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THE EARLY LIFE HISTORY OF CORAL TROUT (PLECTROPOMUS LEOPARDUS) AT GREEN AND ARLINGTON REEFS, AUSTRALIA

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A thesis submitted for the degree of Doctor of Philosophy
in the Department of Marine Biology at James Cook University
of North Queensland, in September 1995.

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ABSTRACT

The relative contributions of pre- and post-settlement processes to the early life history of coral trout were examined, with the aim of understanding how events occurring during the first year of life influence adult demographic parameters. Juvenile coral trout showed distinctive patterns of distribution and abundance at sites around Green Reef, which were consistent in both space (among sites) and time (between years). These patterns were influenced by substratum characteristics, with habitat associations changing as juveniles grew. Newly settled fish initially showed strong associations with low-relief, rubble-covered sand bottoms, but switched to high-relief features such as coral heads and consolidated rubble mounds after approximately two months of benthic life. Post-settlement processes (mortality and movement) for new recruits appeared to be influenced by the amount of sand-rubble habitat available; individuals occupying areas containing relatively high amounts of this substratum suffered less mortality and were more inclined to be site-attached than those from alternate habitats. Temporal patterns of recruitment were variable, but a strong settlement event coincided with the November new moon in all years of the study.

Following settlement, juveniles were site-attached, and occupied home ranges that increased in area as they grew. Home ranges of the smallest recruits (25 - 60 mm SL) showed little overlap, and this pattern appeared to be facilitated by intra-specific aggression. Agonistic behaviour was rarely observed in larger recruits (61 - 102 mm), and home ranges broadly overlapped.

Recruits displayed an ability to return to former locations when displaced short distances (20 m), and the distance from which juveniles could home increased with age. Recruits displayed higher site-fidelity than 1+ fish; 88% of marked 0+ individuals were resighted within 20 metres of their capture point, while only 20% of one year old fish were resighted within these areas.

A change in diet occurred during early growth: diets of newly settled fish consisted mostly of epibenthic crustaceans, whereas larger juveniles (60-100 mm) were mainly piscivorous. Coral trout of all sizes consumed fish, and most piscine prey were recent recruits to the reef. Foraging modes and diurnal feeding patterns differed between size classes: larger juveniles typically fed by ambushing prey (usually small fish), whereas small recruits concentrated feeding activities around morning hours, and typically foraged by striking at invertebrates associated with rubble substrata.

Diets varied spatially for large juveniles, but not for small individuals: large juveniles inhabiting structurally complex habitats (coral heads, rubble mounds) shifted to a primarily piscivorous diet sooner than those from less complex habitats.

Estimates of growth rates of juvenile coral trout were influenced by larval growth histories, size-selective mortality, and variations in water temperature. Significant inter- and intra-annual differences were detected in planktonic growth rate, which were positively correlated with subsequent benthic growth. These initial patterns were accentuated by higher mortality of slow-growing juveniles, which resulted in relatively faster mean growth rates for juveniles collected later in the year. Temperature also had a strong influence on growth, and accounted for 55% of the variability in somatic growth following settlement.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Background

Recruitment of larval fishes to coral reef habitats is a brief demographic event, which precedes a relatively long period of benthic life (Jones 1990). Although the influence of recruitment variation on population structure is well documented (Doherty 1983, Victor 1983), attention has recently been focussed on the numerous ways in which patterns established at the time of settlement may be modified (Jones 1987, 1991).

The increasing interest in post-recruitment processes is driven in part by a number of studies reporting poor correlations between recruitment history and adult population numbers at the patch reef scale (Robertson 1988, Jones 1987, Forrester 1990, but see Doherty and Fowler, 1994). For example, Robertson (1988) found that abundances of adult surgeonfish were not correlated with settlement patterns over a six year period. He attributed these differences to relocation between habitats, and noted that relocation may be the norm in species for which recruits, juveniles, and adults occupy different habitats. Distribution patterns can be expected to be influenced by post-settlement habitat selection and redistribution in highly mobile species (Brock et al. 1979, Jones

1991), or those having different habitat requirements during growth (Choat and Bellwood 1985). However, the contribution of post-settlement dispersal to changes in abundance have rarely been measured for coral reef fishes (Doherty 1982, 1983, Jones 1987, 1988, 1991).

To date, most studies have investigated these processes as they pertain to highly sedentary species such as pomacentrids, and have used small coral reef patches as replicate units. This is because juvenile pomacentrids are relatively abundant, conspicuous, and easily monitored. However, pomacentrids are characterised by specific life history features that influence their settlement patterns and post-settlement processes. Newly settled individuals are large relative to adult size (Wellington and Victor 1989), and as a result they tend to recruit directly into adult habitats from which they rarely move during their lives (Doherty 1983, Williams 1991). Thus, extrapolation of results from studies involving this family may lead to erroneous conclusions when applied to species with different characteristics.

Coral trout, Plectropomus leopardus, are high-level carnivores and the most valuable food fish exploited on the Great Barrier Reef (Williams and Russ 1991). Their large size, elevated position in the food chain, and high mobility as adults make them an interesting contrast to the sedentary pomacentrids upon which most studies of juvenile reef fish ecology have been based. As with most groupers (Richards 1990), much of the early life history is unknown (Leis 1987), due mainly to the cryptic behaviour and relative rarity of the juveniles. Moreover, young serranids often occupy heterogeneous habitats which are not easily sampled by conventional techniques (Ross and Moser 1995). As a result of these difficulties, a large gap exists in our knowledge of grouper ecology.

Although previous studies of coral trout have concentrated on the adult phase (Goeden 1978, Ayling 1991, Kingsford 1992, Ferreira 1994, Davies 1995), the relatively site-attached behaviour of newly settled individuals makes them particularly amenable to the use of mark-recapture techniques for studying movement and growth. Furthermore, fluctuations in abundances of pre-settlement coral trout have been shown to vary with lunar period (Doherty et al. 1994) which may result in the presence of multiple cohorts within a settlement season. These features of the early life history of coral trout make them ideal subjects for intra-specific comparisons of growth, behaviour, and movement.

Demographic parameters of coral reef fish populations are influenced by processes occurring during both planktonic and benthic phases of the life cycle (Sale 1985, Jones 1987, Richards and Lindeman, 1987, Jones 1991). For the past decade, research into the factors affecting reef fish demography has been influenced by the "recruitment-limitation" hypothesis, which proposes that coral reef fish populations are maintained at levels below numbers set by available resources (Doherty 1983, Victor 1983). Based on this hypothesis, numbers of fish recruiting to reefs will be determined by processes occurring within the plankton, and variations in adult populations will reflect numbers of individuals recruiting to benthic habitats. This model draws strong support from studies of widespread natural disturbances such as El Niño events and Acanthaster outbreaks, in which increases in algal food supply have failed to produce corresponding increases in herbivore populations (Doherty 1991).

In contrast, the "resource-limitation" hypothesis (Smith and Tyler 1972, Shulman 1984, Hixon and Beets 1989) proposes that populations are regulated at or around a carrying capacity by competition for limited resources - mainly shelter. According to this model, density-dependent processes should control levels of settlement, growth, and survival of reef fishes. Studies testing these alternate hypotheses have generally concluded that they are extremes in a continuum, and that the limitation of populations by planktonic processes or density dependent post-settlement processes is largely a matter of degree (Forrester 1990, Jones 1990). Furthermore, whether reef fish populations are limited by recruitment or resources may vary between species, or within species in different locations (Williams 1980, Hunte and Côté 1989).

Although considerable progress has been made in documenting numerical aspects of recruitment, little attention has been focussed on qualitative aspects of individuals at the time of settlement. For example, the extent to which variations in body size at settlement biases probabilities of future survival or how such effects are transferred to adult growth have seldom been addressed. These variations may play an important role in predicting demographic parameters of adult populations, because relatively small changes in the previous larval growth rates may result in large variations in the numbers surviving to settlement (Houde 1987, Miller et al. 1988, Pepin and Meyers 1991).

While individuals often differ in size at settlement, their habitat requirements at this time may be quite specific (Sale et al. 1984, Eckert 1985), and these choices may have important consequences for post-settlement ecology. Strong habitat selection often leads to higher densities within settlement areas, with possible compensatory effects on growth (Jones 1987, Forrester 1990). In addition, size-selective predation on smaller size classes is common (Post and Evans 1989), and consequently spatial variability in the availability of suitable shelter may be important in determining predation levels for young fish (Eckert 1985, Aldenhoven 1986, Jones 1988). For example, Shulman (1984) found that settlement and/or post-settlement survival for several families of coral reef fishes (Gobiidae, Pomacentridae, Acanthuridae, Haemulidae) were strongly limited by access to shelter sites. Since availability of shelter and rate of growth are both considered to be major determinants of early juvenile survivorship, newly settled fish may be expected to exhibit behaviour that minimises the risk of predation while maximising growth (Tupper and Boutilier 1995).

The present study examines how demographic parameters of juvenile coral trout are affected by pre- and post-recruitment processes. The principal aim is to assess the relative contributions of these processes to distributions and abundances of juveniles during ontogeny. Specifically, this study describes aspects of the early life history of coral trout from the planktonic stage until entry into the adult population, with particular emphasis on the first several months after settlement. Changes in habitat use, movement patterns, feeding biology, and growth are considered in relation to observed patterns of distribution and abundances. Recruitment patterns are examined, in order to address questions about the timing of recruitment and differences in growth between monthly cohorts. Finally, the influence of larval growth histories on subsequent post-settlement growth is discussed.

This is the first study to examine juvenile demographic factors for a tropical serranid. A growing body of evidence suggests that the first months of benthic life represents a critical "bottleneck" in fish ecology (Werner and Gilliam 1984), during which selective pressure to grow rapidly through vulnerable size classes may be extreme (Post and Prankevicius 1987). By examining changes in habitat preferences, movement, diet, and growth that occur during coral trout ontogeny, the present study identifies these as more than a group of unrelated events, but rather as a suite of simultaneous changes which reflect a major ecological transition in juvenile coral trout.

1.2 THESIS OUTLINE

CHAPTER 2: Recruitment, habitat preferences, and ontogenetic habitat shifts in newly settled coral trout, (Plectropomus leopardus, Serranidae)

The densities of newly settled coral trout and their associated habitats are examined at sites around Green Reef. Specific micro-habitat preferences of newly settled fish are assessed. Observations of marked individuals over time are used to determine if juveniles shift to different habitats as they grow. Temporal patterns in recruitment are evaluated using back-calculated settlement dates. Changes in density are monitored over a two month period at two sites. Possible causes of observed habitat-use patterns are discussed.

Chapter 3: Home range, homing behaviour, and activity patterns of juvenile coral trout _Plectropomus leopardus_.

Observations of marked individuals are used to describe space use patterns of newly settled and older juveniles. Two experiments are described which measured the tendency of juveniles to return to original areas after displacement. Behavioural observations are used to examine the influence of size-specific changes in agonistic behaviour in regulating spacing of individuals. Parameters of the home range are described and used to interpret behavioural data. The importance of home range behaviour for influencing local juvenile density is discussed.

Chapter 4: Spatial and ontogenetic variation in the feeding ecology of juvenile coral trout.

Ontogenetic and spatial variation in diet and feeding biology of juvenile coral trout are examined, with particular emphasis on the implications of a shift towards piscivory. Behavioural observations are used to examine diurnal patterns in feeding behaviour. Foraging styles employed by juveniles are described. The use of samples of regurgitated prey items to estimate total gut content is evaluated. The role of habitat shifts in fostering size-specific asymmetries in feeding ecology is discussed, followed by a discussion of the impact of juvenile coral trout piscivory on the demography of coral reef fish populations.

Chapter 5: The influence of size at settlement, temperature, and size-selective predation on variations in growth rate in juvenile coral trout.

Spatial and temporal variation in growth rates are assessed, using three independent methods of estimation. Daily increment deposition and the correspondence between otolith growth and somatic growth is validated using tetracycline marked field specimens. The influence of seasonal temperature change is evaluated, using instantaneous growth estimates back-calculated from increment widths. Changes in growth parameters are assessed by comparing growth rates of populations collected shortly after settlement with those from later collections. Larval growth histories are compared to subsequent post-settlement growth to determine whether size at settlement and pre-settlement growth determine growth and success during benthic life.

Chapter 6: General Discussion

Chapter 2

RECRUITMENT, HABITAT PREFERENCES, AND ONTOGENETIC HABITAT SHIFTS IN NEWLY SETTLED CORAL TROUT, (PLECTROPOMUS LEOPARDUS, SERRANIDAE)

2.1 Synopsis

The densities of newly settled coral trout (Plectropomus leopardus) and their associated habitats were monitored on Green Reef to assess the extent to which habitat selection and post-settlement habitat shifts influence the distributions of juveniles. Surveys showed that small juveniles did not randomly select settlement sites and that these habitat associations changed as they grew larger. Specifically, coral trout recruited to level patches of rubble substrata > 5 m^2 in area and subsequently shifted to high relief features in the environment. Densities of recruits were related to the amount of rubble substrata available at sites. Loss of individuals from areas was related to density anfd the amount of available shelter. It is hypothesised that initial preferences for these substrata are due to predator avoidance strategies of newly settled fish, and that subsequent habitat shifts are a consequence of changes in the size of refugia required by growing fish.

2.2 Introduction

A significant component of the distribution and abundance of coral reef fish can be explained by spatial heterogeneity within the environment (Smith and Tyler 1972, Luckhurst and Luckhurst 1978, Bell and Galzin 1984). In particular, newly settled reef fish often have restricted depth distributions and are associated with specific habitats (Ehrlich 1975, Sale 1980, Sale et al. 1980, Williams 1980, Doherty 1983, Eckert 1985). One explanation for these patterns is that larval fish possess precise habitat requirements at settlement and actively select these sites (Sale et al. 1980).

Settlement sites selected by reef fish are known for only a few species (Leis 1991). Although numerous field studies have demonstrated apparent selection by juvenile damselfishes (Williams 1980, Sweatman 1988), and other reef-associated species (Sale et al. 1984, Eckert 1985), less is known about the habitat preferences of the juveniles of large, carnivorous fish. In particular, little research has been devoted to the early life stages of serranids (Leis 1986, Richards 1990), primarily because they tend to be cryptic and rare. If newly settled serranids do preferentially associate with specific habitats, information about the characteristics of the preferred substratum could have important implications for the management of this important commercial resource (Keener et al. 1988).

The period following settlement to these habitats is extremely important to the subsequent ecology of reef fish. For example, mortality of a fish cohort has been estimated to be as high as 99% in the first 100 days of life (Cushing 1974). Leis (1991) described the rapid behavioural and morphological changes required by settlement-stage fish during the critical transition from pelagic to reef environments, and emphasised the vulnerability of these potential recruits. Vulnerability to predation usually decreases with size (Jones and Johnston 1977), hence selection may favour rapid growth during this period. Furthermore, to the extent that predation pressure on early stages restricts individuals to particular habitats, local competition for resources may increase - the "recruitment bottleneck" phenomena (Neill 1975). Under these circumstances, it may be advantageous for an individual to switch to an alternate habitat as quickly as possible. Such ontogenetic shifts are not uncommon in fish, particularly in species that attain large sizes (Werner and Gilliam 1984).

Coral trout, Plectropomus leopardus, (Lacepède) are top carnivores and the most valuable food fish on the Great Barrier Reef (Williams and Russ 1991). With few exceptions, previous studies of this fish have concentrated on the adult phase and have considered differences in density at whole-reef scales. Ayling et al. (1991) monitored the abundances of both juvenile and larger coral trout in front and back reef habitats on 26 reefs in the Cairns section of the Great Barrier Reef. They reported variation in the numbers of coral trout recruiting to each habitat, but attributed this to differential removal of cannibalistic adult coral trout, as a result of fishing activities. More recently, Doherty et al. (1994) used light traps to collect pre-settlement coral trout from sites in the same region. In addition to reporting strong lunar periodicity in the abundances of coral trout larvae, they also found that catches were higher at certain sites, indicating that recruitment levels to benthic habitats beneath these sites may also be high.

This information suggests that densities of newly settled coral trout may vary spatially, and raises the possibility that differential mortality rates may exist between locations as a result of density-dependent processes (e.g. competition for food, suitable shelter). Although information concerning mortality is notoriously difficult to obtain, such data is likely to be of major importance in interpreting the dynamics of fish populations (Jones 1991). The limited information available suggests that there is often considerable intra-specific variability in mortality rates at small spatial scales (Aldenhoven 1986, Victor 1986, Mapstone 1988). To date, studies reporting density-dependent mortality have usually examined this process using small units of habitat such as mollusc shells or concrete blocks (Shulman 1985, Hixon and Beets1989). Mortality studies examining variability at within-reef scales are comparatively few, but are essential to identifying variation in abundances among physiographic habitat zones of individual reefs.

The importance of selecting an appropriate sampling scale with which to measure patterns and processes has been emphasised by Ogden and Ebersole (1981). Measurement of patterns of habitat use and recruitment for highly mobile fish such as coral trout may be complicated because they may dramatically increase their range of movements during ontogeny (Davies 1995). Consequently, habitat selection at settlement may be manifest over relatively small distances, reflecting the scales at which larval fish respond to differences in the environment. On the other hand, a sampling scale of hundreds of metres may be necessary to detect changes in the fish-habitat associations of older juveniles resulting from coarse-grained variation in reef morphology. Therefore, several sampling scales may be needed to measure changes in habitat use during ontogeny.

The objectives of this study were:

1) to identify temporal and spatial patterns in coral trout recruitment at Green and Arlington Reefs.

2) to determine if specific sites are occupied by juvenile coral trout at the time of settlement.

3) to establish whether shifts in habitat use occur during growth.

4) to assess the importance of shelter availability and recruit density in influencing post-settlement processes.

2.3 Materials and methods

2.3.1 Study area

The study was conducted at Green Reef, in the Cairns Section of the central Great Barrier Reef Marine Park (Fig. 2.1), between January 1992 and February 1995. Four sites (S1 - S4) were chosen around the periphery of the reef, in depths ranging between 8 - 15 metres (m). Sites were selected in conjunction with another study (Doherty et al. 1994) which identified the presence of pre-settlement coral trout at these locations. S1 was designated the "Primary Area" and was used to make detailed observations on newly settled fish. Within the Primary Area, two sections measuring 50 x 50 m (Site A), and 40 x 100 m (Site B) were gridded and mapped in order to monitor recruitment, densities, and habitat associations of newly settled coral trout. The difference in grid size was necessary due to the configuration of habitats: sand-rubble patches were generally bordered by undulating consolidated rubble mounds. Thus, to ensure that grids compared reasonably similar sections of substrata, dimensions were selected which matched topography.

2.3.2 Distribution and abundance among sites

Timed swims were used to assess the abundance of juveniles at each of the four sites. Each survey consisted of nine replicate 20 minute swims per site, covering a total area of approximately 1500 m^2. Replicates were separated by a short interval (3 - 5 minutes), during which divers were transported by boat to another haphazardly selected starting point. Visual landmarks were noted during each replicate, to insure that the same area was not censused twice during a survey. A zig-zag course was followed, in order to include as many habitat types and depths as possible. One observer (PRL) methodically searched all habitats for the presence of juveniles. Standard lengths for all fish < 200 mm were estimated, and the associated habitat recorded. Sites were surveyed in December 1993 and 1994, and January 1994 and 1995. Two size classes were used in this study: 25 - 105 millimetres (mm), and 140 - 200 mm standard length (SL). The latter size class contained few individuals at the lower end of the range, and no juveniles in the 105 - 140 mm range were seen during the sampling period. As a result of this bi-modal distribution, and based on otolith studies, (Chapter 5) these size classes were considered to represent 0+ and 1+ cohorts. The accuracy of size estimates was checked during a concurrent study by capturing and measuring fish following length estimation; estimates were within 5 mm of actual size for 0+ fish, and within 10 mm of actual size for 1+ fish.

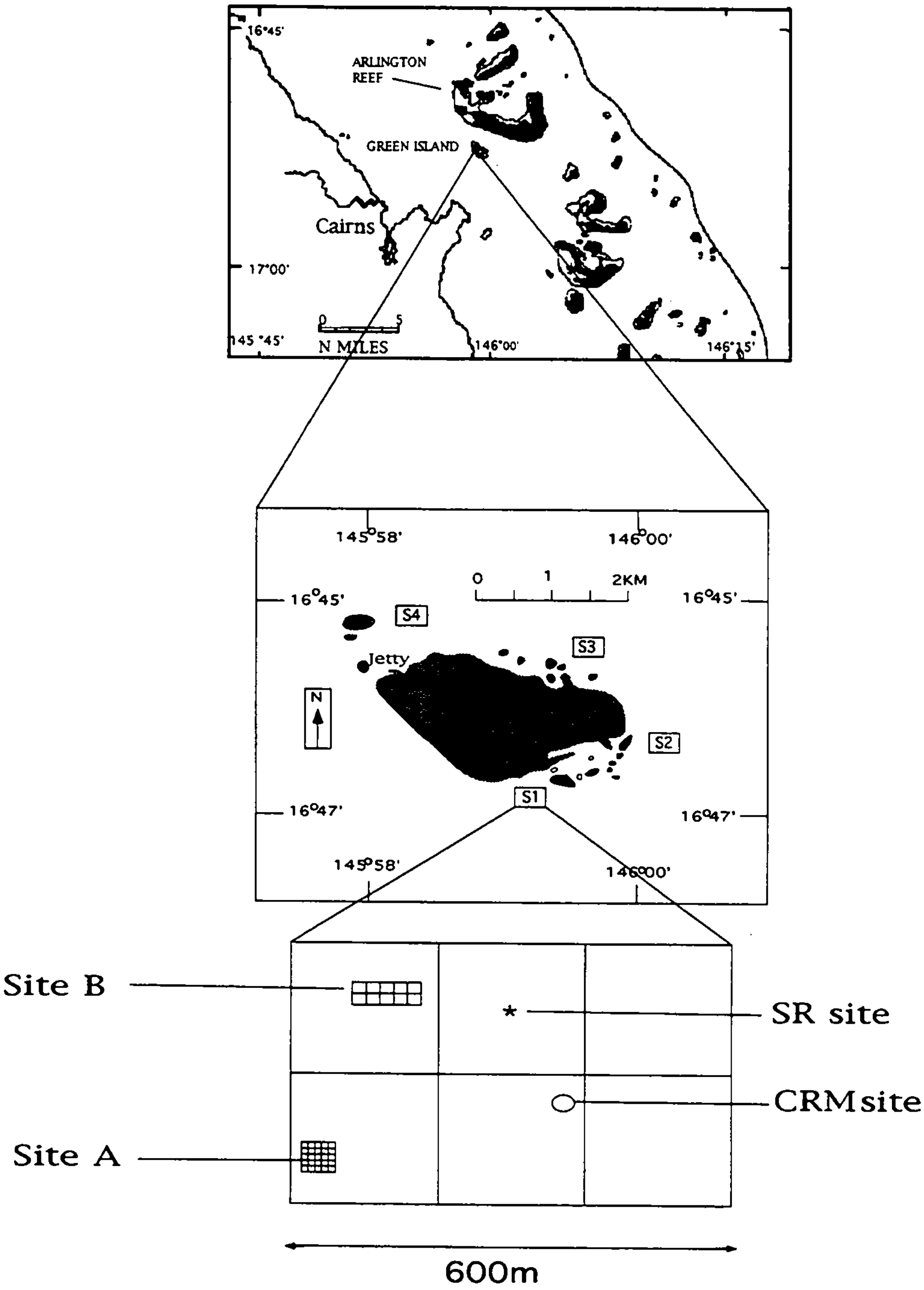


FIGURE 2.1 Location of study sites at Green Reef. **Top inset:** position of Green and Arlington Reefs in the Cairns section of the GBR. **Middle inset:** Green Reef, showing sites S1 - S4 used in visual censuses; S1 = Primary site, S2 = Secondary site. **Bottom inset:** Locations within Primary site used to measure movement and habitat associations. Site A, 50 x 50 m grid;Site B, 40 x 100 m grid; SR site, sand-rubble site used in displacement study; CRM site, consolidated rubble mound site used in displacement study.

2.3.3 Patterns of habitat use among sites

Point - intercept line transects were used to estimate percent habitat cover at each of the sites. Optimal sample size (transect lengths and number of sample points) was determined during a pilot study, by comparing estimates of substrate cover with previously determined values. Consequently, five replicate 50 m transects were placed haphazardly over the substratum., and 8 random points were selected along each transect. The substratum directly below each point was classified into one of four habitats: sand, rubble, live coral, and algae. The resulting 40 random points were used to determine mean (± se) frequency of cover for each of the categories.

2.3.4 Patterns of habitat use by 0+ fish within the primary site

In order to quantify habitat associations of newly settled fish and to determine their positions relative to prominent features in the environment, a 50 x 50 m section within the primary area (Site A) was selected which contained relatively high numbers of recruits and offered a wide range of potential habitats. This section was subdivided into 10 x 10 m squares, and all features within each square (i.e. coral heads, rubble mounds, patches of macro algae, dead coral) were mapped with a resolution of approximately 50 centimetres (cm) and transferred to an X-Y coordinate system. Daily censuses were conducted using SCUBA between 8 December 1993 and 6 February 1994. These consisted of an observer (PRL) swimming up and down the grids while thoroughly inspecting the bottom, and recording the position and identity of each marked fish on an underwater map. Individuals were recorded only once per day. A 30 m strip immediately outside the perimeter of the mapped area was also searched, to census fish which had ranged outside the grid. Censuses required about 45 minutes to complete, and were conducted at randomly selected times of day to minimise the effects of diurnal behaviour patterns.

Habitat was quantified using six replicate point-intercept transects. The resulting 48 points were assigned to the four habitat categories described above, except that rubble habitats were further subdivided into sand-rubble, rubble mounds, and dead coral to allow for finer partitioning of the environment (Table 2.1). Depth was 10 - 11 m. at high tide.

Table 2.1. Habitat types used in use/availability study, and descriptions.

HABITAT	DESCRIPTION
SAND/RUBBLE	Level expanses of sand bottom, covered with medium-grade rubble, <10 cm along major axis.
RUBBLE MOUNDS	Large (>10m^2) piles of consolidated dead branching coral, often covered with macroalgae, (Sargassum, Caulerpa) rising to 5 m above bottom.
LIVE CORAL	hard and soft corals
ALGAE	benthic macroalgae, 5 - 15 cm in height
SAND	uniform patches of sand containing little or no rubble
DEAD CORAL	rocks > 0.5 m

0+ fish were divided into two size classes: 25 - 60 mm, and 61 - 105 mm. Members of the first size class were designated "small recruits" and the latter were considered "large recruits".

In order to identify individuals, selected fish were marked and released. Fence nets were used to capture these juveniles (n = 57), and they were branded with individual marks using a 12 volt soldering tool located on the boat. The branding procedure involved placing the fish on a board with its head covered by a moist towel, and lightly touching the shank of the heating element to the body. This technique cauterised the skin, and produced a white line approximately 0.5 cm wide, which changed to dark gray after 2 - 3 weeks. Although the marks became more difficult to recognise after the colour change they were still visible for two months. Individuals were recognised by different combinations of brand position (left side, middle etc.) and orientation (/, -, <, >, etc.). After branding and measurement, each fish was returned to the exact point of capture, usually within 10 minutes. Observations of branded fish in captivity and in the field indicated that fish were not adversely affected by the procedure (aquaria fish readily consumed prey within an hour of marking, and released individuals were observed to forage and interact with con- and hetero-specifics on the following day).

Daily positions of marked fish were recorded on an underwater map, and the most divergent observation points for each individual were connected to estimate home range. Subsequent plots of the area of these convex polygons and the number of resightings showed that home range was estimated reasonably with a minimum of twelve resightings (Chapter 3). Consequently, the areas of fish with twelve or more resightings were used to indicate their positions relative to spatial reference points inside the grid.

The null hypothesis that juvenile coral trout use habitats in proportion to their availability was evaluated using two tests.

First, resightings of all marked recruits were pooled and divided into the two size classes. Frequency distributions of the number of fish seen on habitats were compared to habitat availability, using Chi-square tests.

As a second test of habitat selection, the Linear Resource Selection Index (Strauss 1979) was used to estimate habitat selection of individual fish:

$$L = r_i - p_i,$$

where L is the measure of preference, r_i = relative utilisation of substratum i (i. e. number of associations of one individual with substratum i divided by the total number of resightings of that individual), and p_i = overall proportion availability of substratum i. Expected values of this index fall between ±1, with zero indicating random association, positive indicating selection of a substratum, and negative values indicating avoidance of the substratum. Selection indices were calculated for all fish resighted 12 or more times, and the means of new and large recruits were compared using Student's t-test. T-tests were also used to assess whether values were significantly different from zero for each habitat ($\alpha = 0.05$) (Morrissey and Gruber 1993).

2.3.5 Timing of recruitment

Juvenile coral trout were collected from Green Reef from 1992 - 1995 for use in an otolith-based study of recruitment and growth (Table 5.1); additional individuals were collected from Arlington Reef during 1992 to assess variation in recruitment between reefs. Sagittae were removed from juveniles, cleaned, weighed and measured. Sagittae from individuals collected in 1992 were prepared and analysed by personnel from the Central Ageing Facility (CAF) in Victoria, and lapilli from the same individuals were used to determine pre-settlement age (Chapter 5). Back-calculated settlement dates were determined for each fish by subtracting total age minus mean pre-settlement age from collection dates. Age and sagittae length were strongly correlated; consequently, this relationship was used to back-calculate settlement dates for juveniles collected during the final two years of the study (Chapter 5).

2.3.6 Changes in density

Density of newly settled individuals were monitored during weekly censuses of both Site A and Site B, between 8 December 1993 and 29 January 1994; Site B was not censused during the first week of this period. New recruits were collected, marked, and returned to the point of capture during each weekly census. Grids were thoroughly inspected during censuses; thus, it was assumed that all individuals present were captured and marked. The number of marked recruits were compared to the number from the previous week, and the percent missing from grids was considered the disappearance rate (losses due mortality and/or relocation). Recruitment rates were estimated from the numbers of unmarked individuals (new recruits) recorded on the grids each week.

2.3.7 Effect of sampling scale on measurement of habitat selection

To determine the spatial scale at which settlement sites differed from randomly chosen sites, 33 recruits (mean SL 36.7 ± 1.2 mm, range 25 - 47 mm) were captured and measured during 1994 - 1995. For each fish located, the surrounding habitat was quantified at three spatial scales using quadrats of nested size (1, 2, and 5 m squared). The quadrat was centred on the position where the fish was first sighted and the surrounding habitat was classified under each of 36 evenly-spaced points into one of 11 habitat categories. These habitat categories were defined as: (1) Rubble - bits of dead coral < 10 cm. (2) Sand - fine grained calcareous sediment. (3) Algae - macro algae (e. g. Halimeda, Sargassum, Caulerpa). (4) Rock - dead coral > 10 cm, firmly embedded in substratum. (5) Live branching coral - (e. g. Acropora, Pocillopora). (6) Live massive coral - (e. g. Porites, Goniopora). (7) Live plate coral - (e. g. Agariciidae). (8) Sponge. (9) Soft coral. (10) Consolidated rubble - mounds of dead branching coral, rising 4 - 8 m above the sea-bed. (11) Consolidated algae/rubble - similar to (10) but encrusted with turf and/or calcareous algae.

To provide a valid comparison, null sites were selected using a compass and sets of two random numbers. The first random number in a set (integer between 1 and 8 inclusive) specified the compass quadrat (to the nearest 45 degrees); the second (0 - 99 inclusive) determined the number of fin strokes to swim from the point of origin. Once the null position was determined, the surrounding habitat was quantified by the same procedures using the same three nested quadrats. The points underlying the quadrats were recorded as above.

Chi-square tests on total frequency counts for each of the 11 habitat groups were used to assess whether habitats selected by recruits differed from null sites. In order to assess whether patterns of habitat use differed between spatial scales, principal component analysis (PCA) was used to reduce the data set to a smaller number of uncorrelated components. The characteristics of the sites selected by the 33 fish were analysed at each scale separately, and for all three scales combined. Principal component axes (PCs) were characterised by their correlations with the original microhabitats: correlations were considered significant if they had an absolute magnitude greater than 0.5 (Paulissen 1988). Microhabitats selected by recruits were expressed as a subset of all microhabitats potentially available at each scale. Means and standard errors of eigenvalues along each PC axis were calculated, and significant differences between selected and random scores were identified at each of the three scales and for all scales combined, using Student's t-test ($\alpha = 0.05$)(Paulissen 1988).

2.4 Results

2.4.1 Distribution and abundance among sites

The pattern of distribution of recruits among sites at Green Island was relatively consistent between years (Fig. 2.2). S1 and S2 received the highest number of 0+ fish in both years sampled, but the overall magnitude was higher in the second year. When counts from both seasons were combined, 63 recruits were recorded from S1 and S2 compared to only three from other sites.

As with 0+ fish, total numbers of 1+ fish recorded during the study were greatest at S1 and S2. However, site by site comparison of the distributions of 0+ fish from the first season with distributions of 1+ fish from the second year, shows that despite a lack of recruits at S3 in 1993 - 1994, 1+ fish were present at this site during the following season, at densities equivalent to S1 and S2.

Analysis of variance of 0+ fish counts using years, months, and sites as fixed factors and number of fish seen per 20 minute swim as the response variable, detected a significant interaction between year and site (Table 2.2), suggesting that

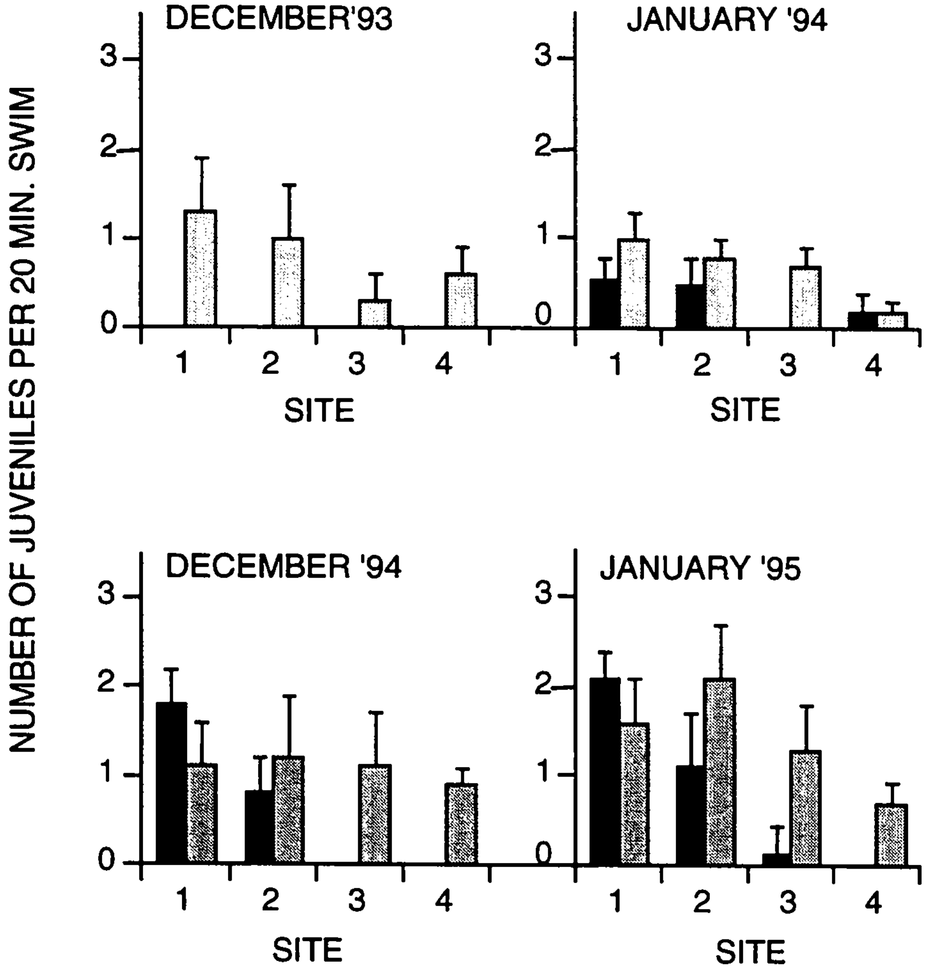


Fig. 2.2. Mean (± SE) number of juveniles seen per 20 minute swim at sites around Green Reef (n = 9 swims per site). Dark bars: 0+ fish, Light bars: 1+ fish.

the magnitude of recruitment to individual sites varied between years . Multiple comparisons revealed higher abundances in 1994 - 1995, and for censuses in January. Recruitment at S1 was significantly higher than at other sites (Tukey's test, $\alpha = 0.05$).

Counts of 1+ fish were also higher in 1994 - 1995. A significant interaction was found between year and month (Table 2.3), indicating that the trend in the distribution pattern differed from that of 0+ fish. Multiple comparisons indicated a more even distribution of 1+ fish relative to recruits: there were no significant differences between abundances at S1, S2, and S3, and fish counts between months did not differ significantly.

Table 2.2. **Table 2.3.** (A) ANOVA of no. of 0+ fish seen per 20 min. swim. (B) Tukey's test of no. of juveniles seen per 20 min. swim. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of juvenile abundance.

A. Source	df	MS	F	P
Year	1	11.67	57.97	<0.0001
Month	1	2.51	12.45	<0.001
Site	3	9.56	47.48	<0.0001
Year x Month	1	0.17	0.86	0.36
Year x Site	3	5.82	28.91	<0.0001
Month x Site	3	0.40	1.97	0.12
Yr x Mo x Site	3	0.06	0.31	0.82
Residual	128	0.20		

B. Main effect				
Year	1993-1994	1994-1995		
Month	December	January		
Site	S4	S3	S2	S1

Table 2.3. (A) ANOVA of no. of 1+ fish seen/20 min. swim. (B) Tukey's test of no. of juveniles seen/20 min. swim. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of juvenile abundance.

A. Source	df	MS	F	P
Year	1	9.0	17.34	<0.0001
Month	1	0.25	0.48	0.49
Site	3	3.72	7.17	<0.005
Yr x Mo	1	2.25	4.33	<0.05
Yr x Site	1	0.80	1.53	0.21
Mo x Site	3	0.82	1.59	0.20
Yr x Mo x Site	3	2.0	1.8	0.20
Residual	128	0.52		

B. Main effect				
year	1993-1994	1994-1995		
month	December	January		
site	S4	S3	S2	S1

2.4.2 Patterns of habitat use among sites

Analysis of transect data detected significant between-site differences in frequency of occurrence of rubble, sand, algae, and live coral (Table 2.4). S1 had the highest proportion of rubble substrata, while S4 had relatively high amounts of coral. S2 had the highest component of algae. Comparison of mean abundance of 0+ and 1+ fish with mean frequency of rubble cover at each site (Fig. 2.3) indicated a positive correlation for 0+ fish, (Spearman's Rank Correlation Coefficient, $r^s = 1.0$, $n = 4$, $p < 0.05$), but not for 1+ fish ($r^s = 0.6$, $n = 4$, $p > 0.05$).

TABLE 2.4. (A) One way ANOVA of habitat cover at four sites around Green Reef, based on forty random points per site. (B) Tukey's test of frequency of habitat at each site. Sites not significantly different at the 0.05 level share an underline. Sites are arranged in increasing order of frequency.

A. SOURCE	df	MS	F	P
RUBBLE	3	6.85	24.91	<0.0001
SAND	3	16.07	21.42	<0.0001
ALGAE	3	15.38	27.97	<0.0001
LIVE CORAL	3	7.8	18.35	<0.0001

RUBBLE	S3	S4	S2	S1
SAND	S2	S1	S4	S3
ALGAE	S4	S3	S1	S2
LIVE CORAL	S2	S1	S3	S4

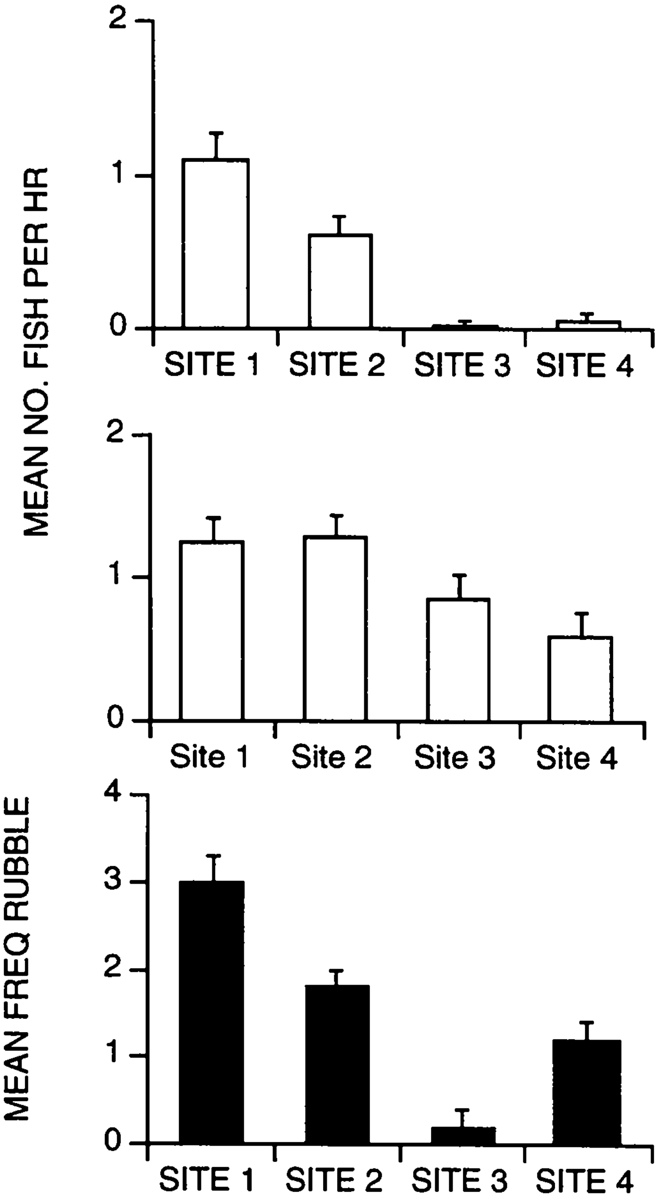


Fig. 2.3. Mean (± SE) number of juveniles seen during timed swims at four sites, and mean (± SE) frequency of rubble at each site. Counts of juveniles are pooled over two seasons (n = 36 swims per site). Frequency of rubble based on 40 random points (see text). Top: 0+ fish. Middle: 1+ fish. Bottom: frequency of rubble at each site.

2.4.3 Patterns of habitat use within a site

Fish-habitat associations were recorded for small recruits (n = 169), and large recruits (n = 239) seen during daily censuses at Site A. Number of resightings per fish ranged from 1 to 17; thus analysing habitat associations from all resightings would bias results towards individuals sighted frequently. Consequently, all habitat associations were analysed for fish seen on up to three occasions; for fish sighted more frequently, three observations were selected at random from the total observations of each individual, and these were used to calculate use/availability indices.

Comparison between numbers of juveniles seen on each habitat, with the availability of each habitat indicated a non-random assortment for both size classes. Habitats were used in proportions that varied significantly from the availability of these substrata, in both small recruits ($X^2 = 92.1$, df = 4, $p < 0.0001$), and large recruits ($X^2 = 72.7$, df = 4, $p < 0.0001$). Sixty one percent of all sightings of small recruits were on the sand-rubble habitat, while this substratum provided only 24% of the total area (Fig. 2.4A). Large recruits were recorded most often on consolidated rubble mounds. Sightings on this habitat comprised 41% of all observations, while this substrata constituted only 21% of the total area (Fig. 2.5A).

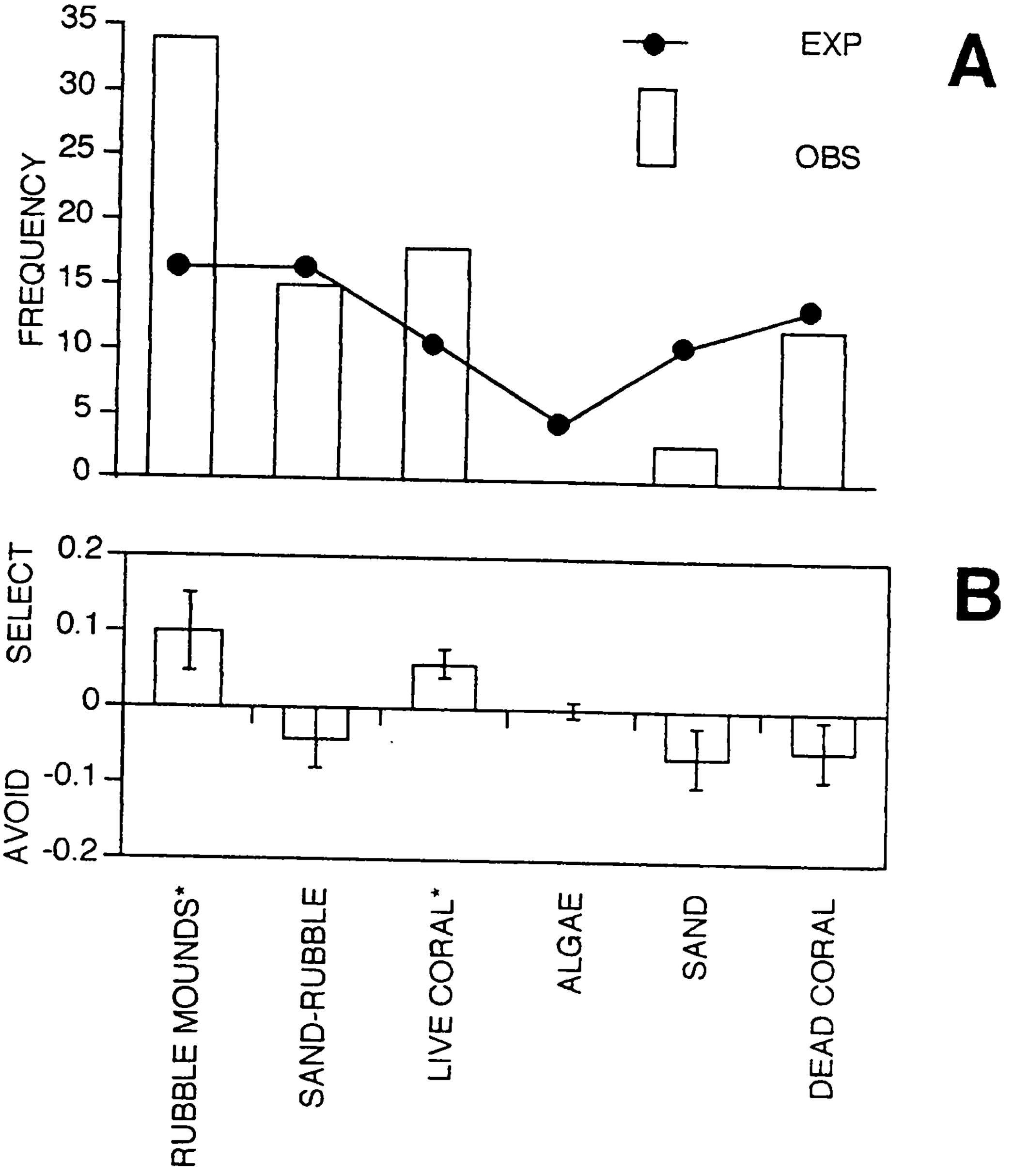


Fig. 2.4. A. Observed (histogram) and expected (circles) frequencies of observations of December recruits (n = 72) seen on habitats within 50 x 50 m mapped area. B. Mean (± SE) index of selectivity values for December recruits resighted 12 or more times (n = 7). * = significantly different from 0, p = 0.05.

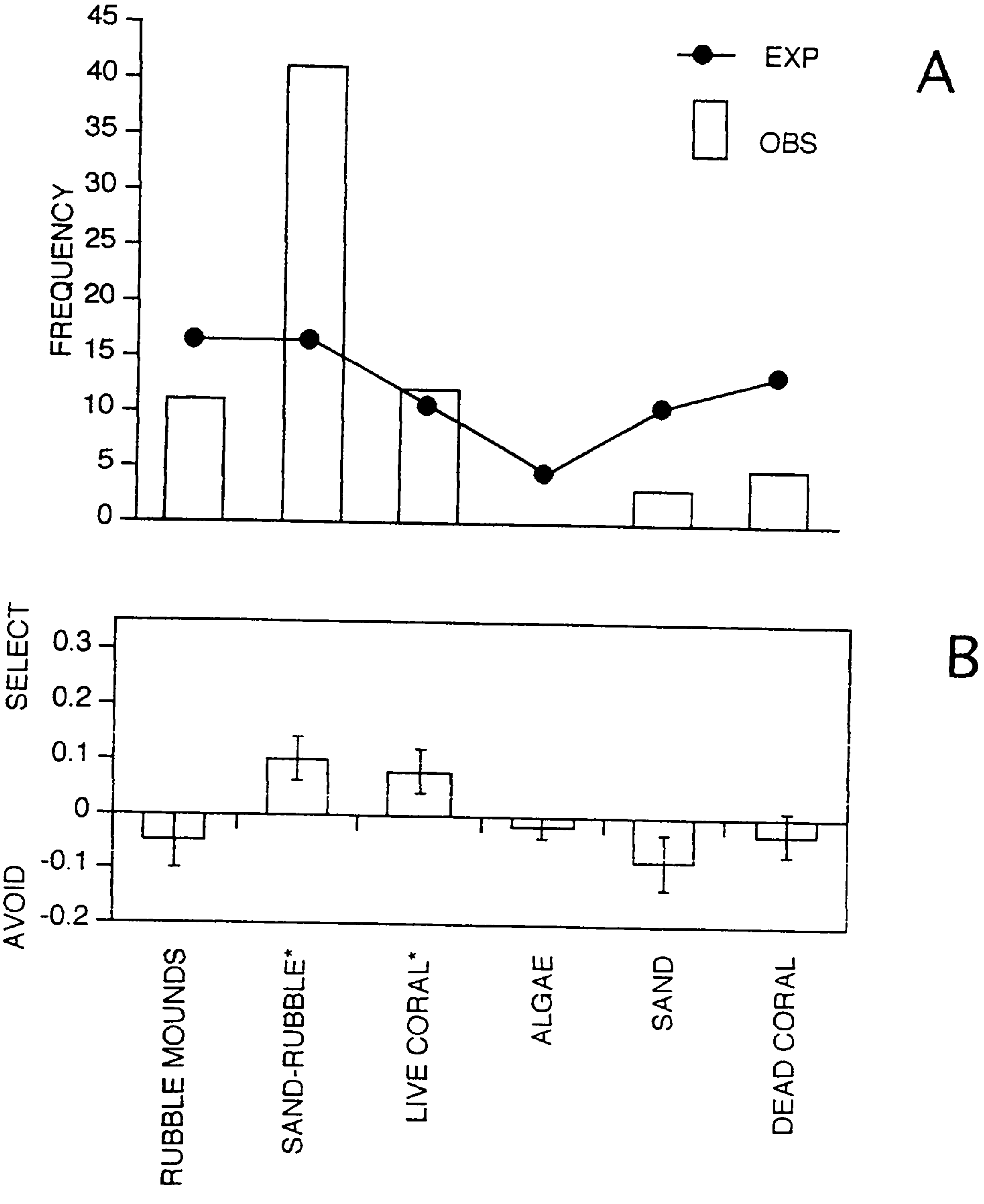


Fig. 2.5. A. Observed (histogram) and expected (circles) frequencies of observations of November recruits (n = 85) seen on habitats within 50 x 50 m mapped area. B. Mean (± SE) index of selectivity values for November recruits resighted 12 or more times (n = 8). * = significantly different from 0, p = 0.05.

Estimates of habitat selection (L) for recruits seen twelve or more times showed that small recruits (Fig. 2.4B) and large recruits (Fig. 2.5B) used substrata in different proportions to their availability within the grid. The greatest change in substrata use involved a transition from sand-rubble habitats to rubble mounds as fish increased in size. The use of the sand-rubble substrata was significantly different between the two size classes ($t = 5.2$, $p < 0.005$), as was the use of the rubble mound habitat ($t = -2.9$, $p < 0.05$). Small recruits used the sand-rubble and live coral habitats in proportions that were significantly different from random ($t = 7.9$, $p< 0.001$; and $t = 5.6$, $p < 0.02$, respectively). Large recruits used rubble mounds and live coral in proportions that were statistically non-random ($t = 5.1$ $p < 0.002$; and $t = 5.60$, $p < 0.001$, respectively). Positions of large recruits were closely associated with high relief structures, and areas used by individuals overlapped with each other (Fig 2.6).

2.4.4 Timing of recruitment

Temporal patterns of recruitment differed between Green and Arlington Reefs in 1991 - 1992 (Figure 2.7). The pattern at Arlington was bi-modal, with peak recruitment approximately coinciding with the November and December new moons. In contrast, recruitment to Green Reef during this year showed little signs of periodicity, and was relatively continuous over a two month period. In 1992 - 1993, only a small number of

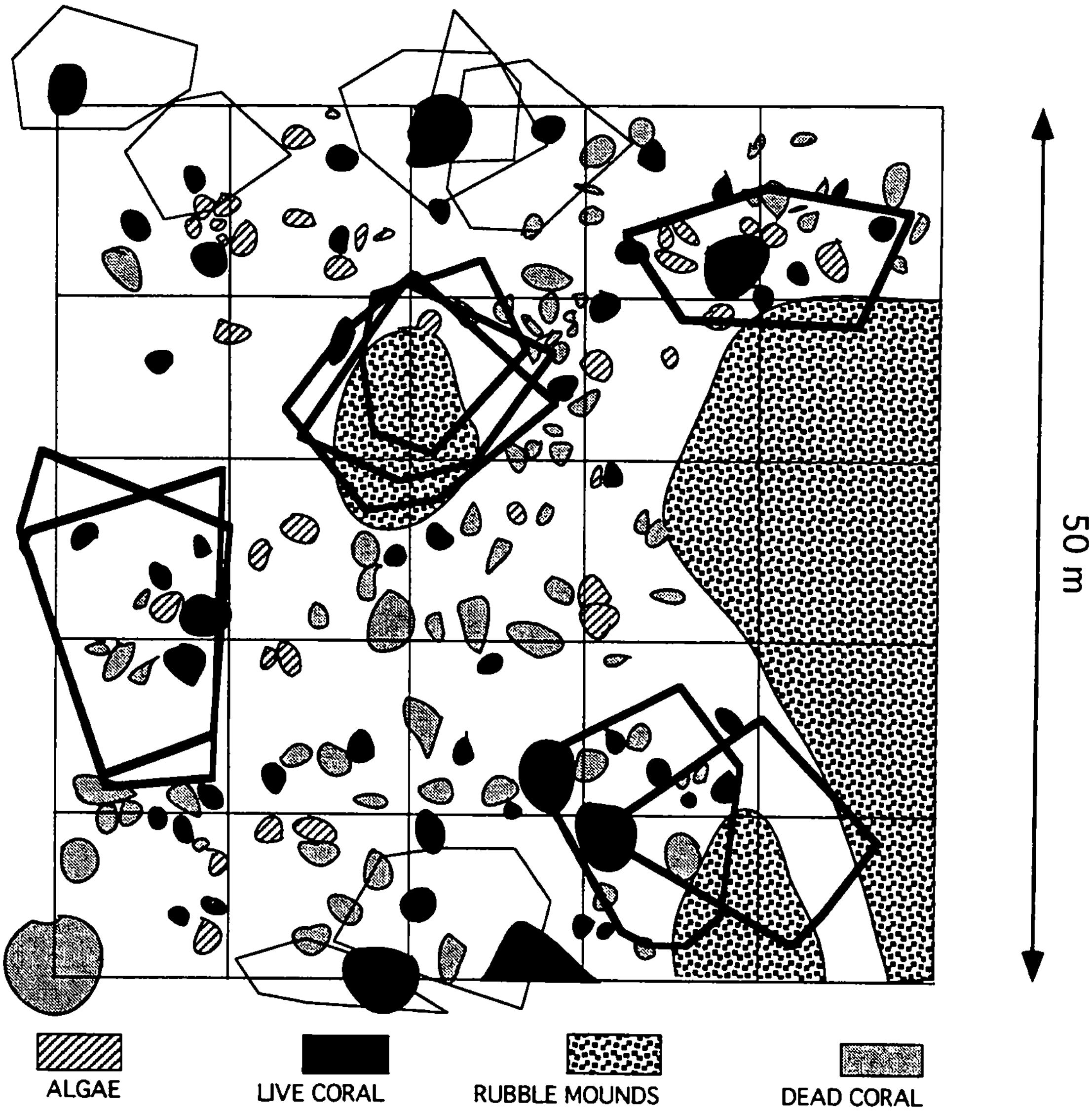


FIG. 2.6. MAP OF SITE A, USED TO MEASURE HOME RANGE AREA FOR 0+ CORAL TROUT. POLYGONS REPRESENT OUTERMOST POINTS OF OBSERVATIONS. LIGHT POLYGONS = RECRUITS ≤ 60 mm, DARK POLYGONS = RECRUITS > 60 mm.

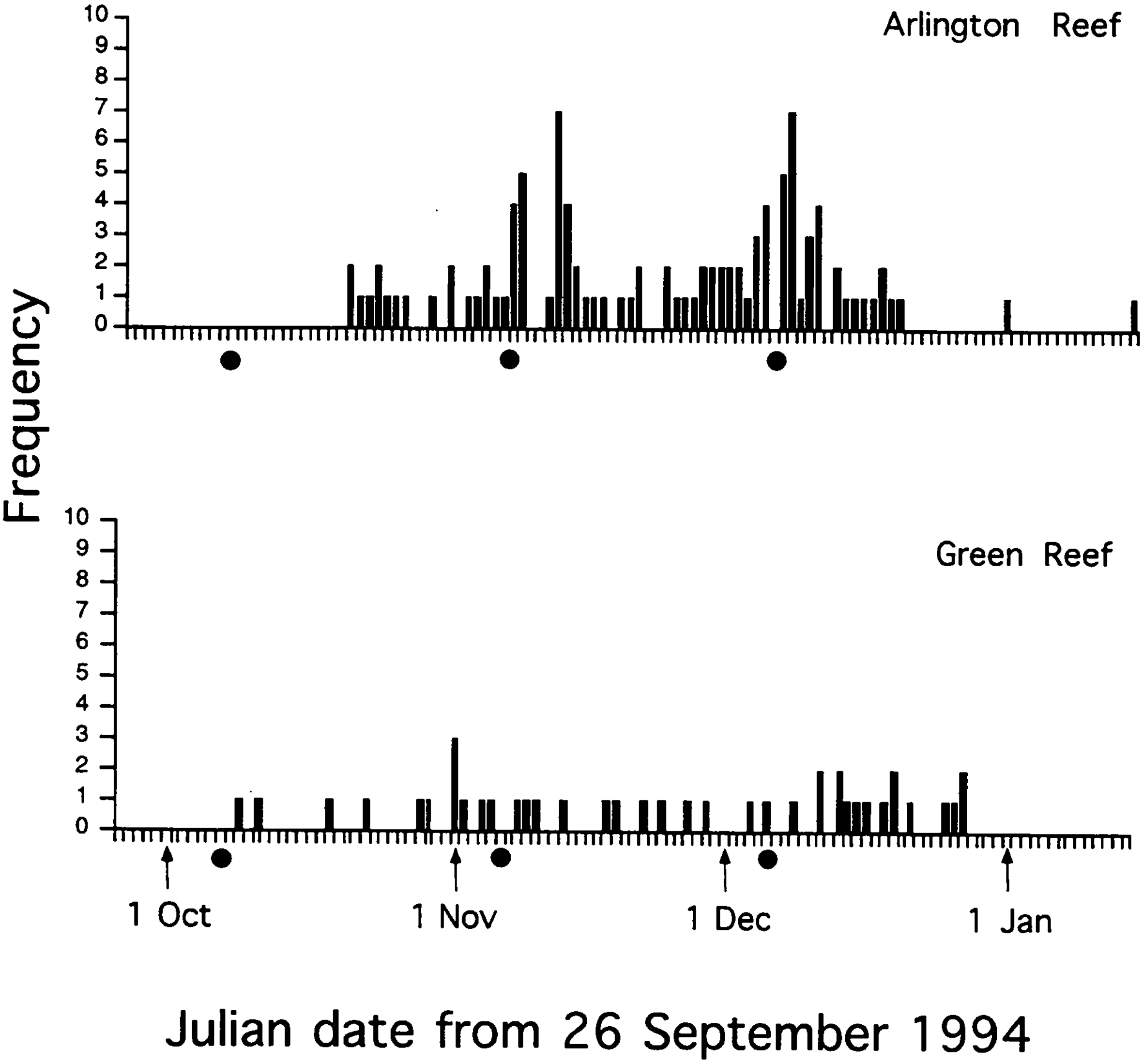


Fig. 2.7. Top: Settlement dates of juveniles recruiting to Arlington Reef during 1991 -1992 (n = 103). Bottom: Settlement dates of juveniles recruiting to Green Reef during 1991 - 1992 (n = 40). Filled symbols represent new moons.

juveniles were collected from Green Reef, precluding analysis of recruitment patterns. In 1993 - 1994, recruitment at Green Reef was characterised by two settlement events occurring during the time of the November and December new moons (Figure 2.8A). Recruitment to Green Reef during the final year of the study was relatively continuous over a one month period, which was approximately centred on the November new moon (Figure 2.8B).

2.4.5 Changes in density

During the 1993 - 1994 censuses, recruitment to both Site A and Site B was highest during the 15 December census (new moon = 13 December) and dropped sharply during subsequent weekly censuses (Figure 2.9A, 2.10A). Mean density (total recruits/m2) during the censusing period was significantly higher at Site A (0.011 recruits/m^2) than at Site B (0.007 recruits/m^2; $t = 2.87$, $p < 0.05$). Mean number disappearing (number disappearing/m^2) was also significantly higher at Site A (0.004 recruits/m^2) than at Site B (0.001 recruits/m^2; $t = 1.97$, $p < 0.05$). Disappearance rate (% disappearing) decreased over the two month period at Site A (Figure 2.9B, Table 2.5) but not at Site B (Figure 2.10B). Disappearance rate and total recruit numbers were significantly correlated at Site A (Spearman's Rank Correlation Coefficient, $r^s = 0.795$, $P < 0.05$), but not at Site B ($r^s = -0.271$, $P > 0.05$). Quantification of habitat cover for each site indicated that sand-rubble

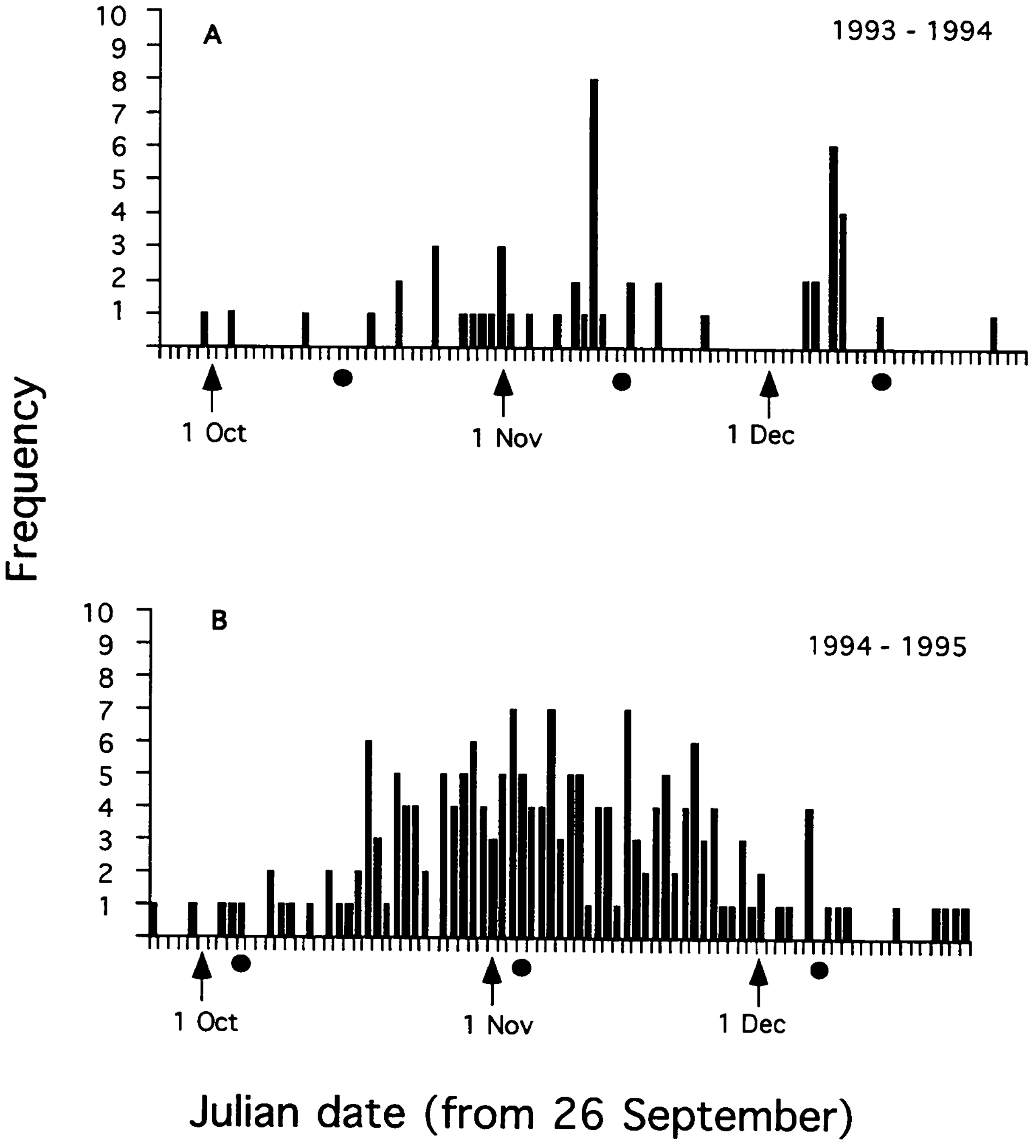


Fig. 2.8. A: Settlement dates of juveniles recruiting to Green Reef during 1993 -1994 (n = 52). B: Settlement dates of juveniles recruiting to Green Reef 1994 - 1995 (n = 185). Filled symbols represent new moons.

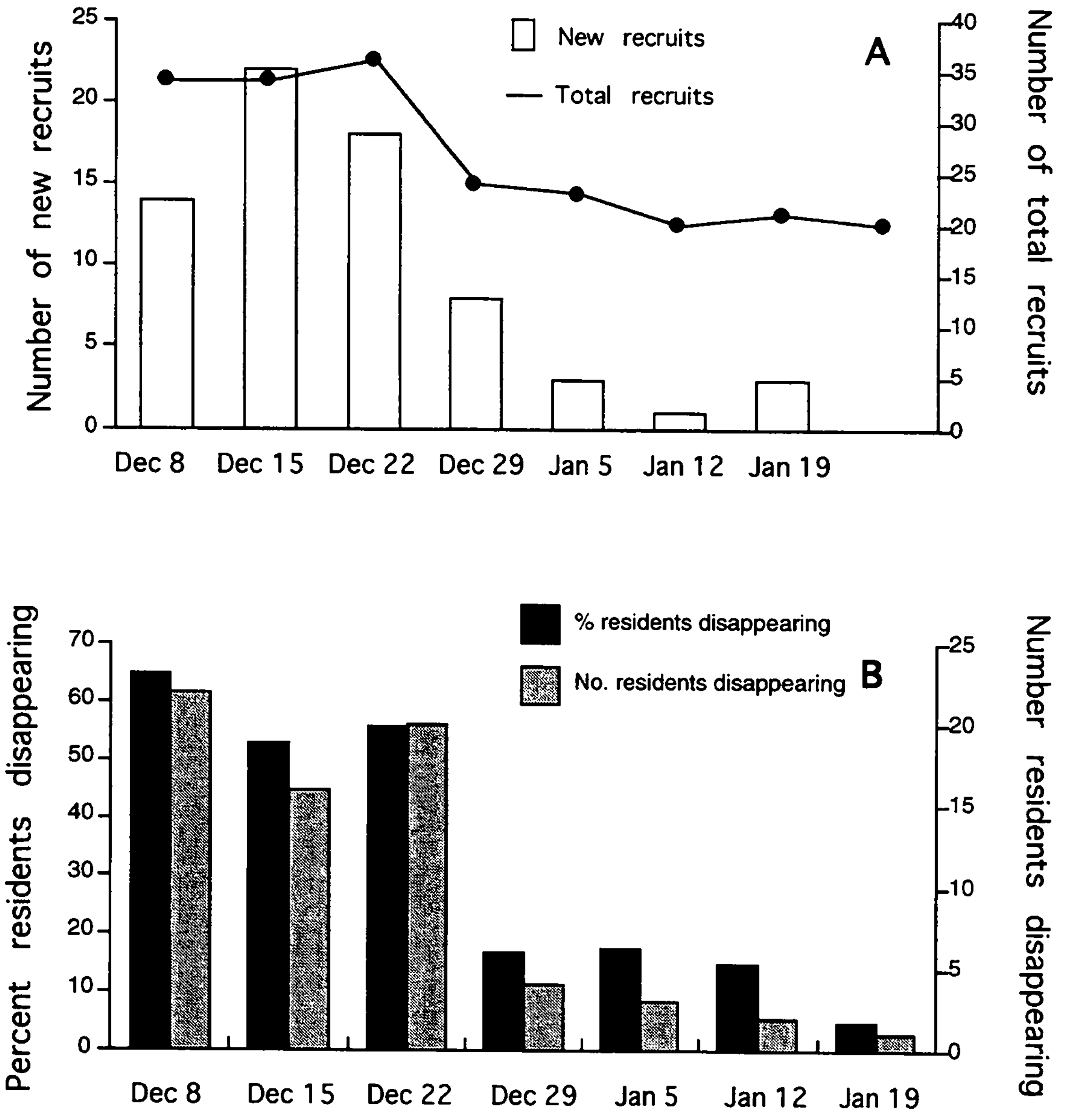


Figure 2.9.A. The number of recruits counted during weekly censuses at Site A, presented separately for new recruits and total recruits. **B.** Disappearance of recruits at Site A, presented separately for disappearance rate (percent disappearing) and number disappearing.

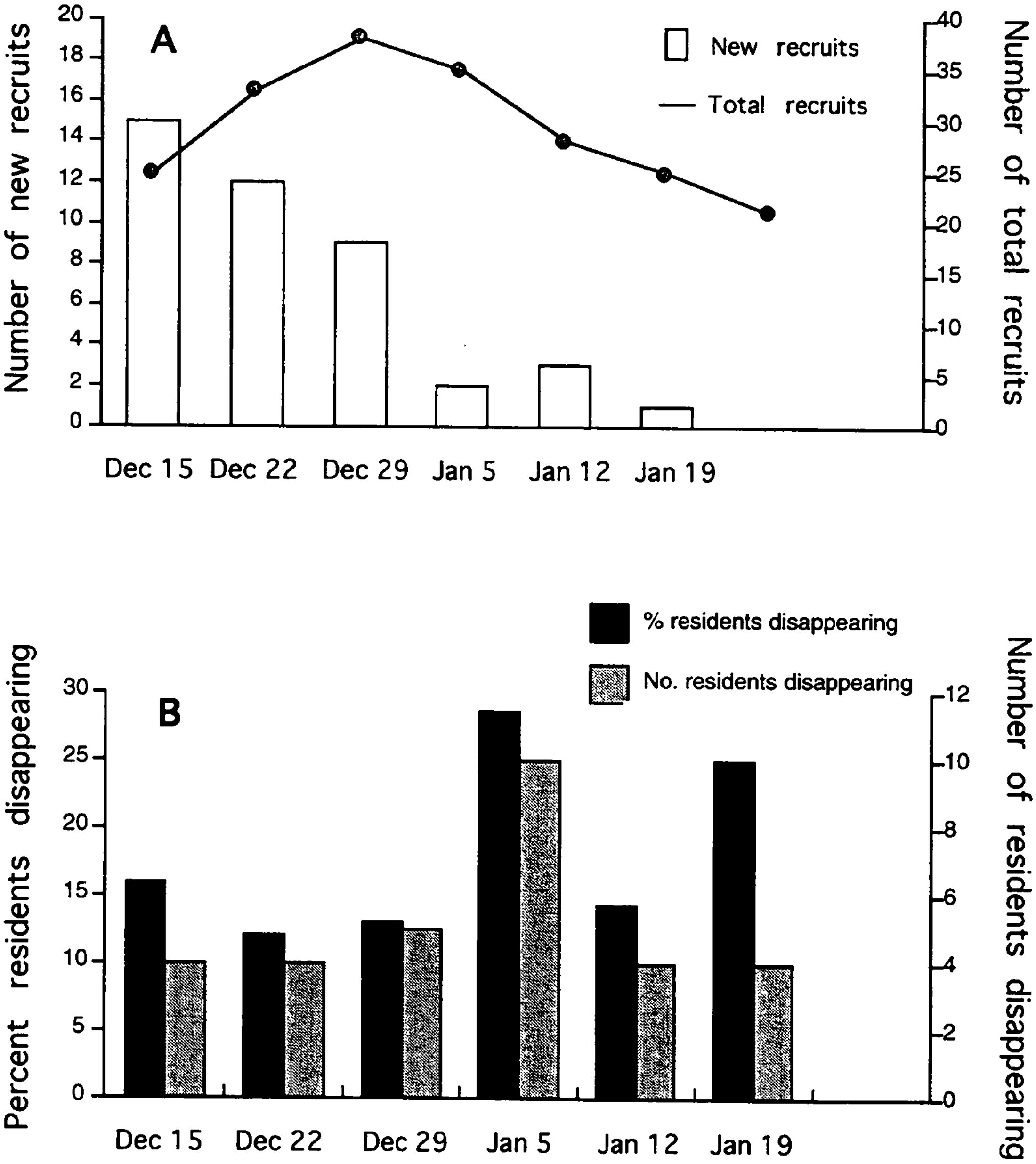


Figure 2.10.A. The number of recruits counted during weekly censuses at Site B, presented separately for new recruits and total recruits. **B.** Disappearance of recruits at Site B, presented separately for disappearance rate (percent disappearing) and number disappearing.

comprised 24% of the area of Site A (Figure 2.6), while this habitat constituted 66% of the area of Site B (Figure 3.10).

Table 2.5. Weekly density surveys at two locations within the Primary Site. Older recruits present during the first weekly censuses represent untagged individuals > 50 mm; older recruits in all other weekly censuses are numbers of tagged fish persisting from the previous week. Mean (± se) SL of new recruits: Site A 43.2(0.6) mm, n = 69; Site B 44.1 (0.4) mm, n = 42.

Week	# New rec.	#Old rec.	rec. (tot)	# persist. to following wk.	Disappearance rate (% missing)
Site A					
8 Dec	14	20	34	12	64.7
15 Dec	22	12	34	18	52.9
22 Dec	18	18	36	16	55.6
29 Dec	8	16	24	20	16.7
5 Jan	3	20	23	19	17.4
12 Jan	1	19	20	17	15.0
19 Jan	3	17	20	19	5.0
26 Jan	0	19	19	-	-

Week	# New rec.	#Old rec.	rec. (tot)	# persist. to following wk.	Disappearance rate (% missing)
Site B					
15 Dec	15	10	25	21	16.0
22 Dec	12	21	33	29	12.1
29 Dec	9	29	38	33	13.1
5 Jan	2	33	35	25	28.6
12 Jan	3	25	28	24	14.3
19 Jan	1	24	25	21	25.0
26 Jan	0	21	21	-	-

2.4.6 Effect of sampling scale on measurement of habitat selection

Mean frequency of occurrence of the 11 microhabitats were plotted for both selected sites (fish present) and null sites (fish absent) at the three scales (Fig. 2.11). There were significant differences between selected and random sites with regard to seven of the eleven microhabitats when data from all grids were pooled. Rubble, algae, and rock microhabitats were most strongly selected by recruits. Frequencies of occurrence for live branched coral, live massive coral, consolidated rubble, and consolidated algal-rubble microhabitats were significantly higher in randomly chosen grids, indicating that recruits tended to avoid these substrata.

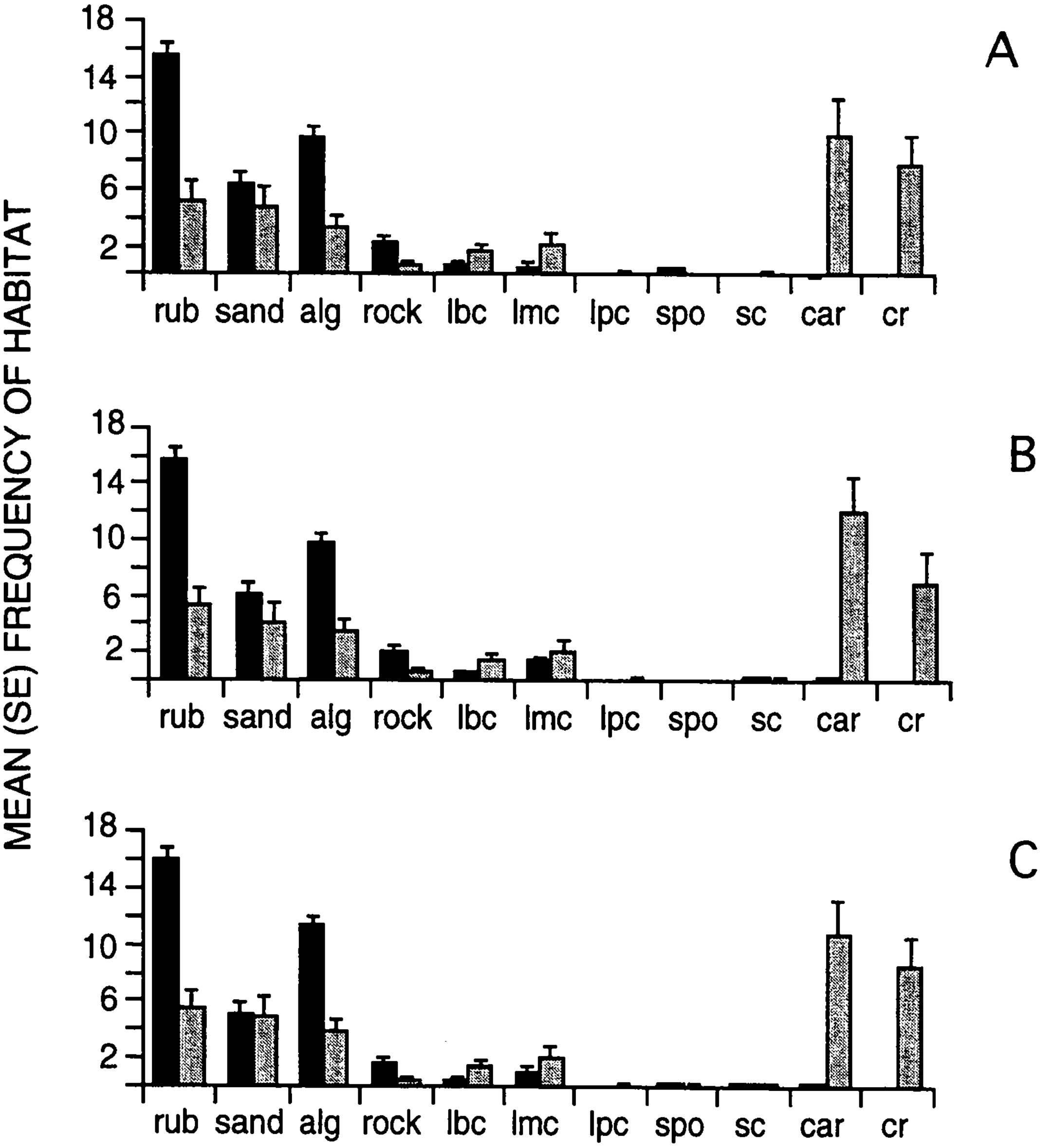


Fig. 2.11. Mean (± SE) frequency of habitat types from nested grid study (see text). Dark bars = values for sites selected by recruits, light bars = random sites. Frequencies are based on 36 points within each grid. A: 1 x 1 m grid. B: 2 x 2 m grid. C: 5 x 5 m grid. Habitat code: rub = rubble, lbc = live branching coral, lmc = live massive coral, lpc = live plate coral, spo = sponge, sc = soft coral, car = consolidated algae/rubble, cr = consolidated rubble.

The first three components accounted for 50.96 percent of the variance in the raw data (Table 2.6). PC-1 was strongly positively correlated with rubble, algae, and rock substrata, and negatively correlated with rubble mounds and live branched coral. Thus PC-1 is interpreted as a relief gradient, with positive values denoting low relief features. PC-2 was strongly positively correlated with live massive, live branched, and live plate coral, and hence describes a living/non-living gradient, with high values associated with live coral microhabitats, and low values representing rubble mounds and other primarily non-living substrata. The third PC was positively correlated with the sand microhabitat.

TABLE 2.6. Means (± se) of PC scores for selected and random grids computed for the total data set and for each grid size. An asterisk denotes a significant difference between random and selected grids, using Student's t-test. * P< 0.05, ** P< 0.01, *** P < 0.0001. LM = Live massive coral, n = number of grids, F = fish-selected sites, R = randomly selected sites.

			PC-1	PC-2	PC-3
COR. WITH PC			RUBBLE (0.5)	LM (0.58)	SAND (-0.54)
% OF VARIANCE			25.51	13.89	11.56
SCALE	n		Score (x ± SE)	Score (x ± SE)	Score (x ± SE)
1 X 1	33	F	1.1898 ± 0.089	0.006 ± 0.075	0.181 ± 0.137
	33	R	-1.148 ± 0.276***	0.129 ± 0.303	-0.163 ± 0.257
2 X 2	33	F	1.229 ± 0.083	0.009 ± 0.098	0.285 ± 0.144
	33	R	-1.066 ± 0.278***	0.003 ± 0.281	-0.081 ± 0.234
5 X 5	33	F	1.174 ± 0.085	0.148 ± 0.100	0.253 ± 0.118
	33	R	-1.069 ± 0.287***	0.541 ± 0.283*	-0.136 ± 0.179*
TOTAL	99	F	1.197 ± 0.049	-0.044 ± 0.053	0.224 ± 0.075
	99	R	-1.095 ± 0.160***	-0.133 ± 0.179	-0.150 ± 0.126**

PC scores from all grids combined (total) showed significant differences between random and selected sites on PC-1 ($t = 13.5$, $p < 0.0001$) and PC-3 ($t = 2.4$, $p < 0.01$), but not on PC-2. When each grid size was analysed separately, selected and random sites differed at all three scales on PC-1. Only the 5 x 5 m grids showed significant differences between random and selected sites on all three PC axes.

Plots of the eigenvalues for each grid size against the first two PCs indicated tight clustering of selected sites as opposed to random sites (Fig 2.12A, 2.12B, 2.12C). Most recruits were strongly associated with low relief features that were intermediate on the living/non-living spectrum. Comparison of these plots with the biplot of habitats (Fig 2.12D) shows that newly settled fish were primarily associated with rubble, algae, and rock habitats.

2.5 Discussion

Habitat associations of newly settled and growing juvenile coral trout are potentially important to the demography of adult populations. Recruitment success appears to be strongly influenced by substratum morphology and the characteristics of available shelter. Newly settled fish occurred within patches of level sand-rubble bottoms, and subsequently shifted to association with high relief features as they grew. One year old fish were distributed more evenly around Green Reef than 0+ fish, suggesting that older fish had moved from initial settlement sites. Spatial variations in recruit density combined with variable amounts of suitable shelter may also have influenced distributions. It is suggested here that distributional patterns of juvenile coral trout at Green Reef are the result of habitat selection and subsequent modification by post-recruitment processes.

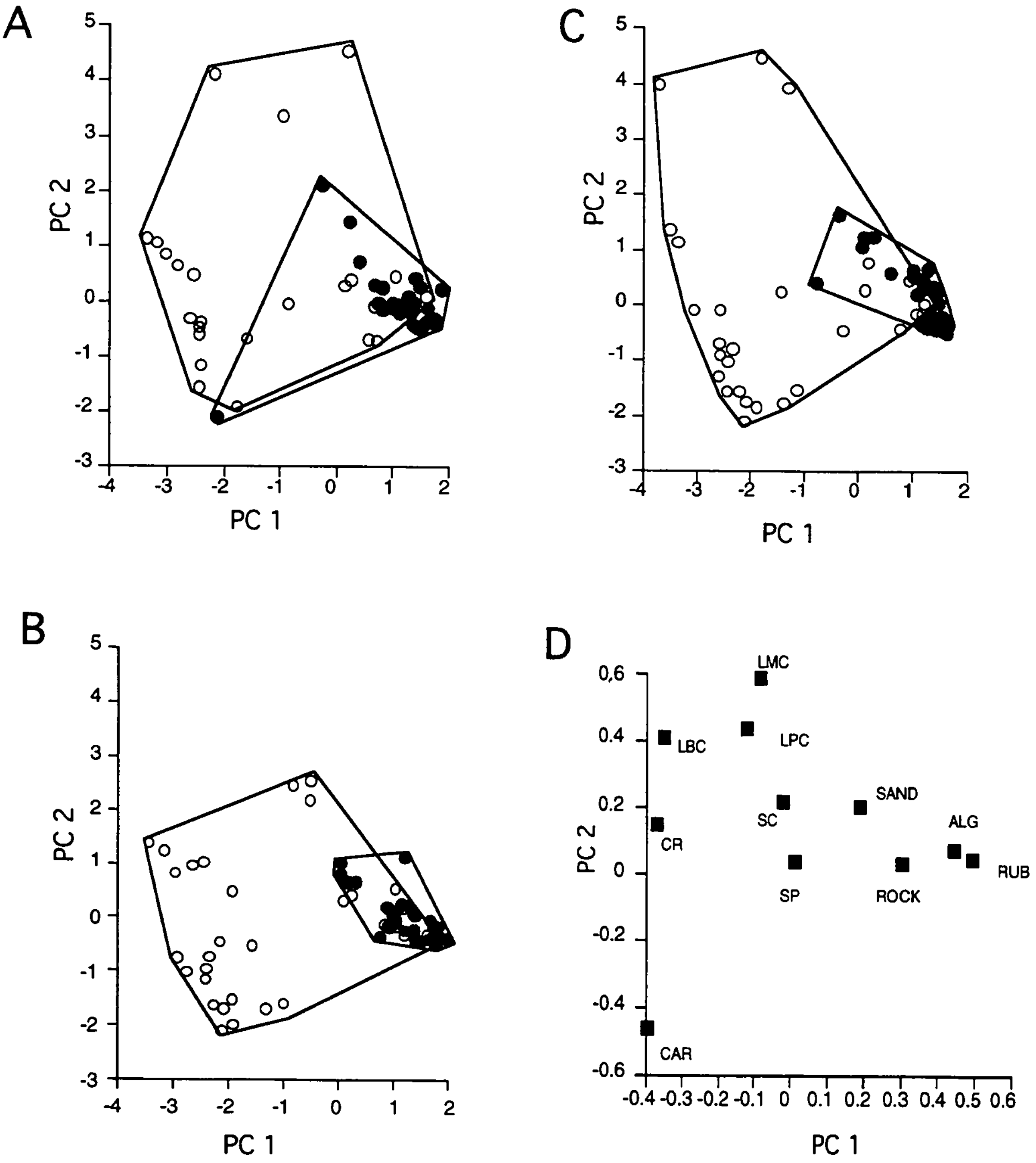


Fig. 2.12. Eigenvalues of sites selected by fish (N = 33, filled symbols), versus randomly selected sites (N = 33, open symbols) at three spatial scales. The most divergent values for each group are connected to indicate habitat space relative to axes. A: Eigenvalues at 1 x 1 m scale, B: Eigenvalues at 2 x 2 m scale, C: Eigenvalues at 5 x 5 m scale, D: Eigenvalues of habitats. All values plotted against PC 1 (25.5 % of variance) and PC 2 (13.9 % of variance). LBC - live branched coral, LMC - live massive coral, LPC - live plate coral, SPO - sponge, SC - soft coral, CAR - consolidated algae-rubble, CR - consolidated rubble.

Effect of sampling scale

The importance of selecting an appropriate sampling unit to measure fish-habitat associations was emphasised in a study by Roberts and Ormond (1987), in which pomacentrid abundances were strongly correlated with habitat at one scale, but not at another. In the present study, the similar ability among all three grid sizes to discriminate between random and selected sites, (Figure 2.12) indicated that the smallest grid size provided sufficient resolution to distinguish selected sites from random ones. Thus, coral trout probably respond to their environment at a scale of approximately one square metre at the time of settlement. Given the similarity of results from the three grid sizes, a sampling unit of 1 x 1 m should provide the best compromise between precision and effort in future efforts to quantify settlement sites for this species.

Habitat preferences at settlement

Settlement sites were readily differentiated from randomly chosen sites, and had distinct microhabitat attributes as characterised by PCA. Most of the variation in the microhabitat data was described by a relief gradient (PC-1), and recruits were strongly associated with low relief features providing shelter that was at, or very close to the sand bottom. These features, (rubble, algae, rocks) appeared to provide recruits with access to shelter as they ranged in search of prey.

Apparently the quality of shelter offered by these habitats makes them attractive to recruits of a variety of species. Coral trout recruits were often observed foraging with groups of newly settled labrids, scarids, and siganids - taxa with broad differences in feeding morphology.

Although new recruits were strongly correlated with habitats offering shelter along PC-1, they settled at sites which had intermediate values along PC-2. This axis describes a continuum between living and non-living habitats, and therefore is also likely to describe variation in the biomass of recruits of other fish species potentially available as prey items (Bell and Galzin 1984). Coral trout undergo a pronounced shift towards piscivory during early growth (Chapter 3), and newly recruited fish form a significant part of their diet after approximately 60 mm SL. The lack of a positive correlation between these presumably food-rich habitats and settlement suggests that selected sites represent a balance between the conflicting demands of energy intake and predator avoidance. Predation pressure has been shown to mediate habitat use by restricting young (vulnerable) fish to patches of protective cover, which may offer less suitable prey resources than alternate habitats. Jones (1984) found that juveniles of a temperate labrid <u>Pseudolabrus celidotus</u> were aggregated as a result of their dependence on shelter (algae), in spite of greater prey abundances on adjacent rock flats Similarly, although the need for shelter provided by the rubble substratum seemed to be of primary importance for coral trout recruits, the availability of food did not appear to strongly influence the choice of recruitment sites.

The smallest recruits encountered in this study, (25 mm) had probably settled less than one week prior to capture. Masuma et al. (1993), reported that coral trout reared during an aquaculture study were morphologically and behaviourally similar, at 20 mm SL, to benthic individuals. In the present study, mean size at settlement was determined as 17.9 (se = 0.15) mm (Chapter 5). These estimates suggest that most recruits used in the nested grid study were captured shortly after settlement. As with many coral reef fish, Plectropomus leopardus recruits are strongly site-attached and initially inhabit very small home ranges. It is therefore likely that the microhabitats occupied by captured fish were the exact ones chosen at the time of settlement.

Narrow microhabitat preferences at settlement have been documented for a number of reef species. Williams (1980) found that two species of pomacentrids recruited to specific sections of patch reefs during three successive years. Sale et al. (1984) showed that sites occupied by eight species of newly settled reef fish could be discriminated from random sites in all but one case, although sites selected by individual species were not significantly different from each other. Ross and Moser (1995) presented evidence that pre-settlement gag, (Mycteroperca microlepis), an epinepheline serranid inhabiting coastal Atlantic waters, selectively recruited to sea-grass habitats. These habitats served as temporary "nurseries" from which they dispersed into surrounding habitats. Similarly, sites occupied by coral trout at settlement may represent centres of dispersal to other areas of the reef.

Broad-scale distribution patterns

Newly settled coral trout were distributed unevenly around Green Reef, and numbers were positively correlated with the presence of rubble substrata at the whole reef scale. Green Reef is classified a fringing/planar reef (Black and Gay 1987), which has periodically been disturbed by natural events including cyclones and Acanthaster outbreaks (Dight et al. 1990). S1 and S2 are located on the exposed south east face, in a section of reef which has received the main impact of several cyclones in the past 30 years (George Craig personal communication). The presence at these sites of extensive mounds of consolidated rubble interspersed with level, rubble-strewn bottom is probably due to these destructive events. Habitat surveys around Green Reef recorded comparatively high amounts of rubble cover at these sites, which also received the highest recruitment during both seasons. These results suggest that distribution patterns of coral trout recruits may be the result of active selection of broad-scale regions of habitat, which are subsequently modified by post-settlement events such as predation and relocation.

A number of alternate explanations could also account for the uneven distribution of recruits around Green Reef. One suggestion is that recruits may be overlooked in certain habitats. This is unlikely, since sites recording the highest recruit numbers were also the most structurally complex and thus would presumably provide more hiding spaces than alternate sites.

Another possibility, differential delivery of larvae to sites, is suggested by hydrodynamic models predicting low residual displacement on the down stream side of reefs (Black 1993). Green Reef may be influenced by the predominantly southward-flowing East Australian Current (Wolanski and Pickard 1985). Hence, if hydrodynamic trapping does occur behind reefs, the highest concentrations of pre-settlement fish should be found at sites on the south edge of Green Reef. Indeed, the highest abundances of recruits were found at S1 and S2, both of which are located close to the south east corner of the reef. However, both light trap samples and visual censuses indicated that recruitment does occur at upstream sites, albeit at lower levels. Thus, models of distribution based solely on hydrographic features cannot account for the uneven distribution patterns seen among Green Reef sites.

Active selection of specific habitats assumes that larvae possess the sensory and behavioural capabilities necessary to evaluate the substratum before settling. Observations of such behaviour is available from both field (Sale et al. 1980, Eckert 1985) and laboratory studies (Marliave 1977). The finding that recruits occupied specific microhabitats shortly after settlement suggests that coral trout may be capable of identifying gross differences in habitat and reef morphology prior to settlement. Spatial variability in recruitment at Green Reef may therefore be the result of broad-scale selection of regions within the reef, followed by differential movement and mortality at smaller scales. Thus, the most parsimonious explanation of the observed distribution patterns appears to include aspects of both pre-settlement and post-settlement processes.

Effects of recruit density and shelter availability on post-settlement processes

Mean recruit density and mean disappearance rate were both significantly higher at Site A than at Site B. Moreover, recruit density was correlated with disappearance rate at Site A but not at Site B. The lack of a correlation at the latter site suggests that density-dependent effects may vary between habitats. Although it was not possible in this study to separate the effects of mortality and relocation, the sedentary behaviour of recruits after settlement (Chapter 3) suggests that mortality due to predation may have been responsible for the majority of losses. Site B had greater proportional coverage of the sand-rubble substrata, and consequently may have provided new recruits with better access to shelter from predation. Aldenhoven (1986) reported spatial variation in mortality rates for Centropyge bicolor at Lizard Island, and Shulman (1984, 1985) suggested that density-dependent predation on several species of Caribbean fishes varied as a function of the amount of available shelter. In the present study, disappearance rate covaried with recruit density, but this relationship was dependent on the amount of available shelter. Thus, shelter may be a limiting resource for coral trout recruits during periods of high density (i. e., during or shortly after recruitment events).

These results must be interpreted with caution for several reasons. First, the limited scope of this study precludes generalisation about other years and locations. Secondly, in species which exhibit seasonal recruitment, age and density will covary (Victor 1986). Consequently, the apparent correlation between density and mortality at Site A may simply be due to higher mortality rates among smaller fish. Finally, adverse effects associated with the tagging procedure may have increased mortality, thus inflating disappearance rates. However, tagging mortality is likely to be size-specific, and recruits tagged on the two grids were similar in mean size. Therefore, although these estimates probably do not represent absolute mortality rates, they may provide an indication of relative rates of post-settlement processes within different habitats.

Temporal patterns in recruitment

Temporal recruitment patterns showed variation between years, and also between reefs within a year. During 1991 - 1992, the bi-modal pattern at Arlington Reef appeared to be correlated with the lunar cycle, while settlement at Green Reef was relatively continuous and non-periodic. The reason for this difference is not clear, particularly in light of the proximity of the two reefs (about 2 km). Doherty et al. (1992) reported that light traps consistently collected higher numbers of pre-settlement coral trout at Arlington Reef compared to Green Reef. They suggested that the larger size of Arlington, and its upstream position with regard to prevailing currents may result in hydrodynamic shadowing of Green Reef. Thus, in 1991 - 1992 Green Reef may have received only a subset of the larvae eventually settling on Arlington. Recruitment at Green Reef during both 1993 - 1994 and 1994 - 1995 showed that most recruitment occurred around the new moon in November, although there appeared to be an additional settlement event during the December 1993 new moon.

Weekly recruitment surveys also indicated a peak in recruitment during the 1993 - 1994 season, which was coincident between both study sites . As these recruits had a mean SL of approximately 43 mm, they had probably settled during the previous new moon in November. These older recruits probably represent members of the November recruitment pulse reconstructed from back-calulation of settlement dates (Fig. 2.8).

Distributions of 1+ fish

Compared to 0+ fish, spatial distribution of 1+ fish at sites around Green Reef was more dispersed, suggesting that ontogenetic changes in movement may have altered distribution patterns established at settlement. Relatively high numbers of 1+ fish were recorded at S3 during 1994 - 1995, although none were seen there during 1993 - 1994. Furthermore, only one recruit was seen at this site during all surveys combined, suggesting that these older juveniles emigrated from nearby sites, probably S1 and S2. Behavioural observations of 0+ and 1+ fish indicate that older fish spend significantly more time moving, and less time under cover (Chapter 3). This increased mobility of larger fish seems to be due to a decreased need for shelter after the first year rather than to a shift in diet, as a change from a predominantly invertebrate-based diet to piscivory occurs well before entry into the 1+ class, (Chapter 4). Since both types of prey are available within the recruitment area, distributions of older fish would be expected to be more concentrated around the main settlement sites if they were primarily related to the distributions of their major prey items.

Ontogenetic habitat shifts

In addition to ontogenetic changes in movement, juveniles also underwent a pronounced shift in habitat use early in their life. Censuses of a mapped portion of the recruitment area showed that this habitat shift occurred at approximately 60 mm SL, when the initial preference of recruits for sand-rubble habitats changed to an association with high relief features. Similar shifts in habitat use by juvenile serranids have been reported in at least three other studies. Ross and Moser (1995) found that several months after settling on sea-grass beds, gag moved from these relatively low relief habitats into complex habitats such as jetties and pilings. In a study of another Atlantic epinephelid, juvenile (3 - 8 cm) Nassau groupers (Epinephelus striatus) were initially observed in close proximity to the sea bed, but moved into holes in the reef as they grew (Beets and Hixon 1994). This species was also reported to undergo an ontogenetic habitat shift from macroalgal-Porites spp. clumps to patch reefs at approximately 120 mm TL (Eggleston 1995).

Shifts in habitat use during ontogeny may be related to size-specific changes in predation risk and foraging patterns (Mittelbach 1981, Jones 1984, Ebeling and Laur 1985).

Initially, distributions of coral trout juveniles appeared to be highly influenced by size-specific predation, which confined them to patches of sand-rubble substrata. As recruits increase in size, there may be a concomitant decrease in dependence on shelter from predation, allowing them to switch to alternate habitats. Alternatively, growing coral trout may need to shift to habitats which provide a better fit between body size and shelter dimensions. Such “shelter scaling” may enhance survivorship by reducing the access of piscivores, and has been documented for both invertebrates (Caddy 1986, Eggleston et al. 1990) and reef fish (Smith and Tyler 1972, Shulman 1985, Hixon and Beets 1989). In coral trout, the shift to alternate habitats was coincident with other major transitions in juvenile ecology. Changes in movement, behaviour, and diet (Chapters 3, 4) occurred at approximately the same time as the shift to association with high relief features in the environment.

Chapter 3

HOME RANGE, HOMING BEHAVIOUR, AND ACTIVITY PATTERNS OF JUVENILE CORAL TROUT PLECTROPOMUS LEOPARDUS.

3.1 Synopsis

Juvenile coral trout, Plectropomus leopardus, were studied using observations of marked and unmarked individuals, to assess whether ontogenetic changes in behaviour affect their space use patterns. Newly settled fish occupied distinct home ranges which increased in size as they grew. There was little overlap between the areas used by the smallest fish, apparently due to higher levels of aggression between newly settled fish. In contrast, large recruits displayed lower levels of aggression towards conspecifics, and home ranges tended to overlap. Home ranges contained both "core areas" of heavy use, and peripheral regions of infrequent use. Recruits returned to former sites after they had been displaced short distances, but this ability diminished rapidly as displacement distances increased. One-year-old fish occupied much larger areas than new recruits, and behavioural observations indicated that these older fish spent significantly more time swimming between feeding locations.

3.2 INTRODUCTION

A thorough understanding of the ecology of an animal must include knowledge of its use of space, and activity patterns (Reese 1978) Most vertebrates confine their activities and movements to specific areas which provide the essentials of food, shelter, and mates (McNab 1963). These areas are commonly referred to as "home ranges" and have been defined by Burt (1943) as "the area, usually around a home site, over which an animal normally travels." Home ranges typically contain "core areas", representing areas of heaviest regular use (Wilson 1975). Although repeated use of an area provides evidence that a home range exists, such information may be equivocal; critical proof of home range behaviour requires demonstration of preference for one site over a comparable one (Baker 1982). Spenser et al. (1990) have suggested that the definition of home range should be modified to include site-fidelity, i.e., the occupation of an area significantly smaller than the area expected from random movement of an individual. The simplest means of obtaining such information is to perform homing or displacement experiments. Hence, one would expect that if an individual possessed a home range, it might try to return there after it had been displaced (Winter 1977).

Coral reef fish are generally sedentary and strongly site-attached (Ehrlich 1975), conditions which often lead to the formation of home ranges (Sale 1978). Although home range areas have been measured for a variety of demersal reef fish (Sale 1978), most studies have focused on adults, and few have considered the larger, more mobile species (Williams 1991). To date no attempt has been made to quantify home range areas for the newly settled individuals of a large predatory species. However, the finding that newly settled coral trout are strongly associated with specific substrata types (Chapter 2) and remain closely associated with them until several months after settlement suggests that they may maintain distinct home ranges, at least during their initial period of residence on the reef.

The size and shape of home ranges can reveal information concerning underlying factors influencing space use, such as distribution of food and shelter (Bowen 1982). The model relating body size to home range area was first developed by McNab (1963). His study of mammalian home ranges led him to conclude that a positive correlation exists between animal size and home range area, which he attributed to bio-energetic considerations. Sale (1978) plotted home range area versus body size for mammals, birds, and reef fish, and found a similar positive correlation in all three groups. He noted that fish occupied areas at least an order of magnitude smaller than those used by similarly sized terrestrial vertebrates, and suggested that additional factors besides availability of food may be responsible for this disparity.

In addition to energetic considerations, behaviour is thought to be a primary factor mediating change in space use (Maza et al. 1973). Patterns of adult fish distribution may be strongly influenced by the spacing behaviour of juveniles during recruitment (Shapiro 1991). After settling within specific microhabitats, juveniles may switch to alternate habitats as they grow, with resultant ontogenetic changes in social behaviour (Helfman et al. 1982). For example, juvenile fish often exhibit higher levels of site-defence than older fish (Ehrlich 1975, Helfman 1978; Leum and Choat 1980, Jones 1984). This behaviour often leads to formation of non-overlapping home ranges, which may be maintained either through actual defence (attacking or chasing rivals) or identifying acts (displays)(Brown and Orians 1970). Hence, one would expect characteristics of an individual's home range to vary with ontogenetic changes in behaviour.

This study addresses the following questions:

1) Are juvenile coral trout site-attached? (i.e. will they return to specific sites after being displaced)?

2) Do juvenile coral trout inhabit home ranges? If so, is there a correlation between the size of a fish and it's home range?

3) Are distributions of juveniles influenced by ontogenetic changes in behaviour such as aggression or foraging?

3.3 MATERIALS AND METHODS

3.3.1 Study site

Observations of juvenile coral trout were made during the recruitment season (November, December, and January), from 1993 - 1995. During 1993 - 1994, home range areas were quantified, homing and persistence experiments were conducted, and behavioural observations were made for 1+ and 0+ juveniles. During 1994 - 1995, time stratified behavioural observations were made.

The study site measured 600 x 400 m, and was subdivided into six contiguous 200 m^2 units, each marked at the corners with buoys (Fig. 2.1). Inside this larger section, 2 smaller areas designated Site A and Site B were gridded and mapped (Chapter 2). Site A was primarily used to quantify home range areas. Fish at both sites were used in an experiment investigating homing ability, and also to quantify differences in the extent of home range overlap between individuals.

3.3.2 Marking of juveniles

With the exception of behavioural observations, all fish used in this study were captured with fence nets, measured to the nearest mm, and marked with a heat branding tool (Chapter 2). During the first year, individuals were branded at the field station and returned to the capture site within 24 hours. In the second year, fish were marked using a portable tool in a boat, and were returned to the capture site within 10 minutes of branding. The size frequency distribution of juveniles captured during the periods of this study was found to be strongly bi-modal (Chapter 2). One cohort ranged in size from 25 mm to 105 mm and were considered to represent 0+ fish, while the other ranged in size from 140 mm to 200 mm and were classified as 1+ fish. Only recruits > 40 mm were branded. Intra-cohort comparisons of 0+ individuals were facilitated by dividing the class roughly in half: 25 - 60 mm SL fish were considered "small recruits" and 61 - 102 mm SL fish were designated "large recruits". These two size classes of 0+ fish were used in all behavioural and home range studies. Underwater visual censuses were conducted as described in Chapter 2.

3.3.3 Calculation of home range area

Home range area was determined by connecting the extreme outermost position points of individuals observed at Site A, thus circumscribing the space used by each fish. This procedure produced a "minimum convex polygon" (MCP) by forming the smallest possible polygon which contains all points (Schoener 1981). Home range area is sensitive to the number of observations (Odum and Kuenzler 1955), which necessitates determination of the minimum number of sightings required to establish an area. Consequently, an observation - area curve (Odum and Kuenzler 1955) was compiled for each fish, showing the cumulative increase in home range area with numbers of observations. The number beyond which each additional observation produced less than a 1 per cent increase in area was determined, and home ranges were calculated at this level. During the homing experiment (see below), areas used by fish before and after translocation were compared. Since it was not necessary to quantify the exact areas used by these fish, only to compare areas at an equivalent number of resightings, a level of seven observations was selected a priori at which to make comparisons.

3.3.4 Parameters of the home range

An index of linearity (IL) was calculated by dividing the maximum length of the home range by the maximum width (Ables 1969).

Values approaching one indicate a symmetrical (circular) home range, while values > 1 correspond to asymmetrical home ranges (Spencer et al. 1990).

The centre of activity (COA) was determined for each individual according to the formula: COA = x/y, where x is the mean of all x coordinates, and y is the mean of all y coordinates for all observations of an individual (Ables 1969). The COA is not necessarily a site of biological importance, but is useful in calculating other characteristics of a home range (Hayne 1949).

Activity radii (AR), were calculated in order to provide an indication of movement within the home range (Cahoun and Casby 1958). AR values represent distance from the COA:

$$AR = [(x_i - x)^2 + (y_i - y)^2]^{1/2}$$

where x and y are the coordinates of the COA, and x_i and y_i are the coordinates of each observation. Values less than the length of the home range indicate disproportionate use of the core area or site fidelity (Morrissey and Gruber 1993).

The frequency distributions of activity radii from the COA were determined for both size classes (Ables 1969; Winter 1977). These distributions were analysed for G1 (the moment coefficient of skewness) and G2 (the moment coefficient of kurtosis). Negative kurtosis is associated with clumped distributions within the home range, and positive skewness is associated with observations concentrated near the COA (Odum and Kuenzler 1955; Ables 1969).

In order to establish the degree of overlap between two activity spaces, an index of reuse (IOR) (McKibben and Nelson 1986; Morrissey and Gruber 1993) was calculated:

IOR = [OV(A1 + A2)]/ (A1 + A2). [OV(A1 + A2)] represents the area of overlap between two spaces, and (A1 + A2) is the combined area of both home ranges. Values range from 0 to 1, with one indicating complete overlap between the areas and a value of zero describing mutually exclusive areas.

3.3.5 Home range of 1+ fish

Movement patterns for one year old fish were estimated for juveniles captured within the 600 x 400 m area. Determination of home ranges for 1+ fish was complicated by the greater range of movements of large fish relative to recruits. To provide an estimate of home range for this size class, and to facilitate comparisons between 1+ and 0+ fish, an alternate method was used. Three nested contours, 20 m, 40 m, and 60 m in radius were marked around the capture point of each 1+ individual, using coloured fish floats to indicate radii distances. After fish were branded and released at the capture point, daily searches were made within each perimeter. The positions of fish sightings were recorded, and the percent of observations within each range (i. e. between perimeters) was calculated. For example, if 10 of 30 fish were resighted within a 40 m radius, the home range estimate would be 33.3% of observations within an area of $\pi(40)^2$m (Mathews 1990). To compare the home range estimates of 1+ and 0+ fish, the number of 0+ fish resighted within 20 m, 40 m, and 60 m of their release points during daily censuses at Site A were tallied. Estimates for 0+ and 1+ fish were compared for an equivalent number of search days, and chi-square tests were used to compare the proportion of home range observations within each radius for the two size classes.

3.3.6 Persistence

In order to examine the extent of site-fidelity in juvenile coral trout, two related questions were asked. First, if juveniles are transplanted to a site, will they remain there? Second, if juveniles do not remain after translocation, to what degree are they able to relocate to former home ranges?

To answer the first question, in 1992 - 1993 two patches of habitat commonly used by juveniles were located within the study site (Fig. 2.1). The first site was labelled the CRM site, and comprised an area of large (> 50 m^2) consolidated rubble mounds separated by narrow sand channels. The second site was designated the SR site, and consisted of a relatively uniform plain of rubble-strewn sand bottom, interspersed with live coral heads. A central buoy indicated the position of each patch, and radii of 30 and 100 meters from the buoys were measured and marked using coloured fish floats. 0+ fish (n = 34), and 1+ fish (n = 62) were captured within both boundaries, then measured and branded. Individuals caught within the 30 m radius were returned to the exact point of capture. Fish collected between the 30 and 100 m perimeters were placed in opaque bags and were transported individually to the central buoys and released. Daily surveys were conducted within the

30 meter perimeter at each site to assess the persistence of the two age classes on each habitat. Fish were considered to persist if they were present within the 30 meter contour after five days.

3.3.7 Homing

In order to assess whether newly settled fish are capable of homing to former sites after displacement, another experiment was conducted within Sites A and B during 1993 - 1994. Nine recruits from each size class (small and large) were captured, marked and released at their capture point within each site, as described above. The positions of fish were recorded during daily censuses, until seven observations per fish were accumulated, following which they were recaptured and assigned to three treatment groups.

1) Control: fish were released at the original point of capture after being retained within a dive bag for 10 - 20 minutes.

2) Displaced 20 meters: fish were placed in a dive bag, moved 20 meters from the recapture point in a randomly selected direction, and released.

3) Displaced 40 meters: fish were placed in a dive bag, moved 40 meters from the recapture point in a randomly selected direction, and released.

Individuals were allowed to adjust to their new surroundings for three days, then censuses were resumed. When an additional seven resightings were made, the areas occupied before and after treatment were transferred to an X-Y coordinate system, and the amount of overlap was calculated as described above. Mean Index of Reuse (IOR) values were determined for each treatment group (n = three fish per treatment group). Fish were considered to have homed if mean IOR values were significantly different from zero (Student's t-test). The amount of overlap between the two areas was tested with analysis of variance, using site, size class, and treatment as fixed factors, and area of overlap as the response variable. ANOVA models were used according to procedures outlined by Underwood (1981). Assumptions of normality and homogeneity of variances were met by the data (Cochran's test). Differences among means were detected using Tukey's multiple comparison test, as recommended by Day and Quinn (1989).

3.3.8 Behavioural observations

Time budgets for 0+ and 1+ fish were compiled during fifteen minute observation periods, conducted at randomly selected times and locations within the study site. Approximately two metres was maintained between the observer and the focal fish, and behaviour appeared unaffected by observer presence. Observation periods were timed with an electronic stopwatch.

Instantaneous sampling (Altmann, 1974) was used to assign behaviour to one of six categories at the start of each minute. Categories were:

1) Stationary - remaining motionless while perched on a rock, or hovering motionless in the water column.

2) Moving - swimming between one point and the next (head not oriented towards substratum), with no clear function other than a change of location; movement to shelter,

3) Under cover - remaining motionless in caves, holes, or under overhanging coral.

4) Foraging/feeding - searching for prey (head oriented towards the substratum while moving slowly over the bottom), striking at prey, feeding.

5) Intraspecific interaction - agonistic encounters between two juveniles: typical behaviour included lateral displays, frontal displays (yawns), chasing, and attacks.

6) Interspecific interaction - all encounters with other species, including cleaning behaviour.

Later, time-stratified observations were made on 0+ fish, which were divided into the two size classes. Observations were stratified into three time periods: 0600 - 1000 hrs, 1000 - 1400 hrs, and 1400 - 1800 hrs, and behaviour was assigned to categories and sampled as described above.

3.4 RESULTS

3.4.1 Effects of branding

No adverse effects were observed to result from the branding technique; both aquarium-reared fish and field specimens appeared to behave normally after marking, (i. e. captive individuals fed well, and there were no differences between branded and unbranded field specimens in intra - or inter-specific behaviour).

3.4.2 Home range

A total of 102 0+ fish were marked; 67 at Site A, and 35 at Site B. Fifty eight fish were resighted one or more times at Site A (mean number of resightings = 6.8, range = 1 - 17). There were 401 resightings of marked fish, and 8 additional sightings of unmarked fish (i. e. fish not captured) (Fig. 3.1).

On average, home range measured 14.13 m x 9.88 m (Table 3.1). A plot of cumulative percent home range area against number of resightings (Fig. 3.2) indicated that increase in area was less than 1 percent for fish seen twelve or more times, which allowed for unbiased estimation of home range areas at this level of sampling. A total of 15 individuals met these criteria; individuals seen on fewer occasions may have suffered

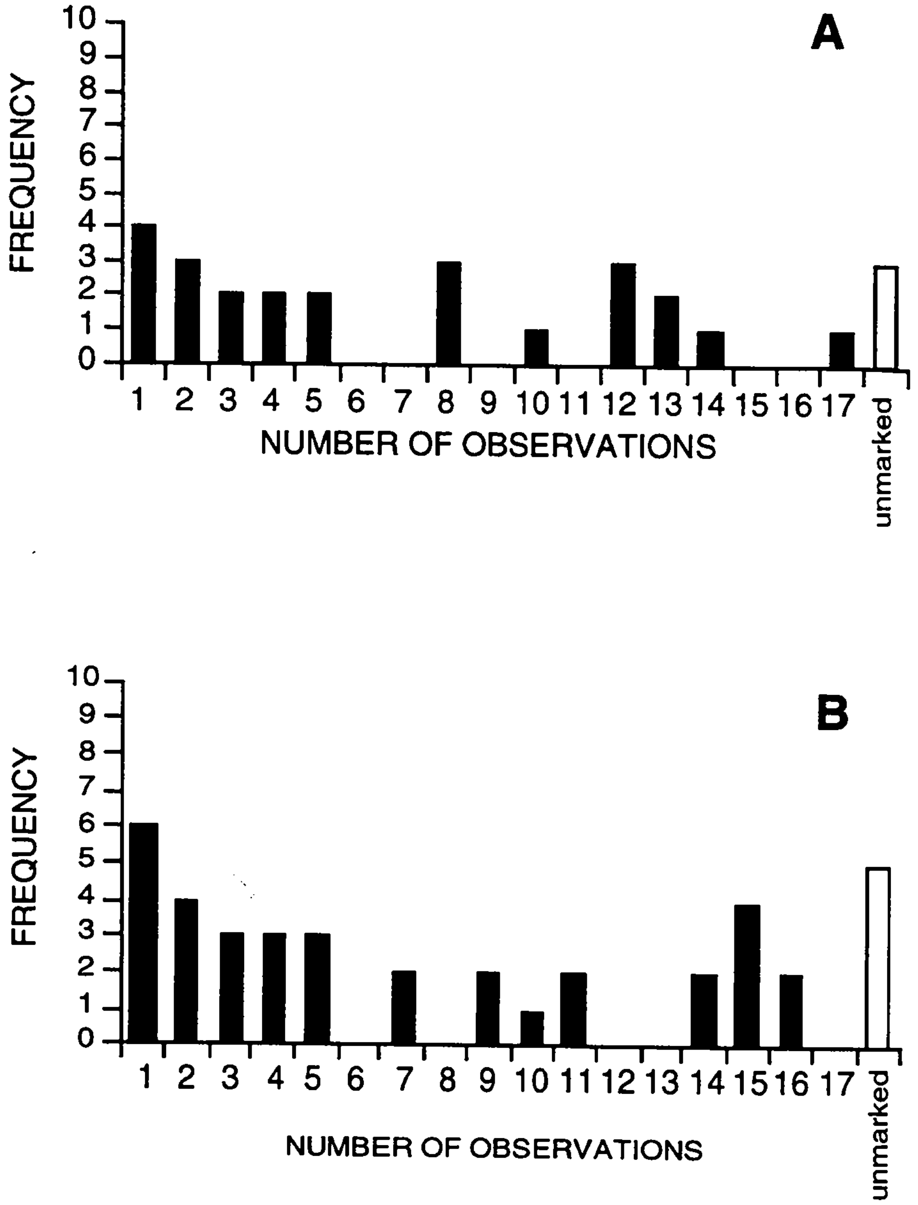


FIG.3.1 FREQUENCIES OF OBSERVATIONS OF MARKED RECRUITS SEEN DURING DAILY CENSUSES OF SITE A. **A:** NEW RECRUITS. **B:** LARGE RECRUITS.

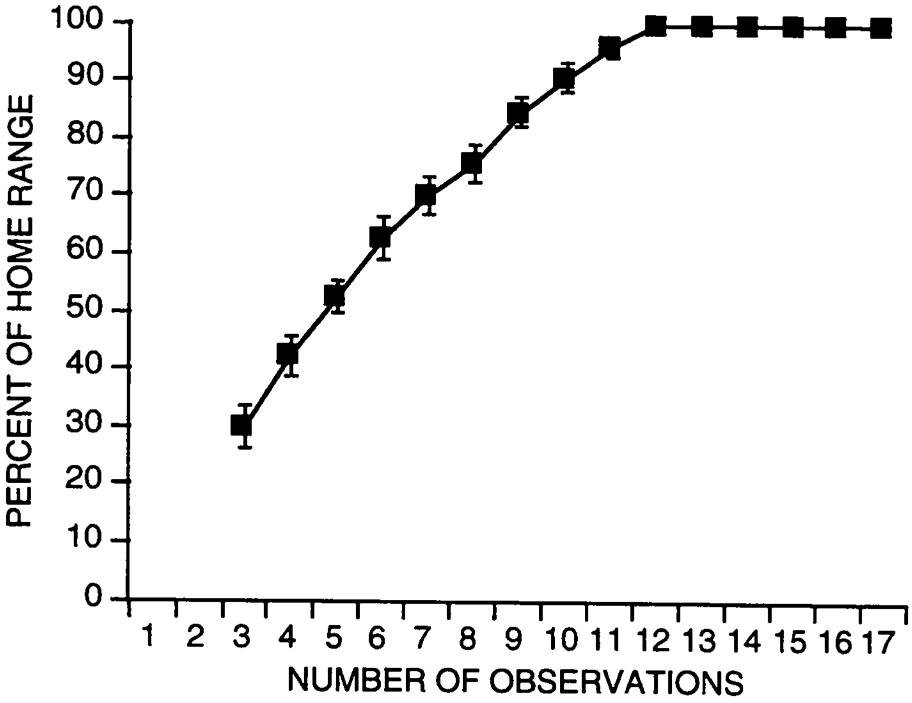


FIG. 3.2. MEAN (+/-SE) CUMULATIVE INCREASE FOR RECRUITS SEEN TWELVE OR MORE TIMES. (N = 15)

mortality, or alternatively, number of observations may have been truncated when the study concluded.

Minimum Convex Polygon (MCP) estimates averaged 84.2 ± 10.3 m^2 (range = 22.4 - 156.5 m^2, n = 15). A comparison of area of home range with standard length, (Fig. 3.3) yielded a significant positive correlation (linear regression, df = 14, $r^2 = 0.70$, $p < 0.0001$). A plot of MCP's relative to habitat features (Fig. 2.6) showed that home ranges of large recruits tended to overlap, and were often centred on prominent features (e.g. coral heads, rubble mounds) The mean index of linearity was 1.5, which did not significantly differ from that of a symmetrical home range (t = 0.15, $P > 0.5$).

Mean AR for all recruits seen twelve or more times was 4.13 m. Mean AR for small fish (3.55 m) was significantly different from the mean for large recruits (4.4 m; t = -2.2, n = 15, $p < 0.05$). Plots of the frequency distributions of activity radii for small recruits and large recruits showed that both distributions were significantly platykurtic and skewed to the right (Fig. 3.4).

A total of 27 1+ fish were marked during 1993 - 1994. Of these, 15 fish were resighted at least once, and there were 25 total resightings. Numbers of fish resighted within 20 m, 40 m, and 60 m were compared to numbers of 0+ fish resighted within these radii at Site A (Table 3.2). Contingency table

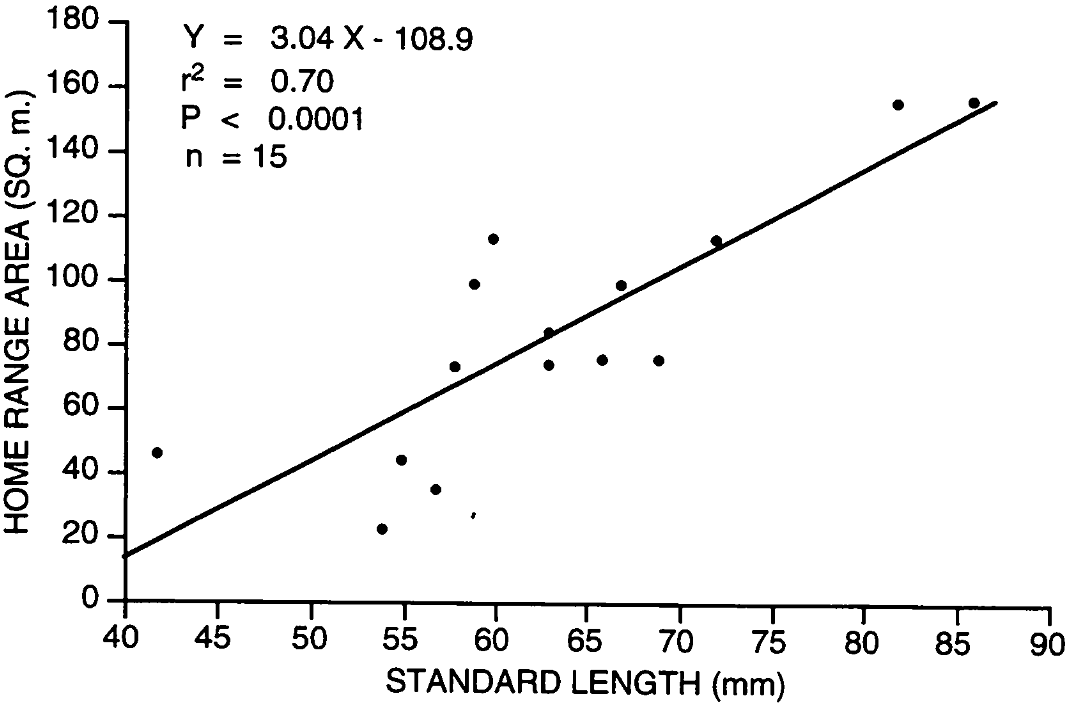


FIG. 3.3. RELATIONSHIP BETWEEN STANDARD LENGTH AND HOME RANGE AREA FOR 15 0+ CORAL TROUT.

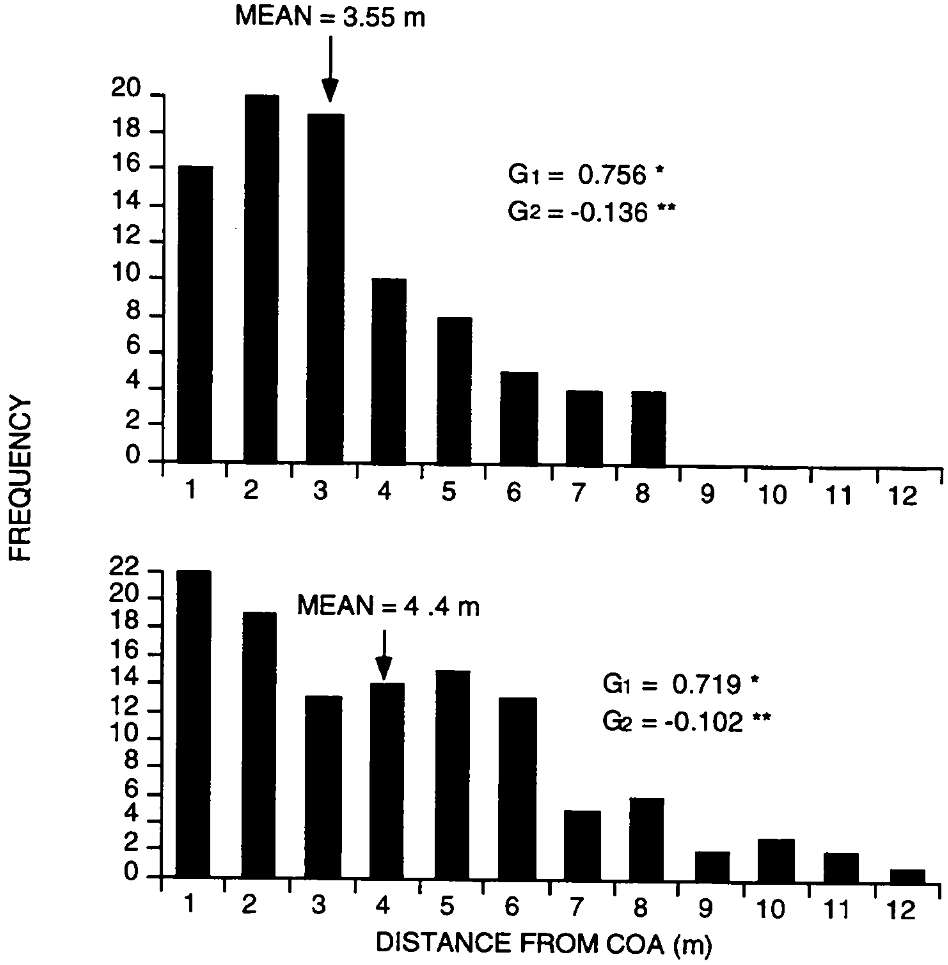


FIG. 3.4. FREQUENCY DISTRIBUTIONS OF ACTIVITY RADII (AR) FOR RECRUITS SEEN 12 OR MORE TIMES. **A:** NEW RECRUITS. **B:** LARGE RECRUITS. G1 = MOMENT COEFFICIENT OF SKEWNESS. G2 = MOMENT COEFFICIENT OF KURTOSIS.
* $P < 0.005$, ** $P < 0.001$.

analysis indicated that frequencies of 0+ and 1+ fish resighted within the three radii differed significantly ($X^2 = 258.5$, df = 2, $p < 0.0001$).

TABLE 3.2 Frequency of 0+ and 1+ fish resighted within three distances from capture point. Positions of 0+ fish relative to capture points were established by overlaying radii on a scale position map and tallying numbers of observations within each radius.

	1+ (n = 25)		0+ (n = 409)	
distance from capt. pt.	freq.	%	freq.	%
0 - 20 m	5	20	360	88
20 - 40 m	6	24	38	9
40 - 60 m	14	56	11	3

3.4.3 Persistence

Of the 96 fish tagged, 37 were resighted at least once, and there were 57 total resightings (Table 3.3). 0+ fish tended to persist on consolidated rubble mounds, and there was no significant difference in persistence between translocated fish and fish released at their original location ($X^2 = 0.75$, NS). However, there was a significant difference between the translocated and non-translocated groups on the sand/rubble habitat ($X^2 = 6.11$, $p < 0.05$): fish persisted when released at their capture points on the sand/rubble habitat but they seldom remained when translocated onto this habitat. In contrast, 1+ fish showed little inclination to remain on either habitat, and the tendency to disperse was not influenced by whether they were translocated or were released at their capture point (CRM: $X^2 = 0.12$, NS; SR: $X^2 = 0.53$, NS).

TABLE 3.3. Numbers of 0+ and 1+ fish persisting on two habitats: SR = sand/rubble, CRM = consolidated rubble mound. Fish were either released at the capture point or translocated to a central location within each habitat. Numbers in parentheses are numbers of fish persisting within a 30 m radius after 5 days.

Habitat	SR		CRM	
Treatment	released at capture pt.	translocated	released at capture pt.	translocated
0+	7(5)	9 (1)	10(7)	8(4)
1+	6(2)	16 (3)	12 (2)	28(6)

3.4.4. Homing

During 1993 - 1994, a total of 36 recruits were marked at Site A and Site B, and used in the homing experiment. Analysis of variance detected no significant differences between sites with regard to the amount of overlap between areas occupied before and after displacement. Consequently, values for the two sites were pooled. IOR values were significantly different from 0 (i.

e. home ranges showed significant overlap) for both size classes in the control treatment, and for large recruits displaced 20 m (Fig. 3.5). (Table 3.4). Analysis of variance (Table 3.5) showed that both size class and the treatment (distance displaced) had a significant influence on the ability of fish to return to their original home ranges. Furthermore, the interaction between treatment and size class was significant, indicating that homing success was significantly affected by the size of recruits.

TABLE 3.4. Mean (±se) Index Of Reuse (IOR) values for homing experiment (see text). Values are pooled for two sites (n = 6 for each group). Values not significantly different from zero indicate no homing.

	SMALL RECRUITS	LARGE RECRUITS
CONTROL	0.68 ± 0.04, $t = 16.41$, $p < 0.0005$	0.69 ± 0.05, $t = 13.51$, $P < 0.0005$
MOVED 20 m	0.07 ± 0.06, $t = 1.22$, NS	0.50 ± 0.09, $t = 5.85$, $p < 0.0025$
MOVED 40 m	0 ± 0 NS	0.10 ± 0.07, $t = 1.48$, NS

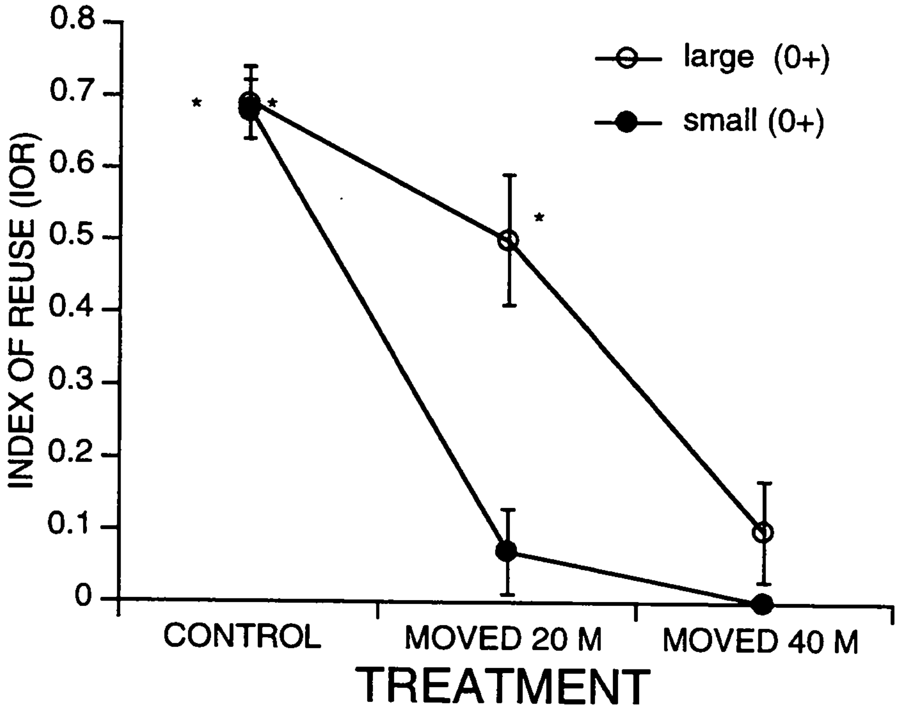


FIG. 3.5. INDEX OF REUSE VALUES (SEE TEXT)
* SIGNIFICANTLY DIFFERENT FROM 0 (P < 0.05).

TABLE 3.5. (A) Results of a two-way ANOVA testing the effects of size class (new, large), and treatment (control, moved 20 m, moved 40 m) on the amount of overlap in areas used by recruits before and after treatment in the homing experiment. (B) Tukey's tests of the mean amount of overlap of areas for the interaction effect of size class* treatment.

A. Source	df	MS	F
Size class	1	52467.0	49.9**
Treatment	2	21270.4	20.2**
Size class*Treat.	2	6443.0	6.1*
Residual	30	1052.0	

**p < 0.0001, * p < 0.001, NS p > 0.05

B. Interaction

treatment	size class	
control	new	large
20 m	new	large
40 m	new	large

size class	treatment		
large	40 m	20 m	control
new	40 m	20 m	control

3.4.5 Home range overlap between neighbouring fish

The activity areas occupied by nine small recruits and nine large recruits at Site B are shown (Fig. 3.6). IOR values for

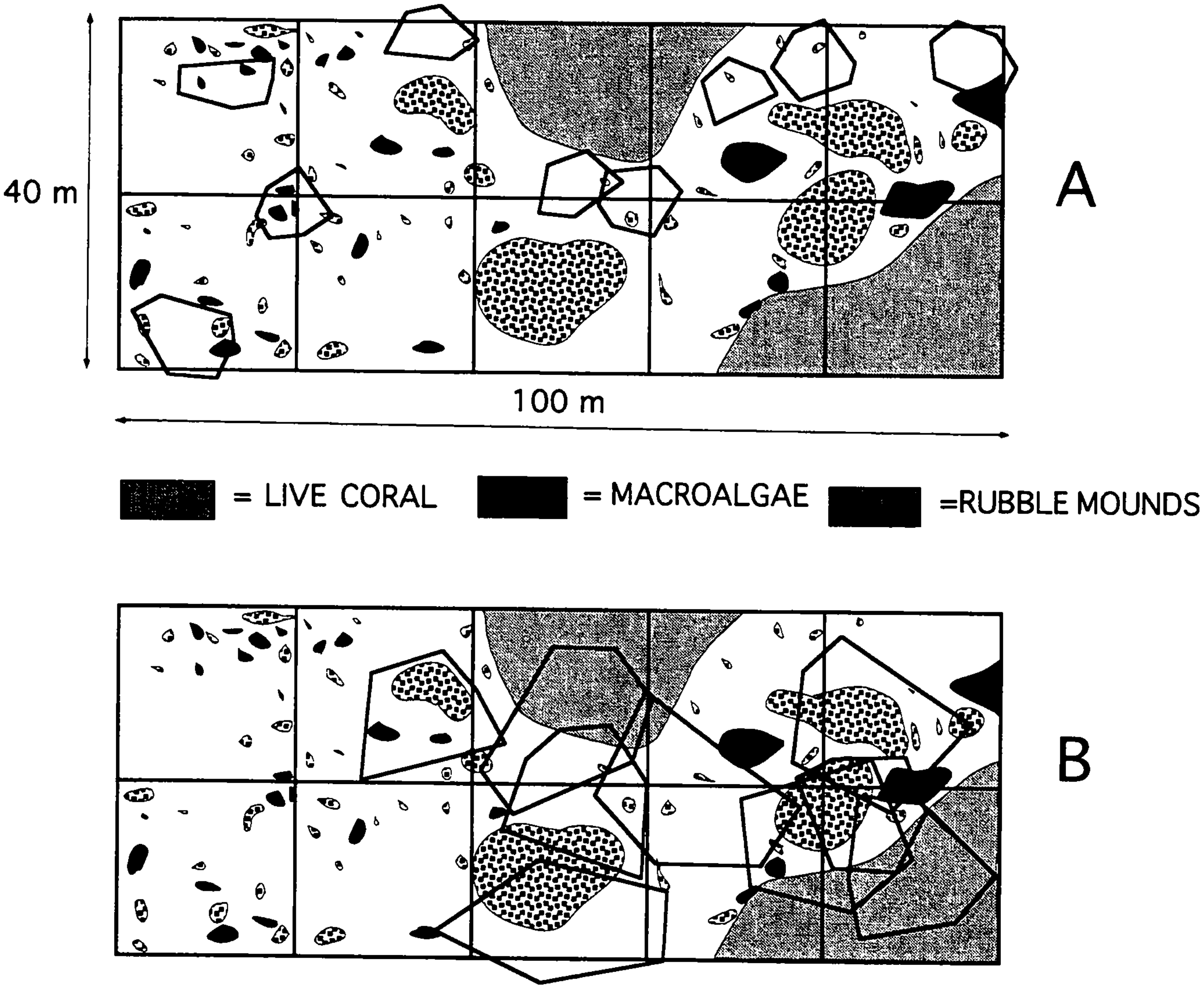


FIG. 3.6. ACTIVITY SPACES OCCUPIED BY RECRUITS WITHIN 40 X100 m GRID, BASED ON 7 OBSERVATIONS EACH. **A:** NEW RECRUITS. **B:** LARGE RECRUITS. UNSHADED AREA = SAND-RUBBLE.

large recruits (mean 0.23 ± 0.05), were significantly different from zero ($t = 4.5$, $p <0.002$), while those for small recruits (mean 0.02 ± 0.01), were not ($t = 1.5$, NS). The mean values for the two groups were also significantly different from each other ($t = 4.0$, $p < 0.005$). Three small recruits had activity spaces which overlapped with those of larger fish, and two of these were completely encompassed by the areas occupied by larger fish. Large recruits were concentrated in the portion of the grid containing high relief features, while smaller fish were more evenly spread over the level sand/rubble bottom.

Home range overlap showed a similar pattern at Site A (Fig. 2.6). IOR values for large recruits (mean 0.41 ± 0.07, $n = 8$), were significantly different from zero ($t = 5.86$, $p < 0.001$), while those for small recruits (mean 0.08 ± 0.04, $n = 7$), were not ($t = 2.0$, NS). The mean values for the two groups were also significantly different from each other ($t = 4.0$, $p < 0.005$).

3.4.6 Behaviour

Mean frequencies of behaviour per 15 minute period were calculated, and Student's t-tests were used to detect differences between size classes. 0+ fish spent significantly more time foraging, and less time moving than 1+ fish (Table 3.6). 1+ fish were most often observed either swimming in a directed fashion, or hovering in the water column, while 0+ fish were usually either stationary or actively searching for food. Closer inspection of the behaviour patterns of 0+ fish using time stratified observations (Table 3.7) showed that small recruits accounted for most of the foraging activity, and also spent less time remaining stationary than large recruits.

TABLE 3.6. Mean (± se) frequency of behaviour per 15 minute observation period, from instantaneous sampling of focal 0+ and 1+ fish. Fish were chosen at random and observed only once. Differences between size classes tested with Student's t-test. ns = no significant difference.

Behaviour	0+ (n = 16)	1+ (n = 16)	t	p
Stationary	5.6 ± 0.97	5.6 ± 0.64	0	n s
Moving	1.1 ± 0.40	5.7 ± 0.58	6.53	$p<0.0001$
Under cover	3.4 ± 0.69	2.4 ± 0.47	-1.19	n s
Foraging	3.2 ± 1.03	0.6 ± 0.3	-2.51	$p<0.05$
Interspecific	1.2 ± 0.34	0.7 ± 0.22	-1.23	n s
Intraspecific	0.5 ± 0.33	0.1 ± 0.06	-1.3	n s

Table 3.7.A. Mean (±se) frequency of behaviour for two size classes of recruits from instantaneous sampling of focal individuals during fifteen minute observation periods. Observations were stratified into three time periods.

A. Behaviour	NEW 0+	LARGE 0+	t	p
0600 - 1000	(N = 16)	(N = 16)		
Stationary	3.9 ± 0.91	9.1 ± 0.95	3.95	$p<0.005$
Moving	0.9 ± 0.35	0.6 ± 0.18	-0.80	n s
Under cover	3.7 ± 1.0	3.6 ± 0.95	-0.09	n s
Foraging	5.6 ± 1.1	1.5 ± 0.45	3.37	$p<0.005$
Interspecific	0.1 ± 0.06	0.1 ± 0.08	0.59	n s
Intraspecific	0.3 ± 0.18	0 ± 0	-1.78	$p<0.05$
1000 - 1400	(N = 16)	(N = 16)		
Stationary	7.5 ± 1.02	8.2 ± 1.18	0.48	n s
Moving	1.4 ± 0.58	1.2 ± 0.32	-0.28	n s
Under cover	3.1 ± 0.93	2.2 ± 0.62	-0.84	n s
Foraging	2.8 ± 0.65	2.1 ± 0.95	0.60	n s
Interspecific	0.2 ± 0.14	1.2 ± 0.25	1.58	n s
Intraspecific	0 ± 0	0 ± 0		n s
1400 - 1800	(N = 16)	(N = 16)		
Stationary	5.8 ± 1.03	7.8 ± 1.08	1.34	n s
Moving	0.9 ± 0.35	0.8 ± 0.36	-0.25	n s
Under cover	1.8 ± 0.53	2.1 ± 0.54	0.33	n s
Foraging	4.2 ± 0.81	3.9 ± 1.02	-0.29	n s
Interspecific	0.5 ± 0.22	0.2 ± 0.14	-0.94	n s
Intraspecific	1.6 ± 0.71	0.1 ± 0.06	-2.11	$p = 0.052$

Pooled	(N = 48)	(N = 48)		
Stationary	5.7 ± 1.03	8.4 ± 1.06	3.09	$p<0.05$
Moving	1.1 ± 0.43	0.9 ± 0.29	-0.69	n s
Under cover	2.9 ± 0.85	2.6 ± 0.73	-0.41	n s
Foraging	4.3 ± 0.98	2.5 ± 0.86	-2.41	$p<0.05$
Interspecific	0.3 ± 0.16	0.5 ± 0.38	1.13	n s
Intraspecific	0.6 ± 0.44	0.0 ± 0.04	-2.34	$p<0.05$

Foraging activity was greatest during morning hours. Recruits often followed multi-specific groups of labrids, scarids, and siganids, striking at small crustaceans and fish displaced by the feeding activities of these schools (Chapter 4). Small recruits also interacted with conspecifics to a greater extent than large recruits, and most interactions took place during morning and afternoon. The majority of interactions occurred along the periphery of home ranges, and generally involved fish of similar sizes. Typical interactions included lateral displays (i. e. orienting parallel to each other), colour changes, yawning (open-mouthed display), and chasing (harassing pursuit, usually lasting < 5 seconds). Encounters were usually followed by the movement of one fish to an adjacent rock or coral, although occasionally both fish remained together.

3.5 DISCUSSION

The results of this study provide evidence that newly settled coral trout occupy specific home ranges, and support McNab's (1963) prediction that home range area will increase in relation to the size of an animal. The ecological importance of these areas was indicated by the tendency of recruits to return to original sites when displaced short distances. Newly settled fish tended to be evenly distributed over flat, relatively uniform bottoms. On the other hand, distributions of larger recruits were aggregated around high relief features, and home ranges tended to overlap. These space-use patterns appeared to be the result of both decreasing levels of intra-cohort aggression and changing foraging behaviour during ontogeny.

Increase in home range area with growth

The first important finding of this study is that coral trout quickly established regular home ranges following recruitment to the reef, and that these areas increased in size as fish grew. Studies investigating ontogenetic changes in the home range areas of fish are relatively few, and have obtained divergent results. Radio-telemetry of small mouth bass Micropterus dolomieu (Todd and Rabeni 1989), and muskellunge Esox masquinongy (Miller and Menzel 1986) failed to find a relationship between size and home range, and a negative correlation was found for bluegills Lepomis microtus (Fish and Savitz 1983). However, the size restriction associated with transmitter implantation has limited most of these studies to larger, mature individuals.

In contrast, a positive relationship between home range area and size has generally been reported when juveniles are included in analyses. For instance, Morrissey and Gruber (1993) demonstrated a significant positive correlation between body length and home range area in juvenile lemon sharks Negaprion brevirostris, as did Jones (1984) for a temperate reef fish Pseudolabrus celidotus, and Leum and Choat (1980) for another cold water species, Cheilodactylus spectabilis. The finding that home range areas of juvenile coral trout also increased with body size, suggests that factors determining the size of these areas may be especially important during early growth.

Compared to newly recruited fish, the estimated home ranges of one year old fish indicated a much greater range of movement. Although the limited number of resightings of these larger fish did not permit measurement of home range areas, comparison of frequencies of resightings within 20, 40, and 60 m of the original capture point indicated a less restricted area of movement relative to newly settled fish. McNab (1968) noted that predators must switch to hunting bigger food items as they increase in size, and consequently must expand home ranges to find sufficient numbers of prey. The much larger range of movement of one year old fish compared to 0+ fish is consistent with his prediction of exponential increase in home range with size.

These extensive home ranges may be related to differences in feeding behaviour between the two size classes. Recruits tended to actively forage early in the day, and were seldom located far from a preferred shelter site (Chapter 4). On the other hand, feeding events in 1+ fish often involved ambush tactics (e.g. strikes at prey from stationary positions). The optimum distance for a consumer to travel is the one which provides the maximum resource yield while minimising risk of predation (Covich 1976). Since vulnerability to predation usually decreases with size in fish (Jones and Johnston 1977), predation pressure may initially restrict recruits to foraging in close proximity to shelter, whereas larger individuals can freely move between feeding areas (Werner and Gilliam 1984). The relatively greater mobility of 1+ fish was evident from comparisons of time budgets, which showed that older fish spent significantly more time moving from one place to another. Thus it appears that strong initial site-attachment of newly settled individuals is the result of their dependence on shelter, and the decreasing need for this resource leads to greater mobility in growing fish.

Persistence

Results of the displacement experiment also indicated decreased site attachment in older fish. 0+ fish released at their original capture points persisted on both sand/rubble and rubble mound habitats. They also remained after translocation to the rubble mound habitat, but not when translocated to the sand/rubble site. In contrast, 1+ fish did not persist on either habitat after displacement, regardless of whether or not they were originally resident there. Similar results were reported from another displacement experiment (Mathews 1990), in which several species of adult rockfish (Sebastes spp.) were displaced between reefs with different characteristics. Rockfish from high relief ("high quality") reefs tended to return there if displaced, but those moved from low relief reefs to high relief reefs usually remained at the high relief reef, suggesting that these habitats were in some way superior. Likewise, the persistence of 0+ coral trout on rubble mounds may reflect preference for this habitat, and fish may lack motivation to leave after displacement there. Although recently settled fish (25 - 50 mm) are strongly associated with the sand/rubble substratum, larger recruits preferred high relief features such as coral heads and consolidated rubble mounds (Chapter 2). As all 0+ fish used in this experiment exceeded 50 mm, their persistence on rubble mounds may be due to a preference for this habitat.

Evidence of site attachment by small recruits is also available from observational data. The low ratio of mean activity radii to mean home range length suggests that recruits rarely approached the perimeters of their activity spaces. Preferential use of core areas is also indicated by measures of skewness and kurtosis for frequency distributions of AR values (Ables 1969). AR distributions of small recruits were significantly skewed to the right, indicating frequent use of central areas, while kurtosis values were significantly negative, indicating clumping (Sokal and Rohlf 1981). Thus the activity spaces of juvenile coral trout appeared to contain heavily used core areas, which presumably contained necessary resources such as shelter or food.

Homing

The importance of these areas to small recruits is indicated by their tendency to return to them when displaced short distances. Large recruits consistently homed to their former areas when displaced 20 m, and were capable of returning after being moved 40 m, although their tendency to home diminished with distance. Smaller recruits showed a similar pattern of decreasing homing performance with translocation distance, albeit at a smaller scale: fish were capable of returning after displacement of 20 m but there were no returns from 40 m translocations.

This pattern may be a consequence of the greater range of movement (higher AR values) of larger recruits. In addition to core areas of intense use, home ranges contain outer areas of infrequent use (Reese 1978), which may represent exploratory excursions to obtain information about alternate habitats, or the presence of conspecifics. Baker (1982) termed these spaces "familiar areas", and hypothesised that they consist of memorised associations between the availability of different resources and the presence of particular landmarks. The familiar area represents the sum of locations visited and remembered during an animal's lifetime, and thus would be expected to increase with age. Therefore, the increased homing performance of larger recruits may be due to their larger familiar areas. Alternatively, displaced fish may fail to return after greater displacements either because the cost of returning is high relative to the benefits offered by the new location, or because habitat quality is suitable at locations encountered during return.

Experimental displacements of fish have generally indicated a strong tendency to home, provided the distance is not too great (Quinn and Dittman 1992). Beets and Hixon (1994) reported adult homing behaviour in two serranids, _Epinephelus_ _striatus_, and _E_. _afer_, in the Virgin Islands. Thirty one tagged individuals were translocated to reefs 140 m away, of which 29 homed to their original reef within 10 days. Studies of adult centrarchids (Parker and Hassler 1959, Messing and Wicker 1986), reported that displaced fish often returned to their place of capture, and that shorter displacements generally resulted in higher proportions of returns and more rapid homing. The evidence indicated that these fish probably had familiar areas well beyond the limits of home ranges measured by the authors, which allowed them to relocate their original areas.

Relatively few studies have examined homing behaviour in juvenile fish. Craik (1981) investigated ontogenetic effects on the homing ability of an intertidal cottid, _Oligocottus_ _maculosus_. Home range fidelity and homing success were found to increase during the first two years of life, after which homing success declined markedly. The increase in homing performance in young fish was suggested to result from "memorisation" of spatial cues during this period. These results closely parallel the findings of the present study, in which the distance over which individuals home appeared to be related to size of the familiar area. In contrast, Thompson (1983) found that both juveniles and adults of a small sub-tidal blenny, Fosterygium varium, returned to their original territories after displacement. Furthermore, juveniles consistently homed after displacements of 200 m, despite occupying territories of 1.5 - 2.0 m^2 for only 1 - 2 months prior to translocation.

These extraordinary distances relative to normal movements, and the undiminished homing performance of adult blennies suggests that the homing mechanism used by this species may be fundamentally different from the one used by coral trout. Temperate species inhabiting turbid, wave-dominated environments may rely on auditory cues such as the acoustic signatures of specific beaches and coves to facilitate homing behaviour, whereas tropical species may be more dependent on underwater guideposts.

Intraspecific behaviour

Recruits were more likely than 1+ fish to engage in agonistic behaviour with conspecifics. In order for an animal to be considered territorial, two criteria must be met: 1) animals must establish home ranges, and 2) competitors must be excluded from some part of this range (Brown and Orians 1970). Defence of an area (via advertisement or actual exclusion), is most common between two similarly sized members of the same species, due to the presumed overlap of resource use (Krebs 1985).

Newly settled coral trout were shown to establish home ranges. The second criterion of Brown and Orians (1970), site defence, is most likely to be manifest as intra-cohort aggression resulting in non-overlap of home ranges. IOR values indicated that little overlap occurred between areas used by small recruits, but considerable overlap was present between those of larger individuals. Home ranges were basically symmetrical, hence they would require less energy per unit space for territorial defence (Ables 1969). Moreover, behavioural observations indicated that small recruits spent proportionally more time engaged in aggressive intraspecific behaviour than large recruits. This aggression often involved identifying acts (i.e. colour changes, displays) which served to maintain separation of home ranges with a minimum of physical contact. Thus, the more dispersed distribution of newly settled fish may be a consequence of an initial tendency toward territoriality, which declines as recruits grow.

Unlike small recruits, home ranges of larger recruits tended to overlap, and were often centred on high relief features. Larger fish were often seen together, but rarely displayed aggression towards each other. Leum and Choat (1980) reported a similar pattern in C. spectablis. Small individuals occupied specific feeding and shelter sites, from which they excluded other small conspecifics, whereas larger fish were not aggressive towards each other, and had overlapping feeding areas. In coral trout, the reason for the more exclusive use of space by small recruits is not apparent, but may be a consequence of the more open and evenly distributed foraging areas of smaller fish. Feeding areas of juveniles may be small enough to be economically defendable, but may become too large to be defended as adults (Jones 1984). Alternatively, gregarious behaviour may have selective value for growing fish. Refuging (Hamilton and Watt 1970) has been defined as the social use of space when exclusive use is too costly relative to the resources derived. This behaviour typically exists where food is widely distributed in an area surrounding principle shelter sites (Reese 1978). Similarly, the high relief features within coral trout settlement sites may represent central refugia which are used as bases for foraging activities.

In conclusion, coral trout exhibited a pattern of space utilisation in which newly settled fish were strongly site attached, possibly as a result of their initial dependence on shelter. A consequence of this site attachment was the formation of well defined home ranges, which increased in area as fish grew. Home ranges contained "core areas" of intense utilisation, and outer regions of diminished use. Initially, high levels of intra cohort aggression maintained a relatively uniform spacing of recruits, but distributions became more clumped as growing fish converged on resources.

Chapter 4

SPATIAL AND ONTOGENETIC VARIATION IN THE FEEDING ECOLOGY OF JUVENILE CORAL TROUT

4.1 SYNOPSIS

Diet and behaviour of juvenile coral trout, Plectropomus leopardus, were studied at Green Reef in the central section of the Great Barrier Reef, Australia, in order to describe ontogenetic and diurnal patterns in feeding biology. Diets of newly settled (25-60 mm) recruits consisted mostly of epibenthic crustaceans, while larger juveniles (60-100 mm) were mainly piscivorous. Coral trout of all sizes consumed fish, and most piscine prey were recent recruits to the reef (mean SL 18.9 mm). Diets varied between habitats for large juveniles, but not for small juveniles, with larger fish consuming higher proportions of piscine prey at the main settlement site. Foraging modes and diurnal feeding patterns differed between size classes: larger juveniles typically fed by ambushing prey (usually small fish), while small recruits concentrated feeding activities around morning hours, and mainly foraged by striking at invertebrates associated with rubble substrata. Analysis of disgorged prey items may yield valuable preliminary information about diet, especially when non-destructive sampling is required.

4.2 INTRODUCTION

Coral reef fish often undergo ontogenetic diet shifts (Gerkin 1994). These changes have the potential to profoundly influence growth rates, and thus to regulate the numbers of small fish recruiting to larger size classes. The transition may be especially critical to fish that are piscivorous as adults (Wicker and Johnson 1987, Van Densen 1985), with piscivores rapidly outgrowing non-piscivorous con-specifics (Juanes and Conover 1994, Fitzhugh and Rice 1995). For example, pike-perch (Stizostedion lucioperca) that do not manage to switch from planktivory to piscivory during their first year grow more slowly, and suffer higher mortality than those that become piscivores (Buijse and Houthuijzen 1992). Since piscivores are likely to be gape-limited (Keast 1985), the close relation between mouth size and body size may result in an ontogenetic "bottleneck" in growth during the onset of piscivory.

Coral trout Plectropomus leopardus (Serranidae) are abundant, top-level carnivores inhabiting shallow tropical and sub-tropical seas in the Indo-Pacific area, and represent the most valuable fish exploited by recreational and commercial fisheries on the Great Barrier Reef (Craik 1989, Williams and Russ 1994). Several studies have examined the feeding biology of adults (Choat 1968, Goeden 1974, Kingsford 1992) and have confirmed their highly piscivorous nature. However, similar information is not available for juveniles; thus it is not known at what size coral trout switch to piscivory, or whether the timing of this transition varies spatially.

Newly settled coral trout are initially restricted to foraging within relatively small home ranges, and habitat requirements may confine individuals to specific areas containing suitable shelter characteristics (Chapter 2). Density-dependent processes within these areas may increase competition for food among con-specifics. Growth depensation is often induced through behavioural interactions, with dominant individuals excluding subordinate individuals from food sources (Koebele 1985). Consequently, fish which are able to make a rapid transition to piscivory may be able to transfer some of the energy reserves used in agonistic behaviour into growth.

The primary purpose of this study was to describe variation in diet and feeding activities of newly settled coral trout among size classes, habitats, and diurnal time periods. An ancillary aim was to test the utility of using samples of prey items regurgitated after capture as a non-destructive alternative to gut content analyses.

4.3 MATERIALS AND METHODS

Research was conducted on Green Reef in the central section of the Great Barrier Reef, between November 1994 and January

1995. The study area was located on the exposed south east corner of the reef (Fig. 1). Within this area, two sites separated by approximately 2 kilometres were sampled. These were designated the “Primary” and “Secondary” sites, and were used to assess variation in diet between habitats. For all analyses in this study, fish were divided into two size classes: Small = 25 - 60 millimetres (mm) standard length (SL), and Large = 60 - 100 mm (SL). Recruitment dates back-calculated from otolith lengths (Fig. 2.8B) indicated that settlement was relatively constant during the period of the study; thus no attempt was made to assign size classes to monthly cohorts as was done for the 1993 -1994 collection (Chapter 2). Data collection involved three phases: 1) behavioural observations 2) collection of specimens 3) stomach content analysis.

4.3.1 Behavioural observations

Time budgets for focal 0+ fish were compiled during observation periods conducted at randomly selected locations within both the Primary and Secondary sites. Observations were stratified into three time periods: morning (0600 - 1000 h), midday (1000 - 1400 h), and evening (1400 - 1800 h). The site-attached behaviour of 0+ fish (Chapter 3) assured that individuals could be differentiated on the basis of location, and thus each fish was observed only once. A total of sixteen observation periods were recorded for each combination of fish size and time period. Observation periods lasted fifteen minutes and were timed with an electronic stopwatch. Approximately two metres was maintained between the observer and the focal fish, and behaviour appeared unaffected by observer presence. Instantaneous sampling (Altmann 1974) was used to assign behaviour to one of four non-resting categories at the start of each minute. Categories were:

1) **Moving** - swimming between one point and the next (head not oriented towards substratum), with no clear function other than a change of location; movement to shelter,

2) **Foraging/feeding** - searching for prey (head oriented towards the substratum while moving slowly over the bottom), striking at prey, feeding.

3) **Intra-specific interaction** - agonistic encounters between two juveniles.

4) **Inter-specific interaction** - all encounters with other species, including visits to cleaning stations.

Foraging/feeding behaviour was sub-divided into 4 mutually exclusive feeding modes:

1) **Ambushing** - striking at prey from a stationary position, either concealed or while assuming camouflage coloration.

2) **Picking** - moving over bottom and striking at prey concealed in substratum.

3) **Following** - Hiding in multi-specific schools of fish and striking at prey dislodged by school.

4) **Joint hunting** - Hunting for food with another fish.

To determine how foraging activity varied according to time of day and size class, a two-way fixed factor ANOVA model was used, with frequency of foraging event per observation period as the response variable, and time of day, and size class as factors. ANOVA models were used according to procedures outlined by Underwood (1981). Assumptions of normality and homogeneity of variances were met by the data (Cochran's test). Differences among means were detected using Tukey's multiple comparison test, as recommended by Day and Quinn (1989).

4.3.2 Specimen collection

Specimens were collected using mono-filament fence nets, and placed in clear 500 ml. plastic jars. Additional specimens were collected to complement fish used in behavioural observations, making a total of 216 recruits (123 small, 93 large). Stress associated with capture and handling often induced fish to disgorge prey items, which were retained for later analysis. No other means (e. g. gastric lavage, emetics) were used to induce regurgitation. Specimens were transported to the field station and preserved by freezing. All specimens were measured to the nearest mm SL. A subsample (n = 92) was eviscerated, and gutted weight was recorded to the nearest 0.01 gram (g).

4.3.3 Stomach content analysis

Stomachs were removed, opened, and the contents placed in a petri dish marked with a grid of 1 mm squares. Prey items were sorted under a low powered binocular microscope, and items were separated by general taxonomic group. General categories were used because not all items were identifiable to species; thus identification of some prey items and not others could bias results. Volume of each item was measured by separating prey into like groups on the petri dish, flattening them to a uniform height (approximately 1 mm), and counting the number of squares under each group. This technique worked well for crustaceans and small well-digested fish, but was problematic for larger prey. These items were first macerated with a scalpel, after which the mass could be easily reduced to 1 mm thickness. Area and volume were considered directly proportional.

Dietary parameters were assessed according to Hyslop (1980). Percent volume (%V) for a prey item was calculated as the proportion of the total prey volume. Percent frequency of occurrence (%F) was the proportional occurrence of a prey item relative to the frequency of occurrence of all prey types. Percent number (%N) equalled the total number of times an item occurred divided by the total number of all items.

An Index of Relative Importance (IRI) was calculated to estimate the contribution of each prey item to the diet (Pinkas et al. 1971): **IRI = (%N + %V) x %F.** This index is considered sensitive to differences in prey abundances and proportions, because it integrates measurements of numbers, volume, and frequency of occurrence. For calculation of IRI values, regurgitated items and stomach contents were pooled, and only fish which had consumed prey were used in analyses.

Diets of recruits were compared for four groups, representing orthogonal combinations of size class and site. Differences in diet between these four groups were analysed using the percent similarity index (PSI)(Whittaker, 1952): $\mathrm{PSI} = 1 - 0.5 \Sigma\ pih - pjh$,

where pi and pj = the proportions by IRI of each prey type (h) in the diets of groups i and j. Percent IRI values were used in the calculation of proportion, p. Values of 0 indicate no overlap and values of 1 indicate complete overlap. PSI values above 0.6 were considered as biologically important overlap (Zaret and Rand, 1971; Wallace, 1981). In order to determine if an adequate sample size had been analysed, cumulative number of prey types was plotted against stomachs examined. The resulting curve was asymptotic, indicating adequate sample size (Cox 1985).

Gut fullness was assessed according to the protocols of Cailliet (1976) for the study of the effects of diurnal variation in feeding. The extent of feeding was estimated using a fullness index subjectively scored as: (A = empty, B = one third full, C = two thirds full, D = full), and a digestion state index (A = well-digested, B = medium digestion, C = some digestion, and D = no digestion). A 4 X 4 matrix of gut fullness by digestive state was constructed with feeding states of: (1) not full or recent, (2) full but not recent, (3) recent but not full, and (4) full and recent. Gut fullness of specimens which had disgorged prey were estimated by comparing the volume of regurgitated items with the remainder of stomach contents, and extrapolating fullness. Regurgitated prey items were compared to total prey consumed using %N of each prey group.

4.4 RESULTS

4.4.1 Behavioural patterns

The amount of time devoted to foraging varied significantly according to size class but not to time of day (Table 4.1A). Analysis of variance revealed that the size class effect was due to significantly higher foraging activity by small recruits (Table 4.1B), which occurred mainly during morning hours (Fig. 4.1A, 4.1B). Small recruits spent significantly more time foraging than large recruits between 0600 and 1000 ($t = 3.37$, $p < 0.005$), but differences during other periods were not statistically significant.

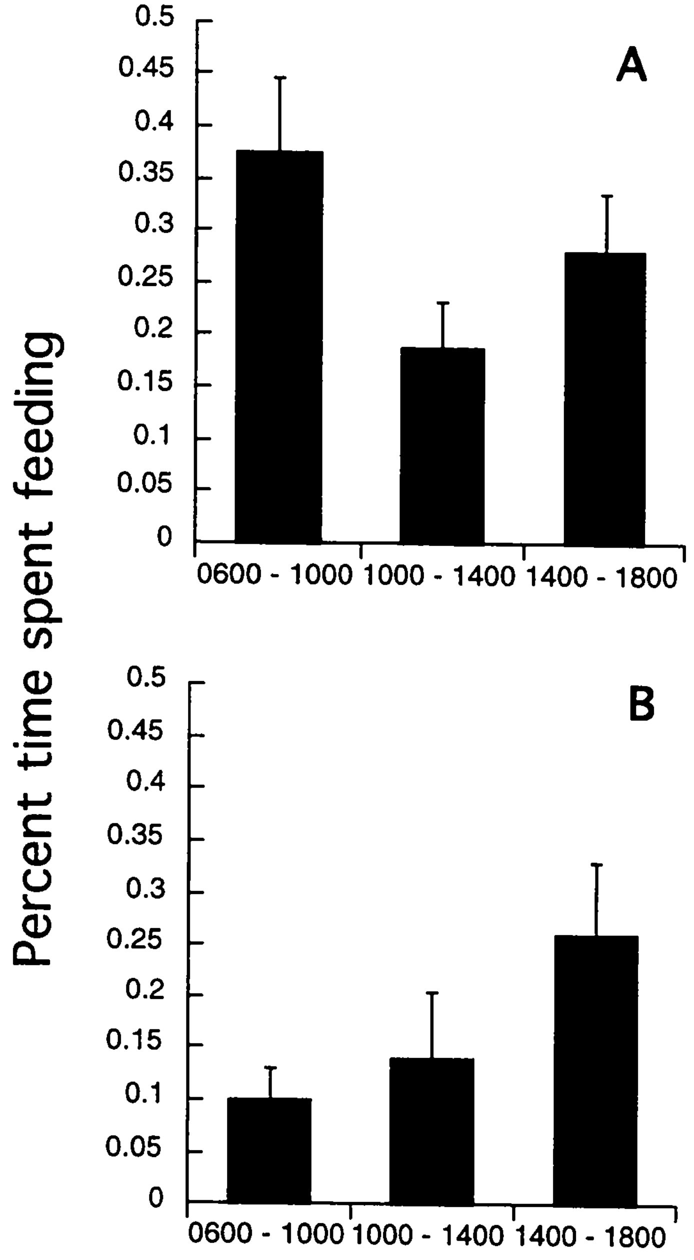


Fig. 4.1. Feeding activity in juvenile coral trout comparing mean (± s.e.) percent of time spent feeding, based on 15 minute observation periods (n = 16 / diurnal period). Diurnal periods: morning 0600 - 1000; mid-day, 1000 - 1400; evening 1400 - 1800. A: small recruits. B: large recruits.

Table 4.1. (A) Results of two-way ANOVA testing the effects of time of day (morning, mid-day, evening) and size (small, large) on frequency of foraging per 15 minute observation period. (B) Tukey's test of frequency of foraging per 15 minute observation period for the main effects of time of day, and size class. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of frequency of foraging.

A. Source of variation	df	MS	F
Time	2	22.88	1.92 NS
Size	1	70.04	5.88*
Time * Size	2	33.45	2.81 NS
Residual	90	11.92	

*p < 0.05. NS p > 0.05

B. Main effect			
Time of day	Midday	Morning	Evening
Size class	Large	Small	

The two size classes also employed different feeding modes (Fig. 4.2). The main feeding mode used by large individuals was ambush (12% of time). This behaviour involved strikes from stationary positions, either while concealed or camouflaged. While in this stationary ambush mode, recruits usually hovered with their heads elevated at a 45 degree angle to the bottom, possibly to increase their range of vision. Large recruits also engaged in joint-hunting behaviour (3% of time), in which recruits followed behind another predatory fish, apparently using the foraging activities of the other fish to locate prey. In contrast, small recruits tended to forage in close

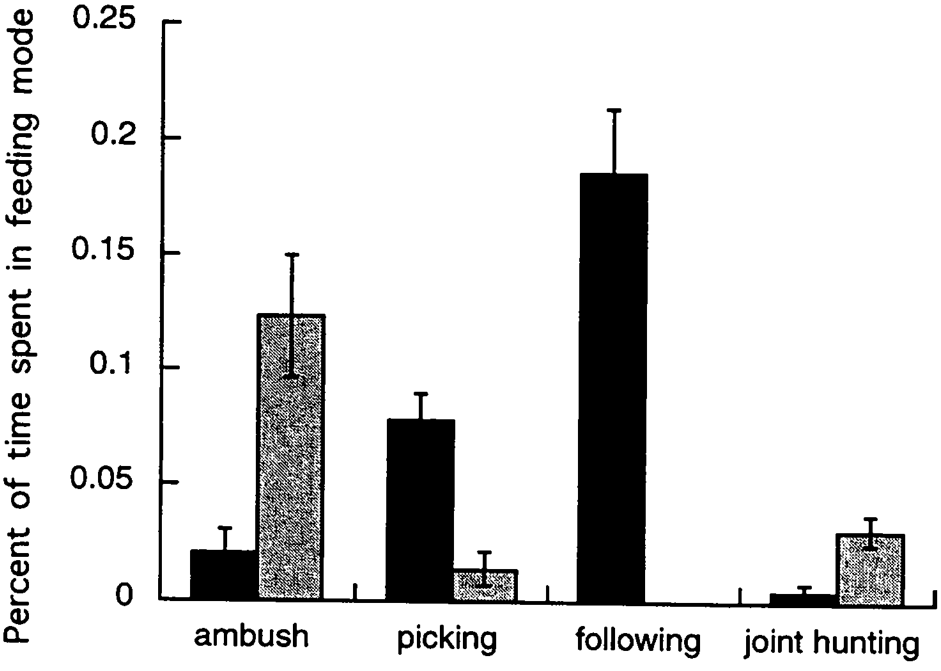


Fig. 4.2. Percent of time spent in feeding modes, based on 15 minute observation periods (n = 48 /size class).

association with the rubble substrata. The main feeding mode used by small recruits consisted of following behaviour (19% of time): hiding in multi-specific schools of juvenile fish, and striking at small prey displaced by the benthic feeding of the school. Small recruits also engaged in "picking" behaviour (8% of time). This feeding mode was similar to following behaviour, except that individuals hunted singly. Inspection of stomachs revealed that these strikes were usually directed at early stage crustaceans, (e. g. zoeae and megalopae).

4.4.2 Stomach fullness/digestive state

There was a general trend among both size classes towards lower numbers of empty stomachs, and higher numbers of full and recent stomachs as the day progressed. Fullness and digestive state of stomach contents of small recruits captured between 0600 and 1000 indicated a bi-modal distribution: most stomachs were categorised as either state 1 (empty/well digested), or state 4 (full/recent) (Fig. 4.3A). A bi-modal distribution was also found for stomachs of small recruits captured between 1400 and 1800.

The stomachs of large recruits (Fig. 4.3B) sampled between 0600 and 1000 also contained high amounts of well digested food, but unlike small recruits, the proportion of full stomachs was low.

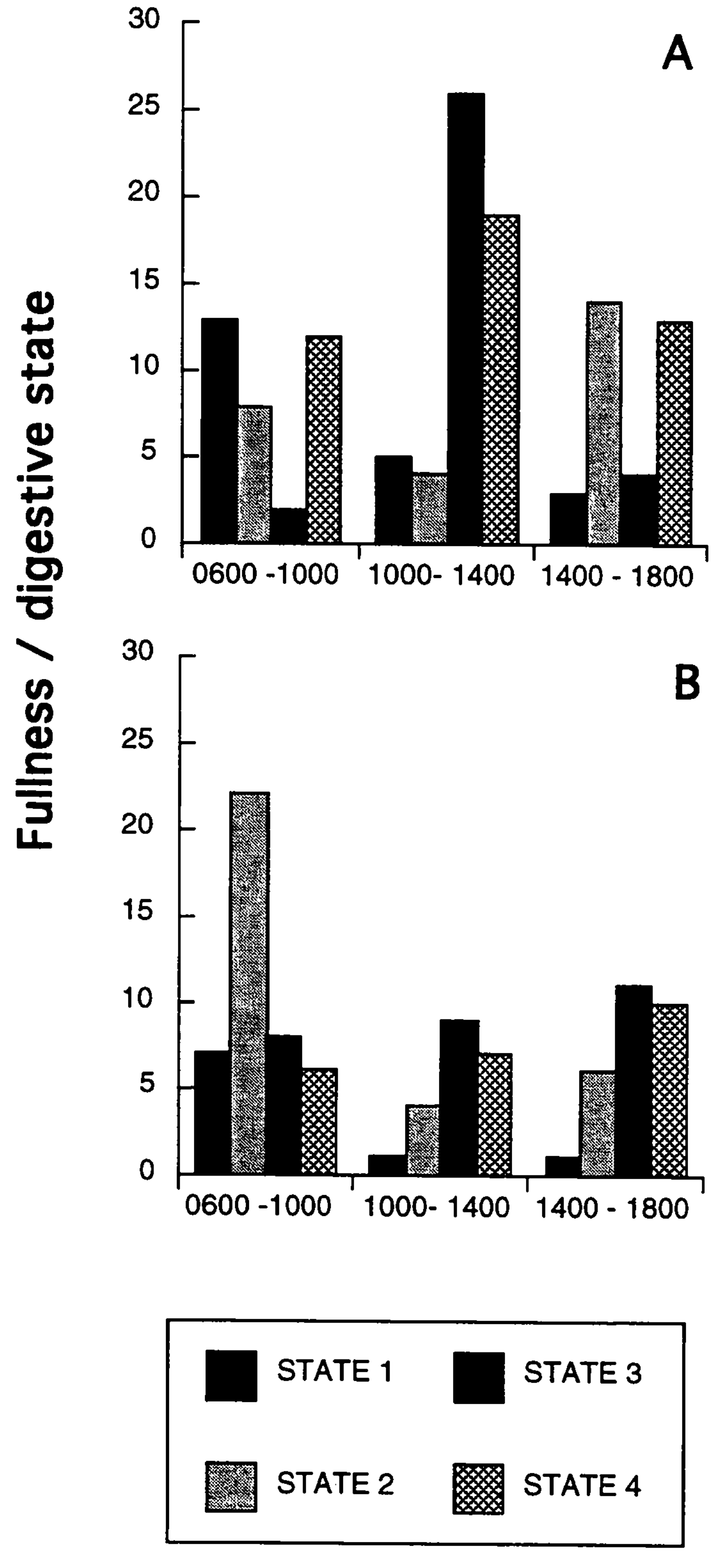


Fig. 4.3. State of feeding of juvenile coral trout comparing index of fullness (see text) as a function of diurnal period: morning 0600 - 1000; mid-day, 1000 - 1400; evening 1400 - 1800. A: small recruits (n = 102). B: large recruits (n = 83).

4.4.3 Stomach contents

Eighty six percent of all stomachs examined contained prey. Of these, eighty four percent contained some crustaceans, and 48% contained only crustaceans. Fifty two percent contained fish, and 16% had eaten only fish.

The most abundant prey were early stage crustaceans (primarily crab megalopae and zoeae). Alpheid shrimp were also numerically important (Table 4.2). Representatives of a number of reef fish families were eaten, including pomacentrids, gobiids, labrids, and siganids. As a result of the advanced state of digestion, many fish could not be identified. Low numbers of most prey items necessitated the pooling of taxa into three main categories: fish, shrimp, and early crustacea.

Table 4.2. Diet of 0+ P. leopardus, pooled data from two habitats (n = 185). Mean size (mm) = mean standard length for fish, mean total length for crustaceans.

Prey item	**n**	**Mean Size, prey**	**Range (mm)**
Total fish	152	18.9	6-42
Pomacentridae	30	12.4	9-15
Pomacentrus amboinensis	6	12	10-13
Dischistodus sp.	2	11	9-13
Pomacentrus nagasakiensis	3	11.3	11-12
Blennidae	1	14	14
Gobiidae	6	16.5	11-27
Trimma sp.	2	13	11-15
Bryaninops yongeii	1	27	27
Labridae	3	25.3	21-33
Stethojulis strigiventer	1	21	21
Thalassoma lunare	1	22	22
Tripterygiidae	1	14	14
Siganidae	2	22	21-23
Scaridae	1	22	22
Apogonidae	1	13	13
Parupeneus multifasciatus	1	42	42
Synchiropus ocellatus	1	23	23
Synodontidae	1	10	10
Unidentified fish	104	22.6	6-37
crustacea			
Alpheid shrimp	193	12.7	7-15
stomatopod	1	1	13
early stage crustacea	246	4.8	3-7

4.4.4 Variation in diet between size classes.

Diets of small and large recruits differed considerably (PSI = 0.46). Small recruits consumed mainly alpheid shrimp (49%), while piscine prey comprised the bulk (72%) of diet for large recruits (Table 4.3). Individuals containing fish remains (63.52 mm SL ± 0.15 s.e.) were significantly larger than those without fish (49.6 mm SL ± 0.14 s. e., $t = 6.6$, $P < 0.0001$). However, both the largest (102 mm) and the second smallest (28 mm) recruits had eaten fish. With the exception of six gobiids and one tripterygiid, all identified fish prey were recent recruits to the reef. Most (86%) P. leopardus that had eaten fish had one or two prey in their stomachs, and the greatest number of fish found in a single individual was six. Overall, small recruits contained more prey items (308) than large recruits (282).

Table 4.3 Variation in diet between small (n = 102), and large recruits (n = 83). Data pooled from two sites.

	small				large			
Main prey categories	% N	% V	% F	%IRI	% N	% V	% F	%IRI
Fish	0.14	0.30	0.28	0.18	0.38	0.71	0.53	0.72
Alpheid shrimp	0.36	0.50	0.39	0.49	0.29	0.21	0.28	.018
Early Crustacea	0.50	0.20	0.32	0.33	0.33	0.08	0.19	0.10

4.4.5 Variation in diet between habitats

There were also differences with regard to the way the two size classes exploited prey at the two sites (Table 4.4). Based on percent IRI, large recruits consumed relatively higher proportions of fish at the Primary site (81%, n = 133) than at the Secondary site (59%, n = 53)(Fig. 4.4).

Table 4.4. Variation in diet between sites. **A.** Primary site (n = 133). **B.** Secondary site (n = 53).

A. PRIMARY SITE	Small			Large		
Main prey categories	%N	%V	%F	%N	%V	%F
Fish	0.15	0.28	0.29	0.47	0.78	0.59
Alpheid shrimp	0.34	0.50	0.33	0.33	0.17	0.25
Early crustacea	0.51	0.22	0.19	0.19	0.05	0.16

B. SECONDARY SITE	Small			Large		
Main prey categories	% N	% V	%F	% N	% V	%F
Fish	0.12	0.36	0.25	0.28	0.61	0.46
Alpheid shrimp	0.50	0.49	0.44	0.25	0.26	0.32
Early crustacea	0.38	0.15	0.31	0.46	0.12	0.22

In contrast, the diets of small recruits were remarkably similar between sites. The highest PSI value (most similar diet) was found between small recruits from the Primary and Secondary

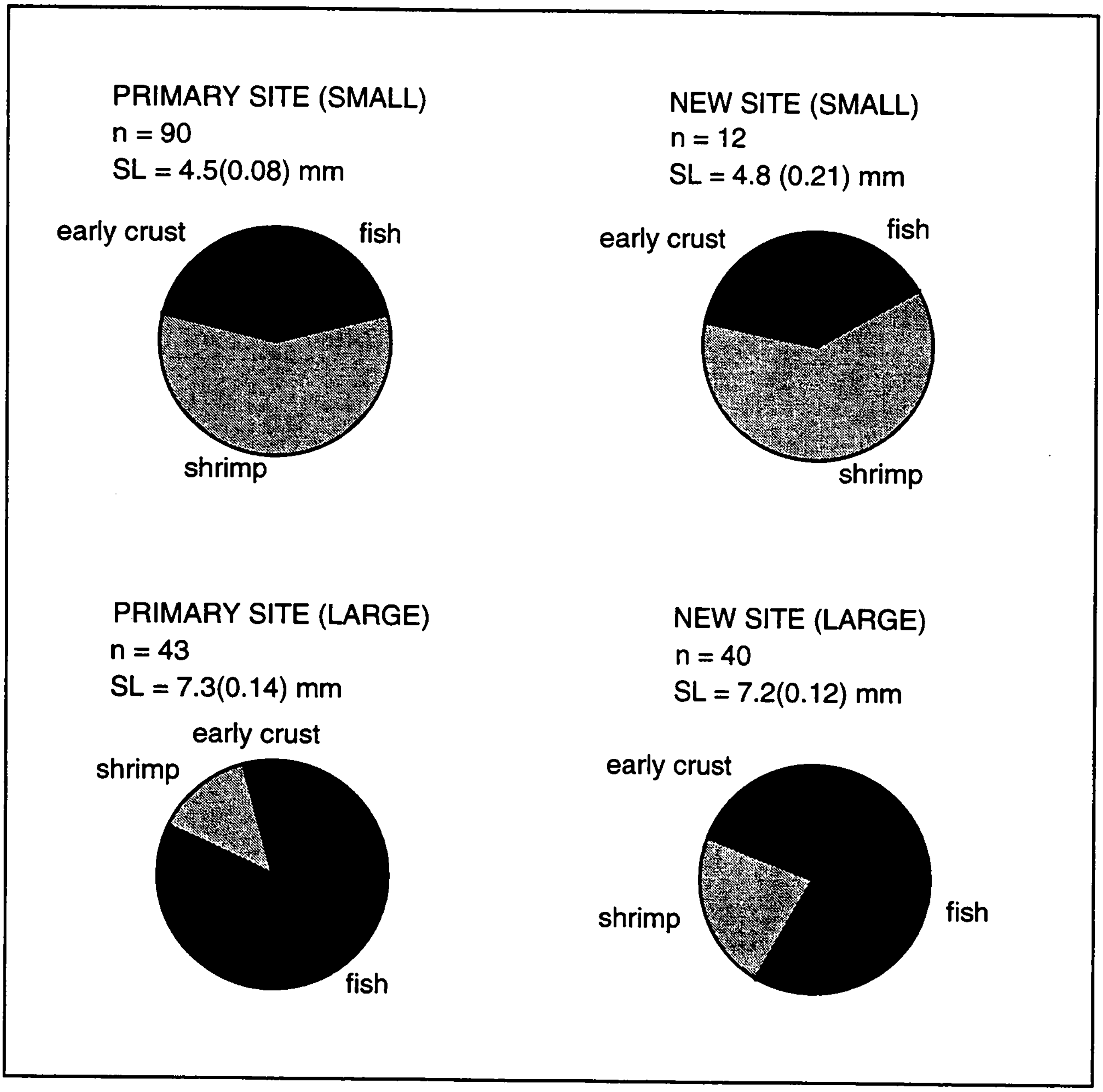


Fig. 4.4. Diet of small versus large recruits based on per cent of toyal IRI (see text)

sites (0.96), while a low index (dissimilar diet) was found between large recruits at the Primary site and small recruits at the Secondary site (0.43) (Table 4.5).

Table 4.5. Percent similarity index (PSI), based on % IRI. Values above 0.60 are considered to be biologically important overlap in diet.

SITE		SECONDARY		PRIMARY	
		SMALL	LARGE	SMALL	LARGE
SECONDARY	SMALL	-	0.58	0.96	0.43
	LARGE	-	-	0.63	0.77
PRIMARY	SMALL	-	-	-	0.4
	LARGE	-	-	-	-

Weight increased exponentially with standard length at both sites. However, the relationship at the Secondary site showed considerably more variation than the relationship at the Primary site (Fig. 4.5).

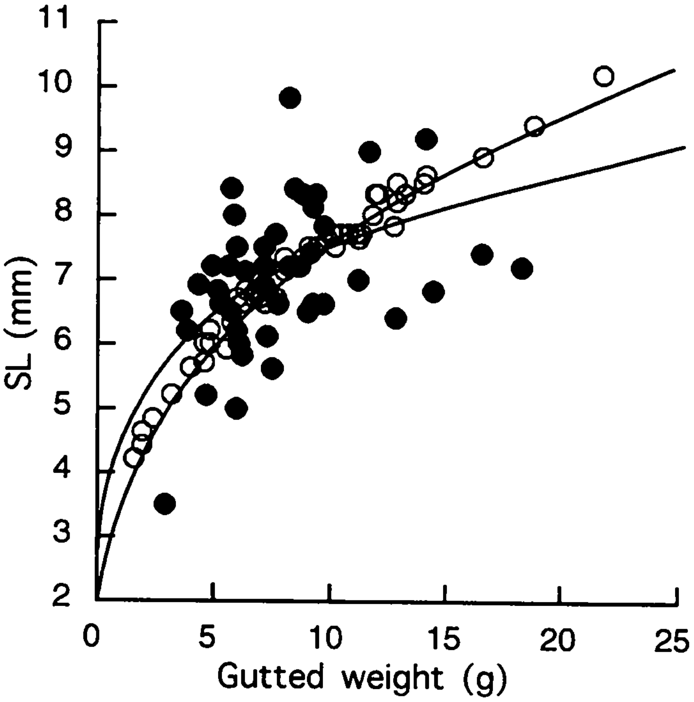


Fig. 4.5. Comparison of gutted weight (grams) and standard length (mm), for two sites. Hollow symbols, Primary site (SL = $34.8(wt)^{0.34}$, $r^2 = 0.99$, n = 46). Solid symbols, Secondary site (SL = $44.6(wt)^{0.37}$, $r^2 = 0.72$, n = 46)

4.4.6 Comparison between regurgitated prey and stomach contents

Thirty six percent (n = 77) of all recruits regurgitated prey after capture. Percent number of fish, shrimp, and early crustaceans were tallied for regurgitated prey versus all prey items recovered from recruits (Fig. 4.6). Regurgitated samples more closely reflected the diets of large recruits than those of small recruits. In general, fish numbers were over-represented, and crustacea were under-represented in the regurgitated material.

4.5 DISCUSSION

Juvenile coral trout underwent a pronounced dietary shift toward piscivory during early growth, with a concomitant change in foraging style and diurnal feeding patterns. Two primary factors probably are involved in producing size-related patterns of feeding among piscivores. First, juvenile fish are constrained by their small size to exploit relatively small food particles (Werner and Gilliam 1984, Keast 1985, Galis 1993). Second, predator-mediated habitat shifts may occur during ontogeny, resulting in different ranges of available prey. The factors influencing feeding ecology will be described, followed by a discussion of the impact of juvenile coral trout piscivory on the demography of reef fish populations.

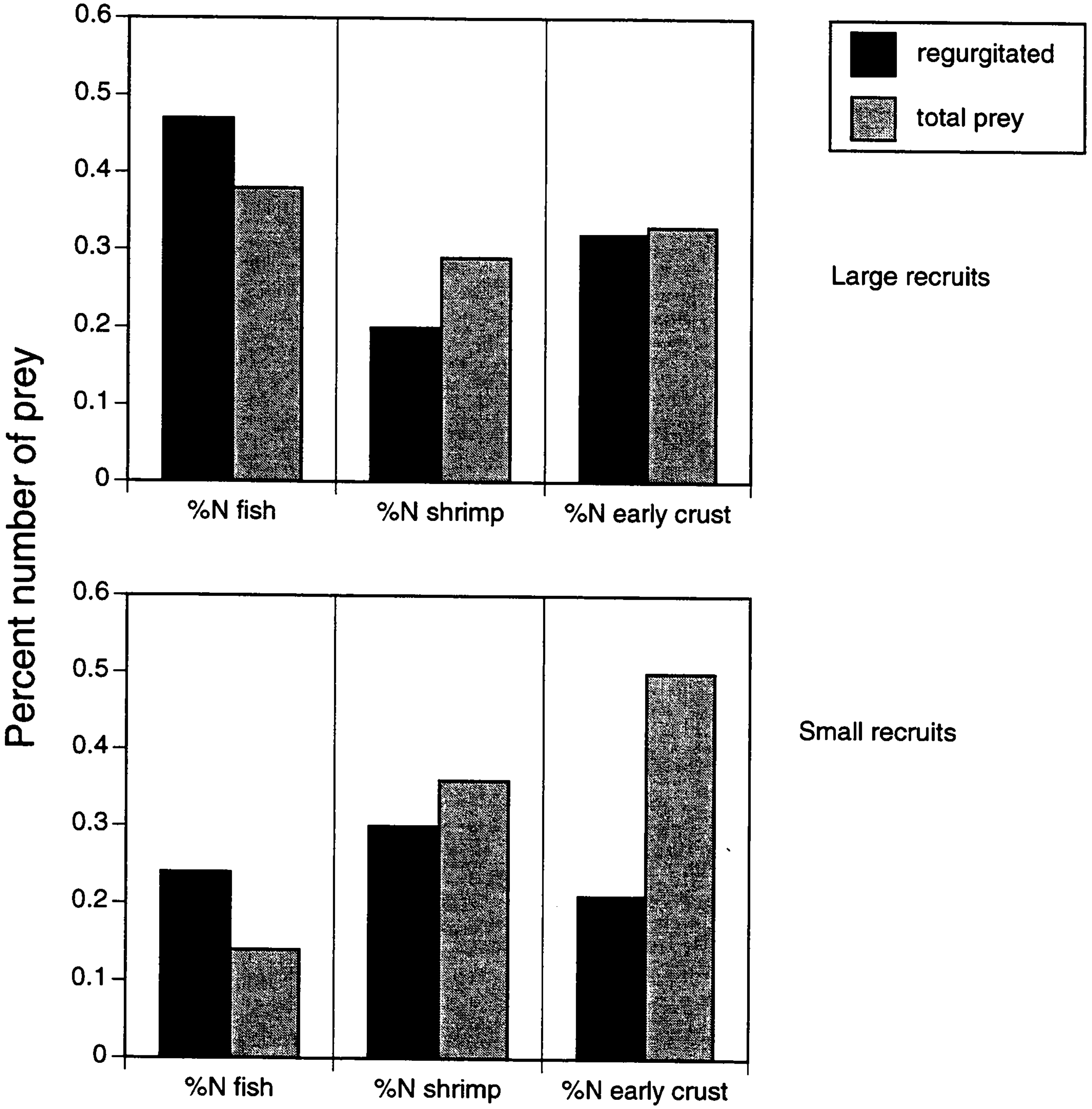


Fig. 4.6. Percent number of prey items from regurgitated (n = 77) and total samples (n = 185). Top: Large recruits. Bottom: small recruits

Foraging behaviour

Small coral trout recruits spent proportionately more time searching for food than larger juveniles, and also consumed greater numbers of prey items. This increased foraging effort may have been due to the high metabolic demands associated with early growth (Smith 1989). In addition, ontogenetic changes in feeding apparatus may allow growing recruits to feed on progressively larger prey (Liem and Osse 1975, Galis 1993), and utilise a greater range of prey sizes (Setran and Behrens 1993, Stoner and Livingston 1984, Schmitt and Holbrook 1984). According to Optimal Foraging Theory (Pyke 1984), feeding strategies should change during growth, as food changes in quantity or size, with the net effect being that energy gain is maximised (Gerkin 1994). A transition towards less frequent feeding on larger prey has two advantages for growing coral trout: (1) consuming larger items results in greater energy returns relative to foraging effort, thus making more energy available for growth, and (2) the reduced time spent foraging decreases the likelihood of being eaten. Both conditions maximise fitness, and favour recruitment into larger size classes.

In addition to variation in the amounts of feeding activity, there were qualitative differences in the predation tactics used by large and small recruits. Small recruits primarily foraged in close proximity to shelter (e. g. rubble-covered bottoms), while larger fish tended to occupy more exposed positions during hunting, suggesting that behaviour may be less influenced by predation at larger sizes. Alternatively, small crustaceans may only be available to recruits foraging close to the substratum, while exposed positions may be best for locating and ambushing piscine prey.

Juveniles of both sizes engaged in feeding activities with other species, but the nature of these associations differed between size classes. Inter-specific feeding associations are common in reef fish (Hobson 1968), and have been reported for several species of serranids, (Diamant and Shpigel 1985, Shpigel and Fishelsen 1989) including coral trout (Goeden 1974, Samoilys 1987, Kingsford 1992). Ormond (1980) defined interspecific joint hunting as association with another predator to enhance prey detection, and following behaviour as following other fish for food items displaced by their activities. Large recruits primarily engaged in interspecific joint hunting with a single fish of similar size (most often Cheilinus trilobatus), while following behaviour in small recruits was typically associated with schools of newly settled labrids, scarids, and mullids, taxa which primarily feed on epifaunal crustaceans as recruits (Green 1994, Bellwood 1986, McCormick 1994).

Diel feeding patterns

Small and large recruits differed with respect to diurnal feeding patterns. Analysis of stomach fullness and the digestive state of prey items indicated a pattern of morning and evening feeding in small recruits. Previous studies have found peaks of feeding activity at dusk and dawn for serranids (Randall 1967, Hobson 1974, Shpigel and Fishelson 1989). Goeden (1974) also reported increased twilight feeding in adult coral trout. Predators are better adapted for foraging during twilight periods because their eyes function more efficiently under these conditions than diurnal or nocturnal prey species (Helfman 1986). However, Hobson (1974) suggested that juvenile fish should be less active during these periods, as a result of their vulnerability to predation. The results of this study indicated increased foraging activity during dusk and dawn, when predation risk is presumably highest. It is possible that the anatomical features which confer superior twilight foraging success in adult coral trout also enable juveniles to avoid predation during these times. Alternatively, the preferred foraging mode of small recruits may represent an adaptation to predation pressure: close association with rubble substrata may provide adequate access to shelter, thus allowing them to feed during periods of high predation risk.

Variation in diet

The relative proportions of prey items consumed by newly settled coral trout changed during early growth: small recruits fed primarily on crustacea while large fish mainly ate fish. A shift from small crustacean prey to piscivory during ontogeny is characteristic of serranids (Shpigel and Fishelson 1989, Brule and Canche 1993, Ross and Moser 1995), and has been reported for juvenile coral trout (Kingsford 1992). For P. leopardus, the timing and success of this transition may be important in determining the number of fish recruiting into larger size classes. Piscivores often must pass through transitory early life history stages during which they are forced to compete with forms that feed exclusively on invertebrates (Werner and Gilliam 1984). Thus it may be advantageous for fish that are piscivorous as adults to switch as soon as possible to a fish-based diet.

In juvenile coral trout, the transition towards a piscivorous diet may be mediated by a habitat shift brought on by release from predation pressure. Habitat shifts may offer recruits a different range of prey types within alternate habitats (Mittelbach 1986, Werner and Gilliam 1984). A pronounced shift in habitat use occurred at approximately 60 mm SL (Chapter 2), which coincided with the observed dietary shift. At this size, recruits switched from association with level, rubble-strewn bottoms to high relief features (e. g. consolidated rubble mounds, coral heads), which may have offered juveniles a different suite of potential prey species.

The transition to piscivory was more pronounced at the Primary site. This site had higher percent cover of rubble mounds, suggesting a correlation between these more complex habitats and the availability of fish prey. Alternatively there may have been differences in the ability of recruits to capture prey in different habitats. Weight of eviscerated juveniles was more closely related to standard length at the Primary site, indicating that resource quality may have been less variable at this site. Site-specific variation in feeding ecology has been documented for several taxa (Cowen 1986, Eckert 1987, Guzman and Robertson 1989, Shpigel and Fishelson 1989). Kingsford (1992) found that predation of adult P. leopardus on reef fish varied between habitats, with coral trout from reef slope habitats taking significantly higher numbers of pelagic fish than at lagoon habitats. Variation in prey availability and quality may influence growth rates of fish (Cowen 1986), with consequent changes in size-based mortality schedules and ultimately, population size (Werner and Gilliam 1984).

Influence of piscivory and diet shifts on reef fish demography

Coral trout settle from the plankton and metamorphose into benthic individuals at approximately 25 mm SL (Masuma et al.

1993). Thus, the smallest fish found to consume piscine prey (28 mm) had probably been resident on the reef for less than one week prior to capture. The finding that _P_. _leopardus_ is piscivorous from the time of settlement has implications for the post-recruitment mortality schedules of many reef fish. Due to increased mobility and rapid growth following recruitment, small changes in the timing of settlement of predator and prey species may result in large differences in predation rates (Sweatman 1993). Furthermore, fluctuations in predator recruitment may have variable impacts on prey populations in different habitats (Eckert 1987).

Hixon (1991) stated that distributions and abundances of prey species should shift in predictable ways as a result of changes in predator density. Coral trout have been reported to influence the mortality rates of juvenile and adult _Acanthochromis polyacanthus_ (Thresher 1983, Connell and Kingsford 1992). In the present study, approximately 50% of recruits had eaten fish, and the majority of these were recent recruits. Thus, newly settled coral trout have the ability to remove large numbers of heterospecific recruits, and may affect populations of prey species from the time of recruitment to the reef.

Use of regurgitated prey samples in diet studies

The analysis of regurgitated prey samples may provide a cost effective means of obtaining estimates of diet, especially where ontogenetic trends are investigated. Based on their lower state of digestion, prey items generally represented recently consumed items, and occasionally were disgorged alive, thus facilitating identification. Another advantage of using this technique is that specimens can be released after sampling, and if individually marked, a serial record of feeding for an individual may be obtained.

Chapter 5

THE INFLUENCE OF SIZE AT SETTLEMENT, TEMPERATURE, AND SIZE-SELECTIVE PREDATION ON VARIATIONS IN GROWTH RATE IN JUVENILE CORAL TROUT.

5.1 Synopsis

The effects of size at settlement, temperature, and size-selective predation on variations in growth rate in juvenile coral trout were examined. Both direct and indirect methods were used to estimate growth parameters to assess temporal, spatial, and ontogenetic variation. Daily deposition of increments within otoliths (lapilli) was validated, and a strong correspondence was found between growth of the lapilli and fish growth. Increment widths were measured within three sections of lapilli and used to compare differences in back-calculated growth rates between years, seasons, and reefs. Significant inter-annual differences were detected in planktonic growth rate, and pre-settlement growth was found to be positively correlated with early post-settlement growth. Mean larval duration was 23.6 (0.23) days, and mean back-calculated size at settlement was 17.9 (0.15) mm SL. Fish recruiting in November 1992 had significantly higher planktonic growth rates than did the December 1992 cohort, and also grew faster as benthic individuals. Temperature had a strong influence on growth, and accounted for 55% of the variability in somatic growth following settlement.

5.2 INTRODUCTION

Variability in growth rates during the early life history of reef fish may potentially influence recruitment of young fish into adult populations. Predation is usually highest among smaller fish (Jones and Johnson 1979, Post and Evans 1989, Pepin 1991), and thus faster-growing fish may suffer less mortality because they are able to pass quickly through vulnerable size classes (Werner and Gilliam 1984, Smith 1985, Post and Prankevicius 1987). Another consequence of enhanced growth is to produce larger individuals with presumed competitive advantages (Werner et al. 1983). Variation in growth among areas may be extreme (Thresher 1983, Jones 1986, Jones 1991). For example, spatial variation has been reported to exceed inter-annual variation in the growth of juvenile Acanthochromis polyacanthus (Thresher 1985). Since size-specific effects may influence the outcome of competitive interactions through mechanisms including social dominance (Coates 1980, Forrester 1990) and food acquisition (Folkvord 1991), information concerning variations in growth parameters is vital to gaining insight into patterns of community structure and population dynamics.

Two primary factors affecting the growth rate of juvenile fish are temperature and food supply (Weatherly and Gill 1987). When food is not limiting, temperature may be the most important determinant of growth (Brett 1979, Pauly 1979, Van der Veer et al. 1990, Sogard and Able 1992), and a number of studies have reported increased post-settlement growth during periods of higher water temperature (Jones 1987, Gladstone and Westoby 1988, Pepin 1991, May and Jenkins, 1992).

Growth rates of larval cohorts have also been shown to increase with water temperature, both within and between years (Crecco and Savoy 1985, Houde 1989, 1990, Pepin 1991, Rutherford and Houde 1995). Other factors contributing to variation in larval growth include food supply (Miller et al. 1988, Pepin 1989, Chesney 1993) and maternal size (Cowan et al. 1993). Simulation studies have demonstrated that relatively small differences in planktonic growth may result in large variations in survival and subsequent recruitment (Chambers and Leggett 1987, Pepin and Meyers 1991, Cushing and Horwood 1994). Thus, larval growth histories have the potential to influence growth parameters of benthic populations, by regulating the numbers and quality of individuals surviving the pelagic stage. (Cushing 1973, Houde 1987, Pepin et al. 1987, Miller et al. 1988, Pepin and Meyers 1991).

Lapilli and sagittae of juvenile coral trout contain daily increments (Doherty et al. 1994), which can be used to reconstruct size at age, providing estimates of relative and absolute growth. It has also been suggested that the width of these increments may correspond to somatic growth (Wilson and Larkin 1982, Volk et al. 1984, Alhoussaina and Pitcher 1988, Sogard and Able, 1992). If so, examination of incremental width could provide estimates of instantaneous growth rates over short time periods corresponding to different points during ontogeny (Thorold and Williams 1989, Campana 1990, Campana and Jones 1992). These estimates can be used to assess growth-dependent survival of cohorts by comparing growth histories of surviving individuals with those of fish collected at an earlier time (Post and Prankevicius 1987, Hovenkamp 1992).

The aims of this study were three-fold:

1) To test the hypothesis that variation in growth in newly settled coral trout is influenced by planktonic growth history
2) To describe the growth dynamics of juvenile coral trout populations at Green and Arlington Reefs.
3) To assess the relative importance of spatial and temporal factors in determining growth rates of juveniles.

5.3 MATERIALS AND METHODS

5.3.1 Sample collection and sites

The study was conducted during four years: 1992, 1993, 1994, and 1995 (Table 1).

Juvenile coral trout were sampled for otolith analysis during 1992, 1993 and 1994 - 1995. In the first two years, fish were collected by spearing on two reefs: (Green and Arlington), and during two seasons: early (February) and late (May 1992, July 1993).

In the third year (1993 - 1994), growth rates were determined for tagged fish released and recaptured at Green Reef. In the final year, (1994 - 1995) juveniles were collected daily at Green Reef from 15 November to 30 January.
Pre-settlement coral trout (n = 12) were collected from light traps (Doherty 1987) deployed around Green and Arlington Reefs during 1992. Fresh standard length (SL) was measured to the nearest 0.1 millimetre (mm).

Table 5.1. Summary of methods used to estimate growth parameters.

YEAR	OTOLITH	TECHNIQUE	COMPARISON
1991 - 1992	sagitta	length at age	inter-reef, inter-season, inter-annual
	lapilli	increment width	inter reef, inter-season, ontogenetic change
	lapilli	increment width	effect of water temperature
	lapilli	width of pre set. region / pre set. increment counts	larval duration, larval growth
	-	modal progression	inter-cohort, pre- vs. post-settlement growth
1992 -1993	lapilli	increment width	inter reef, inter-season, ontogenetic change
1993 -1994	lapilli	somatic growth : fish growth correspondence	back-calculation of somatic growth
	-	mark- recapture	daily periodicity of increment formation
1994 -1995	sagitta	length at age (based on sagitta length)	inter-annual

Standard lengths for all benthic individuals were measured to the nearest millimetre. Juveniles collected during early and late collections in 1992 - 1993 were preserved in 95% ethanol; those collected during other years were measured while fresh. The linear regression of fresh SL (FSL) on preserved SL (PSL) was: FSL = 1.036* PSL ($n = 107$, $r^2 = 0.75$), which indicated shrinkage of 3.6%. This equation was used to calculate the fresh standard length of fish preserved in ethanol.

5.3.2 Water temperature

Water temperature records were obtained from the AIMS weather station at Agincourt Reef, located approximately 85 kilometres (km) from Green Island. Temperatures were recorded from a sub-surface sensor (depth = 2 metres). Daily noon temperatures were averaged for the duration of each sampling period.

5.3.3 Otolith preparation and measurement

•Sagittae

Three pairs of otoliths occur in teleosts: lapilli, sagittae, and asterisci. Sagittae were removed from all juveniles collected during the study ($n = 445$), cleaned, dried, and measured under a stereo dissecting microscope fitted with an ocular micrometer. Left and right otoliths were selected randomly, as paired sample t-tests indicated no significant difference in length between otoliths ($t = 0.853$, $n = 20$, $P > 0.05$). Measurements of whole sagittae were made to the nearest micrometer unit (0.0254 mm at 40X). Each sagitta was measured along the axis of maximum length, which passed through the post-rostrum (i. e. the posterior-most projection of the sagitta).

Sagittae from early and late samples collected during 1992 and 1993 (n = 174) were prepared and analysed by personnel from the Central Ageing Facility (CAF) in Victoria. Transverse sections of otoliths were prepared by polishing in a plane perpendicular to the long axis of the sagittae. The polished surface was then glued to a microscope slide and polished from the opposite direction to produce a thin transverse section. Otoliths were examined randomly and blindly with respect to SL, and increment counts represented the mean of two readings.

•Lapilli

Lapilli were removed and prepared for juveniles collected during 1992 and 1993 (n = 110). Otoliths were ground laterally on a finger tip, and polished using two grades of lapping paper (10 μm and 3 μm) to produce a thin polished section. Preparations were mounted on a glass slide in Euparol medium, and protected by a cover slip. After being left for several weeks for the otolith matrix to clear, measurements and pre-settlement increment counts were made using a Leitz compound microscope (400 X magnification) fitted with an Ikegami high resolution black and white monitor. Measurements of lapilli diameter for individuals collected from light traps were made along the axis of maximum length (Figure 5.1) using a stereo dissecting microscope as described above.

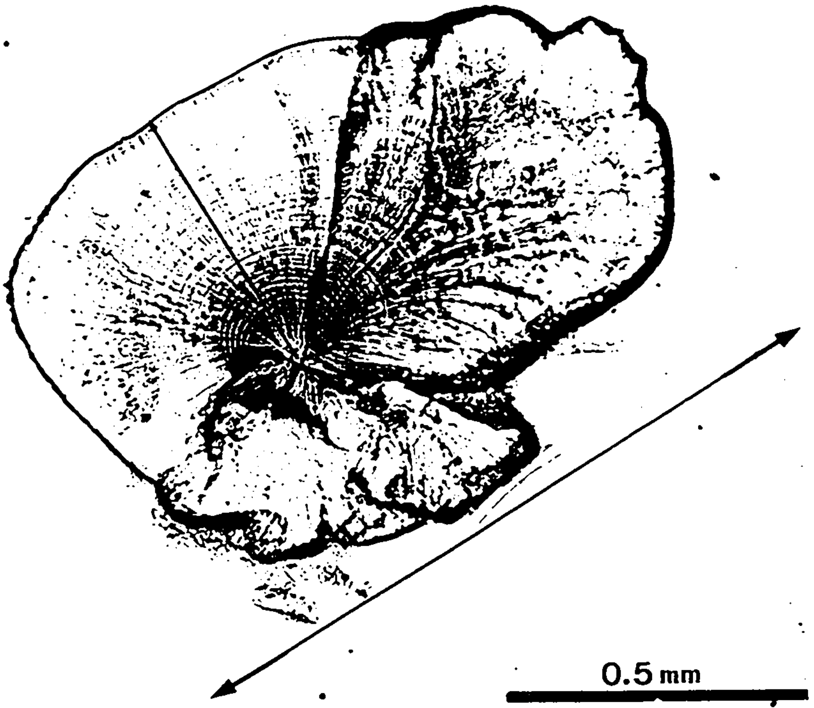


Fig. 5.1. Photomicrograph of lapilli from juvenile coral trout, SL = 140 mm . Long arrow, axis of length measurement. Short arrow, axis of measurement for increment widths. Scale, 75.8 : 1.

5.3.4 Otolith growth - somatic growth correspondence

In order to determine the degree of correspondence between otolith growth (e. g. increment width) and somatic growth, a field study using oxytetracycline marked fish was conducted. Juveniles were caught with fence nets during December 1993 - January 1994, transported to the field station, and measured to the nearest mm. They were then immersed in an aerated bath of oxytetracycline and seawater (concentration = 250 mg/l), and retained in darkness for 18 hours. Juveniles were heat-branded for individual recognition, returned to the study site, and released at the point of capture. Marked individuals were collected and measured in late January 1994, after which lapilli were removed and prepared as described above. Otoliths were examined under both ultraviolet and normal light, and the distance between the fluorescing ring (corresponding to the time of oxytetracycline treatment) and the lapillus edge was measured. This distance was then regressed against the amount of somatic growth occurring since treatment.

To validate daily periodicity of increment formation, increments occurring outside the fluorescent mark were counted, and compared to days since treatment.

5.3.5 Spatial and temporal patterns of growth inferred from variation in increment widths

Increment width measurements of lapilli were made for ten fish selected haphazardly from each orthogonal combination of season, reef, and year. Thus, in both 1992 and 1993, ten fish each were selected from Green early, Green late, Arlington early, and Arlington late, making a total of 80 juveniles sampled.

The microstructure of coral trout lapilli is similar to that of other coral reef fishes, showing a pre-settlement area of relatively broad micro-increments surrounded by a post-settlement area of thinner increments, with the two regions demarcated by a “settlement mark” (Doherty et al. 1994). Accordingly, widths of increments were measured within three sections of each lapilli, designated <u>inner</u>, <u>middle</u>, and <u>outer</u>. Inner increments were those increments deposited immediately interior to the settlement mark, while middle increments were those located just outside the demarcation. Outer increments were those deposited near the edge of the otolith, i. e. just prior to collection. Thus, inner increments represent growth during the pelagic phase, while middle increments reflect growth immediately following settlement. Outer increments reflect growth rates around the collection dates (e. g. early or late).

In each section, the widths of ten increments were measured on a calibrated video analysis system linked to a Leitz compound microscope at a magnification of 400 X. Measurements were made by positioning a cursor to mark the end points of each increment. Widths were measured to the nearest 0.1 µm. Due to the inherent auto correlation of otolith growth, consecutive increment width measurements are not independent of each other (Campana and Jones 1992). Consequently, seven of these measurements were selected haphazardly from each group of ten, and used to calculate mean increment width for each otolith section. If increments were not measurable within all three sections, the otolith was rejected and another lapilli was selected at random.

Due to asymmetrical growth of lapilli, it was necessary to specify an axis along which to measure increment widths. Accordingly, increment measurements were made along a line perpendicular to the longest axis of the otolith (Figure 5.1). This axis consistently provided the best resolution of increments, probably due to the relatively uniform thickness of lapilli in this direction.

5.3.6 Effect of water temperature on somatic growth rate

In order to assess the effect of water temperature on growth rate, mean somatic growth rate was calculated from mean widths of middle increments for juveniles collected during 1992. Middle increments correspond to a specific point during ontogeny (i. e., the period immediately following settlement), and therefore do not confound environmental effects with age-related growth transitions. Growth rates were calculated for each juvenile, based on the mean of seven daily increment widths. As these measurements corresponded to days beginning on the settlement date, length at age estimates for each fish (see below) were used to assign each daily increment to a calendar day. The water temperatures recorded on those calendar days were then averaged to determine the mean water temperature occurring during each measurement interval. Linear regression analysis was used to predict the effect of water temperature on somatic growth rate.

5.3.7 Back-calculation of size at settlement and pre-settlement growth rate

Measurements of lapilli diameters from competent pre-settlement coral trout were regressed against standard lengths. The resulting relationship was used to estimate size at settlement from measurements of pre-settlement areas within lapilli of benthic juveniles collected during 1992 and 1993. Pre-settlement growth rates were determined by dividing estimated size at settlement by the number of pre-settlement increments.

5.3.8 Overall growth rates

Three independent methods were used to estimate overall growth rates of benthic juvenile coral trout.

•Length-at-age estimates

Age estimates were obtained from CAF (see above) and regressed against SL to obtain growth estimates for juveniles collected during 1992 and 1993.

Age was also regressed against sagittae length and sagittae weight for fish collected during these years, and the resulting equations were used to predict ages of juveniles collected in 1994 - 1995.

•Direct measurement

Aquaria study

During 1992 - 1993 pre-settlement coral trout, mean (± se) SL = 17.4 (1.1) mm, n = 4, were collected from light traps. These fish were retained in aquaria and fed ad libitum, initially on small (< 5 mm) guppies, and later with newly settled clupeids. After periods of 6 to 40 days, fish were sacrificed and remeasured.

Tagging experiment

During 1993 - 1994, a tagging experiment was conducted within a 50 x 50 m section of the Primary site. Juveniles (n = 67) were captured with fence nets, measured, and marked with individual patterns (Chapter 2), after which they were returned to their point of capture and released. Juveniles were collected again at the conclusion of the season (n = 33), and the amount of growth occurring during the intervening time was measured.

•Modal progression analysis

To obtain an estimate of growth based on length frequency, newly settled fish (n = 233) were collected daily from 15 November 1994 to 30 January 1995. Sampling was continuous except for the last week in December. Collections were grouped by week, and mean weekly standard length was regressed on time, (i. e. the mean capture date for each weekly sample). The slope of the resulting equation was used as an estimate of daily growth.

5.3.9 Intra-annual growth variation among cohorts

During 1991 - 1992, coral trout recruitment to Green and Arlington Reefs occurred primarily during the months of November and December (Chapter 2). To assess whether juveniles settling in different months grew at different rates, back-calculated settlement dates were used to assign recruits to individuals settling during November 1991 and December 1991. Modal progression analysis was used to compare the mean SL of early and late collections for individuals settling in each month. In addition, back-calculated size at settlement and pre-settlement growth rates were compared between fish settling in November and December.

5.3.10 Data analysis

Somatic and otolith growth were estimated with linear models to permit comparisons between regressions (Ott 1977). To determine how standard length and increment width varied between years, seasons, and reefs, analysis of variance (SAS, 1988) was used, with standard length and increment width as response variables, and reefs, seasons, and years as fixed factors. Tukey's multiple comparison tests were used to detect differences among means (Day and Quinn 1989). Assumptions of normality of residuals were tested using normal probability plots, and homogeneity of variances were tested with Cochran's test. Otolith growth:fish growth relationships were assessed using least squares analysis.

5.4 RESULTS

5.4.1 Relationship between otolith growth and somatic growth

Increments were visible in all fish examined, and the number from the margin to the oxytetracycline mark approximated the days elapsed since treatment (Figure 5.2). Increments from two juveniles could not be reliably counted, and were excluded from the regression analysis. Thus, increment deposition occurs daily in P. leopardus juveniles.

There was a significant correspondence between otolith growth and somatic growth for fish used in the oxytetracycline field experiment (Figure 5.3). Eleven marked recruits (range = 54 - 72 mm SL at first capture) were collected after periods ranging from 15 to 27 days, and oxytetracycline was found to be incorporated into all lapilli examined. Least squares regression yielded the following equation: Δlapillus radius = $2.77*\Delta SL + 0.81$ ($r^2 = 0.86$, $F = 53.42$, $P < 0.0001$).

5.4.2 Spatial and temporal patterns of growth inferred from variation in increment widths

There were significant differences in the widths of inner, middle, and outer increments between seasons. Both inner and middle increments were significantly wider in fish from late collections (7.21 ± 0.15 µm and 4.5 ± 0.09 µm , respectively) than from early collections (6.38 ± 0.21 µm and 3.81 ± 0.21 µm.

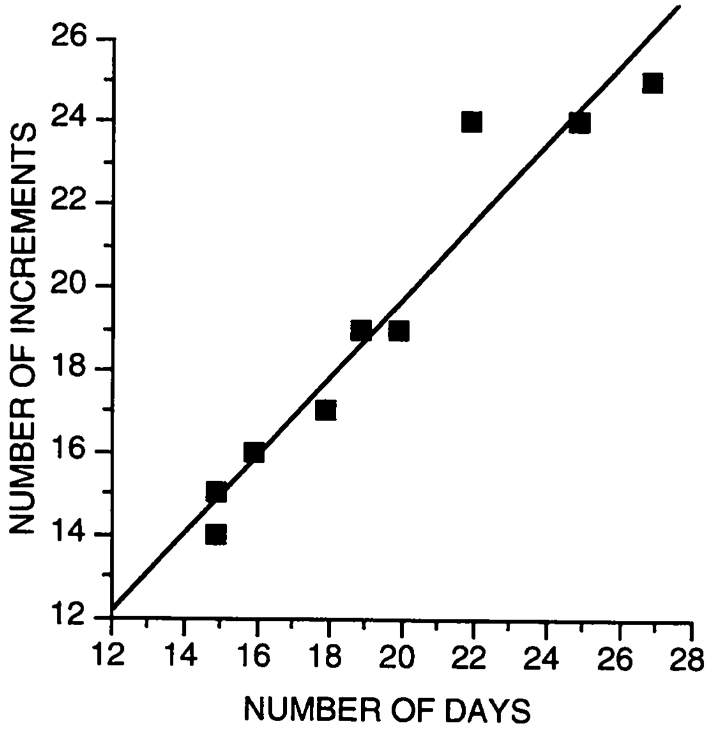


Fig. 5.2. Number of increments deposited outside oxytetracycline induced mark versus number of days at large for heat-branded juvenile coral trout (N = 9). Increments from two otoliths were unreadable. Line represents linear regression between variables.

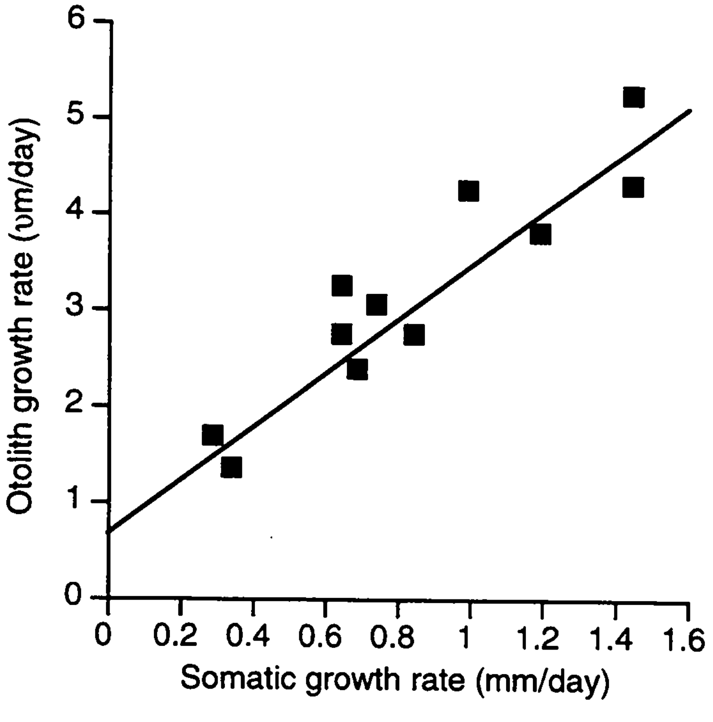


Fig. 5.3. Relationship between otolith growth rate and somatic growth rate for oxytetracycline-marked, heat-branded juvenile coral trout (N = 11).

Table 5.2. ANOVA of inner increment widths of juveniles sampled in 1992 and 1993. Increment width values are means of seven widths selected haphazardly from ten adjacent increments within inner sections. Mean inner increment were greater in 1993 and late collections (7.3 µm and 7.2 µm, respectively) than in 1992 and early collections (6.3 µm and 6.4 µm, respectively).

Source	df	MS	F	p
year	1	19.50	16.74	< 0.001
season	1	14.03	12.04	< 0.001
reef	1	0.23	0.20	0.66
year*season	1	1.65	1.42	0.24
year*reef	1	0.25	0.22	0.65
season*reef	1	0.32	0.28	0.60
year*season*reef	1	0.28	0.24	0.63
residual	72	1.16		

Table 5.3. ANOVA of middle increment widths of juveniles sampled in 1992 and 1993. Increment width values are means of seven widths selected haphazardly from ten adjacent increments within middle sections. Mean middle increment were greater in late collections (4.5 μm) than in early collections (3.8 μm).

Source	df	MS	F	p
year	1	3.28	2.575	0.11
season	1	10.37	8.137	< 0.01
reef	1	0.31	0.245	0.63
year*season	1	0.20	0.157	0.70
year*reef	1	0.08	0.066	0.80
season*reef	1	0.16	0.127	0.73
year*season*reef	1	0.07	0.057	0.82
residual	72	1.27		

On the other hand, outer increments (Table 5.4) were significantly wider in fish collected early in the year (2.43 ± 0.03 μm) than late (1.74 ± 0.04 μm). Comparison of mean settlement dates indicated no difference between early and late collections ($t = 0.03$, $p = 0.49$). Thus, fish sampled in the late collection were members of the same cohort as those sampled in the early collection.

Table 5.4. ANOVA of outer increment widths of juveniles sampled in 1992 and 1993. Increment width values are means of seven widths selected haphazardly from ten adjacent increments within outer sections. Mean outer increment were greater in early collections (2.43 µm) than late collections (1.75 µm).

Source	df	MS	F	p
year	1	0.08	1.58	0.21
season	1	9.6	194.25	<0.0001
reef	1	0.15	3.10	0.08
year*season	1	0.03	0.57	0.46
year*reef	1	0.03	0.57	0.46
season*reef	1	0.001	0.02	0.88
year*season*reef	1	0.001	0.003	0.96
residual	72	0.05		

Coefficients of variation (CV) of increment width were greater in early collections than late collections for both inner (20.83% vs. 13.16%) and middle (34.42% vs. 12.64%) increments.

5.4.3 Post-settlement growth rates calculated from increment widths

Conversion of daily increment widths to daily somatic growth using the regression obtained from oxytetracycline-marked fish indicated strong seasonal variation in post-settlement growth (Figure 5.4). Growth rates derived from middle increments, corresponding to dates immediately after settlement (e. g. November - December), were 1.21 (0.04) mm/day. Estimates from outer increments, corresponding to growth rates around the times of collection (e. g. either February or May/July) were lower 0.46 (0.02) mm/day.

5.4.4 Pre-settlement increment widths

Inner (i. e. pre-settlement) increments were also significantly wider for fish collected late in the year. Furthermore, inner increments were significantly wider for fish collected in 1993 (7.29 ± 0.18 μm) than in 1992 (6.30 ± 0.18 μm) (Table 5.2, Figure 5.5).

5.4.5 Size at settlement and pre-settlement growth rate

Individuals collected from light traps had a mean SL of 16.95 (0.31) mm, range = 14.8 - 18.2 mm, n = 12. The linear regression of lapilli diameter on SL yielded the following equation: SL = 25.4*lapilli diameter + 10.13, (r^2 = 0.88, F = 75.66, $P < 0.0001$) (Figure 5.6). The maximum diameter of lapilli from pre-settlement fish (0.33 mm) fell within the range of diameters of pre-settlement areas measured within lapilli from benthic juveniles (0.20 - 0.42 mm). Thus, it was concluded that the fish length:otolith length relationship

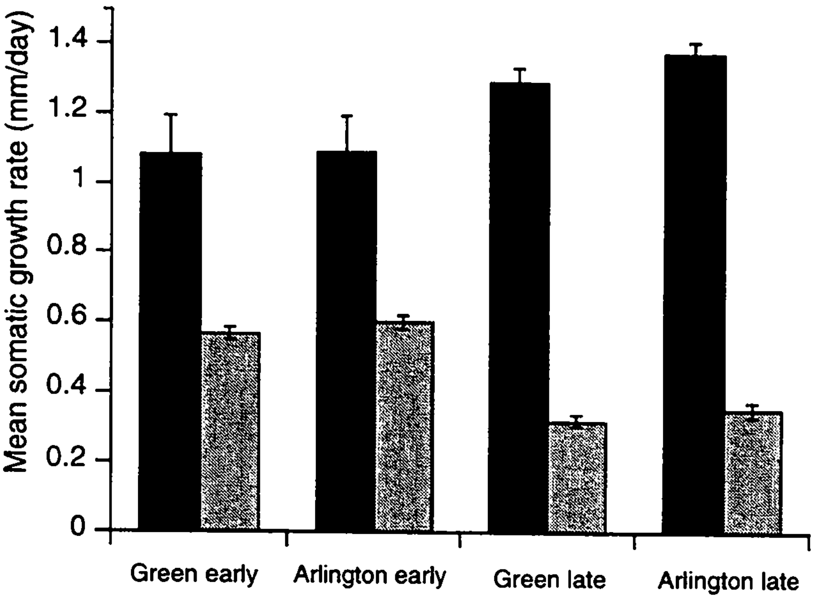


Fig. 5.4. Mean (± se) back-calculated growth rates (mm/day) for juvenile coral trout collected at Green and Arlington Reefs during early and late sampling periods (1992 and 1993 pooled). Dark bars = growth rates back-calculated from middle increments; light bars = growth rates back-calculated from outer increments.

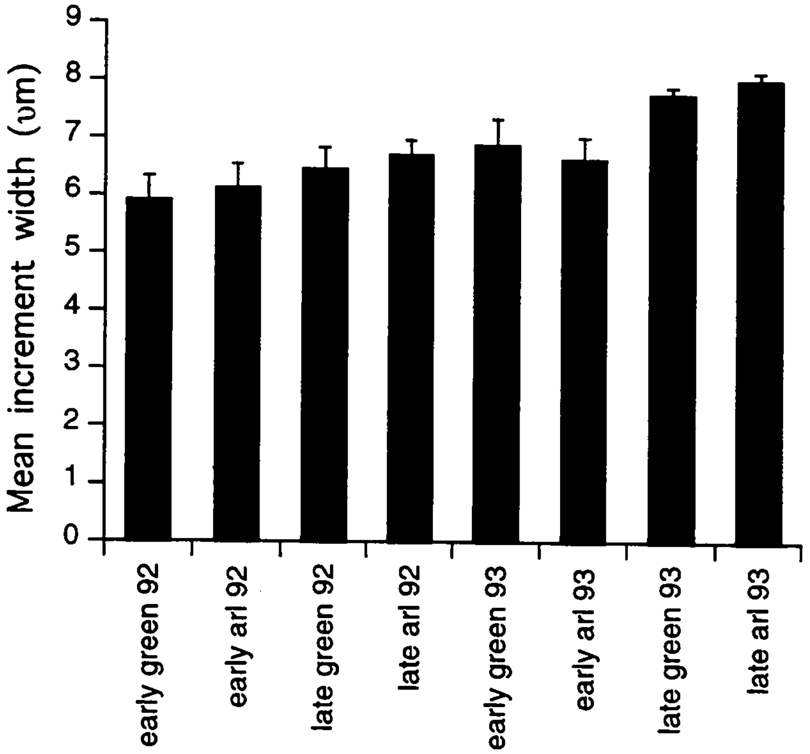


Fig. 5.5. Mean (± se) inner increment widths for juvenile coral trout collected at Green and Arlington Reefs 1992 and 1993.

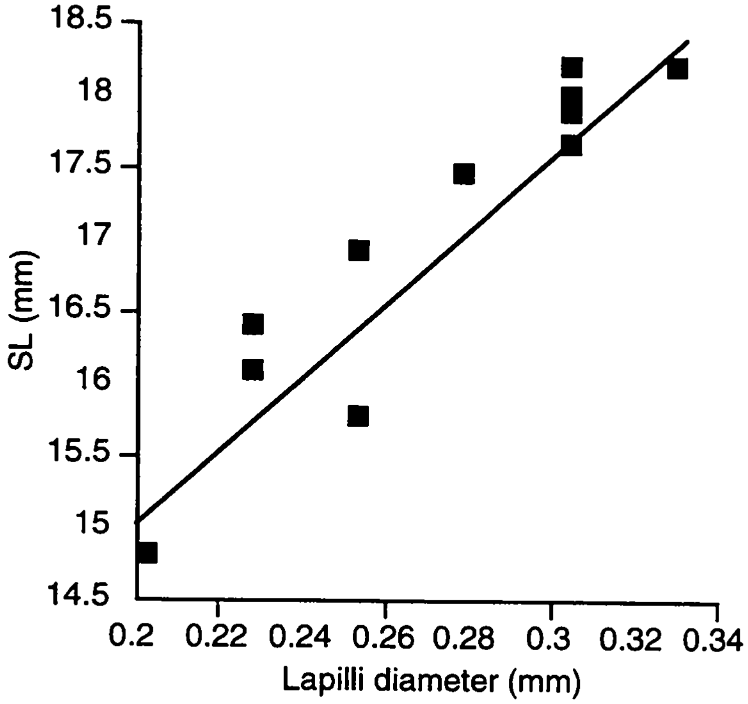


Fig. 5.6. Relationship between lapilli length (mm) and SL (mm) for pre-settlement coral trout collected in light traps in 1992. Line represents linear regression between variables.

derived from the whole lapilli of pre-settlement fish could be used to back-calculate pre-settlement growth parameters for benthic individuals.

Mean (± se) back-calculated size at settlement for all benthic individuals was 17.9 (0.15) mm SL, (range = 15.2 - 20.8 mm, n = 117). Size at settlement was significantly larger for coral trout recruiting in 1992-1993 (18.6 ± 0.22 mm) than in 1991 - 1992 (17.4 ± 0.17 mm, $t = -4.3$, $p < 0.0001$).

Mean (± se) pre-settlement increment number was 23.6 (0.23), n = 102. Mean (± se) pre-settlement growth rate (size at settlement / pre-settlement age) for all juveniles was 0.76 (0.01) mm/day, (range 0.56 - 0.96 mm/day, n = 97). Mean pre-settlement growth did not differ between years ($t = -0.51$, $p = 0.30$).

Both pre-settlement growth (Figure 5.7) and size at settlement (Figure 5.8) showed significant positive correlations with overall growth, as determined by length at age analysis (see below). Linear regression analysis revealed that size at settlement explained 72% of the variation in the overall growth of individuals, while pre-settlement growth rate accounted for 23% of the variation.

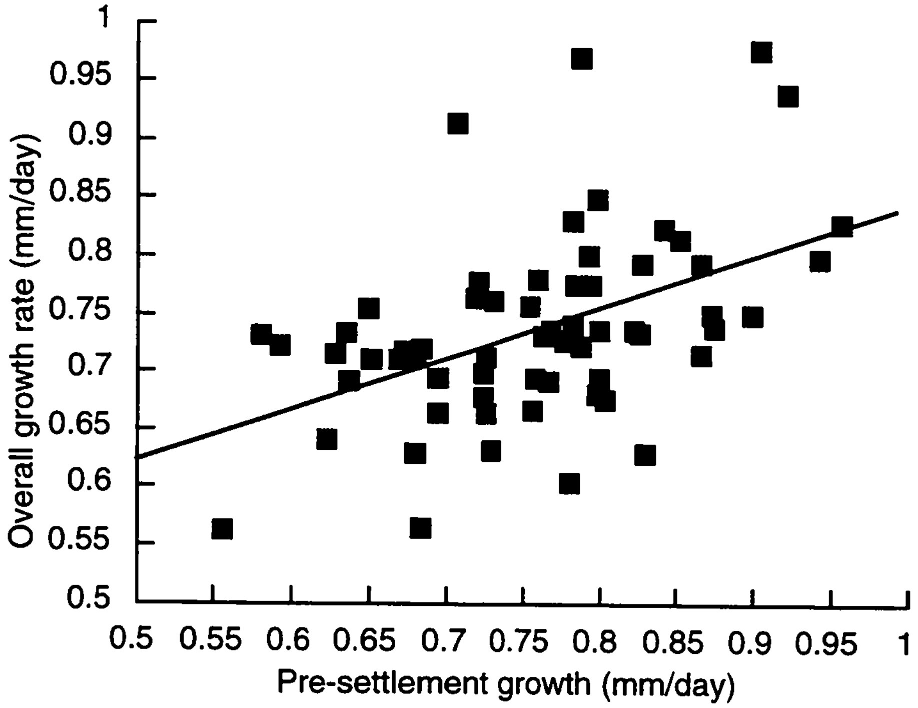


Fig. 5.7. Relationship between pre-settlement growth (mm/day) and overall growth (mm/day) for juvenile coral trout collected at Green and Arlington Reefs 1992 and 1993(see text).

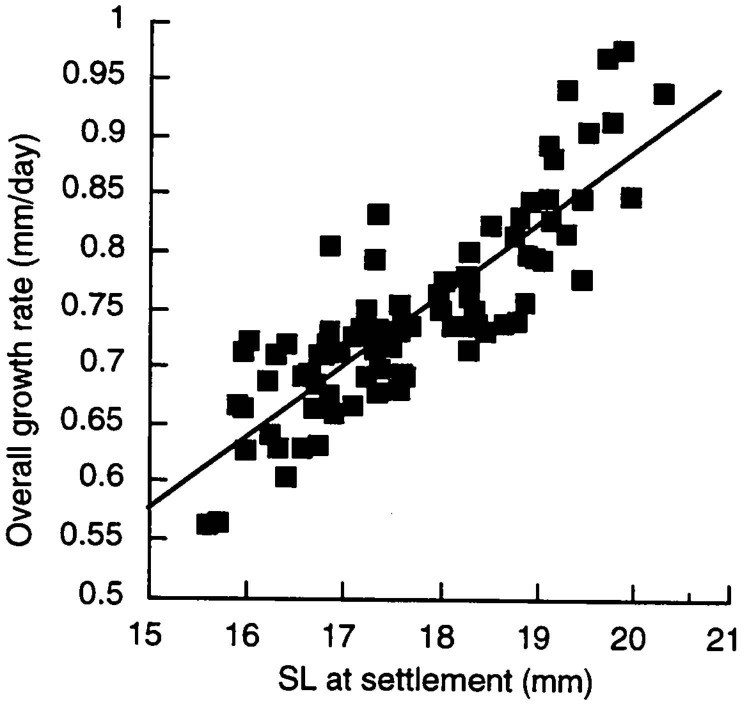


Fig. 5.8. Relationship between size-at-settlement (mm SL) and overall growth (mm/day) (N = 81, see text).

5.4.6 Effect of water temperature on somatic growth rate

Somatic growth rate was positively correlated with water temperature during 1992 (Figure 5.9). The equation for the relationship was: Somatic growth = 0.29*water temp - 6.7, r^2 = 0.52, n = 47. Thus, water temperature accounted for 52% of the variation in somatic growth of juveniles during the period immediately following settlement.

5.4.7 Variation in standard length between reefs, years, and seasons

Analysis of variance of standard lengths for juveniles collected at Green and Arlington Reefs during 1992 and 1993 (Table 5.5) revealed significant differences between the two years, and between fish collected in different seasons. However, the interaction term between years and reefs was significant, thus precluding interpretation of inter-annual change in standard length. As would be expected, juveniles collected late in the year were larger (126.4 mm) than those from early collections (91.4 mm). Standard lengths were not significantly different between reefs.

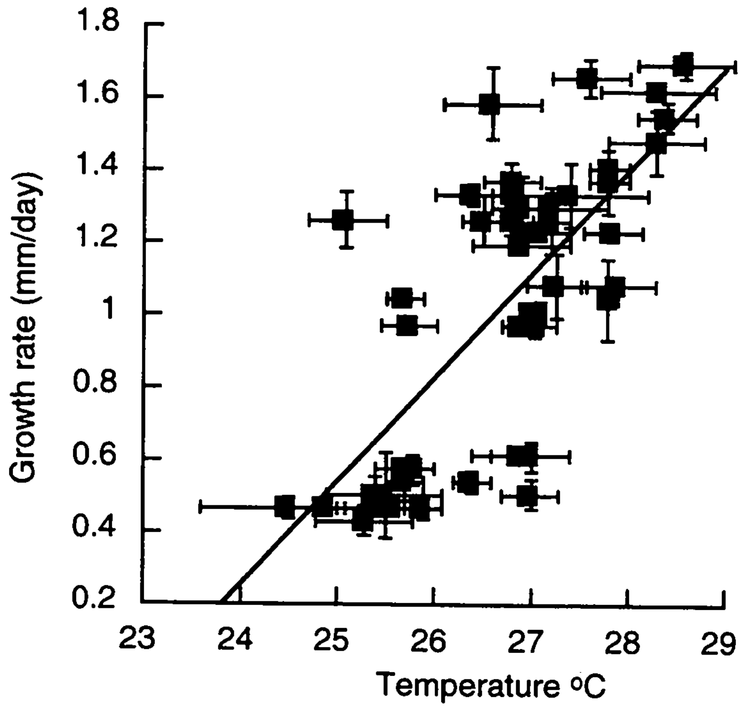


Fig. 5.9. Mean (± se) growth rate (mm/day) for individual juvenile coral trout versus mean (± se) water temperature during each growth period (see text). Temperature data from Agincourt Reef (°C, depth = 2 metres; time = noon)

Table 5.5. ANOVA of SL for all juveniles collected in 1992 and 1993

(n = 240). Mean standard lengths were greater for 1993 and late samples (116.8 and 126.4 mm respectively) than for 1992 and early samples (101.4 and 91.4 mm, respectively).

Source	df	MS	F	p
year	1	10382.19	21.84	< 0.0001
season	1	51984.69	109.33	< 0.0001
reef	1	295.28	0.62	0.439
year*season	1	98.44	0.21	0.654
year*reef	1	4849.16	10.20	< 0.005
season*reef	1	138.77	0.30	0.595
year*season*reef	1	154.11	0.32	0.576
residual	232	475.47		

5.4.8 OVERALL GROWTH

•Length-at-age estimates

Growth during 1992 and 1993

There was a strong linear relationship between age and SL for all juveniles collected during 1992 and 1993. The slopes and intercepts of regression lines did not differ between years for either Green Reef (slope: t = 1.2, p = 0.2; intercept: t = -1.71, p = 0.1), or Arlington Reef (slope: t = - 0.94, p = 0.4; intercept: t =

0.81, p = 0.4); thus years were pooled in comparisons between reefs.

Comparison of pooled regressions between reefs (Table 5.6) indicated a growth rate of 0.68 mm/day for Arlington Reef juveniles, which was significantly higher (t = -2.04, p = 0.04) than the growth rate of 0.58 mm/day for Green Reef juveniles (Figure 5.10).

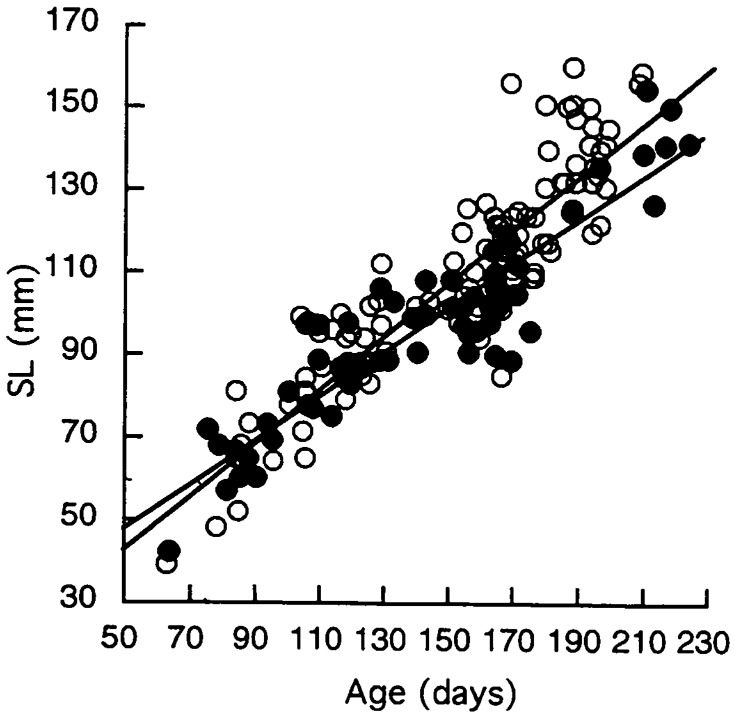


Fig. 5.10. Relationship between age (days) and SL (mm) for juvenile coral trout collected at Green and Arlington Reefs, 1992 and 1993 (years pooled). Solid = Green Reef; Hollow = Arlington Reef.

Table 5.6. Results of regression analysis comparing standard length (mm) with age, for juvenile coral trout collected at Arlington and Green Reefs during 1992 and 1993. n = number of otoliths measured. T-tests were used to test for homogeneity of slopes between years within reefs, years (reefs pooled), and reefs (years pooled).

Collection	n	slope	intercept	r^2	t, p
Green 1992	43	0.54	20.0	0.86	1.2, 0.2
Green 1993	18	0.46	29.9	0.64	
Arlington 1992	100	0.62	13.8	0.68	-0.9, 0.4
Arlington 1993	13	0.74	-6.6	0.97	
1992(reefs pooled)	143	0.63	16.1	0.80	-1.3, 0.2
1993(reefs pooled)	31	0.66	5.4	0.86	
Arlington (years pooled)	113	0.68	9.5	0.81	-2.04, 0.04
Green (years pooled)	61	0.58	18.3	0.85	

Linear regression analysis for all juveniles collected during 1992 and 1993 indicated that sagittae length explained relatively more of the variation in age than did SL (85% versus 81%)(Table 5.7). Linear regression of sagittae weight on age was also significant: age = 19994*(sag. wt.) + 56.3, $r^2 = 0.85$, n = 138.

Table 5.7. Results of regression analysis comparing age with SL, and age with sagitta length for juvenile coral trout collected at Arlington and Green Reefs during 1992 and 1993. n = number of fish measured.

Regression	n	slope	intercept	r^2	F	p
Age vs sag length (mm)	138	44	-44.4	0.85	774.6	<0.0001
Age vs sag wt. (mg)	138	20.0	56.3	0.85	723.3	<0.0001
Age vs. SL(mm)	174	0.61	13.6	0.81	718.6	<0.0001

In 1994 - 1995, it was necessary to obtain age estimates based on one of the above regressions. Although otolith weight has generally been used as a proxy to predict age (Boehlert 1985, Pawson 1990), previous studies have been based on adult fish. Juvenile coral trout sampled in 1994 - 1995 were relatively small (range 26 - 102 mm) compared to those used to establish the above regressions (range 42 - 162 mm). Hence, for 1994 - 1995 juveniles, accuracy and precision were low for otolith weight measurements compared to measurements of sagittae length. Based on the similarity of regressions of sagittae weight and sagittae length on age (Table 5.7) it was concluded that sagitta length could be used as a reasonably accurate predictor of age; consequently growth rates were calculated for the 1994 - 1995 sample using this regression.

The regression of calculated age on SL for all newly settled coral trout collected during 1994 - 1995 at Green Reef was highly significant ($r^2 = 0.94$, $F = 3167.93$, $p < 0.0001$, $n = 186$) (Figure 5.11). The equation was: $SL = 0.55*Age + 16.35$. Thus, juveniles grew at an overall rate of approximately 0.55 mm/day during 1994 -1995.

Otolith length / fish length correspondence

The pooled regression of sagittae length on SL for all individuals collected during the study (excluding pre-settlement fish) was highly significant ($F = 10473.52$, $r^2 = 0.95$, $P < 0.0001$, $n = 478$), and yielded the following equation: $SL = 28.4*\text{sagittae length} - 19.0$. However, the regression was slightly curvilinear (Fig. 5.12), and thus the data were best described by the equation:

$\log(\text{sagittae length}) = 0.034*(SL) + 0.80$, $r^2 = 0.96$.

The sagittae length:fish length regression for pre-settlement fish was also significant ($r^2 = 0.60$, $F = 15.04$, $P < 0.005$, $n = 12$), and yielded the following equation: $\text{sagittae length} = 0.045*SL + 0.003$ (Fig. 5.13).

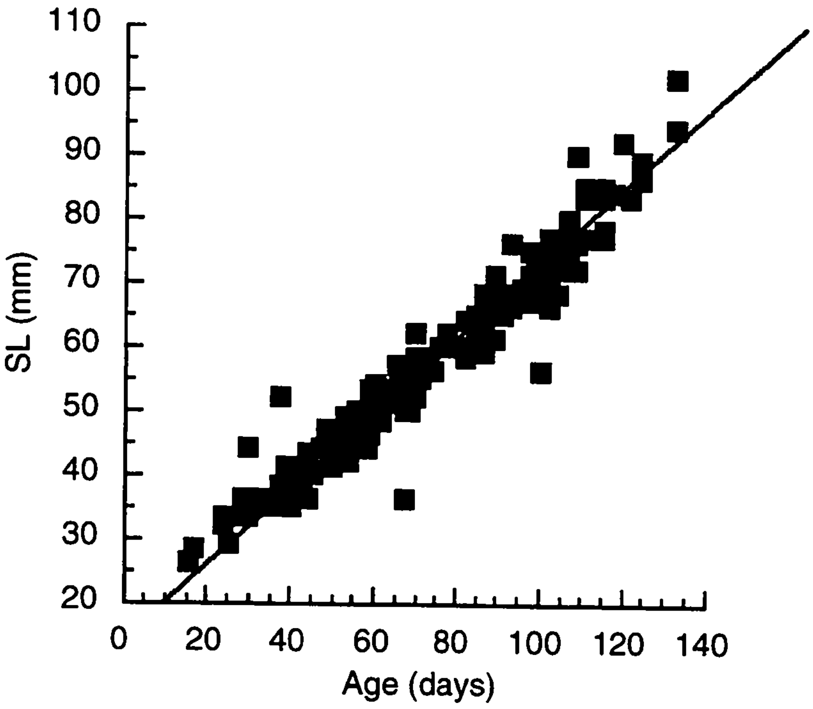


Fig. 5.11. Relationship between age (days) and standard length (mm) for juveniles collected at Green Reef during 1994 - 1995 (N = 186).

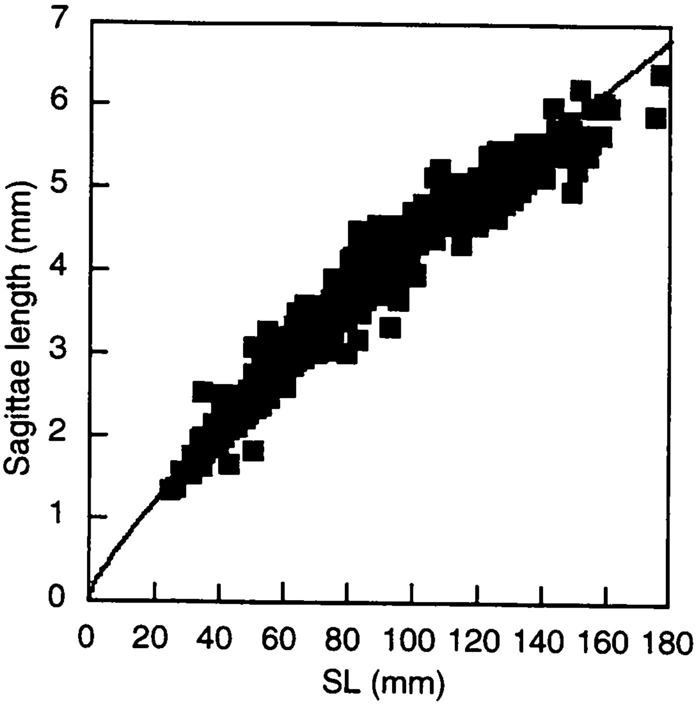


Fig. 5.12. Relationship between sagittae length (mm) and standard length (mm) for all juvenile coral trout collected at Green and Arlington Reefs, 1992 - 1995 (N = 445).

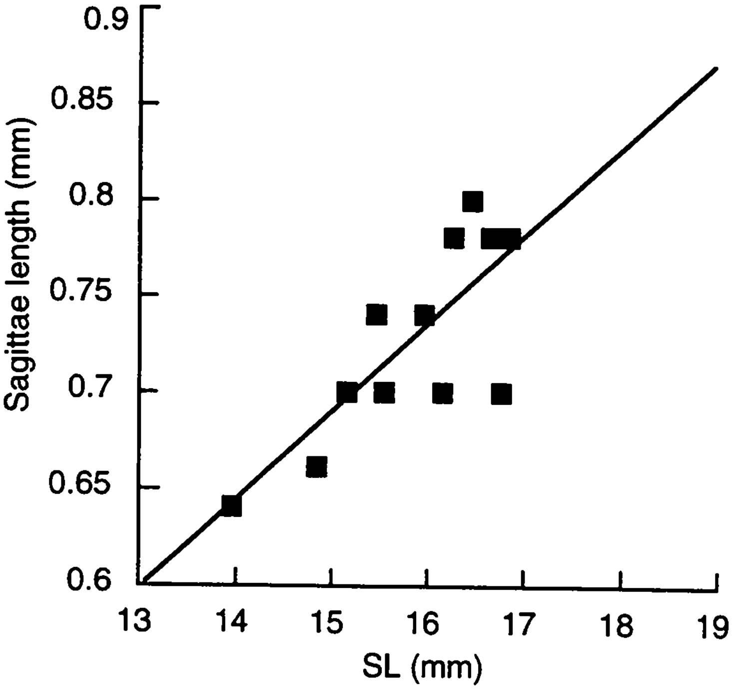


Fig. 5.13. Relationship between sagittae length (mm) and standard length (mm) for presettlement coral trout collected from light traps at Arlington Reef, 1993 (N = 12).

•Direct measurement of growth.

A total of 33 tagged juveniles were recaptured and remeasured during 1993 - 1994. Individuals ranged from 54 mm to 83 mm at the time of first capture. Regression of number of days at large on increase in SL yielded the following equation: Δ SL = 0.60* days - 4.6, $r^2 = 0.60$, $F = 47.37$, $P < 0.05$ (Fig. 5.14).

Mean (± se) growth rate of pre-settlement fish reared in aquaria ($n = 4$) was 1.05 (0.5) mm/day.

5.4.9 Intra-annual growth variation among cohorts

Absolute and specific growth rates based on modal progression analysis (Fig. 5.15) were higher for individuals settling during November 1991 (0.63 mm/day, 0.53%/day SL) than for those settling in December 1991 (0.55 mm/day, 0.51%/day SL).

Linear regression of age on standard length also indicated higher growth rates for individuals settling earlier. The regression for November recruits, SL = 1.33*age + 0.58 ($r^2 = 0.85$, $n = 61$) was approximately 11% higher than the regression for the December cohort: SL = 1.20*age + 24.0 ($r^2 = 0.70$, $n = 59$).

Mean pre-settlement growth rate for November recruits (0.80 mm/day) was significantly higher than for December recruits

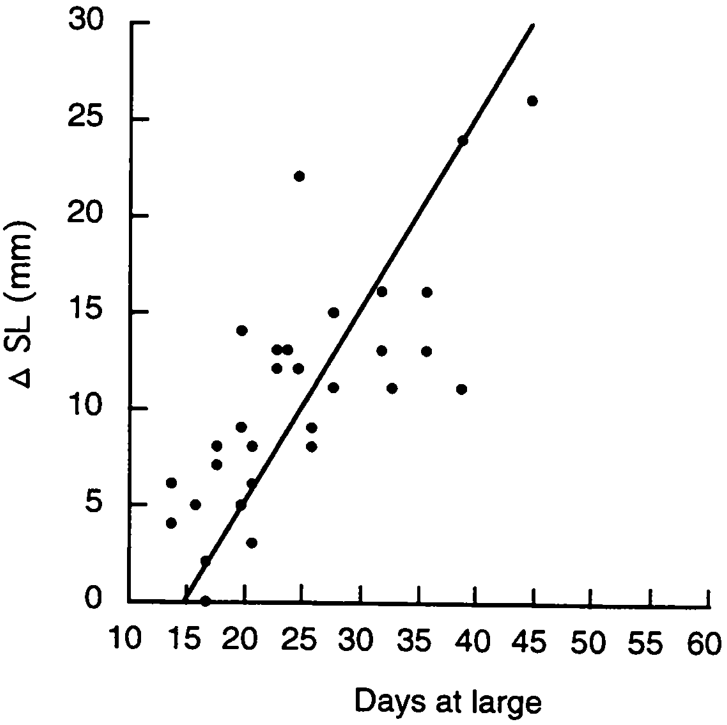
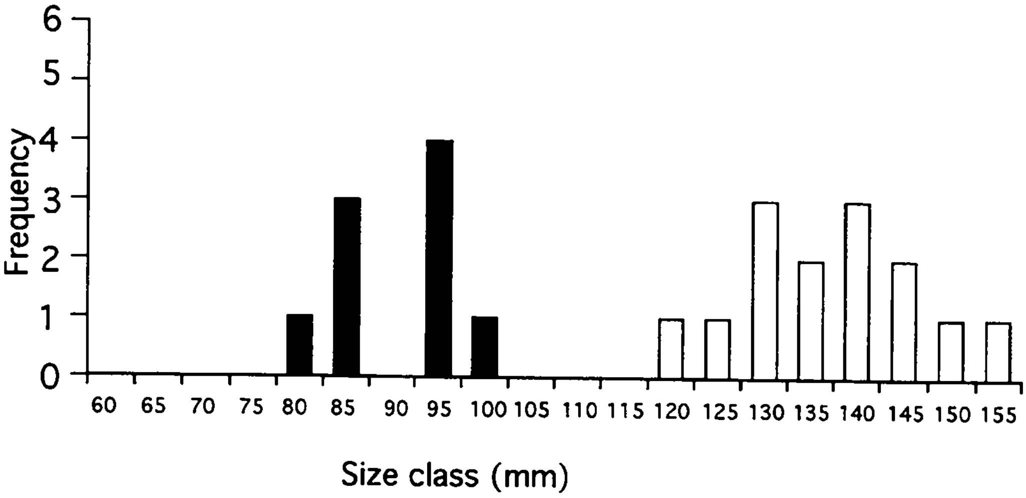


Fig. 5.14. Relationship between change in SL (mm) and number of days at large for coral trout marked and released at Green Reef 1993-1994. (N = 33). Slope of line represents growth rate.



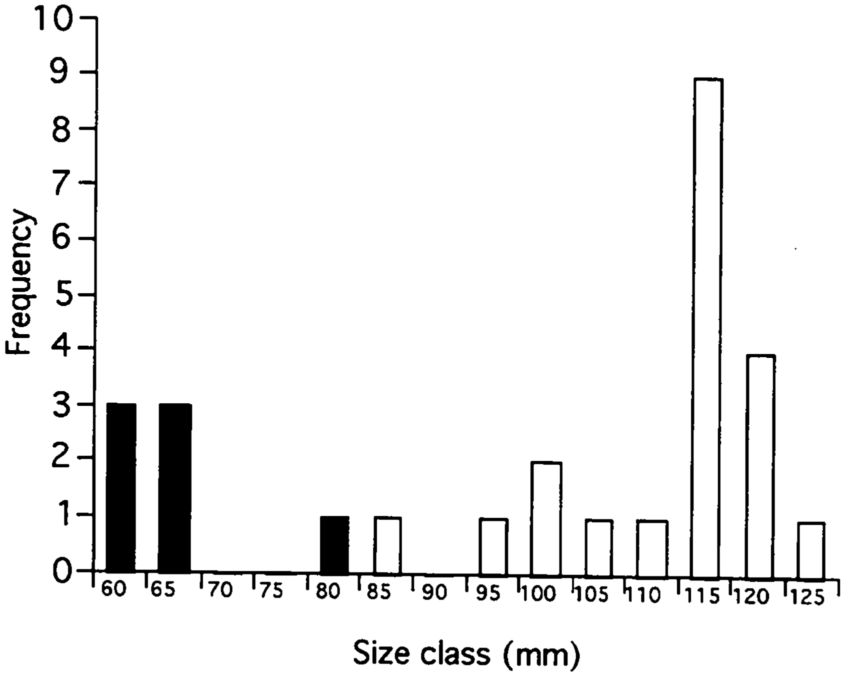


Fig. 5.15. Modal progression of two cohorts of juvenile coral trout at Green and Arlington Reef, 1991 - 1992. Dark bars = early collection. Light bars = late collection. Top, November cohort; Bottom, December cohort.

(0.74 mm/day; t = 2.3 p = 0.016, df = 19.5) Individuals settling in November were larger (17.7 mm SL) than those from the December cohort (17.0 mm SL), although the difference was not statistically significant (t = 1.63, p = 0.057, df = 29.6).

5.5 DISCUSSION

Growth variability in juvenile coral trout appears to be strongly influenced by patterns established during the first few months of life. Intra-cohort variations in pelagic growth rate were correlated with subsequent benthic growth, and both larval growth rate and size at settlement positively influenced overall growth. Following settlement, size selective mortality appeared to be an important determinant of population growth parameters. Somatic growth was positively correlated with water temperature, resulting in strong seasonal variations in growth rate. It is proposed here that variability in growth of juvenile coral trout may be largely determined by intra- and inter-annual differences in growth histories of larval fish, and that size-selective mortality subsequently modifies these initial patterns.

Correlation between pre- and post-settlement growth

Cohort-specific planktonic growth was correlated with post-settlement growth for coral trout recruiting to Green and Arlington Reef during 1991. Intra-annual variation in recruitment during 1991-1992 (Chapter 2) resulted in two recruitment pulses centred around the new moon in November and December 1991. Juveniles recruiting during November were larger, and had experienced higher planktonic growth rates than December fish. Furthermore, November recruits maintained their size advantage up until the May collection, and grew at a faster overall rate than December recruits. These results indicate that the benefits of faster larval growth may result in better physiological condition for recruits settling earlier, and at larger sizes (Cushing 1973). Research on numerous marine and fresh water species has demonstrated that recruitment and post-settlement growth are highest for fast-growing larval cohorts (Crecco and Savoy 1985, Rice et al. 1987, Houde 1987, Rutherford and Houde 1995). Such recruits are likely to have relatively greater energy reserves at settlement (Kerrigan 1995), and consequently may possess adaptive advantages over recruits from slower growing cohorts.

Similar results were reported by Tupper and Boutilier (1995) in a study of juvenile Atlantic cod. Individuals which recruited earlier and at larger sizes grew faster and established larger territories than a subsequent cohort. This was despite more favourable growth conditions experienced by later settlers. In the present study, the December recruitment pulse coincided with the period of maximum water temperature increase, a condition which would be expected to favour growth of these fish. However, the presence of prior recruits within settlement sites may have depressed growth of late settlers, thus offsetting the advantages of settling under more optimal conditions. Newly settled coral trout establish well defined home ranges shortly after settlement, which is apparently facilitated by intra-specific aggression (Chapter 3). Such agonistic behaviour can depress growth by reducing surplus energy available for growth (Forrester 1990). Thus, when recruitment levels are high, as they were in the 1991 - 1992 season, behavioural interactions may be relatively more important than environmental factors in determining growth parameters of young coral trout.

Overall growth rates of juvenile P. leopardus were correlated with both size at settlement and pre-settlement growth, providing further evidence that benefits of settling larger/earlier were expressed as enhanced growth in benthic individuals. Size at settlement had a relatively greater influence on the subsequent growth rates of individuals than pre-settlement growth rate. This finding suggests that events during, and immediately following, settlement played a disproportionate role in establishing benthic growth rates.

Size-selective mortality

Following settlement, size selective mortality appeared to be a major factor in determining the growth dynamics of juvenile coral trout. Lapilli from fish surviving until the late collections had significantly wider inner and middle increments than those from juveniles collected shortly after settlement. This increase in mean increment width is consistent with removal of slower growing individuals from the population through differential mortality, probably due to predation. Moreover, the lower variation in increment widths of late-caught fish also suggests that predation was acting selectively to reduce variability, and supplies further evidence that juvenile coral trout that survived until the late collection were the faster growing members of their cohort.

Effect of water temperature

Temperature also had a strong influence on juvenile coral trout growth. Back-calculated growth rates were positively correlated with water temperature, and otoliths of early-caught fish had wider outer increments than those from later collections. As these increments reflect the growth of individuals immediately prior to collection, they provide an indication of relative growth during these periods. These results agree with several other studies which report a direct correlation between water temperature and increment width (Brothers 1981, Neilson and Geen 1982, Gutiérrez and Morales-Nin 1986, Barkman and Bengtson 1987, Bradford and Geen 1987) but contrast with those of Thorrold and Williams (1989). The finding that in coral trout, somatic growth may be correlated with water temperature must be interpreted cautiously however, because elevated water temperatures may also lead to an increase in feeding rate (Weatherly and Gill 1987), thus confounding the effects of feeding and temperature. Furthermore, higher temperature regimes may also increase growth rates of prey species, thus indirectly resulting in higher growth of predators.

The lack of significant differences in outer increment widths between reefs is puzzling, in light of the asymmetrical collection dates in 1993 (i. e. late collections at Green reef were made in July 1993 versus April 1992). Although July-caught juveniles would be expected to be have thinner outer increments in response to lower water temperatures, July increment widths did not differ from April measurements. One possible explanation is that fish collected in July had been subject to an additional three months of selective pressure, resulting in elimination of slower growing fish. Thus, selective mortality may have produced a faster growing population, and partially compensated for depressed growth during cooler months. Alternatively, uncoupling of the otolith growth:fish growth relationship under sub-optimal temperature regimes (Mosegaard et al. 1988) may have resulted in a conservative response of otolith growth to declining water temperature.

In summary, these findings show that overall growth rates of juvenile coral trout were influenced by growth histories experienced during planktonic life, which were subsequently modified by selective mortality and temperature-dependent growth. Size at settlement was an important determinant of juvenile growth, and population growth parameters were influenced by size-specific mortality, probably as a result of differential predation on slow-growing juveniles.

Chapter 6

GENERAL DISCUSSION

6.1 MAJOR FINDINGS

This study highlights the importance of post-settlement events in influencing the ecology and distribution of juvenile coral trout. Specifically, the study has focussed on the effects of these processes in structuring habitat associations, behaviour, and movement patterns of newly settled individuals. The emphasis on early life history provides a unique focus compared to other studies of this species, because it stresses events and processes occurring during a period of maximum mortality, when selective pressure may also be high. By synthesising information from seemingly disparate events such as recruitment, behaviour, feeding ecology, and growth, it emphasises the interplay of these factors in determining the demography of young coral trout.

Coral reef fish populations have generally been found to vary on a number of spatial and temporal scales (reviewed by Doherty and Williams 1988). However, similar studies examining variation in post recruitment processes are few (Forrester 1990). This is despite the fact that roughly 99% of the potential life span of a reef fish occurs after settlement (Jones 1991). Studies investigating post-settlement processes have generally found that they have the potential to modify recruitment patterns (Aldenhoven 1986, Shulman and Ogden 1987), and in some cases have empirically demonstrated such effects (Robertson 1988, Hixon and Beets 1989). Considering the importance of events occurring both before and after settlement, the most parsimonious paradigm to describe coral reef fish demography may involve a scenario in which local densities reflect the balance between settlement and survivorship (Doherty 1991).

The evidence presented in this study indicates that variations in distributions and abundances of juvenile coral trout on Green Reef are primarily due to predation-mediated post-settlement processes acting upon spatial patterns and conditions established at settlement. Growth rate strongly influenced all aspects of post-settlement ecology. Growth is a sensitive indicator of available resources and is probably the medium through which inter- and intra-specific competition is expressed (Werner and Gilliam 1984). Rapid growth is of paramount importance, not only because it limits the duration of time spent in vulnerable size classes, but also because it results in the production of individuals that may dominate smaller fish in behavioural and competitive interactions. Thus, variations in growth may affect the timing of ecological transitions associated with shifts in habitat, diet, and behaviour.

Variations in growth rates of juvenile coral trout apparently are influenced by three major factors; pre-settlement growth history, size-selective mortality, and temperature. Size at settlement and pre-settlement growth rate explained much of the variation in post-settlement growth. Faster growing fish pass more rapidly through the predator field, and are therefore more likely to be represented in the resulting cohort. Several studies have concluded that relatively small difference in larval growth rates can have dramatic influences on the number of fish in a year class (Houde 1987, Miller et al. 1988, Pepin 1991). Another consequence of rapid larval growth is to produce individuals that settle earlier, and at larger sizes. In juvenile fish, size is often correlated with social dominance and acquisition of food (Coates 1980, Folkvord 1991). Tupper and Boutilier (1995) reported that for Atlantic cod (Gadus morhua), individuals settling earlier and at larger sizes were able to establish and defend larger territories, and consequently grew at faster rates than smaller settlers. In the present study, monthly cohorts had experienced different larval growth rates, and these were positively correlated with subsequent demersal growth. Thus, variations in planktonic growth may result in larger recruits, and competitive and predation-mediated mechanisms may extend this size advantage well into post settlement life.

Size-selective predation also appeared to be a major determinant of juvenile coral trout growth. Large body size can provide a refuge from predation (Werner and Gilliam 1984), and fast growth rates will reduce the amount of time that prey are in the more vulnerable size classes. Therefore, growth parameters and body size during early life may have a significant effect on which individuals recruit into larger size classes. In this study, juveniles surviving until later collections had experienced higher pre- and post-settlement growth than individuals collected earlier, suggesting that slow-growers had been consumed in preference to faster growing fish.

Water temperature was strongly correlated with post-settlement somatic growth, which resulted in pronounced seasonal variations among juveniles collected at different times of the year. This finding has implications for models forecasting growth dynamics for populations recruiting during different seasons, years, and at different latitudes. Future studies will be required to determine the extent to which temperature variations influence planktonic growth parameters for this and other reef species.

Although the results of this study indicate that size and growth histories of coral trout recruits are correlated with their later benthic growth, evidence from laboratory studies is equivocal. In separate studies, both Litvak and Leggett (1992) and Pepin (1992) found that predation rates of sticklebacks (Gasterosteus aculeatus) on capelin larvae (Mallotus villosus) were higher for larger prey. These authors suggested that larger, more active prey had a higher probability of encountering predators, despite larger larvae being less vulnerable due to superior size and mobility. McCormick (1992) used laboratory experiments to investigate predation rates of lizardfish Synodus variegatus on newly settled mullids (Upeneus tragula) and found that predation was random with respect to both size and condition. These studies indicate that the relationship between pre-settlement growth and demersal survival potential may vary between species and habitats.

Sites selected by coral trout at settlement were found to possess specific attributes; recruits were strongly associated with sand-rubble microhabitats. Furthermore, the rate at which recruits disappeared from habitats was related to the availability of this substratum, suggesting that shelter may be a limiting factor in determining abundance patterns. Finally, visual censuses around Green Reef recorded an overwhelming majority of recruits from sites adjacent to the reef front, which also had the highest proportional cover of rubble substrata. These observations support the hypothesis that distribution patterns of young P. leopardus among sites around Green Reef are primarily due to active selection of specific settlement sites, with subsequent modification by differential mortality. As with most coral reef fish (Doherty and Williams 1988) recruitment of coral trout is highly variable (Doherty et al. 1994). However, high variability does not necessarily imply that recruitment must be random with respect to features of the habitat, or that interactions with predators or competitors have no effect on distribution patterns.

Hypotheses predicting predation effects on reef fish populations are based on the premise that predators can cause prey to compete for refuge space (Holt 1987, Hixon 1991). Such predation-induced competition has been suggested as the means by which the allometry between shelter space and fish dimensions may limit population size (Randall 1963, Smith and Tyler 1972, Smith 1978). Moreover, several authors have reported that fish defend shelter holes (Robertson and Sheldon 1979, McFarland and Hillis 1982) indicating that suitable shelter is in short supply. In the present study, coral trout recruits quickly established sites that appeared to be selected on the basis of shelter characteristics (e. g. small bits of rubble which provided shelter that was very close to, or at the level of the sand bottom). Furthermore, they exhibited higher levels of intra-cohort agonism, and occupied more exclusive home ranges than larger recruits, suggesting that suitable shelter sites for these small fish were limited.

Although recruits were initially restricted to specific habitats, a major habitat shift occurred at about 60 mm SL, at which time individuals switched to association with high relief features, including coral heads and consolidated rubble mounds. During the course of ontogeny, prey fish may outgrow juvenile refuges, and/or be subject to a different range of predators, resulting in "ontogenetic niche shifts" between different microhabitats. In fish, size-specific ontogenetic habitat shifts are often correlated with diet shifts, as well as with discrete growth periods (Werner and Gilliam 1984). Juvenile coral trout were found to undergo a dietary transition towards piscivory, which roughly coincided with a shift to an alternate habitat. Moreover, the transition to piscivory was shown to vary spatially, and recruits from more structurally complex habitats shifted to a piscine diet at an earlier point, suggesting that shelter characteristics may influence the timing of major ecological transitions in juvenile coral trout.

Foraging styles of the smallest recruits also appeared to be mediated by predation pressure. The overall cryptic behaviour of these individuals, their close association with the substratum while foraging, and the association with multi-specific schools of heterospecific recruits all suggest that predation is a powerful influence on feeding behaviour at this point in ontogeny. Size-specific asymmetries were apparent in other types of behaviour as well: one year old fish spent more time moving between locations than smaller individuals, providing further evidence that behaviour patterns were modified by predation pressure.

6.2 CONCLUSION

Variations in juvenile coral trout distributions result from both planktonic and post-settlement processes. The interaction of biotic and environmental variables in the planktonic phase results in variations in recruit size, which are translated to differences in post-settlement growth. Following settlement, differential mortality selectively removes smaller and slower-growing individuals. Shelter from predation appears to be critical throughout the early post-settlement period

A major ecological transition in habitat, diet, and behaviour occurs after several months on the reef, which may be due to changing shelter needs, and the timing of this transition may vary spatially. This study indicates that coral trout recruitment, although variable, is not independent of habitat structure. When combined with recruitment information, investigations of post-settlement processes have the potential to contribute to our understanding of the way spatial patterns of population density vary through space and time.

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