DEPARTMENT OF CONSERVATION, FORESTS AND LANDS
FISHERIES DIVISION

STOCK ASSESSMENT OF BLACKLIP ABALONE (HALIOTIS RUBRA) IN VICTORIA

FINAL REPORT
(FISHING INDUSTRY RESEARCH TRUST ACCOUNT 85/16)

Paul E. McShane

June 1989

Internal Report Number 176
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MARINE SCIENCE LABORATORIES

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Marine Science Laboratories
Queenscliff, Victoria
Australia

AIMS AND OBJECTIVES

Aim

To conduct an assessment of the degree of exploitation of Victorian abalone stocks.

Objectives

1. To construct a population model for abalone incorporating a stock-recruitment relationship.

2. To describe the biological consequences of varying levels of fishing effort for Victorian abalone stocks.

Supplementary funding to support nearshore studies of water movement on an abalone reef. was provided from the Fishing Industry Research Trust Account (FIRTA) during 1986-87. This supplementary research program was primarily aimed at predicting larval dispersal in abalone so as to support continuing field studies of stock and recruitment. The objectives of this supplementary research program were as follows:-

(i) To investigate near-shore, water movement at a coastal site in Victoria, in relation to prevailing winds and tide.
(ii) To predict the passive dispersal of abalone larvae from reef to reef using the water movement results.
(iii) To determine the potential of using a 2-dimensional numerical hydrodynamic model of the region to predict passive dispersal of abalone larvae.

SUMMARY

An early focus of research was the basic biology of the blacklip abalone (*Haliotis rubra*) because so little information on the early life history of the species was available. This research was conducted at several coastal sites identified as supporting commercially valuable stocks of abalone and included studies of reproductive biology, growth, movement, mortality and demography. The results were consistent with some of those from studies of other species of abalone. *H. rubra* spawns annually and is relatively slow growing, sedentary and patchilly

distributed on coastal reefs. But contrary to existing notions, settlement of *H. rubra* is often very dense (many thousands per square metre).

The most important findings of this study relate to recruitment. Detailed field studies revealed that settlement of larval *H. rubra* is mostly localised; one corollary is that the Victorian abalone resource is composed of many isolated substocks each confined to individual reefs or reef complexes.

Recruitment (post-settlement abalone observed) varies spatially and annually. Annual variation in recruitment, of several orders of magnitude is attributed to stochastic variation in larval availability. Spatial variation in recruitment (also high) is primarily due to water movement. Evidence from the study suggests that abalone larvae released from exposed reefs are mostly flushed away from suitable habitat whereas those released from sheltered reefs can complete their larval life near the parent stock. The dense growth of sea weeds and the complex topography typical of many abalone reefs attenuate water movement so that larval dispersal is localised. Although abalone larvae would survive being dispersed long distances during the 5 - 10 days of their larval life, few would find suitable habitat on which to settle. Survival of larvae would be highest if larvae settled on the same reef as their parents, that is local dispersal.

Of the abalone that settle, few survive the first 2 - 3 months. This finding of high juvenile mortality is contrary to existing notions of low natural mortality for most other species of abalone.

There is no evidence of recruitment overfishing of abalone on any of the Victorian reefs studied. Even on reefs that commercial fishermen considered to be "fished out" of abalone, recruitment was substantial. Indeed, the research showed that fishing has little impact on the overall stock abundance of abalone on a particular reef. The general fishing behaviour of abalone divers in Victoria is such that stocks are unlikely to be fished down so far that recruitment is deleteriously affected. In the abalone stocks of Victoria, recruitment is determined by factors other than stock density.

Indeed, of all the findings of the study, the most relevant to management is that which shows that recruitment of abalone is unrelated to stock density. The absence of a stock recruitment relationship is due to the enormous variation in recruitment from year to year. This variation is not surprising considering that stock density is but one of a suite of factors that influences recruitment. Other

life history events that are obviously important are larval availability and larval survival. Variation in these will similarly influence settlement and therefore recruitment. Findings relating to recruitment variation are consistent with those from other studies of marine invertebrates.

While recruitment varies from year to year as a result of, for example, variation in larval survival, recruitment to the fishery (those abalone reaching harvestable size) is apparently stable. *H. rubra* grow so slowly and variably that recruitment to the fishery generally occurs after 4 - 10 years. Thus variation in settlement is dampened because, for any year, the annual recruitment to the fishery may be composed of several year-classes. The simple model for the fishery is related to identifying the "stable" annual recruitment. When a catch quota equivalent to the annual recruitment is set, the fishery will be stable, and productivity can be controlled by strategic implementation of size limits.

INTRODUCTION

The Victorian abalone fishery started in the early 1960s. After a rapid increase in the number of operators, licence limitation was introduced in 1968. At that time, for the purposes of management, the Victorian coastline was sub-divided into three zones; eastern, central and western. Divers operating in each of these zones had non-transferable entitlements until recently when, in 1984, transferability of licences was introduced. Because there was widespread concern that Victorian abalone stocks were being over-exploited, the Government, seeking to reduce or control fishing effort, issued new licences on a two- for - one basis. Thus, to gain entry to the fishery, an operator had to purchase two existing entitlements in the zone he decided to fish in. Initially, the combined "value" of two licences was relatively low and reflected, at the time, the uncertainity of abalone export markets. Within two years, however, accompanying the introduction of catch quotas in the large Tasmanian abalone fishery, the world abalone shortages and the decreasing value of the Australian currency, the landed price of abalone quadrupled. Consequently, the value of licences increased dramatically as the fishery became more profitable. The entry of keen young divers eager to repay large loans taken out to gain entry to the fishery was the most significant change in the Victorian abalone fishery since licence limitation was introduced.

In the absence of reliable information, a research program designed to investigate the "health" of Victoria's abalone fishery was instigated at the Marine Science Laboratories (MSL). Because the blacklip abalone (*Haliotis rubra*) forms more than 90 % of the annual Victorian catch of abalone the study was concentrated on the population biology of this species. The focus of the research was the relationship between stock and recruitment - a relationship that is ill-defined for abalone in general. There is evidence, however, that the stock-recruitment relationship in abalone is a sensitive one; the collapse of many of the world's abalone fisheries has been attributed to recruitment failure.

RESULTS AND DISCUSSION

Most of the results obtained during the three year study have been published (see Appendix 1 for a list of reports) and the reader is referred to specific reports for more detailed descriptions of research results.

Historical research data

Previously unpublished data for reef by reef catch rates, reproductive biology and growth/morphometry of Victorian abalone have been analysed and summarised (McShane *et al* 1986a,b, 1988a). Some of the more important conclusions are repeated here.

Generally, no discernible trend in catch rates is evident in the six years of data examined. Relatively few reefs supply large catches of abalone. A few "major" reefs located around headlands provide most of the annual catch in Victoria.

Seasonal variation in a macroscopic gonad index (data for males and females combined) for *H. rubra* from populations on the Victorian coast at Lorne, Point Lonsdale, Portsea and Flinders indicated that three of the populations spawn during summer; the population at Flinders appears to release gametes throughout the year. The population at Portsea spawned twice, during summer and autumn. Although the populations at Point Lonsdale and Portsea were only 4 km apart, their spawning is asynchronous. At both these sites sea temperature correlates inversely with reproductive maturity, but has little correlation with the onset of spawning.

The relationship between size of oocyte and frequency of occurrence revealed ovarian development to be consistent with changes in the macroscopic gonad index, as did histological examination of ovarian tissue.

Variation of fecundity with length showed that one *H. rubra* longer than 100 mm can produce more than half a million eggs.

The morphometric characteristics, for example, the relationship between shell length and total weight,of various *H. rubra* populations studied in the early 1970 s are different.

In each population the meat yield for a given shell length varies seasonally, with lowest yields in summer and highest in winter. This seasonal difference of up to 20% sufficient to allow the development of harvesting strategies which take into consideration fluctuating yields.

Growth rates estimated from the results of tagging studies at several different locations showed that the growth rates of the various populations are different. Growth rate is related to the degree of exposure of a reef; the more exposed the

reef the more available is food in the form of drifting seaweed. Thus, in general, abalone on exposed reefs than those on relatively sheltered reefs.

Tagging studies

During the MSL studies, several populations of *H. rubra* were tagged with a small plastic disc glued to the shell (McShane 1989) so that the movement and the growth of *H. rubra* could be measured.

Movement

Tag recoveries indicated post-tagging movement of up to 40 m. However, most tagged abalone remained near the point of release. Even so, movement and recovery of tagged individuals in the various populations are different perhaps because of habitat differences, for example, in food availability.

Growth

Measurements of growth from tag recapture studies confirmed the results of earlier studies which revealed that growth varied between populations (McShane and Smith in prep. a). However, the later results showed that growth rates of *H. rubra* have been significantly underestimated in the past because they were estimated for populations in relatively sheltered waters. Results of studies on relatively exposed populations revealed that growth rates could be comparatively fast; some individuals reached 120 mm in 4 years. Growth rate during the first 4 years is more adequately described by a simple linear model rather than by the traditional von Bertalanffy function.

Demography

Population censuses were undertaken at several sites by semi-destructive sampling. Boulders were overturned, epi-biota was removed and each site was thoroughly searched in an attempt to count the entire population within the sample area. The density and size composition of *H. rubra* varied from site to site. The size distributions were skewed towards larger individuals indicating that many juveniles were not sampled. Cohorts became difficult to distinguish in size frequency distributions after the first three years of growth because fast-growing and slow-growing year classes merged.

Reef re-stocking

Stick reef in Port Phillip Bay, a reef which once supported a commercially viable population of abalone was chosen for an assessment of the practicality of restocking reefs with abalone. Results showed that re-stocking was impracticable mainly because of predation of the *H. rubra* released (McShane and Smith 1986).

Fecundity

The relationship of between fecundity and length of *H. rubra* is linear, but fecundity depends on age and not length (McShane *et al* 1988a). *H. rubra* becomes reproductively mature after 4 years of age and produces substantial numbers of eggs (1 million or more) at age 6. As a result, harvestable *H. rubra* from fast-growing populations may be reproductively immature or producing relatively few eggs. On the other hand, slow-growing ("stunted") stocks may produce eggs for several years before the mature individuals reach harvestable size.

Larval biology

McShane et al (1988b) conducted surveys of larval *H. rubra* on and near three closely located reefs near Mallacoota. Although more than 100 thousand litres of seawater were filtered from 15 sites, only one abalone larva was positively identified. This larva was found near the seabed off Sandpatch reef.

Measurements of horizontal water velocities near the bed and at the surface of one reef showed that larvae entering the water column by leaving the shelter of local reef topography were dispersed. This dispersal was confirmed by results from numerical, hydrodynamic and dispersion modelling which simulated the temporal and spatial variation of wind-driven currents near the reef. Results from the models also demonstrated that larvae from the reef have little chance of either returning to their parent reef or of settling at another suitable site during a typical 5 - 10 day pelagic phase. Measurements and simulations of water movement near a typical reef suggest that abalone settle most successfully when the larvae remain on their parent reef i.e. local dispersal. This local dispersal could be achieved if larvae remain where water movement is mild, for example, sheltered reef topography, in rock crevices or within dense kelp beds. Because its larvae are dispersed locally, *H. rubra* completes its life cycle near the parent stock.A corollary of this hypothesis is that reefs support discrete stocks and that

sheltered reefs will have higher recruitment per unit stock than reefs with violent water movement, for example, exposed headlands. Another corollary is that long-distance dispersal, i.e. between reefs, is possible but that colonization rates would, in all probability, be very low.

Recruitment

McShane and Smith (1988) used a method similar to that of Prince and Ford (1985) to survey a reef near Tullaburga Island (N.E. Victoria) for post-settlement abalone. The reef has extensive sea-urchin barrens depauperate of mature *H. rubra* and provided an opportunity to monitor settlement of *H. rubra* distant from the parent stock. Substantial settlement of abalone was evident up to 50 m from the nearest mature *H. rubra*. The result implies a dispersal of at least this distance and is contrary to that of Prince *et al* (1987) whos suggested that larval *H. rubra* disperses only a few metres.

Although many different types of substrate surfaces of sponges, bryozoa, ascideans and kelp holdfasts were examined, recruitment occurred only on surfaces containing encrusting coralline algae.

Visual surveys of recruitment are unreliable because tiny abalone are difficult to see and, near the time of settlement, are always undersampled. Similarly, the technique of Prince and Ford (1985) does not permit *in situ* surveys of recruitment in abalone. To obtain more reliable estimates of recruitment in abalone (numbers of post-settlement juveniles), McShane and Smith (1988) developed an underwater venturi-suction sampler. A comparison with two other methods, anaesthetic and underwater searching, revealed that the suction sampler collected significantly more juveniles. More than 12000 *H. rubra* were counted in a single square metre sample - by far the highest recruitment ever recorded for any species of abalone.

Surveys of recruits confirmed that at each site there was a single settlement of larvae each year but that this settlement could occur over 1 or 2 months. A secondary settlement occurred at one site (in May) off Bastion Point . Although recruitment to the various stocks differed quantitatively, most of the larvae settled at the same time of the year (December).

On three closely located reefs off north-east Victoria, recruitment to the various populations of *H. rubra* depended on the relative abundance of adults (McShane

et al 1988b). This early result provided evidence of a stock recruitment relationship; however, later studies of recruitment revealed no significant relationship between stock density and recruitment. In each population the abundance of adults remained largely unchanged over time; in other words recruitment to the adult stock is effectively balanced by mortality. In stark contrast, however, recruitment (as post-settlement juveniles) varied widely (several orders of magnitude) over time. Variation in larval availability is suggested as the primary cause of this variation. Survival of larval invertebrates is characteristically very low. Therefore, the more time a relatively short-lived larva such as *H. rubra* spends in the plankton, the less will be its chance of surviving. Temperature has a pronounced effect on the duration of larval life and therefore could have a marked influence on larval survival and subsequent settlement success. Because temperature control of coastal waters and control of other environmental conditions are outside the domain of fisheries managers so to is recruitment of abalone; a stock recruitment relationship for an abalone fishery is practically unattainable (McShane and Smith in prep. b).

Spatial variation in recruitment was due mainly to differences in water movement at the various sites. At sheltered sites, namely those protected from violent water movement by complex reef topography and dense seaweeds , recruitment was high.

Juvenile mortality

Contrary to the prevailing view, post-settlement survival in *H. rubra* is very low (McShane and Smith in prep. b); fewer than 1% survive the first 2-3 months. Density- dependent survival was evident from relatively poor survival of recruits that had settled in high numbers. Contributary factors implicated by results of the present study are, "bull dozing" by conspecific adults and other grazing epibiota (e.g. sea urchins), predation by terebellid worms and fish, and removal by wave action.

Fishing mortality

Fishing mortality in a population of *H. rubra* was estimated in an experiment during which commercial abalone fishermen were asked to fish on a reef until they considered their catch rates to be unprofitable (McShane and Smith in press). To maximise the catch, fishermen were not subject to the usual daily catch quota and the minimum length of *H. rubra* that could be taken was reduced

from 120 mm to 90 mm. The divers considered the reef to no longer yield profitable catches of abalone after two days fishing. Although catch per unit effort was significantly lower for the second days fishing, estimates of fishing mortality from tagging studies during the experiment were surprisingly low. Stock size was the same before and after fishing.

The reason for these paradoxical results lies in the fishing behaviour of abalone divers. Fishermen target only large aggregations of H. rubra so as to minimize their searching time and maximizes their catch rates. By knowing the location of the main aggregations of *H. rubra* on a reef and by moving from reef to reef, fishermen maintain good catch rates. Unlike the fishermen, the divers from MSL did not tag *H. rubra* living in large aggregations. While tagged abalone were released in proportion to their abundance on the reef surface, fishermen did not search much of the area occupied by tagged abalone. Consequently, the fishermen, by fishing only on the main aggregations of *H. rubra*, had a lower catch rate on their second day's fishing but returned few tagged abalone. Results from the tag-recapture experiment revealed little change in the overall abundance of abalone due to fishing because MSL divers sampled the whole population not just the large aggregations.

The main observation of this study of fishing mortality is that present fishing practices have little impact on the overall breeding stock. Fishermen are reluctant to fish a reef down to a stock density where breeding success is threatened. Rather they will move to another reef where their preferred catch rate can be supported. However, one corollory is that fishing behaviour might change due to, for example; incentive. If the price of abalone is high enough, fishermen may tolerate lower catch rates and fish a stock down to a density at which level where recruitment fails.

IMPLICATIONS FOR MANAGEMENT

The Victorian stock of abalone is composed of several discrete substocks each confined to individual reefs or reef complexes. Management must take into account variability in the population biology of these substocks.

At present there is no evidence of recruitment overfishing of abalone in Victoria; even on heavily fished reefs annual recruitment is often high. Because the stock density of *H. rubra* remaining on reefs in Victoria is so high, recruitment is independent of stock density. The resource should therefore be managed to

ensure that recruitment failure does not occur in the future. The principal management tools in this regard are size limits and catch quotas.

Size limits

Four legal minimum sizes govern capture of abalone in the Victorian fishery. Greenlip abalone (*Haliotis laevigata*) has a minimum harvestable size of 130 mm; but blacklip abalone has three minimum sizes 120,110 and 100 mm.

The rationale behind multiple size limits arose from a notion of different growth rates of *H. rubra* on various parts of the Victorian coast. Thus, in the central zone of Victoria, large areas of coastline are subject to a particular minimum size. While the results of the present study demonstrate that the growth rates of sub-stocks of *H. rubra* are different, the results also indicate that imposition of a minimum size limit on a regional basis can be inappropriate for sensible management of the fishery.

Fundamental to the sensible management of any fishery is the concept that sufficient spawning stock must remain after fishing so that recruitment is not endangered. All too often, however,the minimum size chosen maximizes the yield to the fishery rather than the yield of eggs because egg production is related to age whereas yield is related to size. Thus, for a fast-growing sub-stock, a relatively large minimum size is appropriate to maximize both egg production and yield. On the other hand, "stunted" sub-stocks reach reproductive maturity when the abalone are comparatively small and much of the yield would be lost through natural mortality should the size limits be the same as that for a fast-growing sub-stock.

The available evidence supports a revision of the present minimum size limits. That such limits are imposed on the basis of zones rather than growth characteristics is inappropriate. Furthermore management of a fishery having multiple size limits would be burdensome. Fast growing stocks support most of the Victorian catch of *H. rubra*; yet these stocks, particularly those with low minimum size limits (100 and 110 mm) are most in danger of being overfished. Conversely, the "stunted" stocks are relatively immune from overfishing - they have many years in which to breed before reaching harvestable size.

The legal minimum size of *H. rubra* taken in Victoria should be at least 125 mm. Several strategies to implement this limit could be considered; for example, a

new size limit could be phased in over a three year period with say 5 mm increments. This recommendation is clearly aimed at protecting the fast-growing stocks, those located in exposed waters for example around large headlands (McShane and Smith 1989). Although the stunted stocks cannot be harvested efficiently under such a management regime, a uniform size limit is recommended in the interests of simplified administration. The stunted stocks which, after all, probably make up most of the total stock in Victoria, could be exploited on periodic fish-down days. This system, successfully implemented for the past 10 years in the eastern zone and recently adopted (following recommendations from MSL staff) by the Western Australian abalone fishery, allows for stunted stocks to be fished at a low size limit. The results of the MSL study have shown that if fishing is conducted on discrete days after the reef has been closed to fishing (by imposition of a high size limit) then the effect on the stock is minimal.

The results have also shown that the distinction between fast-growing and stunted stocks can be tenuous. So as to encourage the targetting of stunted stocks on fish-down days an upper as well as a lower size limit could be introduced. In this way, those areas supporting fast- growing, and therefore larger, stocks could be protected. Fishing of stunted stocks to 90 mm would provide reasonable sustainable yields from stunted stocks without compromising recruitment. An upper size limit of 120 mm would discourage exploitation of fast-growing stocks.

Catch quotas

That abalone fisheries are vulnerable to overfishing is widely recognised; the collapse of many abalone fisheries in the world is evidence of this. Fearing a collapse of the Tasmanian abalone fishery, divers in that State have supported a catch quota as a means of achieving a large reduction in effort. A catch quota in the Victorian abalone fishery was considered necessary to maintain the present conservative fishing practices.

Although recruitment (settlement of larvae) varies considerably from year to year, annual recruitment to the fishery is apparently stable because during the years it takes an abalone to recruit to the fishery, variability is dampened by fast-growing year-classes merging with slow-growing ones. A catch quota equivalent to this annual recruitment - the surplus remaining after growth and mortality- should result in a stable fishery. However, the concept of a catch quota assumes an evenly distibuted fishing effort. Because the abalone resource in Victoria is

composed of many discrete substocks, uneven distribution of effort might still result in the overfishing of some substocks. Judicious implementation of appropriate size limits is one strategy that could control polarization of fishing effort.

At first, the catch quotas set were little more than educated guesses because there was no information on the numbers of harvestable *H. rubra* recruited annually to the fishery. Taking into account past catches and the need for conservative management, a catch quota in the form of a total allowable annual catch (TAC) was set for each zone. The TAC s were 700, 280 and 480 tonnes for the central, western and eastern zones respectively. By monitoring the relative abundance of abalone of all major sub stocks, the proximity of the TAC to the annual recruitment may be assessed. Thus, if the TAC is greater than the surplus generated by recruitment then a decrease in the overall stock abundance should be evident from surveys and vice versa. In this way, the TAC can be fine tuned and by adaptive management a quota that reflects the annual surplus can be set.

CONCLUSIONS

. The Victorian abalone fishery is in no imminent danger of collapse

. The Victorian abalone fishery shows no evidence of recruitment overfishing

. The Victorian abalone stock comprises several discrete substocks each confined to an individual reef or reef complex.

. Recruitment in abalone is independent of stock density over the range existing for Victorian abalone.

. Settlement of abalone larvae is controlled primarily by water movement; localised dispersal of larvae and subsequent high survival rate for recruits is possible only in sheltered waters e.g. on reefs protected by dense seaweed and complex topography

. Temporal variation in recruitment is controlled primarily by larval availability which in turn is influenced by environmental factors e.g. temperature

. Recruitment to the fishery (those abalone reaching harvestable size) is apparently stable

. Fecundity is related to age; egg production begins at age 4 years

. Abalone fishing effort is concentrated on fast-growing populations which are generally found in exposed waters, for example around headlands

. Abalone fishing has little impact on the overall abundance of abalone on a particular reef

. Stunted stocks of abalone are in little danger of being overfished and could best be exploited during periodic fish-down days for which minimum legal size is lowered

. Catch quotas and size limits are recommended as the management tools most suited to controlling productivity to an abalone fishery

. Catch quotas should reflect annual recruitment

. Monitoring of the relative abundance of abalone stocks will provide information on the sustainability of catch quotas and, over time, provide realistic estimates of sustainable yield

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Appendix 1. List of reports available

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Department of
Conservation
Forests & Lands
Fisheries and Wildlife Service

ABALONE REEFS IN VICTORIA - A RESOURCE ATLAS.

by

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- A RESOURCE ATLAS

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S. Foley

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ABSTRACT

McShane, P.E., *Beinssen, K.H.H., and Foley, S. (1986). Abalone reefs in Victoria - a resource atlas. Mar. Sci. Lab. Technical Rep. 47. 50 pp.

We describe the distribution of reefs, supporting populations of the two species of abalone which are fished commercially, in Victoria. Estimated surface area together with annual catch and catch-rate statistics are described for each reef of commercial significance. An estimated total of 121 square kilometers of reef supports abalone (Haliotis ruber and Haliotis laevigata) populations in Victoria. Total catch data reveal that most abalone taken in Victoria are H. ruber although relatively large areas of reef support H. laevigata populations. Of the many reefs in Victoria on which abalone are found, relatively few supply large catches of abalone. Indeed, a few 'major' reefs, located around large headlands, provide most of the annual catch in Victoria. Generally, no discernible trend in catch-rates is evident on abalone reefs over the six years data have been recorded.

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INTRODUCTION

Abalone are marine, prosobranch gastropods which, since the early nineteen-sixties, have been harvested commercially from South-Eastern Australian waters.

In Victoria, two species of abalone have been harvested commercially; Haliotis ruber Leach (blacklip abalone) and Haliotis laevigata Donovan (greenlip abalone). The commercial fishery is divided into three zones and is managed under a limited-entry policy which allows each licensed operator to take abalone for sale within a single zone. Licences are transferable to new operators but are not transferable between zones. Divers with commercial entitlements collect abalone from coastal reefs using 'hookah' diving apparatus from a small, high-speed boat as they do in most other abalone fisheries (Mottet 1978).

Here, we present an atlas of abalone reefs in Victoria. The abalone resource is described in terms of reef area and species composition. An indication of the relative commercial importance of each abalone reef is provided by the annual in catch. Catch per unit effort data are shown for individual reefs.

METHODS

The coastal outlines were derived from large-scale aerial photographs and used as reference points by commercial divers who drew reefs on transparencies which, in turn, were used to form composite maps. Those reefs that supported populations of H. ruber, H. laevigata or both were mapped following consultation with commercial abalone divers, 'ground-truth' diving where possible and examination of commercial catch records. Total area of each abalone reef was estimated using a planimeter.

Abalone fishermen in Victoria are required to submit monthly returns detailing total daily catch of abalone (by species), hours spent diving for abalone and the location of fishing activities. We used these data, which have been collected on a reef by reef basis since 1979, to obtain catch and catch per unit effort for each reef. Descriptions of abalone fishing practices were based largely on discussions with Victorian abalone divers.

RESULTS AND DISCUSSION

An estimated total of 121 square kilometers of reef supports abalone populations in Victoria. This total, comprising 94.2, 15.1 and 11.7 square kilometers, for the central, eastern and western zones respectively

(Figs. 1, 2, 3, 4, 30 and 40), is reef area on which commercial divers have collected or observed abalone. Other reefs, not shown in this report, may provide habitat for abalone, but do not have commercial significance or are inaccessible to divers.

The distribution of abalone reefs along the Victorian coastline is described in figures 5 to 46. In most cases, for a given reef, annual variation in catch and catch per unit effort is slight, although substantial variation occurs from reef to reef. Notable exceptions to this are aerodrome reef (Fig. 38), where catches have varied due to the periodic imposition of closures and Kirk's Point (Fig. 13) where catches have declined annually. The results, however, cannot account for large scale changes which may have occurred since the fishery begun, as data have only been available since 1979.

Generally, the total annual catch at each reef bears little relation to reef area. For example, outside Cape Schank reef (Fig. 20), one of the state's most productive abalone reefs, comprises only 0.2% of the total reef area in the central zone. Yet this reef provides over 10% of the annual catch in the zone. On the other hand, many reefs with relatively large reef areas yield comparatively low catches, for example; Dutton Way (Fig. 43), Split Point to Danger Point (Fig. 10), San Remo to Kilcunda (Fig. 23) and Inverloch Reef (Fig. 25). The reef area estimate can only be used as relative indications of availability of abalone habitat. The topography of a reef will considerably influence the actual surface area available for colonization by abalone. This, and the nature of the habitat, including food availability and reef community structure, will affect the abundance of abalone at each reef. Similar factors will influence the abalone species composition on a reef. Haliotis ruber is the dominant species on most of the abalone reef in Victoria. This is reflected by the comparative annual catches of H. ruber and H. laevigata (Table 1) which clearly show that H. ruber comprises most of the Victorian catch. The low catches of greenlip abalone reflect the sparse distribution and low abundance of this species off Victoria, probably resulting from the scarcity of habitat that satisfies its particular needs (Shepherd 1973).

Clearly, there is abundant abalone habitat in Victoria, as is shown by the numerous abalone reefs described in this report. However, relatively few reefs yield large catches of abalone. In the central zone, more than half the annual catch of abalone is provided by only eight reefs. These reefs may be grouped into three areas; Cape Schank (Inside and Outside reefs', Portsea Back Beach) (Figs. 18-20), Port Phillip Bay (Point Cook, Kirk's Point and She Oak reef) (Figs. 13-15) and Cape Otway (Figs. 7-8). Similarly, in the eastern zone, much of the annual abalone catch comes from Sand Patch reef (Fig. 37) which together with Gabo Island (Fig. 39), Pt. Hicks (Fig. 35), Island Point (Fig. 36) and Big Ram Head, (Fig. 36), supply most of the abalone caught in the zone. The western zone, which had less abalone reef than either the eastern or central zone has major reefs surrounding Cape Nelson (Fig. 42) and Cape Bridgewater (Fig. 41). Other important reefs in the western zone are located near Port Fairy, in particular, the Crags Reef (Fig. 44).

All these more productive reefs, with the exception of Port Phillip Bay, share a common feature. They are all located around large headlands, close to shore. Not only do the headlands provide good habitat for abalone, but they often form a refuge or lee to divers, who, by the nature of the fishery, depend on favourable sea conditions. Indeed, degree of exposure of a reef, its accessibility and the depth of water covering the reef, are all factors which influence the periodicity of visits by abalone divers. This, and the abundance of legal-sized abalone, will determine the catch and catch per unit effort. Thus, reefs which are relatively sheltered from hostile sea conditions, for example those in Port Phillip Bay (Figs. 12-17) may be visited more frequently by divers than reefs which are relatively exposed, for example Cape Schank (Fig. 20), Cape Nelson (Fig. 42), Cape Bridgewater (Fig. 41), Cape Otway (Figs. 7 & 8), The Crags (Fig. 44) and Aerodrome reef (Fig. 38). Furthermore, reefs which are distant from safe ports for example Wilson's Promontory (Figs. 27-29), Point Hicks (Fig. 35), and Moonlight Head (Fig. 6) tend to be dived less often than reefs which are close to ports for example the Passage (Fig. 42), Portsea Back Beach (Fig. 18), Gabo Island (Fig. 39), and Phillip Island (Fig. 22).

ACKNOWLEDGEMENTS

We thank the abalone divers of Victoria, too numerous to mention by name, who participated in discussions on abalone diving practices and in the preparation of reef maps. Terry Walker provided commercial catch data. Initial drafts of this report were reviewed by R. Winstanley, D. Bulthuis and D. Gwyther who provided helpful suggestions.

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Mottet; M.G. (1978). A review of the fishery biology of abalones. State of Washington Dept. of Fisheries Tech. Rep. No. 37.

Shepherd, S.A. (1973). Studies on southern Australian abalone (Genus Haliotis). 1. The ecology of five sympatric species. Aust. J. Mar. Freshwat. Res. 24: 217-57.

TABLE 1. Comparison of total annual catches of blacklip (H. ruber) and greenlip (H. laevigata) abalone in Victoria. Total catches of each species is expressed as tonnes live weight.

Year	Western Zone		Central Zone		Eastern Zone	
	H. ruber	H. laevigata	H. ruber	H. laevigata	H. ruber	H. laevigata
1979	186	0.8	590	8.9	582	3.5
1980	228	0.2	745	4.2	567	0.4
1981	319	0.6	655	2.7	458	8.1
1982	277	0.0	659	1.7	402	0.9
1983	101	0.0	666	2.4	561	0.4
1984	273	0.0	712	5.2	543	0.0

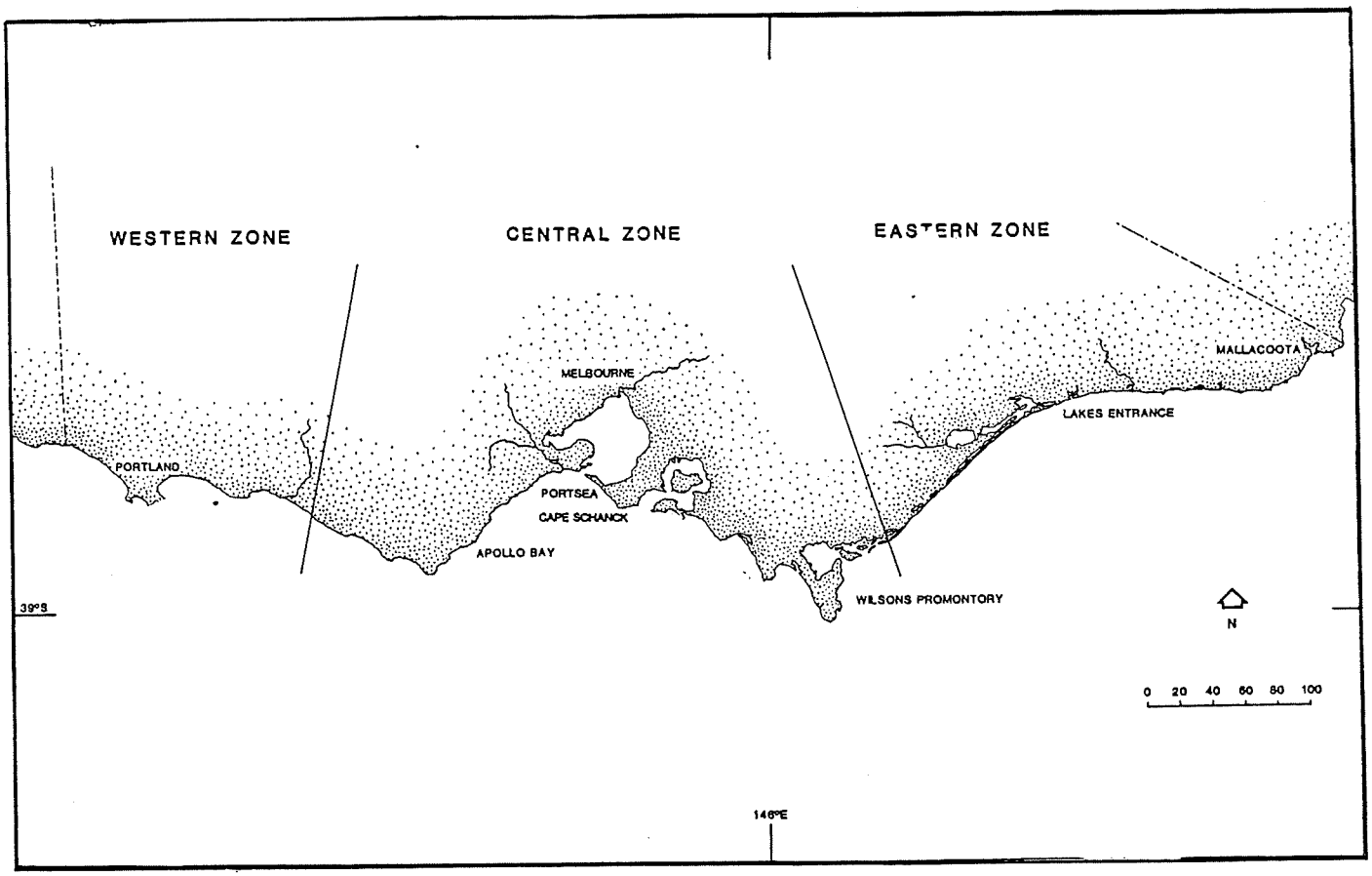


Figure 1. Map of Victoria indicating zones for management of abalone fishing.

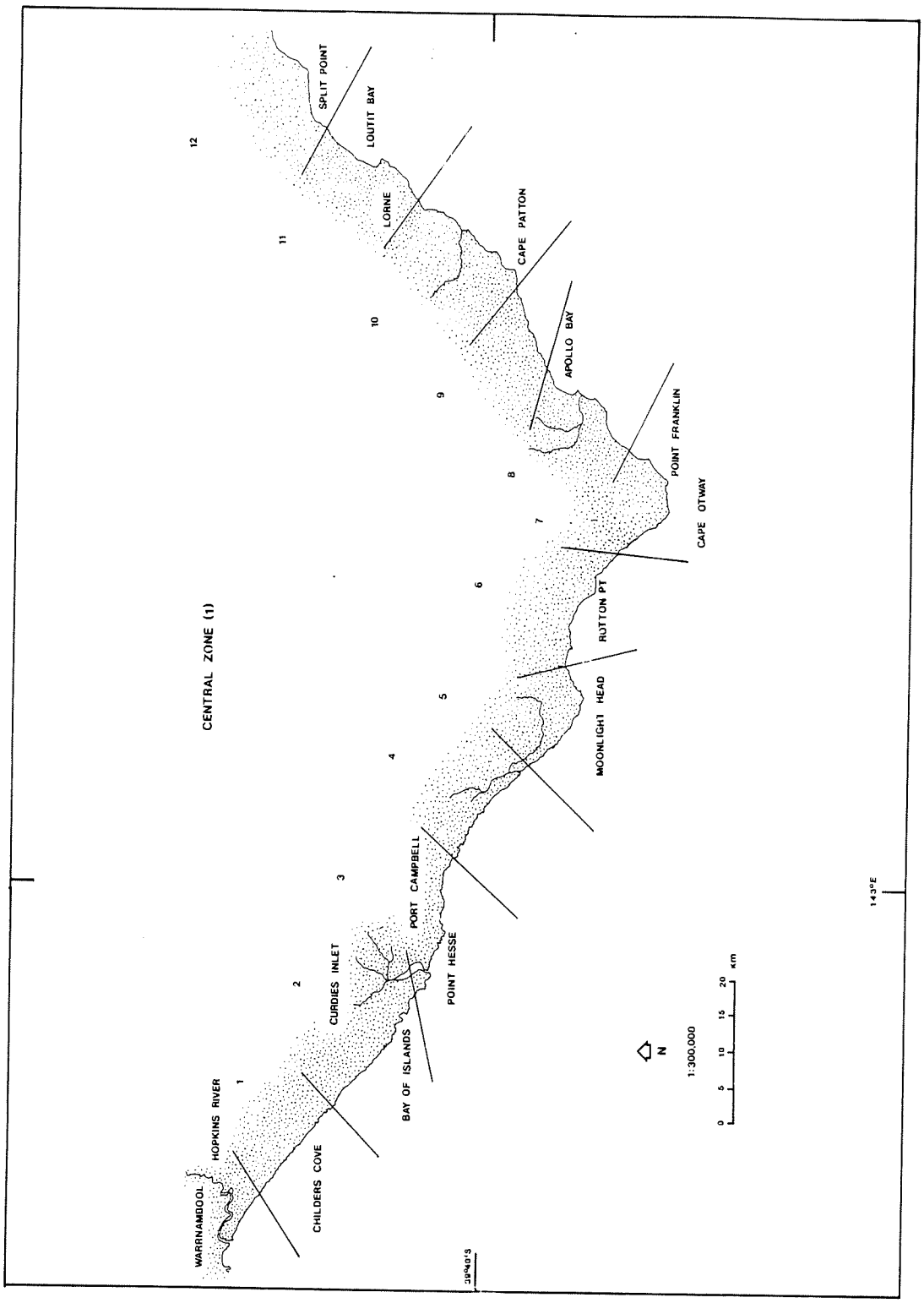


Figure 2. Map of the central zone, (Warrnambool to Lorne), showing the sections of coastline used in the survey of abalone reefs.

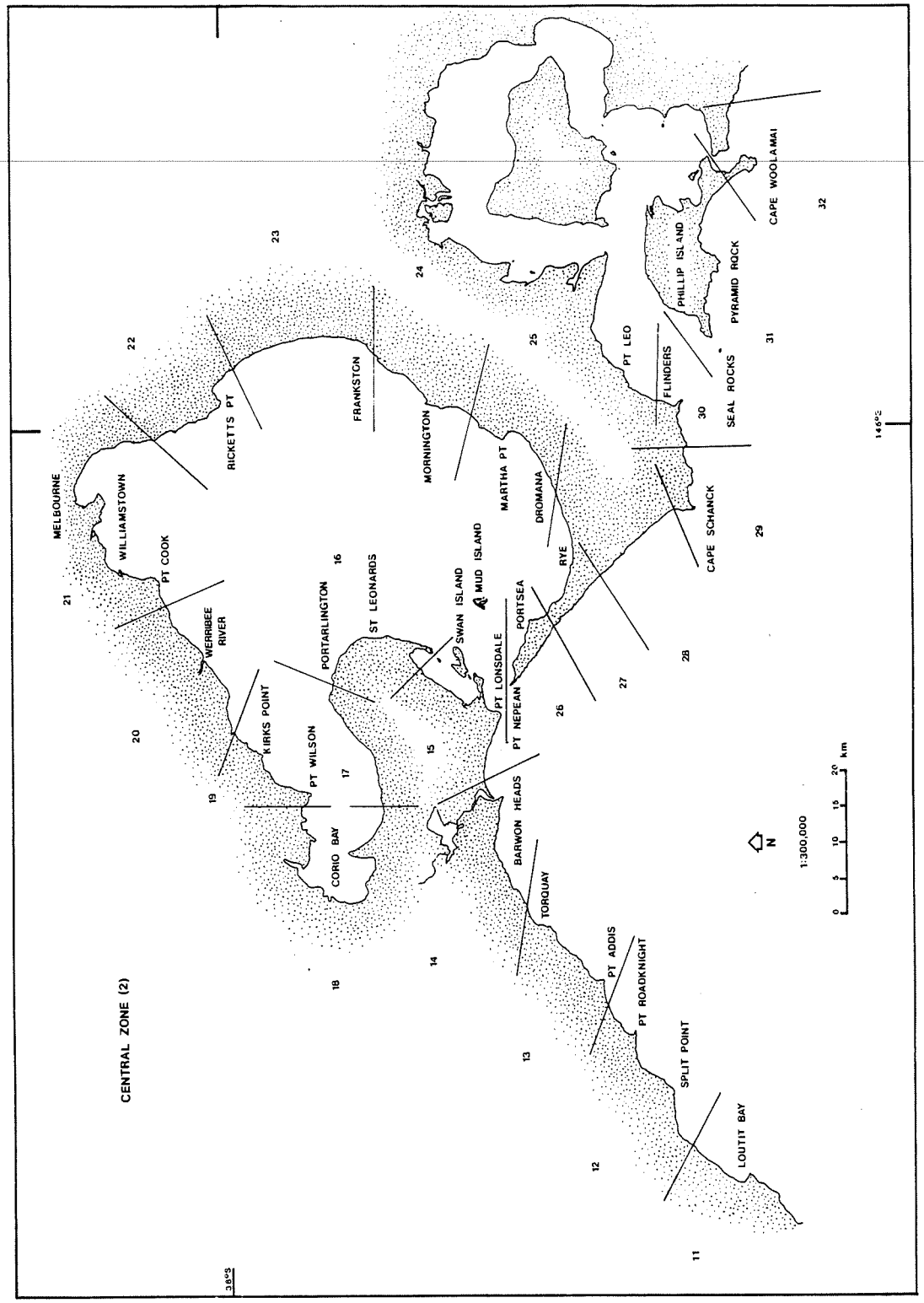


Figure 3. Map of the central zone, (Lorne to Phillip Island), showing the sections of coastline used in the survey of abalone reefs.

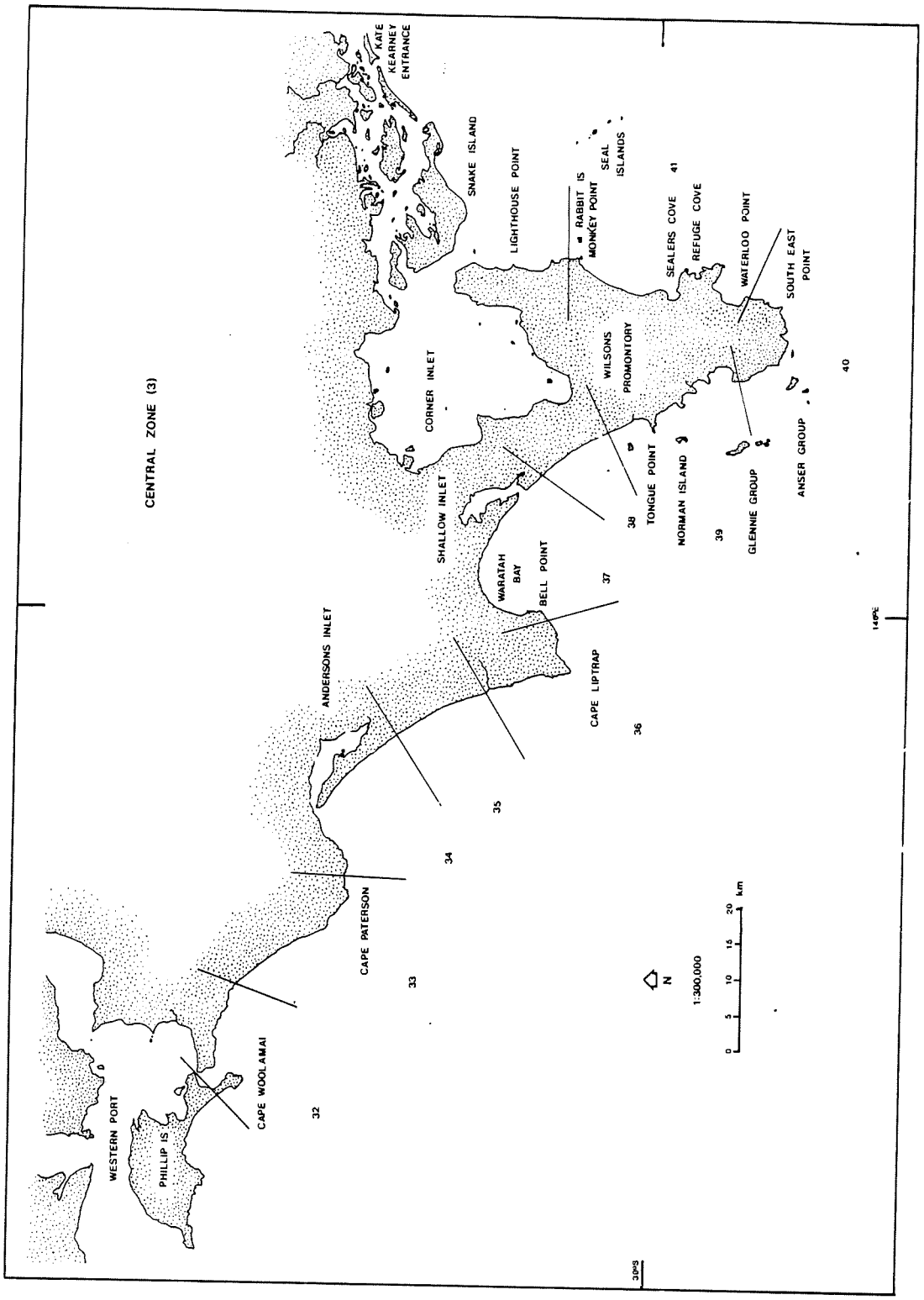
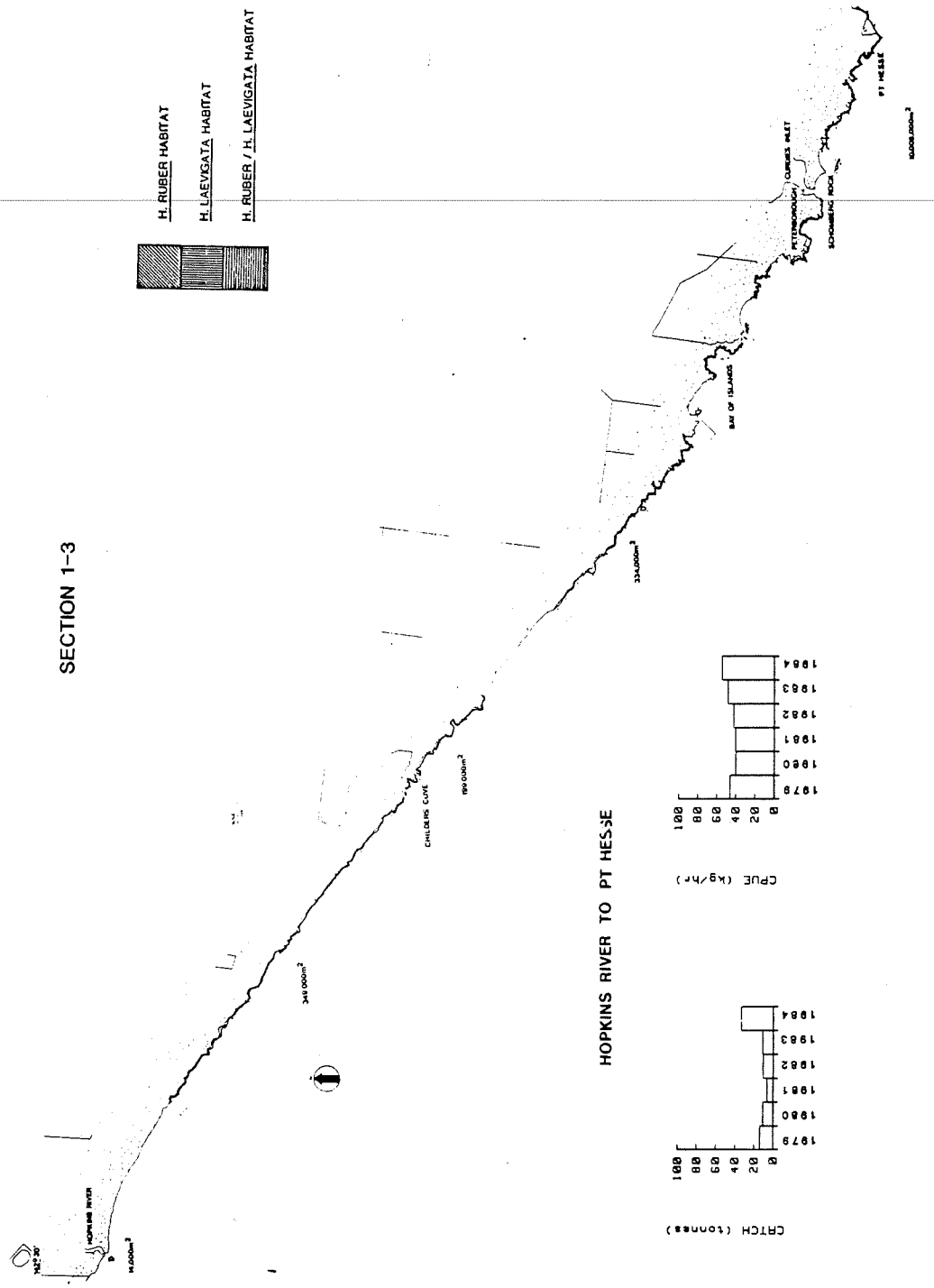


Figure 4. Map of the central zone, (Phillip Island to Wilson's Promontory), showing the sections of coastline used in the survey of abalone reefs.



Figures 5 to 29. Maps of sections of coastline in the central zone indicating abalone reef, estimates of reef area (m^2) and species distribution (H. ruber or H. laevigata).

Annual catches and catches per unit effort are shown for specific reefs or sections of coastline of commercial significance.

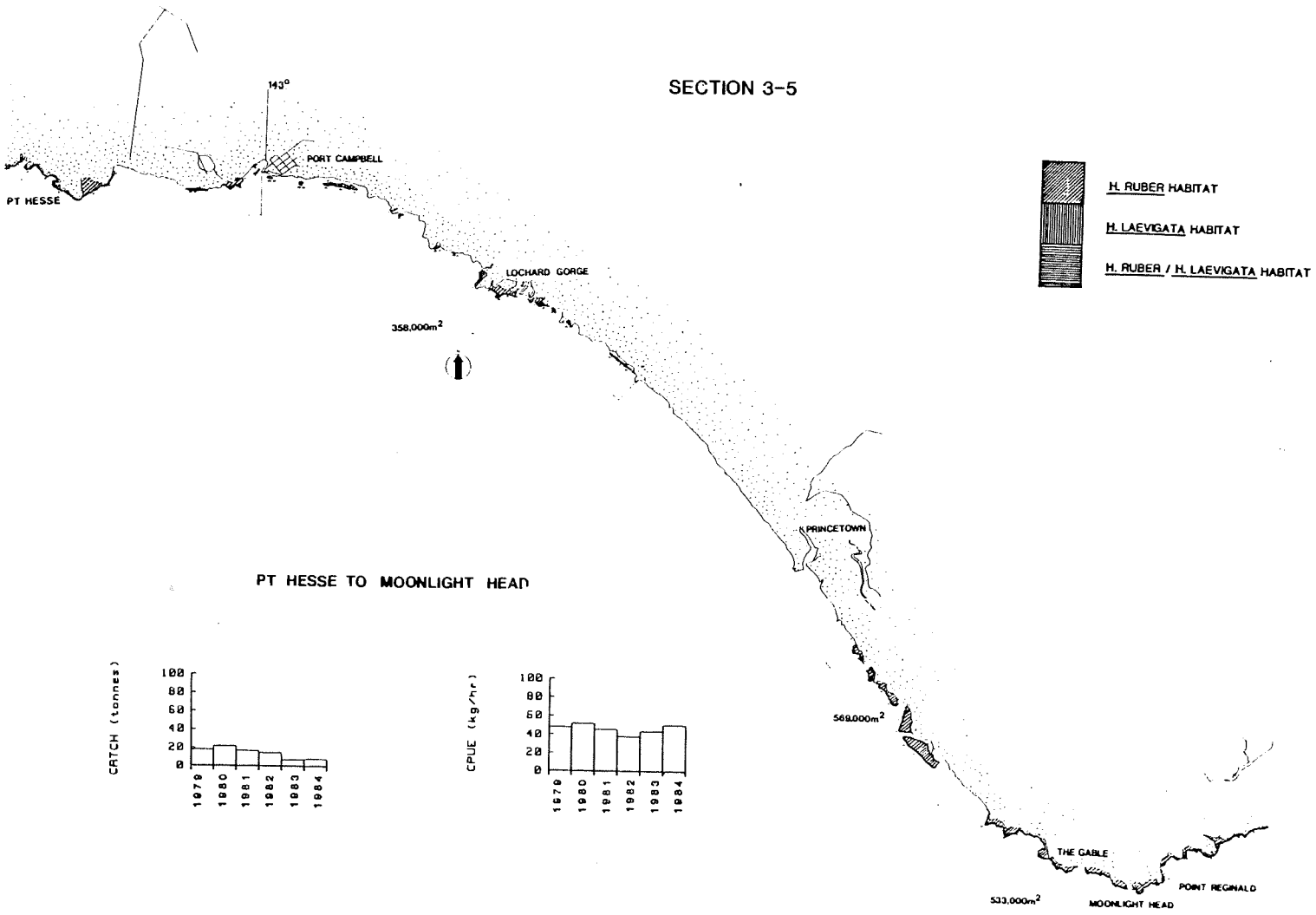

SECTION 3-5
143°
PORT CAMPBELL
PT HESSE
LOCHARD GORGE
358,000m²
PRINCETOWN
569,000m²
THE GABLE
POINT REGINALD
533,000m²
MOONLIGHT HEAD
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
PT HESSE TO MOONLIGHT HEAD
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 6.

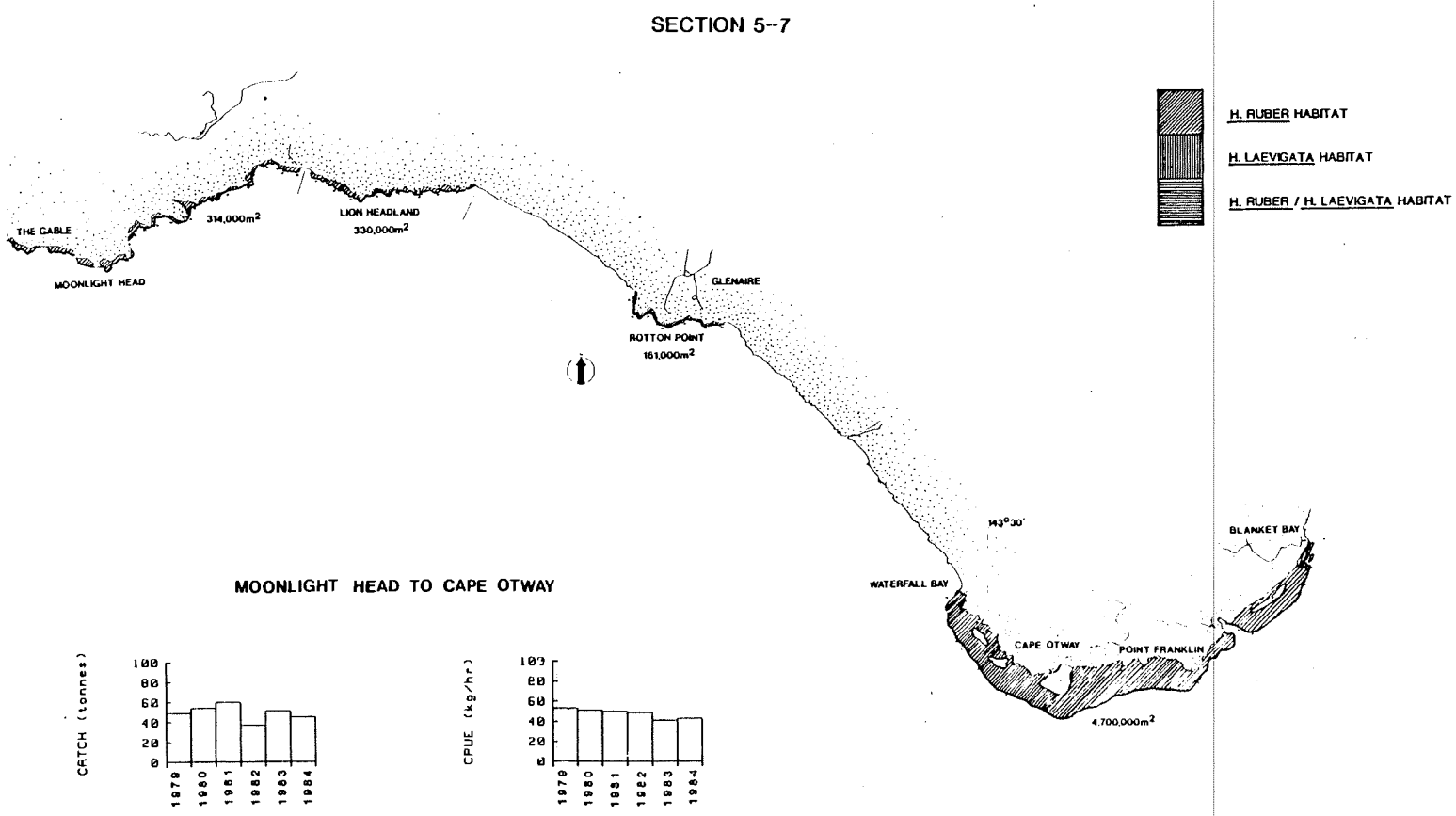

SECTION 5--7
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
THE GABLE
MOONLIGHT HEAD
314,000m²
LION HEADLAND
330,000m²
GLENAIRE
ROTTON POINT
161,000m²
143°30'
BLANKET BAY
WATERFALL BAY
CAPE OTWAY
POINT FRANKLIN
4,700,000m²
MOONLIGHT HEAD TO CAPE OTWAY
CATCH (tonnes)
CPUE (kg/hr)
1979
1980
1981
1982
1983
1984

Figure 7.

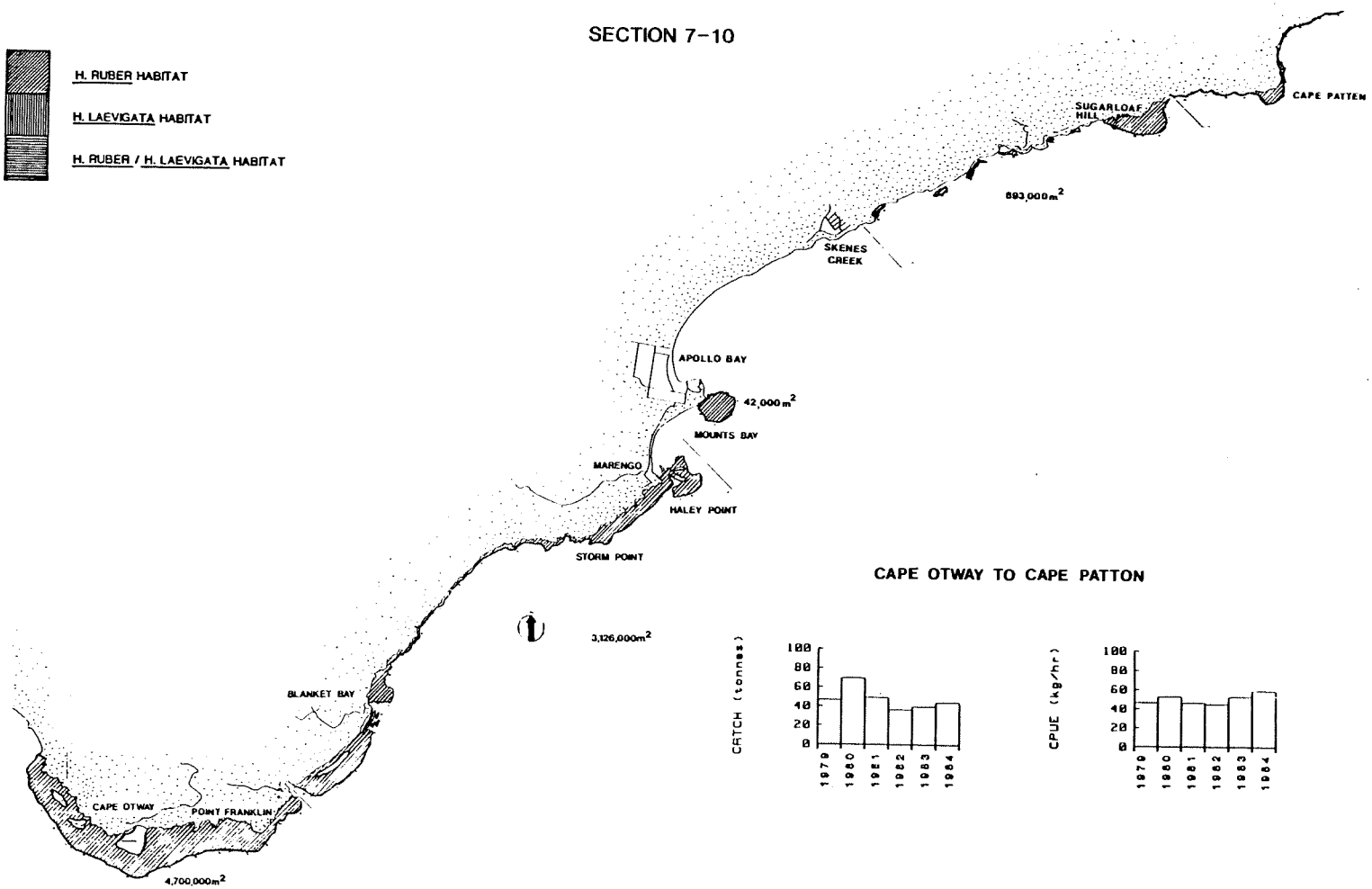

SECTION 7-10
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
CAPE PATTEN
SUGARLOAF HILL
893,000m²
SKENES CREEK
APOLLO BAY
42,000m²
MOUNTS BAY
MARENGO
HALEY POINT
STORM POINT
3,126,000m²
BLANKET BAY
CAPE OTWAY
POINT FRANKLIN
4,700,000m²
CAPE OTWAY TO CAPE PATTON
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 8.

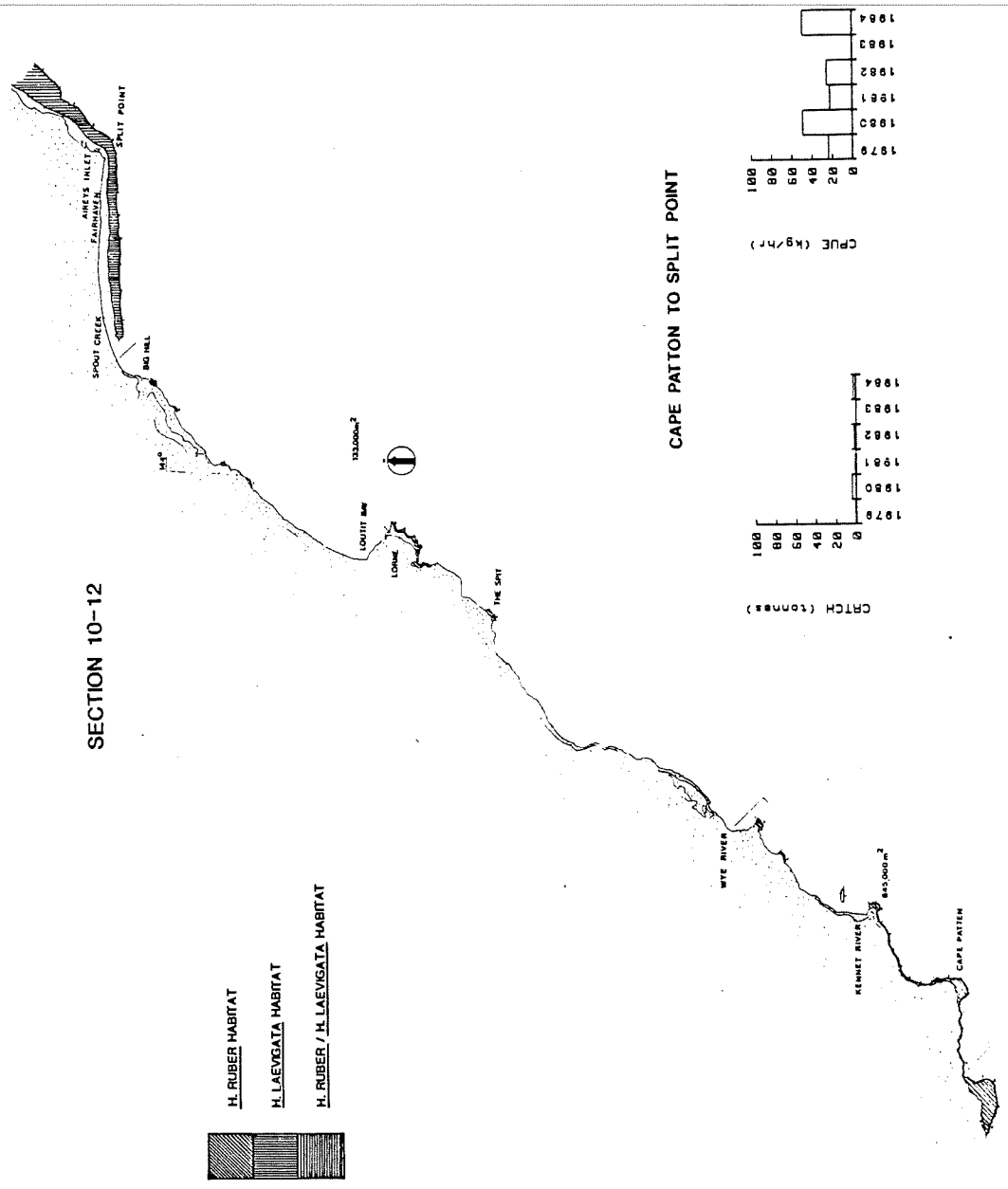

SECTION 10-12
CAPE PATTON TO SPLIT POINT
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
SPLIT POINT
AIREYS INLET
FAIRHAVEN
SPOUT CREEK
BIG HILL
LOUISE BAY
LORNE
THE SPIT
WYE RIVER
KENNET RIVER
CAPE PATTON
CATCH (tonnes)
CPUE (kg/hr)
1979
1980
1981
1982
1983
1984
0
20
40
60
80
100

Figure 9.

SECTION 12-13
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
TORQUAY
DANGER PT
BELLS BEACH
174,000m²
POINT ADDIS
ANGLESEA
HUTT GULLY
POINT ROADKNIGHT
URQUHARTS BLUFF
10,434,000m²
AIREYS INLET
FAIRHAVEN
SPOUT CREEK
SPLIT POINT
BIG HILL
SPLIT POINT TO DANGER POINT
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 10.

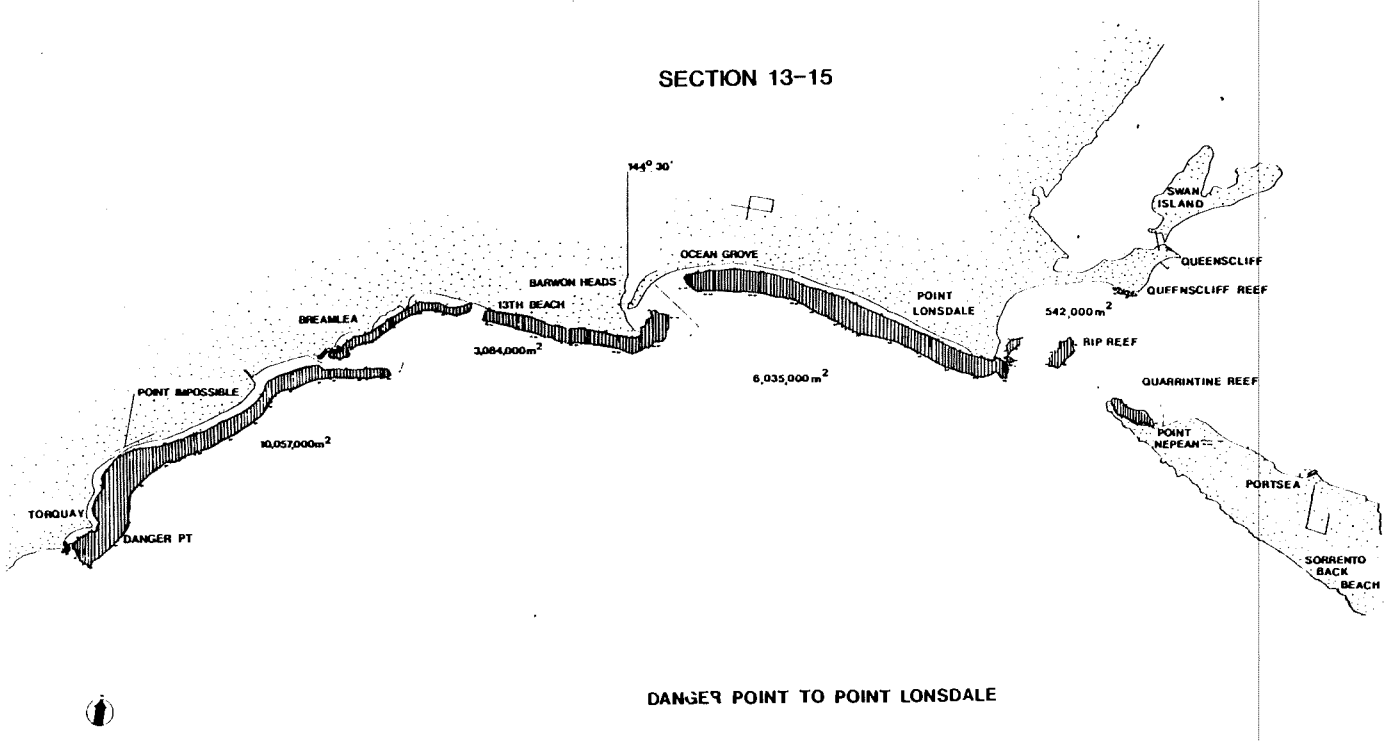
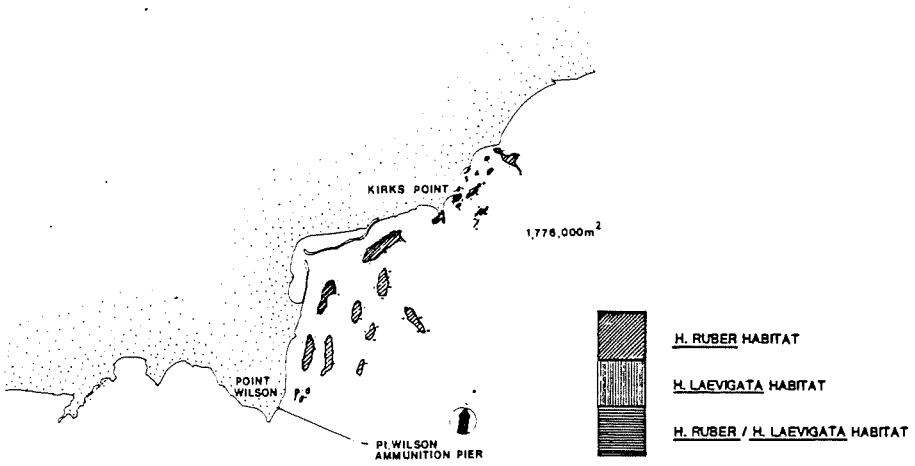

SECTION 13-15
144° 30'
SWAN ISLAND
QUEENSCLIFF
QUFFNSCLIFF REEF
OCEAN GROVE
BARWON HEADS
POINT LONSDALE
542,000m²
BREAMLEA
13TH BEACH
3,084,000m²
RIP REEF
6,035,000m²
QUARANTINE REEF
POINT IMPOSSIBLE
POINT NEPEAN
10,057,000m²
PORTSEA
TORQUAY
DANGER PT
SORRENTO BACK BEACH
DANGER POINT TO POINT LONSDALE
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT

Figure 11.

SECTION 16-18
CORIO
CORIO QUAY
NORTH SHORE
CORIO BAY
GEELONG
POINT HENRY
115,000m²
POINT RICHARDS
PORTARLINGTON
419,000m²
CLIFTON SPRINGS
ST LEONARDS
SWAN BAY
SWAN ISLAND
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT

Figure 12.



KIRKS POINT

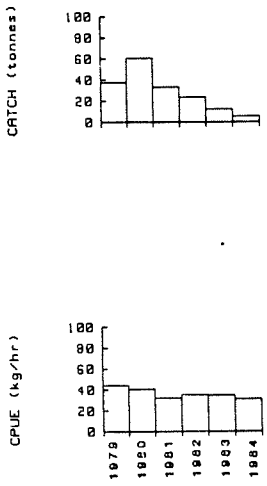
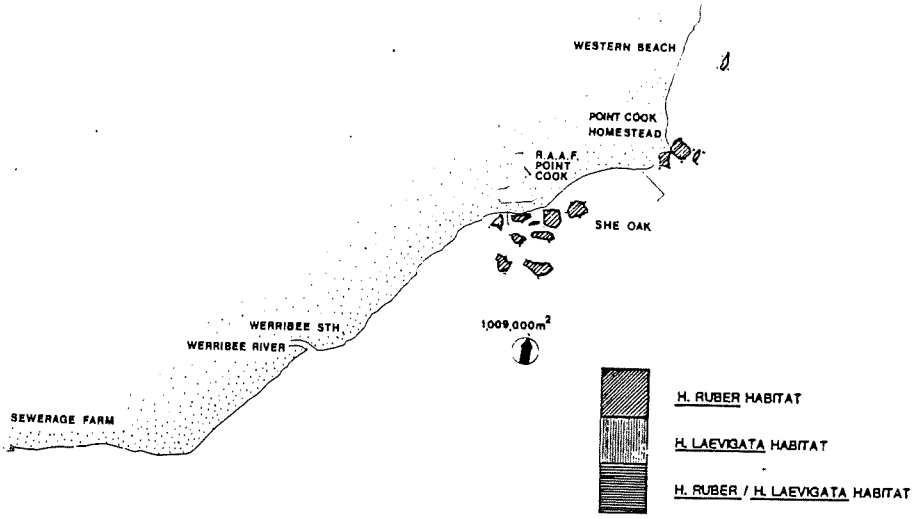


Figure 13.

SECTION 20-21



SHE OAK

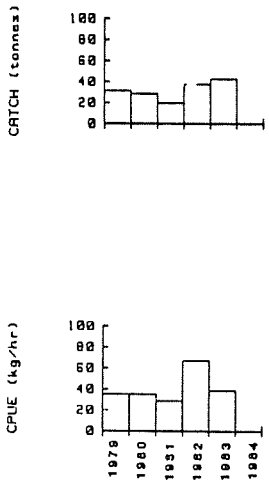


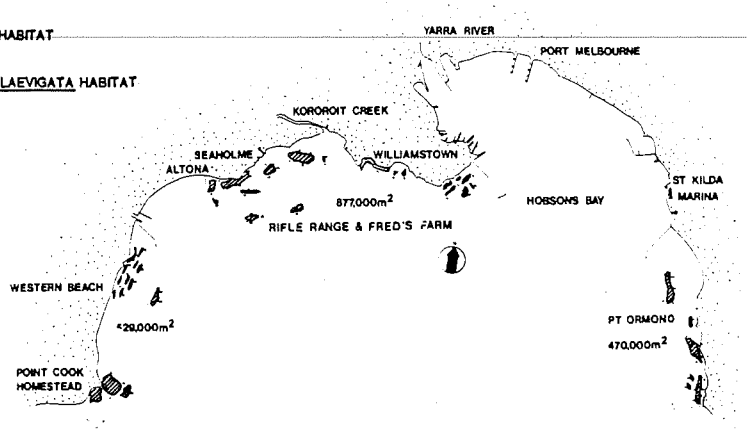
Figure 14.

SECTION 21

H. RUBER HABITAT

H. LAEVIGATA HABITAT

H. RUBER / H. LAEVIGATA HABITAT



POINT COOK

RIFLE RANGE

FRED'S FARM

Figure 15.

SECTION 22-23

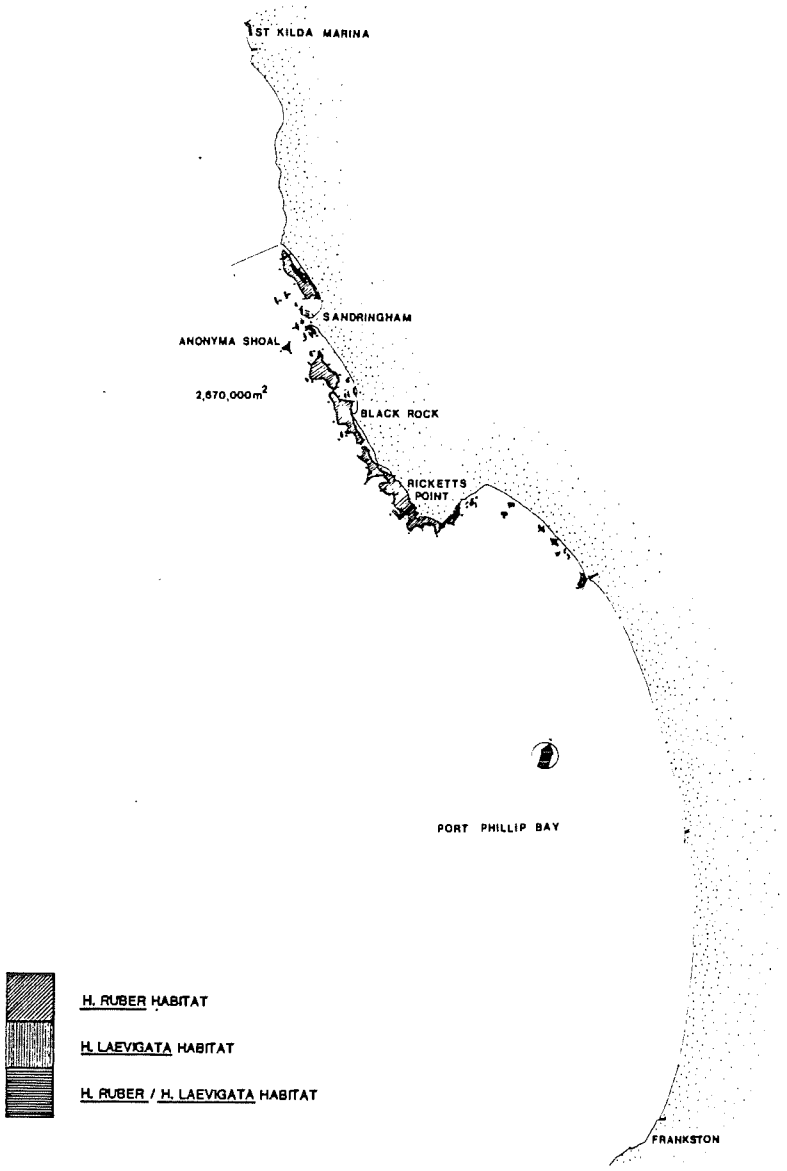
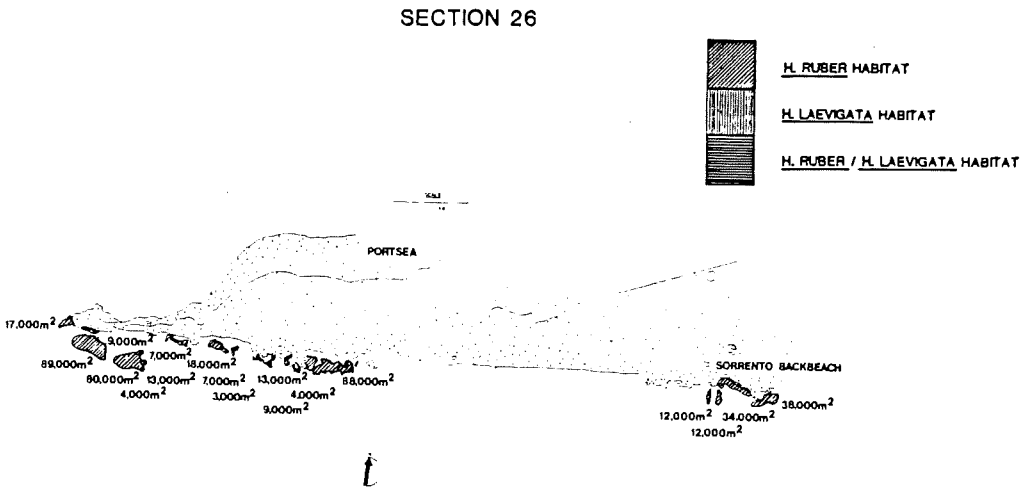


Figure 16.

SECTION 24–27
FRANKSTON
OLIVERS HILL
MORNINGTON
MUD ISLAND
QUARRINTINE REEF
POINT NEPEAN
PORTSEA
SORENTO
RYE
DROMANA
MARTHA POINT
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT

Figure 17.


SECTION 26
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
PORTSEA
SORRENTO BACKBEACH
17,000m²
9,000m²
7,000m²
89,000m²
18,000m²
80,000m²
13,000m²
7,000m²
13,000m²
88,000m²
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12,000m²
34,000m²
38,000m²
12,000m²

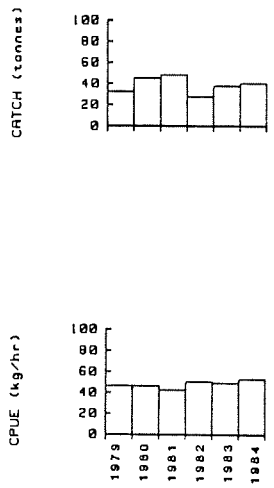

PORTSEA BACK BEACH REEF
CATCH (tonnes)
100
80
60
40
20
0
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 18.

SECTION 28

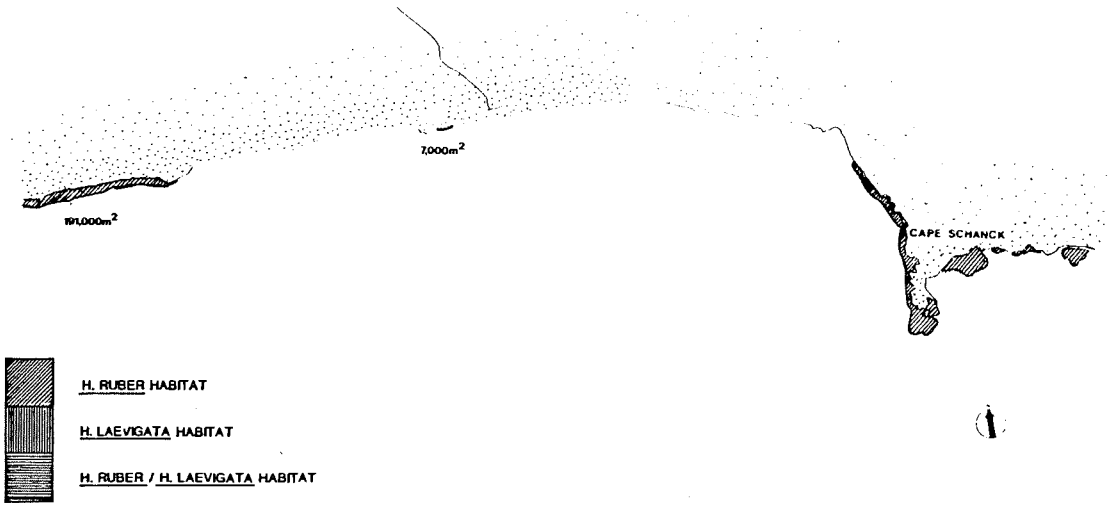


Figure 19.

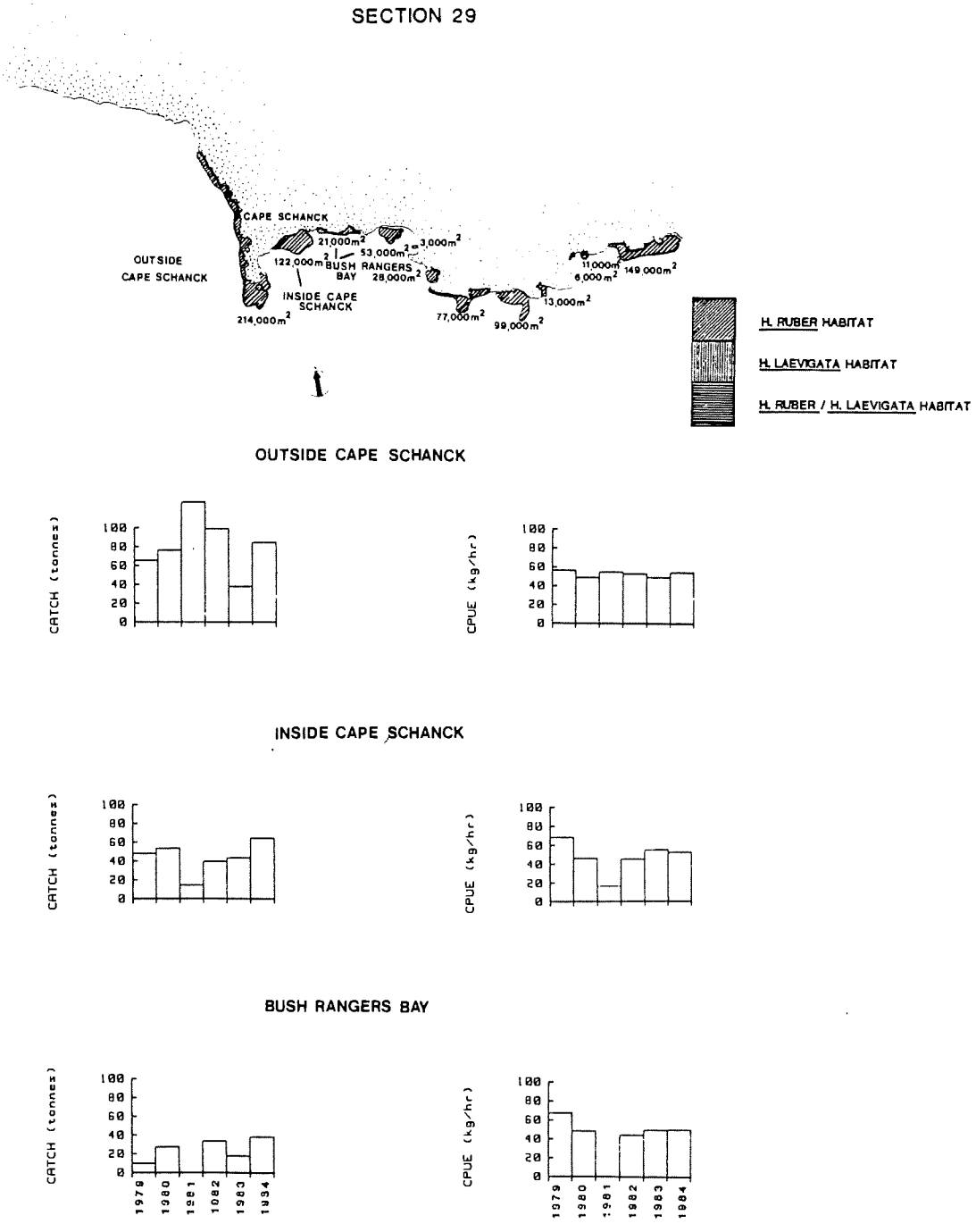
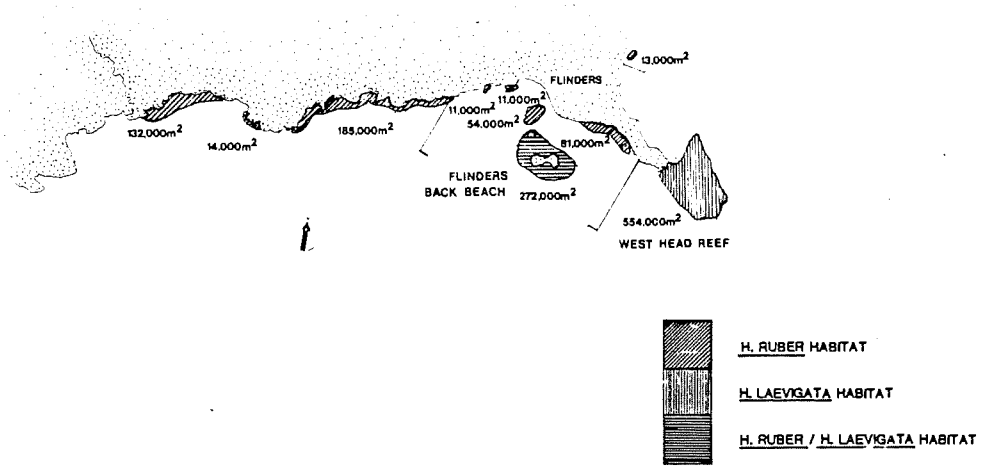

SECTION 29
CAPE SCHANCK
OUTSIDE CAPE SCHANCK
INSIDE CAPE SCHANCK
BUSH RANGERS BAY
214,000m²
122,000m²
21,000m²
53,000m²
3,000m²
28,000m²
77,000m²
99,000m²
13,000m²
11,000m²
6,000m²
149,000m²
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
OUTSIDE CAPE SCHANCK
CATCH (tonnes)
CPUE (kg/hr)
INSIDE CAPE SCHANCK
BUSH RANGERS BAY
1978
1979
1980
1981
1982
1983
1984

Figure 20.



FLINDERS BACK BEACH

WEST HEAD REEF

Figure 21.

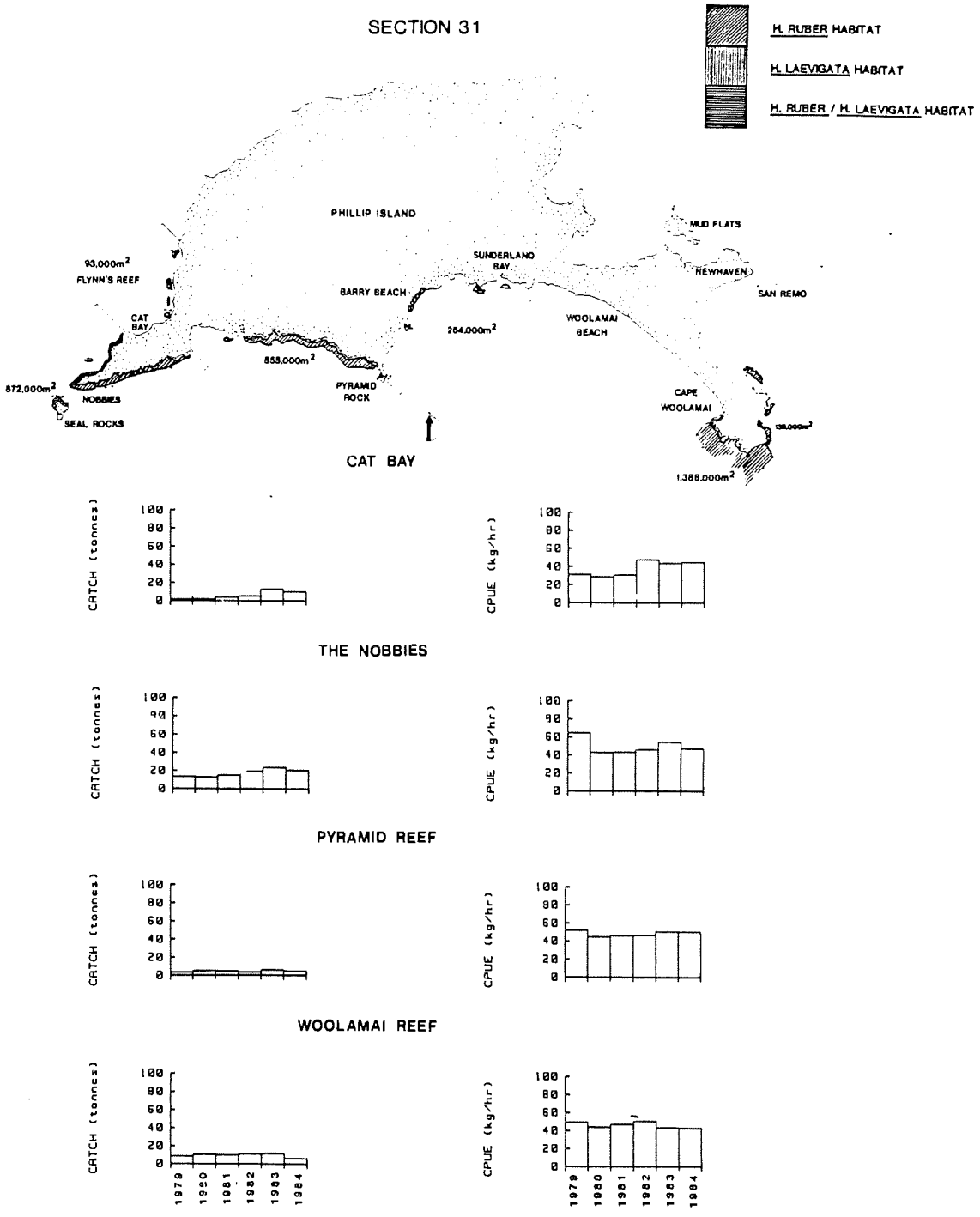
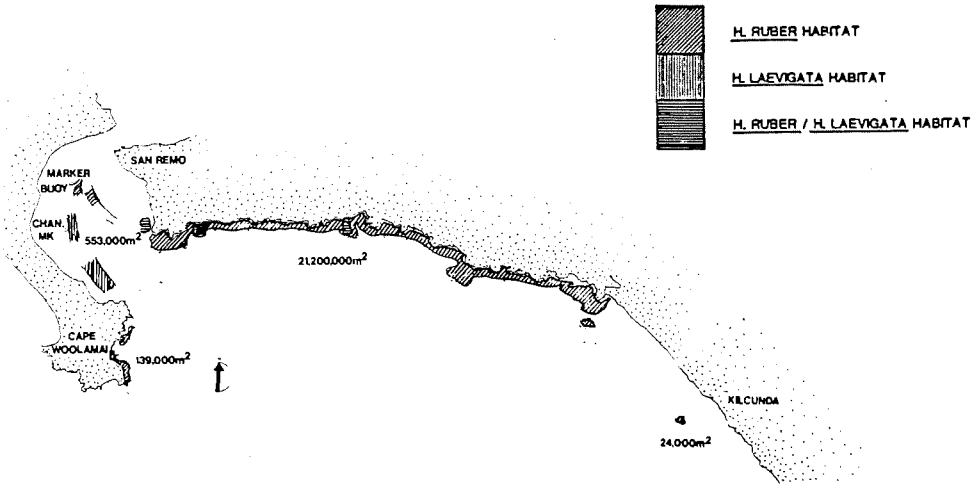

SECTION 31
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
PHILLIP ISLAND
MUD FLATS
SUNDERLAND BAY
NEWHAVEN
SAN REMO
93,000m²
FLYNN'S REEF
BARRY BEACH
CAT BAY
WOOLAMAI BEACH
264,000m²
853,000m²
872,000m²
NOBBIES
SEAL ROCKS
PYRAMID ROCK
CAPE WOOLAMAI
1,388,000m²
CAT BAY
CATCH (tonnes)
CPUE (kg/hr)
THE NOBBIES
PYRAMID REEF
WOOLAMAI REEF
1979
1980
1981
1982
1983
1984

Figure 22.

SECTION 32



SAN REMO TO KILCUNDA

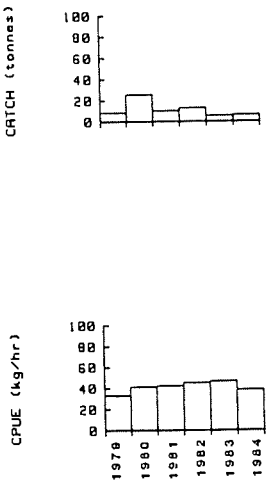
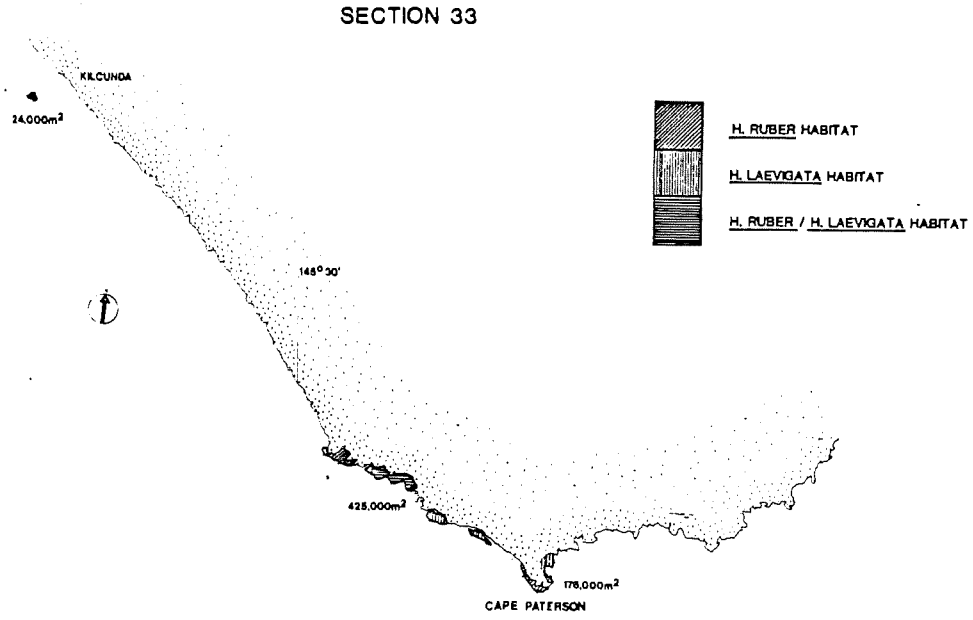


Figure 23.


SECTION 33
KILCUNDA
24,000m²
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
148° 30'
425,000m²
176,000m²
CAPE PATERSON

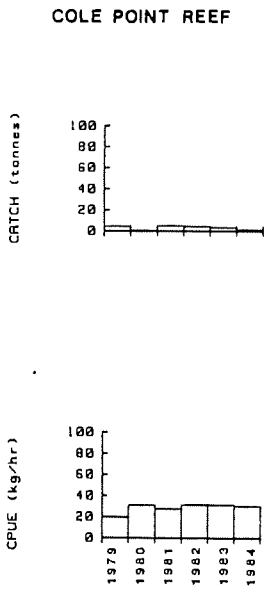
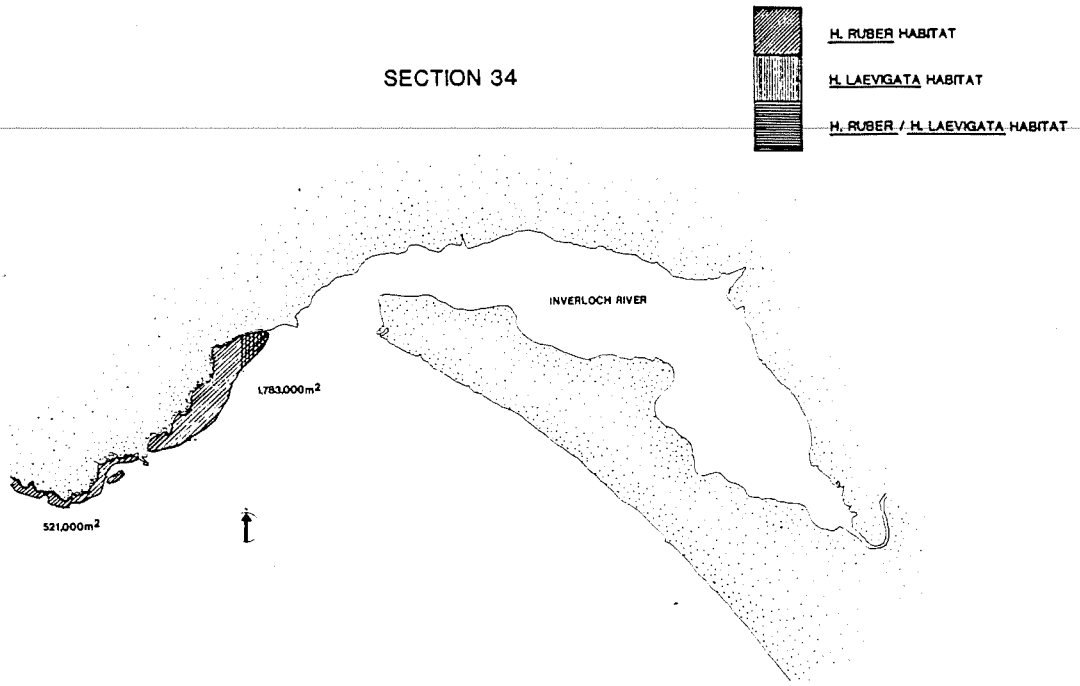

COLE POINT REEF
CATCH (tonnes)
100
80
60
40
20
0
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 24.

SECTION 34



INVERLOCH REEF

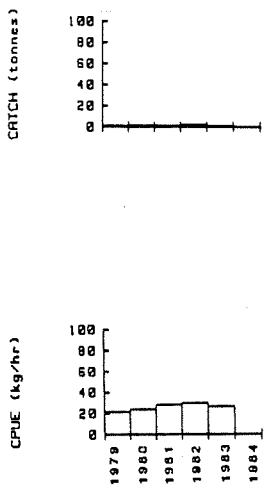
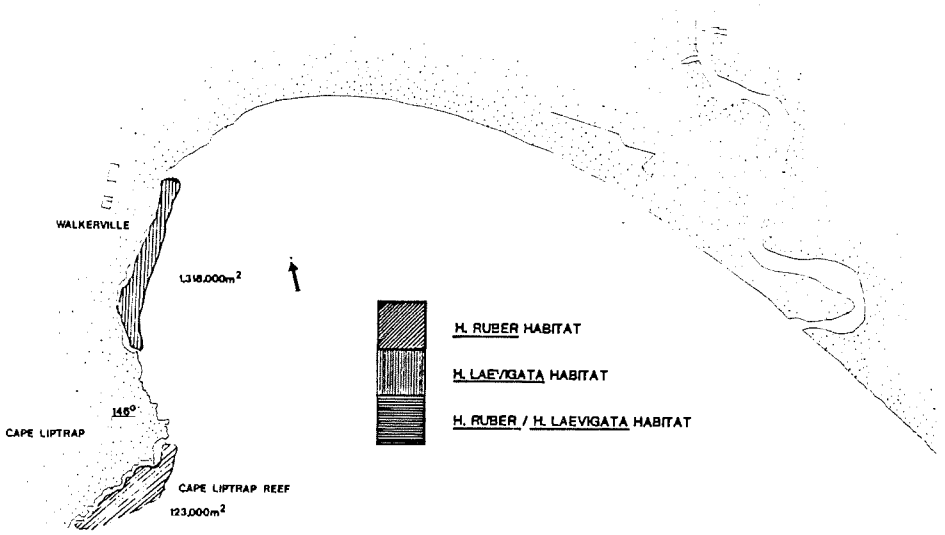
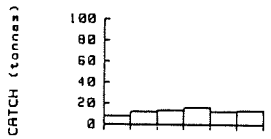


Figure 25.

SECTION 37



CAPE LIPTRAP REEF



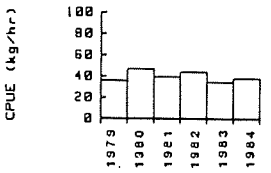
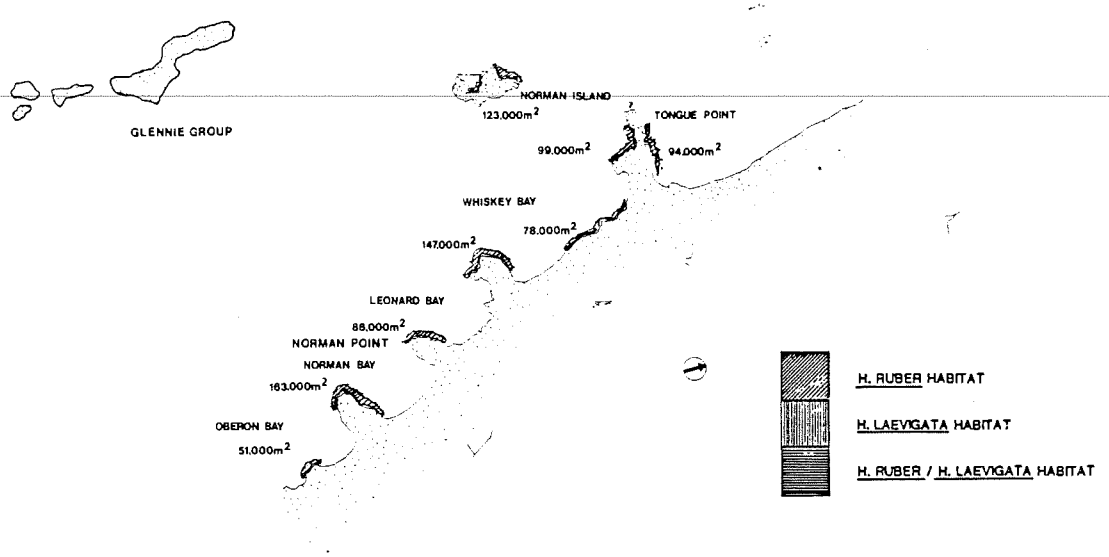


Figure 26.

SECTION 39



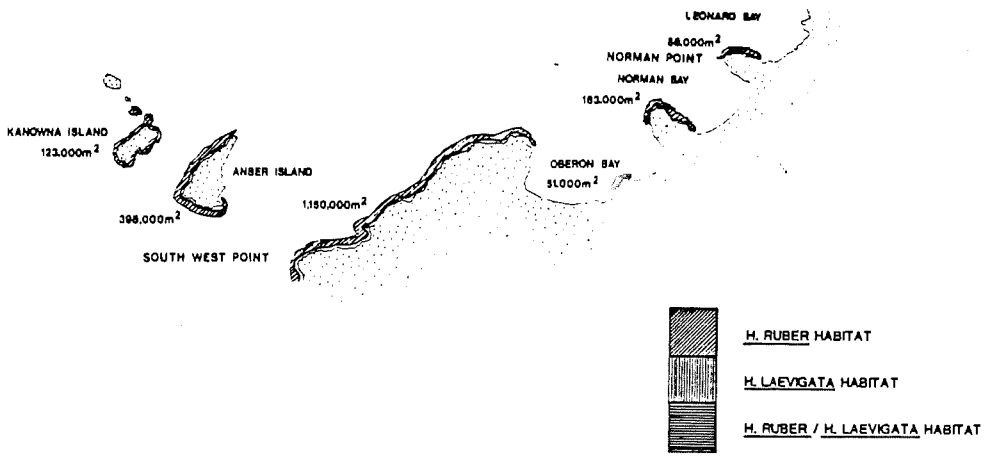
WARATAH BAY TO NORMAN POINT

NORMAN ISLAND

THE GLENNIE GROUP

Figure 27.

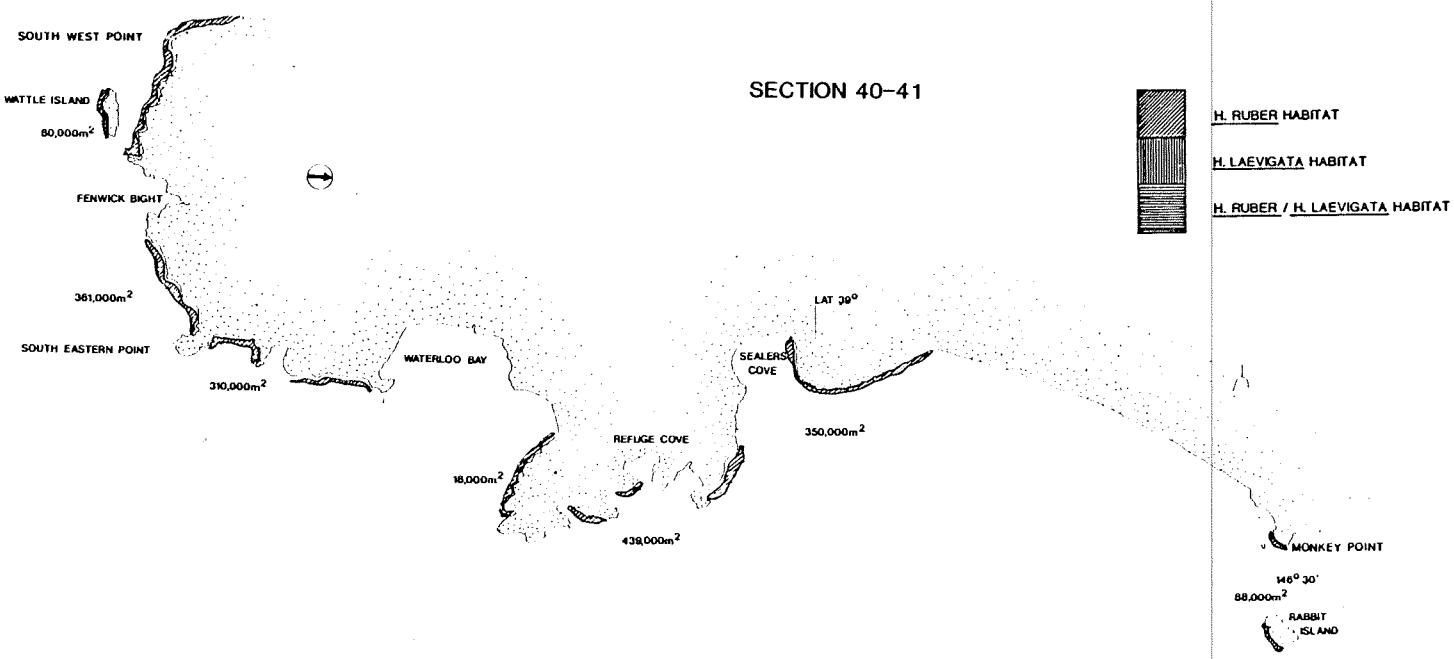
SECTION 40

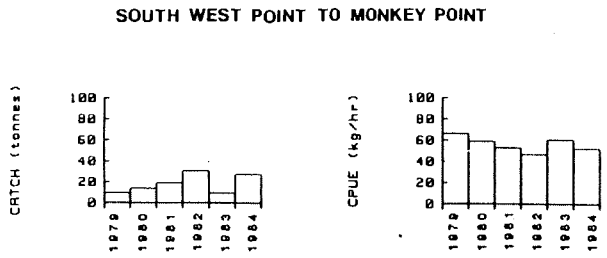


NORMAN POINT TO SOUTH WEST POINT

THE ANSER GROUP

Figure 28.


SECTION 40–41
SOUTH WEST POINT
WATTLE ISLAND
80,000m²
FENWICK BIGHT
361,000m²
SOUTH EASTERN POINT
310,000m²
WATERLOO BAY
REFUGE COVE
18,000m²
439,000m²
SEALERS COVE
LAT 39°
350,000m²
MONKEY POINT
146° 30'
88,000m²
RABBIT ISLAND
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT


SOUTH WEST POINT TO MONKEY POINT
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

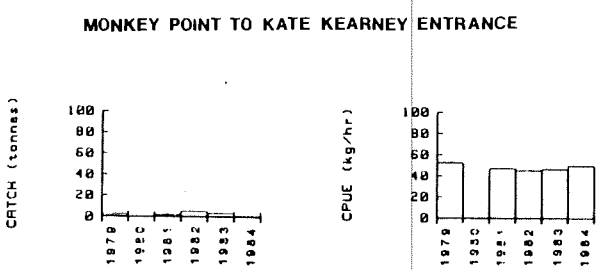

MONKEY POINT TO KATE KEARNEY ENTRANCE
CATCH (tonnes)
CPUE (kg/hr)
100
80
60
40
20
0
1979
1980
1981
1982
1983
1984

Figure 29.

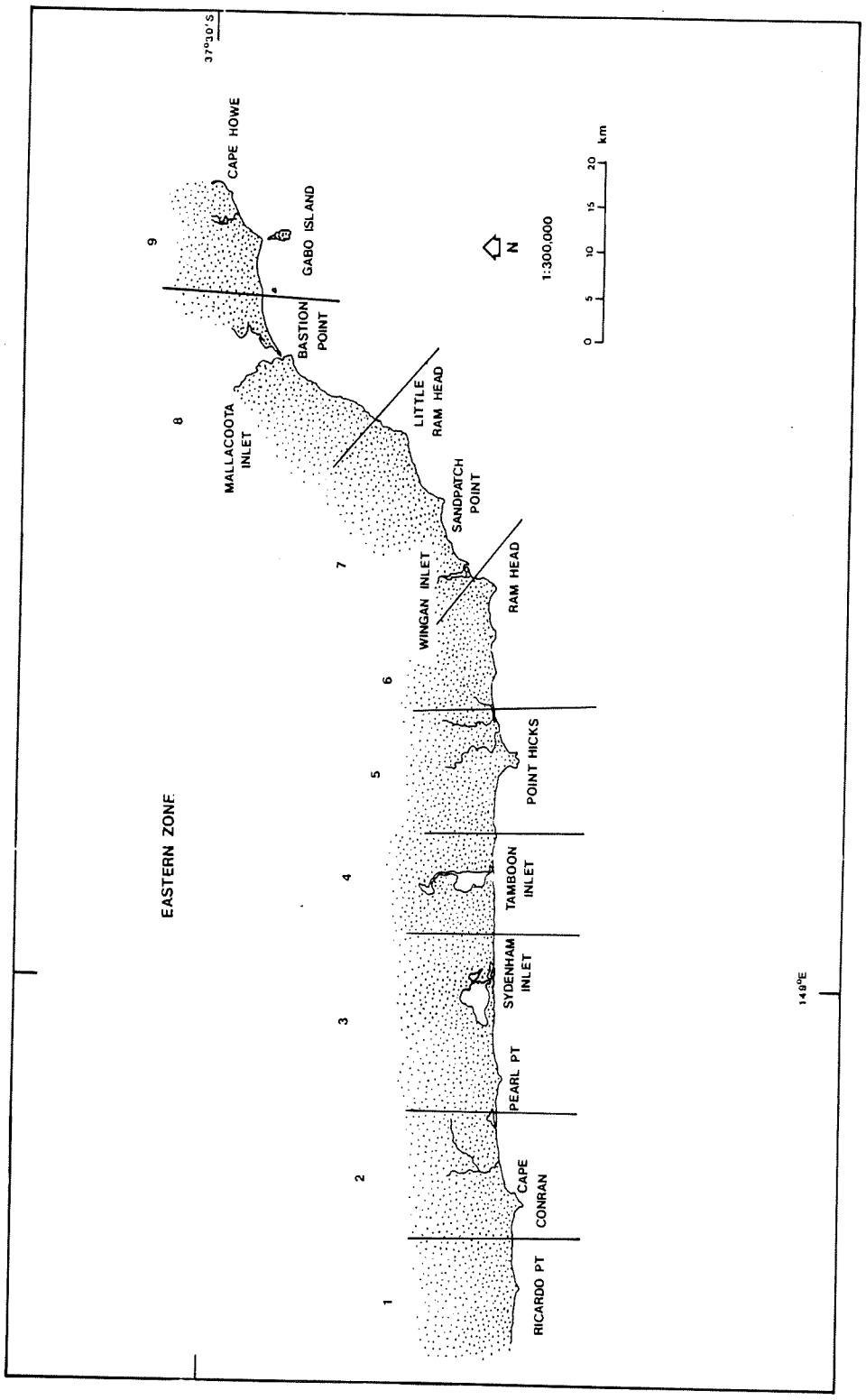
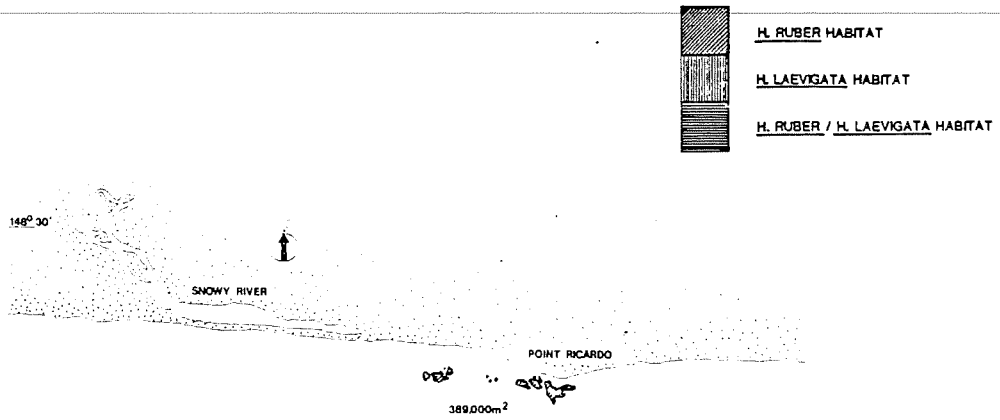
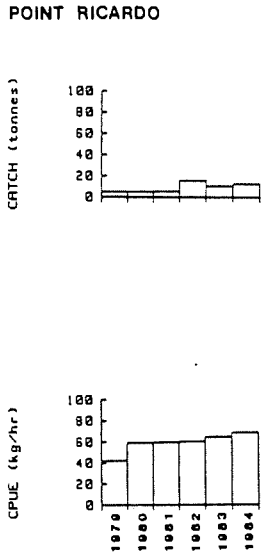


Figure 30. Map of the eastern zone showing the sections of coastline used in the survey of abalone reefs.





Figures 31 to 39. Maps of sections of coastline in the eastern zone indicating abalone reef, estimates of reef area (m^2) and species distribution (H. ruber or H. laevigata).

Annual catches and catches per unit effort are shown for reefs of commercial significance.

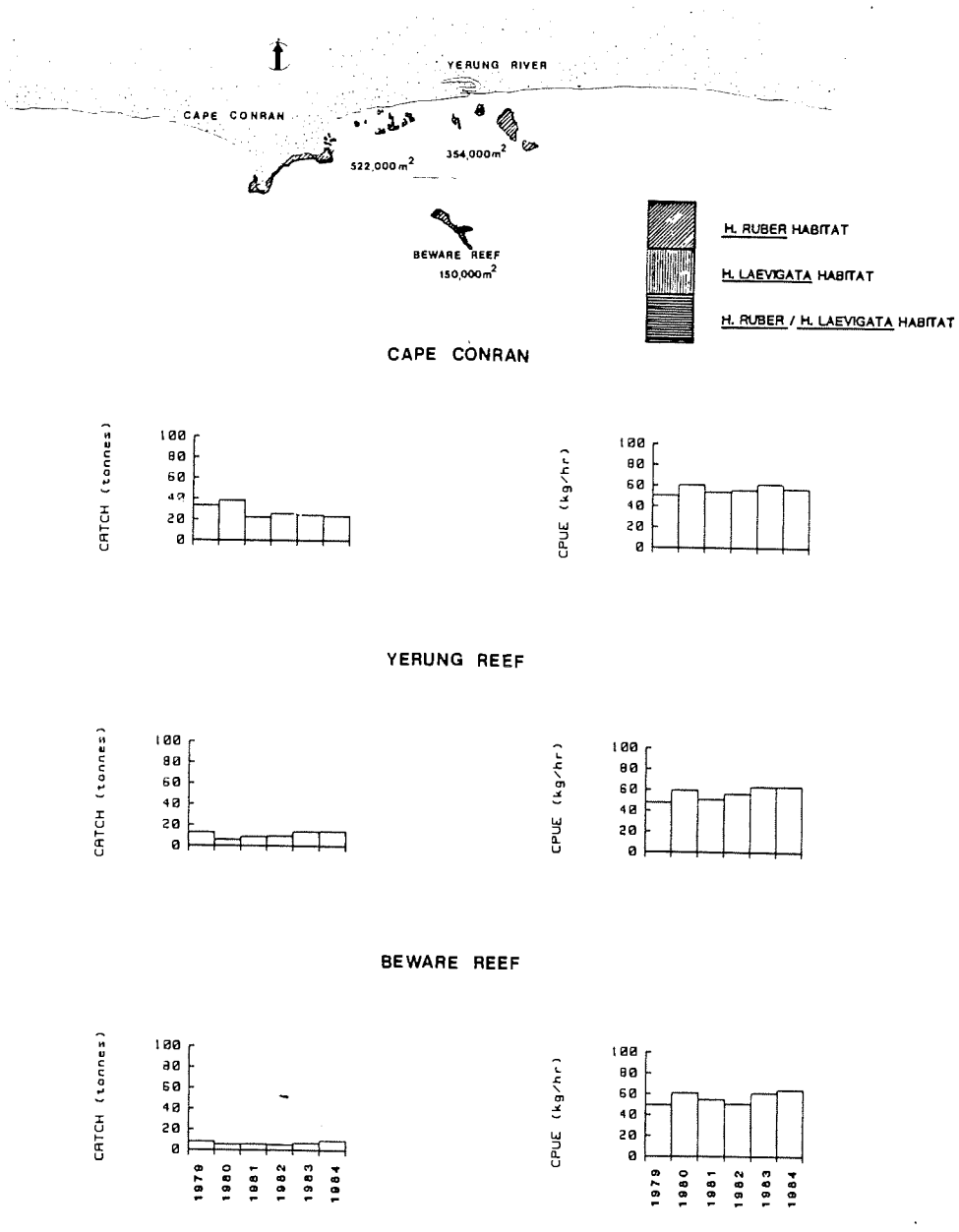
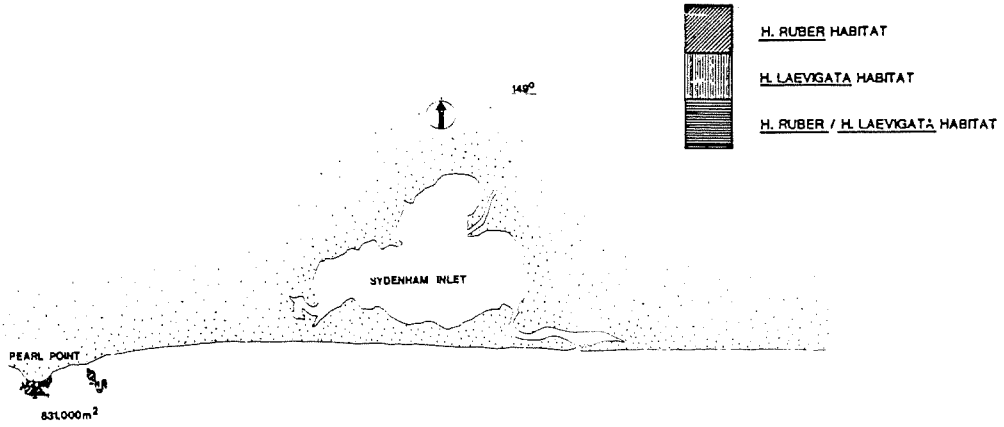

YERUNG RIVER
CAPE CONRAN
522,000m²
354,000m²
BEWARE REEF
150,000m²
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
CAPE CONRAN
CATCH (tonnes)
CPUE (kg/hr)
YERUNG REEF
BEWARE REEF
1979
1980
1981
1982
1983
1984

Figure 32.



PEARL POINT

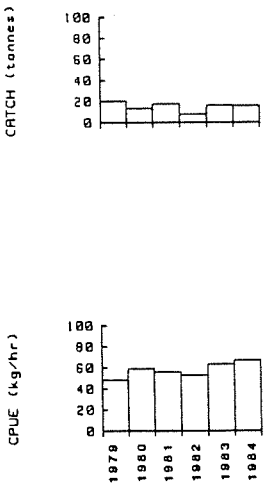
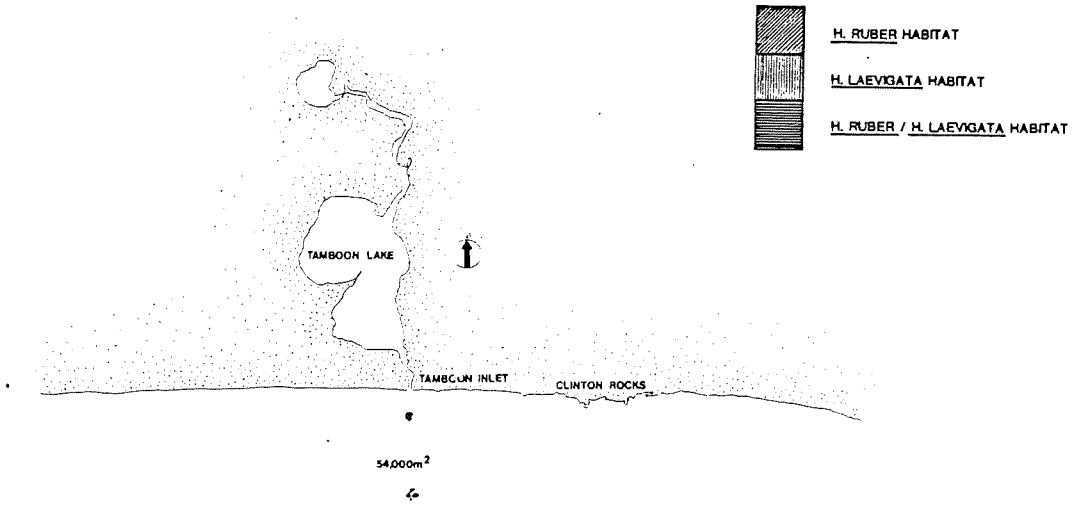
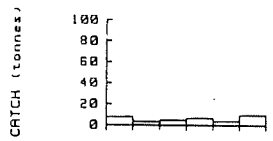


Figure 33.

SECTION 4



TAMBOON REEF



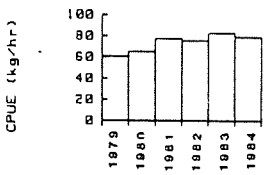
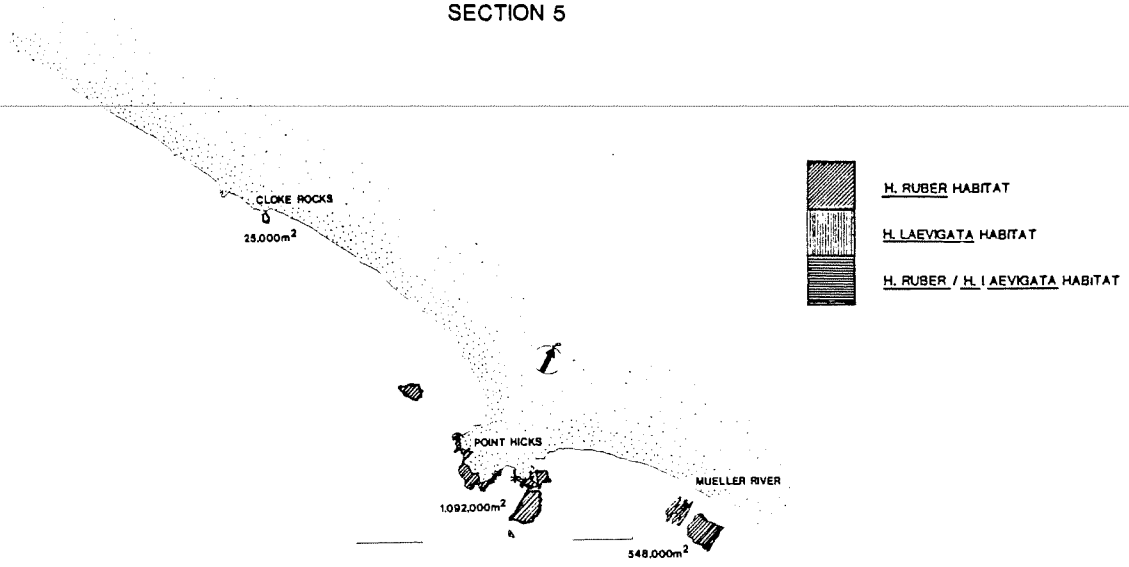


Figure 34.



POINT HICKS

MUELLER REEF

Figure 35.

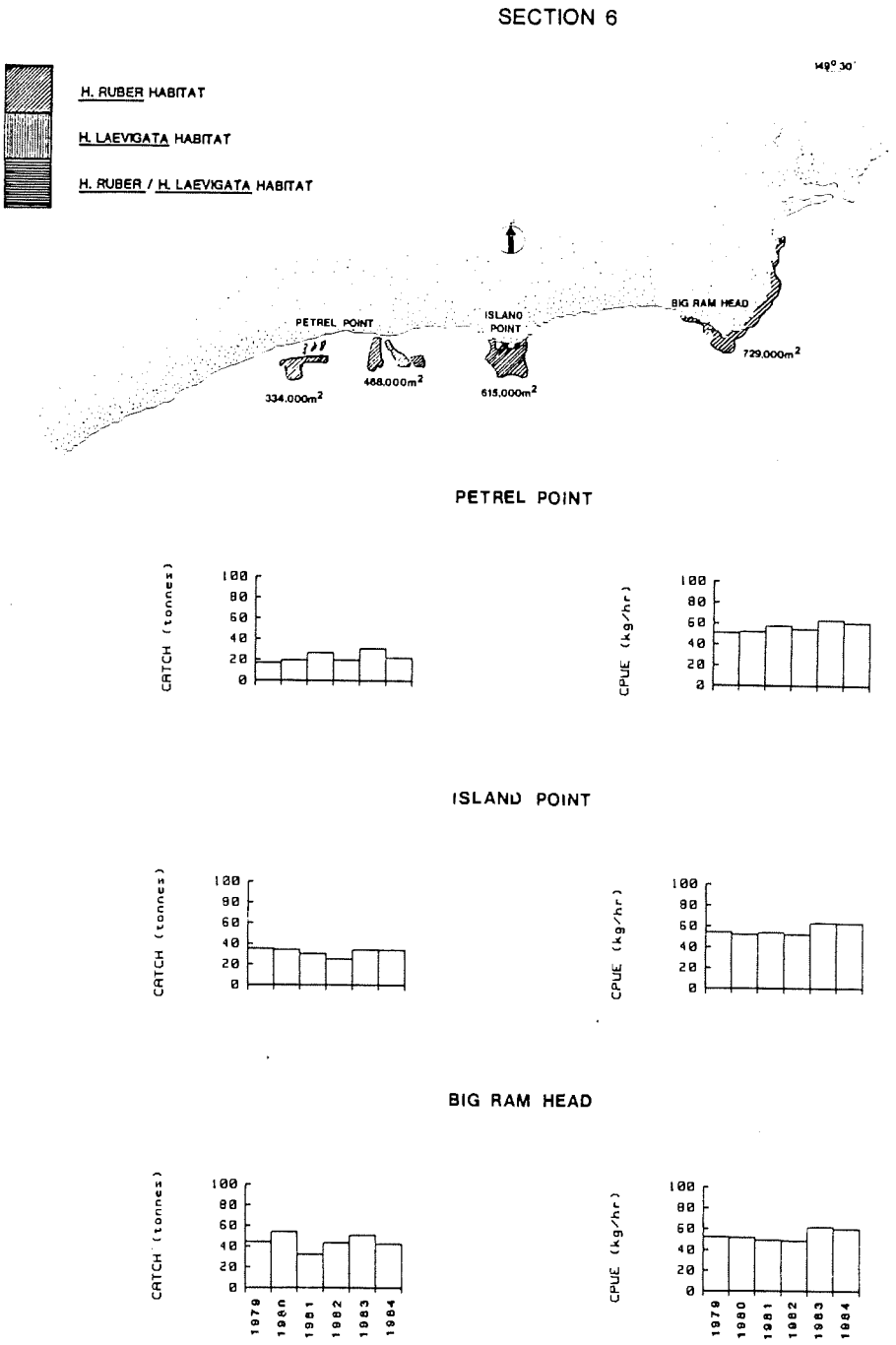
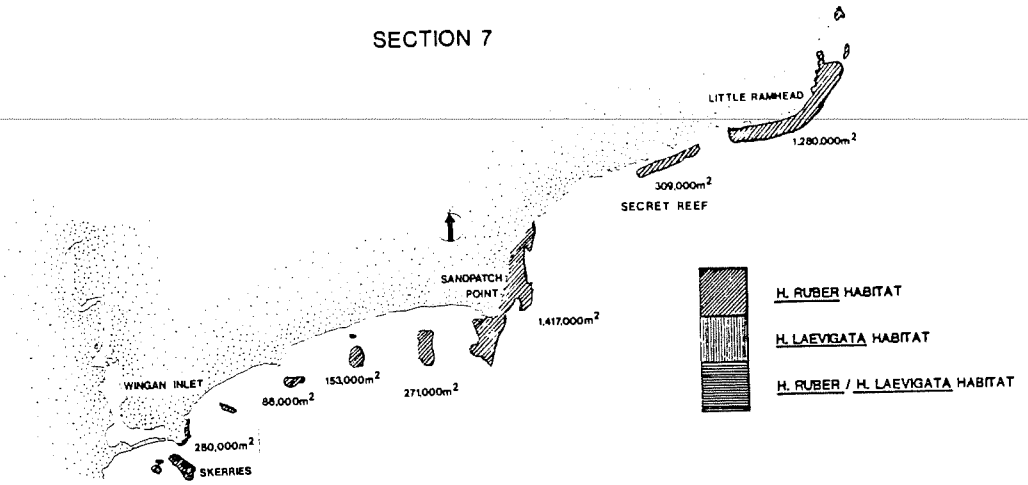

SECTION 6
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
148° 30'
PETREL POINT
ISLAND POINT
BIG RAM HEAD
334.000m²
468.000m²
615.000m²
729.000m²
PETREL POINT
CATCH (tonnes)
CPUE (kg/hr)
ISLAND POINT
BIG RAM HEAD
0
20
40
60
80
100
1979
1980
1981
1982
1983
1984

Figure 36.

SECTION 7



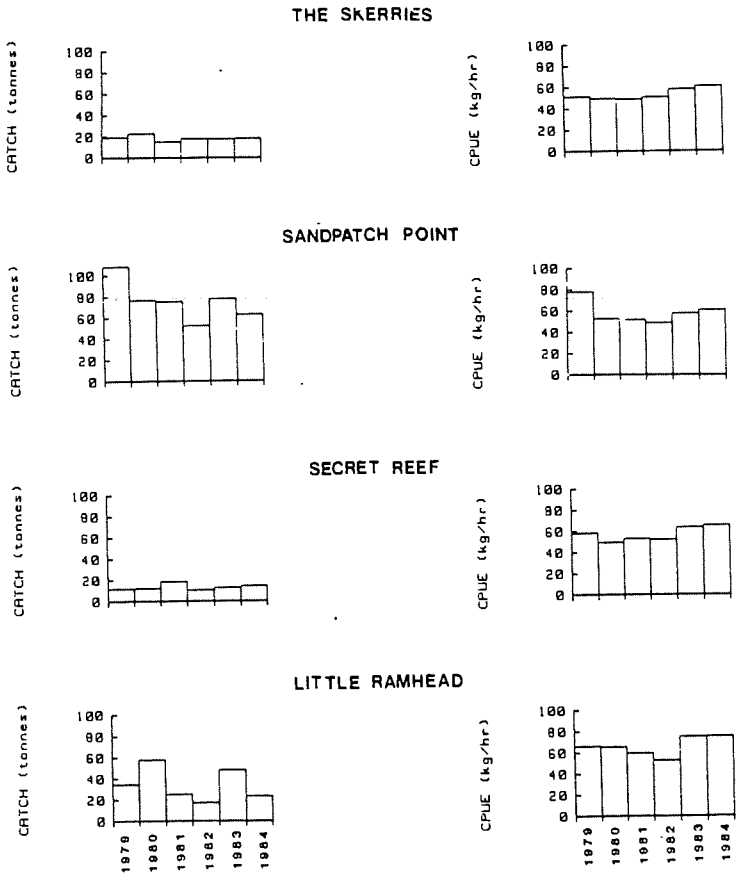
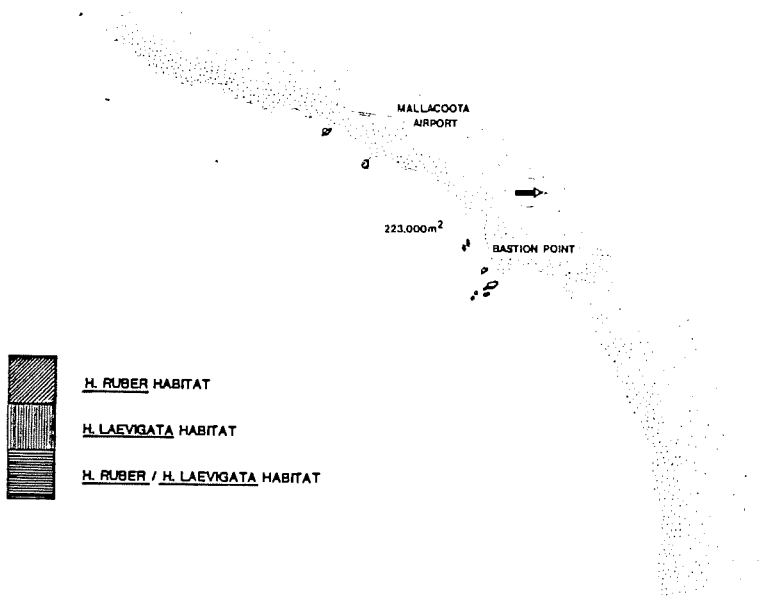


Figure 37.

SECTION 8



AERODROME

BASTION POINT

Figure 38.

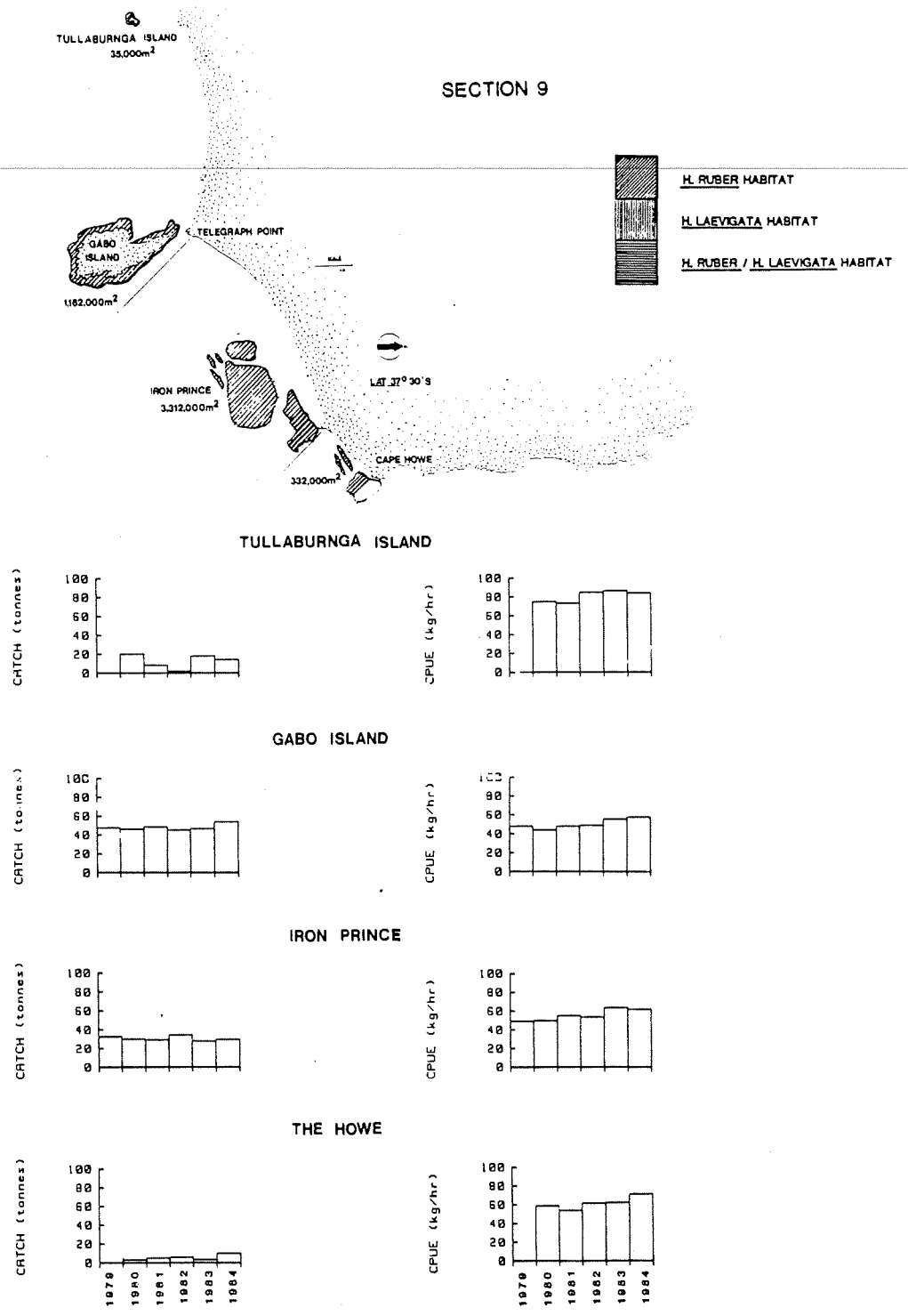

SECTION 9
TULLABURNGA ISLAND
35,000m²
GABO ISLAND
1,182,000m²
TELEGRAPH POINT
IRON PRINCE
3,312,000m²
LAT 37° 30' S
CAPE HOWE
332,000m²
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
TULLABURNGA ISLAND
CATCH (tonnes)
CPUE (kg/hr)
GABO ISLAND
IRON PRINCE
THE HOWE
0
20
40
60
80
100
1979
1980
1981
1982
1983
1984

Figure 39.

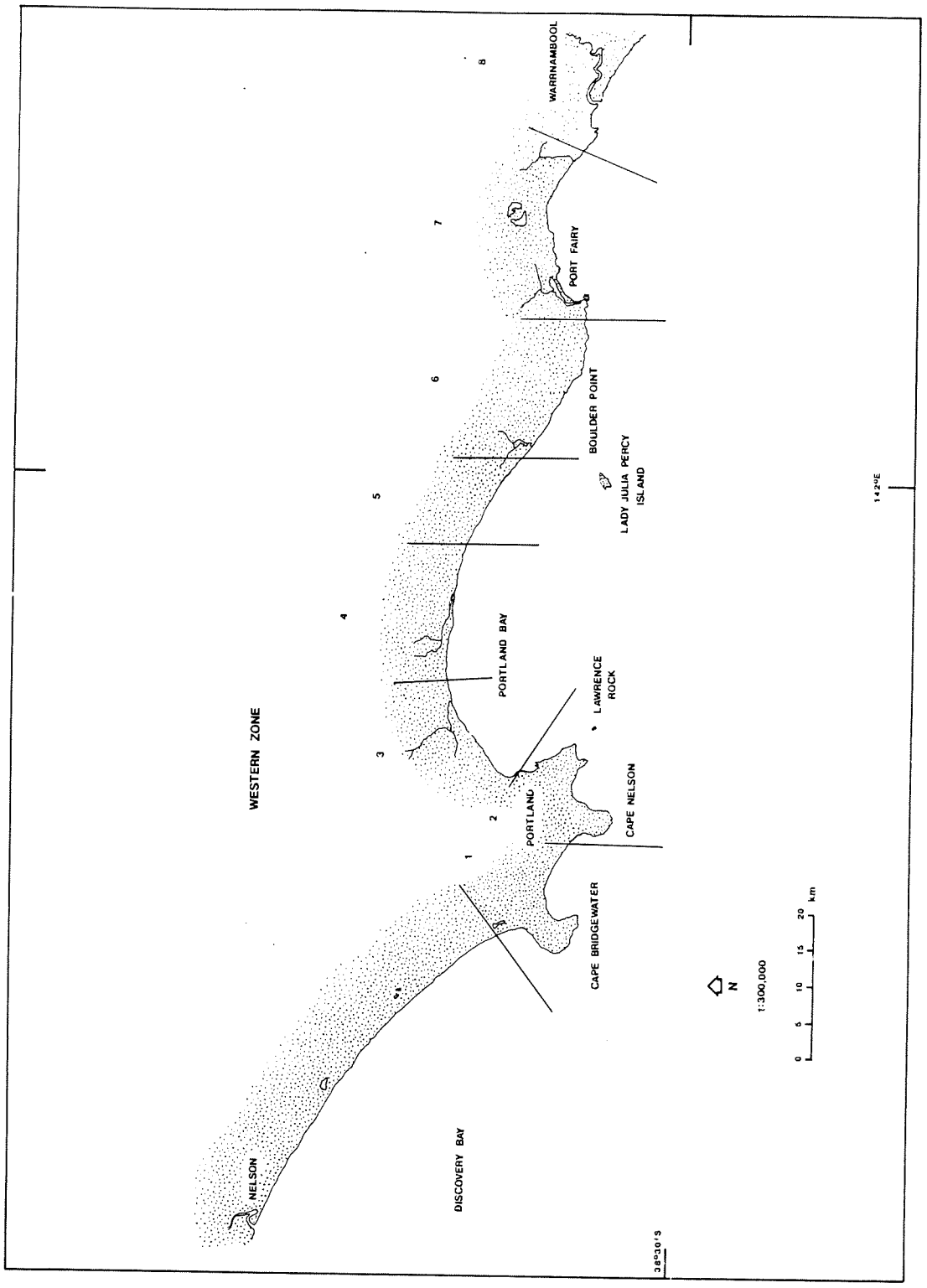
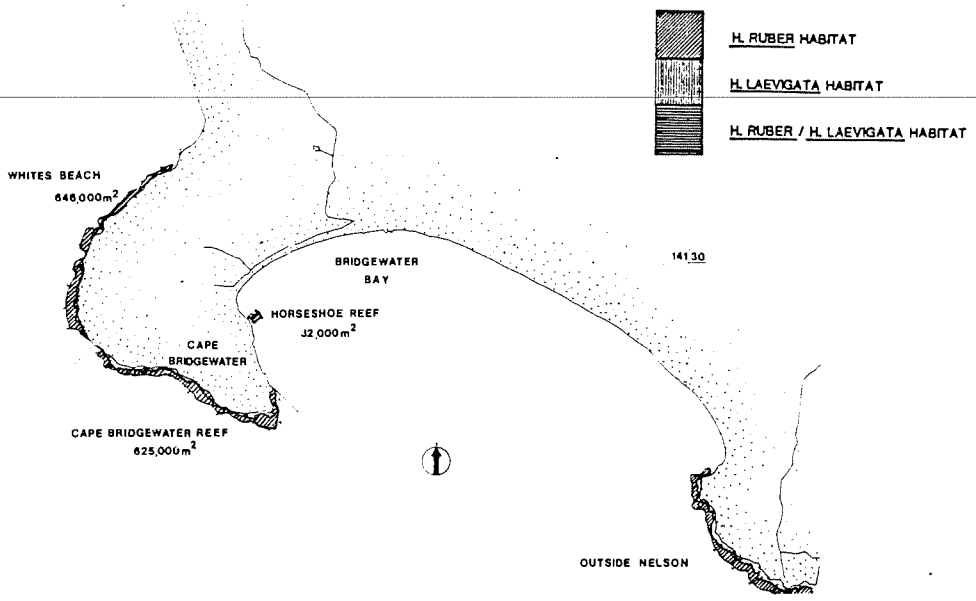


Figure 40. Map of the western zone showing the sections of coastline used in the survey of abalone reefs.

SECTION 1



WHITES BEACH

CAPE BRIDGEWATER REEF

Figures 41 to 46. Maps of sections of coastline in the western zone indicating abalone reef, estimates of reef area (m^2) and species distribution (H. ruber or H. laevigata).

Annual catches and catches per unit effort are shown for specific reefs or sections of coastline of commercial significance.

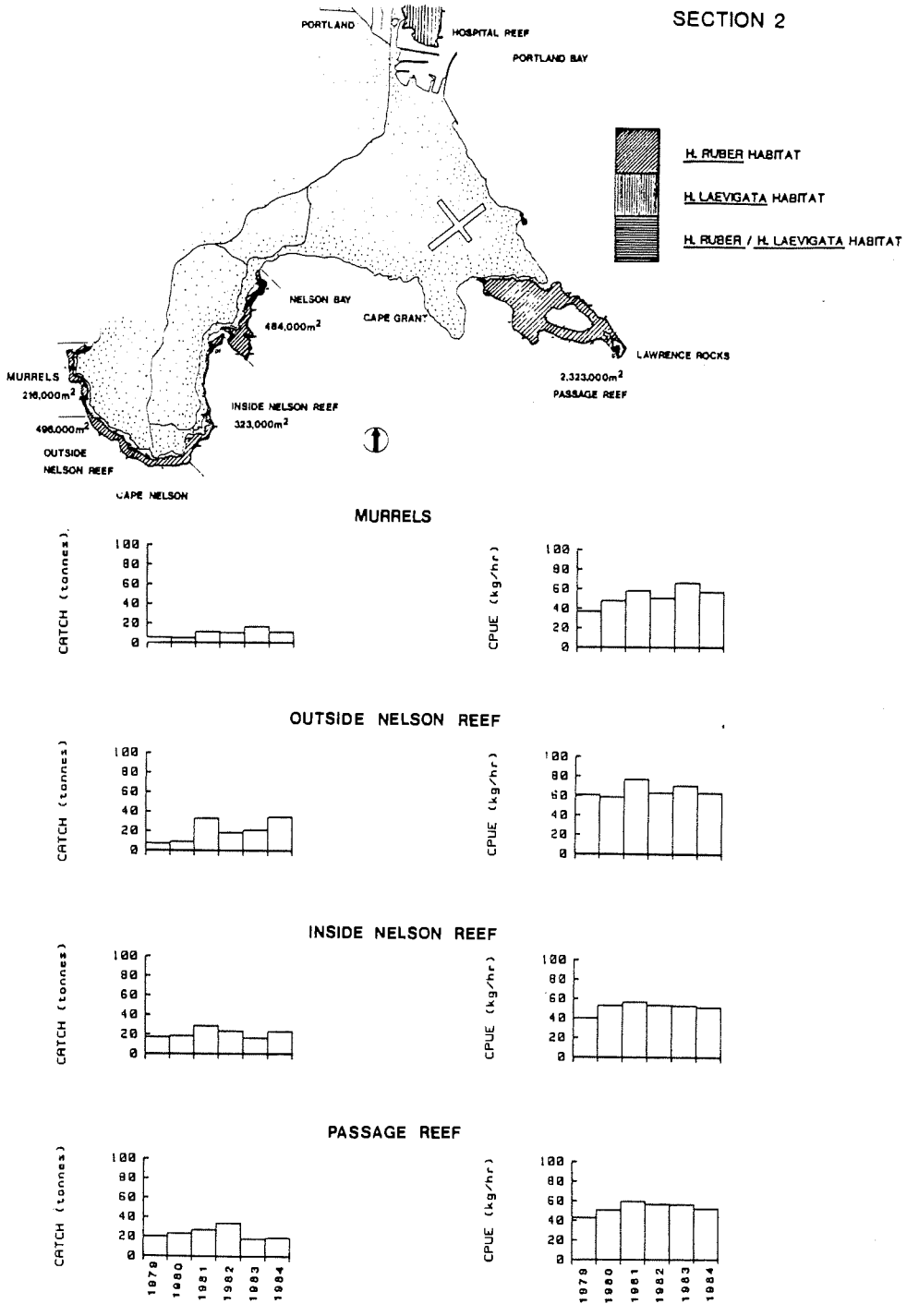

SECTION 2
PORTLAND
HOSPITAL REEF
PORTLAND BAY
H. RUBER HABITAT
H. LAEVIGATA HABITAT
H. RUBER / H. LAEVIGATA HABITAT
NELSON BAY
484,000m²
CAPE GRANT
LAWRENCE ROCKS
2,323,000m²
PASSAGE REEF
MURRELS
216,000m²
498,000m²
INSIDE NELSON REEF
323,000m²
OUTSIDE
NELSON REEF
CAPE NELSON
MURRELS
OUTSIDE NELSON REEF
INSIDE NELSON REEF
PASSAGE REEF
CATCH (tonnes)
CPUE (kg/hr)
0
20
40
60
80
100
1979
1980
1981
1982
1983
1984

Figure 42.

SECTION 3-5

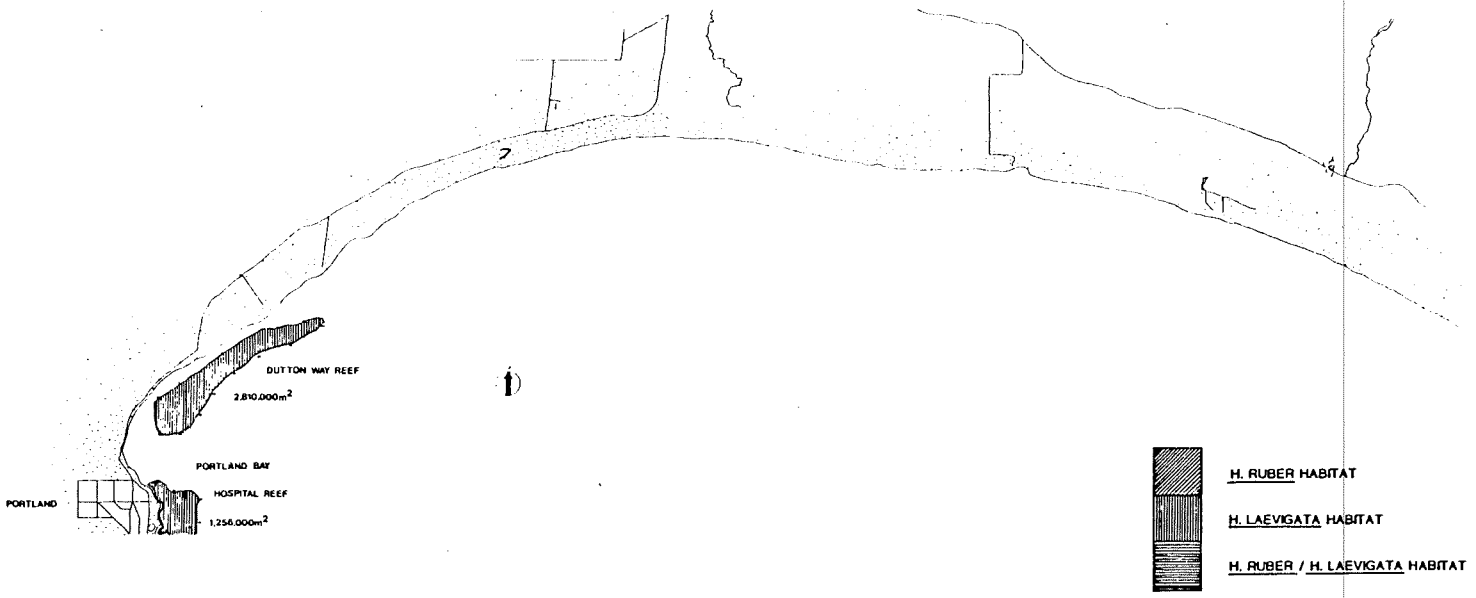
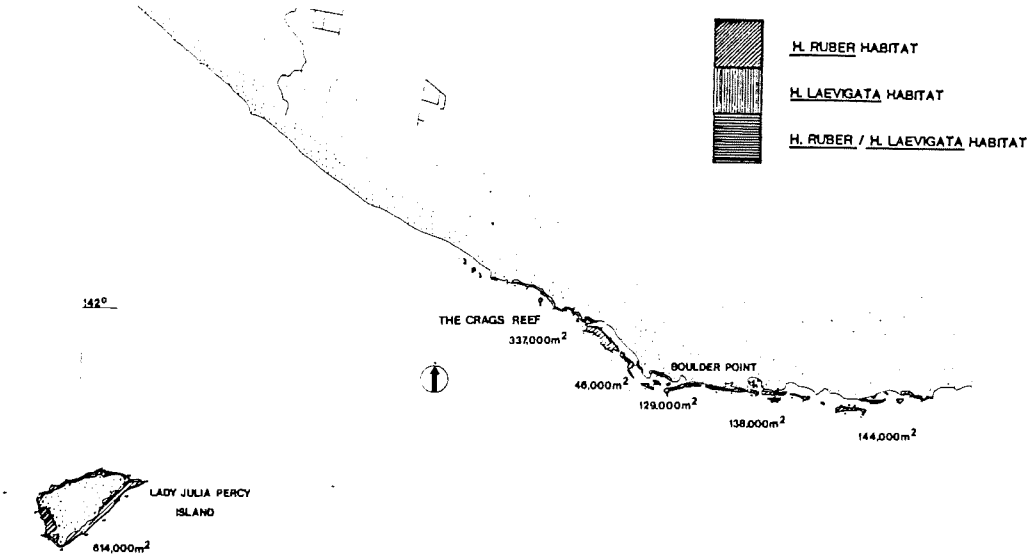


Figure 43.

SECTION 6

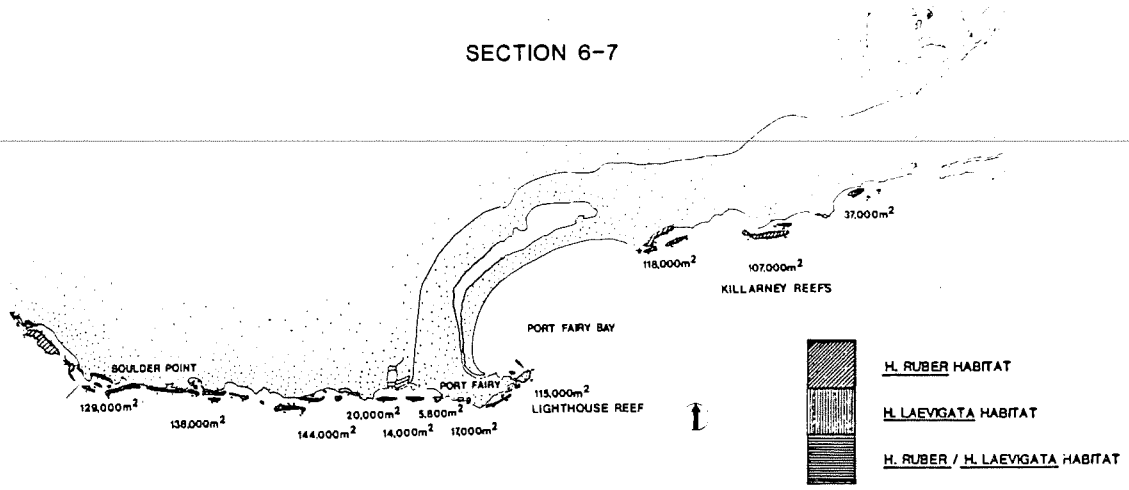


LADY JULIA PERCY ISLAND

THE CRAGS REEF

Figure 44.

SECTION 6-7



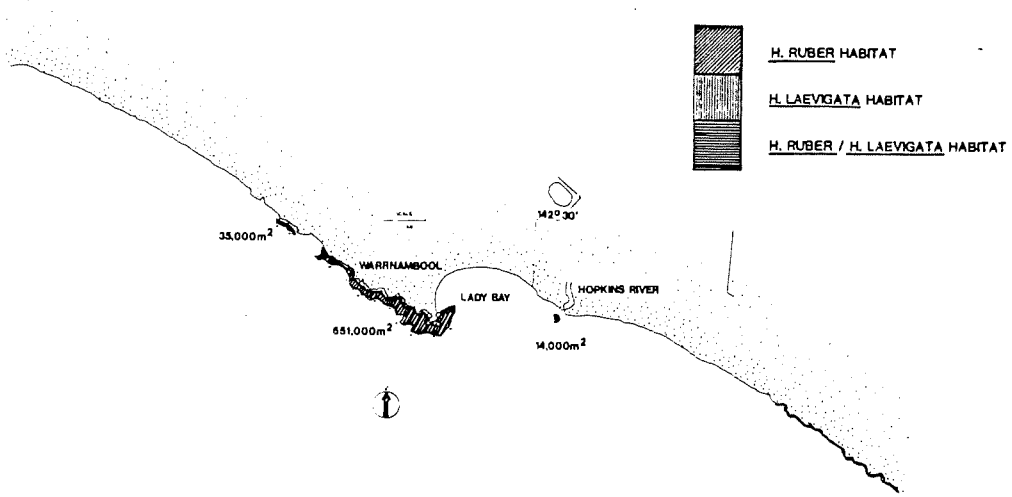
BOULDER POINT TO PORT FAIRY

LIGHTHOUSE REEF

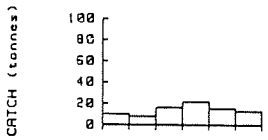
KILLARNEY REEFS

Figure 45.

SECTION 8



WARRNAMBOOL



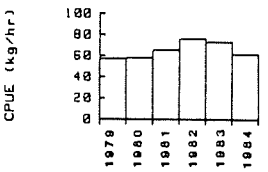


Figure 46.

Department of
Conservation
Forests & Lands
Fisheries and Wildlife Service

REPRODUCTIVE BIOLOGY OF BLACKLIP ABALONE HALIOTIS RUBER LEACH FROM FOUR VICTORIAN POPULATIONS.

by

P.E. McShane,
K.H.H. Beinssen, M.G. Smith,
S. O'Connor, and N.J. Hickman.

May 1986

Technical Report No. 55

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FECUNDITY	3
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SEX RATIO	3
MACROSCOPIC GONAD INDEX	3
GAMETOGENESIS	4
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DISCUSSION	11
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ABSTRACT

McShane, P.E., Beinssen, K.H.H., Smith, M.G., O'Connor, S. and Hickman, N.J. (1986). Reproductive biology of blacklip abalone Haliotis ruber Leach from four Victorian populations. Mar. Sci. Lab. Tech. Rep. 00. 00 pp.

Seasonal variation in a macroscopic gonad index (data for males and females combined) for Haliotis ruber from populations on the Victorian coast at Lorne, Point Lonsdale, Portsea and Flinders indicated that three of the populations spawned during summer; the population at Flinders appeared to release gametes throughout the year. The population at Portsea spawned twice, during summer and autumn. Although the populations at Point Lonsdale and Portsea were only 4 km apart, their spawning was asynchronous. At both these sites sea temperature correlated inversely with gonad index, but had little correlation with onset of spawning. Sea temperature was measured only at Portsea and Point Lonsdale.

The relationship between size of oocyte and frequency of occurrence revealed ovarian development to be consistent with changes in the macroscopic gonad index, as did histological examination of ovarian tissue. Haliotis ruber appeared less fecund than other species of abalone. Variation in fecundity with length showed that one H. ruber longer than 100 mm can produce more than half a million eggs.

Marine Resources Management Branch, Fisheries and Wildlife Service,
Department of Conservation, Forests and Lands, P.O. Box 114,
Queenscliff, Victoria 3225, Australia

INTRODUCTION

The blacklip abalone Haliotis ruber Leach provides the basis of a lucrative fishery in Victoria. Despite this, little published information exists on the biology of Victorian populations of this species. A study of the reproductive biology of populations of H. ruber in South Australian waters (Shepherd and Laws 1974) reveals that their spawning behaviour differs considerably. Consequently the results of that study cannot be used to define the reproductive biology of Victorian populations.

An understanding of the reproductive biology of populations of H. ruber in Victoria is important if we are to gain an insight into their settlement and recruitment processes. Here we describe and compare the reproductive cycles of four Victorian populations. We also estimate their fecundity, sex ratios and gonadal development.

MATERIALS AND METHODS

SAMPLE COLLECTION

Between August 1969 and March 1972, H. ruber were collected each month, whenever possible, from populations at Lorne, Flinders and Portsea; during 1981, when sea temperatures were also measured, samples were taken from Portsea and Point Lonsdale (Fig. 1)

MACROSCOPIC GONAD INDEX

A macroscopic gonad index indicating the relative cross-sectioned surface area of the gonad (Boolotian et al. 1962) was measured for monthly samples of 15-30 abalone of each sex. We selected only animals about 120 mm long since the gonad index has been shown to be independent of size for animals longer than 90 mm (Newman 1967, Hayashi 1980) and errors are minimized by using abalone of similar length. For each animal, a section of gonad, which surrounds digestive tissue, was taken near the main body of the visceral coil (Giorge and De Martini 1977) and preserved in 10% formalin. The perimeters of cross-sections of gonad and digestive glands were traced with the aid of a dissecting microscope equipped with a camera lucida and measured planimetrically (Shepherd and Lowe 1974).

GAMETOGENESIS

The stage of gametogenesis of populations at Point Lonsdale and Portsea was assessed histologically from sections of gonad and digestive tissue taken from next to the visceral coil. Tissues from 3 - 10 animals of each sex were fixed in Bouin's or Davidson's fixative, embedded in paraffin, sectioned to 8 um and stained with haemotoxylin and eosin.

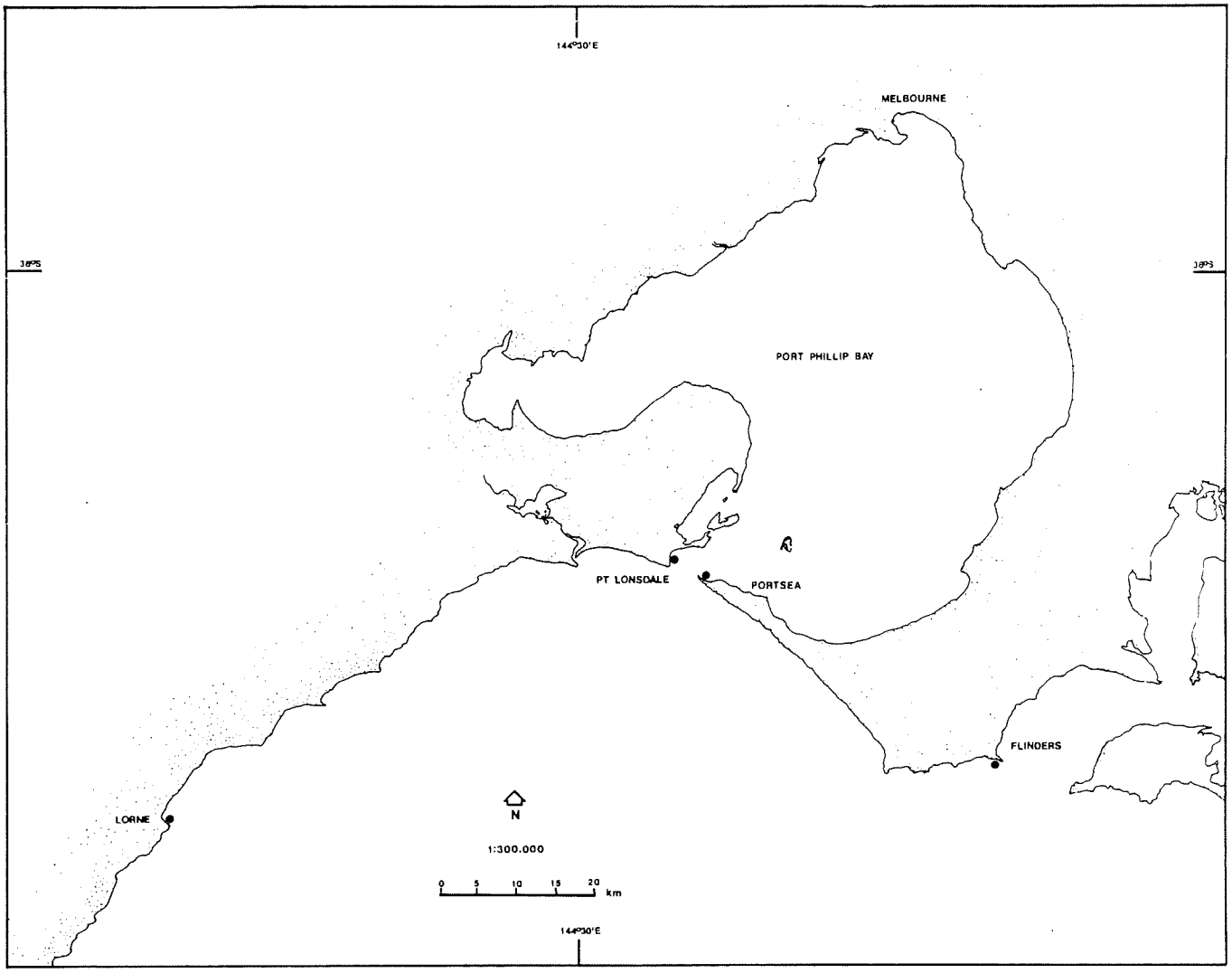

Figure 1. Sample sites on the Victorian coast.

The reproductive states of the gonads of five males and five females taken from as many monthly samples as possible were estimated as being at one of three arbitary stages: stage 1, spawning; stage 2, spent redevelopment; stage 3, mature.

The ovaries of up to ten individuals from each monthly sample were scanned at random and the diameters of at least 50 ova were measured (Webber and Giese 1969). We preferred this method to dissection since small oocytes tend to remain attached to the trabeculae and thus tend to be undersampled (Shepherd and Laws 1974). Oocytes were measured in 25 um size groups and the percentage frequency of occurrence of oocytes of a particular size group was calculated.

FECUNDITY

The fecundity of 24 abalone collected from Portsea during 1971 was estimated according to the method of Newman (1967). Their length (widest shell dimension) was measured to the nearest millimeter and total live body weights were measured to the nearest gram so that relationships between fecundity and length, or fecundity and weight could be determined.

RESULTS

SEX RATIO

A 1:1 relationship existed for numbers of male and female abalone in all populations investigated (Table 1). This was also true for various size classes except for the Flinders population where young males (< 100 mm long) were more numerous than their female counterparts.

MACROSCOPIC GONAD INDEX

The mean gonad index for males was similar to that for females. The results for both sexes were therefore combined to calculate a mean gonad index used to describe the reproductive cycle of H. ruber.

Generally gonad indices were highest during late spring or early summer, indicating gonad maturity during that period. A fall in the gonad index occurred during the late summer often continuing into autumn. The reproductive cycle was completed with a period of rising gonad index values during the autumn/winter months indicative of gonad redevelopment. This pattern was displayed by the Lorne, Portsea and Point Lonsdale populations (Figs 2 and 3). An exception was the Flinders population where no clear seasonality in the gonad index was apparent.

TABLE 1. Numbers of female and male H. ruber in various length classes collected from three populations.

Length class (mm)	Number of H. ruber in length classes at: Portsea		Flinders		Lorne	
	Male	Female	Male	Female	Male	Female
0 - 100	230	203	376*	291*	69	68
101 - 120	338	370	372	381	339	360
> 121	111	112	52	61	327	300
TOTAL	679	685	800	773	735	728

* Significantly different in chi-square test ($P < 0.005$): in no other pair were numbers significantly different.

The timing of spawning and gametogenesis varied from year to year within a population. For example, recovery in the gonad index of the Portsea population commenced during February in 1970 and April the following year (Fig. 2). Highest gonad index values were obtained in December, January or October depending on the year samples were taken. Portsea and Lorne populations displayed similar reproductive cycles, yet a more recent comparison of Portsea and Point Lonsdale populations revealed differences in spawning periodicity even though little distance separates them (Fig. 3). The gonad index of the Point Lonsdale population continued to fall until March whereas recovery at Portsea had already begun. Furthermore, a secondary fall in the gonad index occurred at Portsea after April with subsequent rapid recovery implying a second spawning. A similar occurrence was evident for the Portsea population in 1971 (Fig. 2).

The gonad index of populations at Point Lonsdale and Portsea correlated inversely with sea temperature; however, there was no correlation between the time of spawning and sea temperature (Fig. 3)

GAMETOGENESIS

Figure 4 shows photomicrographs of various stages of gonadal development for males and females. Spawning (stage 1) females had ovaries with large oocytes, 150-250 um in diameter. Many oocytes were free in the lumen and were free of the gelatinous matrix surrounding other mature oocytes. Some oogonia remained attached to the trabeculae. At stage 2, ovaries (spent) were smaller and trabeculae were less closely packed than those of stage 1; open spaces were present in the lumen but very few large oocytes were present. The appearance of numerous small oocytes (< 50 um) attached to

closely packed trabeculae was typical of active ovaries following the spent state. Mature ovaries (stage 3) had densely packed oocytes, each surrounded by a gelatinous matrix. Mature oocytes had large nuclei with a prominent nucleolus and cytoplasm filled with yolk. Oocytes were often tear-drop shaped and attached to the trabeculae.

Reproductive stages in males were harder to distinguish due to the relatively small size of spermatozoa and spermatids. Spawning males had the largest testes with numerous spermatocytes, less densely packed than those of mature testes, and large lumina. The testes of spent males were very much smaller and had large lumina with poorly developed structure and relatively few spermatocytes. Redeveloping testes had densely packed smaller spermatogonia with basophillic nuclei surrounding a well developed lumen structure. In the ripe state testes had densely packed spermatocytes surrounding the lumen. The differences in structure and size between redeveloping, ripe and spawning males were tenuous. Therefore, size may be less reliable than gonad index as a criterion of the reproductive state of H. ruber. In evaluating seasonal variation of gonadal state, we compared only the size of oocytes with their frequency of occurrence (Fig. 5).

During December 1980, when spawning animals were first observed in the Portsea population, the distribution of oocytes in the population was bimodal (Fig. 5a). During the same month most of the Point Lonsdale population was at stage 1 of the reproductive cycle (Fig 5b) and oocytes of three sizes were present. During January 1981 an intermediate mode, although less pronounced than that at Point Lonsdale, was present in the Portsea population. A distinct bimodal oocyte distribution at Point Lonsdale in January reflected an increased proportion of developing individuals although most of the population were still spawning. During February most of the Portsea population were spawning and the frequency of occurrence of mature oocytes (150-200 um) had decreased appreciably although small oocytes (about 50 um) were still present. Indeed small oocytes were present throughout the study period. During March, when the gonads of the Portsea population were recovering, the frequency of occurrence of small oocytes increased while that of mature oocytes declined. Mature oocytes were present infrequently before a secondary spawning of the Portsea population during April. Active gametogenesis was apparent in May with no mature oocytes observed and a dominance of small oocytes in the oocyte size distribution. Most of the population was then in a spent/redevelopment state.

FECUNDITY

The fecundity of H. ruber increased with length (Fig. 6), but fecundity of individuals varied from 14,000 to more than two million. The smallest animal examined (92 mm long) produced 341,000 eggs. The fecundity of H. ruber at Portsea varied directly with body weight, but was less than that of other species of abalone as evident from the variation of fecundity with body weight (Table 2).

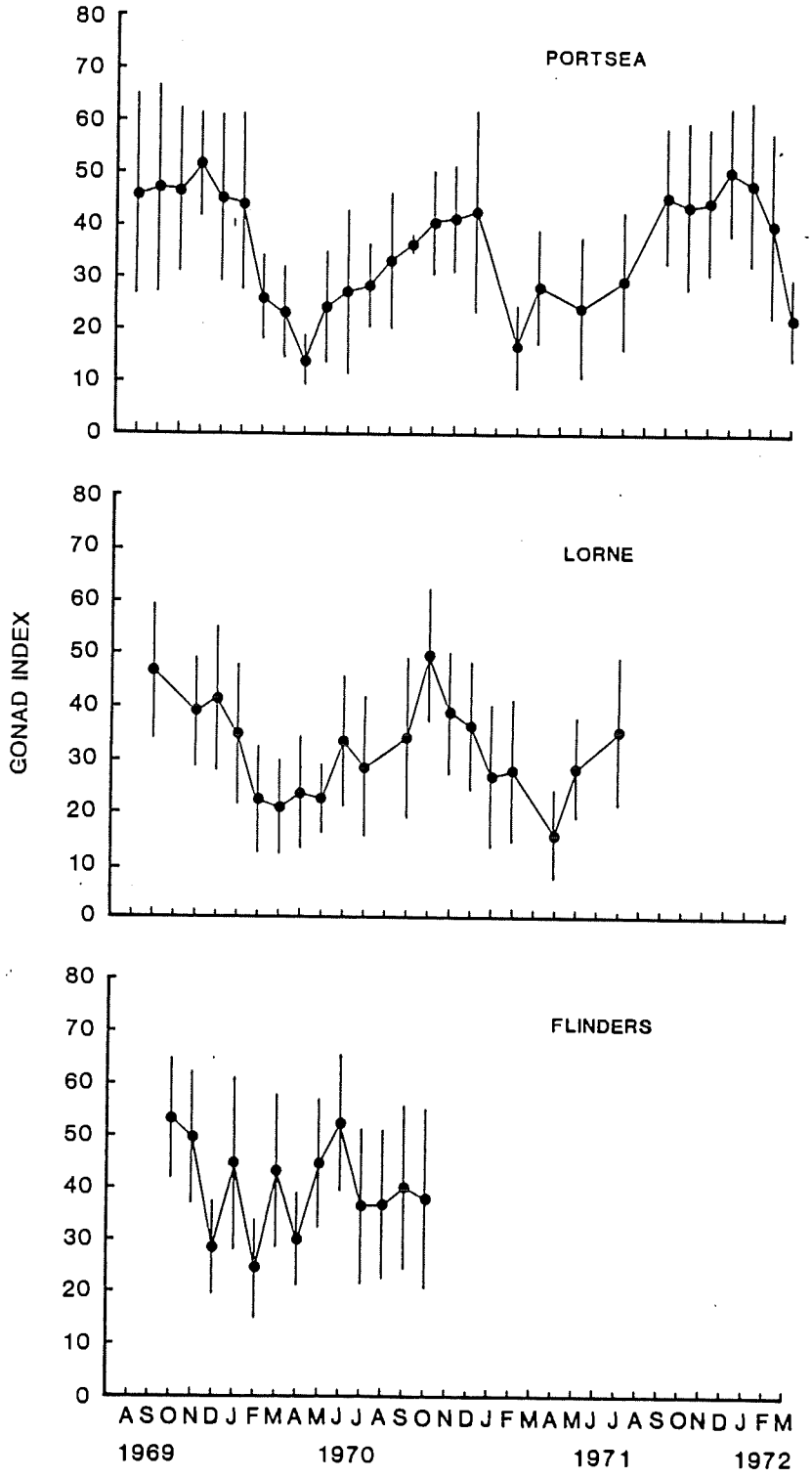

Figure 2. Seasonal variation in the gonad index of H. ruber populations at Portsea, Lorne and Flinders. Data are means ±standard deviation.

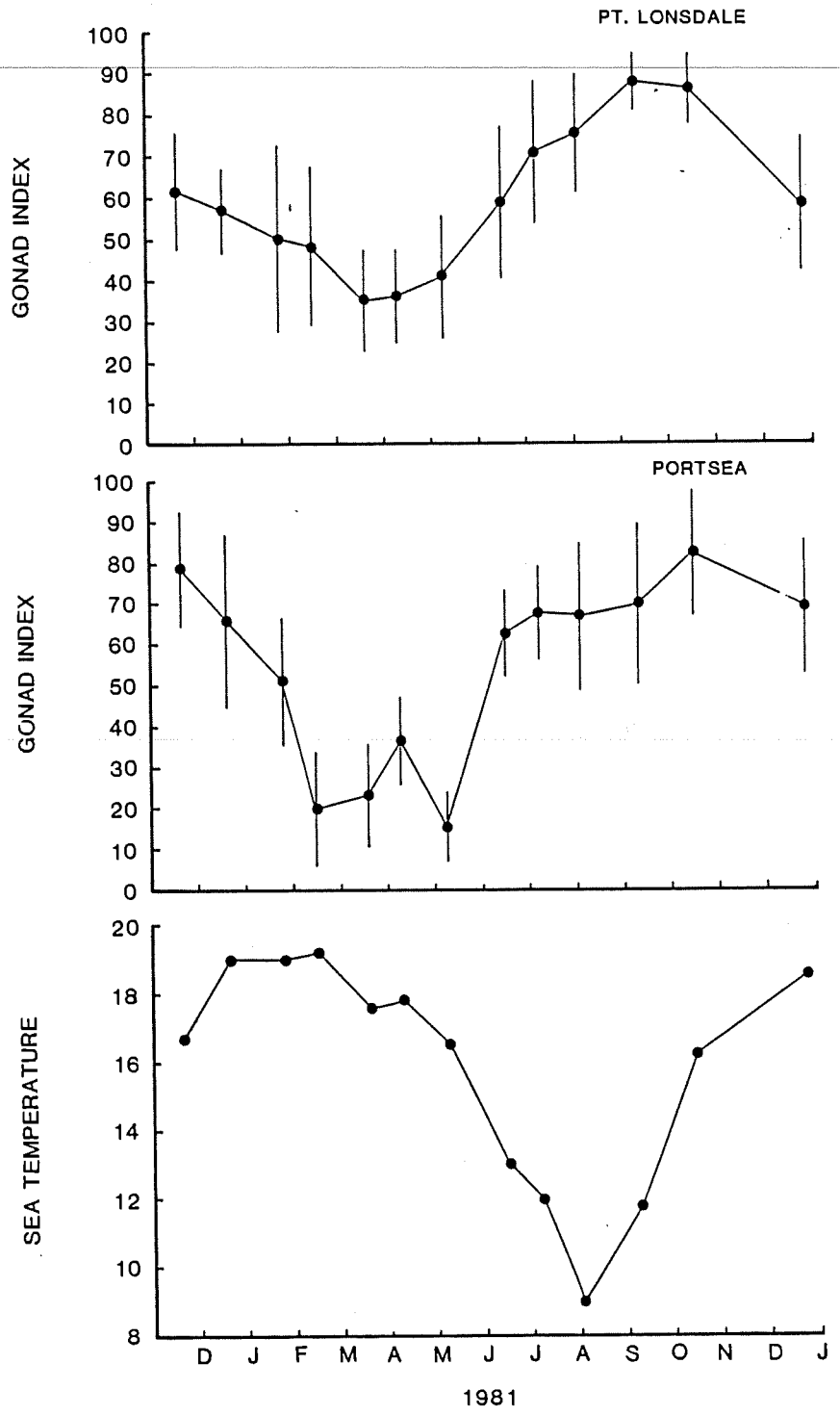

Figure 3. Seasonal variation of the gonad index of H. ruber populations and of sea temperature at Point Lonsdale and Portsea. Vertical bars indicate standard deviations about mean values.

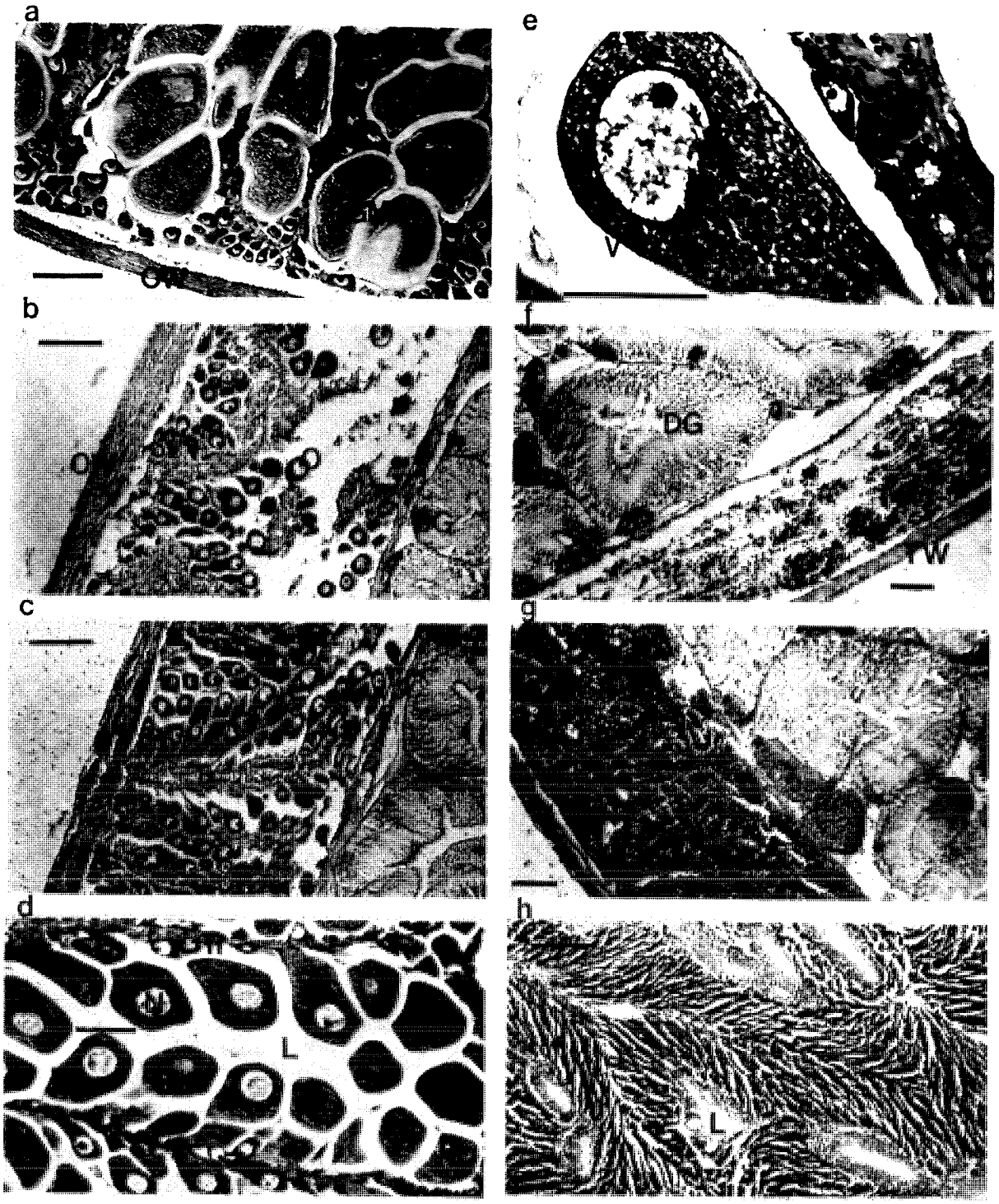

Fig. 4. Photomicrographs indicating various reproductive states of female (a) - (e) and male (f) - (h) gonads of H. ruber.
(a) mature ovary, (b) spent/developing ovary,
(c) developing ovary, (d) spawning ovary, (e) mature oocyte,
(f) spent/developing testis, (g) developing mature testis,
(h) spawning testis.
DG, digestive gland; GM, gelatinous matrix surrounding oocyte;
L, lumen; N, nucleus; O, oocyte; OW, ovary wall; Tr, trabeculae;
TW, testis wall; V, vitelline membrane.
Scale bars indicate 100 um.

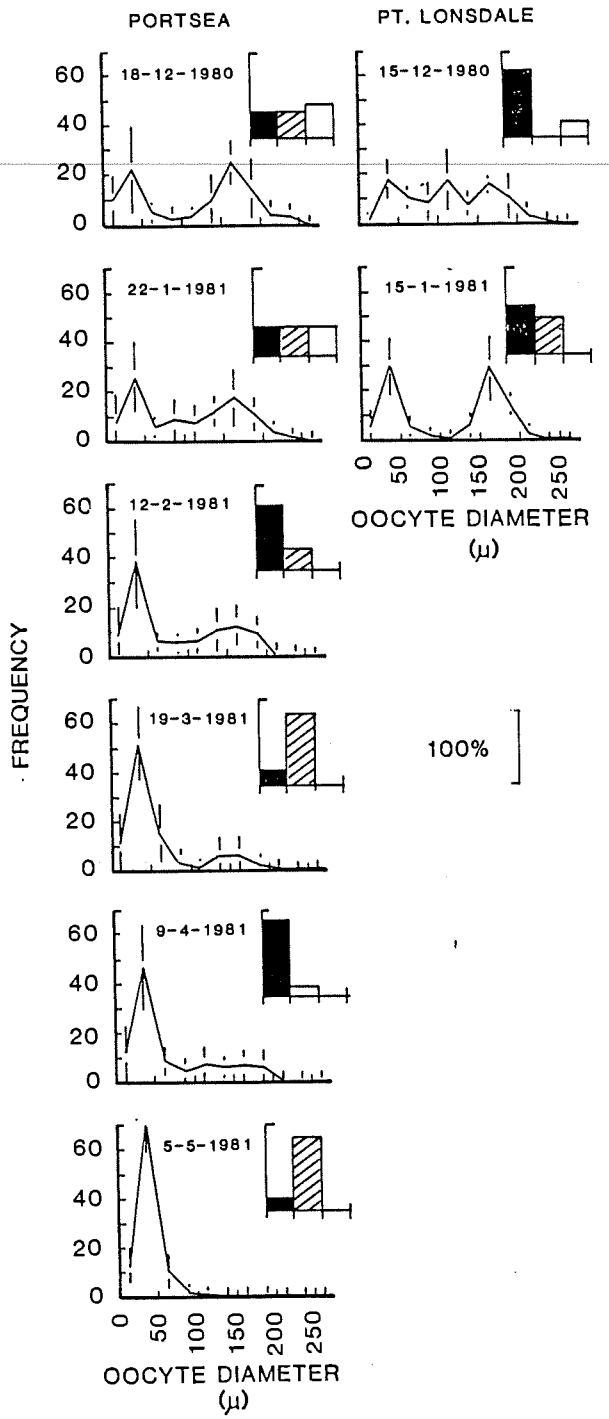

Figure 5. Seasonal variation in size group and percentage frequency of occurrence of oocytes in populations of H. ruber from Portsea and Point Lonsdale. Histograms indicate the reproductive state of ovaries in each sample of the population. Reproductive states are stage 1 (solid shading), stage 2 (hatched shading) and stage 3 (open).

TABLE 2. Comparison of the relationship of fedundity (F) and body weight (W) for several species of abalone. Fecundity is millions of eggs and body weight is grams.

Species		Reference
H. ruber	F = 0.003W +0.215	this study
H. midae	F = 0.0198W -2.196	Newman 1967
H. iris	F = 0.0170W -1.528	Poore 1972
H. australis	F = 0.0005W +1.124	Poore 1972

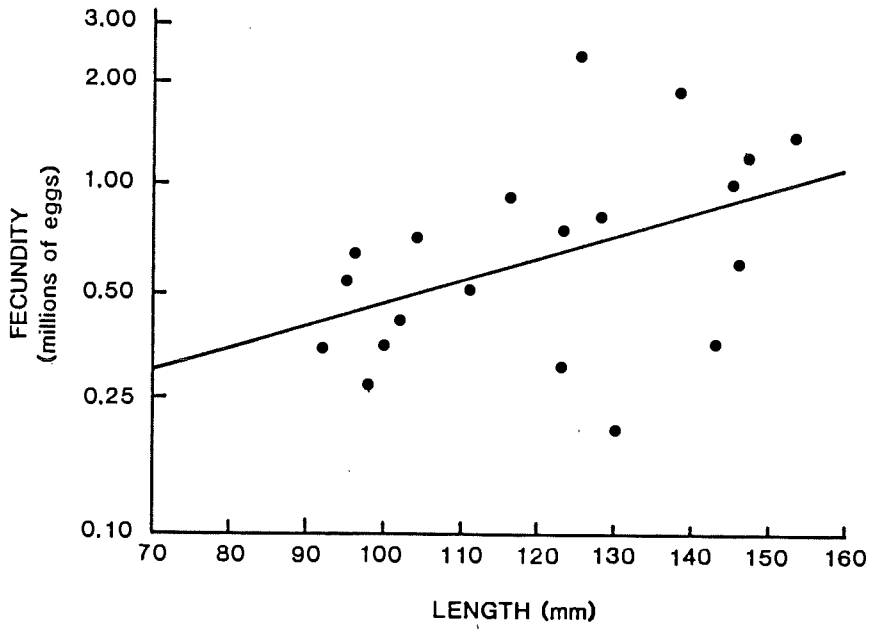

Fig. 6. Variation of Fecundity (F) with shell length (L) in H. ruber where $F = 120.3\ L^{1.79}$

DISCUSSION

The reproductive cycle of H. ruber in the populations at Lorne, Portsea and Point Lonsdale was characterized by a single spawning period extending from late spring over the summer months and, in some cases, into autumn; the fourth population, that at Flinders, was exceptional in that gametes were released throughout the year. Spawning by the three populations is typical of many other species of abalone, generally considered to be summer breeders (Boolotian et al. 1962). Even so, the three populations differed in the timing and periodicity of their spawning. Shepherd and Laws (1974) have reported that populations of H. ruber in South Australia spawned during winter autumn or spring. A Tasmanian population of H. ruber spawned during spring (Harrison and Grant 1971). Thus, depending on locality, spawning populations of H. ruber may be found in southeastern Australia at any time of the year. Differences in spawning cycles of populations of other species of abalone are well established (Cox 1962, Newman 1967, Webber and Giese 1969, Hayashi 1980).

A change in sea temperature has been implicated as triggering gametogenesis in molluscs (Fretter and Graham 1964), stimulating spawning in abalone (Newman 1967, Tomita 1967) and causing differences in spawning behaviour of discrete populations (Newman 1967). The results of our study showed that seasonal change in sea temperature had no correlation with spawning in H. ruber. In contrast, Shepherd and Laws (1974) showed a correlation between a sharp decline in sea temperature and the onset of spawning in a South Australian population of H. ruber. The differences in the spawning behaviour of two very closely located populations, Point Lonsdale and Portsea, and the relatively long spawning season (longer than 3 months) suggests that various factors influence spawning. Shepherd and Laws (1974) found that reproduction in H. laevigata and H. cyclobates, in contrast to that in H. ruber, correlated with food consumption. Giorgi and De Martini (1977) correlated intense gametogenesis in H. rufescens with the appearance of abundant food in summer, yet Webber and Giese (1969) discounted food availability as directly influencing gonadal growth in H. cracheroidii. Reproduction in H. ruber is probably directed by a suite of variables acting contemporaneously rather than by one single environmental factor. Moreover the synchrony of gonadal development in males and females observed in our study suggests that these variables are influencing both sexes simultaneously.

A salient difference between the spawning behaviour of populations at Portsea and at Point Lonsdale was the occurrence of a secondary spawning at Portsea. Notably, no mature oocytes were observed in the population after the second spawning. Incomplete spawning or spawning failure by other species of abalone results in the retention of ripe oocytes and eventual necrosis (Poore 1973, Giorgi and De Martine 1977). We saw no necrotic oocytes in H. ruber. Two discrete spawnings, similar to that reported for H. midae in South Africa (Newman 1967), probably occurred. Minor secondary spawnings have been demonstrated for H. ruber in South Australia (Shepherd and Laws 1974).

In the Flinders population of H. ruber it was apparent from the irregular fluctuations in the gonad index that gametes were being released throughout the year. Continuous spawning in H. ruber has been suggested by Shepherd and Laws (1974) but remains to be demonstrated unequivocally. The results of our study suggest that such a spawning behaviour is unusual for H. ruber as it is for abalone in general. Continuous spawning occurs in few species, notably H. scalaris, H. roei (Shepherd and Laws 1974) and H. rufescens (Boolotian et al. 1962, Cox 1962). The spawning behaviour of populations of H. rufescens was highly variable and discrete spawning on a seasonal basis is the more common pattern (Giorgi and De Martini 1977).

We did not examine development of gametes in the Flinders population. In the other populations; where spawning followed a seasonal cycle, the gonad index was sufficient to indicate reproductive state. In female H. ruber the diameters of oocytes provided a simple and convenient measure of reproductive maturity and such an examination may have provided more information on spawning periodicity at Flinders.

The fecundity of individuals in the populations we studied varied considerably. Shepherd and Laws (1974) have shown that lenght of H. ruber at first maturity varied from 75 mm to 100 mm depending on locality, but that substantial spawning was unlikely to occur for at least another year. This reinforces Poore's (1973) suggestion that the number of eggs produced rather than the presence of a functional ovary constitutes reproductive maturity.

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Starfish vs abalone in Port Phillip Bay

by Paul McShane and Murray Smith

Australian Fisheries Reprint No. 148, 1986

Starfish vs abalone in Port Phillip Bay

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PORT Phillip Bay provides a lucrative abalone resource with annual catches often exceeding 150 tonnes — yet some reefs no longer support viable populations. Research has begun at Altona to assess the practicality of restocking reefs with abalone (*Haliotis ruber*).

Sticks reef was chosen by commercial divers as an appropriate research site as it no longer yielded commercial quantities of abalone, yet provided good abalone habitat in the form of low-relief reef (maximum depth 4 m) with a flourishing macro-algal community. The divers claimed that reefs nearby supported a large population of small abalone which often failed to reach commercial size.

Prior to transferring abalone, we surveyed the density of abalone and dominant epibiota at Sticks reef. The results of that survey form the basis of this report.

Confrontation — starfish are consuming abalone in the bay at a remarkable rate.

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Photographs by John Litchen.

A research site was established at Sticks reef with a length of chain anchored to the sea-floor serving as a permanent transect. This transect was divided into two areas. Area 1 had abundant boulders (average diameter 0.5 m) forming a heterogeneous habitat. Area 2 had fewer boulders, with areas of sand or shell grit. *Ecklonia* sp. was the dominant macro-alga in both areas, although cover rarely exceeded 20 per cent.

Area 1 supported an extraordinarily abundant starfish population (*Coscinasterias calamaria*) with up to 40 starfish a square metre. Often, every available space was occupied by a starfish. Area 2 had significantly fewer starfish. Indeed, Table 1 shows a tenfold variation between the two areas, a result probably due to the difference in physiography of the two areas.

Starfish predation

To check post-tagging mortality, we conducted a thorough search for tagged abalone on our transect and adjacent reef a day later. Remarkably, most of the abalone tagged in area 1 had been consumed or were being consumed by starfish. A much lower incidence of starfish predation was found in area 2 as may be expected (Table 1).

It is likely that prising abalone from the reef, tagging and returning to the reef, shocks or otherwise injures the abalone to the extent that blood or other secretions provides an olfactory cue for starfish predation. We often observed starfish reacting to replaced abalone whereas undisturbed abalone elicited no response. We therefore do not suggest that the high incidence of predation observed on our tagged abalone is typical of that experienced by the natural population.

It nevertheless draws attention to the problems encountered when abalone are removed and replaced (even with extreme care); for example, when divers return undersized abalone. Re-stocking of Sticks reef or other abalone reefs is clearly not viable when *C. calamaria* is abundant.

Starfish 'attack' abalone with one arm extended — and the abalone is too slow to escape.

Coscinasterias calamaria is widely distributed within the Indo-Pacific region and is generally more common in sheltered waters compared with exposed waters. (Reference 1). Pronounced predation of abalone by this starfish has hitherto been unreported. Starfish in general are considered unimportant predators of abalone (Reference 2).

However Shepherd (Reference 3) lists *C. calamaria* as a predator of abalone (including *H. ruber*) and he notes a well developed escape response of abalone to this starfish.

A population census of abalone revealed similar densities in the two sample areas (Table 1). All abalone within a metre of the transect were collected, taken to our research vessel, tagged with a glued plastic disc and returned to the reef within half an hour of collection. Care was taken to return the abalone to their natural habitat. Thus small abalone (less than 40 mm length) were replaced under boulders and larger abalone were returned to home scars where possible.

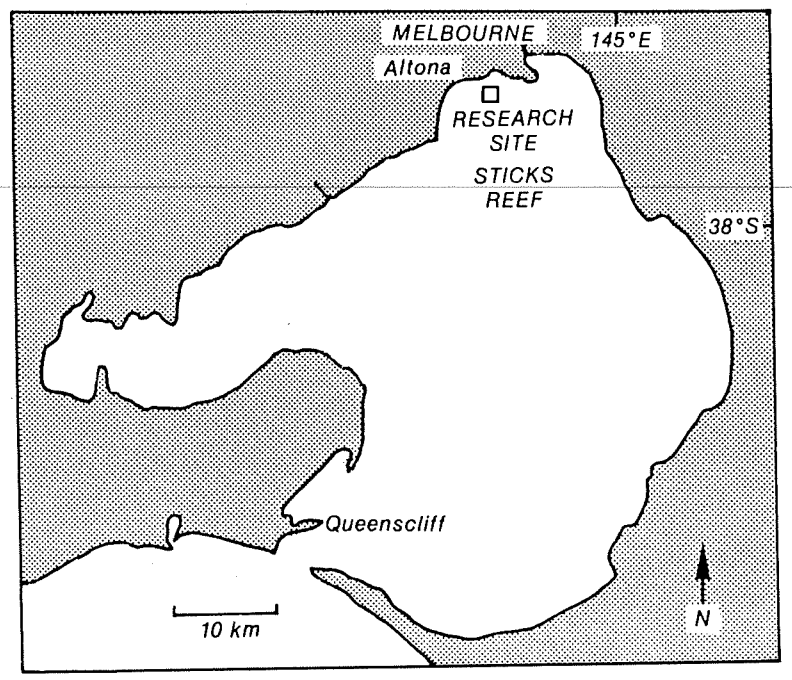
During our studies we have often observed starfish 'attacking' abalone. The starfish approaches an abalone with one of its arms extended, presumably using its sensory tube feet to detect the prey. The abalone often appears to sense the presence of the starfish and moves away. The speed of an abalone is, however, no match for that of a starfish. Upon contact of the abalone by a starfish arm, the abalone vigorously rotates its shell several times. This dislodges the starfish arm but the starfish, undeterred, resumes the attack.

The abalone becomes vulnerable when it reaches a discontinuity in the reef, such as the edge of a boulder or a patch of sand. The starfish then succeeds in placing an arm underneath the abalone and tipping it on its shell. Predation occurs after the abalone is immobilised with the starfish arms. Feeding commences when the stomach of the starfish is everted, after which the abalone is rapidly digested.

Starfish are capable of preying on the full-size range of abalone (up to 140 mm in length).

Potential threat?

Apart from abalone, *C. calamaria* were observed feeding on each other and just about every other epi-benthic species, including algae, sponges, tunicates, crabs, mussels and sea-urchins.



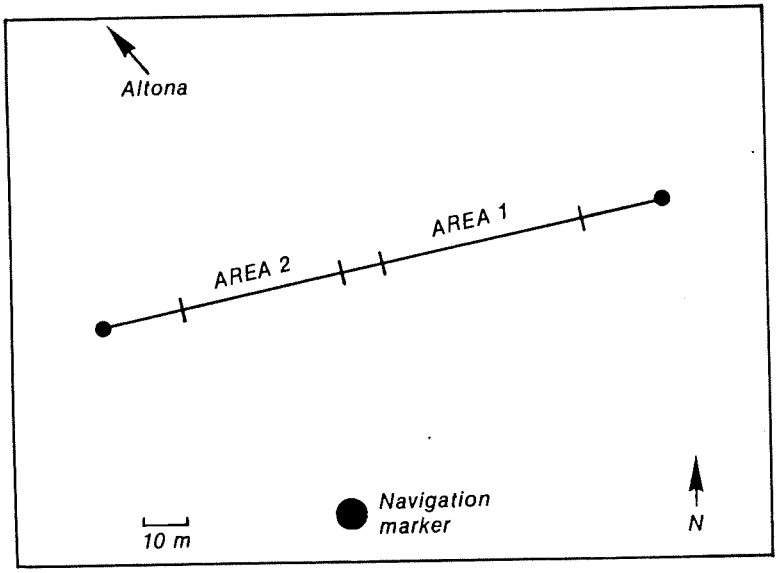


Table 1

Area	*Starfish density (number/m²) ± SD*	*Abalone density (number/m²)*	*Starfish predation (% abalone consumed by starfish)*	*Proportion of starfish feeding (% with stomachs everted)*
1	24 ± 12	1.4	83	19.5
2	2 ± 3	1.5	42	13.4

Our results show that starfish were often feeding (Table 1) and our observations suggest that the starfish are moving over the reef perhaps in search of food.

Our frequent observation of starfish consuming abalone in the natural population and the relatively high number of empty abalone shells suggests that starfish may significantly decrease abalone abundance. Abalone divers report the presence of *C. calamaria* on other reefs in Port Phillip Bay in high numbers.

The abundance of *C. calamaria* at Sticks reef, the species' capacity to reproduce both sexually and asexually (by fission) (Reference 1), the lack of natural predators and its ability to colonise new habitat are portentious. The incidence of *C. calamaria* in Port Phillip Bay evokes comparison with the closely related crown of thorns starfish on the Great Barrier Reef. In both cases the cause of the population increase is unknown. Research efforts currently being undertaken on the crown of thorns starfish may provide insight into the mechanisms controlling *C. calamaria* populations. In the meantime, the abundance of starfish in Port Phillip Bay is a potential threat to abalone stocks, and clearly a greater understanding of the population dynamics and mechanisms controlling feeding responses is needed to determine the nature of this problem.

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Recruitment processes in *Haliotis rubra* (Mollusca : Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae

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Abstract: Our studies of recruitment, adult numbers, and ocean hydrodynamics suggest that recruitment of *Haliotis rubra* is primarily local. In three neighbouring coastal populations of *Haliotis rubra* in southeastern Australia where adult numbers differed significantly, recruitment was found to be correlated with the abundance of adult *H. rubra* counted in each population. Regional larval dispersal was examined using measurements of horizontal water velocities near the seabed and at the surface of one reef. The measurements showed that larvae entering the water column would be dispersed if they left the shelter of local reef topography. This dispersal was confirmed by numerical hydrodynamic and dispersal modelling which simulated the temporal and spatial variation of wind-driven currents near the reefs. The results from the models also demonstrated that larvae entering the water column have a low chance of returning to their parent reef and that recruitment to some reefs from an upstream population was unlikely during a typical 3–7-day pelagic period because some populations were found to be hydrodynamically isolated from their neighbours. This was confirmed by plankton surveys several days after the estimated start of spawning which revealed only one larva of *H. rubra* in ocean water around the reefs surveyed. The measurements and simulation models suggested that settlement of *H. rubra* would be most successful if the larvae remained on their parent reef. The results of additional hydrodynamic studies at the surface of one reef showed that local reef topography attenuated near-bed currents sufficiently for larvae of *H. rubra* to stay on the parent reef, for example, in rock crevices, for the full pelagic period. In this way, *H. rubra* would complete its larval life cycle near the parent.

Key words: Abalone; Dispersal; *Haliotis rubra*; Hydrodynamics; Larva; Recruitment

Introduction

Many abalone fisheries world-wide have collapsed because of recruitment failure (Cicin-Sain *et al.*, 1977; Mottet, 1978; Breen, 1980; Sainsbury, 1982; Sluczanowski, 1984); yet, little is known about recruitment processes in abalone. Prince *et al.* (1987) attributed this paucity of knowledge to the fisheries scientists' incomplete understanding of larval biology and factors influencing settlement. Indeed, the larval stage of marine

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invertebrates is the least understood of all invertebrate life stages (Cameron, 1986; Butman, 1987). This is especially true for abalone whose larval biology has been studied only in aquaria (e.g., Ino, 1952). Laboratory studies of larval behaviour (Yano & Ogawa, 1977; Tanaka, 1978; Lee *et al.*, 1978; Seki & Kan-no, 1981a,b) provide clues as to the behaviour of abalone in their natural habitat, but so few larvae have been found in the sea (Tomita *et al.*, 1977; Tanaka *et al.*, 1986) that their dispersal is poorly understood.

Recently, Prince *et al.* (1987) have proposed that dispersal of abalone larvae is localized rather than pelagic; we have recently obtained evidence which supports their proposal. We used a novel method (McShane & Smith, 1988) to obtain estimates of recruitment of *H. rubra*. To overcome the difficulties associated with accurately estimating breeding stock, we chose three neighbouring reefs which had obviously different densities of adult *H. rubra*. We adopted this approach rather than experimental manipulation (cf. Prince *et al.*, 1987) because we aimed to study recruitment on a large scale and an appropriate experimental design would have been logistically prohibitive. Furthermore, the reefs are so close that we could test the hypothesis of localized dispersal. Should *H. rubra* show pelagic dispersal (Tegner & Butler, 1985), then a relationship between abundance of adults and recruitment on individual reefs would be masked.

Results from studies of water movement have been used to predict larval distribution (Tanaka *et al.*, 1986; and references cited therein). We studied water-movement on one of the reefs. The location of the water-movement study was selected to depict the water circulation in a complex coastal environment subjected to wind, wave, and tidal forces. A nearby entrance to a tidal inlet further compounded the hydrodynamic complexity of the region. Therefore, simplified analytical approximations for the coastal currents were not expected to be a valid substitute for direct measurements. Previous studies of water flow in the region were lacking and we sought to measure the principal components of the regional hydrodynamics. From this, a two-dimensional hydrodynamic numerical model and a larval dispersal model were established. Such models include the regional bathymetry and assess the potential for local retention and exchange of larvae between reefs.

Materials and Methods

PARENT-STOCK ABUNDANCE

The three neighbouring reefs (Fig. 1) at Sandpatch Point, Tullaburga Island, and Bastion Point had similar underwater topography and were composed mainly of granite and sandstone (McCrae-Williams *et al.*, 1981). The reefs were situated at similar depths (8–10 m) and supported communities dominated by the kelp *Phyllospora comosa*. While there were no obvious differences in the overall physical or biological characteristics of the reefs, commercial fishermen have also indicated that the abundance of *H. rubra* between the reefs varied considerably. Catch data (McShane *et al.*, 1986a) have revealed

that the reefs at Sandpatch Point, Tullaburga Island, and Bastion Point are ranked in declining order of catches.

To verify the relative abundance of *H. rubra* we surveyed the population at each reef (Fig. 2). Because much of the habitat of *H. rubra* is cryptic and therefore difficult to sample effectively (Shepherd, 1973; Prince *et al.*, 1987), we estimated the abundance of *H. rubra* by means of three independent methods: transect, random quadrats, and searching. Each method targets larger individuals because juvenile abalone inhabit cryptic habitat (Shepherd, 1973; Prince *et al.*, 1987).

For each sampling method, sites were assigned randomly using a 10 000-m^2 grid, a large scale map of the reef complex, and random number tables. If the site was unsuitable, for example, if the substrate was sand rather than reef, the site was reassigned. At Sandpatch Point and Bastion Point, contiguous 1-m square quadrats on

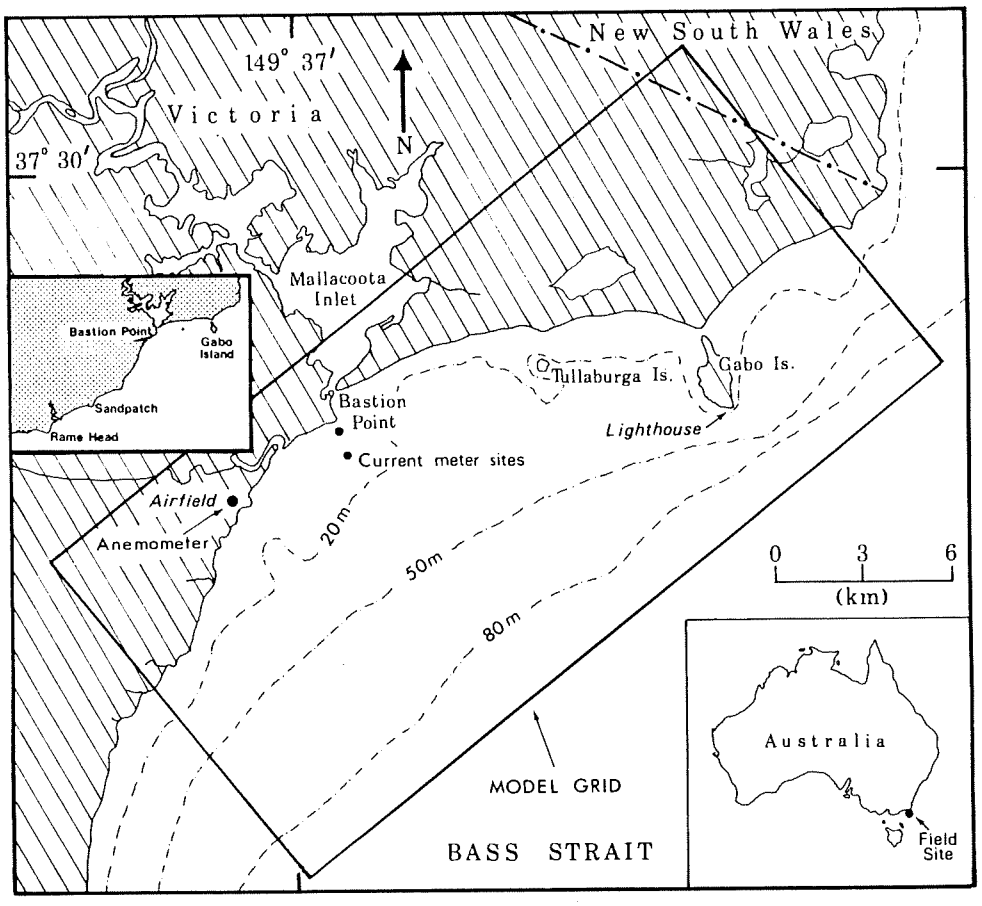


Fig. 1. Map of the study region showing the relative location of the three study reefs and the location of the current meter used in the hydrodynamic studies.

each side of three 50-m transects were surveyed for *H. rubra*. Where possible, abalone divers searched for abalone in cryptic habitat by overturning boulders and removing epibiota (e.g., sponges and sea urchins). On each reef, sites were also assigned for deployment of five 1-m square quadrats from which all *H. rubra* were collected by scuba divers.

On each reef, two divers each collected all the *H. rubra* they saw within a given searching time (10 or 15 min). Preliminary trials revealed a close correspondence

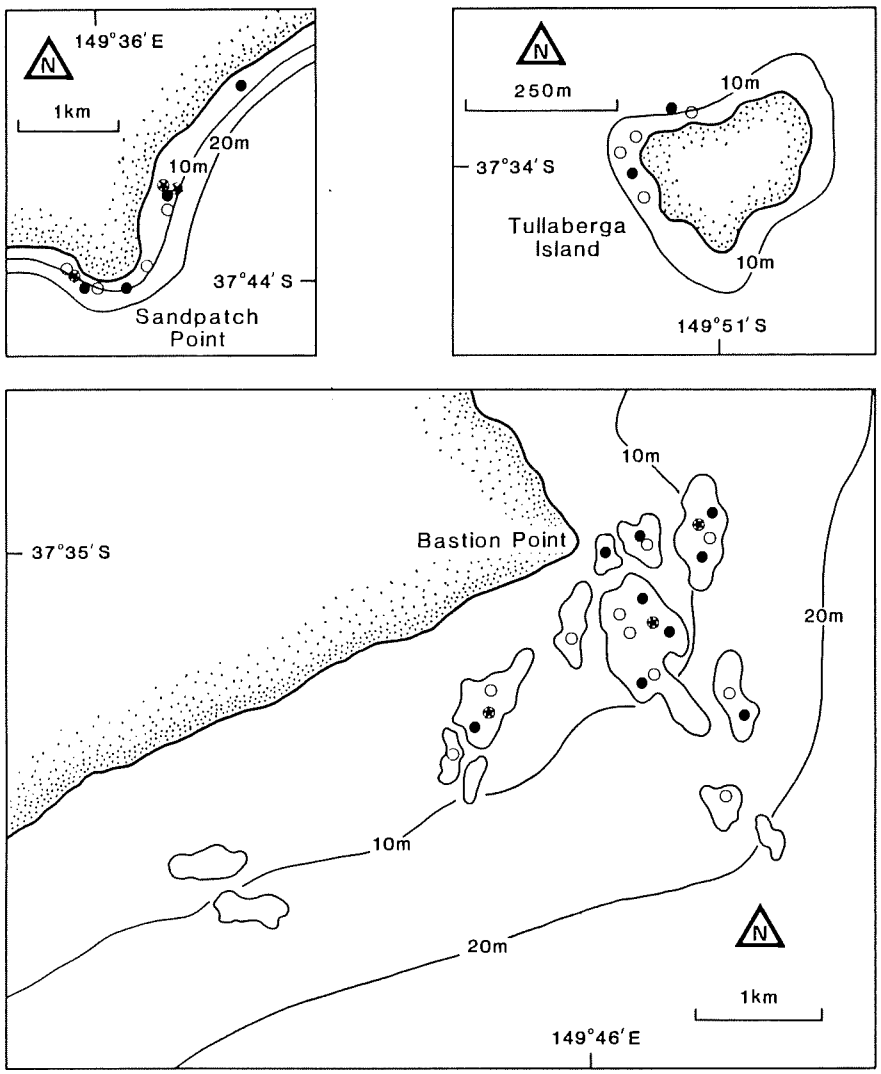


Fig. 2. Sample site locality at Sandpatch Point, Tullaburga Island, and Bastion Point. Sites for surveys of recruits and adults of *H. rubra* (quadrat method) are indicated by solid circles. Sites for transect and searching surveys of adult *H. rubra* are shown by starred and open circles, respectively.

(always $<20\%$ variation) between the number of *H. rubra* collected by scuba divers. Thus, the total number collected at each reef (up to 10 sites surveyed) was used as an index of relative abundance (Beinssen, 1979). The shell length (longest shell dimension) of *H. rubra* collected by each method was measured to the nearest millimetre.

EGG PRODUCTION

In Victorian waters, *H. rubra* are generally considered a summer breeder (McShane *et al.*, 1986b). We assessed the incidence of spawning by examination of gonad fullness.

A macroscopic gonad index indicating the relative cross-sectional surface area of the gonad was measured before the estimated spawning period (summer) on each reef. We selected *H. rubra* ≈ 120 mm long because the gonad index for animals >110 mm (Newman, 1967; Hayashi, 1980) is independent of size and because errors are minimized by using abalone of similar length. From each *H. rubra*, a section of gonad which surrounds digestive tissue was taken near the main body of the visceral coil (Giorgi & De Martini, 1977) and preserved in 10% formalin. The perimeters of cross-sections of gonad and digestive glands were measured planimetrically with the aid of a dissecting microscope equipped with a camera lucida (Shepherd & Laws, 1974).

The fecundity of *H. rubra* collected from Sandpatch Point and Bastion Point during November 1986 was estimated by a method similar to that used by Newman (1967) for *H. midae*. Gonads that had been preserved in 10% formalin were dissected from the digestive gland. Eggs were then carefully dissected from the connective tissue and undamaged eggs were separated with the aid of a 600-μm screen. All the undamaged eggs from all the gonads were kept together in an appropriate volume of preservative. The number of eggs in subsamples of the total volume of preservative was estimated using a counting chamber; the estimates varied by $<10\%$.

REGIONAL HYDRODYNAMICS

Water velocity was measured on three occasions at two sites. The first site was located in water ≈ 18 m deep at the seaward extent of the matrix of reefs at Bastion Point (Fig. 1) and selected to reflect currents in the nearshore environment which could be responsible for pelagic dispersal of *H. rubra* from Bastion Point. Current measurements were made from 10 November to 23 December 1986, from 9 September to 13 November 1987, and from 5 January to 8 February 1988 and wind velocity was measured with an anemometer sited at the nearby airport (Fig. 1). These data were supplemented with observations from the Gabo Island lighthouse (Fig. 1) where wave and wind statistics were recorded every 3 h (Australian Bureau of Meteorology, Melbourne, pers. comm.).

During the first occasion, tidal heights were measured with an Aanderaa RLX4 which recorded water pressure every 10 min. Neil Brown acoustic Smart meters were placed 2.7 and 12.4 m above the seabed and currents and water temperature were measured.

During the second occasion, a Neil Brown acoustic smart meter and an electromagnetic Interocean S4 meter were placed 12.0 and 1.95 m above the seabed, respectively, but the data from the near-surface meter were lost due to a buoy failure. Current velocity and wave orbital motion were recorded at the seabed. Both current meters have a fast-response time which makes them suitable for the coastal environment where the reversing orbital flows under surface waves make impeller-type meters impractical.

Near the site where water velocity was measured, divers found that the predominant bedforms were wave-induced, but echo-sounder records showed the seabed to be otherwise undistinguished. Therefore, the water velocity measurements were not expected to be strongly influenced by the immediate seabed topography except for the normal effect of seabed friction, which causes water velocity to be lower near the seabed.

The second site at which current measurements were taken was located within the reef complex at Bastion Point in a channel enclosed on three sides by large boulders (Fig. 3). Large stands of the kelp *Phyllospora comosa* situated on the reef were expected to attenuate local water movement. This site was chosen as being typical of the sheltered reef habitat of *H. rubra* and selected to examine small-scale flows within the local reef structure. The water depth at the site was 10 m and one Neil Brown current meter was placed at 3 m above the seabed. In contrast to the first site, local seabed topography was expected to exert considerable influence on current strengths at this second site. The meter was deployed from 5 January to 8 February 1988 to coincide with a typical January spawning of *H. rubra*.

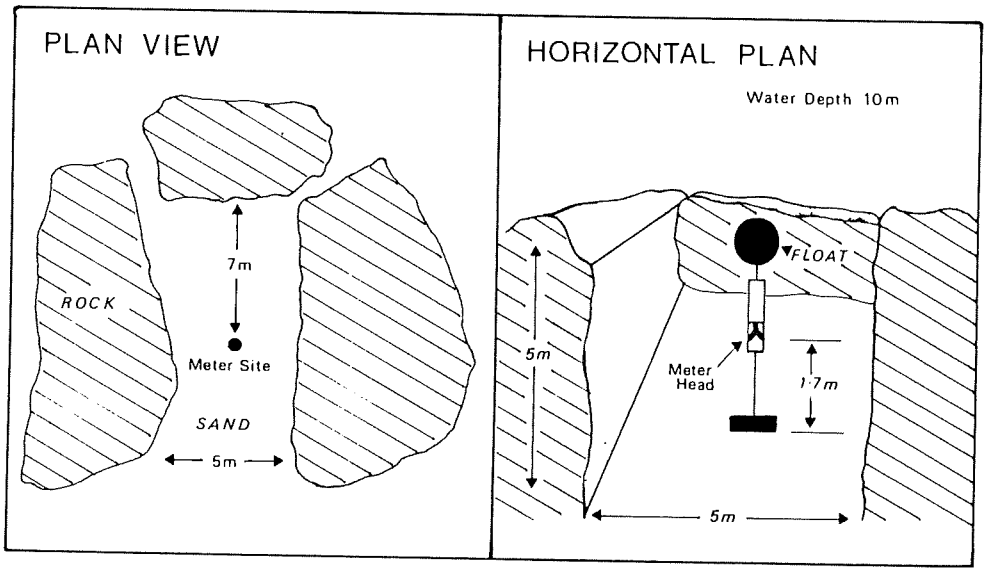


Fig. 3. Schematic diagram showing the reef structure surrounding the current meter at the second study site at Bastion Point.

Applications of the measurements

Measurements of water movements from the first site were examined to assess the hydrodynamic characteristics of the region and to determine the primary forces responsible for pelagic larval transport. The measurements were then employed to calculate larval dispersal rates using a procedure denoted as "particle tracking with spatially uniform velocities". Finally, a two-dimensional numerical hydrodynamic model, calibrated with the water movement measurements, provided a comprehensive specification of regional flow patterns and these were applied in a Lagrangian particle dispersion model. The dispersal patterns from the model assessed the potential for successful pelagic dispersal and interreef larval transfer by simulating the hydrodynamic factors which influence recruitment.

PARTICLE TRACKING WITH SPATIALLY UNIFORM VELOCITIES

For computer simulation of larval dispersal, particles were released at the current meter site (Fig. 1) every 20 min for the duration of the record and tracked for 3–7 days, which is a realistic period for the larval life of abalone (Ino, 1952). During the 3–7 days, the position of each particle was recorded and, by accumulation of all positions, contours of particle numbers per cell were constructed. The results therefore represent the variety of current conditions measured, even though spatial velocity variation is not being considered, and provide an estimate of the likely positions of *H. rubra* larvae from Bastion Point at the time of their settlement.

NUMERICAL HYDRODYNAMIC MODELLING

The numerical hydrodynamic modelling was undertaken with model 2DD of Black (1983) which solves the two-dimensional vertically averaged momentum and continuity equations for an incompressible fluid.

The model is designed to be applicable to shallow- and deep-water environments and includes simulations of the flooding and drying of intertidal zones, the effects of sea gradients, Coriolis force, eddy diffusion, convective momentum, seabed friction and surface wind stress. 2DD has been applied in several instances where detailed field measurements were available for its calibration (e.g., Black, 1987a). For the present study, the model was calibrated with the S4 measurements after being adapted to treat the wave/current interactions which were found to control the wind-driven flow speeds found to be primarily responsible for net larval transport in the study region.

The model grid of 750-m square cells included Bastion Point and Tullaburga Island (Fig. 1) so that the potential for larval exchange between reefs could be assessed. *Haliotis rubra* was estimated to have spawned during late December 1986 when winds were consistently from the southwest quadrant. This period could not be modelled as wave conditions were not measured but a period with similar wind velocities (Fig. 4) was selected from the second deployment (3 October – 14 October 1987). Results for the

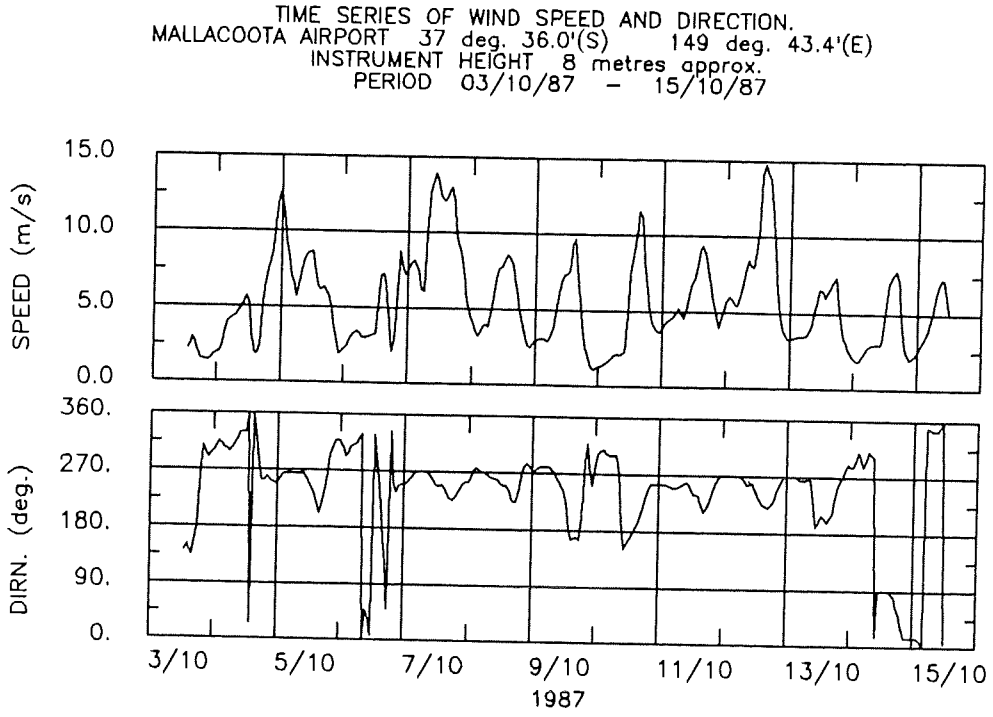


Fig. 4. Winds recorded at Mallacoota airport from 15 October 1987. The directions (0–360°) conform with the standard definition of direction from which the wind blows.

7 days from 1300 on 4 October 1987 are presented; other 7-day time bands within the calibration period (Fig. 4) were simulated but the general results from the model remained unaltered. However, the measurements were made during a predominantly south-to-west-wind period and the wind is later shown to be the major factor determining net larval transport.

LARVAL DISPERSAL MODELLING

Larval dispersal was simulated in the Lagrangian particle tracking model 2AD of Black (in press). The method, which utilizes a full two-dimensional Lagrangian tracking algorithm, eliminates the numerical smearing of concentration gradients that occurs in a Eulerian scheme and so makes possible the examination of concentrations at subgrid scales.

In the dispersal model, water velocities produced by the hydrodynamic model were used to advect particles progressively in time. The advection scheme was second-order accurate, i.e., velocity gradients across the model cells were accounted for. Diffusion was modelled as a "random walk" with flow longitudinal and lateral coefficients set to a selected fraction of the total distance moved each time step (0.2 and 0.05, respectively).

The coefficients, therefore, represented a level of diffusion which was in proportion to local water speed.

Although the dispersal model has the capacity to simulate the larval mortality in open ocean conditions such modelling was not attempted because of the lack of adequate, supportive data. The modelling primarily examines the possibility of larval exchange and a 100% survival rate was assumed so that the interpretation of results was simplified.

LARVAL SURVEYS

Samples of plankton were collected on and near the three reefs (Fig. 5) in an attempt to find larvae of *H. rubra* in the water column. Samples were taken on two occasions; 21 January and 1 February 1987. At each site, ≈ 1000 l of seawater were pumped from within ≈ 1 m of the bottom, from midwater and from within ≈ 1 m of the surface. Plankton was collected by filtering seawater samples through a 200-μm screen and then preserved in 10% buffered formalin. Samples were sorted with the aid of a plankton counting chamber and a dissecting microscope.

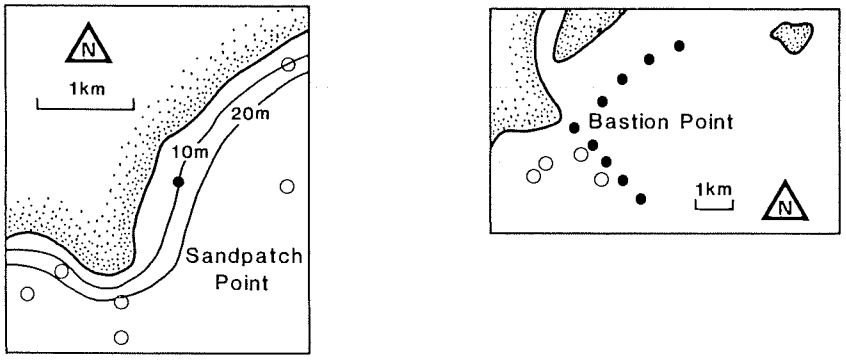


Fig. 5. Sites sampled for larvae of *H. rubra* on 21 January 1987 (solid symbols) and 1 February (open symbols). Solid symbol at Sandpatch Point indicates location at larva sampled.

RECRUITMENT SURVEYS

At each site (Fig. 2), scuba divers used a diver-operated suction sampler (McShane & Smith, 1988) to collect newly settled *H. rubra* from the surface of substratum in each of the five quadrats used in surveys of adult *H. rubra* abundance. All epibiota retained in the 200-μm mesh collecting bag were preserved in 10% formalin, then sorted in the laboratory for *H. rubra* under a dissecting microscope (McShane & Smith, 1988). The method has been shown (McShane & Smith, 1988) to be superior to existing methods of quantifying recruitment in abalone (Prince & Ford, 1985; Shepherd & Turner, 1985).

RESULTS

EGG PRODUCTION

For each population of *H. rubra*, macroscopic gonad indices were similar each month (Fig. 6). During the 3 months September to November, gonad indices increased to prespawning levels (McShane *et al.*, 1986). Commercial fishermen's reports that the gonads of *H. rubra* examined in December had little bulk suggest that spawning had occurred during December. In January, a decrease in the gonad index indicative of spawning/recovery (Fig. 6) supported the fishermen's observations. However, the relatively high variation in gonad indices within populations of *H. rubra* in January indicated that spawning may be asynchronous and that gametes could well be released over a prolonged period.

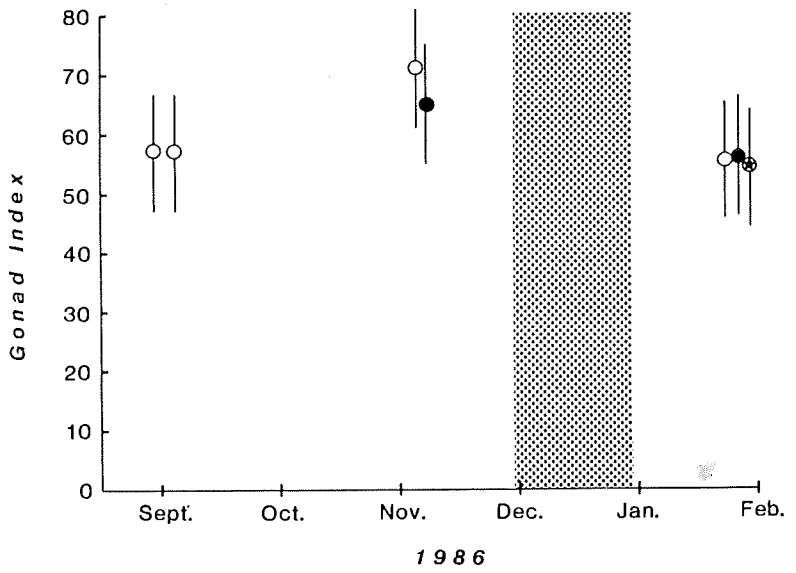


Fig. 6. Monthly variation in the macroscopic gonad index of *H. rubra*. Data are means ± SD. Open symbols represent the Bastion Point population, closed symbols the Sandpatch Point population and the starred symbols the Tullaburga Island population. The estimated spawning period of *H. rubra* is indicated by shading.

The relationship between fecundity and shell length of *H. rubra* was linear over the range of lengths we measured ($r^2 > 0.6$, $P < 0.001$) (Fig. 7). ANCOVA revealed that regressions of the data for *H. rubra* from Sandpatch and Bastion Point were significantly different ($P < 0.05$) and reproductively mature *H. rubra* from Sandpatch Point had a greater mean shell length than did *H. rubra* from Bastion Point. In both populations, however, only those animals > 100 mm shell length may be expected to produce large

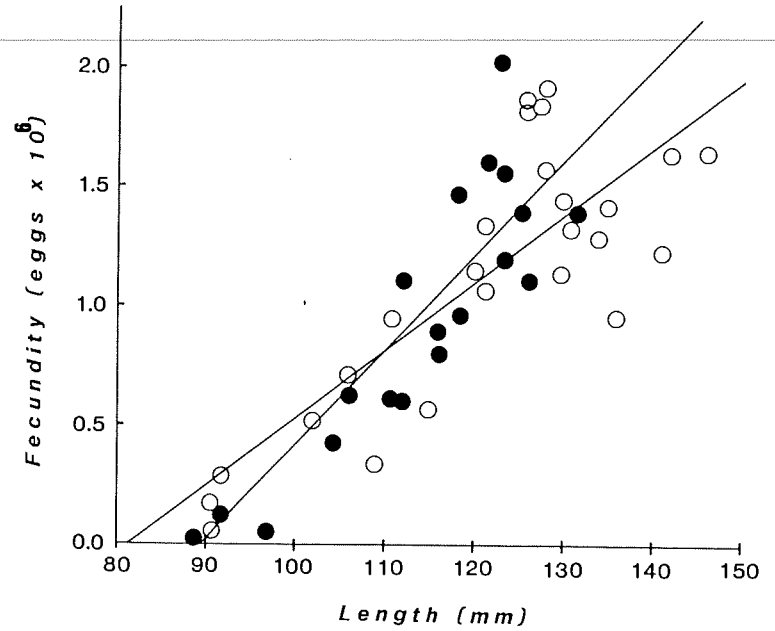


Fig. 7. Relationship between fecundity (F) and shell length (L) of *H. rubra*. Open symbols represent the Bastion Point population and closed symbols the Sandpatch Point population. Least-squares fitted linear regressions (F vs. L) were $F = 0.029L-2.36$ ($r^2 = 0.60$, $n = 24$) and $F = 0.040L-3.62$ ($r^2 = 0.77$, $n = 21$) for the Bastion Point and Sandpatch Point populations, respectively. These regressions compare with a population of *H. rubra* from Tasmania (Prince *et al.*, 1987) where $F = 0.028L-2.4$ ($r^2 = 0.36$, $n = 83$).

numbers of eggs (> 100 000). This is consistent with the findings of Prince *et al.* (1987) who examined a Tasmanian population of *H. rubra*.

LARVAL SURVEYS

Only one larva of *H. rubra* was positively identified from seawater samples on and remote from the three reefs despite our filtering of 43 000 l of seawater from 15 sites. The one larva of *H. rubra* identified was a precompetent veliger (270 μm diameter) found near the seabed on Sandpatch reef (Fig. 5). Numerous larvae of other taxa, including other gastropods, were present in the samples. Many trochophore larvae of gastropods were found but none could be positively identified as *H. rubra*.

PELAGIC DISPERSAL

Although the measured currents exhibited a three-dimensional behaviour, the dominant component of the currents was driven by wind and tidal forcing and directed parallel to the coast (Fig. 8). The current was strongly modified by local wind and therefore larval transport in the vicinity of Bastion Point will be determined mostly by

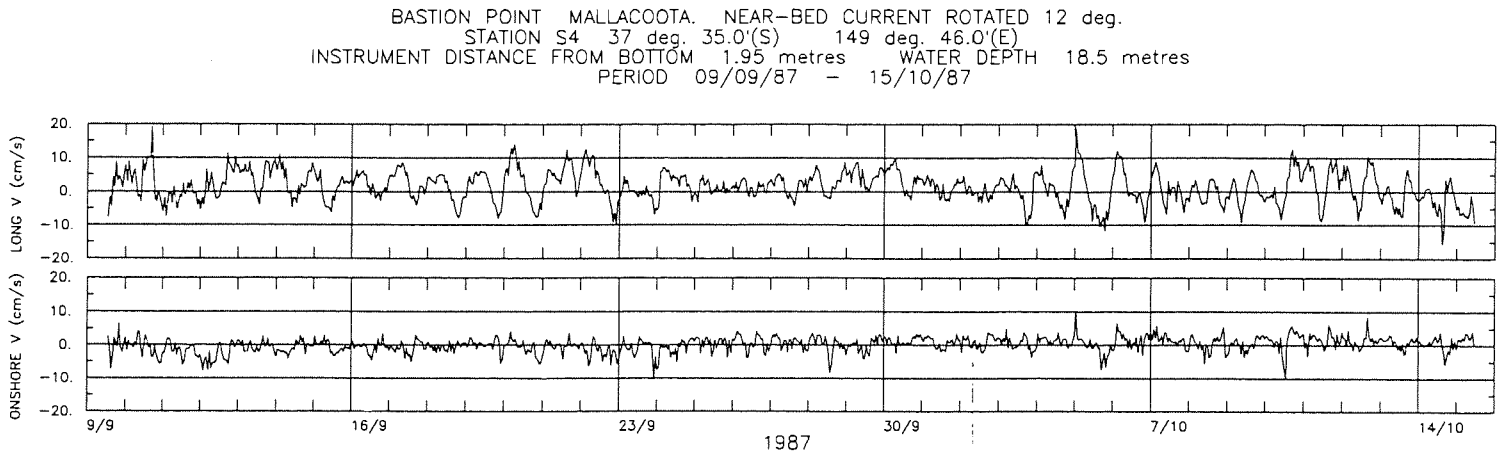


Fig. 8. Longshore and on/offshore velocities recorded at an exposed site at Bastion Point. The current meter was 1.95 m above the seabed. Strongest currents occur in the longshore direction.

the wind velocity at the time of spawning. The wind rose for Gabo Island (Reinson, 1977) shows that south-west and north-east winds are dominant and these winds generate currents headed downwind, parallel to the local shoreline. Residual tidal circulation was near zero and therefore oscillating tidal currents had only a limited capacity to transport material over distances greater than the tidal excursion. The residual longshore currents, that remain after removal of the tidal component from the raw time series were mostly $< 0.10\ m \cdot s^{-1}$. Periods of several days when currents were $< 0.05\ m \cdot s^{-1}$ and oscillating ≈ 0 (e.g., ≈ 27 September) were recorded.

Wave influences

The wind-driven longshore coastal currents were considerably slower than expected. This decrease in velocity was caused by the increase in seabed friction due to combined turbulent seabed stresses associated with the steady current and the components of the wave orbital velocity. The process operates to arrest the longshore transport of larvae during wave events in the nearshore zone and should have a similar effect near any open wave-attacked coastline in intermediate depths.

Thus, the arrival of swell after spawning decreases the dispersal distance compared with similar wind conditions when swell is not present. In the study region, the wind and swell waves were nearly coincident, so that waves reduce the strengths of currents parallel to the coast during most storms.

A second consequence of wave activity is identified in Fig. 9 which shows that surface wave action rapidly dissipated temperature gradients in the vicinity of Bastion Point. This important correlation demonstrates the rapid and thorough vertical mixing that

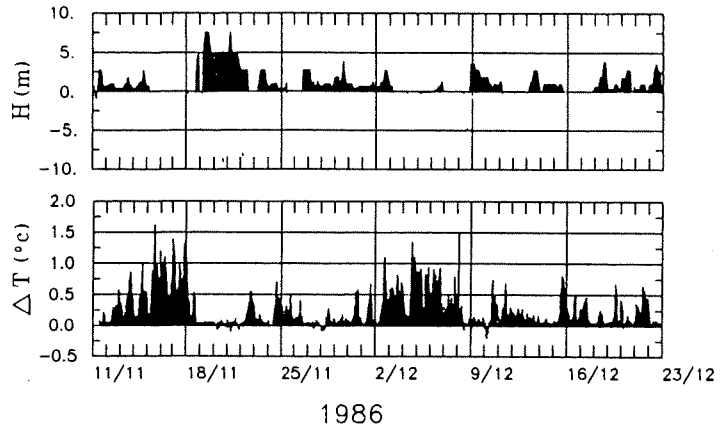
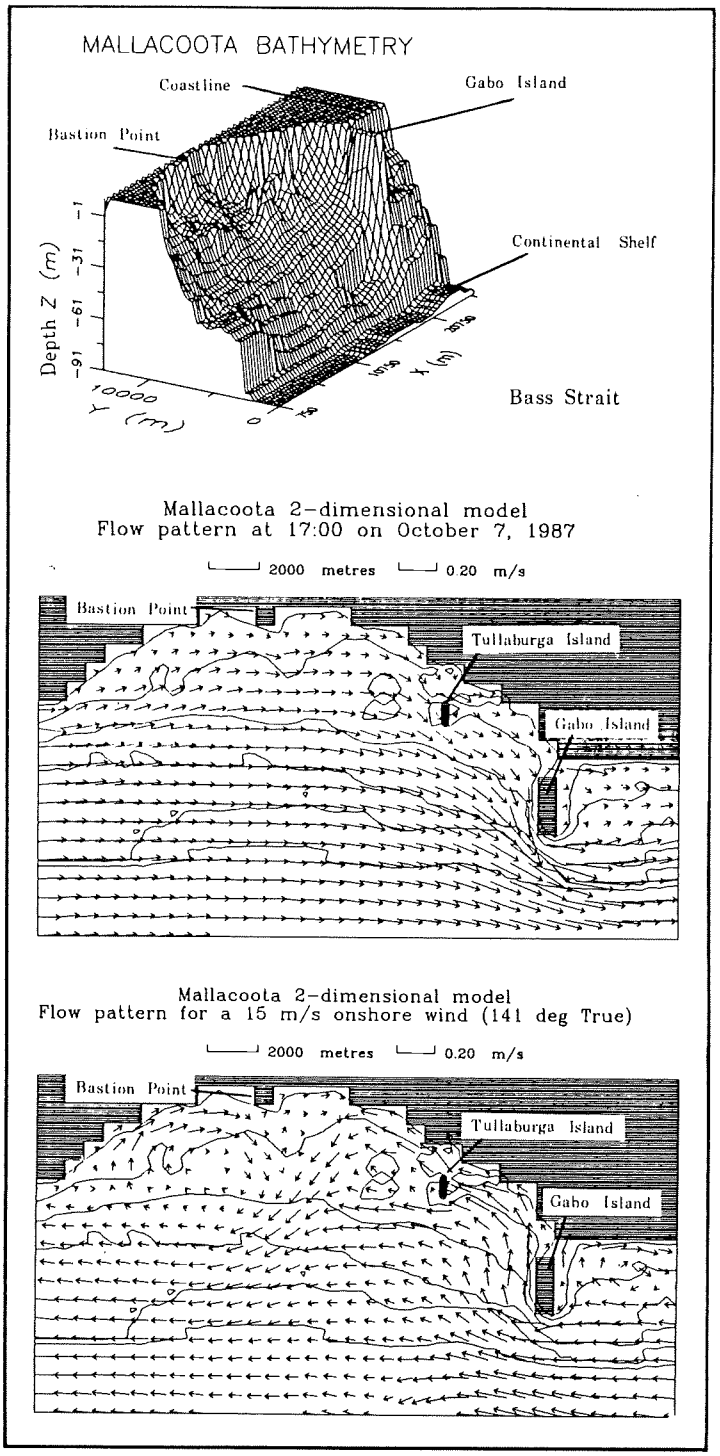


Fig. 9. Wave height observed at Gabo Island (Australian Bureau of Meteorology, pers. comm.) resolved about the onshore normal and the temperature difference between the upper and lower current meters at 12.4 and 2.7 m above the bed, respectively. Positive differences occur when the winter is warmer at the surface. The figure shows that wave mixing dissipates the temperature gradients.


MALLACOOTA BATHYMETRY
Coastline
Gabo Island
Bastion Point
Continental Shelf
Depth Z (m)
-1
-31
-61
-91
10000
Y (m)
0
X (m)
Bass Strait
Mallacoota 2-dimensional model
Flow pattern at 17:00 on October 7, 1987
2000 metres
0.20 m/s
Bastion Point
Tullaburga Island
Gabo Island
Mallacoota 2-dimensional model
Flow pattern for a 15 m/s onshore wind (141 deg True)
2000 metres
0.20 m/s
Bastion Point
Tullaburga Island
Gabo Island

occurs under surface gravity waves and indicates the amount of mixing which larvae of *H. rubra* would be subjected to. The wave turbulence, which effectively neutralized the temperature gradients, would be expected to mix the plankton throughout the water column also, thereby preventing many larvae from remaining at a depth conducive to settlement. In the study region, waves large enough to mix the temperature gradients occurred $\approx 50\%$ of the time (Fig. 9).

Hydrodynamic modelling

Examples of the currents simulated in the two-dimensional hydrodynamic model (Fig. 10a) for the study region are shown for a south-west and an onshore (141°) wind (Figs 10b,c). The south-west wind generates longshore currents and Fig. 10b indicates that there may be some exchange of water between Bastion Point and Tullaburga Island. During the onshore wind (Fig. 10c), when eddies form near Gabo Island, an exchange of water appears less likely, but onshore south-easterlies are not common (Reinson, 1977).

Measurements at one location could not fully treat the complex and spatially variable hydrodynamics of the nearshore zone identified by these model results. The model highlights the variability of flow strength with location. Offshore, where seabed friction is low, the currents are predominantly wind and inertia dependent and behave differently from the currents nearer shore (Fig. 10b) where land sheltering, seabed friction and wave–current interaction play a more important role. This variability is compounded by the unsteadiness of the wind stress which acts quicker as the depth decreases.

The variability in the strength of current flow could strongly influence larval dispersal. For example, larvae reaching the fast-flowing offshore zones would be swept away more rapidly than those remaining near the coast when waves are present. Notably, the current strengths and wave heights at Mallacoota were not exceptional (e.g., Pond & Pickard, 1983) for an exposed coastline.

Larval dispersal simulations

Fig. 11a shows the larval dispersal patterns calculated by particle tracking with spatially uniform velocities. Three distinct peaks of relative larval occurrence, one at 12 km to the east and a pair at ≈ 4 km to the north-east of Bastion Point, represent two distinctive periods in the flow measurements corresponding with an extended interval of easterly flow before a period of near-neutrality of the flow in the later stages of the record.

During the easterly flow period, there was little chance that plankton in the body of

Fig. 10. (a) Two-dimensional model bathymetry, (b) flow pattern under longshore winds from the south-to-west quadrant, and (c) flow pattern under onshore winds.

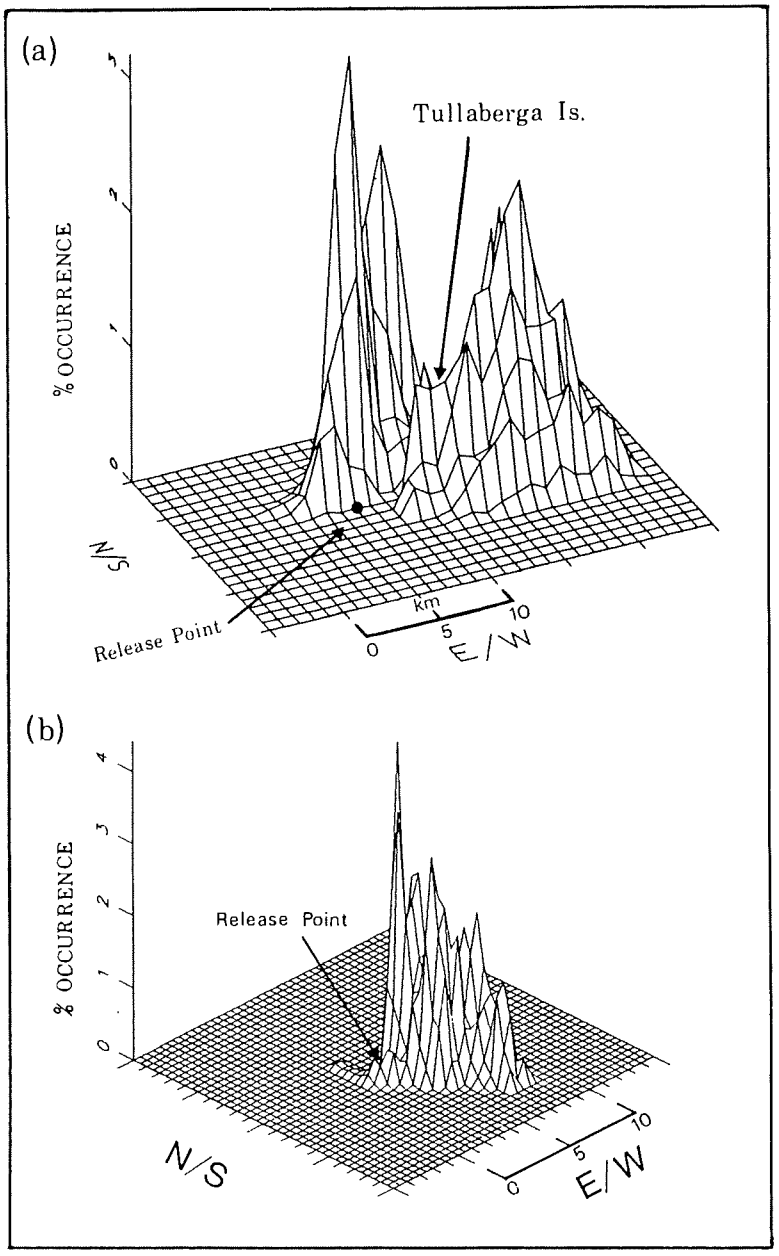


Fig. 11. Larval dispersal 3–7 days after release calculated directly from the current meter measurements and assuming spatially uniform velocities. The contours show relative larval abundance and have no units. (a) Exposed site currents: two distinctive periods were identified; a net easterly movement and a more restricted movement to the north-east. (b) Rock channel currents: the peak of the distribution is within 500 m of the release point, and maximum excursions are much less than in (a).

the water column could remain near Bastion Point. However, during the more neutral phase, the probability of local retention was still low, but the measurements indicate that some free-drifting larvae could remain nearby.

The results (Fig. 11) show that larvae from Bastion Point could be found at Tullaburga Island 3–7 days after spawning. Conversely, for Sandpatch Reef, ≈30 km to the south-west of Bastion Point, these results indicate that the dispersal excursion in the nearshore zone was more restricted and larval transfer between these two reefs is therefore unlikely.

Larval dispersal patterns simulated in the two-dimensional numerical model using near-bed currents from the hydrodynamic model are shown in Fig. 12. In this simulation, when particles were released instantaneously at the sites of interest and subsequently allowed to drift freely with the current, the advecting larval patches travelled predominantly to the east, as identified by the current meter measurements (Fig. 11).

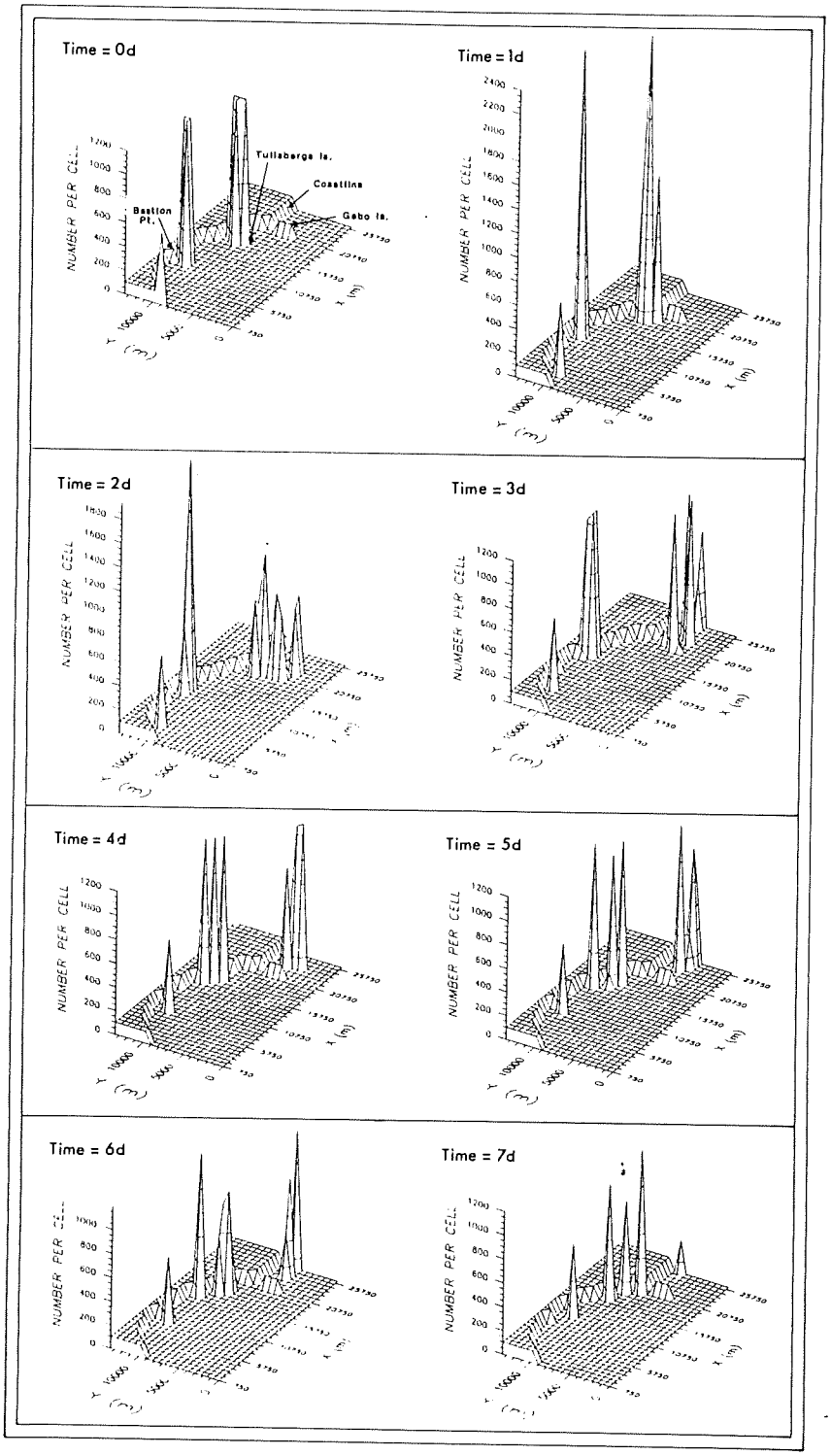
During the first 3 days, larvae from Bastion Point would have moved ≈4 km to the east drifting close to the coast along the shoreline between Bastion Point and Tullaburga Island. By the 5th day (Fig. 12), the Bastion Point patch had split into two components; one trapped near the shoreline and a second near Tullaburga Island. On the 6th day, the currents changed direction and the two components began to link up again. On the 7th day, the larvae would still be very close to the coast near Tullaburga Island. During the 7 days, larvae would have moved a total of ≈10 km. A similar movement pattern of larvae was evident when mean-vertically averaged currents were used in the larval dispersion model but the larval patch split earlier and the nearshore component was swept onto the shore (and disappeared) while the other component travelled toward Gabo Island.

Larvae from Tullaburga Island would be carried by convergent faster currents (Fig. 10b) to the eastern side of Gabo Island within 3 days (Fig. 12). Larvae would then remain in an eddy in the lee of Gabo Island for a relatively long time before passing out of the eastern boundary of the model grid.

Larvae from the western boundary would have travelled 700 m south of Bastion Point in the 3.5–5.5-day interval after release (Fig. 12). However, because Sandpatch Point is 15 km to the west of the model boundary, the arrival of larvae would be delayed by several days and the distance to Sandpatch Point is greater than the maximum excursions over 3–7 days identified by the model and the measurements. In the model, the larvae were also released very close to the land and those initially further offshore at the western boundary passed Bastion Point much further to the south. Both of these factors suggest that larval exchange between Sandpatch Reef and Bastion Point was unlikely. On the 7th day, the western boundary larvae were between Bastion Point and Tullaburga Island.

Local recruitment

The currents measured at the second site in the enclosed channel within the reef matrix were significantly less than the exposed site. Speeds were mostly $< 0.06\ m \cdot s^{-1}$


Time = 0d
Tullaberga Is.
Coastline
Gabo Is.
Bastion Pt.
NUMBER PER CELL
Y (m)
X (m)
Time = 1d
Time = 2d
Time = 3d
Time = 4d
Time = 5d
Time = 6d
Time = 7d

(Fig. 13) including the tidal flows and net flow was also small with currents consistently oscillating ≈ 0 for long periods of time. Reflecting the reduction in flow speeds, particle tracking with spatially uniform flows (Fig. 13) shows most of the larvae would be within 500 m of the release point in the 3–7-day period typical of the larval life of *H. rubra*. While the assumption of spatially-uniform velocity within the rapidly-varying reef topography is unsatisfactory, the results indicate that the irregular reef topography sufficiently attenuates the flows to allow larvae to remain within a channel or rock crevice for extended periods. A greater speed reduction than that measured in the reef channel could be expected to occur in habitat offering greater protection from water currents, for example, narrow rock crevices.

PARENT-STOCK ABUNDANCE

The abundances of *H. rubra* on the three reefs were different regardless of the method used to measure abundance. This result supports our acceptance of the reefs as having "high", "medium", and "low" abundance (Table I). On every reef, however, *H. rubra* were observed to be patchily distributed and aggregated in gutters or under ledges of the rocky substratum. This patchiness is reflected in the relatively high error in abundance estimates from the results of the quadrat method. Both the quadrat and transect methods provided more realistic estimates of the population abundance than the searching method because *H. rubra* from cryptic habitat (e.g., under boulders) can often have been missing in the sample obtained by searching. However, an unreasonably large sample size would be necessary to provide precise estimates of population abundance and even then juvenile cohorts, typically found in cryptic habitat (Shepherd, 1973; Shepherd & Turner, 1985), would be undersampled. The searching method selects for larger *H. rubra* (Fig. 14) but data from the searching method indicated that the relative proportion of parent stock (those *H. rubra* > 100 mm shell length) in each of the three populations was similar.

RECRUITMENT SURVEYS

On the three reefs a total of 72 1-m square quadrats were surveyed for post-settlement *H. rubra*. Except when a quadrat had landed on sand, no attempt was made to relocate randomly placed quadrats. Thus divers sampled a variety of substrata ranging from bare flat rock to heterogeneous habitat of kelp, boulders and encrusting biota. The physical substrate sampled ranged from horizontal to nearly vertical; our estimates of population density (Table I) are therefore not strictly comparable because surface area was not measured, logistically an impossible task. Nonetheless, the results are presented as $n \cdot m^{-2}$ (per quadrat surveyed), so that the results can be compared with those of other

Fig. 12. Near-bed dispersal patterns predicted by the two-dimensional hydrodynamic and dispersal models showing particle numbers in 750-m square cells at daily intervals for 7 days.

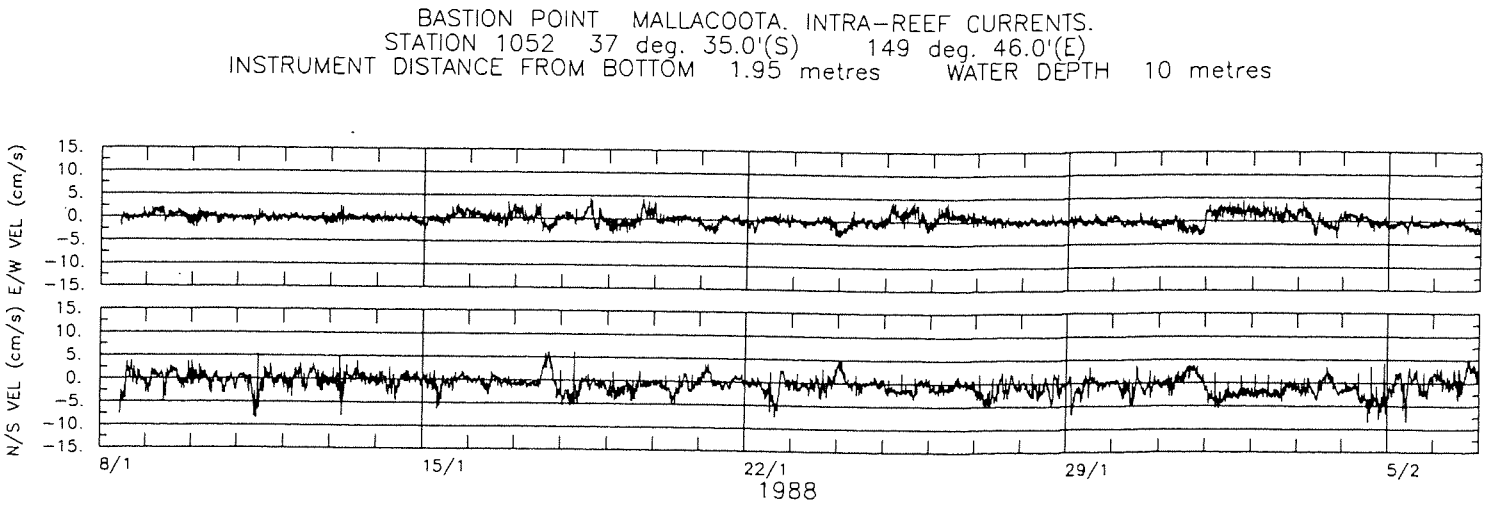


Fig. 13. East/west and north/south velocities recorded at a sheltered site in a reef channel at Bastion Point. The flows are often very slow ($< 0.05\ m \cdot s^{-1}$).

TABLE I

Mean population abundance of three populations of *H. rubra*.

Population	Mean population abundance ($n \cdot m^{-2}$) (SE)		
	Transect	Quadrat	Searching
Sandpatch Point	2.1 (0.3)	1.5 (0.5)	372 (53)
Tullaburga Is.	–	1.2 (0.4)	285 (42)
Bastion Point	0.6 (0.1)	0.9 (0.2)	159 (19)

studies. Densities of *H. rubra* recruits sampled varied from 0 to $246 \cdot m^{-2}$ and were much higher than those from other comparable studies, for example, Prince & Ford (1985) ($0–15 \cdot m^{-2}$) or Shepherd & Turner (1985) (up to $13 \cdot h^{-1}$ searching time). The size range of recruits sampled on the three reefs were similar. The mean shell length (mm) (SD), length range of recruits sampled, and sample size (n) was 1.03 (0.44), 0.41–3.95, and n = 538, 0.78 (0.37), 0.51–2.19, and n = 146, and 0.80 (0.42), 0.45–4.90, and n = 218 for the Sandpatch Point, Tullaburga Island, and Bastion Point populations respectively. The wide range of sizes of recruits of *H. rubra* within a population on a reef supported the suggestion from the gonad index results that settlement on each reef was asynchronous. Abalone settle when they are 300–500 μm (Ino, 1952; Grant, 1981). Thus, the size range of recruits sampled (420–620 μm) is consistent with recent settlement of *H. rubra*.

Site to site variation in recruitment of *H. rubra* on each reef was high (Table II). However, recruitment varied between the three reefs with the mean recruitment of *H. rubra* reflecting the abundance of parent stock. Thus, at Sandpatch Point which supported a relatively high abundance of adult *H. rubra*, mean recruitment was $31.1 \cdot m^{-2}$ compared with 16.8 and $5.8 \cdot m^{-2}$ at Tullaburga Island and Bastion Point, respectively.

All three reefs supported communities dominated by dense stands of the kelp *Phyllospora comosa*. Relative area of encrusting coralline algae varied within a given reef (Table I) yet there was no correlation between recruitment of *H. rubra* and relative cover of coralline algae. The relative cover of coralline algae was similar between the three reefs (Table II).

DISCUSSION

The results of our study, in which we used the best method available for measuring recruitment, provide realistic estimates of recruitment in *H. rubra*. Previous studies of abalone have underestimated recruitment because juvenile abalone are difficult to detect by searching (Saito, 1981; Sainsbury, 1982; Shepherd & Turner, 1985) or because only recruits on removable substrata were counted (Prince & Ford, 1985). Our results show

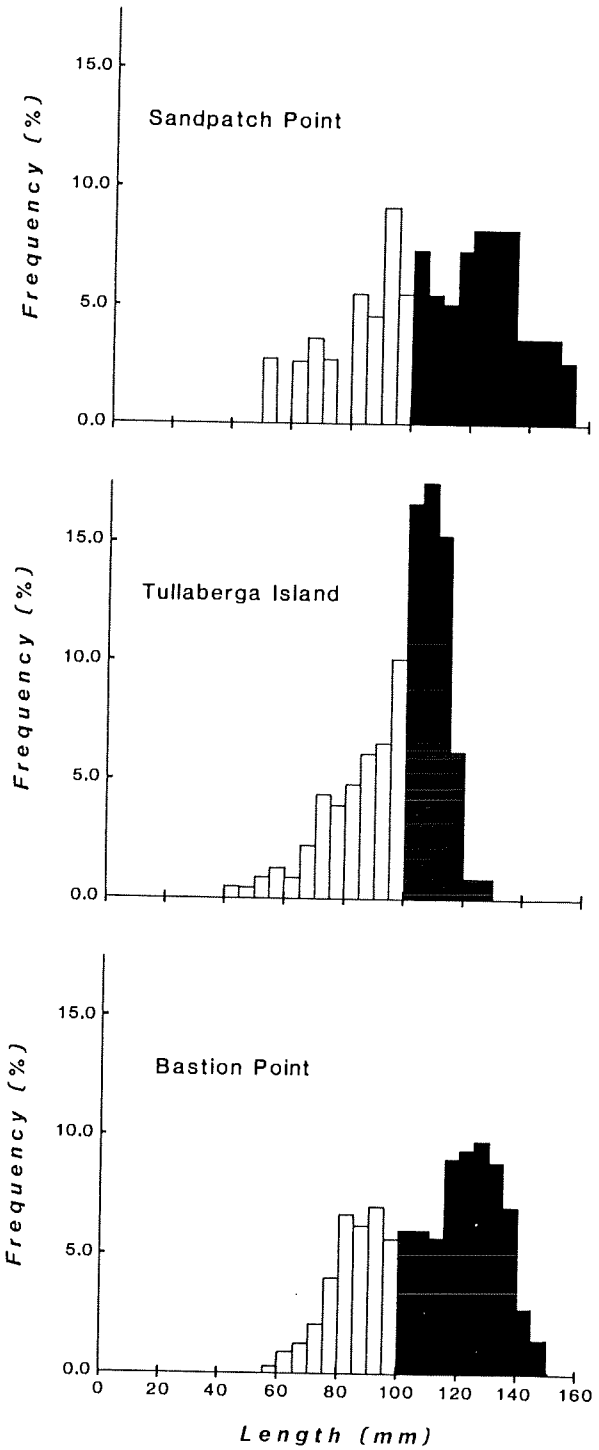


Fig. 14. Length frequencies of three populations of *H. rubra*, Sandpatch Point, Tullaburga Island, and Bastion Point sampled by searching (see text). Frequencies in each case are expressed as percentage of the total sample (n). The relative proportion of estimated parent stock is indicated by shading.

TABLE II

Relationship of recruitment of *H. rubra* to adult abundance and the relative cover encrusting coralline algae on three neighbouring reefs. Data are means (SE). ANOVA revealed that mean coralline algal cover was homogenous between reefs ($F_{2,69} = 0.54$, $P > 0.4$) but that mean recruitment of *H. rubra* varied between reefs ($F_{2,69} = 15.5$, $P < 0.001$).

Reef	Site	*n*	Coralline algal cover (%)	Recruitment ($n \cdot m^{-2}$)
Sandpatch	1	6	26 (9)	13.8 (6.4)
Point	2	5	54 (21)	16.8 (11.6)
	3	5	60 (19)	69.4 (22.1)
	4	4	52 (10)	22.7 (6.7)
Tullaburga	1	5	48 (16)	19.0 (6.8)
Island	2	5	66 (17)	14.6 (6.7)
Bastion	1	5	28 (16)	5.8 (2.1)
Point	2	5	23 (18)	12.4 (5.8)
	3	5	20 (18)	2.4 (0.8)
	4	4	24 (19)	4.0 (1.4)
	5	5	17 (14)	6.6 (1.8)
	6	4	47 (5)	2.5 (1.6)
	7	5	42 (11)	3.8 (2.0)
	8	4	29 (18)	8.8 (6.2)
	9	5	32 (23)	6.0 (3.4)

that recruitment of *H. rubra* on each of the reefs is related to the abundance of adults on that reef. We propose that our results for recruitment in *H. rubra* can be explained by settlement of larvae near the parent reef, i.e., local dispersal of larvae.

Recruitment of *H. rubra* on any reef will be influenced by (a) larval availability, (b) larval mortality, and (c) availability of substrate (Keough & Downes, 1982; Connell, 1985). We assume in the following discussion that larval availability is controlled by the hydrodynamics directing larval transport and by production from the parent stock.

PELAGIC DISPERSAL

Results from studies of water movement have prompted hypotheses of pelagic dispersal of abalone larvae (e.g., Tegner & Butler, 1985) and indeed our results from modelling show that pelagic dispersal of *H. rubra* can occur. However, dispersal from Bastion Point was to the east and no upstream source to replace the larvae lost was identified by the modelling or measurements. Furthermore, near spawning time, we found only one larva of *H. rubra* in waters surrounding the reefs. Our lack of success in finding larvae is consistent with results by Breen & Adkins (1980) and others. Tomita *et al.* (1977) and Tanaka *et al.* (1986) have reported both trochophore and veliger larvae of abalone in the open sea, but the small numbers they and we found are low considering the high numbers of recruits we record on the reef surface. Larval mortality of abalone is doubtless high, as it is for other marine invertebrates with a pelagic larval phase (Cameron, 1986), and so, if high recruitment was the result of pelagic dispersal of larvae, huge numbers of larvae must have been present in the plankton before settlement. While

our studies of dispersal have accented the difficulty of attempting to randomly sample for a small, mobile, larval patch (the chance of finding larvae is relatively low unless hydrodynamic model predictions, such as ours, or simultaneous oceanographic measurements, are made in conjunction with on-site diver identification of the time of spawning), they equally demonstrate that the probability of large numbers of larvae of *H. rubra* being over suitable substrate at the time of settlement is low.

LOCAL RETENTION OF LARVAE

Prince *et al.* (1987) have suggested that dispersal of abalone larvae is local because spawning by abalone is triggered during periods of calm weather when wind-driven currents are low. However, calm conditions would have to persist for the larval life of an abalone (3–7 days) to avoid dispersal. Our results show that calm conditions are unlikely to persist that long in our study area. Rather, we suggest that calm conditions are the optimum for fertilization of eggs for dioecious and broadcast spawners such as abalone. Eggs of abalone are negatively buoyant (Ino, 1952) and slight water turbulence may assist the mixing of gametes such that fertilization is enhanced. On the other hand, the water velocities that we measured in open water could cause such diffusion of sperm that fertilization would be impeded.

Our studies of the hydrodynamics within the habitat of *H. rubra* suggested that dispersal of larvae was local. The crevices in the reef habitat of *H. rubra* provide shelter from the tidal and wind-driven flows of the region and a site for fertilization of eggs. Larvae can settle near their parents by remaining in the local rock fissures or under the protection of epibiota very near the seabed where currents are strongly attenuated. These locations may provide a suitable habitat for abalone during the pelagic phase of its life cycle. Our hypothesis is supported by finding high recruitment of *H. rubra* ($> 100 \cdot m^{-2}$) in sheltered habitat (surrounded by large boulders and dense kelps) but low recruitment in comparatively open habitat (no kelp, bare flat reef). Moreover, in sheltered habitat, larvae would be more able to remain in contact with the reef surface.

The hypothesis that calm conditions are conducive to settlement of abalone larvae is supported by the association of adult abalone with kelp communities (Shepherd, 1973; Hines & Pearce, 1982; this study). Kelps can be effective attenuators of water movement (Bernstein & Jung, 1979; Jackson & Winant, 1983) and so kelps may function to assist larval trapping such that the entire larval life can be completed in an area close to the parent (Jackson & Strathmann, 1981).

The high level of turbulence induced by surface waves would be expected to reduce the larval retention rate, and the measurements in the exposed location suggest that larvae moving into the water column would be dispersed. The several orders of magnitude between recruit numbers and larvae released is indicative of these processes. However, because of the large difference in numbers, many larvae can be lost due to intermittent periods of wave turbulence without totally depleting local stocks. Of these lost from the reef, random turbulent currents acting on negatively bouyant eggs and

precompetent larvae would be expected to return some of those near the seabed into more sheltered locations.

The hypothesis of localized dispersal of abalone larvae also implies that individual reefs harbour discrete parent stocks of abalone. While other factors may be important, the number of recruits produced from a population should reflect the abundance of adults. Our results show that for populations of *H. rubra* this is indeed so.

It is noteworthy that the few reports of abalone larvae in the sea have been in the regions of eddies (Tomita *et al.*, 1977; Tanaka *et al.*, 1986). Eddy formation is a common feature of continental shelf flows (Black & Gay, 1987). Black (1987b, in press) found that circulation patterns around coral reefs on the Great Barrier Reef caused free-drifting larvae to remain longer in some regions than others. The pattern of larval retention to the east of Gabo Island is similar to this. The higher residence time of larvae to the east of Gabo Island suggested a higher probability of larval settlement in proportion to the total time that larvae spend in the area. The eastern side of the island supports a relatively large number of *H. rubra* (McShane *et al.*, 1986) and the abundance of juveniles is relatively high (McShane, unpubl. data). Similarly, our hydrodynamic studies show that the predominant westerly water currents in the study area should cause eddy formation on the eastern side of headlands, for example our study site at Sandpatch Point. Recent surveys of *H. rubra* in the study region have revealed relatively few juveniles on the western compared with the eastern side of headlands despite no obvious difference in habitat (McShane *et al.*, unpubl. data). Moreover the lowest number of recruits recorded at Sandpatch Point in the present study was on the western side of the headland. The model result therefore indicates a correlation between the hydrodynamic processes and recruitment of *H. rubra*. Indeed the relative abundance of parent stock on the three reefs may also be explained by the hydrodynamic processes in the region.

VARIATIONS IN ADULT ABUNDANCE

Sandpatch Point and Tullaburga Island offer more shelter from currents than Bastion Point. Furthermore our measurements of current velocities and the numerical modelling both showed that larvae entering the water column on the open coast at Bastion Point are likely to be dispersed from their parent reef. Our studies show that exchange of larvae between Sandpatch Point and Bastion Point is improbable and so only those larvae trapped within local reef topography are likely to successfully settle at Bastion Point. Thus the hydrodynamic processes which influence recruitment are evidently responsible for the abundance of adults on a particular reef.

Larval mortality

As an alternative hypothesis, differences in recruitment on the three reefs could have been the result of differential mortality, due to, for example, temporal differences in settlement. But our results of both the reproductive state of adults and the comparative

size range of recruits of *H. rubra* indicated similar patterns of settlement between the three reefs. Different abundances of predators on the reefs is unlikely because the reefs had similar topography, were in the same geographical area, had similar relative cover of crustose coralline algae and supported apparently similar communities.

Availability of substrate

Abalone are reported to settle exclusively on coralline algae (Saito, 1981; Shepherd & Turner, 1985; Clavier & Richard, 1986; McShane & Smith, 1988). Yet, the recruitment observed during our study was not related to the relative cover of coralline algae. Chemicals available only on the surfaces of crustose coralline algae have induced settlement and metamorphosis of abalone in the laboratory (Morse *et al.*, 1979a,b, 1980). However, chemical cues are effective only if a larva is in direct contact with, or in close proximity to the substrate containing the chemical (Morse *et al.*, 1980; Banse, 1986; Butman, 1987) which further suggests that sheltered habitat provides the most suitable location for settlement of *H. rubra*. For example, orbital velocities under waves were ≈ 0.1–$1\ m \cdot s^{-1}$ in the study region (Black & McShane, 1988) which is several orders of magnitude greater than the mobility of most invertebrate larvae (Mileikovsky, 1973; Banse, 1986).

CONCLUSIONS

The absence of adequately defined stock–recruitment relationships for abalone (Mottet, 1978) arises from two main sources: a failure to detect recruits, and a lack of understanding of larval dispersal. We believe that the results of our study serve to redress the lack of knowledge in these areas. We predict that, at the time of spawning, larval concentration of *H. rubra* will be highest in sheltered habitat near the reef surface; larvae entering the water column by vertical diffusion or wave-induced turbulence will be dispersed. We have discussed the mechanism of pelagic dispersal of larvae in *H. rubra*. Typically, the larvae travelled ≈ 10 km from the parent reef at Bastion Point. However, the larvae probably had little chance of encountering suitable substrate on which to settle. Larvae entrained in discrete areas by current eddies could be the exception. However, many, if not most, abalone reefs are not subject to current eddies particularly where variable tidal flow and weather patterns cause eddies to dissipate when flow patterns change.

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Measuring Abundance of Juvenile Abalone, *Haliotis rubra* Leach (Gastropoda : Haliotidae); Comparison of a Novel Method with Two Other Methods

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Abstract

An underwater venturi-suction sampler is described, suitable for sampling fauna on structurally-complex sublittoral reefs. Abundance of juvenile *Haliotis rubra* was estimated from the samples collected with the suction sampler; this was compared with estimates obtained at the same time by two other methods, an anaesthetic method and a searching method. Off Sandpatch Point (south-eastern Australia) during January 1987, the mean number (s.e.) of *H. rubra* per square metre of substrate was 68·7 (s.e., 39·2) by the suction method, 25·6 (s.e., 16·1) by the anaesthetic method and 7·7 (s.e., 3·0) by the searching method. Off Cape Schanck, the respective numbers were 1·3 (s.e., 0·5), 1·2 (s.e., 0·5) and nil. Juveniles found in the population off Sandpatch Point were of a size range (430–1020 μm) consistent with recent settlement of *H. rubra*. The suction method has three main advantages over the other two methods: unlike the anaesthetic technique it is not destructive and is not restricted to removable substrate; it is readily applied to most reef substrata by one diver spending relatively little time under water; and the sampler is sufficiently powerful to remove all juvenile abalone from the reef surface.

Introduction

Abalone are herbivorous gastropods (family Haliotidae) common on coastal reefs in temperate waters. Because of their considerable commercial value, much scientific effort has been expended in defining the population biology of abalone (see review by Mottet 1978). Yet the early life history of abalone is poorly understood, primarily because the abundance of newly-settled individuals is difficult to estimate (Prince and Ford 1985; Shepherd and Turner 1985). Very small abalone in the complex habitat typical of sublittoral reefs generally elude detection by divers. This prompted Prince and Ford (1985) to develop an anaesthetic technique for removing juvenile abalone from substrata. Although this method provides more realistic estimates of abalone abundance and is less operator-dependent than standard searching methods, it relies on the removal of suitable substrata from the bottom for examination. Thus the method is destructive, and examination of abalone abundance is restricted to those substrata (e.g. small boulders) that can be taken by a diver to the surface.

To overcome these limitations we have developed a diver-operated suction sampler suitable for collecting newly-settled abalone (*Haliotis rubra*) from structurally complex reef habitat. The suction samplers already available are suitable for sampling fauna from soft-bottomed habitat (Barnett and Hardy 1967; Christie 1976; True *et al.* 1968; Bussers *et al* 1983; Stoner *et al.* 1983) and from hard substrata on structurally simple but not structurally complex reef (Kennelly and Underwood 1985). Our sampler operates on the venturi principle and has a more powerful suction than the pump-driven sampler of Kennelly and Underwood (1985).

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This paper describes the suction sampler and the way it was used to collect samples from which was estimated the abundance of juveniles of *H. rubra* in populations off Sandpatch Point and Cape Schanck in Victoria. These results were compared with estimates of abundance obtained by two other methods, the anaesthetic method and the searching method.

Materials and Methods

To investigate the habitat specificity of juvenile *H. rubra*, reefs off Tullaberga Island (37°34'S., 149°51'E.) were examined by searching and by the anaesthetic technique of Prince and Ford (1985). Replicate 1-m square quadrats were randomly placed on the reef and thoroughly searched by divers who overturned boulders where appropriate, removed epibiota and examined cracks and crevices. If the quadrat was placed on habitat (e.g. sand) not suitable for *H. rubra*, or if the quadrat lay on habitat inaccessible to divers (e.g. deep crevices), the quadrat was replaced. At the same time, substrata removable by divers were taken to the surface for treatment with anaesthetic (Prince and Ford 1985); various seaweeds (e.g. the kelps *Phyllospora comosa* and *Ecklonia radiata*), large tunicates and small boulders were removed from the reef. Material was placed in a 200-μm mesh bag to avoid loss of *H. rubra* during its transport to the surface.

These two methods were used to obtain estimates of abundance of juvenile *H. rubra* on a reef off Sandpatch Point (37°44'S.,149°36'E.) during January 1987 and off Cape Schanck (38°29'S.,144°53'E.) during April 1987; these were compared with those obtained from samples collected from 1-m square quadrats with the venturi-suction sampler (Fig. 1). For the anaesthetic method, divers collected only boulders because studies at Tullaberga Island had shown that recruits of *H. rubra* were present only on hard substrata.

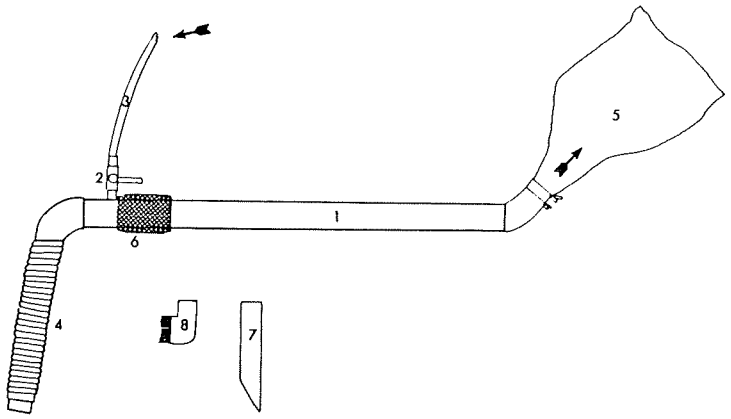

Fig. 1. The suction sampler employed: *1*, 55-mm diameter PVC tube; *2*, 12-mm ball valve; *3*, compressed-air inlet; *4*, flexible vacuum-cleaner hose; *5*, 200-μm mesh bag; *6*, 2·5-kg shot weight; *7*, crevice suction attachment; *8*, brush for normal flat-surface sampling. Arrows show the passage of air through the sampler.

The venturi-suction sampler is driven by the diver's air supply. The use of surface-supplied air (hookah), rather than SCUBA, permits longer sampling time under water. The diver controls the sampler's suction by means of a hand valve, which is attached directly to the body of the device using commercially available plumbing fixtures. Epibiota are drawn from the reef through commercial vacuum-cleaner attachments; brushes for encrusting biota, or a nozzle for cracks or crevices. Attachments are easily interchanged under water, as are the sample-containing bags made from 200-μm plankton mesh.

Material removed from the substrata by either the suction sampler or by anaesthetic was preserved in 10% buffered formalin. In the laboratory, material was sorted by means of a 2-mm mesh screen and then a 500-μm screen (fine sievings). The approximate diameter of newly settled abalone is 400 μm (Ino 1952), and it was assumed that this selective screening would speed the sorting process. Nevertheless, both coarse and fine screenings were retained for analysis and the relative sorting times were recorded.

Samples were sorted with the aid of a dissecting microscope and the longest shell dimension of *H. rubra* was measured, to the nearest micrometre, with a calibrated eyepiece graticule.

Because it was impossible to measure surface area available for settlement by *H. rubra*, the abundance of juveniles was expressed as number per square-metre quadrat. As with the reef surface contained within a quadrat, the actual surface area of a boulder will depend on its topography. Therefore, in order to get comparable estimates of juvenile abundance of *H. rubra* across methods, an approximate value for the flat surface area of each boulder was recorded and each estimate was adjusted to one square metre.

Results

Many types of substratum including seaweed, surfaces of sponges, tunicates and bryozoa were examined at Tullaberga Island both by searching and by anaesthetic treatment. Careful searching revealed juvenile *H. rubra* (< 5 mm shell length) only on encrusting coralline red algae; thorough searching of five quadrats gave a mean of 0·7 (s.e., 0·5) per quadrat. From 19 boulders treated with anaesthetic, the mean number of juvenile *H. rubra* collected per quadrat was 8·4 (s.e., 3·7).

Mean shell length of *H. rubra* juveniles collected by anaesthetic sampling of substrata from Tullaberga Island was 2·3 (s.e., 0·3) mm whereas that of *H. rubra* detected by searching was 4·8 (s.e., 0·8) mm. It was, however, difficult to measure very small *H. rubra* *in situ* because many were lost while being removed from the substratum for measurement. Others were present in depressions in the coralline algae whose colour is so similar to their shell colour that many juveniles probably remained undetected.

Table 1. Mean abundance (s.e.) and mean length (s.e.) of *H. rubra* juveniles off Sandpatch and Cape Schanck

Sample size (no. of 1-m square quadrats or equivalents) is 5 in all cases. Total effort is sampling and sorting time per 1-m square quadrat. *Significantly different by ANOVA ($P < 0·05$)

Sampling method	Juvenile abundance (abalone m^{-2})		Length (mm) of juveniles		Total effort (h)
	Sandpatch	Cape Schanck	Sandpatch	Cape Schanck	
Suction	68·7 (39·2)	1·3 (0·5)	1·4 (0·2)	1·8 (0·8) } *	5–10
Anaesthetic	25·6 (16·1)	1·2 (0·5)	1·2 (0·1)	3·4 (0·5) } *	2–6
Searching	7·7 (3·0)	0·0	1·5	–	1–2

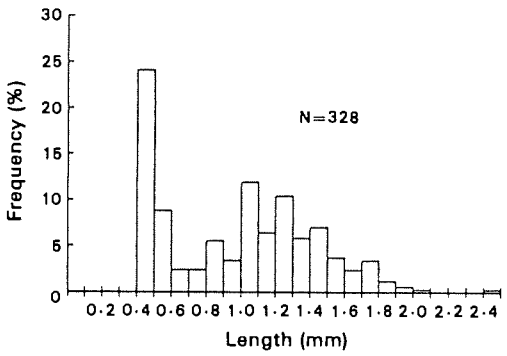

Fig. 2. Length-frequency distribution of *H. rubra* recruits sampled by suction from Sandpatch Point (coarse and fine sievings). Frequencies are percentages of the total sample (*N*).

At each sampling site, the abundance of *H. rubra* juveniles estimated by the venturi-suction method or by the anaesthetic method was not significanly different (by ANOVA $P > 0·05$), but the searching method seriously underestimated abundance (Table 1). However, even the first two methods underestimated abundance, because only *H. rubra* individuals retained by a 500-μm screen were counted. Examination of fine sievings from Sandpatch revealed numerous *H. rubra* individuals ranging from 430 to 1020 μm in shell length (Fig. 2). Consideration only of coarse screenings underestimated the total abundance by a mean of 67%. Therefore the mean abundance at Sandpatch was 115 per square metre,

which is more than an order of magnitude greater than the mean estimated by searching. No additional *H. rubra* juveniles were found in the fine sievings of samples from Cape Schanck. Fine sievings derived from anaesthetic samples were not examined but, because the same screens were employed for both methods, the underestimate may be of similar proportions.

Sorting the coarse screenings was laborious; more so for those obtained from the suction method than for those from the anaesthetic method (Table 1). Generally, a greater surface area was sampled by suction than with anaesthetic so that the former method produced more material to be sorted. Sorting the fine sievings was even more time consuming. An additional 10 person hours per sample was necessary, on average, to sort fine screenings for *H. rubra*. However, more recent studies (McShane and Smith, unpublished data) revealed that this sorting time could be at least halved using rhodamine dye. By using a 0·1% solution of the dye in 95% ethanol and applying this to formalin-treated samples (Hamilton 1969), all invertebrates were stained bright pink; this made the task of sorting *H. rubra* from inorganic material (e.g. sand) much less time consuming. Inclusion of fine screenings from one sample at Sandpatch yielded the highest estimate ever made for juvenile abundance in a population of abalone, namely 246 juveniles per square metre.

Discussion

The study has shown that reasonable estimates of juvenile abundance of *H. rubra* are attainable; these will greatly assist understanding of recruitment processes which, to date, are poorly understood for abalone in general.

Estimates of juvenile abundance of *H. rubra* at the two sampling sites were significantly different, but one site was sampled in January, the other in April; therefore, differential mortality could account for the observed disparity. To avoid errors due to, for example, differential mortality, it is advisable to measure recruitment as soon as possible after settlement (Keough and Downes 1982). Victorian populations of *H. rubra* generally spawn during summer (McShane *et al.* 1986); therefore the present survey of juveniles at Cape Schanck during April may have been compromised by a time lag between settlement and date of sampling. Evidence for this is the relatively low abundance of juveniles of *H. rubra* at Cape Schanck and their comparatively large size.

The sizes of juveniles in the screened samples taken at Cape Schanck by the suction method and by the anaesthetic method were significantly different (Table 1). A likely explanation is that the suction was not applied to the undersides of boulders. Abalone are known to migrate to cryptic habitat such as the undersurfaces of boulders after first settling on coralline algae (Shepherd 1973; Witherspoon 1975; Prince and Ford 1985; Shepherd and Turner 1985; McShane and Smith, unpublished observations). The size of juvenile *H. rubra* in the screened samples taken at Sandpatch by the suction method and by the anaesthetic method were not significantly different (Table 1). Difficulties associated with *in situ* measurement of all *H. rubra* found by searching prevented an accurate assessment of the size of *H. rubra* detected by that method.

The size of *H. rubra* juveniles sampled at Sandpatch ranged from 430 μm (in the fine sievings) to 2500 μm. It showed a bimodal distribution (Fig. 2) reflecting a discrete settlement revealed only by examination of the fine sievings. The size distribution of juvenile *H. rubra* sampled by suction at Sandpatch indicated at least two periods of settlement. In the absence of reliable growth data, the precise timing of settlement cannot be accurately estimated; however, the mean size of the first post-settlement cohort of *H. rubra* is similar to that typical of competent larvae (Ino 1952; Grant and Sumner, personal communication for *H. rubra*). Thus, the data from Sandpatch suggested that *H. rubra* juveniles were settling very near the time of sampling. If surveys are timed to coincide with the period immediately following spawning, such as at Sandpatch, then realistic estimates of recruitment of abalone are attainable using the present method.

The main advantage of the suction method is that it is simple to use, it permits *in situ* sampling of most *H. rubra* habitat and it allows samples to be collected rapidly. Typically, a sample can be removed from a 1-m square quadrat within 20 min. *In situ* observations of juveniles of *H. rubra* on the reef revealed that most were removed with a single pass of the suction sampler and all were removed with two or more passes. Because of the obvious physical constraints of underwater sampling, time saved under water is valuable, especially as opportunities to sample the shallow sublittoral reefs generally populated by abalone are relatively few.

The main limitation to the suction method is the time taken to sort the samples collected. More than a hundred taxa of various epibiota were encountered in the suction samples. Because *H. rubra* is the only species of abalone common at both sites, identification of juveniles was relatively simple but, even with selective screening of sample material, sorting was very time consuming. Use of fluorescent dyes (Hamilton 1969) is one way in which sorting time can be reduced.

Our results show, as did those of Prince and Ford (1985), that searching is an inaccurate method of measuring abundance of abalone. Prince and Ford (1985), in evaluating their anaesthetic method of measuring juvenile abundance, showed that searching is operator-dependent and underestimates abalone measuring less than 20 mm. Although searching provides poor quantitative data on recruitment, it is useful for acquiring qualitative information such as habitat preference, especially if enhanced by underwater magnification (Kennelly and Underwood 1984; Shepherd and Turner 1985). Only careful underwater searching revealed the phenomenon of settlement of *H. rubra* exclusively on crustose coralline algae (Saito 1981; Shepherd and Turner 1985; Clavier and Richard 1986; the present study).

The suction sampler described might equally well be applied to the sampling of other epibiota. Application of an airlift (venturi principle) ensures considerable suction (Barnett and Hardy 1967), unlike the sampler of Kennelly and Underwood (1985) which lacked efficiency in turfing algal habitats. Despite the removal power of the suction sampler, few *H. rubra* samples were damaged while being removed from the reef, even though newly-settled individuals were fragile. Thus, the method may be widely applicable to the sampling of delicate taxa.

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Growth and Morphometry in Abalone (*Haliotis rubra* Leach) from Victoria

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Abstract

Several Victorian populations of the abalone *Haliotis rubra* were studied. A comparison was made of relationships of the dependent variables, shell width, shell height, foot weight and total weight with shell length of abalone collected from several sites at different seasons. Male and female *H. rubra* were morphometrically similar. In contrast, the morphometrics for abalone collected from the same site at different times were significantly different, as were the morphometrics of abalone collected from different sites at the same time. Weight yields (foot weight relative to total weight) from Portsea and Apollo Bay were highest in winter and lowest in summer. This correlated with the known reproductive cycle in *H. rubra*, suggesting a relationship of gonad fullness and somatic tissue weight. Morphometric heterogeneity was attributed to differences in growth rates between sites. Growth rates were estimated at three sites and significant between-site variation was shown.

At Mallacoota, *H. rubra* tagged with a threaded wire tag yielded lower estimates of growth rate than those to which tags were affixed with glue. Differences in growth rate, exclusive of tagging method, were attributed to difference of exposure between the study sites.

Introduction

Victoria has a lucrative commercial fishery for the abalone *Haliotis rubra* (McShane *et al.* 1986*a*). As in other abalone fisheries (Mottet 1978), legislation determines the minimum length of capture and therefore the size of *H. rubra* available to the fishery. Victorian fishermen are paid according to the total weight (including shell) of *H. rubra* but generally only the large muscular foot is processed for export markets. Therefore a knowledge of the species' morphometric characteristics and their relationships to the weight of *H. rubra* (total weight and edible flesh weight) is an important consideration in the development of optimal harvesting strategies. Another important consideration, the growth rate of the species, has been studied by Shepherd and Hearn (1983). They found that the growth rates of geographically distinct populations of *H. rubra* in South Australia were different, a phenomenon common for haliotids in general (e.g. Newman 1968; Poore 1972). It is therefore inappropriate to apply growth estimates derived from South Australian populations to Victorian populations. This and the fact that little is known of the morphometry of *H. rubra* has prompted this study.

In this paper we describe the morphometry of several populations of *H. rubra* in Victoria, including the relationship of shell height or width with shell length and the relationship of total weight or flesh weight with shell length. We also compare the effect of sex, location and season on these relationships. In our study we used the mark–recapture method to measure growth rates, but used two types of tag and compared the effects of the different types of tag.

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Materials and Methods

Morphometry

Haliotis rubra was sampled at seven sites along the Victorian coastline (Fig. 1) during the 3 years August 1969–March 1972. Weather conditions made it necessary to use a flexible sampling strategy and at some sites *H. rubra* could not be collected more than once.

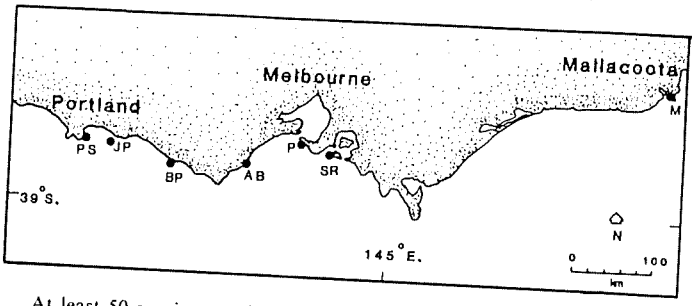

Fig. 1. Localities where samples of *H. rubra* were collected (PS, the Passage; JP, Lady Julia Percy Island; BP, Boulder Point; AB, Apollo Bay; P, Portsea; SR, Seal Rocks; M, Mallacoota).

At least 50 specimens of *H. rubra* were collected from each site by research or commercial divers, monthly where possible. The length and width of each shell was measured to the nearest millimetre with vernier calipers. Shell height was measured with an apparatus, similar to that described by Newman (1968), which measured the distance between the ventral plane of the shell and the apex of the spire. Shell length, width or height is hereafter referred to as length, width or height respectively. Total weight was recorded to the nearest gram and the muscle tissue of the foot (foot weight) was weighed after dissection from the shell and viscera. The sex of each animal was recorded wherever possible.

Regression analyses with length as the independent variable were carried out. The relationship between weight X (either total weight or foot weight) and length (L) was assumed to be:

$$X = aL^b$$

Therefore weight and length were converted to logarithms so that regression analysis could be used to estimate a and b.

Growth

For measurement of growth, more than 1000 individuals were tagged at three sites; Seal Rocks, Mallacoota and Boulder Point (Fig. 1). At each site where they were collected, tagged and measured for length, the time of emersion was always less than 1 h. Two tagging methods were used. In one method, a numbered plastic tag (22 × 12 mm) was attached with rapid-setting epoxy glue to a part of the shell from which epibiota had been removed and the surface quickly dried with compressed air (Forster 1967). In the other method, tags were attached to the shell with stainless-steel wire (0·5 mm diameter) threaded through two adjacent respiratory pores.

Growth increments were determined by periodic recoveries and measurement of tagged abalone. Tagged individuals that had been recovered were not replaced but additional abalone were tagged during each visit to a site, so that data were obtained for individuals that had been at liberty for different times.

Growth increment were fitted to a von Bertalanffy growth equation: $L = L_\infty\{1 - \exp[-K(t - t_0)]\}$ where L is the length of the animal at age t, L_∞ is the theoretical maximum length, t_0 is the hypothetical age at which L is zero and K is the growth constant which indicates the rate of increase in length towards L_∞. The parameters L_∞, K and t_0 were estimated according to the method of Fabens (1965).

Results

Morphometry

From measurements of 5461 individuals from seven sites on the Victorian coastline, we calculated mean ± standard deviation and range, respectively, for length (108 ± 18 mm; 36–164 mm), width (86 ± 15 mm; 7–136 mm), height (31 ± 6 mm; 10–55 mm), total weight (200 ± 94 g; 8–576 g) and foot weight (85 ± 40 g; 4–260 g). That few small specimens (length less than 70 mm) were collected at any site is reflected in the relatively high mean shell

length (108 mm) of the total sample. However, the range of values for each morphometric parameter was wide and facilitated correlation between any two morphometric variables. Comparison of the relationships between the various shell dimensions and between length and weight at any site revealed that males and females were morphologically similar ($P > 0{\cdot}25$). We therefore pooled the data for both sexes at each site for comparisons of morphometric relationships of *H. rubra* from different sites and the changes in morphometric relationships with time.

Pooled data from populations at Apollo Bay, Seal Rocks, Mallacoota and Portsea were sufficient for us to compare the morphometric relationships of each population at different times. Analysis of covariance of morphometric regressions for each of the populations showed that morphometric relationships varied with time (d.f. 34, 1448 F = 1·8, $P < 0{\cdot}001$). For the Portsea and Apollo Bay populations, the meat yield (foot weight relative to total weight) was lowest in summer and highest in winter (Fig. 2). We were unable to detect trends in the weight yield of other populations because the data were insufficient.

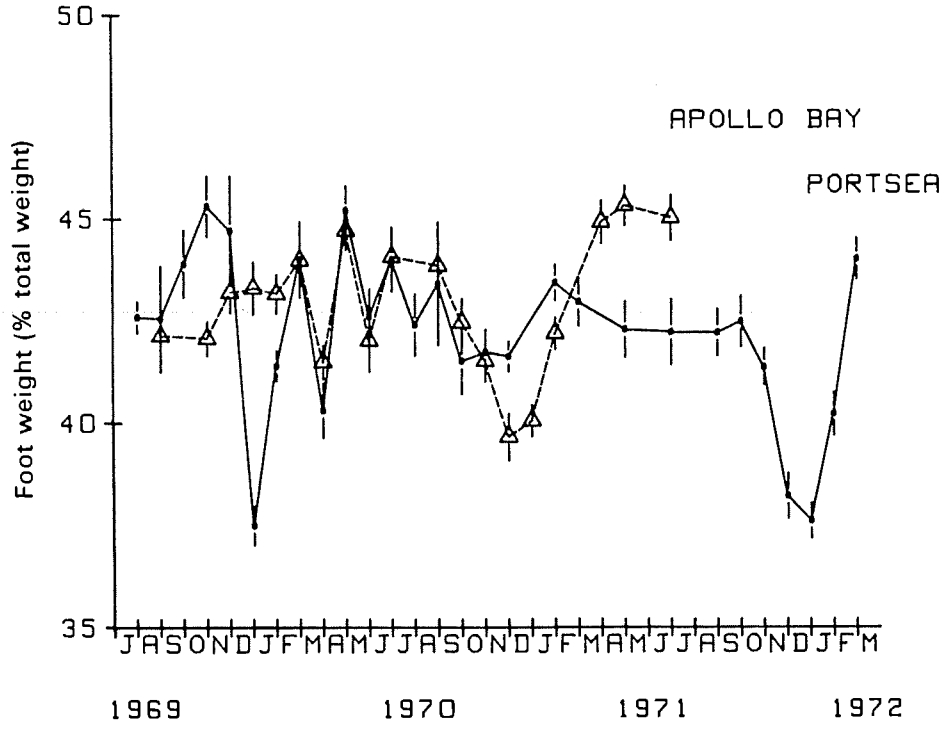

Fig. 2. Variation in meat yield from *H. rubra* from Portsea and Apollo Bay. Data for Portsea (—●—) and Apollo Bay (- -△- -) are means ± s.d.

We used all data from any one population to generate morphometric regressions with length as the independent variable (Table 1). All linear regressions had slopes significantly different from zero ($P < 0{\cdot}0001$), and coefficients of determination indicated excellent 'goodness of fit' of linear regression models (Table 1). Analysis of covariance of morphometric characteristics revealed significant differences between populations from different sites (d.f. 8, 5622 F = 1753, $P < 0{\cdot}0001$). This was true for all dependent variables compared with length. For example, samples from Mallocoota yielded a lower foot or total weight for a given length than any other population examined, whereas those from Seal Rocks

yielded the highest weights of any population studied. Similarly, samples from Mallacoota had a lower height for a given length than those from the other sites.

Table 1. Relationships between morphometric variables in *H. rubra* populations
Values are given for regression constants a and b (with standard error), sample size n and coefficient of determination r^2. Weights in grams, shell dimensions in millimetres

Relationship	Sampling site	a	$b \pm$s.e.	n	$r^{2\wedge}$
Total weight (T) *v.* length (L) $T = aL^b$	Apollo Bay	$8{\cdot}13 \times 10^{-5}$	$3{\cdot}12 \pm 0{\cdot}03$	1555	0·90
	Mallacoota	$1{\cdot}44 \times 10^{-4}$	$2{\cdot}98 \pm 0{\cdot}06$	301	0·90
	Seal Rocks	$1{\cdot}00 \times 10^{-4}$	$3{\cdot}08 \pm 0{\cdot}03$	1491	0·90
	Portsea	$1{\cdot}34 \times 10^{-4}$	$3{\cdot}01 \pm 0{\cdot}02$	1805	0·94
	Julia Percy I.	$7{\cdot}58 \times 10^{-5}$	$3{\cdot}14 \pm 0{\cdot}12$	102	0·87
	Boulder Point	$5{\cdot}12 \times 10^{-4}$	$2{\cdot}76 \pm 0{\cdot}19$	86	0·70
	The Passage	$4{\cdot}68 \times 10^{-4}$	$2{\cdot}74 \pm 0{\cdot}13$	121	0·78
Foot weight (F) *v.* length (L) $F = aL^b$	Apollo Bay	$6{\cdot}31 \times 10^{-5}$	$2{\cdot}99 \pm 0{\cdot}03$	1484	0·83
	Mallacoota	$8{\cdot}91 \times 10^{-5}$	$2{\cdot}87 \pm 0{\cdot}02$	301	0·89
	Seal Rocks	$1{\cdot}10 \times 10^{-4}$	$2{\cdot}89 \pm 0{\cdot}03$	1491	0·84
	Portsea	$8{\cdot}71 \times 10^{-5}$	$2{\cdot}92 \pm 0{\cdot}02$	1805	0·91
Width (W) *v.* length (L) $W = aL + b$	Apollo Bay	0·84	$-3{\cdot}78 \pm 0{\cdot}01$	1484	0·94
	Mallacoota	0·79	$0{\cdot}38 \pm 0{\cdot}05$	301	0·94
	Seal Rocks	0·79	$-0{\cdot}67 \pm 0{\cdot}01$	1491	0·89
	Portsea	0·82	$-4{\cdot}49 \pm 0{\cdot}01$	1805	0·93
Height (H) *v.* length (L) $H = aL + b$	Apollo Bay	0·31	$-2{\cdot}44 \pm 0{\cdot}01$	1484	0·69
	Mallacoota	0·31	$-4{\cdot}74 \pm 0{\cdot}02$	301	0·71
	Seal Rocks	0·35	$-6{\cdot}43 \pm 0{\cdot}01$	1491	0·65
	Portsea	0·31	$-2{\cdot}54 \pm 0{\cdot}00$	1805	0·73

$^{\wedge}$ Log (T) *v.* log (L), log (F) *v.* log (L), W *v.* L, H *v.* L.

Growth

Estimates of growth rates were obtained for populations tagged at Seal Rocks, Mallacoota and Boulder Point (Table 2). The time for which tagged individuals were at liberty varied

Table 2. Comparison of von Bertalanffy growth parameters for three populations of *H. rubra* using two tagging methods

Population	Tag method	No.	K ± s.e.	$L_\infty \pm$s.e.
Seal Rocks	glue	228	$0{\cdot}29 \pm 0{\cdot}001$	117 ± 2
Mallacoota	wire	538	$0{\cdot}02 \pm 0{\cdot}01$	$129 \pm 2^{\wedge}$
	glue	101	$0{\cdot}35 \pm 0{\cdot}03$	121 ± 3
Boulder Point	wire	44	$0{\cdot}21 \pm 0{\cdot}03$	142 ± 2
	glue	397	$0{\cdot}27 \pm 0{\cdot}01$	133 ± 1

$^{\wedge}$ Significant difference between tag methods (ANOVA $P < 0{\cdot}05$).

between 79 and 3980 days at all sites. A time at liberty of more than 10 years was demonstrated by periodic recoveries of tagged *H. rubra* by commercial divers after our field studies had finished. The growth parameters K and L_∞ were correlated in all cases ($r^2 > 0{\cdot}72$) invalidating comparison of individual parameters. However, comparison of the residuals of

the von Bertalanffy regressions revealed that the growth rate of animals tagged with glue varied between the three sites studied ($P < 0{\cdot}05$) (Table 2). A similar comparison showed that the method of tagging influenced the growth rate. At Mallacoota, abalone to which tags had been glued grew significantly faster than those to which tags had been attached with wire, although this difference was not evident at Boulder Point (Table 2).

Discussion

Our results show that the morphometric relationships within each of three populations of *H. rubra* changed with time; hitherto, no such change has been recorded for a population of any species of abalone (cf. Newman 1968). The differences in morphometric relationships within each population, although statistically significant, were not large. Our findings of temporal changes in morphometric relationships were probably due to small-scale differences in growth patterns within each population. Because *H. rubra* lives in a heterogenous habitat and can occupy 'cryptic' home sites (Shepherd 1973), differences in food availability arising from small-scale differences in habitat may be manifest as different growth rates (Shepherd and Hearn 1983).

The meat yield from *H. rubra* within two other populations also varied with time, but this variation was closely allied to the annual reproductive cycle of *H. rubra* (McShane *et al.* 1986*b*). In common with most other haliotids (Fretter and Graham 1964), *H. rubra* generally spawns once a year (McShane *et al.* 1986*b*), and redevelopment of the gonad after spawning is reflected as a relative increase in somatic tissue weight. Our results are similar to those of Webber (1970) for *H. cracheriodii*. Webber concluded that the foot of an abalone can function as a nutrient store from which glycogen can be metabolized during gametogenesis. Our results have shown that meat yield can vary by as much as 20% during a year—sufficient to allow the development of harvesting strategies which take into consideration fluctuating yields.

Our results on the differences in morphometric relationships of geographically-distinct populations of *H. rubra* are consistent with the results obtained for other species of abalone (Newman 1968; Poore 1972; Breen and Adkins 1982; Shepherd and Hearn 1983). These differences have also been attributed to differences in food availability associated with habitat type (Shepherd 1973). However, in our experiments the method of tagging also had a demonstrable effect on the growth rate of *H. rubra*. Tags attached with wire threaded through a respiratory pore could have interfered with the abalone's natural behaviour, although Poore (1972) found no evidence of this in species of *Haliotis* from New Zealand waters. The trauma associated with removal of abalone from their natural habitat to tag them could have decreased growth rate, but for both the tagging methods used for *H. rubra* the abalone were out of the water for similar periods. Clearly, care must be taken to avoid significant underestimation of growth rates from the results of mark–recapture studies.

Our growth estimates for *H. rubra* are, in all cases, lower than those of Shepherd and Hearn's (1983) for three South Australian populations of *H. rubra*. The fastest growth rate estimated (glue tags) from our results was that at Mallacoota which was also the most exposed to rough seas; this result suggests a positive relationship between water movement and growth rate. Shepherd (1973) notes that *H. rubra* feeds best in conditions of moderate water movement and poorly in rough water. During a recent study (McShane, unpublished data) growth rates of *H. rubra* in very exposed waters were high. Mark–recapture studies of growth rates tend not to be conducted in exposed waters because of problems in collecting regular samples—problems that we have encountered in the present study. Yet we suggest that the continual churning action of rough seas on seaweed beds results in regular supplies of drift algae, the principal food of abalone (Cox 1962; Leighton and Boolotian 1963). Thus, reefs in exposed waters probably provide more food for abalone than those in relatively sheltered waters. This suggestion is reinforced by commercial catch data which reveal that reefs near exposed headlands supply most of the abalone caught in Victoria (McShane *et al.* 1986*a*).

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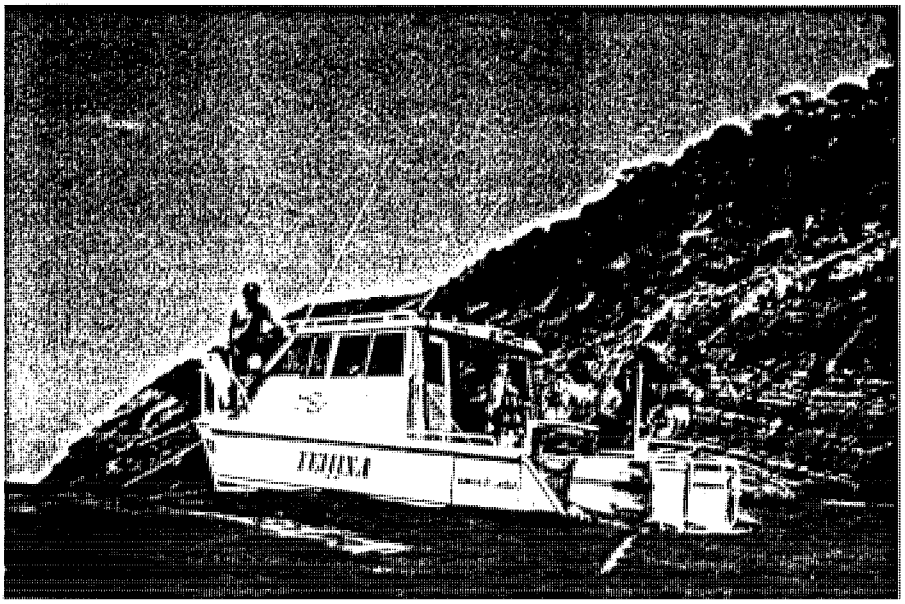
Focus on Victoria's abalone fishery

Market trends for banana prawns

Industry training dilemma

Victoria's abalone fis

Paul McShane and Murray Smith recently completed a five year study of Victoria's abalone fishery. Their verdict — the fishery is in good shape.



The research vessel used in Victorian abalone research which was equipped with twin 'hookah' diving rigs to allow extended diving time.

In the early 1980s an ageing population of Victorian abalone divers expressed concern at the lack of transferability of licences and the possibility of overexploitation of the abalone resource. At the time the only information on the state of the abalone stocks in Victoria was the mandatory catch and effort data from fishermen's returns — research had ceased in 1970.

Understandably government and industry alike feared a collapse in the Victorian abalone fishery, a fate that has befallen many of the world's abalone fisheries.

Transferability of licences was introduced in 1984. However, recognising the dangers of overfishing, especially with the entry of highly motivated young divers, the Victorian Government required new entrants to purchase two existing entitlements. Such a strategy was aimed at reducing the number of divers and therefore the risk of overfishing. At the same time, a detailed research program designed to investigate the health of the Victorian abalone resource was launched.

Basic biology

An early focus of the research program was the basic biology of the commercially valuable blacklip abalone (*Haliotis rubra*) — the predominant species of abalone in the Victorian catch — about which little was known.

Studies of the growth rates of abalone revealed differences from site to site. Abalone grew faster on exposed reefs than on sheltered reefs because these weed eating marine snails do not normally go looking for food. Water currents, generated by wave action or tide, increase the likelihood of bits of weed brushing past the nose of an abalone, thus providing more food and leading to a faster growth rate. Divers claim good regrowth in tidal areas such as 'the tide' near Cape Otway. In contrast 'stunted stocks' are typically found in sheltered areas such as Port Fairy Bay and some bays between Cape Schanck and West Head.

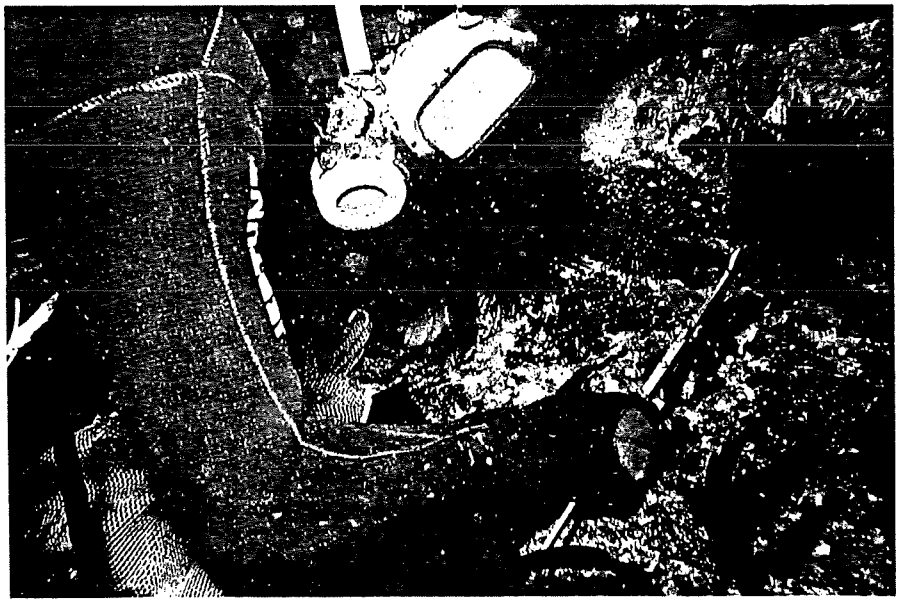
In 1984 it was presumed that the planktonic larvae of abalone floated in the sea for up to 10 days and were therefore capable of being dispersed over large distances. But supporting evidence was lacking. We therefore developed a technique which allowed us to study this dispersal and to relate the reproductive success of a stock of abalone (production of juveniles) to stock size.

Our study showed that if abalone larvae rose above the cover of dense seaweed and the protection of the reef surface they would most likely be swept away by coastal water currents. We also found that larvae successfully settle only on crustose coralline red algae (the pink encrusting material covering much of the rocky surface of a reef). Therefore, the chances of abalone larvae encountering such substrate after being flushed from the reef of their parents into the open sea during their short life in the plankton are remote.

Survival rate

The chances of larvae surviving and settling successfully are therefore much greater if the abalone can complete its

Measuring the growth of tagged abalone reveals that many populations of abalone are 'stunted'.



shery in good shape

An underwater suction sampler is used to collect juvenile abalone from the reef surface.

larval life cycle within the shelter of the reef surface where there are abundant sites for settlement and subsequent development. Indeed we found large numbers of juveniles (more than 12 000 abalone per square metre) on the the most sheltered parts of the reef surface (in narrow rock channels protected by dense stands of seaweed) and relatively few on the exposed flat surfaces of reef. This supports the fishermen's and our observations of high numbers of juveniles on reefs occupied by stunted stock, which are areas of low water movement and therefore there is less flushing of larvae from the reef surface.

The effect of the mostly local dispersal of abalone is that the Victorian abalone resource can be considered as being composed of a number of discrete substocks each confined to a single area of reef. If a reef is 'fished down' of abalone then recovery will depend on larval production from that reef and not from neighbouring reefs. That is not to say that abalone cannot travel from reef to reef but only that most larvae successfully settle on the reef of their parents.

Having settled on the reef surface, the life of the juvenile abalone is a hazardous one. Not only must the young abalone escape the jaws of numerous marauding fish, they must also avoid being bulldozed by their larger cousins and other grazing animals such as sea urchins. The end result is that of the juveniles that settle, few survive the first two months. Those that do seek the shelter of the undersurfaces of boulders, narrow cracks and crevices emerging to feed at night when the fish are sleeping.

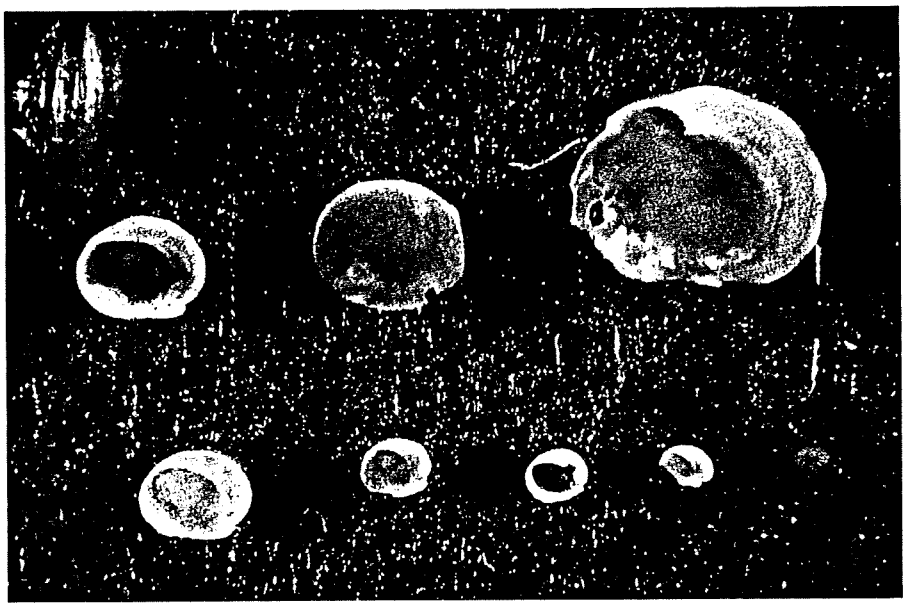
The Victorian abalone fishery depends on the annual recruitment of abalone growing larger than the legal minimum size. Our studies of the production of juveniles, following annual spawning, show extreme variation from year to year for a typical stock. Most fishermen are well aware of the difference between good and bad years that generally arise from variation in reproductive success. Unlike many fisheries, the Victorian abalone fishery appears reasonably stable because the difference between good and bad years is evened out over the four to 15 years it takes abalone to recruit to the fishery.

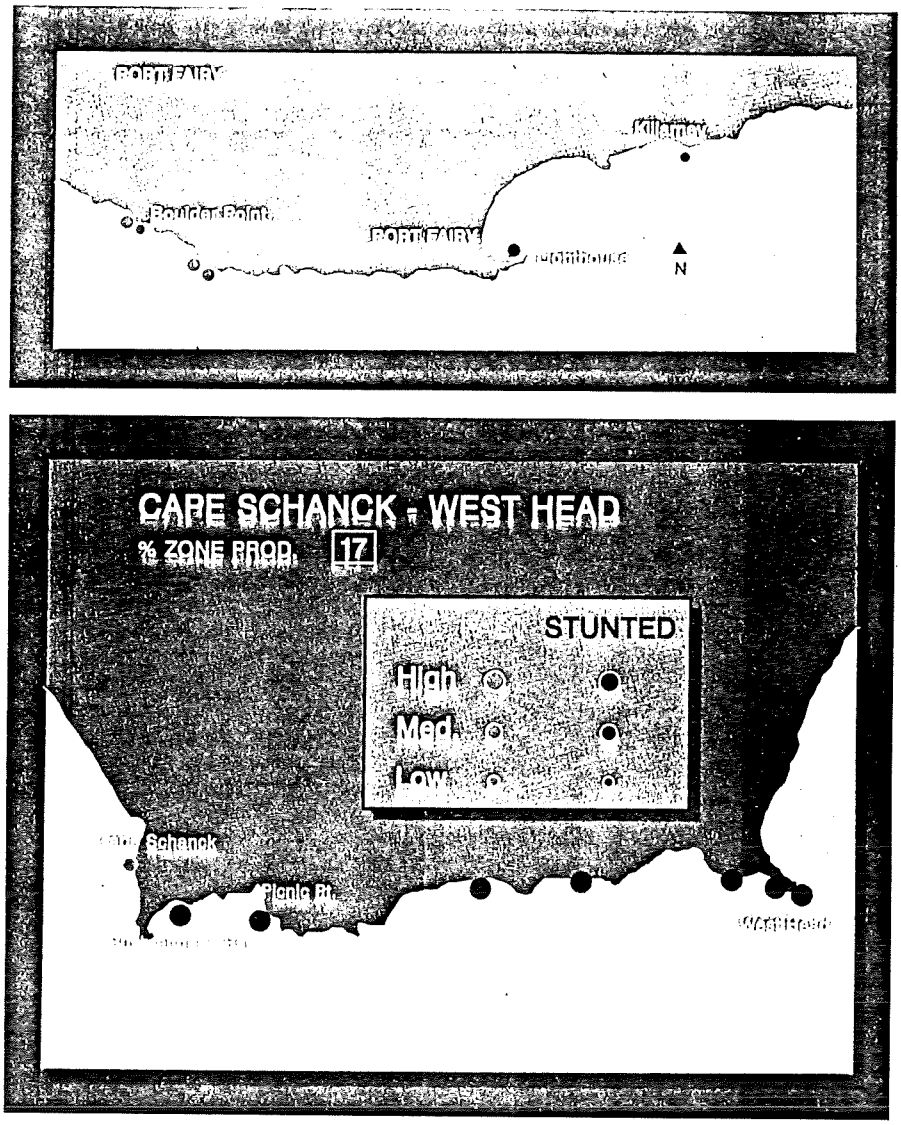
The fishery

What impact can abalone fishing have on the abalone population on a reef? We addressed this question by involving the abalone divers of Mallacoota. They were requested to fish a reef (Bastion Point) until, in their opinion, it was fished out. We measured the abundance of the stock before and after the fishing and the abundance of juveniles produced after spawning by the 'fished down' stock.

The results were surprising. The divers removed approximately 13 tonnes of abalone from the reef in two days fishing. The catch rate of abalone was so low on the second day that the divers were

Typical size range of juveniles sampled using the suction sampler. A guide to the size is provided by the pin head in the top left hand corner.





Distribution of stunted and fast-growing populations of abalone near Port Fairy and Cape Schanck. The relative abundance of abalone at each site is indicated by the size of the circles. Fast growing populations of abalone are generally found off exposed coasts whereas stunted stocks inhabit sheltered waters.

torian fishery? The answer is, as it is for any abalone fishery, that no one knows.

An annual catch quota was introduced to the Victorian fishery in 1988 in an attempt to reduce and stabilise fishing effort. The quota system in Victoria, based on equivalent systems already operating in Tasmania and South Australia, means that each diver is allocated an equal share of the total annual catch which is set each year.

But because under-reporting of catches is a time-honoured practice in fisheries, the catch data available for the Victorian abalone fishery were considered unreliable indicators of the annual catch taken over the past few years. Discussions with fishermen yielded what may loosely be termed the 'true' catch.

The setting of the first annual catch quota for each of the three fishing zones was little more than an educated guess taking into account the 'true' catch for the past five years. The initial catch quotas of 280, 700 and 480 tonnes for the western, central and eastern zones are considered sufficiently conservative so as to not endanger the fishery in the short term. By fixing an initial 'best guess' quota and allowing sufficient time for monitoring the impact of the quota on the state of the stocks (at least a few years) a true sustainable catch may be determined.

Monitoring the fishery

Monitoring of the abalone stocks is necessary for an assessment of the effectiveness of management strategies (size limits, quotas) applied to the Victorian abalone fishery. An emphasis on our monitoring program (commenced December 1988) is to assess the state of the stocks on all abalone reefs in Victoria receiving heavy fishing effort. Our aim is to establish a data base that will serve as a yard stick for the state of the stocks. Such a data base includes relative stock abundance on the reef — if the overall abundance of abalone increases with time then the resource is being underutilised and vice versa. Data on relative size distribution provides information on the intensity of fishing on a particular reef — if most of the abalone are near legal size then the reef is being fished down and may need a respite from fishing. Monitoring of juvenile abundance on reefs provides information on the breeding success of the stock. If there are problems of recruitment failure we will detect them at this stage, early enough to implement corrective strategies. Estimation of the growth rate of individual stocks will allow us to determine whether stocks are stunted or fast growing, important when considering sensible size limits.

We already have much of this information and with further monitoring we will have a much sounder base for management of the Victorian abalone fishery. The results of the annual monitoring are published each year and circulated to all abalone fishermen. With constructive feedback from industry we can fine tune management of the resource, ensuring both its longevity and perhaps increasing its productivity.

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unwilling to continue fishing the reef, considering it to be well and truly fished out.

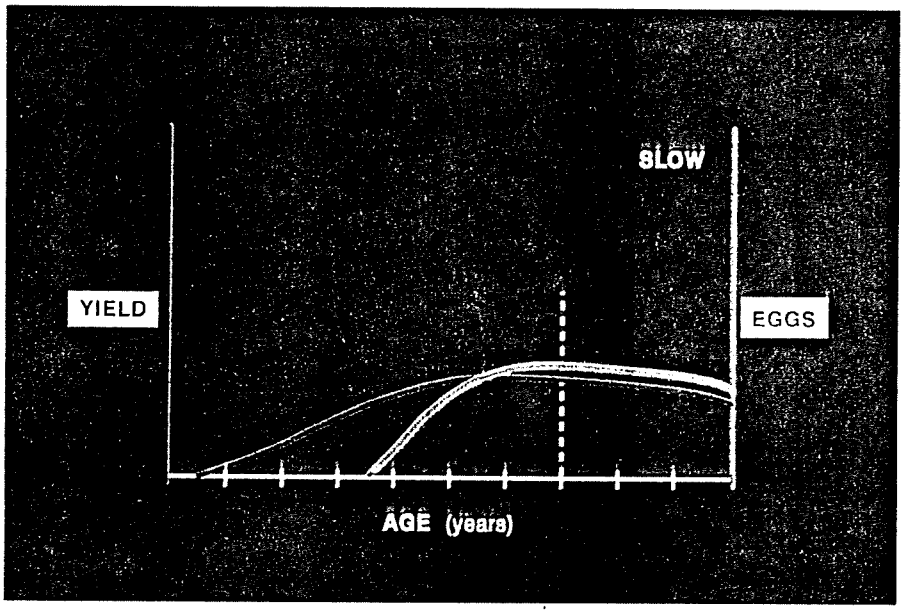
Our surveys showed that in fact the divers had taken only a a small portion of the fishable stock. Our count of juveniles following spawning after the reef had been 'fished out' were high enough to suggest that reproduction of the stock remained healthy. Yet the stock had been subjected to extraordinarly high levels of fishing. Rarely would nine divers fish within a couple of hose lengths of each other on a single reef for two days in succession. If this amount of fishing had minimal impacts on the stocks what is the effect of 'normal' fishing? Why do divers take such a relatively low proportion of the fishable stock of abalone from a reef?

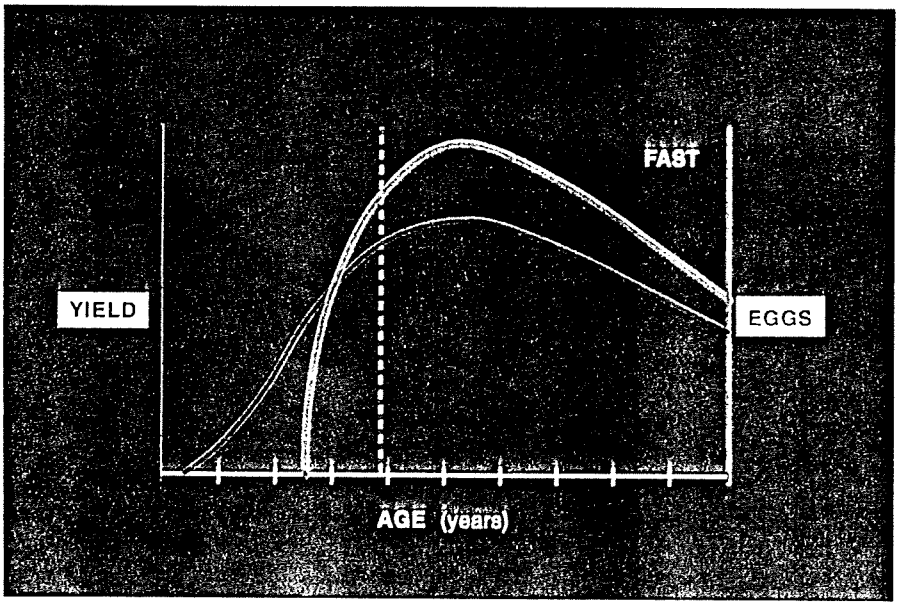
Comparison of the relative yield and egg production from slow-growing 'stunted' and fast-growing populations of abalone. Present size limits for Victorian abalone are indicated by the dashed line. Stunted populations could be efficiently harvestered by periodic 'fish down' days when abalone can be taken at a low size.

Abalone form aggregations usually in rock gutters aligned with the direction of water movement (tide or swell). Fishermen have a good knowledge of the location of the aggregations on a reef and direct their fishing accordingly. However, most of the abalone stock is in the form of small aggregations or is inaccessible to divers (in nooks and crannies).

Because divers fish only the large aggregations most of the stock remains unfished.

The substantial reduction in the catch rate that we observed on the second day of our experiment was due to the removal of the large aggregations on the first day. Only by painstakingly swimming and searching for those abalone scattered over the less accessible areas of the reef surface could the divers remove most of the stock. Understandably most divers are unwilling to do so which is good news for those seeking to conserve the stock. However, this perhaps unintended conservative fishing practice is at the whim of fishermen's behaviour.





In Victoria, an abalone diver aims for a catch rate of at least 100 kg/h. New divers lacking pre-conceived notions of high catch rates might be prepared to search for smaller aggregations and so reduce some stocks to dangerously low levels.

This possibility in itself is an argument for maintaining a relatively small pool of fishermen in the limited entry Victorian abalone fishery. One only has to consider the now collapsed Californian fishery that was, and still is, open to all. In that fishery fishermen usually count the daily catch of individual abalone on two hands.

Management

SIZE LIMITS

Fundamental to the successful management of any fishery is that sufficient breeding stock must remain after fishing so that annual production is maintained. Size limits are, in part, a valuable management tool in this regard. All too often though a legal minimum size is chosen to maximise the yield to the fishery rather than egg production.

The growth rate of abalone will determine the rate of recruitment to a particular minimum size. In fast growing populations — for example, those off exposed headlands — the number of abalone above the minimum size will be replaced relatively rapidly and such stocks will recover from fishing in a short time (good regrowth). On the other hand stunted stocks may consist of some abalone that never reach fishable size. Ideally, size limits should allow efficient harvesting of both fast and slow-growing stocks. However it would be burdensome to manage a fishery with multiple size limits.

Size limits should be aimed at protecting the fast-growing populations, those which support the fishery and those most at risk of overfishing. Stunted stocks, which consist of individuals more likely to die of old age than be taken by abalone divers, can be exploited by periodic fish-down days. On such days, the stunted stocks are open to fishing at a low size limit. With sensible size limits the stocks can be conserved while at the same time supporting a productive fishery.

CATCH QUOTAS

Abalone fisheries are vulnerable to overfishing; the collapse of almost all abalone fisheries elsewhere in the world is evidence enough of this. Catch quotas must be sufficiently conservative to maintain a viable breeding stock whilst providing a reasonable yield to the fishery. The quota should be equivalent to the average annual recruitment (the weight of abalone growing beyond the legal minimum size each year). If the annual quota is greater than the annual recruitment then the breeding stock will be reduced until the fishery collapses. What is the average annual recuitment in the Vic-

Direct measurement of fishing mortality in abalone (*Haliotis rubra*) off southeastern Australia.

McShane, P.E. and M.G. Smith

Fisheries Research in press (not to be cited)

ABSTRACT

McShane, P.E. and Smith, M.G., 198-. Direct measurement of fishing mortality in abalone (*Haliotis rubra*) off southeastern Australia. *Fish Res.* 00

Daily fishing mortality in a population of abalone (Mollusca:Gastropoda: *Haliotis rubra*) off southeastern Australia was estimated from the number of tagged *H. rubra* recovered by commercial abalone divers who participated in experimental fishing. Instantaneous fishing mortality rates were 0.16 and 0.02 on successive days. Fishermen stopped fishing after only two days fishing because they believed that the reef was "fished out" ; yet we detected no change in overall population abundance of *H. rubra* due to fishing. We postulate that fishing mortality was comparitively low because commercial abalone divers target only large aggregations of *H. rubra*. The low fishing mortality implies that the abundance of *H. rubra* will be little affected by the catch of commercial abalone divers. However, exploitation of aggregations of *H. rubra* may, in the long term, affect reproduction of the population. *H. rubra's* choice of cryptic habitat may make the species less vulnerable to overfishing than other species of abalone.

INTRODUCTION

Abalone are herbivorous gastropod molluscs that are common on coastal reefs in temperate waters (Mottet 1978). Their high market value has resulted in the rise and fall of many abalone fisheries around the world due to overfishing (Cicin-Sain *et al* 1977, Breen 1980, Sluczanowski 1984) ; yet little is known about fishing mortality in any abalone fishery. Indirect estimates of fishing mortality have been variously reported as high off Victoria (southeastern Australia) (Beinssen 1979a) and as low off British Columbia (Breen 1980).

Beinssen (1979a) involved commercial abalone divers who were invited to search for and return tags from cement-filled drink cans used to simulate abalone (*Haliotis rubra*). *Haliotis rubra* is known to inhabit cryptic habitat (Shepherd 1973, Witherspoon 1975, Prince & Ford 1985, McShane & Smith 1988). This and the presence of thick kelp on reefs off southeastern Australia (McShane *et al* in press) can make the detection of *H. rubra* by divers difficult. However, Beinssen (1979a) concluded that fishing intensity on *H. rubra* was high. Results such as this have led to fears of overfishing in the Victorian abalone fishery - fears expressed by those associated with other abalone fisheries (e.g. Breen 1980, Sainsbury 1982).

In this paper we provide direct estimates of the fishing mortality in a population of *H. rubra* off southeastern Australia near the site of Beinssen's (1979a) study. Our estimates were based on the number of tagged *H. rubra* recovered by commercial divers.

MATERIALS AND METHODS

Experimental fishing for *H. rubra* was conducted on a reef complex at Bastion Point off southeastern Australia (Fig.1) where *H. rubra* is the only abalone species of commercial importance. Only the middle reefs (estimated surface area 0.7 km ^{2}) were available for fishing in the experiment. The reef complex comprised discrete reefs separated by sand (Fig.1) and was closed to fishing prior to and after experimental fishing.

Traditional sampling methods (e.g. transect censuses) haved proved to be inaccurate in estimating abalone abundance because abalone are so patchilly distributed (Sainsbury 1982, McShane *et al* in press). To determine the effect of intense fishing on the abundance of a population of abalone off Bastion Point we used a searching method. The number of abalone found within a specified searching time was assumed to be proportional to abalone abundance (Beinssen 1979b, Shepherd 1985, McShane *et al* in press).

Prior to experimental fishing, a population census of *H. rubra* was undertaken. Nine sites on the reef complex were chosen at random (Fig.1). At each site two research divers each collected all the *H.rubra* they saw within a specified searching time. At most sites searching time was 10 min but at some sites, where the abundance of *H. rubra* was low, searching time was 15 min. Although searching efficiency can vary between individual divers (Shepherd 1985), preliminary trials revealed close correspondence (less than 20% variation) between the number of *H. rubra* collected by the two research divers.
As with commercial divers, the area swept in searching for abalone is limited by the length of the "hookah" diving hose (approximately 100 m). Estimates of diving power suggest that approximately 200 m^2 can be searched for abalone in 10 min. (Beinssen 1979b, Shepherd 1985).

All *H. rubra* collected were measured with vernier calipers for shell length (longest shell dimension) to the nearest millimeter, tagged with a polyethylene disc (6 mm diameter) glued to the shell (Forster 1967) and returned to the reef within 30 min of collection. In this way the number of tagged *H. rubra* placed on the reef was in proportion to the abundance of *H. rubra* on the reef. Although abalone were clearly marked, the relatively small size of the tag meant that the tag was conspicuous to divers only at close range. Thus, commercial divers were unlikely to selectively target for tagged *H. rubra* and the probabilities of catching a tagged and non-tagged *H. rubra* being caught were considered similar for the purposes of the experiment. Tagging took place the day before experimental fishing on each of two occasions in September and November 1986.

Commercial divers at Bastion Point are normally restricted to a daily quota of 300 kg. During our experiment the daily quota was rescinded and the permissible length at first capture was reduced from 120 mm to 90 mm. Removal of these constraints was expected to increase fishing mortality rates beyond those normally expected. Because fishing was conducted only on discrete days, the reef was believed to be subject to maximum fishing pressure by each of the commercial divers involved in the experiment.

On each occasion, commercial divers were directed to take as many *H. rubra* as they could in a day's fishing. Further fishing days were to be conducted until, in the opinion of the commercial divers, the reef complex was "fished out". The fishing pattern of each commercial diver was monitored by observers off Bastion Point and included location of fishing effort, total time spent fishing at each location, weight of *H. rubra* caught, size composition of the catch and number of tagged *H. rubra* returned. The crew of each diver's vessel were directed to separate tagged from non-tagged *H. rubra*. To ensure that no tagged *H. rubra* captured by the divers were

missed, we searched a subsample of the catch of each diver for tagged *H. rubra*. Additionally, the local processors of *H. rubra* were directed to monitor all *H. rubra* for the presence of tags immediately after the experiment. After the each day's fishing the research divers repeated their searching so that the abundance of *H. rubra* could be estimated.

Fishing mortality (F) is related to total mortality (Z) after Beverton and Holt (1957) ; $m/T = (F/Z)(1 - e^{-Zt})$,
where T is the total number of *H. rubra* tagged on each occasion and surviving at the time of the experiment and m is the number of tagged abalone caught after time t (days). Natural mortality in *H. rubra* was assumed to be 0.2 per annum (Beinssen & Powell 1979), M_t was therefore negligible and F was assumed equal to Z. Thus,
$m/T = 1 - e^{-Ft}$. (1)

$T = T_0 - M_t - M_{tag} - L$

where T_0 is the number of *H. rubra* tagged at the commencement of the experiment; M_t is natural mortality occurring in t days; M_{tag} is mortality due to tagging during time t and L is tag loss during time t. Because tag recoveries on each occasion took place the day after *H. rubra* were tagged, t = 1.

Preliminary trials with double tagging (McShane unpublished data) showed that M_{tag} was negligible but that L was 0.2. Initial tag loss was high because poorly glued tags were lost soon after tagging (McShane unpublished data). Thus, $T = 0.8\ T_0$ and, from (1), F is approximated by $m/0.8\ T_0$

The catchability (q) is given by $q = F/f$ where f is fishing effort (the total number of hours each commercial diver spent underwater fishing for *H. rubra* on each occasion).

RESULTS

In the opinion of the commercial divers participating in the experiment, the reef complex at Bastion Point no longer supported a commercially exploitable population of *H. rubra* after the second fishing day.

The results of the two experiments are presented in Table 1. On the first day of the experiment eight divers caught 3635 kg of *H. rubra*. Crews aboard the diver's boats found 105 tagged *H. rubra* in the total catch; processors found none. We found no tagged *H. rubra* in the subsamples we took of the catch.

Six divers participated in the second experiment and caught a total of 1302 kg. of *H. rubra*. Because the tags used in the two experiments were easily distinguishable, only the recently tagged *H. rubra* were used in calculations of F and q for the second experiment. Only 13 tags were returned by the fishermen. None were found by processors or in our sub-samples of the catch.

Prior to fishing there was no significant difference in abundance of abalone between individual reefs off Bastion Point. Thus data for all reefs were pooled for comparison of the effect of fishing on abundance of *H. rubra* (Table 2).

Catch per unit effort decreased on successive days fishing although there was no significant difference in relative population abundance (Fig.2, Table 2). However, a comparison of the relative size composition before and after fishing showed an increase in the relative proportion of small abalone (Fig.3, Table 2). This result may reflect an emergence of *H. rubra* from cryptic habitat or, more likely, it may be that smaller individuals were more visible after larger *H. rubra* were removed by fishing.

Mean fishing effort was 6.1 h per diver for the first fishing day and 5.1 h per diver for the second. During both experiments each diver visited up to four locations on the reef complex with most divers fishing three locations (Fig. 1). Examination of the fishing patterns of divers in the two experiments revealed that fishing was concentrated in the shallow reefs and that the fishing pattern was similar for the two fishing occasions (Fig. 1). The time spent fishing at a site by individual fishermen varied from 1 to 5.5 h.

Figure 1 shows relatively little overlap between the distribution of tagged abalone and the location of fishing effort on both occasions. Abalone divers can search approximately 1000 m^2/h (Beinssen 1979b, Shepherd 1985). Therefore an estimated total of 48500 m^2 and 30500 m^2 was searched in fishing for *H. rubra* on the first and second fishing occasions respectively. With an estimated 700000 m^2 of reef area available for fishing only 7 and 4% of the reef surface was searched for *H. rubra* on the respective fishing days.

DISCUSSION

Contrary to our expectations, fishing mortalities calculated from the results of the experimental fishing were low despite the extraordinarily high fishing effort applied to the *H. rubra* population at Bastion Point. We had several reasons for expecting fishing mortality to be high. Firstly, fishing effort was concentrated in a relatively small area. Usually, abalone divers are generally unwilling to fish as close together as they did in our study. Secondly, *H. rubra* are sedentary and adults are easily detected by divers, especially those familiar with the habitat of *H. rubra*. Thirdly, Bienssen (1979a) claimed high fishing mortality by abalone divers fishing in the area of our study. Finally, the removal of constraints in our experiment (daily catch quota and minimum length at capture) would be expected to increase fishing mortality rates beyond those normally experienced.

The fishing effort applied had no measurable effect on the abundance of *H. rubra* on the reef complex at Bastion Point. While this result suggests relatively low fishing mortality, there was a significant decline in catch per unit effort on successive fishing days. Furthermore, the commercial divers considered the reef complex to no longer hold a commercially exploitable abundance of *H. rubra* and would not undertake further fishing after the second day. The population biology of *H. rubra* and the fishing behaviour of abalone divers are important factors in explaining our results.

Abalone normally aggregate (Shepherd 1973, 1986, Breen and Adkins 1980). Fishermen target on aggregations of abalone to maximize their catch rate (Beinssen 1979b). But the aggregations of *H. rubra* are patchilly distributed and occupy a relatively small area of the available reef surface. This was evident from our observations of populations of *H. rubra* off Bastion Point and the fact that divers searched a relatively low proportion of the total reef surface area before considering the reef complex fished out.

Unlike the fishermen, we did not select large aggregations in tagging *H. rubra*. While our tagged abalone were released in proportion to their abundance on the reef surface, fishermen did not search much of the area occupied by tagged abalone. Consequently, the fishermen, in removing the main aggregations of *H. rubra*, reduced their catch rate on the second day's fishing but returned few tagged abalone. We observed little change in the overall abundance of *H. rubra* due to fishing because we sampled the whole population, not just the large aggregations.

Beinssen (1979a) considered annual fishing mortality on *H. rubra* high. However, using his estimates of F and f, catchability of *H. rubra* was lower than that estimated in our study. In Beinssen's (1979a) study their was little incentive for fishermen to return tags from the drink cans used to simulate abalone. Thus, the catchability and

the daily fishing mortality estimated from Beinssen's (1979a) study of *H. rubra* was probably lower than that normally applied. An annual fishing mortality cannot simply be extrapolated from the results of daily fishing events; nor are annual rates appropriate for an abalone fishery. Typically, abalone reefs are fished intensely over a short period and then left to recover (Sluczanowski 1984). Our study shows that a reef can be "fished out" of abalone after two days of intense fishing. While our daily fishing estimates are high compared to natural mortality, the annual exploitation rate was relatively low considering that fishermen were unwilling to refish the area within twelve months of our experiment.

We propose that abalone fishing in Victoria impacts mainly on large aggregations of *H. rubra*. When these aggregations of *H. rubra* have been removed, fishermen are unwilling to fish smaller or less accessible aggregations. Rather they will fish other areas of a reef, as shown in our study, or move to other reefs in the region. However, aggregations can reform after fishing. Commercial divers fishing on Bastion Point, approximately a year following experimental fishing, recorded catch rates of over 70 kg. h^{-1} ; a return to pre-experimental fishing levels. This result cannot be explained by recruitment alone because the fishermen were constrained to the usual minimum length of capture (120 mm shell length).

The fishing behaviour evident in our study has important consequences for stock conservation. Most of the available population of abalone on a reef will remain unfished at any time leaving broodstock sufficient to maintain recruitment. The abalone fishery in Victoria is composed of a number of sub-stocks (McShane *et al* 1986, in press). Catch rates will remain stable provided that there are aggregations of abalone, within these sub-stocks, sufficient to maintain the diver's expected catch rate. Indeed catch rates of abalone in Victoria have remained stable since 1965 (Anon 1982). However, in the absence of constraints, overfishing could reduce the number of aggregations of abalone available to fishermen (e.g. Cicin-Sain *et al* 1977). Under these circumstances the "expected" catch rate could be lower and tolerable if the price of abalone is sufficiently high. In this way it is economically viable to reduce the abundance of an abalone population to a dangerously low level.

While the tendency of *H. rubra* to inhabit cryptic habitat may protect some aggregations and may make this species less vulnerable to recruitment overfishing than other species of abalone, the removal of aggregations, necessary for successful fertilization of eggs in dioecious and broadcast spawners such as *H. rubra* (Shepherd & Laws 1974), may deleteriously affect recruitment. Management of abalone stocks should provide for the conservation of large aggregations thereby ensuring adequate recruitment and a viable fishery.

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TABLE 1. Parameter estimates from experimental fishing of a tagged population of *H. rubra*.

Parameter	Experiment	
	September	November
To	647	573
m	105	13
F	0.16	0.02
f	48.5	30.5
q	3.3×10^{-3}	7×10^{-4}

TABLE 2 Relative abundance of *H. rubra* before and after experimental fishing (November 1986). Data are mean numbers of *H. rubra* (standard deviation) collected per 15 min searching period.

	Relative abundance of *H. rubra*	
	Before fishing	After fishing
H. rubra > 90 mm shell length	75.8 (21.0)	60.5 (28.3)
H. rubra < 90mm shell length	9.9 (4.9)	27.0 (10.4) *
Total *H. rubra*	85.7 (23.7)	87.5 (36.8)

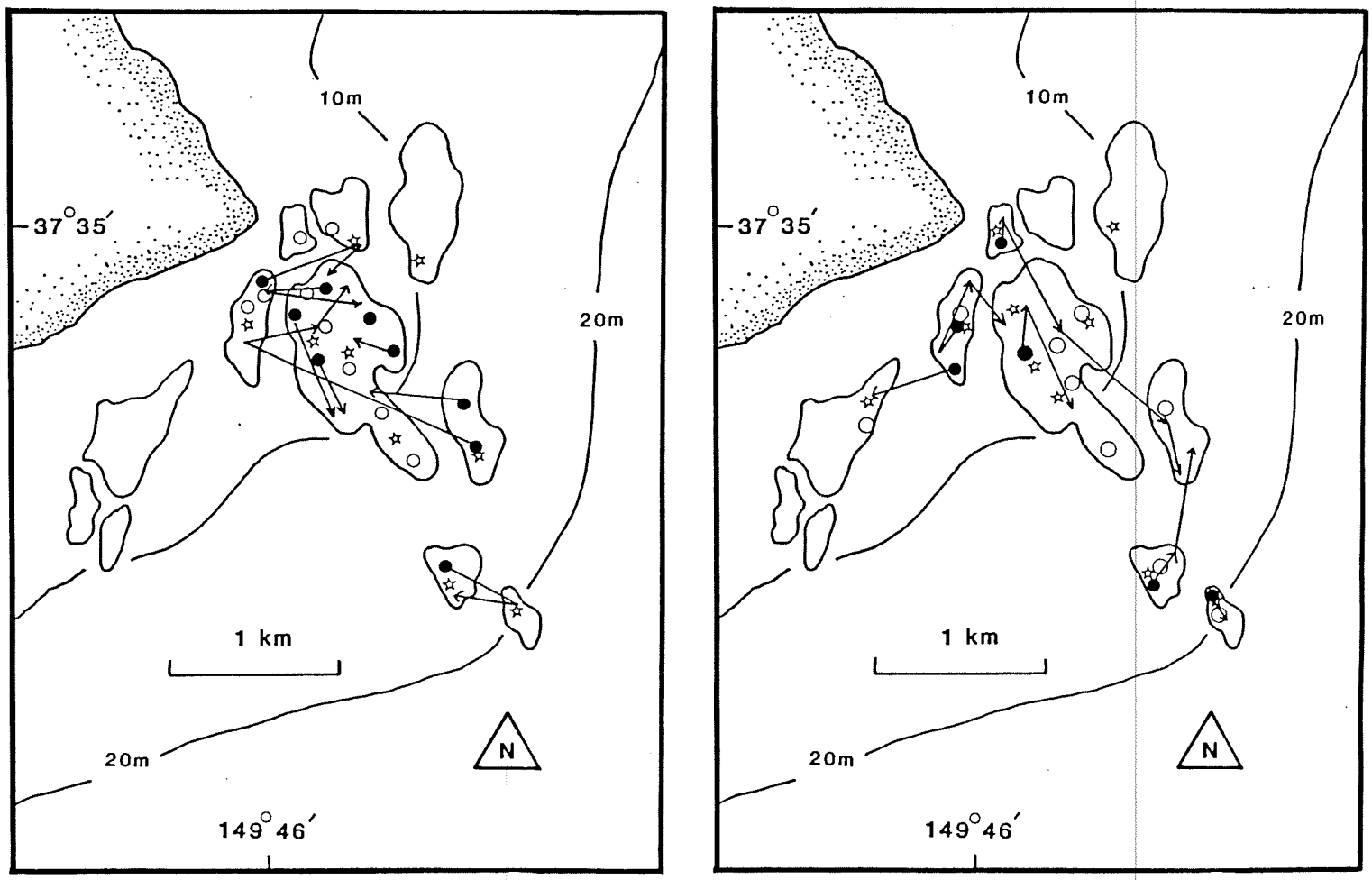
* Analysis of variance revealed a significant difference for *H. rubra* < 90mm shell length due to fishing ($p < 0.05$).

FIGURE CAPTIONS

Figure 1. Site locality, Bastion Point, southeastern Australia for experimental fishing; (a) September and (b) November. Bathymetry is indicated in each case. Location of fishing effort on each occasion is indicated by solid symbols and arrows depicting movement of individual fishermen. Open symbols represent sample sites (before fishing) and location of release of tagged abalone. Sample sites (after fishing) are indicated by stars.

Figure 2. Comparison of relative abundance (number of *H. rubra* > 90 mm shell length collected per diving hour) before and after experimental fishing in September (dark shading), and catch per unit effort (kg. *H. rubra*/h) (light shading) on successive fishing days. Standard errors for mean values are indicated.

Figure 3. Comparison of the length composition of *H. rubra* sampled (a) before experimental fishing (b) after experimental fishing (c) from the catch. Data are expressed as percent of the total sample (N) and represent the September experiment.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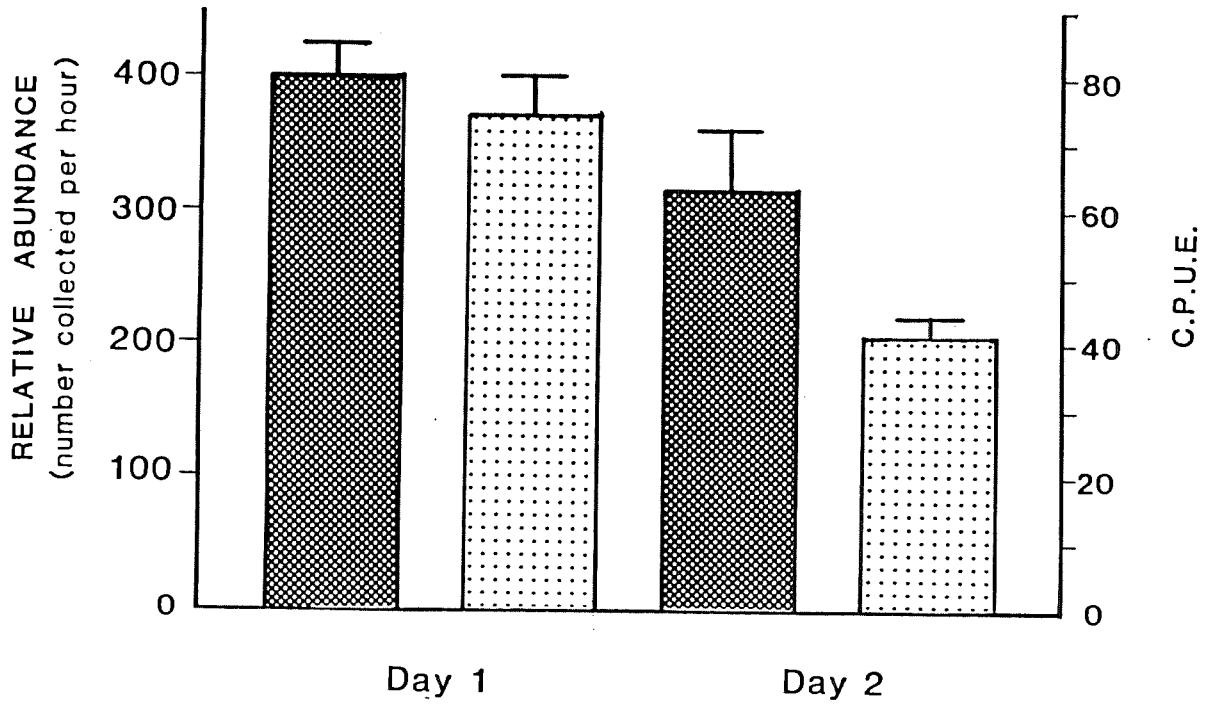
RELATIVE ABUNDANCE
(number collected per hour)
400
300
200
100
0
80
60
40
20
0
C.P.U.E.
Day 1
Day 2