	Syngnathidae	59	Schindleriidae
17	Sphyraenidae	33	Nemipteridae
15	Plesiopidae	24	Syngnathidae
12	Siganidae	22	Acanthuridae
12	Holocentridae	19	Scorpaeninae
7	Scorpaeninae	18	Caesionidae
6	Pseudoplesiopidae	16	Labridae

Appendix 2E. Relative abundance of the 20 most abundant families collected from Helix Reef in two consecutive years of sampling.

1990/1991		1991/1992	
12044	Clupeidae	3584	Clupeidae
2411	Pomacentrinae	1678	Pomacentrinae
327	Apogonidae	858	Monocanthinae
239	Atherinidae	353	Apogonidae
151	Monocanthinae	266	Blennidae
149	Chrominae	224	Chrominae
146	Blennidae	123	Bregmacerotidae
98	Nomeidae	84	Carangidae
39	Gobiidae	68	Atherinidae
23	Carangidae	59	Gobiidae
22	Synodontidae	57	Nomeidae
16	Holocentridae	46	Holocentridae
10	Labridae	36	Synodontidae
6	Scorpaeninae	17	Caesionidae
6	Lethrinidae	17	Lethrinidae
6	Pseudochromidae	15	Pempheridae
5	Pempheridae	11	Labridae
3	Caesionidae	9	Myctophidae
2	Grammistidae	8	Microdesmidae
2	Mullidae	6	Siganidae

Appendix 2F. Relative abundance of the 20 most abundant families collected from Faraday Reef in two consecutive years of sampling.

1990/1991		1991/1992	
5112	Clupeidae	5126	Pomacentrinae
645	Pomacentrinae	2905	Clupeidae
246	Apogonidae	1242	Chrominae
225	Chrominae	967	Blennidae
117	Atherinidae	897	Apogonidae
106	Nomeidae	287	Atherinidae
74	Blennidae	135	Gobiidae
43	Gobiidae	60	Scorpaeninae
37	Holocentridae	55	Nomeidae
29	Labridae	51	Labridae
26	Carangidae	49	Monocanthinae
20	Synodontidae	46	Schindleriidae
17	Scorpaeninae	37	Synodontidae
15	Monocanthinae	36	Carangidae
7	Schindleriidae	24	Bregmacerotidae
3	Myctophidae	9	Pseudochromidae
2	Lutjanidae	8	Lethrinidae
1	Uranoscopidae	8	Caesionidae
1	Kyphosidae	5	Eleotridae
1	Syngnathidae	5	Acanthuridae

Appendix 2G. Relative abundance of the 20 most abundant families collected from Myrmidon Reef in two consecutive years of sampling

1990/1991		1991/1992	
2396	Clupeidae	11580	Clupeidae
1037	Pomacentrinae	4018	Pomacentrinae
299	Holocentridae	1439	Chrominae
272	Apogonidae	695	Apogonidae
245	Chrominae	328	Pseudochromidae
55	Blennidae	319	Atherinidae
39	Labridae	287	Blennidae
15	Atherinidae	241	Gobiidae
13	Nomeidae	131	Synodontidae
11	Synodontidae	66	Schindleriidae
7	Gobiidae	65	Scorpaeninae
7	Pomacanthidae	37	Labridae
6	Carangidae	21	Bregmacerotidae
6	Scorpaeninae	19	Holocentridae
5	Pseudochromidae	13	Nomeidae
5	Monocanthinae	12	Pempheridae
3	Myctophidae	12	Myctophidae
2	Siganidae	11	Carangidae
1	Schindleriidae	5	Amphiprioninae
1	Pseudoplesiopidae	4	Caesionidae