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Patterns of movement of three species of coral reef fish on the Great Barrier Reef

Thesis submitted by

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for the degree of Doctor of Philosophy
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Abstract

The patterns of movement of three species of coral reef fish were investigated in two tagging studies on the Great Barrier Reef. In the first study, done within the lagoon at Lizard Island on the northern GBR, the frequency of movement of *Lutjanus carponotatus*, *Plectropomus leopardus* and *Siganus doliatus* within and among sites and three habitat categories were examined in a multiple capture-recapture fish trapping study spanning a period of 22 months. Rates of growth, mortality and tag loss were estimated from the capture-recapture data also. The second study was a large-scale tag-recovery program designed to estimate the extent of movement of *Plectropomus leopardus* within and among five individual coral reefs in the Cairns Section of the Great Barrier Reef Marine Park. The rates of loss of t-bar anchor tags and dart tags were compared as was the frequency of loss of different coloured t-bar anchor tags.

A total of 4,736 fish from 21 families and 109 species were trapped over the duration of the small-scale movement study in the Lizard Island lagoon. The catch was dominated by the Siganidae, Lutjanidae, Lethrinidae, Serranidae, Haemulidae and Acanthuridae, which collectively comprised over 88% of the catch at each site. *Siganus doliatus* and *Lutjanus carponotatus* were the two most common species and together accounted for 36 % of the total catch. *P.leopardus* was less common accounting for less than 5% of the catch at each site. Catch per unit effort (CPUE) of *P.leopardus*, *L.carponotatus* and *S.doliatus* varied among the three sites. However, the CPUE of each species was highest in the reef habitat and lowest in the sand habitat at all sites. Fish trappping proved to be an effective, but selective, technique to simultaneously sample these species of coral reef fish at many locations and across a variety of habitats with limited logistical support.

The patterns of movement of the three species within the Lizard Island lagoon were found to differ considerably. *P.leopardus* regularly moved among trapping positions and across habitat types while the movements of *L.carponotatus* and *S.doliatus* were considerably more restricted. The majority of individuals of *L.carponotatus* (68%) and *S.doliatus* (69%) were recaptured at the position of release while the majority (66%) of *P.leopardus* recaptures had moved among trapping positions. *L.carponotatus* exhibited a strong fidelity for the habitat of release. The frequency of movement among habitat categories for fish released in the reef habitat was considerably (although marginally significant) lower than for fish released in the patch or sand habitat categories. *S.doliatus* was found to show a strong fidelity for the habitat of release also.

However, the frequency of movement among the reef and patch reef habitats was higher than observed for *L.carponotatus*. This may be related to be related to foraging patterns of siganids which feed over the reef flat at high tide. The results indicate that the movements of *L.carponotatus* and *S.doliatus* are generally restricted to less than a few hundred meters with the majority of fish not moving from their position of release. The frequency of movement of *L.carponotatus* and *S.doliatus* across reef-sand habitat boundaries was considerably lower than the frequency of movement across reef-patch reef or patch reef-sand habitat boundaries. This suggests that reef-sand habitat boundaries may represent less permeable management boundaries than arbitrary boundaries located within continuous sections of reef mosaic.

Estimates of survivorship for each species were made from the multiple capture-recapture data using program RELEASE version 2.6. The estimates of survivorship for *L.carponotatus* and *S.doliatus* for the reef and patch reef habitats suggested that survivorship was higher (but not significantly at α= 0.05) in the reef habitat than in the patch reef habitat. There were insufficient data to examine the effect of habitat on survivorship for *P.leopardus*. Estimated survivorship also appeared to vary among sampling periods. The estimates of survivorship were adjusted for tag loss and converted to estimates of annual rate of natural mortality. These were very high for each species, in comparison to estimates available in the literature, which suggest that there may have been a significant effect of capture and tagging. The results suggest that survivorship may vary among habitats and over time. Consequently, the common assumption of constant mortality within and among populations and over time requires greater scrutiny.

Rates of growth for *P.leopardus*, *L.carponotatus* and *S.doliatus* were estimated using growth increment data from the small-scale tagging study. Estimated von Bertalanffy growth equation parameters, L_∞ and K, were 576 mm and 0.21 for *P.leopardus*, 357 mm and 0.12 for *L.carponotatus* and 201 mm and 0.71 for *S.doliatus*. There was evidence of high individual growth variability for each species. This, combined with the lack of data for individuals in the lower end of the size range of each species, suggests that the estimates of L_∞ are likely to be positively biased, and hence the estimated K negatively biased. The age-based parameter estimates for *L.carponotatus* obtained from the same location suggested this was the case, with L_∞ and K estimated to be 312 mm and 0.31, respectively. There was considerable variation in size at age for *L.carponotatus*, again suggesting that there may be significant variation in growth among individuals. This highlights the need for age-based estimates of population parameters for

coral reef fish as length is likely to be a poor proxy for age. The relationship between estimates of age from readings of sectioned and whole otoliths and otolith weight were examined for *L.carponotatus*. Readings of whole and sectioned otoliths were the same up until age 5-6 after which readings of whole otoliths tended to underestimate age relative to readings of sectioned otoliths. There was a high correlation ($r^2 = 0.94$) between otolith weight and age from sectioned otoliths of *L.carponotatus*, indicating otolith weight may be an objective and cost-effective alternative for obtaining age-based estimates of population parameters for some coral reef fish.

All *P.leopardus* and *L.carponotatus* were double tagged in both studies. The Bayliff and Morbrand model was used to estimate rates of tag loss. Type I tag loss was not significant for *L.carponotatus*. However, the instantaneous rate of loss of t-bar anchor tags was high (0.0034, ±95% CI = ±0.0021). Type I tag loss was significant for t-bar anchor tags for *P.leopardus*. The estimate of the proportion of tags remaining following type I tag loss for *P.leopardus* was 0.8927 (95% CI = 0.8140-0.9791), while *L*, the instantaneous rate of tag loss was 0.0010 (±95% CI = ±0.0005). The estimated proportion of t-bar anchor tags lost annually were 72% and 60% for *L.carponotatus* and *P.leopardus*, respectively. This clearly demonstrates that tag loss rates can be substantial and assuming they are negligible will result in seriously biased parameter estimates. Dart tags were found to be shed at a significantly greater frequency than t-bar anchor tags (Likelihood $\chi^2_{0.05,1,} = 10.678$; $p < 0.005$) suggesting that t-bar anchor tags are the less effective of the two tag types used. The colour of the t-bar anchor tags used didn't significantly effect their frequency of loss (Likelihood $\chi^2_{0.05,5,243} = 1.902$; $p < 0.8625$). This demonstrates that different colours of tag may be used to batch code releases of reef fish without incurring differential frequencies of tag loss due to the colour of the tags.

A total of 8,043 fish were caught from the five reefs over five trips of the large-scale tagging study. Catch was dominated by Serranidae, Lutjanidae and Lethrinidae which comprised greater than 97% of the total catch. The species composition was dominated by six species, *Plectropomus leopardus* (57%), *Cephalopholis cyanostigma* (12%), *Lutjanus carponotatus* (6%), *L.bohar* (3%), *Lethrinus miniatus* (3%) and *L.atkinsoni* (4%). The contribution of these six dominant species to the catch varied significantly among trips and reefs. *Plectropomus leopardus* comprised a greater proportion of the catch on the trips done during the spawning season (September 1992 and October 1993). This may indicate an increase in the catchability of *P.leopardus* during the spawning season. The difference among reefs was mainly due to the higher proportion of *Cephalopholis cyanostigma* and *Lutjanus bohar* and the lower proportion of *Lethrinus miniatus* and *Lutjanus carponotatus* at two reefs compared to the other three reefs studied. Catch Per Unit Effort of *P.leopardus* varied significantly among trips and within reefs. However, there was no significant difference in CPUE among reefs. The pattern of CPUE among trips and within reefs indicated that the observed increase in CPUE that occurs during the spawning season is likely to be the result of an increase in the catchability of *P.leopardus* when the fish are aggregated to spawn.

The average size (mean length to caudal fork) of *P.leopardus* decreased significantly over the five trips, with a monotonic reduction in average size from April 1992 to February 1994. Mean size of *P.leopardus* varied significantly among reefs and blocks (1.5-2.5 km strip of reef perimeter) also, with Taylor Reef having a significantly greater average size than the other reefs and Beaver Reef having a significantly smaller average size than all other reefs. Although the overall reduction in mean size of *P.leopardus* across all reefs is indicative of fishing and cause for concern, in the absence of size-at-age information it is not possible to accurately interpret these effects in terms of differences in the population dynamics of *P.leopardus* among reef or over time. The significant effect of block on mean length of *P.leopardus* suggests that there may be significant differences in either age-structure or growth rates within reefs also. These results highlight the need for rigorous and powerful sampling programmes, which include within reef strata, for monitoring changes in relative abundance and size and age-structure of exploited populations of coral reef fishes.

A total of 4,627 *P.leopardus* were tagged and released on the five reefs with a total of 443 recaptured; 300 from the public and 143 from the four tag-recovery exercises. Ninety-nine percent of the research returns of *P.leopardus* were returned from the reef of release. One inter-reef movement was recorded from Taylor to Beaver Reef. These results indicate that the extent of inter-reef movement was negligible. In contrast, 36% of the public returns were returned from reefs other than the one on which they were released. The majority of inter-reef movement from the public returns was from Beaver (Closed) to Taylor reefs and from Potter Reef to other reefs in the cluster. The disparity in the extent of inter-reef movement of *P.leopardus* from Beaver Reef (Closed to fishing) between the public and research returns appears to be the result of infringement and misreporting of location of capture by the public. It is suggested that the level of fishing effort on Beaver Reef (Closed to fishing) indicated by the tag returns may be sufficient to negate the potential effects of protection from fishing. This was supported circumstantially by the CPUE and length frequency data for *P.leopardus*. In contrast to the negligible level of inter-reef movement by *P.leopardus*, there was considerable movement within reefs. On average 35% of the *P.leopardus* returned had moved out of the 1.5-2.5 km block in which they were released. The extent of movement varied among reefs and appeared to be related to movement to, or from, spawning aggregations. The results of the large-scale movement study suggest that partial reef closures may not effectively protect the populations of more mobile reef fish such as *P.leopardus*, due to their relatively high frequency of movement within reefs, and that it would be more effective to use individual reefs as the minimum spatial unit for reserve design.

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Chapter 1

Introduction

1. Introduction

Coral reef fish stocks support important commercial, recreational and artisinal fisheries around the world. These stocks are receiving an increasing level of fishing pressure due to a combination of factors, including; rapid population growth in tropical regions, expanding recreational fleets and the relative proximity of many coral reefs to major population centers. Marine Fisheries Reserves (MFR) have been widely touted as a potential technique to maintain, or enhance, reef fish stocks by protecting a minimum proportion of the stock from exploitation. An implicit assumption of this approach is that movement of adults from designated refugia is minimal. However, there is little data available on the extent to which reef fish (tropical or temperate) move within or among individual reefs. The objective of this research was to determine the extent to which coral reef fish move within and among the major spatial scales found on coral reefs, *ie* within and among habitats and within and among individual coral reefs.

1.1 Coral reef fisheries

In most tropical regions of the world coral reef fish communities are exploited by various types of fishing (Russ 1991). Levels of exploitation are particularly high in the islands of South-east Asia and the Caribbean, where fish is the major source of animal protein for rapidly expanding populations, and fishing provides one of the only sources of income and employment in depressed economies (Munro 1983; Koslow *et al* 1988; Russ 1991). In the face of uncontrolled fishing effort and markets for most sizes and species of reef fish, many of the reefs in these regions are over-exploited (Russ 1991), in some cases to the extent of ecosystem overfishing (Koslow *et al* 1988; Russ and Alcala 1989; Hughes 1994). Clearly, there is an immediate need to manage these fisheries in a more sustainable manner. However, unless the socio-economic problems of these regions improve, the very existence of these reefs and their fisheries may be under threat (Munro and Williams 1985; Russ 1991).

High levels of fishing pressure on coral reefs and its effects are not confined to artisinal and subsistence fisheries in developing regions. Reef fish stocks in the southern United States have been fished to dangerously low levels of spawning stock biomass by commercial and recreational fisheries (Plan Development Team (PDT) 1990). This has occurred even though this fishery is perhaps the best studied coral reef fishery in the world (Russ 1991). On the Great Barrier Reef

(GBR) there is also concern over the effects of present levels of commercial and recreational effort on the sustainability of the reef line fishery (Craik 1979,1989; Goeden 1980; 1982; Gwynne 1990; Blamey and Hundloe 1993; Williams and Russ, 1994). Hence, there appears to be a general need around the world for more effective management of coral reef fisheries.

A number of factors have impeded successful management of coral reef fisheries. They include their complexity, the lack of basic demographic information for even major target species and a general paucity of funding for research and management in comparison to larger, more economically important fisheries (PDT, 1990; Russ 1991). Furthermore, and perhaps most importantly, in most coral reef fisheries there is little or no control of fishing effort (Munro, 1987). This is often due to a lack of alternative opportunities for employment or, as is the case of the United states, statutory limitations, which make reduction of fishing effort difficult, if not impossible (Munro 1987; PDT, 1990; Russ 1991). The combined effect of these factors makes the implementation of conventional harvest strategies, such as constant stock size or constant exploitation rate, effectively impossible.

The complexity of coral reef fisheries results as much from the heterogeneity of the fishery as from the diverse range of life history characteristics displayed by reef fish. Coral reef fisheries are multispecific, involve a diverse range of gears, including hook and line, spear, traps, trawls and gill nets, and catches are landed at a large number of small sites spread over a wide geographic area. Consequently, basic catch statistics are rarely available (Munro 1987; PDT, 1990). Furthermore, even when catch statistics are available, they are generally not sufficiently detailed to satisfy the intense data requirements for multispecies stock assessment models (PDT 1990; Hilborn and Walters 1992; but see Ralston and Polovina, 1982).

The ecological diversity of coral reef fisheries results from the extreme range of life histories displayed by coral reef fishes and their inter- and intra-specific interactions. For example, small, planktivorous fusiliers, such as *Pterocaesio pisang*, which have a maximum longevity of 2-3 yrs (Russ *et al* 1993), may be harvested within the same fishery as large epinepheline groupers that grow to three meters in length and live for over thirty years (Bullock *et al* 1992). Obviously, the population dynamics of such species will differ dramatically, as will their population response to different fishing regimes. Consequently, a harvesting strategy which may be optimal for one species is unlikely to be optimal for others (Dugan and Davis 1993b).

Although population parameters may vary considerably among species of coral reef fish, a number of common life-history characteristics have been identified which may make them more vulnerable to overfishing than species which commonly support higher latitude fisheries. As many species of coral reef fish exhibit strong habitat and depth preferences (Munro and Williams, 1985; Williams 1991) they may be targeted very efficiently with specific gears (Russ and Alcala 1989). They are commonly considered to be sedentary or territorial, with limited home ranges and mobility also (Ehrlich 1975; Sale, 1980; 1991; PDT 1990; Russ 1991). As a result, it may be possible to concentrate fishing effort to a greater extent on coral reef fishes than is possible in higher latitude fisheries, where the stocks are more widely ranging and distributed (Koslow *et al*, 1988). Consequently, coral reef fish stocks may be particularly vulnerable to local depletion. This has led many workers to suggest that spatial closures may be an effective technique for the management of reef fish stocks (Davis 1977; Davis and Dodrill 1980; Russ 1985,1989,1991; Alcala 1988; Buxton and Smale 1989; Davis 1989; Russ and Alcala 1989; Alcala and Russ 1990; Roberts and Polunin 1991,1993; PDT 1990; Dugan and Davis 1993 a&b; Polunin and Roberts 1993).

1.2 Marine Fishery Refugia

The concept of Marine Fishery Reserves (MFR), defined as permanent spatial closures to fishing, has received substantial attention recently as a potential management tool for exploited stocks of reef fish (Davis 1989; Alcala and Russ 1990; PDT 1990; Roberts and Polunin 1991,1993; DeMartini 1993; Dugan and Davis 1993a; Russ *et al* 1993). Much of the enthusiasm for MFR has arisen from the perception that conventional fisheries management techniques, based on input or output controls, are inappropriate or ineffective for complex multispecies reef fisheries and that MFR may represent a viable alternative (Munro and Williams, 1985; PDT 1990; Roberts and Polunin 1991; Russ 1991). However, despite a growing literature on MFR and their potential benefits, there is little empirical evidence with which to evaluate their potential to maintain or enhance yields of reef fisheries (Roberts and Polunin 1991; Dugan and Davis 1993a).

A number of potentially beneficial effects of MFR have been identified (Davis and Dodrill 1980; Russ 1985; PDT 1990; Roberts and Polunin 1991; Dugan and Davis 1993b; Carr and Reed 1993). Those more directly related to maintaining or increasing fisheries yields include:

conservation of spawning stock biomass above a critical minimum, provision of a source of recruitment for surrounding fished areas, maintenance of population age structure, protection of intraspecific genetic diversity, an insurance policy against management failure in areas open to fishing, enhancement of yield in the area immediately surrounding MFR through emigration, simplified enforcement and ease of public understanding.

There is some evidence to suggest that implementation of MFR will increase the abundance and size of target species and overall species diversity of fish within the MFR relative to adjacent fished areas (see reviews by Russ 1991, Roberts and Polunin 1991 and Dugan and Davis 1993b and references therein). However, empirical evidence of the effect of MFR on reproductive output of the protected part of the stock or on levels of recruitment in fished areas adjacent to the MFR is not available for either temperate of tropical reef fishes (Dugan and Davis 1993b) and there is little information on the extent of movement of adult fishes across MFR boundaries (Roberts and Polunin 1991; DeMartini 1993). Furthermore, there is only one empirical example to suggest that MFR will enhance yields of coral reef fishes in adjacent fished areas (Russ 1985; Alcala, 1988; Alcala and Russ, 1990). Thus, despite the cited potential benefits of MFR, their ability to enhance or maintain yields of reef fishes remains virtually untested.

The potential of MFR to maintain or enhance yields of reef fishes in adjacent fished areas will depend on two main mechanisms: 1) the export of larvae which recruit to adjacent fished areas, and 2) movement of post-settlement stages (adults or juveniles) from the MFR to the adjacent fished areas (Davis 1977; Russ 1985; Polacheck 1990; PDT 1990; Roberts and Polunin 1991; DeMartini 1993; Dugan and Davis 1993b; Carr and Reed 1993). The relative importance of these two mechanisms will depend on the abundance and spawning potential of the reserve population, the population dynamics and exploitation schedules of the target species and the relative rates of transfer of post-settlement and larval life-history stages across reserve boundaries. There is little empirical evidence to evaluate the potential of these mechanisms to enhance fishery yields in fished areas adjacent to MFR. However, two recent simulation studies have provided some insight into their relative importance.

Russ *et al* (1994) modelled the effect of random fluxes of adults of a small caesionid, *Pterocaesio pisang*, across reserve boundaries on yield per recruit (Y/R) at Sumilon Island, central Philippines. They found that the presence of a 25% spatial closure would only increase Y/R at moderate to high levels of fishing mortality (F=2.5-4.0) and that this increase would be relatively small. They concluded that the increase in total yield at Sumilon Island in the presence of a 25% closure, documented by Alcala and Russ (1990), may have resulted from active emigration of adult fishes from higher density in the reserve to the adjacent fished area of the reef. They highlighted the need for quantitative estimates of rates of flux of adults across reserve boundaries for effective design of MFR.

DeMartini (1993) simulated the effects of MFR on spawning stock biomass per recruit (SSB/R) and Y/R of three "model" types of coral reef fish over a range of reserve sizes, transfer rates and fishing mortalities. The results of his extensive simulations supported the findings of Polacheck (1990) and Russ *et al* (1994), in that MFR will only increase Y/R at high levels of fishing mortality and relatively high rates of transfer. Under such circumstances any increase in yield is likely to be restricted to the area immediately surrounding the reserve.

In terms of SSB/R, the DeMartini (1993) demonstrated that MFR could enhance SSB/R significantly. Maximum gains in SSB/R were found for a fast growing, relatively vagile "surgeonfish" type, with life-history characteristics selected to be typical of many medium-sized reef fish. Gains in SSB/R for the larger, "jack" species, characterised by greater longevity, lower rate of natural mortality and higher age at recruitment and sexual maturity, were only attainable with large MFR size and relatively low fishing mortality (F=0.3). Importantly, the simulations indicated that even small compensatory increases in rates of emigration from the MFR, which may result from density gradients between MFR and adjacent fished areas, will potentially negate the observed gains in SSB/R due to the presence of the reserve (DeMartini 1993).

These simulation studies clearly demonstrated the need for estimates of movement of adult fishes across reserve boundaries to evaluate the effectiveness of MFR as a management tool for coral reef fisheries. This applies not only in terms of their potential as growth refuges and to increase Y/R, but particularly for their potential to increase SSB/R by effectively protecting a proportion of the spawning stock. Furthermore, the potential influence of growth and mortality schedules on Y/R and SSB/R from MFR (DeMartini 1993) highlights the need for estimates of rates of growth and mortality and size at maturity for exploited species.

1.3 The role of movement in the population dynamics of large reef fish

The role of movement in population dynamics has received relatively little attention in the ecological literature (Hestbeck *et al* 1991; Nichols 1992). The central debate in reef fish ecology over the past fifteen to twenty years has focused on the relative importance of recruitment variation and post-settlement processes in determining the abundance and distribution of reef fishes (for reviews see Sale, 1991 and chapters therin). The extensive literature on capture-recapture models is almost entirely devoted to the estimation of rates of mortality, capture probabilities and population size (Nichols 1992). More recently, the failure of these hypotheses and models to satisfactorily explain the dynamics of many animal populations has resulted in an increasing focus on the influence of movement (immigration/emigration) on population regulation (*eg*. Robertson 1988; Hestbeck *et al* 1991; Hilborn and Walters 1992; Schweigert and Schwarz 1993).

Movement may influence the dynamics of reef fish populations in ways which are important both to our understanding of their ecology and for their management. The description of the distribution and abundance of populations in space and over time forms a major component of ecological study (Andrew and Mapstone 1987). Movement may result in changes in distribution and abundance over a variety of spatial and temporal scales, including: diel migrations to feeding grounds (Hobson 1972;1973; Helfman *et al* 1982; Holland *et al* 1993), ontogenetic shifts among habitats (Beaumariage 1969; McFarland 1979; Quinn and Kojis 1985; Smith and Jamieson 1990; Frank 1992; Nakashima 1992; Rountree and Able 1992), spawning migrations (Johannes 1978; Johannes and Squire 1988; Hampton 1991a; Colin 1992; Samoilys and Squire 1994) and movement in response to density gradients and, or, exploitation (Robertson 1988; Hilborn and Walters 1992). Incorporating estimates of movement into models of population dynamics of reef fish may substantially increase our understanding of the mechanisms which regulate their abundance and distribution (Robertson 1988).

There are several potential effects of movement on stock assessment and management of reef fishes. Changes in the distribution of exploited species, as a result of directed movement, can potentially bias estimates of stock size from catch per unit effort (CPUE) data by maintaining a constant density in fished areas even as the total stock size is reduced (Hilborn and Walters, 1992). As already outlined above, the extent of movement across management boundaries between fished and unfished areas will be a critical factor in determining the effectiveness of MFR to enhance SSB/R and Y/R (Polacheck 1990; DeMartini, 1993; Russ *et al*, 1993).

The importance of movement among spatial strata applies also to adaptive management experiments designed to examine the response of fish populations to varying levels of fishing effort (Walters and Hilborn 1976,1978; Walters 1986). In this case, compensatory movement of target species among experimental replicates in response to fishing may effectively mask imposed treatment effects (Walters and Sainsbury, 1990). Knowledge of patterns of movement is also important in determining the boundaries of fish stocks and the extent of fishery interactions, relationships between spawning, nursery and feeding sites within a stock and estimating rates of survival and exploitation (Sibert 1984; Hilborn 1990; Schwarz and Arnason 1990; Hampton 1991a).

Despite the potential importance of movement in ecology, stock assessment and management, there is relatively little information available on the extent of movement of species of commonly exploited reef fish (PDT, 1990; Roberts and Polunin, 1991; Williams and Russ, 1994). This is in part due to the fact that a large proportion of research on the population dynamics and ecology of coral reef fish has concentrated on small, sedentary pomacentrids and labrids as model species (reviewed in Sale 1991 and chapters therein). These species are abundant, can be censused visually and are amenable to manipulation. This makes them ideal candidates to experimentally investigate the relative importance of pre- and post-settlement processes. Generally, these studies have incorporated small patch reefs (natural or artificial) separated by expanses (<50 m) of open sand and their focus has been the relative importance of pre- and post-settlement processes in the dynamics of reef fish populations. In these studies, movement among replicates has generally not been considered and all losses have generally been assumed to be the result of mortality, as migration among patch reefs is considered unlikely (Doherty and Williams, 1988; Hixon and Beets 1993).

These studies may have biased the perception of the importance of movement in the population dynamics of reef fishes. The study species are small, generally display the same specialised habitat requirements at settlement and as adults, and often have complex social organisation within individual aggregations (Sweatman 1985; Doherty and Williams 1988). As such, they are likely to lie at one extreme of the spectrum of life-history traits of coral reef fish. Secondly, the use of isolated patch reefs is likely to reduce the probability of movement in comparison to areas of continuous reef mosaic (Doherty 1983; Robertson 1988). On the basis of these studies alone, there appears to be little reason to assume *a priori* that larger species of reef fishes, such as serranids, lutjanids and lethrinids, will display the same degree of site attachment.

There are relatively few studies in which directly estimating the extent or degree of movement of large coral reef fish has been the primary objective. Several studies have demonstrated that individuals of various species of large reef fish may be resighted or recaptured in the same location for periods ranging from a few days to over a year (Bardach 1958; Randall 1961; Beaumariage 1969; Samoilys 1986; Recksiek *et al* 1991; Hixon and Beets 1993). This has generally been inferred as evidence of their sedentary, site attached nature. However, a feature of many of these studies has been that recapture effort has generally not been distributed beyond the release sites, the majority of the returns are recaptured shortly after release in close proximity to the release sites, and the duration of the studies have been short in relation to the average longevity of the target species. Consequently, the generality of the results are restricted to relatively small spatial (100's m) and temporal (< 1 yr) scales.

Bardach's (1958) study of movement of reef fish in the Virgin Islands is often cited as an example of the limited mobility of coral reef fish (PDT 1990; Recksiek *et al* 1991). Bardach conducted two separate experiments; a "homing" experiment in which fish were translocated between adjacent reefs (about 500 m apart) and monitored over a period of eighty days, and a study of the movements of several species within one reef over a period of about 3 months. The "homing" experiment demonstrated that the majority of the serranids (*Epinephelus guttatus* and *E. striatus*) returned to their original reef, while less than 5% of the translocated pomacanthids were capable of homing. The second study demonstrated that the serranids ranged over a considerably larger area within a single patch reef (approximately 100 m in diameter) than the pomacanthids. Bardach suggested that the maintenance of a larger home range, and thereby familiarity with the area to which they had been translocated, may have explained the ability of the serranids to return to their original reef.

Bardach also observed that there was a high level of "natural turnover" among the study reefs and suggested that no serranid stayed on the study reefs for more than one month. Therefore, while Bardach (1958) certainly demonstrated the ability of large reef fish to return to their original location of capture, he equally clearly demonstrated that they naturally range over considerable areas, including large expanses of open sand, and raised the question of the temporal stability of home ranges.

More recent studies of the coral trout, *Plectropomus leopardus* (Serranidae), on the Great Barrier Reef (GBR) have indicated that this species may regularly range over large areas within individual coral reefs. Samoilys (1986), in a study combining tagging and underwater observation at Heron Island on the southern GBR, found that although the majority of *P.leopardus* resighted were located within an 18,000 m^2 study area, they were estimated to spend 90% of their time outside that area. Furthermore, over 40% of the *P.leopardus* tagged were never resighted. She concluded that although *P.leopardus* showed some affinity for certain locations, particularly cleaning stations, they generally ranged over a much larger area (> 2,000 m^2).

Beinssen (1989b; 1990) observed considerable movement of *P.leopardus* within a 4 km section of reef crest at Heron Island on the southern GBR. The study site included a boundary between Marine Park B (closed to fishing) and Marine Park A (open to limited fishing). Twenty-nine percent of the *P.leopardus* resighted over a period of approximately three weeks were found to have moved out of the 500m section of reef in which they were originally released (Beinssen 1989b). A second survey, done three months after the initial release, suggested that the overall density of *P.leopardus* had decreased by almost 50% and that the dispersion of *P.leopardus* throughout the study site had continued (Beinssen 1990). Results for two other species, *Lethrinus miniatus* and *Lutjanus adetii*, from the same study indicated that they dispersed through the study site with time also, although at a lower rate than *P.leopardus*. Beinssen suggested that the practice of closing a section of an individual reef to fishing, with the objective of protecting a part of the population from effects of fishing, may not be effective for *P.leopardus* due to the extent this species moves within reefs.

The information available on movement of large reef fish suggests that the extent of movement varies considerably among species and, although a large percentage of fish may remain in the same area over the short-term, there is a tendency for individuals to disperse with time. In the case of medium to large serranids, they may move considerable distances (up to several kilometres) within individual reefs over relatively short periods (a few months). The majority of studies have focussed on detailed movements at relatively small sites within individual reefs. Furthermore, the sampling effort in the majority of studies has been concentrated into a few periods and the total duration of the study has generally been less than a year. Consequently, our present knowledge of movement of large reef fish is confined to relatively small spatial and temporal scales. In order to evaluate the importance of movement in the population dynamics of exploited reef fish and the management of reef fisheries, information on the extent of movement on large spatial scales, particularly among individual reefs, over longer periods is required.

1.4 Age, growth and mortality of coral reef fish

Until relatively recently, coral reef fishes were generally perceived to be short lived and fast growing with relatively high rates of natural mortality (Ehrlich 1975; Sale 1980). This was largely due to a lack of age determination studies of tropical species as a result of the perception that they did not deposit daily or annual bands due to the lack of seasonal variation in the tropics (Longhurst and Pauly 1987). Subsequently, annual bands have been documented to occur in hard parts (principally otoliths) in a wide range of genera of tropical reef fish (*eg*. Pomacentrids: Fowler 1990; Epinepheline serranids: Ferreira and Russ 1991;1993; Bullock *et al* 1992; Lutjanids: Davis and West 1992; Newman 1995; Sheaves 1995; Scarids: Lou 1992;1993). These studies have demonstrated that tropical reef fish are considerably longer lived than previously considered and have correspondingly lower rates of growth and natural mortality.

Greater longevity and lower rates of growth and mortality of exploited species have considerable implications for the effectiveness of MFR. DeMartini (1993) used estimates of longevity, growth and mortality derived from a variety of published sources to provide parameters estimates for three "typical" types of reef fish; a *pomacentrid*, *surgeonfish* and *jack*. The maximum longevity estimates used for each of the three fish types were 3, 5 and 15 years for the *pomacentrid*, *surgeonfish* and *jack*, respectively. The results of recent age determination studies suggest that the parameter estimates used for the long lived, slow growing, low mortality *jack* are likely to be representative of many small to medium reef fish. This includes many of the smaller serranids, lutjanids, scarids and acanthurids, that were classified the *surgeonfish* type, and which are commonly exploited in many coral reef fisheries. If this is the case, significant gains in SSB/R for these species may only be achievable with large reserves and low levels of fishing effort, unless the transfer rates of these species between the reserves and fished areas are low.

1.5 Objectives and outline of this thesis

The complexity of coral reef fisheries, and the failure of traditional fisheries management techniques to effectively manage them, has resulted in an increased interest in the potential of Marine Fisheries Reserves as a management alternative. While intrinsicly appealing in theory, there is limited empirical evidence on which to evaluate their potential effectiveness or to use as a basis for reserve design. The need for quantitative data on movement of target species at spatial scales appropriate to their management has been widely identified as a priority (PDT 1990; Russ 1991; Roberts and Polunin 1991; Dugan and Davis 1993; DeMartini 1993; Russ *et al* 1993).

The central objective of this thesis was to estimate the extent of movement of large coral reef fish within and among the major spatial scales found on coral reefs, with the aim of providing information that could be used to evaluate the effectiveness of spatial closures (MFR) as a management tool for coral reef fish. This was achieved through two separate tagging studies; i) a small-scale study of patterns of movement of three species of coral reef fish among habitats and sites within an individual reef, and ii) a large-scale study of the patterns of movement of the epinepheline serranid, *Plectropomus leopardus,* within and among five individual coral reefs separated by distances ranging from 200 m to 10 km.

1.5.1 Small-scale study

The small-scale study was done in the Lizard Island lagoon on the northern GBR and was based on a multiple capture-recapture study that covered spatial scales from 100 m, within and among habitats, to kilometres among sites. The principle objective of the study was to estimate the extent of movement of three species of reef fish, *Plectropomus leopardus*, *Lutjanus carponotatus* and *Siganus doliatus*, within and among three major habitat categories and three sites within the lagoon (Chapter 6). The species were selected to provide a range of life history characteristics. A secondary objective of the study was to obtain estimates of rates of growth (Chapter 4), tag loss (Chapter 5) and natural mortality (Chapter 6). The general methods for the small-scale study are described in chapter 2 and the catch composition and catch per unit effort from the trapping study are presented in chapter 3.

1.5.2 Large-scale study

The large-scale study involved a tagging programme at a cluster of five reefs in the central GBR over a period of approximately two years. The objective was to examine the patterns of movement of the common coral trout, *Plectropomus leopardus*, at spatial scales of a few kilometres within individual reefs to tens of kilometres among individual reefs. The catch statistics from this study are the subject of chapter 7. The large-scale patterns of movement of *P.leopardus* are examined in chapter 8.

The results of each of the data chapters are drawn together in chapter 9 (General Discussion), where their implications are discussed with respect to the potential effectiveness of MFR as a management tool for reef fisheries, and priorities for future research are identified.

Chapter 2

Sampling design and methods for the Lizard Island lagoon study

2.1 Introduction

A multiple capture-recapture study was implemented to describe the small-scale patterns of movement and rates of mortality and growth of three common species of reef fish within the lagoon at Lizard Island. Fish traps were used to implement a sampling design in which the total sampling effort was evenly distributed across the study area in the form of 3 permanent trapping grids which were sampled 7 times over a period of 21 months. This chapter describes the study site, experimental design and sampling schedule, trap design and trapping and tagging methods of that study. The sampling design and methods described in this chapter are of direct relevance to chapters 3, 4, 5 and 6.

2.2 Study site

The study was done in the lagoon of Lizard Island (Lat. 14° 40' S Long. 145° 28' E) (Figure 2.1) on the northern GBR between 20 July 1990 and 24 November 1992. Lizard Island is a high (continental) island, located approximately 30 km from the east coast of north Queensland, Australia. Lizard and two neighbouring islands, Palfrey and South, enclose a triangular lagoon (Figure 2.1). The lagoon is relatively shallow, ranging in depth from 1 - 15 m and has been protected from fishing since 1983 (GBRMPA, 1983).

Three sites were established within the Lizard Island lagoon so that each site covered one of the three major entrances to the lagoon and so that the sites were relatively equally spaced within the lagoon (Figure 2.1). The sites were separated by approximately 300-500 m and hereafter will be referred to as Loomis, Mangrove and South (Figure 2.1).

Loomis was the shallowest of the three sites (1 - 5 m). The majority of Mangrove was also shallow (1 - 5 m), however, the eastern border of this site extended into the main channel of the lagoon (8 - 10 m). South had the greatest depth range of the three sites (1 - 14 m) with approximately 40 % of the site being deeper than 5 m.

Three major categories of habitat were identified within the lagoon: i) *Reef* - defined as consolidated reef structure. ii) *Patch reef* - defined as small patch reefs (< 10 m in diameter) interspersed by areas of open sand. iii) *Sand* - defined as large expanses of open sand, devoid of any major structural features. The number of trapping positions in each habitat category at each site are given in Table 2.1. The number of trapping positions in each habitat at each site was proportional to the occurrence of the habitat at each site as the positions were distributed in a systematic sampling grid (see below - 2.3.1).

2.3 Sampling design and sampling schedule

2.3.1 Trapping grids

A regularly spaced permanent trapping grid was marked at each site. Each grid consisted of 36 trapping positions in a 6 x 6 configuration marked with steel pickets hammered into the substratum. Adjacent positions were approximately 100 m apart. Thus, each site was approximately 500 m x 500 m and covered a total area of about 250, 000 m^2 (Figure 2.1).

The location of each picket within each grid was determined in the following way. The western boundary of each grid was marked by divers on SCUBA. A compass was used to ensure each position was in line and two 50 m measuring tapes used to ensure the positions were separated by 100m. A buoy attached to a 600 mm long metal picket was used to mark each position. The bearing of the row and the alignment of the positions were checked from the boat and any positions deviating from the main bearing were corrected. When all positions were correctly aligned the pickets were driven into the substratum with a sledge hammer.

This procedure was very time consuming. Consequently, a more efficient method was developed for locating the remaining stations on each grid. The western boundary transect of each site was used to calibrate the time taken for the boat to travel, at full speed, the 100 m between adjacent stations. The boat was driven along the entire length of the transect at full speed and the time taken to travel each 100m interval between positions was measured using a digital stop watch. Three replicate runs were made along the western boundary row at each site, giving 15 estimates of the time taken to travel 100 m. The mean of the 15 time intervals was used as the time taken by the boat to travel 100m. Care was taken to ensure the boat was at full speed before commencing each run and all runs were done in the same direction at each site.

The remaining transects of each grid were marked from the boat using the compass bearing of the western boundary and the estimated time taken for the boat to cover 100 m. The boat was driven at full speed along the prescribed compass bearing and buoys attached to metal pickets were dropped from the side of the boat at the mean time interval. The position of each picket was adjusted following the completion of each run so that all six stations within each row lay along the correct bearing. The pickets were then hammered into the substrate on snorkel. Using this procedure it was possible to mark an entire grid within a day.

Each station was marked initially with a surface buoy for ease of location from the boat. However, considerable loss of buoys due to boat traffic and rough weather resulted in subsequent removal of the majority of the buoys to avoid further losses. Large (300 mm) "dan" buoys were used to mark the corners of the grids and act as reference points for the remaining trips. The original pickets within the grid were then marked with flag tape or, in the case of deeper positions, with sub-surface buoys, which could be located easily from the surface.

2.3.2 Trap sampling protocol

Each of the trapping grids was sampled using six traps. Thus, eighteen traps were deployed at any time. Eighteen was the maximum number of traps which could be hauled and reset within a day given the logistic support available. Three day soaks were used throughout the study as they included the optimum length of soak for the target species; *Plectropomus leopardus, Lutjanus carponotatus* and *Siganus doliatus* (Davies, 1989).

Traps were set in rows of six traps at each site and fished without buoys. The rows were orientated so that where possible a combination of the three habitat categories were sampled during each set. It took six sets of six traps to sample all stations within each grid. Thus, using 3 day soaks and 18 traps in total, it took at total of 18 days to trap the 36 stations in each grid at all sites. The row first sampled in each grid sampling was randomly selected (with replacement) from the 6 possible rows at each site. The remaining rows were sampled sequentially according to their location with respect to the initial row.

The time taken to haul, clear and reset the traps varied according to the number of fish caught and the weather conditions. Large catches increased the catch processing time whilst rough weather conditions increased both the time required to locate traps and the travelling time between traps and sites. On average it took approximately 2.0 - 2.5 hr /site, a cumulative total of 6.0 - 7.5 hr for the 3 sites.

The full sampling design including grids at all three sites was implemented in March 1991 and was repeated on each of the 4 subsequent trips. On two of these sampling trips, July/August and October/November 1991, each grid at each site was sampled twice. During all other trips each grid at each site was sampled once only. Therefore, each site was sampled a total of 7 times following implementation of the full sampling design.

Seven field trips were done over the course of the study (Table 2.2). The majority of time during the first two trips was spent completing the construction of the traps at Lizard Island. As traps were completed they were used to trial aspects of the logistics of the project during which fish were caught, tagged and released. These early trials were done initially at Loomis, and during the second trip, at Mangrove also. Tagging data from these initial trips has been used in estimation of rates of growth and tag loss only. Only fish tagged after the implementation of the full sampling design will be considered in the analysis of movement and mortality.

2.4 Trap design and trapping method

2.4.1 Trap design

The sampling in this study was based on the use of Antillean Z-traps. The design used was identical to that described by Davies (1989) and similar to those used by Munro and Co-workers in the Caribbean (Munro *et at*, 1971; Munro, 1974; Munro 1983; Munro, 1986). A total of 18 traps were constructed for the study.

Each trap was 2.4 m long, 1.2 m wide and 0.6 m high and made from 25 mm x 3 mm angle-iron frames which were covered with 42 mm hexagonal, galvanised wire mesh, lashed to the frame with 16 gauge galvanised tie wire (Figure 2.2). Each completed trap weighed approximately 25 kg. Traps each had two horse-head funnels with an outer aperture of 400 x 200 mm and an inner aperture of 250 x 150 mm. Doors were made by making an L-shaped cut in the mesh at the top corner of each trap (Figure 2.2) which were sealed by stitching plastic-coated copper wire through the mesh (Munro, 1986). Opening and closing of these doors proved to be very time consuming and resulted in early corrosion of the mesh surrounding the door. As a result the area around the door was reinforced with extra mesh. It is recommended that in future steel-framed, hinged doors be incorporated into the trap design to avoid this problem and improve access to the catch. Munro (1986) provides detailed instructions on the construction of Z-traps and other commonly used trap designs.

2.4.2 Baiting Method

Traps were baited with approximately 500 g of West Australian pilchards, *Sardinops neopilchardus*. Whole pilchards were put in bait containers made from 90 mm PVC stormwater pipe sealed with PVC end-caps. Each container was 250 mm long with 5-6, 20 mm horizontal slits in either side. A 200 mm length of plastic-coated copper wire was used to secure each container to the top of each trap so that the bait container hung free in the centre of the trap (Figure 2.2).

2.4.3 Trap sampling method

Traps were set and hauled from a 4.1 m aluminium dingy anchored above the trap. Traps were hauled by hand using a 16 mm sheet rope which was clipped onto the trap by free-diving to each trap from the boat. The catch was removed from the trap as quickly as possible and placed in plastic bins (650 x 400 x 400 mm) of fresh seawater, from which all fish were identified to species and their length to caudal fork (LCF) and standard length (SL) measured to the nearest millimetre on a 1 m measuring board. A wet towel or piece of foam rubber (25 mm thick) was used to keep fish wet and to shield their eyes during the handling process. Data were recorded onto prepared data sheets on waterproof paper. Identifications of species were made according to Allen (1985) (Lutjanidae), Carpenter and Allen (1989) (Lethrinidae) and Randall *et al* (1990) (all other taxa).

All species of Serranidae, Lutjanidae and Lethrinidae and common species of Nemipteridae, Haemulidae, Labridae, Siganidae, Scaridae and Acanthuridae were tagged. Common species of Serranidae, Lutjanidae and Lethrinidae were injected with oxy-tetracycline. Details of the tagging and injection methods are described in section 2.5. All fish, with the exception of target species sacrificed for otoliths (see Chapter 4), were released. Fish sacrificed for otoliths were collected from the last samling trip only.

When the catch had been processed the trap was rebaited and moved to the next position. Traps were never set in the same position over consecutive soaks (see section 2.3.2). In the 'patch reef' habitat category, traps were always set on the sand adjacent to patch reefs, less than 1 m from the nearest reef structure. Traps were orientated so that the entrance funnels were parallel to the prevailing current direction at each site.

During the study, the mesh of many of the traps was damaged. Minor repairs were done on the boat during regular sampling. When it was necessary to replace large sections of the mesh the repairs were made at the research station and, in the 3 cases where this was necessary, it resulted in the loss of a replicate for that trap set. Such instances were invariably the result of sharks or large groupers damaging the trap.

Between sampling trips the traps were left in the water. This maintained the algal and invertebrate growth on the traps and reduced the time and effort required to reset the traps at the beginning of each sampling trip. The traps were kept at one place at each site, located outside the sampling grid, with funnels and doors open. Leaving the traps with doors and funnels open was found to be more effective in preventing accidental capture of fish than attempting to completely close the traps, as fish would inevitably find a way into the traps through even the most securely closed funnel.

Where greater logistic support is available it is recommended that traps are removed from the water between sampling periods. This would increase the longevity of the mesh and eliminate any variability in the growth of algae and invertebrates among traps. Although not quantified in this study, it is considered that factors such as algal and invertebrate fouling, trap "age" and extent of repair, which may vary between traps may contribute substantially to the variation in CPUE and species composition of the trap catches (CRD personal. observation; M. J. Sheaves, personal comment). Thus, it is strongly recommended that all feasible steps be taken to standardise these factors among traps.

2.5 Tagging Method

2.5.1 Tagging Equipment

Hallprint® standard and fine t-bar anchor (TBA) tags and standard dart tags were used throughout this study. The standard and fine TBA tags were applied with Monarch 3030 and 3000 tagging guns, respectively, and the dart tags were applied using a standard stainless steel tagging needle. All tags were yellow, individually numbered and had "**JCU-MB**" (James Cook University - Marine Biology) and a contact telephone number printed on them.

Standard TBA tags were used to tag all fish greater than 150 mm LCF. This included the majority of serranids, lutjanids and lethrinids caught in the traps. The fine TBA tags were used to tag all size classes of siganid, as their high degree of lateral compression meant that even the largest individuals could be tagged successfully with the fine TBA tags. All individuals of other species less than 150 mm LCF were tagged with fine TBA tags also.

Dart tags were used initially to tag large (>500 mm LCF) *Plectropomus leopardus* and *Epinephelus* species. However, due to the greater degree of damage caused by the application of the dart tags and the larger and more persistent tagging wounds observed on fish tagged with dart tags, in comparison to fish tagged with standard t-bar anchor tags, the use of dart tags was discontinued after the second field trip (Table 2.2). On subsequent trips all fish greater than 150 mm LCF were tagged with standard t-bar anchor tags. In the case of large serranids the location of the tags was shifted, relative to smaller fish, so that the tags could be applied successfully. Chaetodontids, pomacentrids and rare species were not tagged.

2.5.2 *Tagging and tetracycline method*

Following removal from the trap fish were held in plastic bins full of fresh sea water (see section 2.4.3). Before tagging commenced, fish which were badly embolised were "pricked" to release pressure from the swim bladder. This was done by inserting a sterile hypodermic needle though the body wall into the swim bladder. The fish was then held in the water, with the needle in place, and the excess pressure allowed to escape. The correct insertion point varied between species but in general was located at the posterior tip of the pectoral fin, when the fin was layed flat against the body wall. Embolisms were most common in lethrinid and haemulid species.

Fish were taken from the bins by hand and placed on a 1 m measuring board, measured and tagged. The tags were gently pulled to test that they were securely anchored before the fish was released. If a tag was not secure it was removed and a second tag applied. In the case of recaptured fish, the tags were read and checked that they were secure. Tags which were loose or damaged were removed and a new tag applied. Fish which had been double tagged and were recaptured with a single tag had a second tag applied.

Tags were applied through the dorsal musculature and between two pterygiophores so that the t-bar of the tag locked firmly behind the pterigyophores. Care was taken not to damage the pterigyophores when inserting the tagging needle as this has been shown to be a major source of tagging mortality (Whitelaw and Sainsbury 1986).

The exact application procedure varied slightly between species but, in general, the first tag was applied between the third and forth dorsal spine approximately 5 mm below the base of the dorsal fin. The second tag was also applied to the left hand side of the fish 5 - 10 mm posterior to the start of the soft dorsal fin.

All species of serranid, lutjanid and lethrinid were double tagged over the duration of the study to obtain estimates of rates of tag loss (see Chapter 5). All other species were tagged with a single tag only. *Siganus doliatus* was initially double tagged; however, given the relatively small size of this species (< 220 mm LCF) and the fact that no individuals which had been double tagged were recaptured, all species of siganid were tagged with a single tag only after the second field trip (Table 2.2). All tagging was done by CRD, except on one occasion (19.11.1991) when it was done by an experienced assistant (D. Zeller).

In collaboration with B. P. Ferreira, all *Plectropomus leopardus, Lethrinus* species and approximately 50% of *Lutjanus carponotatus* and *L. fulviflamma* were injected with oxytetracycline hydrochloride for validation of increments in otoliths. The prescribed dosage of oxytetracycline hydrochloride, 50 mg kg^{-1} body weight (McFarlane and Beamish 1987), was injected into the coelomic cavity, below and to the posterior of the pelvic fin, at a concentration of 50 mg ml^{-1} of sterile saline solution . Fish to be injected were returned to a separate bin following tagging while the correct dosage of tetracycline was prepared, then the fish injected and released.

Table 2.1: The percentage of the total area of each site covered and the number of trapping positions in each habitat category in each sites in the lagoon at Lizard Island.

	Loomis	**Mangrove**	**South**
Habitat	No. trap positions	No. trap positions	No. trap positions
Reef	5	4	10
Patch reef	16	15	14
Sand	15	17	12
Total	36	36	36

Table 2.2 : Summary of sampling schedule for study in the lagoon at Lizard Island. The distribution of sampling effort between the sites, Loomis (L), Mangrove (M) and South (S), within trips and over the duration of the study is given. The level of sampling effort within each trip is given in parentheses e.g. L(2) = the Loomis grid was sampled twice. (p) = preliminary trapping done while traps were being built.

	Time of year		
Year	Feb - Mar	Jun - Aug	Oct - Dec
1990	-	L(p)	L(p) M(p)
1991	L(1) M(1) S(1)	L(2) M(2) S(2)	L(2) M(2) S(2)
1992	L(1) M(1) S(1)	-	L(1) M(1) S(1)
Total	L(2) M(2) S(2)	L(3) M(2) S(2)	L(4) M(4) S(3)

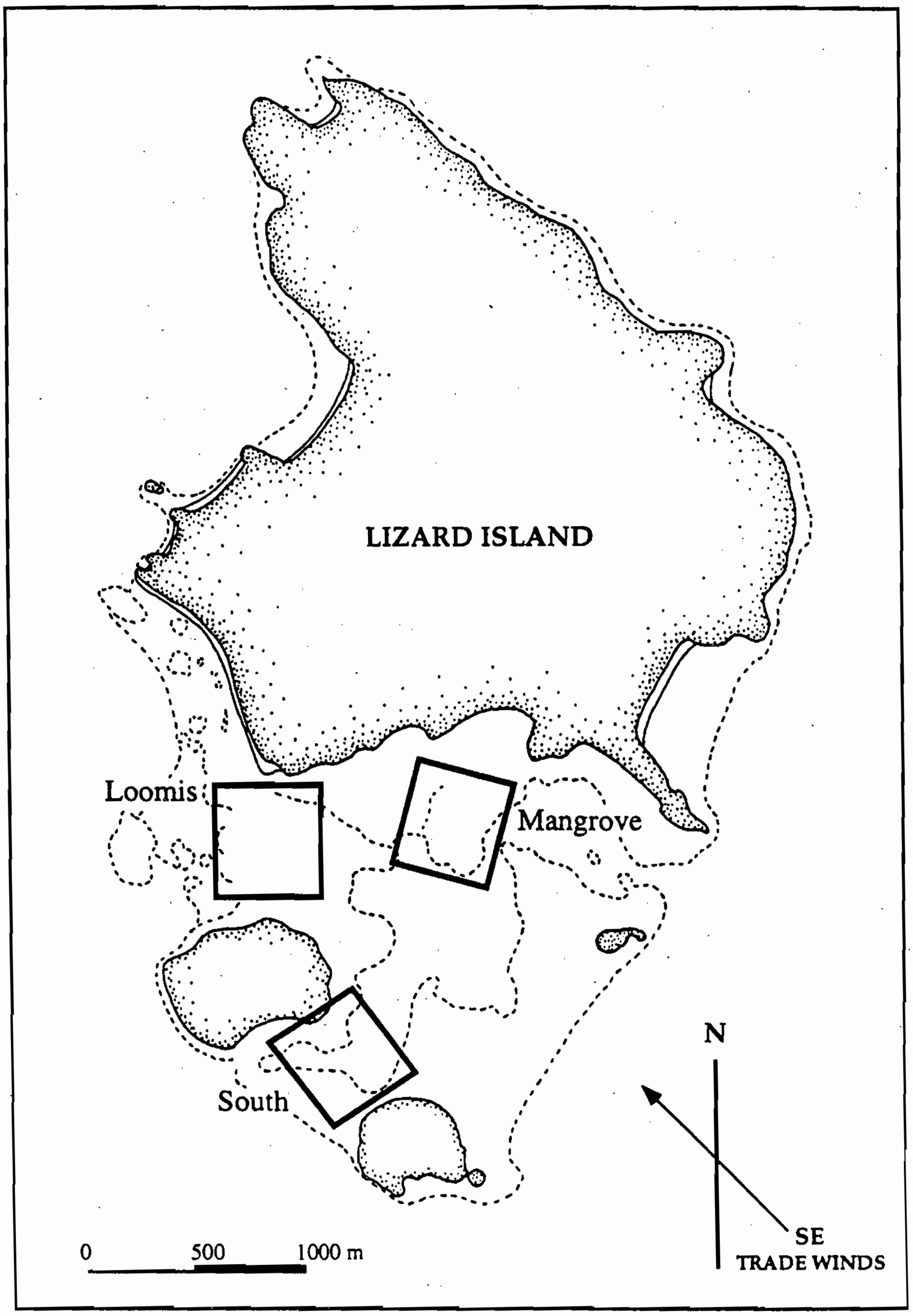

Figure 2.1: Map of Lizard Island and the lagoon indicating the location of the three sampling grids.

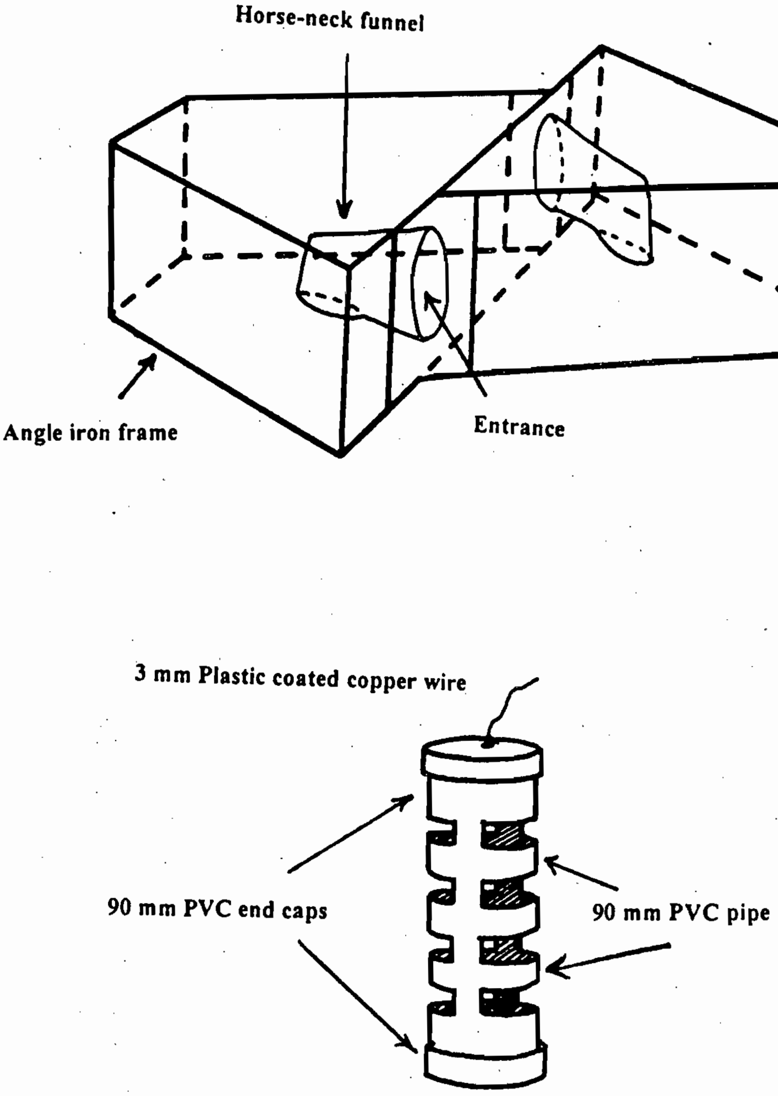

Figure 2.2: Schemmatic diagramme of : a) a Z-trap showing positon of entance funnels and doors for removing catch and b) the PVC bait container used to bait the traps.

Chapter 3

Catch composition and catch per unit effort of Z-traps in the Lizard Island Lagoon

3.1 Introduction

Fish traps have been used extensively in the Caribbean as a sampling tool for stock assessment of reef fishes (Munro 1974; Wolf and Chislett 1974; Stevenson and Stuart-Sharkey 1980), exploratory fishing (Wolf and Rathjan 1974) and for monitoring the effects of fishing on exploited fish stocks (Ferry and Kohler 1987; Koslow *et al* 1988). More recently, traps have been used in the tropical Pacific in exploratory fishing and as an alternative to traditional fishing technologies (Papua New Guinea: Dalzell and Aini 1987; New Caledonia: Kulbicki and Mou-Tham 1987; Tonga: Felfoldy-Fergusson 1988; Vanuatu: Blanc 1988; New Caledonia: Desurmont 1989; Northwestern Australia: Whitelaw *et al* 1991). However, until recently (Davies 1989; Newman 1990) they have been little used on the Great Barrier Reef (GBR).

Traps have a number of features which make them an attractive technique for sampling reef fish. Many traps may be fished simultaneously over relatively large spatial scales (Miller and Hunte 1987). They can be set in most types of habitat found on coral reefs and they catch a wide range of taxa, including all trophic groups (Munro 1974; 1983; Dalzell and Aini 1987; Davies 1989; Blanc 1988). The catch is alive, and in most cases unharmed, and previous studies indicate that the rates of recapture obtained using traps, particularly for serranids and lutjanids, are high (Bardach 1958; Randall 1962; Davies 1989; Sheaves 1992;1993).

Fish traps were chosen as the principle method of capture for the small-scale study of patterns of movement in the Lizard Island lagoon as it was necessary to sample relatively large spatial scales simultaneously, across a variety of habitats, with limited personnel (i.e. CRD and an assistant). Furthermore, previous work (Davies 1989; Newman 1990) had indicated that traps would be an effective means of capture and recapture for the three target species; *Lutjanus carponotatus, Plectopomus leopardus,* and *Siganus doliatus.*

This chapter descibes the species composition and catch rates of the traps at three sites within the lagoon over a period of 21 months. The aim was to describe the general patterns of distribution and relative abundance of the three target species, among habitats and sites within the lagoon.

3.2 Methods

The experimental design, sampling schedule (section 2.3) and trap sampling protocol (section 2.4) for the Lizard Island lagoon study have been described in Chapter 2. Only data from the seven sampling periods following the implemetation of the full sampling design are included in the results (Table 2.2). The distribution of trap positions among habitats and sites is given in table 2.1 and a summary of the trapping effort among habitats and sites over the seven sampling periods is given in table 3.1. Positions 31-36 at Loomis, 6, 12, 18, 24, 30, 36 at Mangrove and 1, 7, 13, 19, 25 and 31 at South were not sampled on trip one and a further 3 replicates were lost, 1 during trip 3b and 2 during trip 5.

All data are expressed as numbers of fish per trap. Only fish which were alive when the trap was hauled have been included. Fish which were dead, or had been regurgitated by other fish, were excluded. For comparison of CPUE of families between sites, mean CPUE was calculated from the pooled catch of each family at each site for each sampling period and has been standardised as catch per sampling period (i.e catch from 36 trap hauls, using a 3 day soak). Similarly, the percent of total catch by family was calculated by pooling the catch by family and site for each sampling period and dividing by the pooled total catch for each site for each sampling period.

The experimental design for this study involved repeated sampling of the same positions over time, therefore, the replicate samples from each trapping position cannot be considered independent (See Chapter 6). It was not possible to use repeated measures analysis of variance to examine the effects of site, habitat or time on the catch rates of the target species as the data failed to meet the assumptions of homogeneity of variances and normality, even following transformation. This was largely the result of the high percentage of zero values in the data for all species. Furthermore, the experimental design was not balanced across habitats and repeated measures ANOVA techniques are not robust for unbalanced designs, especially with hetergeneous data. Consequently, the data have been presently graphically as mean CPUE of each taxon among habitats and sites pooled across the seven sampling periods. This serves to illustrate the major patterns in relative abundance of the four target species among habitats and sites which were consistent across the seven sampling periods. All total catch and catch rate data are by numbers of individuals (*ie* not weight).

3.3 Results

3.3.1 Catch composition

A total of 4,736 fish from 21 families and 109 species were caught over the duration of the study in the lagoon from a total of 735 trap hauls (Appendix 1). The total catch, pooled over sites, ranged from 352 fish on trip 5 to 885 fish on trip 3b (Table 3.2). The total catch at Loomis was consistently lower than Mangrove and South, with the exception of trip 5, despite the relatively high variability in total catch within sites and among trips (Table 3.2).

Although a total of 21 families and 109 species were caught during the study, the catch was dominated by a few families. The six most abundant families, the Siganidae, Lutjanidae, Lethrinidae, Serranidae, Haemulidae and Acanthuridae, collectively comprised over 88% of the catch at each site. The Siganidae and Lutjanidae were the most abundant families in the catches at each site with their combined catch accounting for 54%, 63% and 68% of the total catch at Loomis, Mangrove and South, respectively. (Figure 3.1). The two most common species of siganid and lutjanid, *Siganus doliatus* and *Lutjanus carponotatus* comprised 36 % of the total catch collectively. *Siganus doliatus* accounted for 61 % of the total catch of siganids and *Lutjanus carponotatus* 52% of the lutjanid catch. The percent composition of the Lutjanidae and Serranidae was higher at Loomis than the other sites while the Siganidae were consistently in higher proportions in the catches at Mangrove and South (Figure 3.1). The Lethrinidae comprised similar proportions of the catches at each site. The Haemulidae and Acanthuridae each comprised between 7-10% at Loomis and Mangrove while they each made up less than 3-4% of the catch at South (Figure 3.1).

The six dominant families included 57% of the species trapped during the study. Of these species, the ten most common in the trap catches accounted for more than 60% of the catch at each site (Table 3.3). Almost 60% percent of the species trapped during the study were rare (i.e. represented less than 0.5% of the total catch) (Appendix 1). The three most common species, *Siganus doliatus, Lutjanus carponotatus* and *L.fulviflamma,* comprised 33%, 42% and 53% of the total catch at Loomis, Mangrove and South, respectively (Table 3.3).

S.doliatus constituted a greater proportion of the catch at South and Mangrove than at Loomis (Table 3.3). In contrast *P.leopardus* was more common in the catch at Loomis than at the other sites, while *L.carponotatus* comprised similar proportions of the catch at each site (Table 3.3).

3.3.2 Distribution and relative abundance

Distribution and relative abundance of dominant families by site

The patterns of relative abundance between sites for the dominant families were similar to those described for the catch composition. Mean CPUE of siganids was substantially higher at South and Mangrove than at Loomis, as was mean CPUE of lutjanids (Table 3.4). In contrast, mean CPUE of serranids was greater at Loomis than at Mangrove or South (Table 3.4). Mean CPUE of Lethrinidae was higher at South than at Loomis or Mangrove, whilst mean CPUE of acanthurids and haemulids was higher at Loomis and Mangrove than at South (Table 3.4).

Distribution and relative abundance of target species by habitat and site

There were marked and consistent patterns in relative abundance (mean CPUE) of the three target species, *L.carponotatus, P.leopardus* and *S.doliatus*, among sites and habitats. Among sites, mean CPUE of *S.doliatus* and *L.carponotatus* was higher at Mangrove and South than at Loomis (Table 3.5). In contrast, mean CPUE of *P.leopardus* was substantially higher at Loomis than at the other sites (Table 3.5).

Lutjanus carponotatus

Mean CPUE was consistently higher in the reef habitat and lower in the sand habitat at all sites (Figure 3.2). The difference in CPUE between the reef and patch reef habitats was greatest at Mangrove and least at South. CPUE in the sand habitat was slightly higher at South than at the other sites.

Plectropomus leopardus

Mean CPUE for *P.leopardus* was very low in comparison to the other species with the exception of the reef and, to a lesser extent, the patch reef habitats at Loomis. The catch of *P.leopardus* at Loomis accounted for 62% of the total catch of *P.leopardus* caught during the lagoon study (Table3.5). There was little difference in Mean CPUE among habitats at Mangrove or South.

Siganus doliatus

Mean CPUE for *S.doliatus* was the highest of the three target species and was consistently higher in the reef habitat at all sites. Among sites, CPUE in the reef habitat was highest at Mangrove and lowest at Loomis while CPUE in the patch reef habitat was highest at South and lowest at Loomis with Mangrove intermediate. Catches and CPUE in the sand habitat at Loomis and Mangrove were negligible while it was slightly higher at South

In contrast to the general pattern of the three target species, CPUE for *Lutjanus fulviflamma*, the third most common species in the trap catches, was highest in the sand habitat even though it was commonly seen in large aggregations on the reef during the day (CRD personal observation). These patterns in relative abundance of target species among habitats across sites were consistent among sampling periods.

3.4 Discussion

Trapping studies in the Caribbean (Munro *et al*, 1971; Munro, 1974; Stevenson and Stuart-Sharkey, 1980) and Papua New Guinea (Dalzell & Aini, 1987) have shown that a few species of roving, herbivorous fish typically dominate trap catches in shallow water on coral reefs. Acanthurids dominated trap catches at Kavieng Harbor, Papua New Guinea, with one species *Acanthurus xanthopterus* constituting 28% of the total catch (Dalzell & Aini, 1987). Scarids tended to dominate shallow water trap catches in the Caribbean (Munro 1974; Koslow *et al* 1988). In contrast to these results, catches from trapping studies in Tonga (Felfoldy-Fergusson 1988) and New Caledonia (Kulbicki and Mou-Tham 1987) were dominated by carnivorous species. Serranids, lutjanids and lethrinids accounted for 80% of the catch taken in Z-traps set in depths of up to 40 m in the New Caledonia lagoon by Kulbicki and Mou-Tham (1987) while mullids comprised nearly 50% of the total catch of Z-traps in the lagoon at Tonga (Felfoldy-Fergusson 1988). Deep-water trapping studies in other tropical regions have reported lutjanids and lethrinids to be the dominant component of catches also (Wolf and Chislett 1974; Sylvester 1974; Blanc 1988; Desurmont 1989; Whitelaw *et al* 1991).

The catch composition from the Lizard Island trapping study was dominated by six families; the Siganidae, Lutjanidae, Lethrinidae, Serranidae, Haemulidae and Acanthuriidae. Of these six families the Siganidae and Lutjanidae were the most abundant accounting for 63% of the total catch during the study. At a species level the composition of the catches was dominated by two species, *Siganus doliatus*, *Lutjanus carponotatus* which collectively accounted for 36 % of the total catch. This supports the results of previous trapping studies on the central GBR (Davies 1989; Newman 1990) in which trap catches on shallow coral reefs at Orpheus Island, central GBR, were dominated by *Siganus doliatus*.

The overall pattern in catch composition by family was consistent among the three sites although the relative contribution of some families varied slightly. The higher abundance of the Siganidae in the catches at Mangrove and South may be related to the more windward location of these sites relative to Loomis and the greater abundance of siganids on the windward sides of coral reefs on the GBR (Russ 1984a).

The Serranidae were three times more abundant in the catches at Loomis than at either of the other sites. This difference was largely the result of the higher catches of *Plectropomus leopardus* at Loomis. The other common species of serranid in the catches, *Epinephelus malabaricus*, was equally common at Loomis and South but less so at Mangrove (Appendix 1). There is no apparent reason for this pattern among sites. Loomis was the shallowest of the three sites and does not have steep slopes or deeper regions (present at the other sites) that are habitat characteristics commonly associated with abundance of serranids (Russ, 1989). In fact many of the large *E.malabaricus* caught were in the patch reef habitat in less than 2 m of water. The presence of these larger serranids in shallow water may reflect the absence of fishing pressure in the lagoon. The very low abundance of large serranids in trap catches from the shallow reefs and banks in the Caribbean has been related to fishing pressure (Munro, 1983; Koslow *et al* 1988).

Results of a recent trapping study on the central GBR, in depths of 10 - 40m, indicate that lutjanids and lethrinids constitute a larger proportion of the catch of traps set at greater depth (Williams *et al* 1992). Lutjanids and lethrinids comprised a significant proportion of the trap catches in the Lizard Island study also, with *Lutjanus carponotatus*, *L.fulviflamma*, *Lethrinus nebulosus* and *L.atkinsoni* collectively accounting for 22.4% of the catch over the three sites. The majority of the catches of *Lutjanus fulviflamma* and *Lethrinus nebulosus* were taken in the sand habitat where they dominated the catch composition. These species tend to aggregate around the reef structure during the day and disperse at night to feed on invertebrate infauna over the sandy substrates (Jones *et al* 1990). Mullids and haemulids display the same type of diel movement patterns also (Hobson 1978; Holland et al 1993). The water depth over this sand habitat tends to vary among coral reefs depending on the geomorphology of individual reefs (Hopley 198?) and may range from less than 1 m (*eg* Lizard Island lagoon) to greater than 40 m in New Caledonia (Kulbicki and Mou-Tham 1987). Thus the occurence of these species in trap catches may be more related to the distribution of this habitat type rather than water depth *per se*.

There appears to be a general pattern in the species composition of trap catches on coral reefs. Herbivorous species dominate shallow water trap catches while serranids, lutjanids and lethrinids are predominant in deeper water catches. It is well documented from visual census studies that herbivorous coral reef fish occur in greater abundance in shallow (<15m) zones of coral reefs (e.g. Bouchon-Navaro and Harmelin-Vivien 1981; Russ 1984b). Little information is available on the distribution of many of the lutjanid and lethrinids species on the GBR (Williams 1991; Williams and Russ 1991) as many of these species are found in greater abundance at depths greater than 10 - 15m (Allen 1985; Carpenter and Allen 1989; Williams 1991) and are not amenable to visual census surveys (Williams and Russ 1994). It is likely that the observed differences in catch composition of traps set in different depths and habitats is a direct reflection of the spatial distribution and abundance of these trophic groups on coral reefs. Thus, traps may represent an effective technique for examining the patterns of distribution and relative abundance of these large, exploited species over the complete depth and habitat range of coral reefs.

Trap catches on coral reefs around the world are generally characterised by a large number of species and high variation in CPUE at a species level. Although a large number of species are caught in traps, the majority are rare, only being represented by one or a few individuals (Munro

1974; ; Dalzell and Aini 1987; Koslow et al 1988; Davies 1989; this study). Trap catches from tropical estuaries have been found to have similar characteristics (Sheaves 1992). This suggests that while fish traps may catch a wide range of species of coral reef fish, they may only be used effectively to examine the patterns of abundance and distribution of the most common species in the catches.

Table 3.1: Distribution of sampling effort amongst habitat categories (reef, patch reef and sand) and sites (Loomis, Mangrove and South) over seven sampling periods in the Lizard Island Lagoon. Each sampling unit represents one trap haul. Dates of each sampling period are given in Table 2.2.

	Loomis			**Mangrove**			**South**		
Sampling period	reef	patch reef	sand	reef	patch reef	sand	reef	patch reef	sand
1 (F/M'91)	5	12	11	3	15	12	8	12	10
2a (J/A'91)	5	16	15	4	15	17	10	14	12
2b (J/A'91)	5	16	15	4	15	17	10	14	12
3a (O/N'91)	5	16	15	4	15	17	10	14	12
3b (O/N'91)	5	16	15	3	15	17	10	14	12
4 (F'92)	5	16	15	4	15	17	10	14	12
5 (N'92)	5	16	15	4	13	17	10	14	12
Total	**35**	**108**	**101**	**22**	**103**	**114**	**68**	**96**	**82**

Table 3.2: Total trap catch (by numbers) for each site for each sampling period of the Lizard Island lagoon study.

Sampling period	**Loomis**	**Mangove**	**South**	**Total**
1	159	301	239	699
2a	137	226	258	621
2b	151	319	121	591
3a	167	287	373	827
3b	217	316	352	885
4	124	243	396	763
5	133	88	131	352
Total	1,088	1,780	1,870	4,738

Table 3.3: Total catch and percent of total catch for the 10 most abundant species caught in Z-traps at three sites over seven sampling periods in the Lizard Island Lagoon study.

	Loomis		**Mangrove**		**South**	
Species	Total	%	Total	%	Total	%
Plectropomus leopardus	62	5.7	15	0.85	23	1.23
Lutjanus carponotatus	122	11.21	179	10.11	207	11.11
L.fulviflamma	128	11.76	139	7.85	112	6.01
Lethrinus atkinsoni	31	2.85	15	0.85	34	1.83
L.nebulosus	38	3.49	50	2.82	64	3.44
Diagramma pictum	46	4.23	97	5.48	14	0.75
Siganus doliatus	107	9.83	428	24.17	677	36.34
S.lineatus	105	9.65	22	1.24	37	1.99
S.punctatus	70	6.43	118	6.66	64	3.44
Acanthurus xanthopterus	33	3.03	86	4.86	27	1.45
Total	**742**	**68.18**	**1149**	**64.89**	**1259**	**67.59**

Table 3.4: Summary of trap catch by family for each site in the Lizard Island lagoon study. Data are the total catch (by number) and mean total catch/site/trip and standard error over the 7 sampling periods. Only families which consituted greater than 5% of the total catch/site/trip on at least one sampling period are presented.

	Loomis			**Mangrove**			**South**		
Family	Total	Mean	SE	Total	Mean	SE	Total	Mean	SE
Serranidae	95	13.6	1.77	55	7.9	1.50	64	9.1	2.26
Lutjanidae	274	39.1	5.17	358	51.1	5.93	354	50.6	9.26
Lethrinidae	97	13.9	1.94	117	16.7	3.21	200	28.5	2.59
Nemipteridae	35	5.0	0.76	94	13.4	4.51	68	9.7	1.90
Haemulidae	103	14.7	2.60	142	20.3	2.45	42	6.0	1.51
Siganidae	312	44.6	7.18	753	107.6	19.74	916	130.9	25.24
Acanthuridae	86	12.3	4.64	130	18.6	6.45	64	9.1	2.14
Pomacentridae	11	1.6	0.69	67	9.6	2.42	34	4.9	1.67
Labridae	24	3.4	0.84	29	4.1	0.74	34	4.9	1.34

Table 3.5: Summary of Z-trap catch of *L.carponotatus, L.fulviflamma, P.leopardus* and *S. doliatus* at three sites in the Lizard Island lagoon study. Data are total catch (number), mean CPUE (no.fish trap^{-1} haul^{-1}) and standard errors for each species at each site over the seven sampling periods.

	Loomis			**Mangrove**			**South**		
Species	Total catch	Mean CPUE	SE	Total catch	Mean CPUE	SE	Total catch	Mean CPUE	SE
L.carponotatus	122	0.50	0.06	179	0.73	0.10	207	0.84	0.09
L.fulviflamma	128	0.52	0.08	139	0.57	0.09	112	0.46	0.07
P.leopardus	62	0.25	0.05	15	0.06	0.02	23	0.09	0.03
S.doliatus	93	0.38	0.11	428	1.74	0.34	677	2.5	0.50

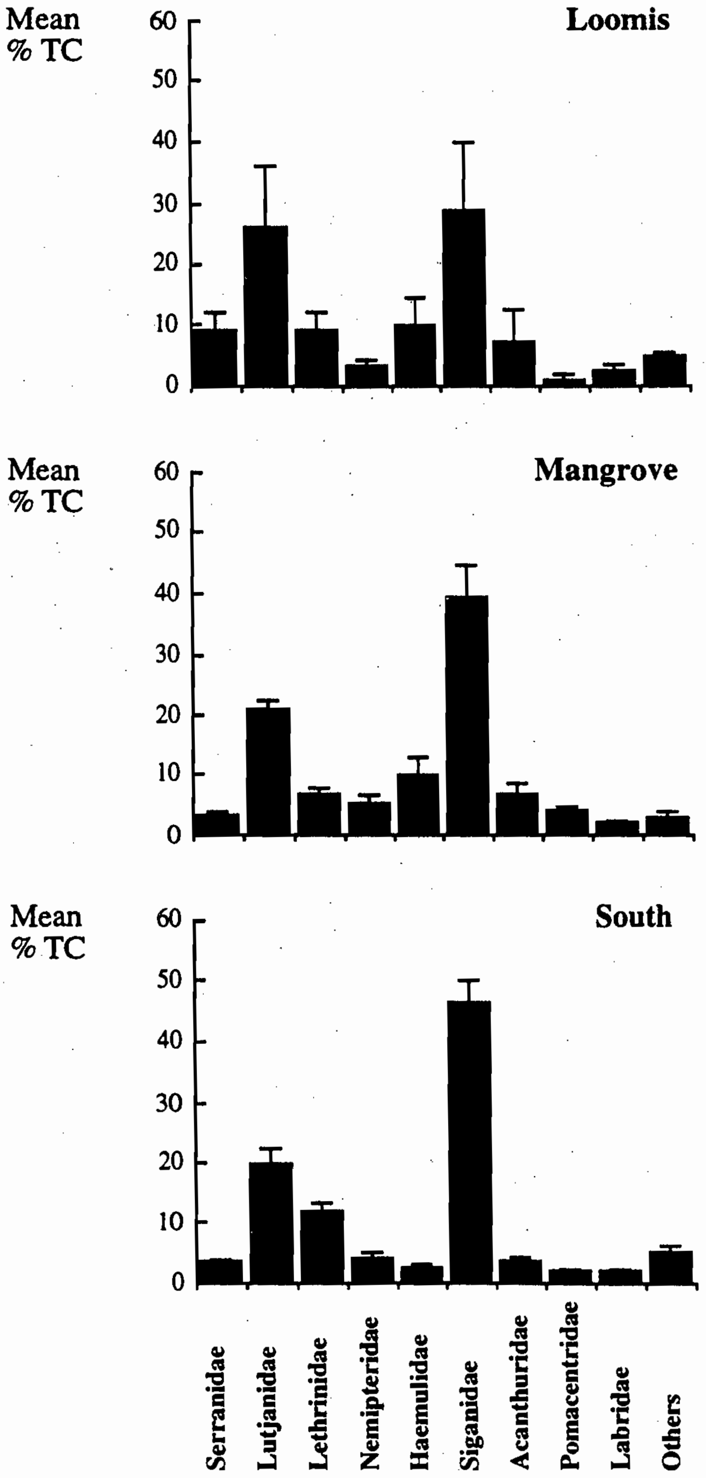

Figure 3.1: Composition of Z-trap catches by family at Loomis, Mangrove and South. Data are mean percent of total catch at each site over the 7 sampling periods (n=7). Error bars are one standard error of the mean. Only families which comprised greater than 5% of total catch for at least one sampling period are presented.

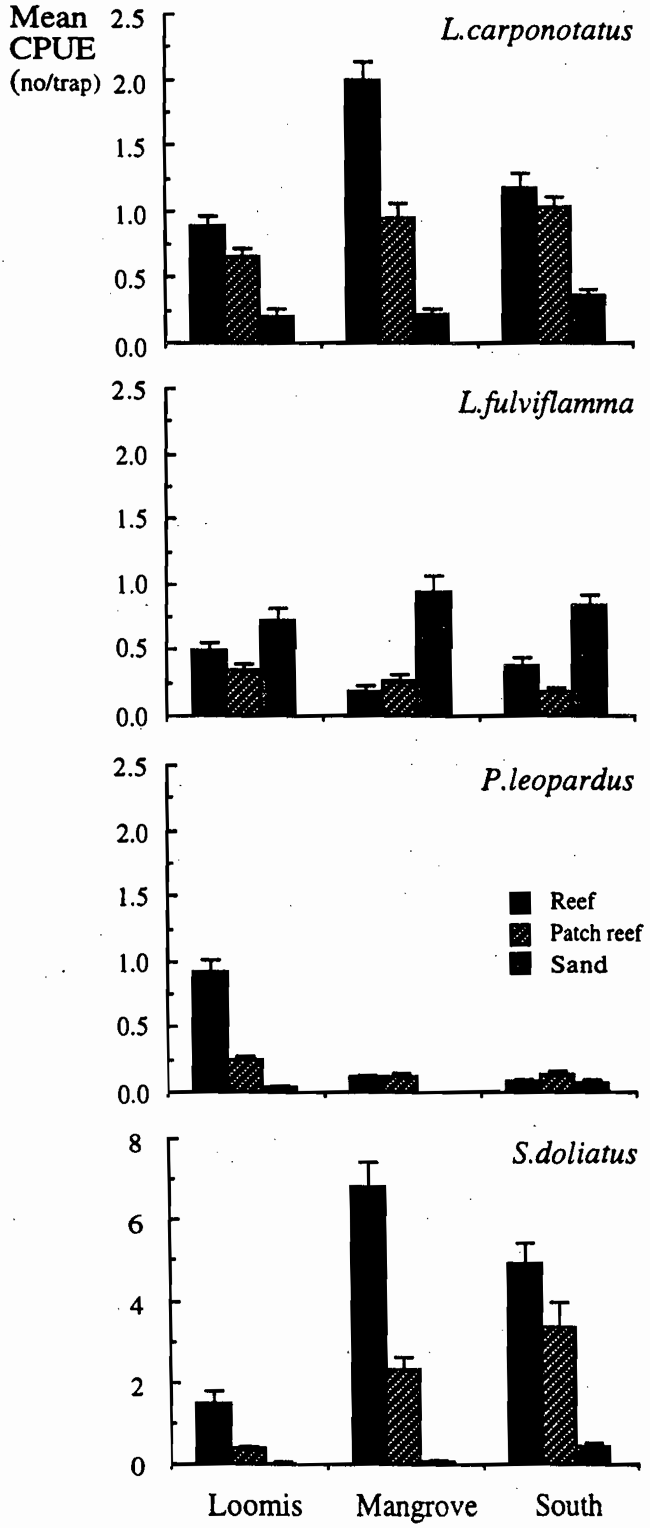

Figure 3.2: Summary of variation in mean CPUE (no.fish trap^{-1} haul^{-1}) of *L.carponotaus*, *L.fulviflamma*, *P.leopardus* and *S.doliatus* among habitats (reef, patch reef and sand) and sites. Error bars are one standard error of the mean. Note difference in scale for *S.doliatus*.

Chapter 4

Estimates of rates of growth of *Lutjanus carponotatus, Plectropomus leopardus* and *Siganus doliatus*

4.1 Introduction

Estimates of rates of growth form a central element of most stock assessment models (Beverton and Holt 1957; Gulland 1988; Hilborn and Walters 1992). However, in many coral reef fisheries there is little data available on the rates of growth for many of the species exploited (Manooch 1987; PDT 1990; Williams and Russ 1994). This lack of information is the result of relatively little research on the demography of exploited tropical species (Russ 1991) and the perceived difficulty in aging tropical fishes (Panella 1980; Brothers 1982; Campana and Neilson 1985; Longhurst and Pauly 1987). Length-based methods have been widely recommended for estimating growth rates and for stock assessment of tropical species (Pauly 1984; Munro 1987; Pauly and Morgan, 1987). However, given the highly variable size at age documented for many species of reef fish, their greater longevity and protracted spawning period, it is likely that estimates of rates of growth and mortality from length-based methods will be biased (Sainsbury, 1980; Davis and West 1992; Hilborn and Walters 1992; Ferreira and Russ 1994; unpublished manuscript).

Tagging techniques are used extensively in fisheries biology to estimate rates of growth and represent a valuable alternative when age or length based methods cannot be applied (Jones 1976). However, they have been relatively little used for coral reef fishes. In a recent review of available data on exploited species of reef fish on the Great Barrier Reef (GBR) (Williams and Russ 1994), none of the published growth studies cited had used growth increment data from tagging studies to estimate rates of growth.

The use of tagging data to estimate rates of growth assumes that the process of capture, tagging and the presence of the tag do not significantly bias the rate of growth of tagged individuals (Jones 1976). This assumption is difficult to test without growth increment information from untagged fish, which can usually only be obtained from aquarium trials. Comparison of estimates of growth parameters from tagging studies with an alternative estimate, such as size at age data, from the same study or other studies may provide some insight of the extent to which this assumption is violated. However, they will only provide a general indication of the extent of the effect, as growth parameters from growth increment data and size at age data are not strictly comparable (Francis 1988).

A number of recent studies have validated the presence of annual bands in the otoliths and other calcified structures of a range of genera of coral reef fish (*eg*. Pomacentrids: Fowler 1990; Chaetodontids: Fowler 1989; Epinepheline serranids: Ferreira and Russ 1991;1993; Bullock *et al* 1992; Sadovy *et al* 1992; Lutjanids: Davis and West 1992; Newman 1995; Scarids: Lou 1992).

These studies have demonstrated that coral reef fishes are considerably longer lived than previously considered and exhibit considerable individual variability in rates of growth. The majority of these studies have focussed on estimating age from sectioned otoliths. Preparation and reading of sectioned otoliths is time consuming, expensive (Boehlert 1985) and requires equipment and a level of training not often available in many tropical countries (Munro 1987). The reading of whole otoliths or the use otolith weight to estimate age of tropical reef fish may represent economic alternatives to sectioning otoliths that provide less biased estimates of growth and other population parameters than length-based methods (Boehlert 1985; Fletcher 1991; Ferreira and Russ 1994).

There are currently no published estimates of rates of growth for *Lutjanus carponotatus* for the GBR. An estimate is available for *L.carponotatus* from Papua New Guinea from length frequency data (Wright *et al*, unpublished; cited in Williams and Russ 1994, Chapter 5, Table 10). There are no published information on the growth of *Siganus doliatus*. *Plectropomus leopardus* is the most studied species of exploited reef fish on the GBR and estimates of rates of growth are available from size at age data (McPherson *et al* 1988; Ferreira and Russ 1993; unpublished manuscript) and length-frequency data (Goeden, 1978; Pauly and Ingles 1981; Ralston 1987).

The aims of this chapter were: 1) to estimate the rates of growth of the three target species from growth increment data from the tagging study at Lizard Island, 2) compare estimates of age of *L.carponotatus* obtained from whole and sectioned otoliths and examine the relationship between fish age and otolith weight and fish length, and 3) obtain estimates of growth from size at age data for *L.carponotatus*.

4.2 Methods

4.2.1 Trapping and tagging methods

All fish used to estimate growth from tagging data were captured in the Z-trap sampling programme in the lagoon at Lizard Island. Details of the trapping, tagging and tetracycline methods have been described in Chapter 2 (see sections 2.4.3 and 2.5, respectively).

4.2.2 Collection of L.carponotatus otoliths

Ninety-two *Lutjanus carponotatus* were collected by spear during the final sampling trip (November 1992) for estimating rates of growth from bands in the otoliths. An effort was made to obtain an equal sample size (8-10 individuals) for each 30 mm size class, as the objective was to obtain size-at-age information for growth curves, rather than a representative sample of the age-structure.

4.2.3 Otolith processing

Following collection, fish were dissected and sagittal otoliths (hereafter referred to simply as "otoliths") removed. Otoliths were cleaned of any residual material, washed in fresh water, dried and stored dry in 5 ml plastic vials. Whole left and right otoliths were weighed to the nearest 0.001g on a balance accurate to 0.00001g. Whole otoliths were immersed in eucalyptus oil and read under incident light using a stereo dissecting microscope, following the method described by Ferreira and Russ (1991). Otoliths were selected at random for reading, without knowledge of fish size or preference for left or right otolith. Counts of opaque bands were made along the dorsal surface, from the focus to the dorsal edge of the otolith. Each otolith was read twice by the same reader (CRD) with a period of about 2 months between readings.

The methodology for sectioning otoliths follows that described by Ferreira and Russ (1991). Otoliths were set in epoxy resin, mounted on a glass microscope slide with Crystal bond 509 adhesive and sectioned transversely through the core with a Buehler low-speed Isomet saw. Completed sections were mounted on glass slides with Crystal bond 509 adhesive and finished on 500 and 800 grit wet and dry paper to remove saw marks; then polished with 0.3 μm aluminium powder. Sections were read using a high powered microscope with transmitted light at 10x and 40 x magnification. A drop of oil (immersion/eucalyptus) on the section was found to improve the clarity of the opaque bands.

Counts of bands were made along the axis from the focus to the internal dorsal surface. Each section was read twice by the same reader over a period of 3 months (CRD). All repeat counts of whole and sectioned otoliths were made "blind" without reference to previous readings. A count was accepted if the same count resulted from both readings. If the initial two counts differed a third reading was done. The otolith was accepted if the third reading corresponded with one of the former two. If not, it was considered unreadable and omitted from the analysis.

4.2.4 Analysis

Length-frequency distributions of releases and returns of tagged individuals of each species were compared with 2-way contingency tables using likelihood chi-squared tests (SAS 1989) to examine the effect of size class on frequency of return. Data were excluded from analysis of the growth increment data for each species based on the following criteria, in an attempt to exclude the potential effects of capture, tagging and measurement errors,: i) time at liberty must exceed 30 days, ii) growth increment must be greater than 2 mm, and iii) in the case of multiple observations of the same fish, the observation with the greatest time at liberty was used. Additional outliers were identified using scatter plot matrices and 95% density ellipses in JMP (SAS 1989).

Fabens (1965) nonlinear form of the von Bertalanffy Growth Equation (VBGE) for growth increment data was initially fitted to the reduced data sets for each species using the Gauss-Newton method with step-halving in the nonlinear fitting platform of JMP (SAS 1989). The minimisation procedure failed to converge or the parameter estimates were highly unstable over a range of initial parameter values for each species. Consequently, estimates of L_∞ and K were obtained by fitting Gulland and Holt's linear model (in Pauly 1984);

$$L_2\text{-}L_1/t_2\text{-}t_1 \approx a - b\, L_m$$

$$\text{where, } L_\infty = -a/b$$
$$\text{and, } K = -b$$

where, L_2 and L_1 are the lengths at recapture and release, respectively, t_2 and t_1 are the dates of recapture and release, respectively, L_m is the mean length over the time at liberty (L_2-$L_1/2$) and a and b are the regression parameters (The equation above does not include the additional parameter, D, found in Pauly due to the lack of data for these species (1984)).

The periodicity of the bands in the otoliths of *L.carponotatus* are unvalidated. However, several individuals which had been injected with tetracycline and released during this study have since of been recaptured. Therefore validation should be completed in the near future. Nevertheless, as the periodicity of the bands has not been validated, the measure of age used throughout this chapter is referred to simply as the number of bands.

The relationship between age, otolith weight and fish length was examined using scatter plot matrices (SAS 1989). Otolith weight was regressed on age (from sectioned otoliths) to test for a significant linear relationship. There was little difference in the counts of whole and sectioned otoliths. However, counts of whole otoliths tended to be less than those of the sectioned otoliths after age five. Thus, it was assumed that the counts of sectioned otoliths were a more accurate estimate of age than counts from whole otoliths, at least for older age classes. The difference in the estimates of age from whole and sectioned otoliths was examined by plotting the mean difference between the age estimates from sectioned and whole otoliths by the age from sectioned otoliths.

The nonlinear form of the VBGE for size-at-age data,

$$L_t = L_\infty \left[1 - e^{-K(t - t_o)}\right]$$

was fitted to the *L.carponotatus* data for sectioned otoliths using the same minimisation procedure described above. L_∞ ,K and t_o are the von Bertalanffy parameters and t is the estimated age at length, L_t . In this case the parameter estimates were stable over a range of initial values and repeatedly converged at the same minima.

4.3 Results

4.3.1 Growth increment data

A summary of the tagging data for each species is presented in table 4.1. The selection criteria resulted in more than half the available growth increment data being discarded (Table 4.1). The reduced data sets resulted in 41 observations for *L.carponotatus*, 16 for *P.leopardus* and 102 for *S.doliatus*. The majority of data discarded failed to meet criteria i), for minimum time at liberty, resulting from recaptures within the same sampling occasion. The mean time at liberty for the reduced data sets for each species ranged from 136 days for *L.carponotatus* to 236 days for *P.leopardus*. The size range of the fish used in the growth increment analysis was generally less than half of the observed size range for each species (Table 4.1). The relative frequency of recapture did not vary significantly among size classes for any of the three species (Figure 4.1). This suggest that the potential effect of tagging (*eg*. tag induced mortality) did not effect size classes of each species differentially.

Significant Gulland and Holt plots were obtained for the reduced data sets for each species (Figures 4.2-4.4). There was considerable variation in individual growth increments at length among similarly sized individuals. This was particularly evident for *L.carponotatus* and

S.doliatus, where the larger sample sizes allowed better comparison of growth increments among individuals of similar length (Figures 4.2 and 4.4). For example, individual growth increments of *S.doliatus* of 15-16 cm length (LCF) ranged from 0.14-0.47 cm/mth (Figure 4.4). Estimates of L_∞ and K for each species are presented in table 4.2.

4.3.2 Otolith weight for Lutjanus carponotatus

The length-frequency distribution of the *L.carponotatus* collected for size at age data is presented in Figure 4.5. As expected there was a high positive correlation between fish age and length and age and otolith weight. However, the correlation between age and otolith weight was substantially higher (age and otolith weight correlation coefficient = 0.94; age and length correlation coefficient = 0.84). Otolith weight increased exponentially with length for *L.carponotatus* (Figure 4.6) and was linearly related to age (Figure 4.7). This demonstrates that the otoliths of *L.carponotatus* continue to increase in mass with age after growth in fish length has almost ceased. There was reasonable variation in otolith weight within age classes also.

4.3.3 Size at age for Lutjanus carponotatus

Otolith description

The sagittal otoliths of *L.carponotatus* were large relative to the size of the fish which appears to be a feature of the genus *Lutjanus* (personal observation). The nucleus was generally opaque and encircled by alternating translucent and opaque milky bands. The milky bands were broad and diffuse, without a distinct margin, and were clearly visible under a dissecting microscope using reflected light and black background. The first two bands were particularly broad and in some cases the initial band was difficult to identify. The distance separating adjacent opaque bands decreased with distance from the nucleus until the 5-6th band after which bands were relatively uniformly spaced. The highest count from whole readings was 13.

Growth from size at age data for *Lutjanus carponotatus*

There was a tendency for counts of whole otoliths to underestimate the number of bands relative to counts of sectioned otoliths, particularly after age 5. However, the difference was small with the exception of the two oldest age classes (age 12 and 13) (Figure 4.8) and given the small sample sizes for these age classes the comparison was equivocal.

There was considerable variability in size at age for *L.carponotatus* (Figure 4.9 and 4.10). Mean size at age increased rapidly to 250 mm at approximately age 4, after which growth slowed considerably (Figure 4.9). There was little difference in mean size between 4 and 13 years (Figure 4.9). However, the sample sizes for the older age classes were very small. The parameter estimates of the VBGE from the nonlinear fit (Figure 4.10) of the size at age data from the sectioned otoliths were L_∞ = 312 mm (LCF), K=0.31 and t_o = -1.05, respectively (Table 4.3)

4.4 Discussion

The estimates of growth for *L.carponotatus* from this study are the first available for the Great Barrier Reef (GBR). The estimate of *K* from growth increment data (0.127) is considerably lower than the only other estimate available for this species. Wright *et al* (unpublished; cited in Williams and Russ 1994, Chapter 5, Table 10) estimated *K* and L_∞ from length-frequency data to be 0.31 and 560 mm (LCF), respectively, for *L.carponotatus* from Kavieng in Papua New Guinea. The L_∞ estimated by Wright *et al* is high, and exceeds by more than 150 mm the largest recorded size for this species from the Lizard Island study and the GBR (400 LCF mm, Randall *et al* 1990). This may reflect geographic variation in the maximum size reached by this species. Geographic variation in maximum size has been reported for other species from the GBR, such a *Plectropomus leopardus* (see Williams and Russ 1994) and *Lethrinus miniatus* (Walker 1975, Church 1989, in Williams and Russ 1994; Loubens 1980b) and suggests that growth parameters may vary among regions.

There is very little information available on the growth of siganids, even though they represent a major component of the herbivorous fish community on Indo-Pacific coral reefs (Russ 1984 a&b; Woodland 1990) and form a significant proportion of catches in subsistence fisheries (Woodland 1990). The estimate of *K* (0.71) for *S.doliatus* from this study suggests that this species approaches the estimated L_∞ (202 mm) very rapidly. Estimates of rates of growth of other species of siganid, from direct observation in mariculture, indicate that the early phase of growth may be very rapid, with *Siganus canalicullatus* (L_∞ =278 mm TL *K*=1.73; Bwathondi 1982) and *S.vermiculatus* (L_∞ =278 mm TL *K*=1.73; Gundermann *et al* 1983) reaching close to their maximum size in less than one year. These estimates may be considered high and unrepresentative of wild populations as they were derived from populations under "favourable" growth conditions.

On the basis of the high estimate of K and its small maximum size, traditional fisheries theory suggests that *S.doliatus* should have a relatively high rate of natural mortality and short longevity

(Beverton and Holt 1956; Pauly 1980). Unfortunately, there are no estimates of mortality or longevity available for *S.doliatus,* or any other species of siganid, to test this. However, a recent study of small acanthurids on the northern GBR (Howard Choat personal Dept. Marine Biology James Cook University communication) has validated the presence of annual bands in several species and estimated maximum longevity's of up to 35-40 years. Maximum recorded longevity's of two species of similar size and habit to *S.doliatus, Ctenochaetus striatus* (L_{max} =260 mm FL) and *Acanthurus nigrofuscus* (L_{max} =210 mm FL), were 35 and 15 years, respectively.

Although these species may be long lived, they are not slow growing. The majority of growth is occurring in the first two or three years of life after which it slows to almost negligible levels. Similar patterns of growth, *ie* a period of fast initial growth followed by an extended period of very slow or zero growth, have been demonstrated for other species of small reef fish (*Centropyge bicolor,* Aldenhoven 1986; *Pomacentrus moluccensis,* Mapstone 1988; Fowler 1990; *Lutjanus russelli,* Sheaves unpublished manuscript; *Lutjanus adetii* and *L.quinquilineatus,* Newman in press, *Acanthurus nigrofuscus,* Hart unpublished manuscript; *Lutjanus carponotatus,* this study).

Plectropomus leopardus is the most studied of the exploited species of reef fish on the GBR. Estimates of VBGE parameters for *P.leopardus* are available from a number of studies in different regions of the GBR (Williams and Russ, 1994). Pauly and Ingles (1981) estimated L_∞ and K to be 647 mm standard length(SL) and 0.25, respectively using ELEFAN and data from Goeden (1978). This estimate was based on a maximum longevity of 5 years. Ralston (1987) made an estimate of K=0.13 based on the analysis of the same data. McPherson *et al* (1988) provided the first parameter estimates from size at age data for *P.leopardus* from the GBR, based on readings of whole otoliths of *P.leopardus* from the Cairns region of the GBR. They suggested that *P.leopardus* was living to at least 7 year, with L_∞ and K estimated to be 598 mm (SL) and 0.25, respectively.

More recently, Ferreira and Russ (1994) validated the periodicity of the bands in sectioned otoliths of *P.leopardus* as annuli and estimated L_∞ and K at 522 mm fork length (FL) and 0.354, respectively, at Lizard Island. Their data were unusual in that they included the full age/size range of the species, from about 66 mm to 645 mm FL and ages from 0+ to 15. They demonstrated that the VBGE parameters were very sensitive to the omission of the smaller age/size classes from the estimation procedure and that this resulted in substantially different parameters estimates (with omission of first two age classes L_∞ = 613 mm FL and K=0.132) (Ferreira and Russ 1994). Their study demonstrated *P.leopardus* is considerably longer lived than previously thought and suggested that earlier estimates of growth parameters, which did not include small, young fish which are not commonly caught in the fishery, may have over-estimated L_∞ and underestimated K.

The estimates of L_∞ and K for *P.leopardus* from the Lizard Island tagging study are similar to those made by McPherson *et al* (1988) from size at age data. The estimate of L_∞ is larger and, consequently, the estimate of K lower than those made by Ferreira and Russ (1994) for *P.leopardus* from the same location (*ie* Lizard Island). The comparison of parameter estimates derived from growth increment data and size at age data is not strictly valid (Francis 1988a), as discussed below in relation to the estimates of growth for *L.carponotatus* from the two techniques. However, the same factors are likely to affect the estimates of growth parameters from the growth increment data, namely high variability in growth rates among individuals and incomplete size range of samples, which will result in positively biased estimates of L_∞ and negatively biased estimates of K (Sainsbury 1980).

The variation in growth increments for *P.leopardus* was extreme in some instances, there being as much as 4 mm/mth difference in growth increment between similar sized individuals. This occurred among both large (>500 mm FL) and small (<400 mm) size classes. Similar variability in growth has been observed in size at age data for *P.leopardus* (Ferreira and Russ 1994; in press), *P.maculatus* (Ferreira and Russ, 1992) *Epinephelus malabaricus*, and *E.coioides* (Sheaves 1995). Such variability in individual growth rates will inevitably obscure recruitment modes in length data for species with greater longevity's (>5-6 yrs). Hence the observed modes will contain more than a single age class and estimates of growth parameters based on length-frequency techniques are likely to be biased (Ferreira and Russ 1994).

The estimates of rates of growth for *L.carponotatus*, *P.leopardus* and *S.doliatus* from growth increment data from this study must be considered underestimates for two reasons. Firstly, the estimated growth rates can only be considered representative of tagged fish. As the growth of tagged individuals may be retarded by the presence of the tag and the process of capture, handling and tagging it is likely that the estimated rate of growth is less than that of untagged fish (Saunders and Allen 1967; McFarlane and Beamish 1989). Secondly, estimates of VBGE parameters from growth increment data are likely to be biased due to individual growth variability, resulting in overestimation of L_∞ and underestimation of K (see discussion below). There was substantial variation in growth increments among individuals of the same length. This suggests that the growth rate of untagged fish are likely to be higher than reported here.

The estimate of K for *L.carponotatus* from the growth increment data is low in comparison to the estimate derived from the size at age data (0.127 and 0.31,respectively). Although it is not strictly valid to compare parameter estimates derived from the two techniques (Francis 1988a), doing so provides some insight into the factors affecting the estimation of the VBGE parameters. Firstly, the size range included in the estimates of VBGE parameters for *L.carponotatus* from growth increment data did not include fish smaller than 180 mm LCF. The VBGE is very sensitive to the distribution of the data (Mapstone 1988; Hampton 1991) and the omission of data in the lower size/age classes has been shown to result in positively biased estimates of L_∞ and consequently, negatively biased estimates of K (Ferreira and Russ 1994). This suggests that the lack of growth increment data for individuals of *L.carponotatus* less than 180 mm may have resulted in K being underestimated. The negative effect of carrying a tag (s) may also have reduced the rate of growth of tagged fish compared with the untagged individuals used for the size at age estimates.

Of a more fundamental nature are the expected differences in the parameter estimates obtained from VBGE from the two types of data. The VBGE was derived based on the metabolic processes of individual animals (Richards 1959; Ursin 1967), and hence the parameters L_∞ and K describe the growth of an individual, not a population (Sainsbury 1980). Therefore, it is not a valid progression to fit the standard VBGE to data for a group, and doing so is likely to result in biased parameter estimates (Sainsbury 1980; Kirkwood and Somers, 1984; Hampton 1991). This is likely to be most serious in the case of growth increment data, where variation in L_∞ among individuals will result in a positively biased estimate of L_∞ and, consequently, an underestimate of K (Sainsbury 1980; Hampton 1991). The estimates of L_∞ for *L.carponotatus* from the two types of data conform to this expected pattern. The estimate of L_∞ from growth increment data was almost 50 mm greater than that estimated from the size at age data and larger than any individual in the combined samples.

Parameter estimates from the two types of data would also be expected to differ due to the difference in the definition of L_∞ when the VBGE is fitted to size at age data and growth increment data (Francis 1988 a and b). In the case of size at age data, L_∞ is the asymptotic mean length at age, *ie* the age beyond which any increase in mean length is negligible. Given individual variability in growth parameters it would be expected that some individuals would have lengths greater than L_∞. Furthermore, as some fish will not have stopped growing at L_∞, their growth increment over a period will be greater than zero. When fitting the VBGE to growth increment data, L_∞ is defined as the length at which the expected growth increment is zero. Under this definition L_∞ is the maximum length achieved in the population and, by definition, would be expected to be greater than an estimate of L_∞ from size at age data for the same population (Francis 1988a). The VBGE parameter estimates from size at age and growth increment data for *L.carponotatus* from this study conform to this pattern, and support Francis' (1988) contention that estimates of VBGE parameters derived from the two methods should not be compared in an attempt to validate one or the other.

Examination of whole and sectioned otoliths of *Lutjanus carponotatus* revealed the occurrence of clearly identifiable bands. The oldest individuals (n=2) aged from sectioned otoliths in the sample had 13 bands and were 300 mm fork length. This is not likely to represent the maximum longevity of this species given the size of the sample (n=79) and the fact that individuals up to 380 mm LCF were caught during the trapping study. It is likely that a larger sample size and range of sizes may reveal individuals of greater age than represented here. Brown *et al* (1993) found *L.carponotatus* greater than 350 mm LCF to be relatively common in spear and line fishing catches from four mid-shelf reefs in the Cairns section of the GBRMP. A large proportion of the *L.carponotatus* in their samples were estimated from counts of annulli in sectioned otoliths to be between 5 and 11 years, with a number of individuals estimated to be up to 15 years of age.

Other studies of age and longevity of other small-medium tropical reef lutjanids have recorded high longevities. Loubens (1980a) estimated maximum longevities of 12, 18, 22, 23 years for *Lutjanus vitta, L.gibbus, L.quinquilineatus* and *L.fulviflamma,* respectively, from New Caledonia from readings of whole and broken otoliths. Davis and West (1992) recorded ages of up to 8 years for *Lutjanus vittus* on the Northwest Shelf of Australia. Preliminary counts of whole otoliths of *L.fulviflamma* from Lizard Island indicate potential ages of up to 16 years (CRD, unpublished data) and validated estimates of maximum longevity for *L.adetii* and *L.quinquilineatus* indicate that these two small lutjanids may reach up to 24 and 31 years, respectively (Newman 1995). Thus, it appears that although many of the common species of lutjanids associated with coral reefs in the Indo-Pacific region have a relatively small maximum length, they are considerably longer lived than is widely recognised. Furthermore, within the species for which data are available, maximum longevity does not appear to be related to maximum length.

The relationship between readings from whole and sectioned otoliths was good up until about 5 or 6 years, after which there was a tendency for whole readings to underestimate age. However, sample sizes were small and comparison of a larger number of otoliths from older fish is required to determine the true nature of the relationship between readings of whole and sectioned otoliths over the entire range of age classes. Ferreira and Russ (1994) found similar levels of correspondence between readings of whole and sectioned otoliths for *P.leopardus* up to age five from Lizard Island. The divergence between readings of whole and sectioned otoliths in the older age classes was greater than for *L.carponotatus,* however. The same pattern of agreement between readings in younger age classes and divergence in older age classes, has also been described for species of *Sebastes* (Boehlert 1985). This suggests that reading of whole otoliths may be used routinely for aging at least the younger age classes of reef fish. As these younger age classes invariably comprise the greater proportion of age samples, especially in heavily exploited stocks, this would significantly reduce the time, expense and degree of expertise required to obtain age-based estimates of growth and other population parameters.

The linear relationship between otolith weight and estimated age was very good (r^2 =0.94). This suggests that otolith weight may be a useful, objective criteria for aging *L.carponotatus* and potentially other species of tropical reef fish. Several studies have investigated the relationship between age and otolith weight and many have included other independent variables (fish length and weight, otolith dimensions) to increase the proportion of the variance explained by the regression model (Boehlert 1985; Fletcher 1991; Ferreira and Russ 1994; Newman 1995). The relationships between age and otolith parameters in most of these studies have been good, with otolith weight generally explaining the majority of the variance. However, the relationship has been observed to vary substantially among species, even among closely related species (Boehlert 1985; Newman 1995).

The use of otolith weight as an estimate of fish age shows considerable promise as a objective, low cost, low training, substitute for reading sectioned or whole otoliths that may be considerably more reliable than length frequency methods. A comprehensive comparison of the range of available techniques (sectioned, whole, weighed otoliths and length frequency analysis) across a range of species and spatial scales should be a priority of future studies of age and growth of reef fish.

This chapter examined the rates of growth of *L.carponotatus*, *P.leopardus* and *S.doliatus* using growth increment data from tagging. It has provided the first estimates of growth parameters for *L.carponotatus* and *S.doliatus* for the GBR, and the first estimates from growth increment data for *P.leopardus* for the GBR. A feature of the tagging data for all three species was the high variation in growth increments among individuals of similar size, indicating that there may be considerable individual variation in rates of growth for these species. This suggests that the parameter estimates (K) from the growth increment data are likely to be negatively biased. The observed variation in growth rates among individuals will also result in a number of age classes occurring within individual length classes. The inability to discriminate among age classes on the basis of length means that growth parameter estimates based on analysis of length frequency distributions are likely to be biased, and that this bias will increase with the longevity of the species.

The description of growth of *L.carponotatus* based on size at age data demonstrated that this species grows quite rapidly, approaching the average asymptotic length in the early stages of growth followed by an extended period of little, or no growth. Considerable variation in growth rates among individuals was evident also in the size at age data. This supports the observations from the growth increment data and highlights the need for age based estimates of growth and other important population parameters, such as mortality and reproduction. The favorable comparison between age estimates from whole and sectioned otoliths suggests that the training and technology required to obtain age estimates from sectioned otoliths may not be necessary, at least for the younger age classes which commonly represent a large proportion of samples. Furthermore, the strong relationship between otolith weight and estimated age for *L.carponotatus* suggests that objective criteria, such as otolith weight, may provide an efficient means for obtaining age based estimates of population parameters without the expense, technology and training required to prepare and interpret sectioned otoliths.

Table 4.1: Summary of tagging data used to estimate rates of growth of *Lutjanus carponotatus*, *Plectropomus leopardus* and *Siganus doliatus*, with number of releases and number returned, number of observations used in analyses (n) and the range, mean and standard error (below in parentheses) of length (LCF mm) at release and time at liberty (t_i, d).

Species	Released	Returned	*n*	Range LCF	Mean LCF	Range t_i	Mean t_i
L.carponotatus	377	96	41	165-335	263.5	69-365	136.0
					(0.66)		(10.37)
P.leopardus	83	28	16	336-605	460.2	69-554	235.8
					(1.40)		(15.93)
S.doliatus	1039	221	102	106-203	168.0	33-696	156.9
					(0.15)		(14.35)

Table 4.2: Estimates of VBGE parameters, L_∞ and K, from Gulland and Holt plots for *Lutjanus carponotatus*, *Plectropomus leopardus* and *Siganus doliatus* (see figures 4.2-4.4) from Lizard Island lagoon, northern Great Barrier Reef. Sample size (n), r^2 and ANOVA results for model fit are presented also. Standard errors of parameter estimates are given below in parentheses.

Species	n	r^2	L_∞	K	F-ratio	df	Pr>F
L.carponotatus	41	0.51	35.69	0.1268	40.8599	1,39	0.001
			(4.36)	(0.0198)			
P.leopardus	16	0.35	57.60	0.2143	7.5246	1,14	0.0159
			(16.55)	(0.0781)			
S.doliatus	102	0.48	20.19	0.7123	90.6899	1,100	0.001
			(1.81)	(0.0748)			

Table 4.3: Estimates of VBGE parameters, L_∞ ,K and t_o from nonlinear fit to size at age data from sectioned otoliths for *Lutjanus carponotatus*. Approximate standard errors of estimates, model fit (Adjusted r^2), Mean Square Error (MSE) and degrees of freedom for the model fit are given also.

Parameter	Estimate	Approx SE	Adjusted r^2	MSE	df
L_∞	312.14	9.111	0.856	52545.69	75
K	0.31	0.043			
t_o	-1.05	0.287			

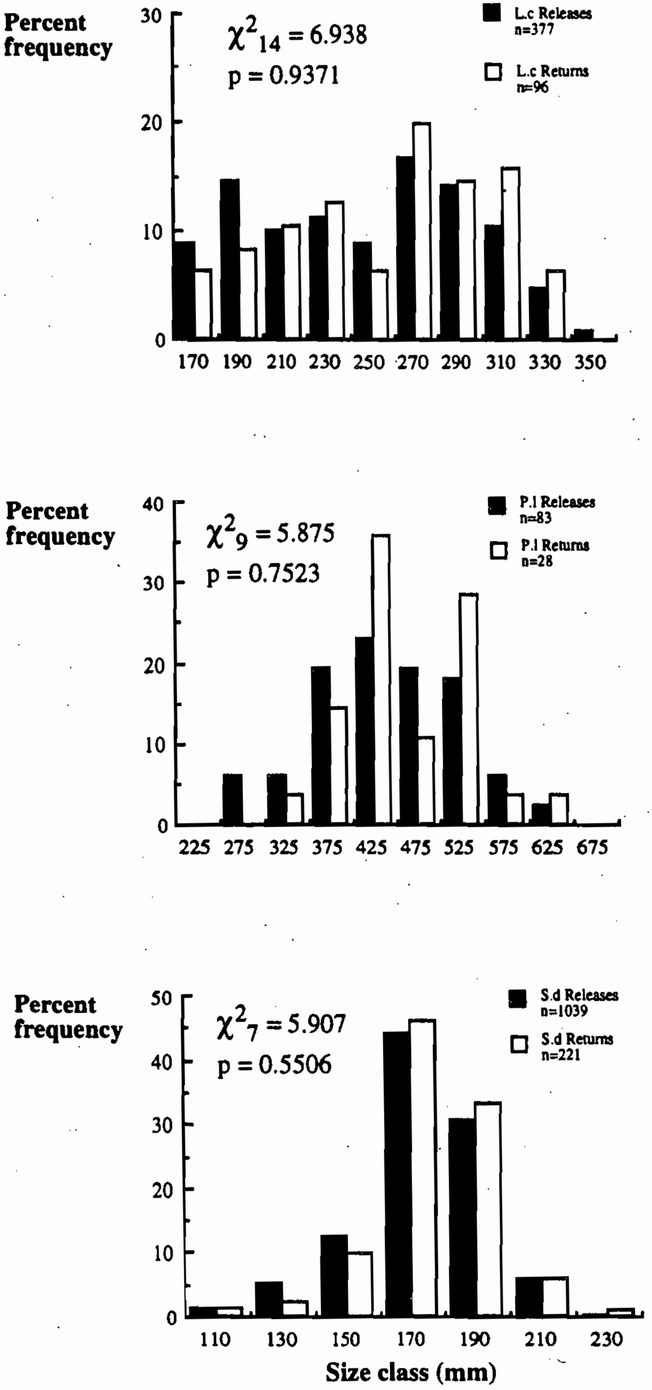

Figure 4.1: Length frequency distributions of releases and returns of *Lutjanus carponotatus*, *Plectropomus leopardus* and *Siganus doliatus* caught in Z-traps and tagged with standard t-bar anchor tags in the Lizard Island lagoon, northern Great Barrier Reef. Mid-point of size classes is given. Sample sizes (n) and results of Chi-square comparisons are presented also.

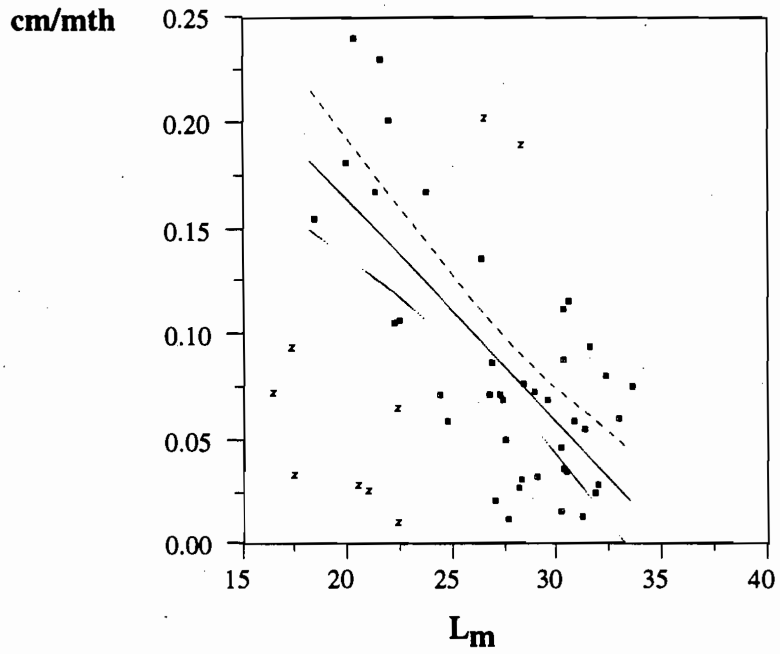

Figure 4.2: Regression of growth increment (cm/mth) against mean length (L_m (cm)) for *L.carponotatus*. The regression is significant ($F_{0.05\ 1,39}$=40.8599; p=0.001; n=41). Parameter estimates for VBGE are L_∞=35.69cm (SE=4.36cm), K=0.1268 (SE=0.0198). Dashed lines represent 95% CI of regression line (solid line), "z" are points omitted as outliers from the regression analysis.

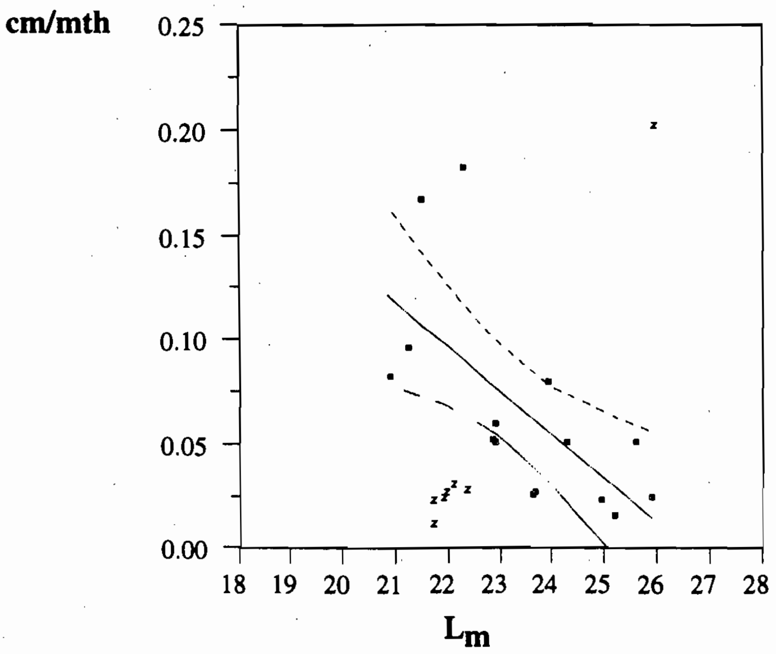

Figure 4.3: Regression of growth increment (cm/mth) against mean length (L_m (cm)) for *L.fulviflamma*. The regression is significant ($F_{0.05\ 1,13}$=10.0259; p=0.0074; n=15). Parameter estimates for VBGE are L_∞=26.7cm (SE=7.42cm), K=0.2535 (SE=0.0801). Dashed lines represent 95% CI of regression line (solid line), "z" are points omitted as outliers from the regression analysis.

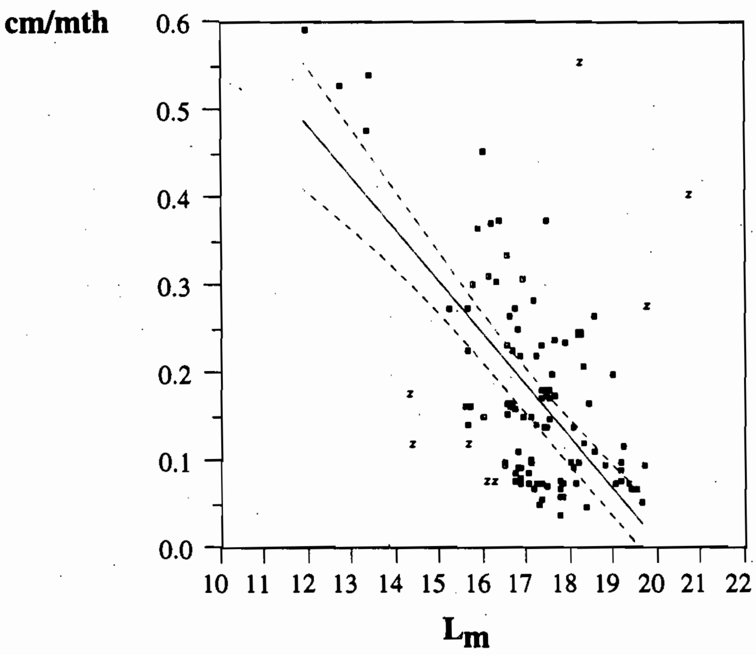

Figure 4.4: Regression of growth increment (cm/mth) against mean fork length (L_m (cm)) for *Siganus doliatus*. The regression is significant ($F_{0.05\ 1,100}$=90.6899; p=0.001; n=102). Parameter estimates for VBGE are L_∞=20.19cm (SE=1.81cm), K=0.712 (SE=0.0748). Dashed lines represent 95% CI of regression line (solid line), "z" are points omitted as outliers from the regression analysis.

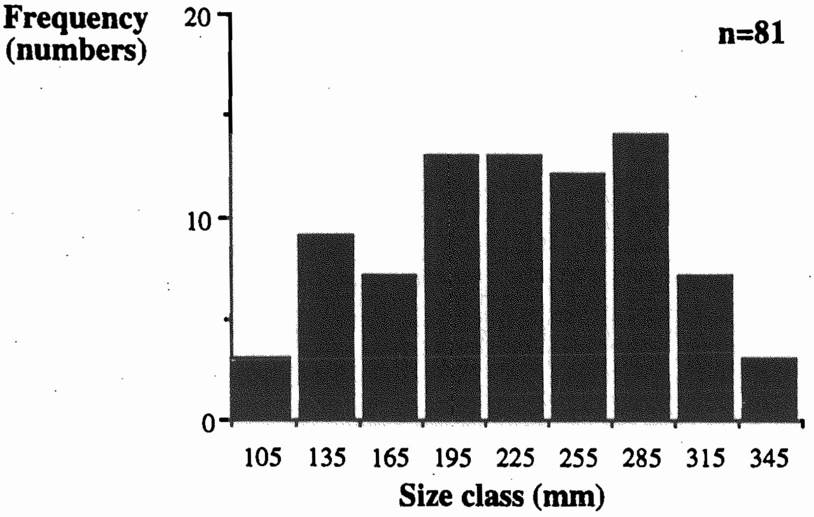

Figure 4.5: Length-frequency distribution for *Lutjanus carponotatus* collected for size-at-age data. Mid-point of 30 mm size classes is given. Sample size (n) is 81.

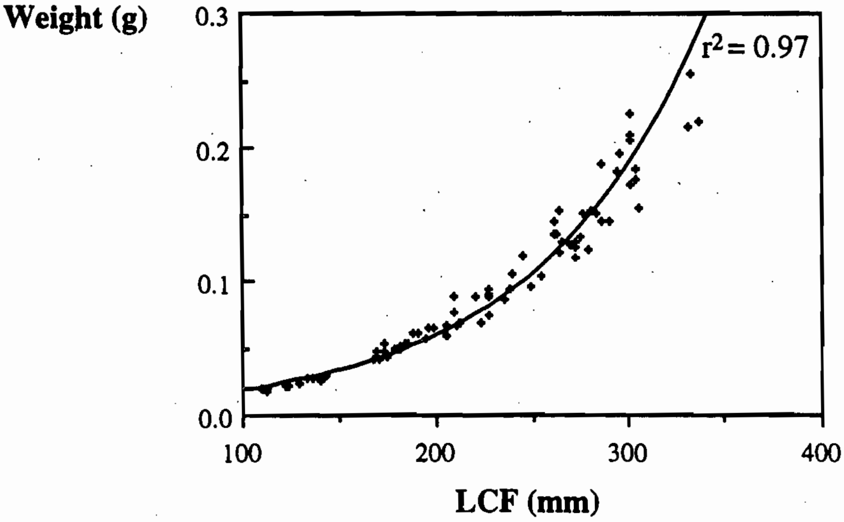

Figure 4.6: Plot of otolith weight (g) by fork length (LCF mm) for *Lutjanus carponotatus*. Fitted line is an exponential function of fork length, $r^2 = 0.97$.

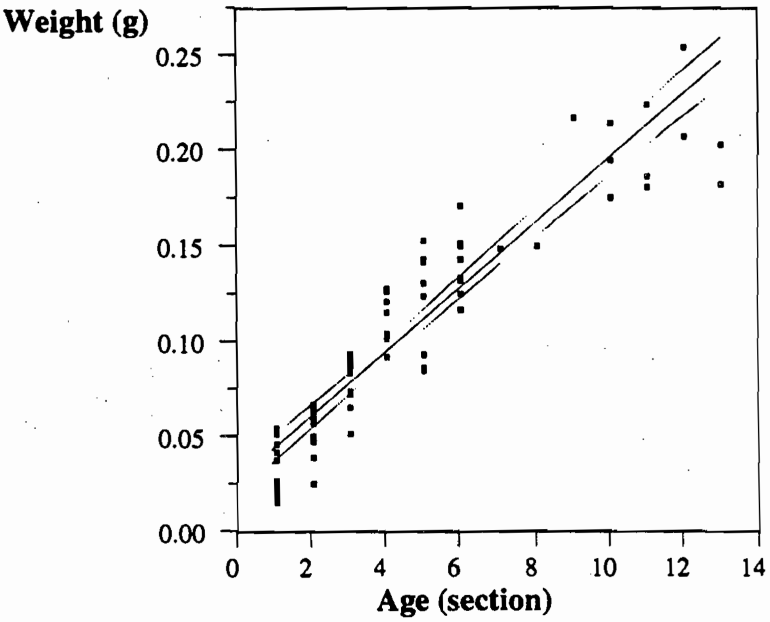

Figure 4.7: Otolith weight by age from sectioned otoliths for *Lutjanus carponotatus*. The regression is significant ($F_{0.05,\ 1,\ 77} = 553.51$; $p=0.0000$; $r^2 = 0.94$). Dashed lines represent 95% confidence intervals of the regression line.

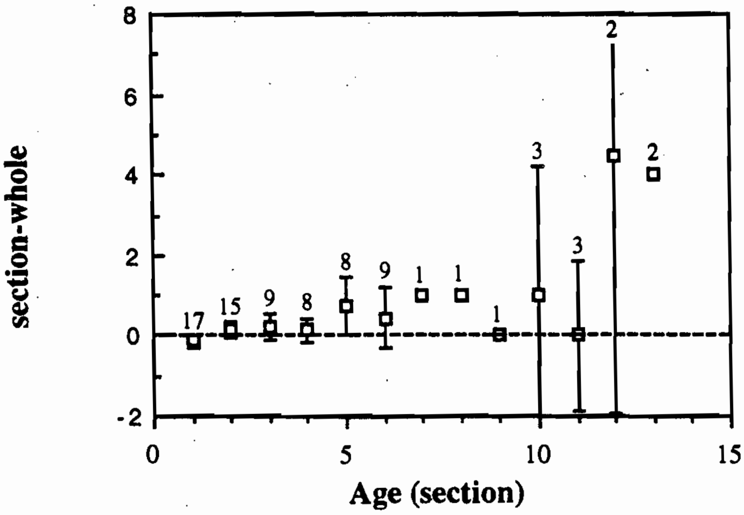

Figure 4.8: Mean difference (sectioned - whole) in estimated age by age class (sectioned) of *Lutjanus carponotatus* from readings of sectioned and whole otoliths. Error bars are 95% confidence intervals. Sample sizes for each age are given above each point.

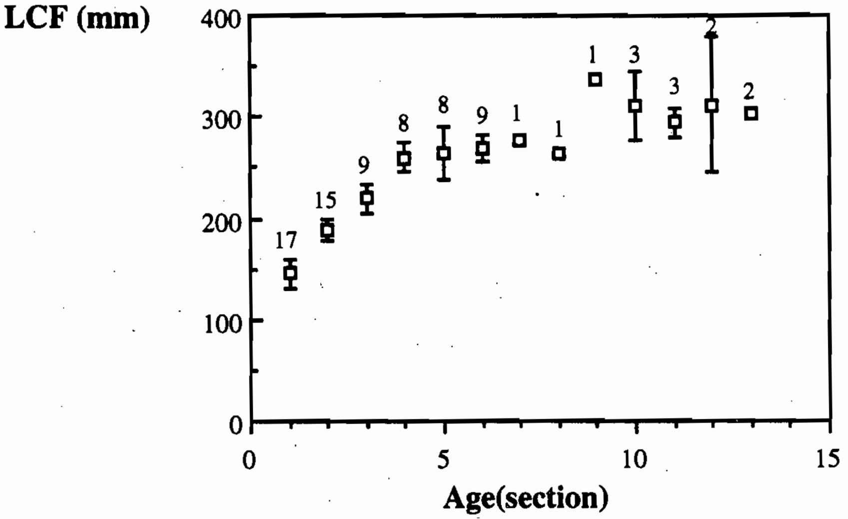

Figure 4.9: Mean length (LCF mm) by age class for *Lutjanus carponotatus* from size at age data from sectioned otoliths. Sample sizes for each age class are given above each point. Error bars are 95% confidence intervals.

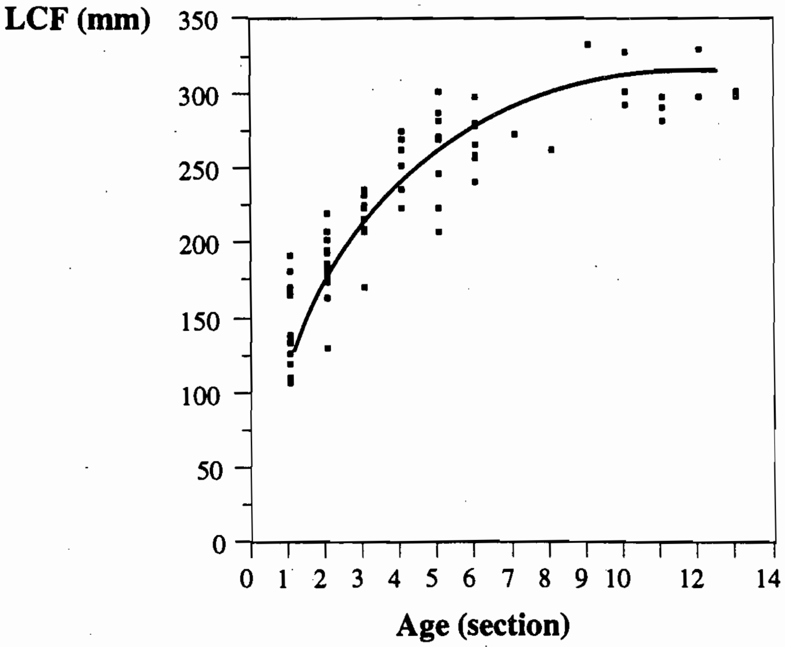

Figure 4.10: Nonlinear fit of VBGE to size-at-age data for *Lutjanus carponontatus* from sectioned otoliths. L_{∞}= 312.1 mm (approx.SE= 9.11) and K= 0.31 (approx.SE=0.043) (SSE = 52545.69, n=75).

Chapter 5

Estimates of rates of loss of t-bar anchor tags and dart tags from *Lutjanus carponotatus* and *Plectropomus leopardus*.

5.1 Introduction

Techniques designed to estimate rates of mortality or movement, by following marked individuals through time, assume that all sources of loss from the tagged population can be accounted for and that the dynamics of the tagged population are representative of the untagged population. The latter of these assumptions is virtually impossible to test directly (Lebreton *et al* 1992, but see McFarlane and Beamish 1990). However, with suitably designed tagging experiments, it is possible to obtain estimates of the three sources of loss from the tagged population, ie. mortality, emigration and loss of tags.

Tag loss is generally catergorised into two components referred to as type I and type II tag loss (Beverton and Holt 1957). Type I tag loss occurs immediately following release and results from mortality due to the tagging and handling process and nonreporting and nonrecovery of tags. Type II tag loss refers to the gradual loss of tagged individuals from the tagged population over an extended period and may result from the loss of tags or mortality due to the effect of carrying the tag(s). Type II tag loss is often assumed to occur at a constant rate. Both forms of tag loss can be significant sources of bias in parameter estimates from tagging experiments and generally will cause parameter estimates to be negatively biased (Beverton and Holt 1957; Ricker 1958; Wetherall 1980; Kirkwood 1981; Seber 1982). Consequently, estimating rates of tag loss should be a regular feature of any tagging programme concerned with estimating rates of movement, mortality, exploitation or population size (Bayliff and Morbrand 1972; Wetherall 1982; Treble *et al* 1993).

There are two main strategies for estimating rates of tag loss. Commonly, a small double-tagging experiment is performed to obtain estimates of tag loss parameters, which are then used to correct population parameters estimated from a larger single-tagging experiment. Conversely, all fish may be double-tagged throughout the main experiment. The second approach has the advantages that tag loss parameters may be estimated directly from the main experiment and the exclusive use of double-tagged fish increases the expected rates of recovery (Bayliff and Morbrand 1972; Wetherall 1980). In this study the latter of these approaches was adopted.

Two separate tagging studies were performed to examine patterns of movement and estimate rates of natural mortality and growth of several species of reef fish. In both studies all fish were double-tagged. The aim of double tagging in the Lizard Island lagoon study was to obtain estimates of rates of tag loss which could be used to correct estimates of mortality of each of the target species (see Chapter 6). In the study of patterns of movement of *Plectropomus leopardus* among reefs (see Chapter 8), the principle reason for double-tagging all fish was to maximise recovery rates. An ancillary part of that study was a comparison of the rates of tag loss of t-bar anchor (TBA) tags and standard dart tags. Furthermore, the use of different colour TBA tags in the latter study, to colour-code releases by reef, and returns from both the public and research recovery exercises provided the opportunity to test for the effect of colour and source of returns (public or research) on estimates of tag loss.

5.2 Methods

5.2.1 Tag types and tagging method

The trapping and tagging methods for the Lizard Island study have been described in Chapter 2 (sections 2.3.2, 2.4 and 2.5). For *Siganus doliatus*, the smallest target species from the Lizard Island study, double-tagging was abandoned following the second sampling trip due to the lack of returns of any double-tagged individuals. Consequently, data for estimates of tag loss for this species are not available.

The sampling protocol for the large-scale movement study is described in Chapter 7 (section 7.2). The tagging methods are described below and are relevant to Chapter 8 also.

Tag Type

Standard t-bar anchor (TBA) tags and standard dart tags, manufactured by Hallprint® (Holden Hill, SA), were used in the large-scale study (only fish tagged with standard t-bar anchor tags are considered for the Lizard Island study) . Tags were labelled with an individual number, a toll-free telephone number and the words "RESEARCH-REWARD". In all other respects the tags were identical to those used in the Lizard Island study (see section 2.5). The standard TBA tags were colour-coded (green, orange, pink, grey, blue and yellow) for each reef in the study. The dart tags were yellow and were used with yellow TBA tags only.

Tagging Technique

All fish were double-tagged. The first tag was applied between the 3rd and 4th dorsal spine approximately 5-10 mm below the base of the dorsal fin. The second tag was applied approximately 10 mm posterior to the commencement of the soft dorsal fin, on the same side as the anterior tag. All tags were tested to ensure that they were secure and any tag which was not secure was removed and a new tag applied. During the first four tagging exercises all species of serranids, lutjanids and lethrinids were tagged. For the final research recovery exercise only *Plectropomus leopardus*, *Cephalopholis cyanostigma*, *Lutjanus bohar*, *L.carponotatus*, *Lethrinus atkinsoni* and *L.miniatus* were tagged. However, return rates of all species, except *P.leopardus*, were too low to yield useful data sets (See Chapter 8). Therefore, only data for *P.leopardus* are presented here.

The main objective of this double-tagging study was to compare the effectiveness of standard TBA tags and dart tags for use on large reef fish. Approximately one third of the total number of *P.leopardus* greater than 350 mm fork length (LCF) were tagged with one standard TBA tag and one dart tag. Fish smaller than 350 mm (LCF) were considered to be too small to be tagged with dart tags (Davies and Reid, 1982; personal observation). The locations of the tags were the same as described above and the relative positions of the two types of tag were alternated. All other fish were tagged with two standard TBA tags.

Captured fish were dehooked by the fisher and placed in either the kill bin, a self-draining bin permanently fixed to the centre of the "dory" (5 m tender vessel), or a plastic "nelly" bin (600 x 400 x 400 mm), filled with fresh sea water. Fish were taken from the bin with a piece of foam rubber and placed on a 1 m wooden measuring board where they were measured, tagged and released. The following data were recorded for each fish: species, length to caudal fork (to the nearest mm) and standardised comments on the condition of the fish at release. The entire process generally took less than 45-60 seconds per fish to complete.

Research returns were obtained from 4 research recovery exercises evenly spaced over a period of 22 months following the initial tagging exercise (Dates of research trips are given in Chapter 7, Table 7.1) . Fish were tagged and released on each of these exercises also. Public returns were obtained through a publicised reward programme coordinated by the Great Barrier Reef Marine Park Authority (GBRMPA) from April 1992 to February 1994.

5.2.2 Data sets

Three main data sets arose from the two studies. Firstly, as the Lizard Island study was a multiple release-recapture study, all returns were obtained by CRD and individual fish were often captured on multiple occasions. This is in contrast to the common fisheries situation (release-recovery) where multiple recaptures are rare (Hilborn 1990; Schweigert and Schwarz 1993). The use of multiple observations of the same individual to estimate rates of tag loss raises the question of independence among observations. Consequently, the last observation of each fish when one, or both, of the original tags were still present was used to estimate the probability of tag retention in the Lizard Island study. This provides a larger number of observations at greater times at liberty than if only the first observation was used.

There were two main data sets from the large-scale study; 1) the comparison of TBA and dart tags from fish tagged with both tag types, and 2) the comparison of different coloured TBA tags from fish tagged with TBA tags only. Both these data set may be divided further by the source of the returns (public or research). Only the first observation of fish recaptured multiple times have been used in the analysis of these data.

5.2.3 Analysis

Diagnostic plots of ln K_i by t_i were used to identify the most appropriate model to fit to the different data sets, where

$$K_i = 2r_{di} \;/\; r_{si} + 2r_{di}$$

where, r_{di} is the number of returns retaining 2 tags, r_{si} is the number of returns retaining a single tag and t_i is the mid-point of the *i* th period since release, where the 2 tags are identical and assumed to have the same probability of being shed. In the case of the comparison of the dart tags and the TBA tags, alternative estimators were used for the two tag types:

$$K_{Ai} = r_{di} \;/\; r_{Bi} + r_{di}$$

and,

$$K_{Bi} = r_{di} \;/\; r_{Ai} + r_{di}$$

where, K_{Ai} is the estimated probability that a TBA tag is retained, K_{Bi} is the estimated probability that a dart tag is retained, r_{di} is the number of returns retaining both tags, r_{Ai} is the number of returns retaining only the TBA tag and r_{Bi} is the number of returns retaining only the dart tag.

A plot of Ln K_i against t_i will be linear if type II tag loss (following the terminology of Bayliff and Morbrand 1972) is constant. In this case the linear models of Chapman *et al* (1965) and Bayliff and Morbrand (1972) are most appropriate. If the plot is non-linear, it suggests that type II tag loss is increasing (concave downwards) or decreasing (concave upwards) over time and a more complex non-linear model may be warranted (Kirkwood 1981; Wetherall 1982).

In all cases the 2 parameter Bayliff and Morbrand (BM) model

$$\ln(K_i) = \ln p - Lt_i$$

(where, ln*p* is Type I tag loss which occurs immediately following release, *L* is the instantaneous constant rate of tag shedding (Type II tag loss) and t_i is the mid-point of the *i* th period since release) was fitted using a weighted linear regression, with r_i (number of returns per t_i) used as the weighting factor. The model assumes that instantaneous tag shedding (Type II tag loss) is constant with time, that fishing mortality is constant within t_i and returns are evenly distributed within t_i. The BM model was fitted as the plots were generally of a linear form and suggested a negative intercept, and therefore the possibility of Type I tag loss.

Returns of *P.leopardus* from the research exercises and from the public from the large-scale tagging study were analysed separately and the regression parameter estimates compared by ANCOVA (Zar 1984). When the parameters did not differ significantly, new parameter estimates were computed from a common regression. Two-way contingency tables (using Likelihood Chi-squared test (SAS 1989)) were used to test for the effect of tag type (dart tags and TBA tags), tag colour (Yellow, Green, Orange, Pink, White, Blue for TBA tags only), and source of returns (public and research) on the frequency of tag loss for the large-scale study.

5.3 Results

5.3.1 Rate of loss of t-bar anchor tags from the Lizard Island study

Summaries of the data sets used for *Lutjanus carponotatus* and *Plectropomus leopardus* from the Lizard Island study are presented in Tables 5.1 and 5.2, respectively. A significant fit of the BM model was obtained for *L.carponotatus* (r^2=0.84; $F_{0.05\ 1,4,}$=21.1933; p=0.0100) (Figure 5.1) but not for *P.leopardus* (r^2=0.12; $F_{0.05\ 1,2,}$=0.2931; p=0.6425) (Figure 5.2).

There was no significant type I tag loss for *L.carponotatus* ($t_{0.05\ (2),4,}$= -0.33; p=0.7546) (Table 5.3). The estimated instantaneous rate of tag loss (type II) for *L.carponotatus* was 0.0034 (± 95% CI=0.0021) (Table 5.3). The estimated proportion of TBA tags lost after 100 days and after 1 year for *L.carponotatus* 0.32 and 0.72, respectively.

The lack of fit for *P.leopardus* is likely to be due to the few incidences of tag loss and the very small sample size (n=26) for this species from the Lizard Island study. Only 6 of the 26 observations had lost a tag. Five out of the six fish which had lost a tag were recaptured within 250 days (Table 5.2). In contrast, there were 9 observations of individuals at liberty for greater than 250 days, and 6 for greater than 350 days, returned with both of the original tags. Furthermore, the individual at large for the greatest time at liberty (600d) was returned with both tags. The overall probability of tag retention was high (K_i =0.870, SE=0.022). Although the data are few, this suggests that the overall rate of loss of TBA tags for *P.leopardus* is likely to be low and may decrease with time following an initial period of loss.

5.3.2 Rates of loss of t-bar anchor tags and dart tags for P.leopardus from the large-scale study

The model fits for TBA tags and dart tags for *P.leopardus* from the public returns from the large-scale study were not significant (TBA: $F_{0.05\ 1,4}$=2.4183: p=0.2602 darts: $F_{0.05\ 1,3}$=1.1328: p=0.3987). It was not possible to fit a regression to the data from the research returns as there were too few observations for each time interval. Consequently, data from both sources were pooled (Table 5.4). The regression for TBA tags for the pooled data was significant ($F_{0.05,1,5}$=16.22; p=0.01) (Figure 5.3), with significant intercept ($t_{0.05\ (2),5}$ = -3.75; p=0.013) and slope ($t_{0.05\ (2),4}$=-4.03; p=0.01), and parameter estimates of p=0.7160 and L=0.001593 (Table 5.5). However, the fit for dart tags was poor (r^2=0.542) and not significant (F=$_{0.05,1,3}$=3.5471; p=0.1562) (Figure 5.4). Consequently it was not possible to make valid parameter estimates for dart tags (Table 5.5). The estimated proportion of TBA tags lost after 100 days and after 1 year were 0.39 and 0.60, respectively.

5.3.3 Comparison of frequency of return of t-bar anchor tags and Dart tags for P.leopardus

There was a significantly higher frequency of retention of TBA tags than dart tags for *P.leopardus* tagged with both tag types and recaptured during the research recovery exercises (Likelihood Chi-sq$_{0.05,1,}$ =10.678; p<0.005). However, this difference was not significant for the data from the public returns (Likelihood Chi-sq$_{0.05,1,}$ = 0.6127; p>0.25). The significant difference in the frequency of tag loss among tag types from the research returns suggests that the dart tags are shed more frequently than the TBA tags. This is supported by the plots of the probability of tag retention over time for the two tag types (Figures 5.3 and 5.4). The lack of a significant effect from the public returns suggests that the larger dart tags are more likely to be observed and reported by the public than the smaller TBA tags and that this compensates for their higher rate of shedding.

5.3.4 Rate of loss of t-bar anchor tags for P.leopardus from the large-scale study

A summary of the TBA tag data by source of returns for the large-scale study is given in table 5.6. There was no significant difference between the model fits for the research and public returns ($t_{0.05(2),8}$ =-1.105: p>0.5). The common regression from the research and public returns is illustrated in Figure 5.5. Both the intercept ($t_{0.05(2),5}$=-3.01; p=0.0299) and slope ($t_{0.05\ (2),4}$ =-5.58; p=0.0.0025) were significantly different from zero (Table 5.7), indicating both Type I and Type II tag loss contributed significantly to the tag shedding process. The estimate of the proportion of tags remaining following type I tag loss, p, for the TBA tags was 0.8927 (95% CI=0.8140-0.9791), while L, the instantaneous rate of tag shedding was 0.0010 (±95% CI=0.0005) (Table 5.7). The estimated proportion of TBA tags lost in the first 100 days and the first year following release were 0.19 and 0.38, respectively.

5.3.5 Effect of colour on the frequency of return of t-bar anchor tags for P.leopardus

A summary of the pooled public and research returns of TBA tags by colour is given in table 5.8. There was no significant difference in the frequency of loss of the 6 different colours of TBA for the public returns (Likelihood Chi-sq $_{0.05,5,154}$=1.413; p=0.9299), the research returns (Likelihood Chi-sq $_{0.05,5,83}$=5.438; p=0.3648) or the pooled data (Likelihood Chi-sq $_{0.05,5,243}$=1.902; p=0.8625) (Figure 5.6). This suggests that the colour of TBA tags had no significant effect on the frequency of loss or reporting.

5.4 Discussion

Several studies using TBA tags have found type I tag loss for TBA tags to be low or insignificant. Whitelaw and Sainsbury (1986) reported that short-term (55 days) loss of Floy FD-67 TBA tags from *L.carponotatus* was low (6.1%). Sheaves (1993), using similar trapping and tagging techniques to those used in this study, found that type I loss was not significant for several estuarine species tagged with Hallprint® TBA tags. Davis and Reid (1982) suggested that sufficient handling time to ensure the t-bar was securely anchored and prior experience in tagging the target species contributed to the absence of type I tag loss in their estimates of rates of loss of Floy TBA tags from *Lates calcarifer*. Similar circumstances existed in this study, in that time out of the water was not as critical as is considered for pelagic species and the tagger (CRD) had considerable experience with the target species prior to the commencement of the study. This may have reduced type I tag loss to insignificant levels.

There are relatively few estimates of tag loss available for TBA tags for tropical species of demersal reef fish (Whitelaw and Sainsbury 1986) and less where tag loss parameters have been estimated from a formal model. The estimates of instantaneous tag loss, L, for TBA tags for *L.carponotatus* (0.0034), from the Lizard Island study, and *P.leopardus* (TBA only: 0.0010, TBA/Dart: 0.0018), from the large-scale study, are similar to those reported by Davis and Reid (1982), for Floy FD-67 tags for *Lates calcarifer* (0.0018), and Sheaves (1993), for TBA tags for several estuarine species combined (0.0011).

Although these rates may appear small when expressed in an instantaneous form, over the course of a capture-recapture study tag loss will contribute substantially to the attrition of tags from the tagged population. Even in short-term experiments (100 days), such as that described by Davis and Reid (1982), these rates will result in a large proportion of tags being lost. Using the rate of tag loss for *L.carponotatus* from the Lizard Island study, and the case where fish are tagged with a single tag only, approximately 32% of the tagged population will have lost their tags and not be identifiable on recovery within the 100 day period. If all fish were double-tagged, the loss of identifiable individuals decreases to approximately 10%.

This highlights the need to estimate rates of tag loss in order to obtain unbiased estimates of population parameters from tagging experiments (Beverton and Holt 1956; Baglin *et al* 1980; Wetherall 1982; Treble et al 1993). Moreover, as parameter estimates from tagging data are limited by the number of recoveries, it suggests that it may be more cost-effective to double-tag all fish purely for the expected increase in recoveries (Bayliff and Morbrand 1972; Baglin *et al* 1980; Wetherall 1982). This is particularly likely to be the case for tagging studies where expenses include ship time or bench fees at research stations. In these situations the additional cost of applying two tags rather than one are small in relation to the overall cost of the study.

T-bar anchor tags and dart tags are the two most commonly used tags for demersal reef fish. However, results of studies comparing the two tag types are equivocal. Davis and Reid (1982) compared rate of loss Floy FT-2 dart tags and FD-67 anchor tags for the barramundi, *Lates calcarifer*, and found the FD-67 anchor tags had a significantly higher rate of shedding. However, the two tag types were used on different size classes of fish. Consequently, the comparison of tag type was confounded with size. They concluded that FD-67 tags did not penetrate deeply enough to successfully lock the anchor behind the pterygiophores and that the pterygiophores of the barramundi were too widely spaced to secure both sides of the t-bar anchor. They also noted that FD-67 tags were prone to separating at the joint between the monofilament anchor and the plastic tubing, particularly when fish were removed from gill nets.

In contrast, Whitelaw and Sainsbury (1986) found Floy FT-2 tags to have a significantly higher frequency of loss than FD-67 tags for *Lutjanus carponotatus*. They demonstrated that the higher rate of loss of the FT-2 tags was the result of pterygiophores being broken during the tagging process, resulting in poor support for the tag and high mortality. This did not occur with the FD-67 anchor tags. From these studies it would appear that the more appropriate type of tag will depend on the size, lateral compression and spacing of the pterygiophores of the target species and the method of recovery.

In this study the loss of standard dart and TBA anchor tags (Hallprint®) were compared using a range of sizes of *P.leopardus* (350 - 680 mm). The frequency of return of TBA tags was significantly higher than the dart tags for the research returns and, although the model fit was not significant, the rate of loss of the dart tags appears to be considerably higher than that for the TBA tags. This suggests that the dart tags are lost more frequently than the TBA tags and this may be the result of damage to the pterygiophores, as found by Whitelaw and Sainsbury (1986).

Contrary to the results of Davis and Reid (1982) working with barrumundi, the TBA tags were found to penetrate sufficiently to lock behind the pterygiophores of even large *P.leopardus* (>550 mm). The use of "long" tagging needles for the tagging guns and "long shaft" TBA tags provided extra penetration. In the case of larger fish (>650 mm) sufficient penetration was achieved by applying the tag closer to the posterior end of the dorsal fin where the body is more laterally compressed. Using this tag location, large serranids (*Plectropomus leopardus* up to 680 mmLCF, *Epinephelus fuscoguttatus* and *E.malabaricus* >700 mm LCF) have retained both TBA tags for more than 2 yrs (CRD, unpublished data). The results of this comparison suggest that TBA tags are more appropriate for use on *P.leopardus* than dart tags.

In contrast to the results from the research returns, there was no difference in the frequency of return of the two tag types from the public returns. A potential explanation for this is the larger dart tags are more likely to be observed and reported by the public and this compensates for their higher frequency of shedding. Over the course of the large-scale study several fishers reported that they did not discover the tag until they came to cleaning the fish, as the tag was covered in a thick coat of algae. Filamentous algal growth is common on tags and will completely cover a TBA tag in a few weeks (personal observation). The effects of this on detection rates could be minimised by a well planned public participation and advertising campaign prior to the commencement of the tagging study to inform the public of the location and size of the tag being used and by providing examples of the likely appearance of the tag(s) after various times at liberty, not only when they are first applied.

The use of different colour tags is a common technique used to differentiate among individuals or, as was the case in the large-scale study, between batch releases in different spatial or temporal strata (creeks, reefs, releases). Therefore, it is of interest to know whether tags of different colours have different frequencies of loss. A potential mechanism for differences in the frequency of loss of different tag colours is if fish which feed on ectoparasites selectively remove tags of a particular colour(s) from tagged fish. Incidences of tags being "bitten off" at the shaft are common, particularly for tropical species (Sheaves, 1993, personal observation, Mike Hall, Hallprint®, SA, personal communication). The results from this study demonstrated there was no significant difference in the frequency of loss of the six colours of TBA used. This is not necessarily a surprising result as the colour of the tag will be visible only for the first few weeks following release due to the rapid growth of algae on the tags (see above). However, it does indicate that the use of tags of different colour to colour-code releases should not result in different frequencies of loss among tag colours.

Tagging studies are widely used in fisheries biology to estimate a variety of population parameters, including natural and fishing mortality, population size and movement (Beverton and Holt 1957; Ricker 1958; Jones 1979; Burnham *et al* 1987; Gulland 1988). However, failure to account for the shedding of tags from tagged fish may lead to serious bias in these parameter estimates (Wetherall 1980; Treble *et al* 1993). The estimates of tag loss obtained in this study indicate that tag loss can be considerable and therefore, assuming that it is negligible is unjustified. Furthermore, given the relatively high rates of tag loss observed for both species and types of tag examined in this study, double tagging of all fish should be a common feature of future tagging studies, rather than an exception. This would increase the rate of recovery and provide corresponding increases in the precision of tag loss parameter estimates.

Table 5.1: Summary of tag loss data for TBA tags for *Lutjanus carponotatus* from the Lizard Island study. t_i is the mid-point of the *i* th time period (60 days) since release, r_{di} is the number of fish returned with 2 tags in the *i* th period, r_{si} is the number of fish returned with one tag in the *i* th period and K_i is the estimated probability of tag retention at t_i . * denotes data omitted from the analysis.

t_i (days)	r_{di}	r_{si}	K_i
30	21	6	0.875
90	16	12	0.727
150	3	5	0.546
210	3	10	0.375
270	3	5	0.546
330	1	5	0.286
390*	1	2	0.500
450*	0	1	-
510*	1	0	1

Table 5.2: Summary of tag loss data for TBA tags for *Plectropomus leopardus* from the Lizard Island study. t_i is the mid-point of the *i* th time period (120 days) since release, r_{di} is the number of fish returned with 2 tags in the *i* th period, r_{si} is the number of fish returned with one tag in the *i* th period and K_i is the estimated probability of tag retention at t_i . * denotes data omitted from the analysis.

t_i (days)	r_{di}	r_{si}	K_i
60	6	2	0.875
180	4	2	0.800
300	6	1	0.9231
420	3	1	0.8571
540*	0	0	-
660*	1	0	1.000

Table 5.3: Estimates of tag shedding parameters ***p*** (type I) and ***L*** (type II) from the Bayliff and Morbrand (1972) tag shedding model for TBA tag returns for *Lutjanus carponotatus* from the Lizard Island study. Sample size (n), proportion of total variance accounted for by the model (r^2) and significance level of parameter estimate (Pr>t) are given also. Ninety-five percent confidence intervals of parameter estimates are in given below in parentheses.

Species	n	r^2	$\ln p$	Pr>t	p	L	Pr>t
L.carponotatus	90	0.84	-0.0390 **ns**	0.7546	0.9618	-0.0034 **	0.010
95% CI			(0.2622 to -0.3402)		(1.2997 to 0.7117)	(-0.0013 to -0.0055)	

Table 5.4: Summary of tag loss data for TBA tags and dart tags of *P.leopardus* tagged with both tag types from the pooled public and research tag returns from the large-scale study. t_i is the mid-point of the *i* th time period (60 days) since release, r_{di} is the number of fish returned with 2 tags in the *i* th period, r_{Ai} is the number of fish returned with one TBA tag in the *i* th period, r_{Bi} is the number of fish returned with one dart tag in the *i* th period, A_i is the estimated probability of tag retention of a TBA tag at t_i and B_i is the estimated probability of tag retention of a dart tag at t_i. * indicates points omitted from analysis.

			Public and Research		
t_i (days)	r_{di}	r_{Ai}	r_{Bi}	A_i	B_i
30	7	1	1	0.8750	0.8750
90	5	8	4	0.5556	0.3846
150	8	11	7	0.5333	0.4211
210	2	3	2	0.5000	0.4000
270	2	11	2	0.5000	0.1538
330*	0	0	2	-	-
390*	2	5	3	0.4000	0.2857
450*	1	1	2	0.3333	0.5000

Table 5.5: Estimates of tag shedding parameters ***p*** (type I) and ***L*** (type II) from the Bayliff and Morbrand (1972) tag shedding model for TBA tags and dart tags from the common regression for the pooled public and research returns of *P.leopardus* from the large-scale study. Sample size (n), proportion of total variance accounted for by the model (r^2) and significance level of parameter estimate (Pr>t) are given also. Ninety-five percent confidence intervals of parameter estimates are in given in parentheses.

Tag type	n	r^2	ln *p*	Pr>t	*p*	*L*	Pr>t
T-bar Anchor	48	0.76	-0.2880	0.025 *	0.7498	-0.0018	0.008 *
			(-0.0661 to -0.5099)		(0.9361 to 0.6005)	(-0.0007 to -0.0029)	
Dart	74	0.38	-0.5202	0.184		0.00582	0.137
			ns			ns	

Table 5.6: Summary of tag loss data for TBA tags from public and research tag returns of *P.leopardus* tagged with 2 TBA tags from the large-scale study. t_i is the mid-point of the *i* th time period (60 days) since release, r_{di} is the number of fish returned with 2 tags in the *i* th period, r_{si} is the number of fish returned with one tag in the *i* th period and K_i is the estimated probability of tag retention at t_i. * denotes data omitted from the analysis.

	Public			Research		
t_i (days)	r_{di}	r_{si}	K_i	r_{di}	r_{si}	K_i
30	20	11	0.7843	9	0	1.0000
90	24	11	0.8135	14	11	0.7180
150	23	11	0.8070	10	9	0.6897
210	9	3	0.8571	4	4	0.6667
270*	10	10	0.6667	1	4	0.3333
330	7	2	0.8750	2	3	0.5714
390	1	0	1.000	5	9	0.5263
450	4	11	0.4211	0	0	-

Table 5.7: Estimates of tag shedding parameters ***p*** (type I) and ***L*** (type II) from the Bayliff and Morbrand (1972) tag shedding model for the public, research and pooled returns of *P.leopardus* tagged with 2 TBA tags from the large-scale study. Sample size (n), proportion of total variance accounted for by the model (r^2) and significance level of parameter estimate (Pr>t) are given also. Ninety-five percent confidence intervals of parameter estimates are in given in parentheses.

Source	n	r^2	ln ***p***	Pr>t	***p***	***L***	Pr>t
Public	136	0.89	-0.0959	0.04 *	0.9086	-0.0009	0.01 **
			(-0.0128 to -0.1789)		(0.9872 to 0.8361)	(-0.0004 to -0.0013)	
Research	80	0.82	-0.1446	0.10 **ns**		-0.0013	0.01 **
			(0.0258 to -0.3150)			(-0.0005 to -0.0022)	
Pooled	217	0.86	-0.1135	0.03 *	0.8927	-0.0010	0.002 **
			(-0.0212 to -0.2058)		(0.9791 to 0.8140)	(-0.0005 to -0.0015)	

Table 5.8: Summary of tag loss data by tag colour for TBA tag returns of *P.leopardus* tagged with 2 TBA tags from the large-scale study. r_d is the number of fish returned with 2 tags, r_s is the number of fish returned with one tag and K is the estimated probability of tag retention.

Tag Colour	r_d	r_s	K
Yellow	33	19	0.78
Green	21	12	0.76
Orange	54	32	0.77
White	48	29	0.77
Pink	47	26	0.78
Blue	46	22	0.81
Total	249	140	0.78

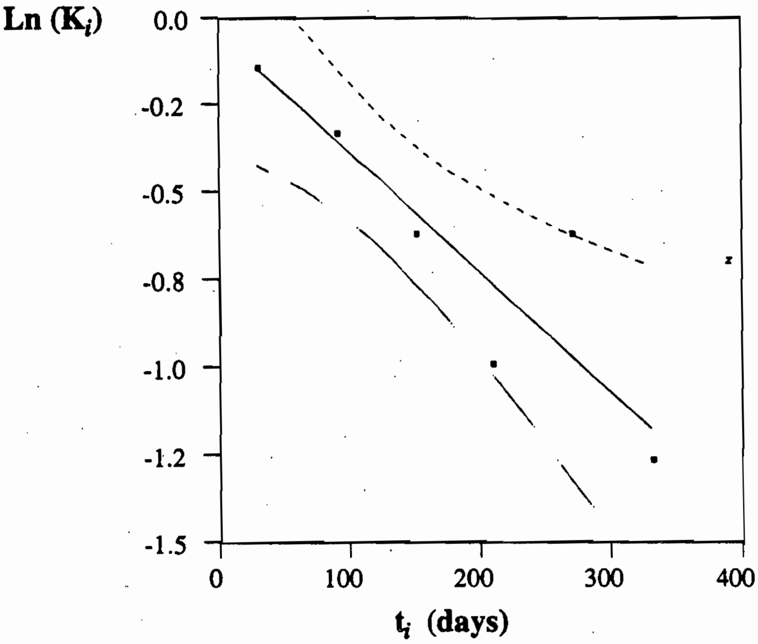

Figure 5.1: Natural logarithm of estimated proportion of t-bar anchor tags retained ($Ln(K_i)$) over time (t_i), for *Lutjanus carponotatus* tagged with 2 t-bar tags. Dashed lines are 95% confidence curves. The regression is significant ($F_{0.05,1,4}$ =21.1933, p=0.0100).

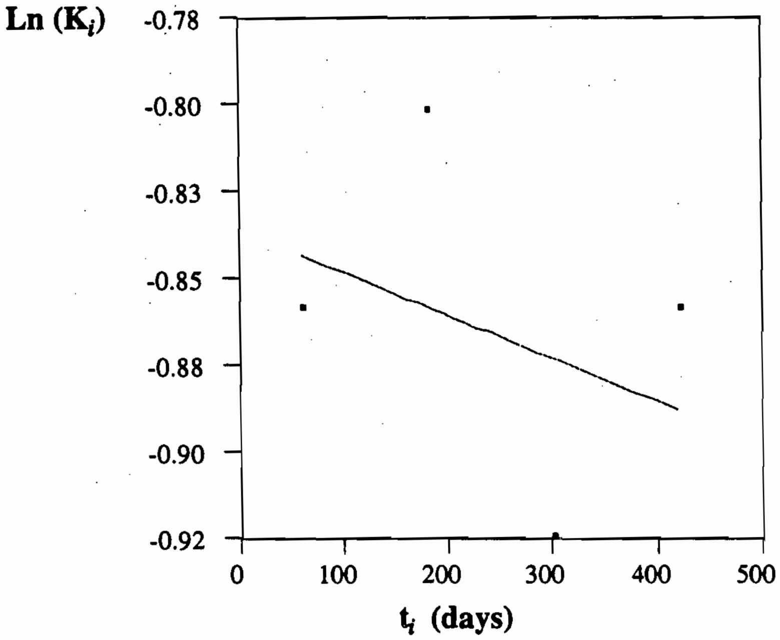

Figure 5.2: Natural logarithm of estimated proportion of t-bar anchor tags retained ($Ln(K_i)$) over time (t_i), for *Plectropomus leopardus* tagged with 2 t-bar tags from the Lizard Island study. Dashed lines are 95% onfidence curves. The regression is not significant ($F_{0.05,1,2}$, =0.2931, p=0.6425).

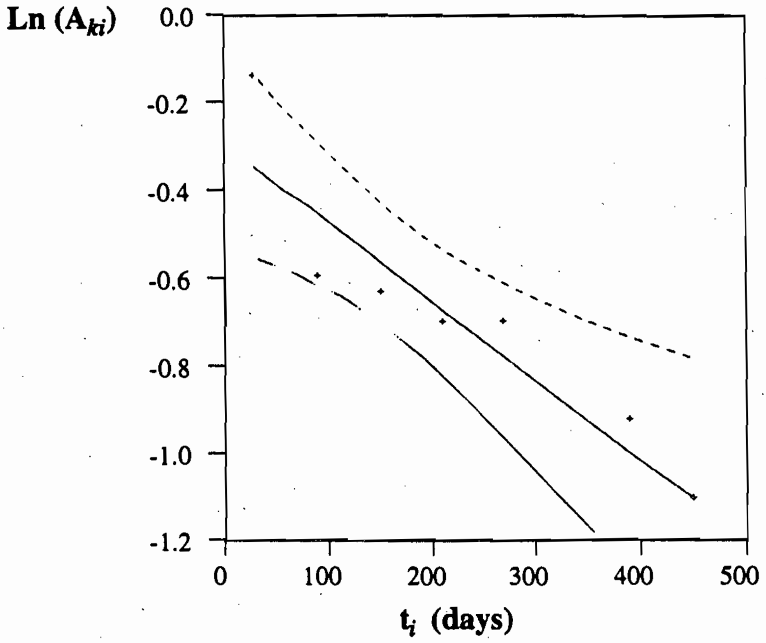

Figure 5.3: Natural logarithm of estimated proportion of t-bar anchor tags retained (Ln(A_{ki})) over time (t_i), for pooled public and research returns of *Plectropomus leopardus* tagged with one t-bar and one dart tag from the large-scale study, with confidence curves (95%). The regression is significant ($F_{0.05,\ 1,5,}$ =18.6048, p=0.0076).

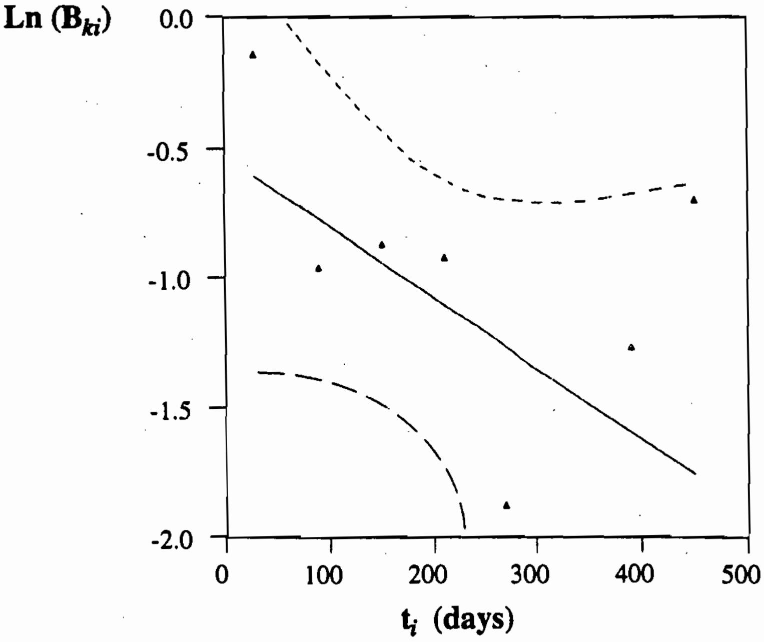

Figure 5.4: Natural logarithm of estimated proportion of dart tags retained (Ln(B_{ki})) over time (t_i), for pooled public and research returns of *Plectropomus leopardus* tagged with one t-bar and one dart tag from the large-scale study, with confidence curves (95%). The regression is not significant ($F_{0.05,\ 1,3,}$ = 3.1350, p=0.1368).

Chapter 6

Patterns of movement and rates of natural mortality of *Lutjanus carponotatus*, *Siganus doliatus* and *Plectropomus leopardus* from Lizard Island lagoon.

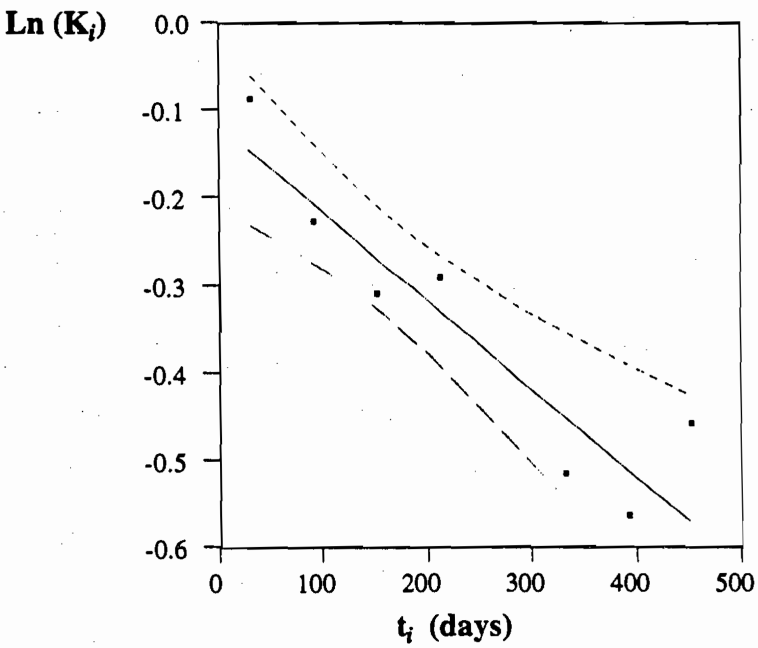

Figure 5.5: Natural logarithm of estimated proportion of t-bar anchor tags retained (Ln(K_i)) over time (t_i), of pooled public and research returns for *Plectropomus leopardus* tagged with t-bar tags only from the large-scale study. Dashed lines are 95% confidence curves. The regression is significant ($F_{0.05,1,5,}$ = 31.1344, p=0.0025).

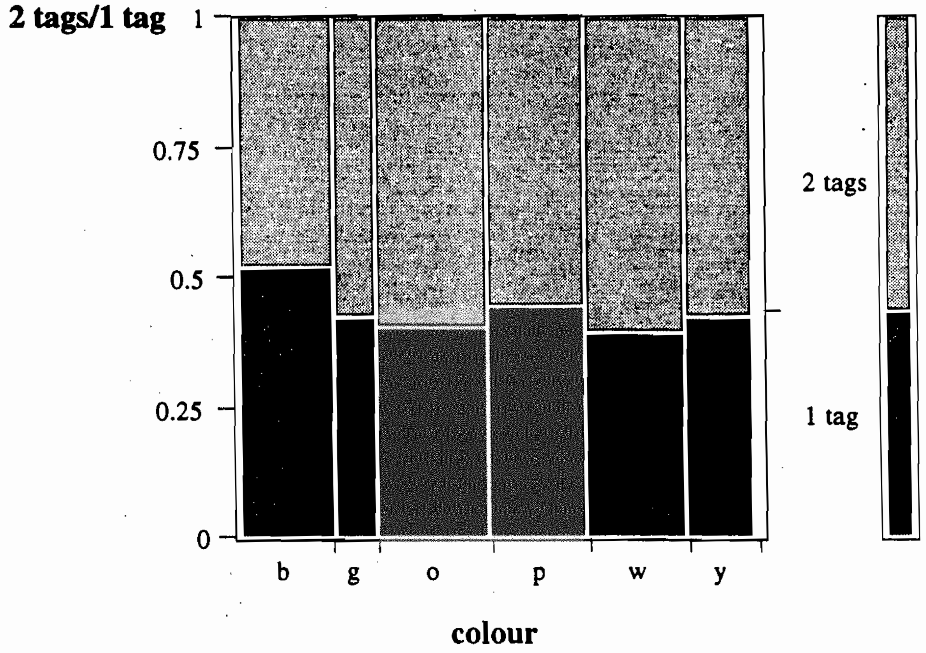

Figure 5.6: Mosaic plot from 6x2 contingency table analysis of proportion of *Plectropomus leopardus* returned with oneor two t-bar anchor tags by tag colour from the large scale experiment. Tag colours were blue (b), green (g), Orange (o), pink (p), white (w) and yellow (y). There was no significant difference in the frequency of returns among the six colours of tags (Likelihood $\chi^2_{5,\,243,}$= 1.902; p=0.8625).

6.1 Introduction

The concept of Marine Fishery Reserves (MFR), defined as permanent spatial closures to fishing, has received substantial attention recently as a potential management tool for exploited stocks of reef fish (PDT 1990; Roberts and Polunin 1991; Dugan and Davis 1993a). Closures may vary in spatial extent from sections of individual reefs to individual reefs or clusters of reefs (Russ *et al* 1994). Theoretically, MFR function by protecting a minimum proportion of the spawning stock and providing a form of growth refuge for target species (Davis 1989; PDT 1990; Polacheck 1990; Roberts and Polunin 1991; Russ 1991; DeMartini 1993; Dugan and Davis 1993b). There are two potential mechanisms by which MFR may maintain or enhance fisheries yields. Firstly, they protect the spawning stock from falling below a theoretical minimum and thereby ensure a recruitment supply to fished areas via the export of pelagic larvae. Secondly, they protect a portion of the stock from fishing, allowing them to attain a larger average size and reproductive output. It is assumed that, as a result of the increase in density of target species within the MFR, a certain percentage of these fish will move out of the reserve which will also enhance the fisheries in adjacent areas (Alcala and Russ 1990; PDT 1990; Polacheck 1990; DeMartini 1993; Russ *et al* 1993).

Simulation studies have indicated that the proportion of the population moving across MFR boundaries into the fished areas will be a critical parameter in determining the effectiveness of MFR for increasing or maintaining fisheries production (Polacheck 1990; DeMartini 1993; Russ *et al* 1994). However, at present there is little empirical information on the extent to which exploited species of coral reef fish move among the various spatial strata found on coral reefs or across management boundaries (PDT 1990; Roberts and Polunin 1991; Dugan and Davis 1993b). Hence, there is an urgent need for information on the frequency of movement among spatial strata within individual reefs, in the case of partial reef closures, and among individual reefs for whole reef closures, in order to fully evaluate the potential of MFR (Roberts and Polunin 1991; Russ 1991; Dugan and Davis 1993b). Quantitative information on the frequency of small-scale movement within and among habitats is of particular importance in the case of partial reef closures as it may be used to select appropriate MFR boundaries based on the "permeability" of different categories of habitat (Schonewald-Cox and Bayless 1986; Buechner 1987; DeMartini 1993).

The objective of the small-scale movement study was to examine the patterns of movement of three common species of reef fish within the lagoon at Lizard Island and investigate the implications of these for the design of MFR which include partial reef closures. The study addressed three spatial scales of movement; among sites within the lagoon (km's), among habitats within sites (100's m), and within sites (100's m). The first aim of the study was to determine how the frequency of movement varied among the spatial scales and among the three target species. The second aim was to obtain estimates of rates of natural mortality for each of the species from the capture-recapture data and to determine whether mortality varied seasonally or among habitats.

6.2 Methods

The study of the small-scale movements of *P.leopardus*, *L.carponotatus* and *S.doliatus* was done in the Lizard Island lagoon on the northern Great Barrier Reef. A multiple capture-recapture study was implemented using fish traps as the sampling method with 7 sampling occasions over a period of 22 months. The details of the study site, sampling design, sampling protocol, traps and tagging methods have been described in chapter 2.

Estimates of capture and survival probabilities for each species were obtained using RELEASE 2.6 (Burnham *et al* 1987). An excellent review of capture-recapture theory and model selection procedure is given by Lebreton *et al* 1992. Burnham *et al* 1987 provide a comprehensive coverage of the model fitting procedure for estimating survival and capture probability parameters and statistical detail of program RELEASE. Capture-recapture notation and symbols follow Burnham *et al* 1987. Data was input as full capture history matrices for each species. The first recapture event of an individual in any sampling occasion was used in the analysis and subsequent recaptures in the same sampling occasion were omitted. There were only sufficient data to examine the effect of habitat (patch reef and reef categories only) on estimates of survivorship and recapture probabilities for *L.carponotatus* and *S.doliatus*. There were insufficient data for comparisons among habitats for *P.leopardus*.

The distribution of releases and returns of each species were mapped for each site to graphically display patterns of distribution and movement within and among habitats within sites. The effect of site and habitat on the frequency of movement was examined using contingency table analyses in *JMP 2.0* (SAS, 1989).

6.3 Results

6.3.1 Estimates of survivorship

A total of 65 *P.leopardus*, 373 *L.carponotatus* and 825 *S.doliatus* were tagged and released over the 7 sampling occasions from March 1991 to November 1992 (Table 6.1). Due to the relatively low number of releases (and recaptures) in each cell it was necessary to pool across sites to obtain sufficient data for estimating survivorship. This was particularly the case for *P.leopardus* and *L.carponotatus*. A summary of releases of each species by trip and habitat is given in Table 6.1.

Data were pooled across sites, rather than habitats, as the pattern of distribution of the target species among habitats was relatively consistent, while among sites it was not. Furthermore, differences in survival (and movement) among habitats were considered of greater general interest than differences among sites. Release and return data were pooled across sampling occasions for trips 2 a&b and 3 a&b also. Summaries of the capture-recapture data sets, in the form of reduced *m*-arrays (Burnham *et al* 1987; Lebreton *et al* 1992), used to estimate survivorship and recapture probabilities for each species are given in tables 6.2-6.4. The total number of releases in each of the m-arrays do not exactly correspond to those in table 6.1 as a result of fish recaptured within sampling periods being excluded from the analysis.

Lutjanus carponotatus

The full Cormack-Jolly-Seber (CJS) model was fitted to *L.carponotatus* data with each habitat considered as a separate group. The fit of the model , TEST 2 (Burnham *et al* 1987), was reasonable ($\chi^2_{2} = 1.7665$, $p = 0.4134$). However, TEST 3 (Burnham *et al* 1987) was significant ($\chi^2_{8} = 39.3989$, $p < 0.0001$) in both habitats, indicating there may have been heterogeneity in capture histories at occasions 2 and 3. The result of TEST 1, which tests for the overall effect of habitat on survivorship, was not significant at $\alpha=0.05$ level ($\chi^2_{7} = 11.9304$, $p = 0.1029$). However, survivorship in the reef habitat was consistently higher than in the patch reef habitat over the five sampling occasions (Figure 6.1). There was considerable variation in the estimates of survivorship (pooled across habitats) among occasions with estimates ranging from 0.1660, between occasion 3-4, to 0.4743, between occasions 2-3 (Table 6.5).

Plectropomus leopardus

The capture-recapture data for *P.leopardus* were too sparse for the effect of habitat on survival to be examined. Therefore data were pooled across habitats (Table 6.4) and the full CJS model fitted to the pooled data. The fit was reasonable considering the available data (TEST 2 + TEST 3 ($\chi^2_5 = 7.7840$, $p = 0.1685$). There were not sufficient data to compute TEST 2 and 3 separately. The resulting estimates of survivorship were generally higher than the estimates for *L.carponotatus* and exhibit a similar pattern of variation among occasions, with intermediate values between occasions 1-2 , a peak between 2-3 and a sharp decline between 3-5 (Figure 6.3).

Siganus doliatus

The full Cormack-Jolly-Seber (CJS) model was fitted to *S.doliatus* data with each habitat considered as a separate group. The model fitted the data well (TEST 2 + TEST 3 (χ^2_{10} = 6.3150, p = 0.0.7881) and there was no evidence of heterogeneity in capture histories among occasions (TEST 3 ($\chi^2_7 = 4.5172$, $p = 0.7186$). However, survival and capture probabilities for occasion 4 (ϕ_3 and p_4) were unidentifiable. Although, the effect of habitat on survival was not significant at $\alpha = 0.05$ level (TEST 1 ($\chi^2_6 = 10.1652$, $p = 0.1179$), estimated survival probabilities in the reef habitat were higher than the patch hatch habitat between occasions 1-2 and 2-3 (Figure 6.2). The overall pattern in estimates of survival across occasions was the same as for *L.carponotatus* and *P.leopardus*, with an increase from ϕ_1 to ϕ_2 and then a sharp decline after occasion 3 (Figure 6.3).

6.3.2 Estimates of natural mortality

The survivorship estimates were used to calculate estimates of mortality for each interval. The resulting estimates of mortality were adjusted for tag loss, using the rates of tag loss for *L.carponotatus* from Chapter 5, and converted to instantaneous rates of mortality by dividing each estimate by the number of days between the corresponding sampling occasions (Lebreton *et al* 1992). It should be noted that rates of tag loss were assumed to be constant among habitats, as there was not sufficient data to estimate rates for each habitat. The estimates for each species are presented as estimates of the annual rate of natural mortality for each sampling period, and the mean rate for the whole study period (Table 6.8).

6.3.3 Estimates of Movement

Lutjanus carponotatus

Sixty-eight percent of the 110 recapture observations of *L.carponotatus* were recaptured at the same trapping location where they were released. There were only two recorded movements between sites (Figure 6.4 a,b,c). Both incidences involved movements from Mangrove to the same vicinity of South (positions 20 and 21) and back to Mangrove during the second sampling occasion of the November 1991 trip (Figure 6.4 a,b,c). There was no significant difference in the frequency of movement away from the position of release (moved vs not moved) among the three sites (Figure 6.5) (Likelihood $\chi^2{}_{65} = 1.213$, $p = 0.5451$) or among habitats among sites (Reef: Likelihood $\chi^2 = 1.368$, $p = 0.5046$, Patch: Likelihood $\chi^2 = 1.676$, $p = 0.4326$, Sand: (Likelihood $\chi^2 = 5.661$, $p = 0.0590$ (high proportion of cells with zeros)). Therefore, data were pooled across sites to examine frequency of movement among habitats.

There was a highly significant effect of habitat of release on habitat of recapture for *L.carponotatus*, including all observations (*ie* moved and not moved) (Likelihood $\chi^2{}_{95} = 64.262$, $p < 0.0001$) (Figure 6.6). Partitioning of the contingency table indicated there were highly significant differences in the habitat of recapture for fish released in the reef as compared to fish released in the patch or sand habitats (Reef by Patch: Likelihood $\chi^2 = 54.928$, $p < 0.0001$ Reef by Sand: Likelihood $\chi^2 = 24.479$, $p < 0.0001$ Reef by Patch and Sand: Likelihood $\chi^2 = 54.928$, $p < 0.0001$ Patch by Sand: Likelihood $\chi^2 = 5.483$, $p = 0.0.0645$). Examination of figure 6.5 shows that fish which are released in the reef habitat are highly likely (87%) to be returned in the reef habitat. Similarly, fish which are released in the patch habitat are highly likely (83%) to be recaptured in the same habitat. In contrast, fish that are released in the sand habitat are more likely to be returned from the patch habitat (58%) than the sand habitat (33%). This suggests that *L.carponotatus* released in the reef and patch habitats have a strong fidelity to that habitat and are not likely to transverse habitat boundaries. In particular, the frequency of movement from the reef to sand habitat was low (8%). Whereas fish released in the sand habitat were more transient and likely to move among sand and patch reef habitats.

The contingency table analysis for the smaller data set of only *L.carponotatus* which had moved among trapping positions (*ie* excludes observations of fish recaptured at the same position) highlights the difference in the frequency of movement among habitats. The overall analysis was not significant at $\alpha = 0.05$ level (Likelihood $\chi^2{}_{29} = 8.677$, $p = 0.0697$). However, examination of the mosaic plot (Figure 6.7) from the analysis indicates a quite different pattern of movement among habitats in comparison to the full data set. While the majority (63%) of fish released in the reef habitat were recaptured in the same habitat, fish that were released in the patch habitat, and moved among positions, were equally likely to be recaptured in either of the three habitats (Reef 42%, Patch reef 29%, Sand 29%). Furthermore, fish that were released in the sand habitat, and moved among positions, were more likely to be returned from the patch reef (70%) than the sand (20%) habitat.

Again, this indicates that *L.carponotatus* which were released in the reef habitat are more likely to recaptured from that habitat, even when they moved among trapping positions, and that they are more likely to move from reef to patch reef rather than reef to sand. In contrast, fish which were released in the patch reef and sand habitats, and moved among trapping positions exhibited a much higher frequency of movement among habitats, with fish released in the patch reef habitat more likely to move to the reef habitat, and fish released in the sand habitat more likely to move to the patch reef habitat.

Plectropomus leopardus

The total number of *P.leopardus* tagged and recaptured during this study was low; a total of eight, three and six returns from Loomis, Mangrove and South respectively. The majority of *P.leopardus* were released and returned from Loomis and there was also a high proportion of multiple observations data for individuals in comparison to the other sites. However, due to the low number of total observations, it was not possible to do formal analysis of the frequency of movement of *P.leopardus* among sites and habitats.

The pattern of movement of each individual has been mapped on the grids for each site (Figures 6.8 a,b,c) . From these figures it is apparent that *P.leopardus* ranged over relatively large distances within each site, especially in comparison to the average movement of *L.carponotatus* and *S.doliatus* (Figures 6.4 a,b,c and 6.9 a,b,c). The largest individual movement observed was approximately 415 m at Loomis between positions 8 and 18 (Figures 6.8 a,b,c). It is also clear that *P.leopardus* moved across the three habitat categories and traversed open expanses of sand (30-60 m) among isolated patches of reef structure. A feature of the patterns of movement at Loomis was the extent of overlap in the movement of individuals, particularly around the large area of reef habitat between grid transects 7-12 and 13-18 (Figures 6.8a). Another point of interest was the location of two exceptional captures of 6 and 4 *P.leopardus* in a single trap, one at position 1 and one at position 32 at Loomis. Of the 10 fish released none were recaptured during the trap sampling. However, one of the individuals released at position 32 in February 1992 was resighted on SCUBA 5 days later on Vicki's Reef, approximately 300-400 m to the west of the release site. It was possible to identify the individual as one which had been released at position 32 as all *P.leopardus* in that release had been tagged with dart tags, due to a shortage of t-bar anchor tags at the time. These results suggest that *P.leopardus* ranges over distances of 200-300 m and that the type of habitat or the presence of large expanses of open sand (>50 m) do not prevent them from moving between large patches of reef structure within reefs.

Siganus doliatus

The patterns of movement of *S.doliatus* were relatively similar to those of *L.carponotatus* in that the majority of the recaptures were returned at the position of release and there was limited movement among habitats (6.9 a,b,c). Of the 197 recaptures of *S.doliatus* the majority (69%) were recaptured at the same trapping position at which they were released. There was no significant difference in the frequency of movement away from the position of release (moved vs not moved) among sites (Figure 6.10) (Likelihood $\chi^2_{194} = 0.481$, $p = 0.7863$) or among habitats among sites (Reef: Likelihood $\chi^2 = 0.042$, $p = 0.9791$, Patch: Likelihood $\chi^2 = 0.866$, $p = 0.6485$). Data were pooled across sites to examine the frequency of movement among habitats. There were insufficient releases of *S.doliatus* in the sand habitat to include sand as a release category in the contingency table analysis of the effect of habitat of release on frequency of movement among habitats.

Figure 6.11 is a mosaic plot from the contingency table analysis for the effect of habitat of release on the frequency of movement among habitats for all observations (*ie* moved and not moved). There was a highly significant effect (Likelihood $\chi^2_{194} = 110.756$, $p < 0.0001$) similar to that observed for *L.carponotatus*. Overall the frequency of movement among habitats was very low, with 90% and 77% of the fish released in the patch reef and reef habitats returned from the same habitat. There was a greater tendency for *S.doliatus* to move from the reef to patch reef habitats (19%) than from patch to reef (8%) while there was negligible movement from either the reef (3%) or patch reef (1%) habitats to the sand.

The contingency table analysis of the effect of habitat of release on the frequency of movement among habitats for only *S.doliatus* which moved among trapping positions shows that the habitat of release had little effect on the frequency of movement among habitats (Likelihood $\chi^2_{57} = 0.914$, $p = 0.6330$). The majority of releases in both the reef (54%) and patch reef (64%) habitats were recaptured in the patch habitat (Figure 6.12) indicating a high frequency of movement of *S.doliatus* from the patch reef to the reef (32%) and from the reef to the patch reef (54%) habitats. Movement from either the patch reef or reef habitats to the sand habitat was low. The relatively high value for frequency of movement from the reef habitat to the sand derives from a single trapping position at South Island, located between a narrow gutter (Figure

6.9c). Although the analysis of movement among habitats for the subset of *S.doliatus* which had moved among trapping positions shows that the movement among the patch and reef habitats was high, it must be remembered that the observations of fish which did move among habitats only accounted for 17% of the total observations. That is 83% of the *S.doliatus* recaptured were recaptured in the same habitat as they were released.

6.4 Discussion

The use of tagging studies to examine the patterns of movement of fishes requires a rigorous sampling design in which tagged fish are released in all spatial strata (*ie* habitats) and the amount and distribution of recovery effort are known (Hilborn 1990; Schwarz and Arnason 1990; Schweigert and Schwarz 1993). In the absence of this information it is not possible to determine to what extent the pattern of tag recoveries represents the distribution of fishing effort or real patterns of movement. The sampling design used in this study provided a uniform distribution of effort across the three sites within the lagoon at regular intervals over about a two year period. An additional feature of this study was that each trapping position was sampled once only during any sampling occasion. Other tagging studies of coral reef fish have involved relatively long periods (several weeks to months) of continuous sampling of the same position (*eg* Bardach 1958; Randall 1961; Recksiek *et al* 1991). This is likely to result in "trap happy" fish, particularly if the traps are baited, which are continually recaptured at the same position. This was deliberately avoided in this study. There was generally greater than two months between successive sampling of the same position. It was considered that this combined with the longer duration of the study would reduce the occurrence of "trap happy" fish and, hence, provide more representative movement data.

The major aim of the small-scale study at Lizard Island was to quantify the frequency of movement of three species of reef fish among three spatial scales within the lagoon: among sites, among habitats within sites and among trapping positions within habitats. There was little evidence of movement among sites for any of the species. This suggests the frequency of movement over the largest spatial scale accounted for in this study (500 m - 1000 m) is negligible, particularly for *L.carponotatus* and *S.doliatus* whose range of movement within sites was small also.

The patterns of movement of the three species studied differed considerably. The most immediate difference was the greater distances moved by *P.leopardus* in comparison to both *L.carponotatus* and *S.doliatus*. The data for *P.leopardus*, although sparse, show that *P.leopardus* readily and frequently moved among positions and over much greater distances than *L.carponotatus* and *S.doliatus*. In contrast, the majority of recaptures of *L.carponotatus* and *S.doliatus* were recaptured at the same position (68% and 69%, respectively) and of those that did move among positions the majority moved to the next adjacent position. The pattern from the multiple recapture data for both species reinforces the suggestion that the range of movement of *L.carponotatus* and *S.doliatus* are confined to a small area in comparison to *P.leopardus*. This is consistent with findings from earlier studies of movement of reef fish where different species of serranid have been found to move over greater distances and exhibit less site fidelity than smaller bodied fishes, such as holocentrids, small lutjanids and acanthurids (Bardach 1958; Randall 1961; Beinssen 1989b).

The patterns of movement of *P.leopardus* from this study support the earlier conclusions of Samoilys (1986) and Beinssen (1989b; 1990) that *P.leopardus* ranges over relatively large areas within individual reefs. In particular, the movement of one individual from the Loomis sampling grid to Vicki's Reef, a straight line distance of approximately 400 m, indicates that individuals *P.leopardus* do move large distances within reefs and that they are capable of transversing relatively large expanses of open sand. There were insufficient releases and recaptures of *P.leopardus* in this small-scale study at Lizard Island to infer what proportion of the population may move to the same extent as the single example given above. However, data obtained during the large-scale study of movement of *P.leopardus* (Chapter 8) suggest that a substantial proportion of the population on an individual reef may move over two kilometres or more within a reef. This suggests that partial reef closures may not effectively protect *P.leopardus* from fishing due to the potentially high rates of transfer between the fished and unfished areas within an individual reef.

The importance of movement in animal population dynamics and their management is becoming increasingly apparent (Hetsbeck *et al* 1991; Nichols 1992). This is particularly the case in design of Marine Fisheries Reserves (MFR) as the degree of immigration and emigration of post-settlement fish to or from the reserve may determine its effectiveness (Polacheck 1990; DeMartini 1993 Russ *et al* 1993). In this respect, MFR boundaries should be selected so that emigration from the reserve to adjacent areas that are open to fishing is minimised. The rate of emigration of a species across reserve boundaries is likely to be a function of the perimeter to area ratio of the reserve, the permeability of the reserve boundaries, the patterns of movement and habitat preferences of the species, the overall size of the reserve and the existence of biological or physical gradients between the reserve and non-reserve areas (Buechner, 1987). Of these factors, differences in boundary permeability are likely to have large effects on the frequency of movement across reserve boundaries (Buechner 1987; Stamps *et al* 1987).

It has been suggested that naturally demarcated boundaries, such as sharp changes in habitat, may form less permeable reserve boundaries (Buechner 1987; Stamps *et al* 1987; DeMartini 1993). However, previous to this study, there was no empirical data available on the effect of different habitats on the frequency of movement of coral reef fishes. Habitat of release was found to have a considerable effect (although not significant at $\alpha = 0.05$) on the frequency of movement of *L.carponotatus* among habitats. There was a lower frequency of movement of *L.carponotatus* from the reef to sand habitats than from patch reef to sand habitats. The pattern was similar for *S.doliatus* in that movement from either the reef or patch reef habitats to the sand habitat was low. However, the frequency of movement among the reef and patch reef habitats was higher than found for *L.carponotatus*. This may be related to the feeding behaviour of *S.doliatus*. *S.doliatus* is a roving herbivore which often forms mixed feeding schools with acanthurids and scarids that move across the reef flat behind the reef crest at high tide to graze on turf algae (Russ 1984b; CRD personal observation). The majority of the observed movement of *S.doliatus* among habitats involved movement from the patch reef habitat behind the reef flat up onto the reef flat/crest, which was generally a movement between adjacent trapping positions (approximately 100 m).

The low frequency of movement of both *L.carponotatus* and *S.doliatus* between the reef and sand habitats suggests that reef-sand habitat boundaries may form less permeable, or “harder edged” (Stamps *et al* 1987) boundaries than patch reef - sand or patch reef - reef habitat boundaries. The use of sharp natural demarcations on coral reefs for MFR boundaries, such as large sand channels, would also have the advantage of being more readily identified by fishers on the water in comparison to arbitrary boundaries which fall within a continuous section of reef mosaic. This may be an important consideration in the design of MFR to reduce the level of incidental infringements within the reserve area (PDT 1990; Caddy 1993; Chapter 8 this study).

The rate of natural mortality is a critical parameter in fisheries population dynamics and is generally one of the most difficult to quantify (Vetter 1988; Hilborn and Walters 1992). There are a range of methods for estimating the rate of natural mortality which Vetter (1988) classified into three main categories: 1) Catch analysis methods, 2) Correlations with life-history parameters, and 3) Predation methods. The approach that was used in this study, tagging studies, falls into the catch analysis category as does the most commonly used technique in fisheries biology, catch curves. Each method has its particular advantages and disadvantages. Catch curves methods generally make strong assumptions about natural and fishing mortality and catchability being constant among groups of fish and over time and rely heavily on accurate catch and effort data. It is also assumed that the samples used are representative of the composition of the population (Ricker 1975; Vetter 1988; Hilborn and Walters 1992).

The important assumptions of tagging studies with respect to estimating mortality include: 1) the tagged population is representative of the untagged population, 2) all sources of loss from the tagged population, including the loss of tags and permanent emigration from the study area, can be accounted for, 3) the process of capture, handling and carrying a tag(s) does not affect the survival of tagged individuals. The estimated rates of natural mortality for each of the species in this study appear to be very high and are unlikely to be representative of the untagged population. This is most likely to be due to a violation of assumption 3 above as the movement data indicated that movement out of the study area was negligible, particularly for *L.carponotatus* and *S.doliatus*, and tag loss has been accounted for. An independent estimate of total mortality for *P.leopardus* from Lizard Island, derived using age-based catch curve analysis is available (Brown 1994). This estimate (Z = 0.12 (95% CI = 0.11-0.34)) is substantially lower than the estimated rate of natural mortality from the capture-recapture data in this study (M = 1.72 SE = 0.30). Similarly the estimate of M for *L.carponotatus* is considerably higher than published estimates of either natural or total mortality for similar species of lutjanids (Ralston 1987; Acosta and Appeldoorn 1992; Davis and West 1992; Newman 1995). There is no published estimate of mortality for *S.doliatus* or any other species of siganid. However, the recent estimates of the longevity of several species of small acanthurid on the Great Barrier Reef suggest that many of these species of small herbivorous fishes may live for 10 to 20 years, if not longer (Howard Choat, Department of Marine Biology, James Cook University, personal comment.) (See Chapter 4). This would suggest that the true rate of natural mortality of *S.doliatus* would be considerably less than reported here.

Theses results indicate that the estimated rates of mortality (or survival) may not be representative of the untagged population due to the effects of capture and tagging. However, if the effect(s) are constant across the tagged population for each species, then the relative differences in estimates of survival among habitats for each species will reflect real differences in survivorship (Burnham *et al* 1987; Lebreton *et al* 1992). There was a consistent difference in the estimated survivorship of both *L.carponotatus* and *S.doliatus* between the reef and patch reef habitats with survivorship of both species being higher in the reef habitat. The variation in the estimates for each habitat was largely due to the relatively low number of observations at each sampling occasion. As a result the observed differences in survivorship were not significant at $\alpha = 0.05$. However, the relatively high χ^2 statistic for both species in the test for the effect of habitat suggests that the effect may be real. The data also suggest that survivorship may vary within years, with a peak in the July - November period. However, as the estimates of capture probabilities were poorly defined, due to the relatively few recapture occasions, it is difficult to discount that this pattern is not the result of variation in catchability (Lebreton *et al* 1992).

Variation in survivorship/mortality within populations has been documented previously for coral reef fish (Aldenhoven 1986) and in a variety of species from other marine and freshwater systems (Vetter 1988). The results of this study suggest that mortality may vary among habitats within reefs. This has important implications for stock assessment and for the design of MFR, particularly if mortality also varies among larger spatial scales such as reefs or regions. Mortality is a critical parameter in the estimation of sustainable exploitation rates from most stock assessment models (Hilborn and Walters 1992) and mortality schedules have a large effect on the effectiveness of MFR to enhance or maintain fisheries production (DeMartini 1993). In the case of MFR, the assumption that natural mortality is constant over a series of reserves that include different proportions of different habitats or that are located in different positions on the continental shelf may result in a net loss of fisheries production in some areas if the rate of natural mortality is over-estimated for that area. Given that natural mortality has been found to vary over space and time in most cases where it has been examined (Vetter 1988), it may be more appropriate that mortality is assumed to vary and efforts be focussed to determine at which scales this variation is most important, than to continue to assume that it is constant within populations (Vetter 1988).

This chapter focussed on the frequency of movement of *P.leopardus*, *L.carponotatus* and *S.doliatus* among trapping positions, habitats and sites within an individual reef. *P.leopardus* was found to range over larger distances across habitats within sites while *L.carponotatus* and *S.doliatus* exhibited a strong fidelity for position and habitat of release. Furthermore, the reef - sand habitat boundary was found to be less permeable to movement of either *L.carponotatus* or *S.doliatus* than the reef - patch reef or patch reef - sand habitat boundaries. This supports the assertion that reserve boundaries which incorporate strong contrasts in habitat will reduce the frequency of movement of coral reef fish between protected and unprotected areas relative to arbitrary boundaries located in sections of continuous reef mosaic (Buechner 1987; Stamps *et al* 1987; DeMartini 1993).

There are two important limitations to the generality of these findings. Firstly, the three species studied are strongly associated with hard reef structure at all stages of their life-history. The patterns of movement of other species groups, such as haemulids, lethrinids, some lutjanids and mullids, which are associated with hard reef structure during the day but disperse to feed over sand flats or off reef habitats at night (Hobson 1972, 1973; Holland et al 1993) will be very different to those described here. Therefore, caution should be taken in extrapolating the patterns described here to other species of coral reef fish. More importantly, from a management perspective, the movement patterns described in this chapter come from unfished populations. How the patterns of movement of these species may change in the presence of varying levels of fishing pressure is unknown. Compensatory movement from protected to fished areas may potentially undermine the effectiveness of MFR (DeMartini 1993). Future movement studies should incorporate experimental manipulations of density to determine the response(s) of populations to density gradients between fished and unfished areas.

Table 6.1: Distribution of releases of *Plectropomus leopardus*, *Lutjanus carponotatus* and *Siganus doliatus* by samping occassion (k) and habitat pooled across sites.

		Habitat Category			
Species	*i*	Reef	Patch	Sand	Total
L.carponotatus	1	30	42	8	80
	2a&b	26	51	15	92
	3a&b	39	81	18	138
	4	10	16	12	38
	5	9	8	8	25
	Total	114	198	61	373
P.leopardus	1	13	0	3	16
	2a&b	3	7	0	10
	3a&b	3	8	1	12
	4	2	16	3	21
	5	3	3	0	6
	Total	24	34	7	65
S.doliatus	1	113	39	2	154
	2a&b	128	168	2	298
	3a&b	113	141	5	259
	4	35	10	24	69
	5	35	8	2	45
	Total	424	366	35	825

Table 6.2: Reduced *m*-array of capture-recapture data for *Lutjanus carponotatus* by habitat (patch reef and reef).

i	**R(*i*)**	m_{ij}				**Never Recaptured**
		2	**3**	**4**	**5**	
Patch reef						
1	42	8	1	0	0	33
2	59		13	0	0	46
3	95			15	0	80
4	21				1	20
Reef						
1	30	8	2	0	0	20
2	34		11	3	0	20
3	52			5	1	46
4	18				1	17

Table 6.3: Reduced *m*-array of capture-recapture data for *Plectropomus leopardus*.

i	R(*i*)	m_{ij}				Never Recaptured
		2	3	4	5	
Patch reef						
1	16	5	1	0	0	10
2	15		4	2	0	9
3	17			4	0	13
4	27				5	22

Table 6.4: Reduced *m*-array of capture-recapture data for *Siganus doliatus* by habitat (patch reef and reef).

i	R(*i*)	m_{ij}				Never Recaptured
		2	3	4	5	
Patch reef						
1	39	8	1	0	0	30
2	165		42	4	0	119
3	184			24	0	160
4	38				0	38
Reef						
1	111	20	6	1	0	84
2	145		51	6	0	88
3	170			14	2	154
4	56				0	56

Table 6.5: Summary of estimates of survival (ϕ) and capture probabilities (p) (pooled across habitats) between sampling occassions for *Lutjanus carponotatus* made under the Cormack-Jolly-Seber model (ϕ_t, p_t).

Occasion	ϕ	SE(ϕ)	p	SE(p)
Mar'91-Jun'91	0.3500	0.0898	0.6012	0.1549
Jul'91- Nov'91	0.4743	0.1343	0.4813	0.1424
Nov'91-Feb'92	0.1660	0.0523	0.7426	0.2083
Feb-Nov'92			0.1154	0.0443

Table 6.6: Summary of estimates of survival survival (ϕ) and capture probabilities (p) between sampling occassions for *Plectropomus leopardus* made under the Cormack-Jolly-Seber model (ϕ_t, p_t).

Occasion	ϕ	SE(ϕ)	p	SE(p)
Mar'91-Jun'91	0.4554	0.1755	0.6667	0.2534
Jul'91- Nov'91	0.6971	0.3545	0.3704	0.2201
Nov'91-Feb'92	0.2353	0.1029	1.0000	-
Feb-Nov'92			0.1852	0.0748

Table 6.7: Summary of estimates of survival (ϕ) and capture probabilities (p) between sampling occassions for *Siganus doliatus* made under the Cormack-Jolly-Seber model (ϕ_t, p_t).

Occasion	ϕ	SE(ϕ)	p	SE(p)
Mar'91-Jun'91	0.3462	0.0617	0.5377	0.1016
Jul'91- Nov'91	0.5844	0.0970	0.5067	0.0877
Nov'91-Feb'92	unidentifiable		unidentifiable	
Feb-Nov'92	0.0000	0.0000	0.0000	0.0000

Table 6.8: Estimates of annual rate of mortality for *L.carponotaus*, *P.leopardus* and *S.doliatus*for each interval between sampling occassions and the mean and standard error for the whole study period after adjusting for tag loss. Estimates of instantaneous tag loss of t-bar anchor tags from Chapter 5 have been used for *L.carponotatus* (0.0034) and *P.leopardus* (0.0010). In the absence of an estimate of tag loss for *S.doliatus*, the same estimates as for *L.carponotatus* has been used.

Species	**M'91-J'91**	**J'91-N'91**	**N'91-F'92**	**Mean**	**SE**
L.carponotatus	1.82	1.56	1.93	1.77	0.11
P.leopardus	1.85	1.09	2.21	1.72	0.33
S.doliatus	1.83	1.13	-	1.48	0.28

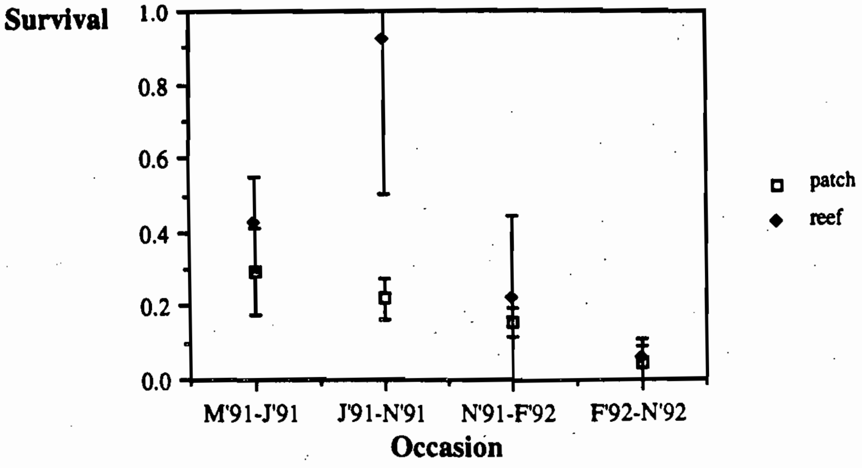

Figure 6.1: Estimates of survival among sampling occasions for *L.carponotatus* by habitat. Error bars are standard errors.

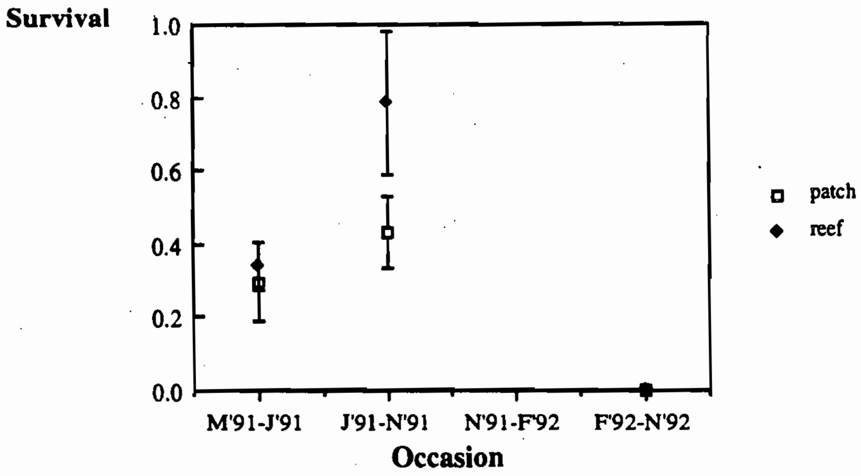

Figure 6.2: Estimates of survival among sampling occasions for *Siganus doliatus* by habitat. Error bars are standard errors.

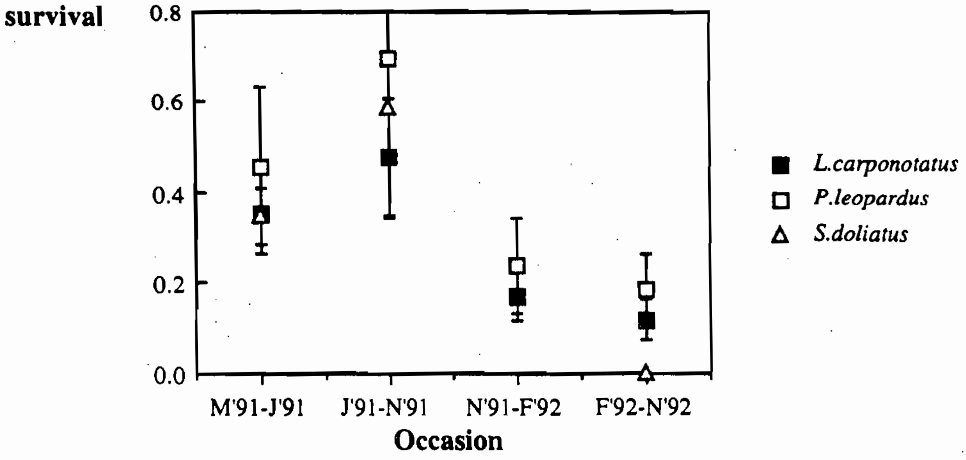

Figure 6.3: Overall estimates of survival among sampling occasions for *Lutjanus carpnontatus*, *Plectropomus leopardus* and *Siganus doliatus* for both habitats patch and reef) combined. Error bars are standard errors.

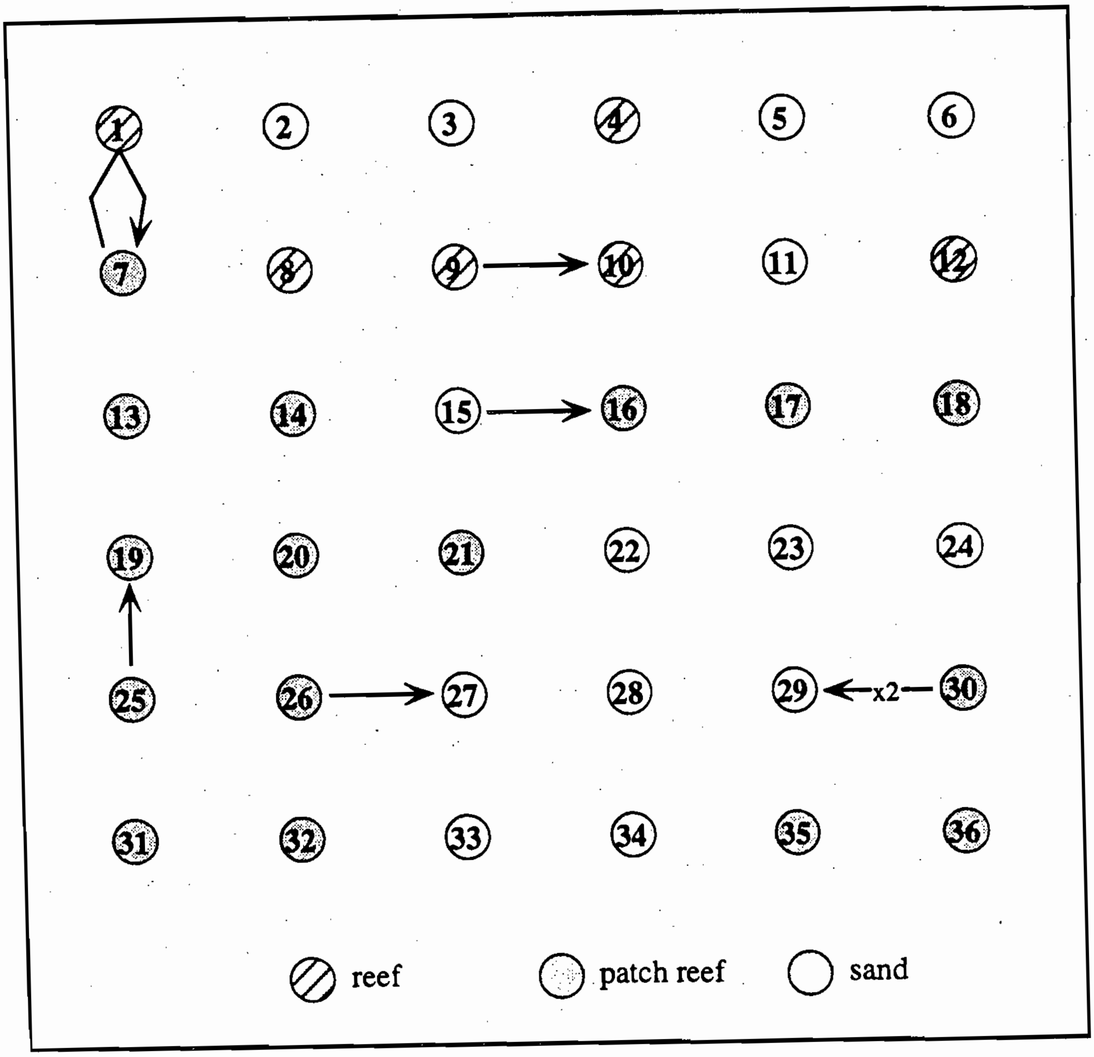

Figure 6.4a: Patterns of movement for *Lutjanus carponotatus* which moved ($n_{(\text{moved})}=7$, $n_{(\text{not moved})}=23$) among trapping positions at Loomis, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

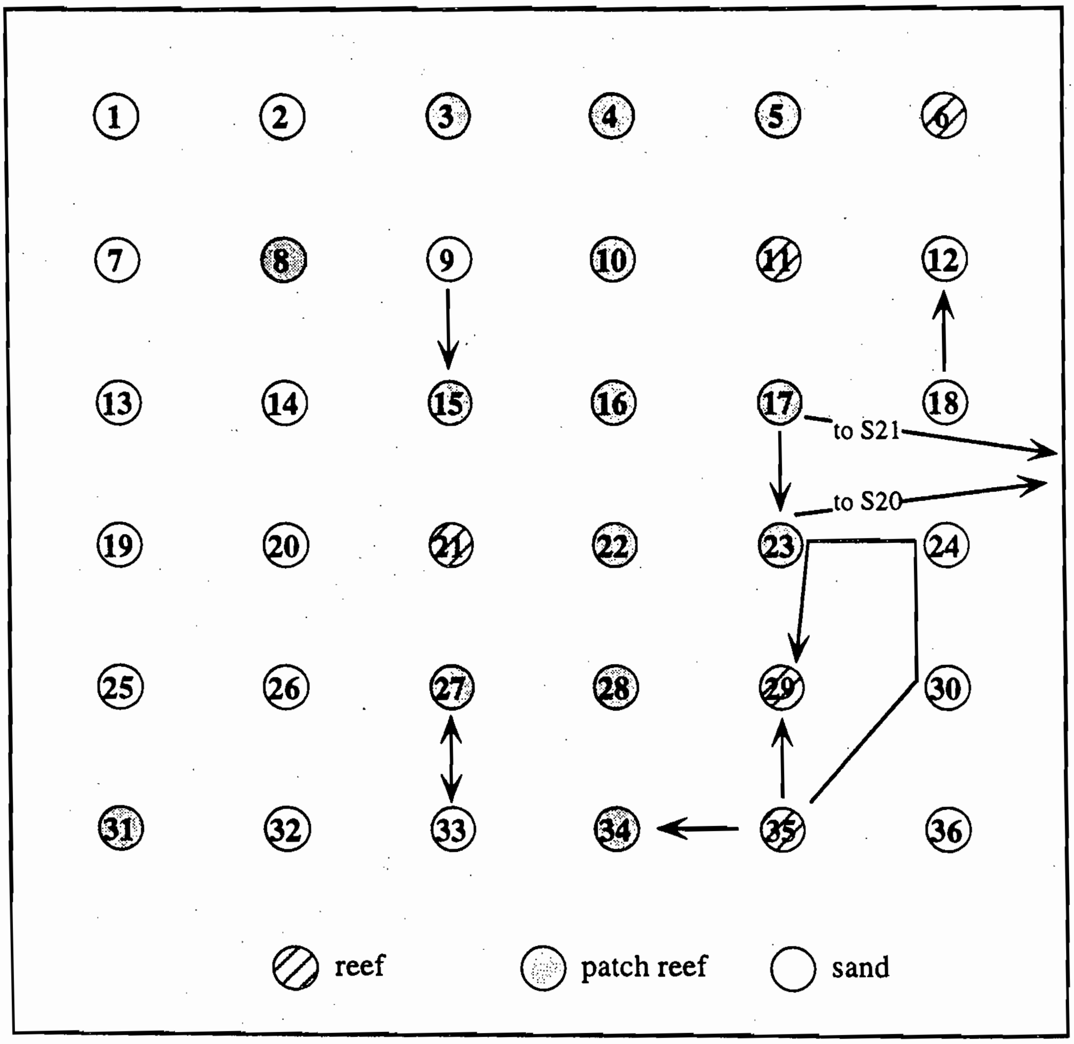

Figure 6.4b: Patterns of movement for *Lutjanus carponotatus* which moved ($n_{(\text{moved})}$ =10, $n_{(\text{not moved})}$ =28) among trapping positions at Mangrove, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

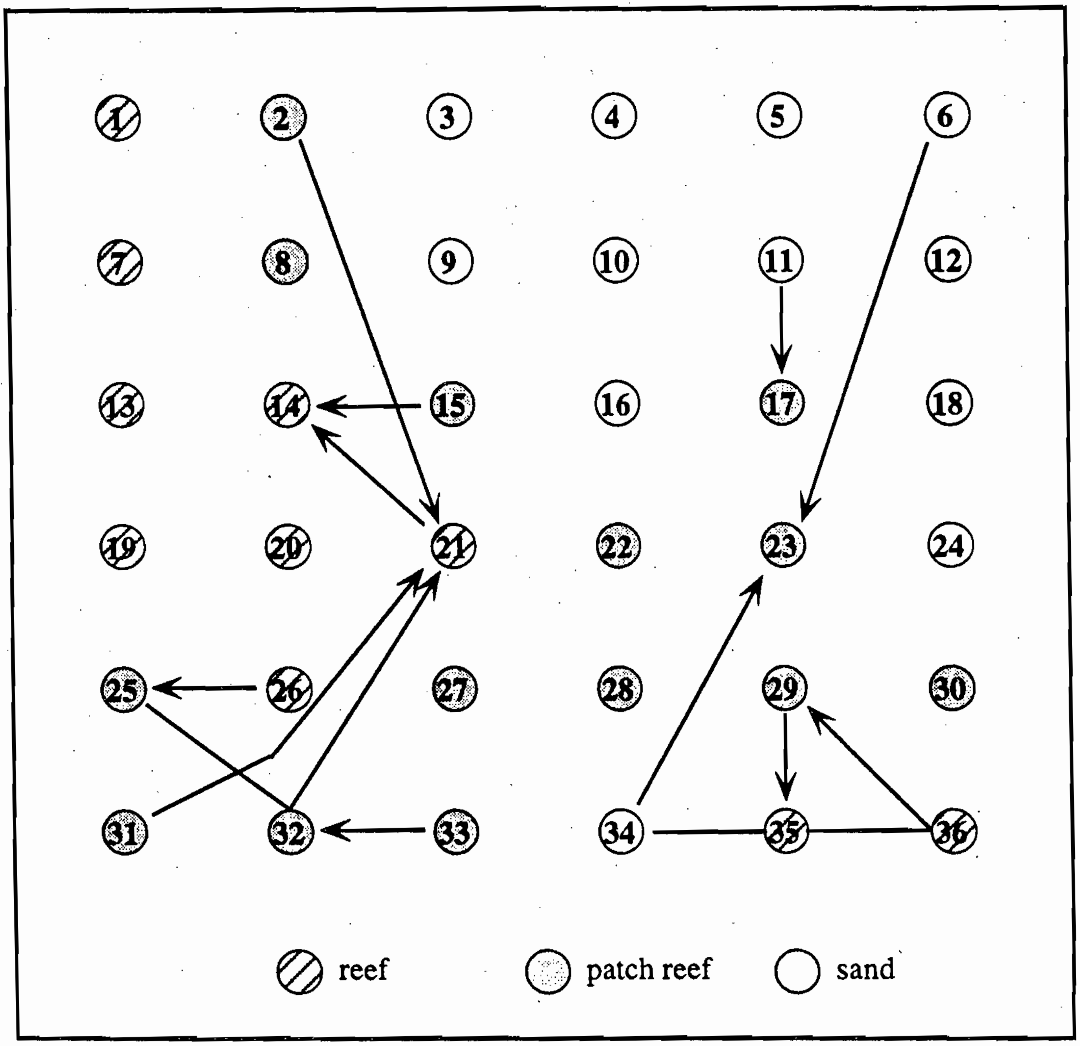

Figure 6.4c: Patterns of movement for *Lutjanus carponotatus* which moved ($n_{(\text{moved})}=12$, $n_{(\text{not moved})}=24$) among trapping positions at South, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

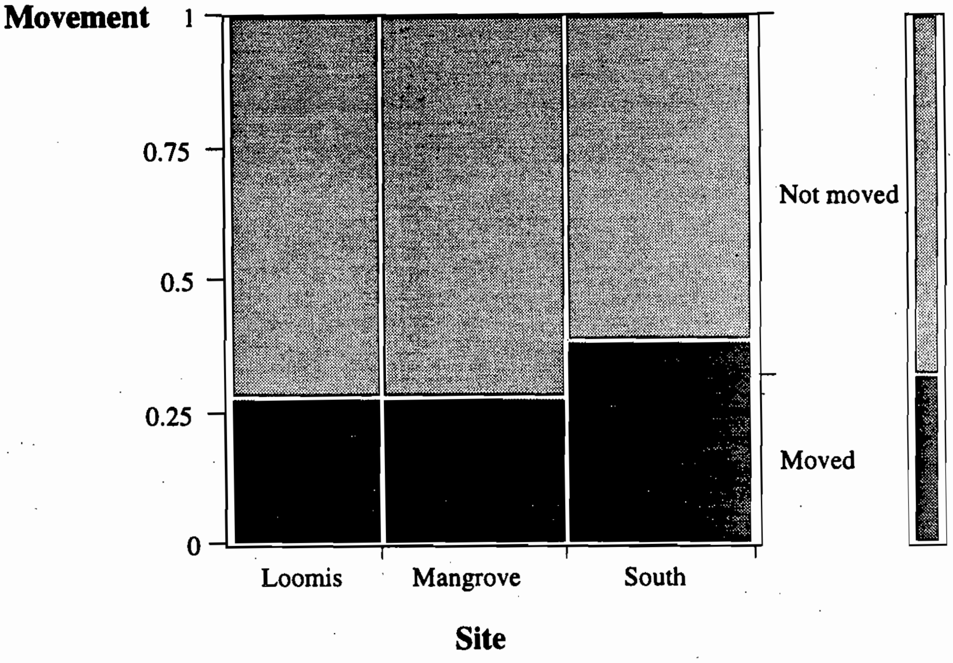

Figure 6.5: Mosaic plot of frequency of moved versus not moved for *Lutjanus carponotatus* for each site. The frequency of movement did not differ significantly among sites. (Likelihood χ^2 = 1.213, p=0.2563).

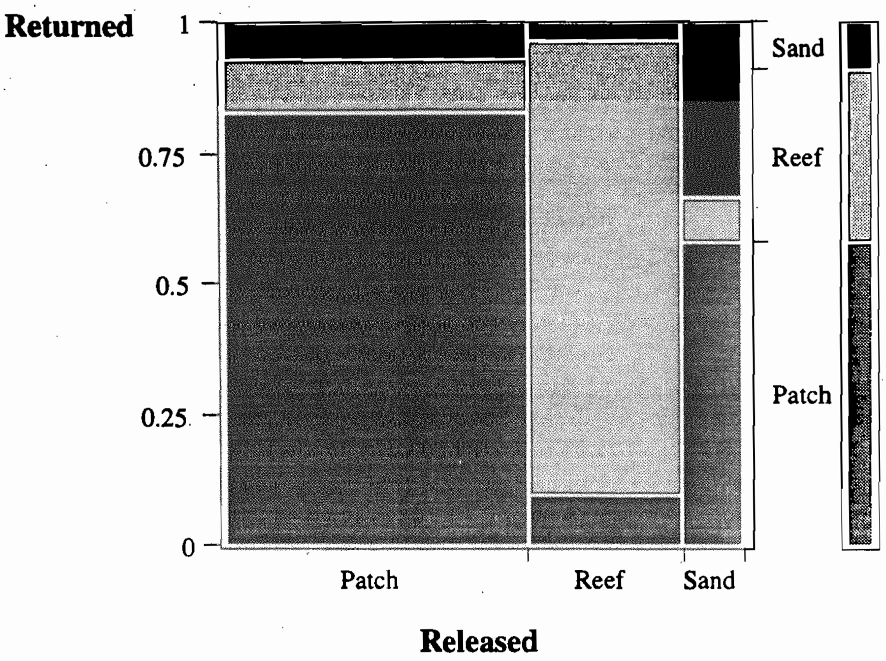

Figure 6.6: Mosaic plot of frequency of movement of *Lutjanus carponotatus* among habitats pooled over sites, including all releases. There was a significant effect of habitat of release on the frequency of movement among habitats. (Likelihood χ^2 = 64.262, p=0.000).

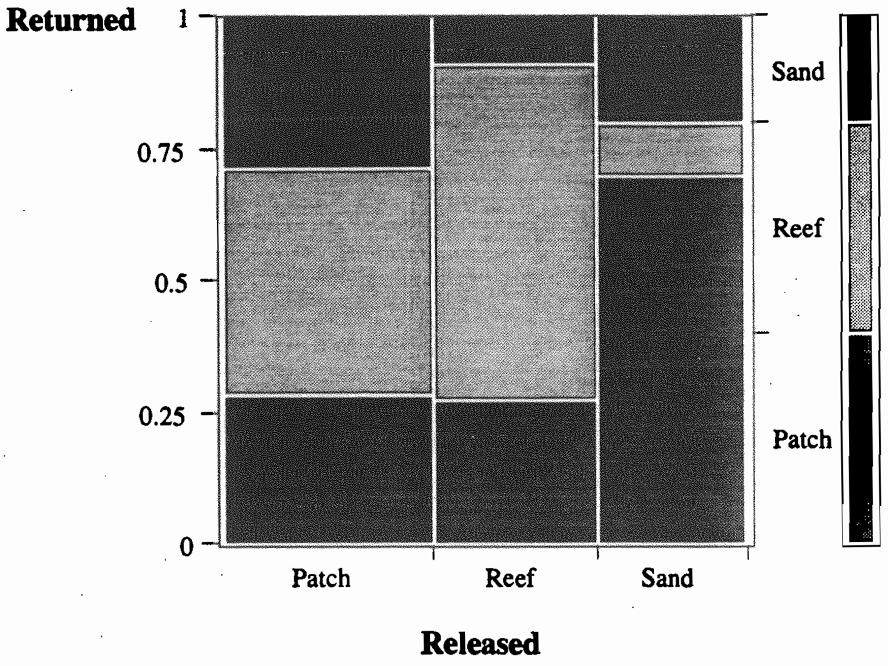

Figure 6.7: Mosaic plot of frequency of movement of *Lutjanus carponotatus* among habitats, pooled over sites, for releases which moved among positions. There effect of habitat of release on frequency of movement among habitats was not significant. (Likelihood $\chi^2 = 8.677$, p=0.0697).

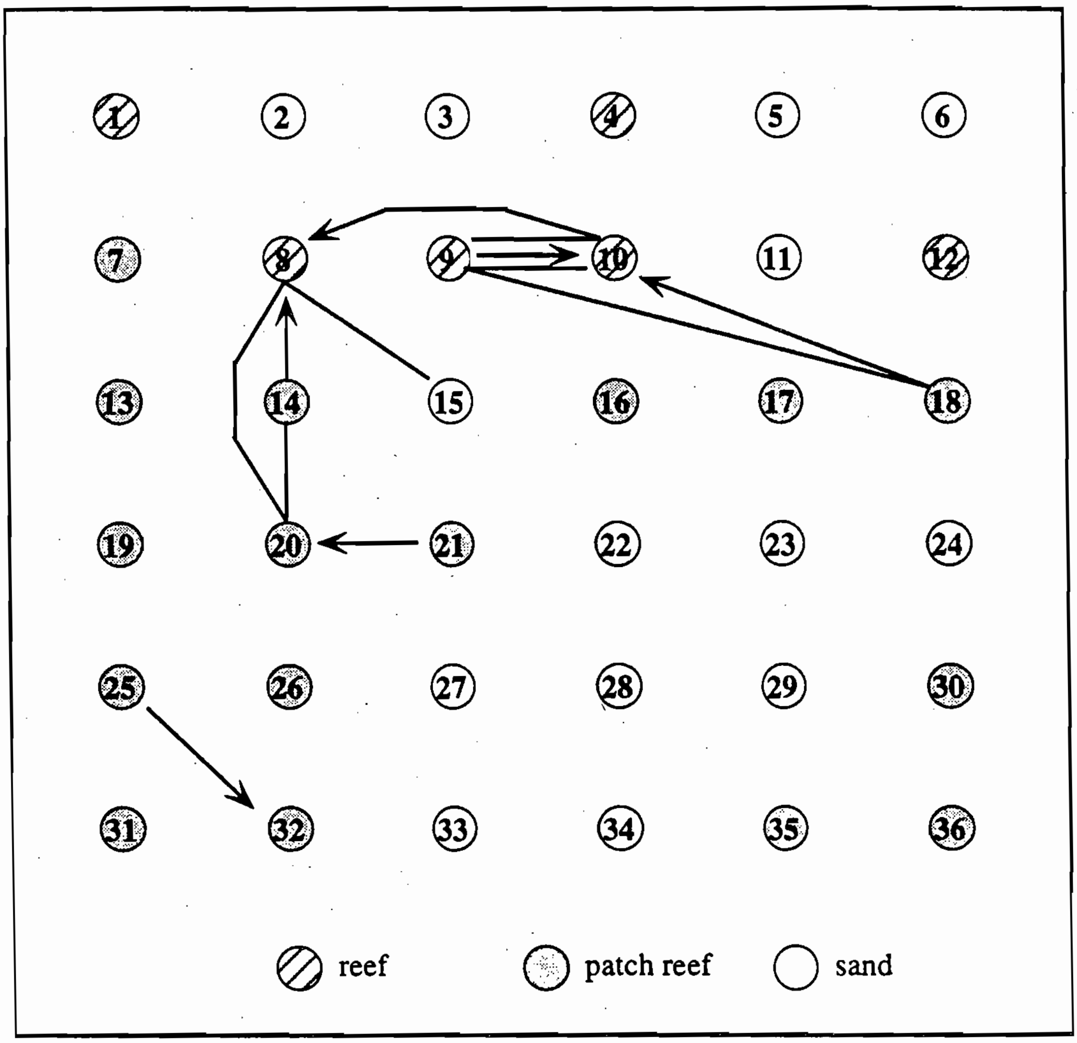

Figure 6.8a: Patterns of movement for *Plectropomus leopardus* which moved ($n_{(\text{moved})}=6$, $n_{(\text{not moved})}=3$) among trapping positions at Loomis, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

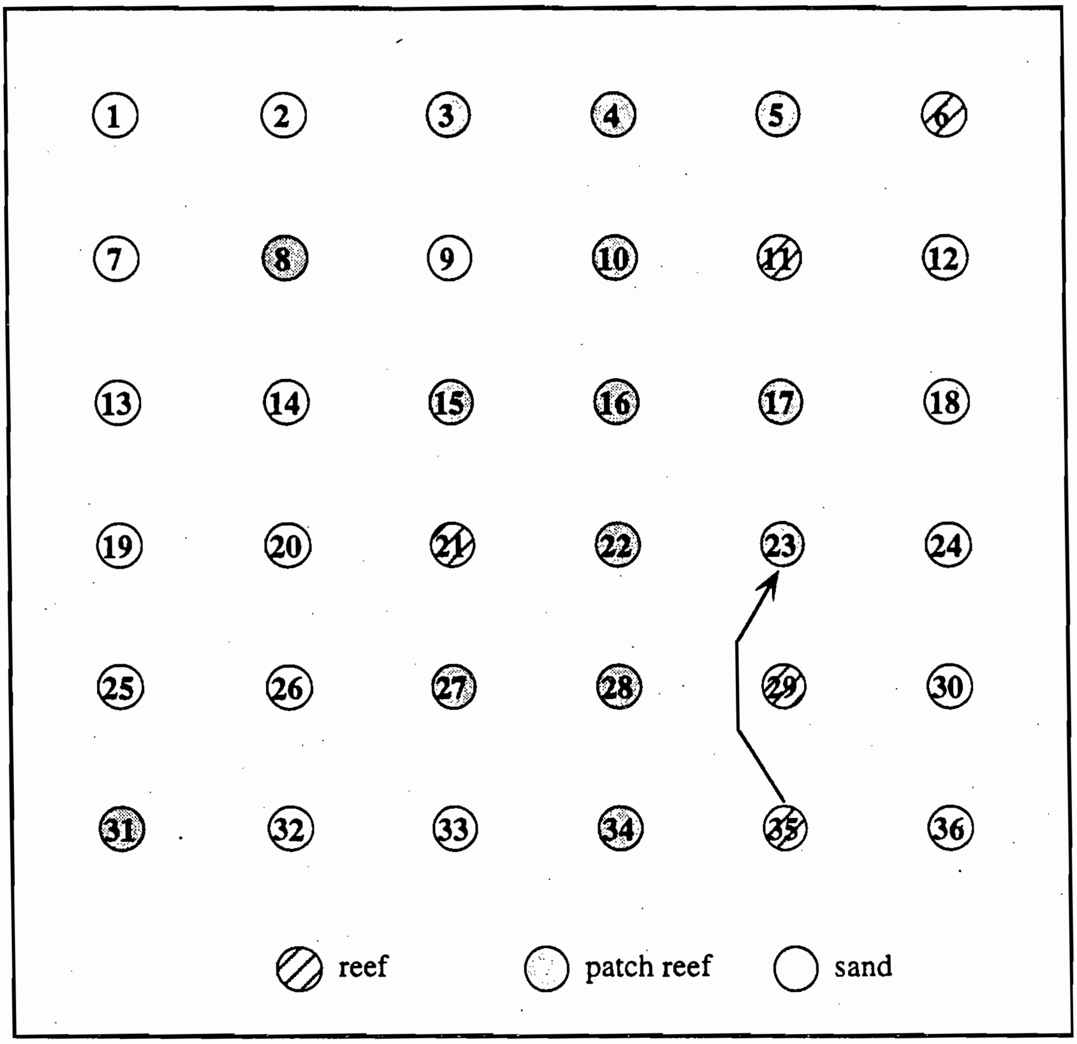

Figure 6.8b: Patterns of movement for *Plectropomus leopardus* which moved ($n_{(\text{moved})} = 1$, $n_{(\text{not moved})} = 2$) among trapping positions at Mangrove, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

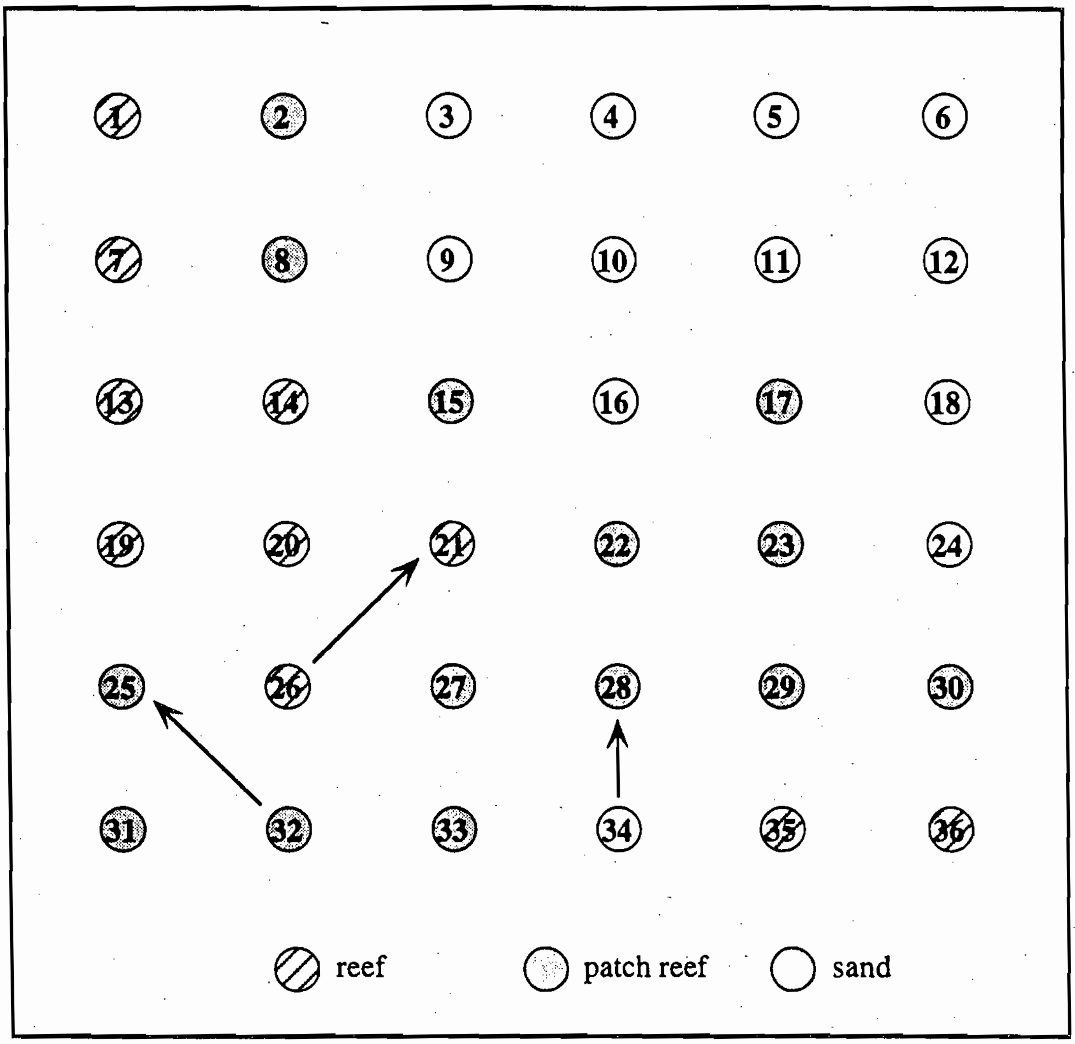

Figure 6.8c: Patterns of movement for *Plectropomus leopardus* which moved ($n_{(\text{moved})}=3$, $n_{(\text{not moved})}=2$) among trapping positions at South, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

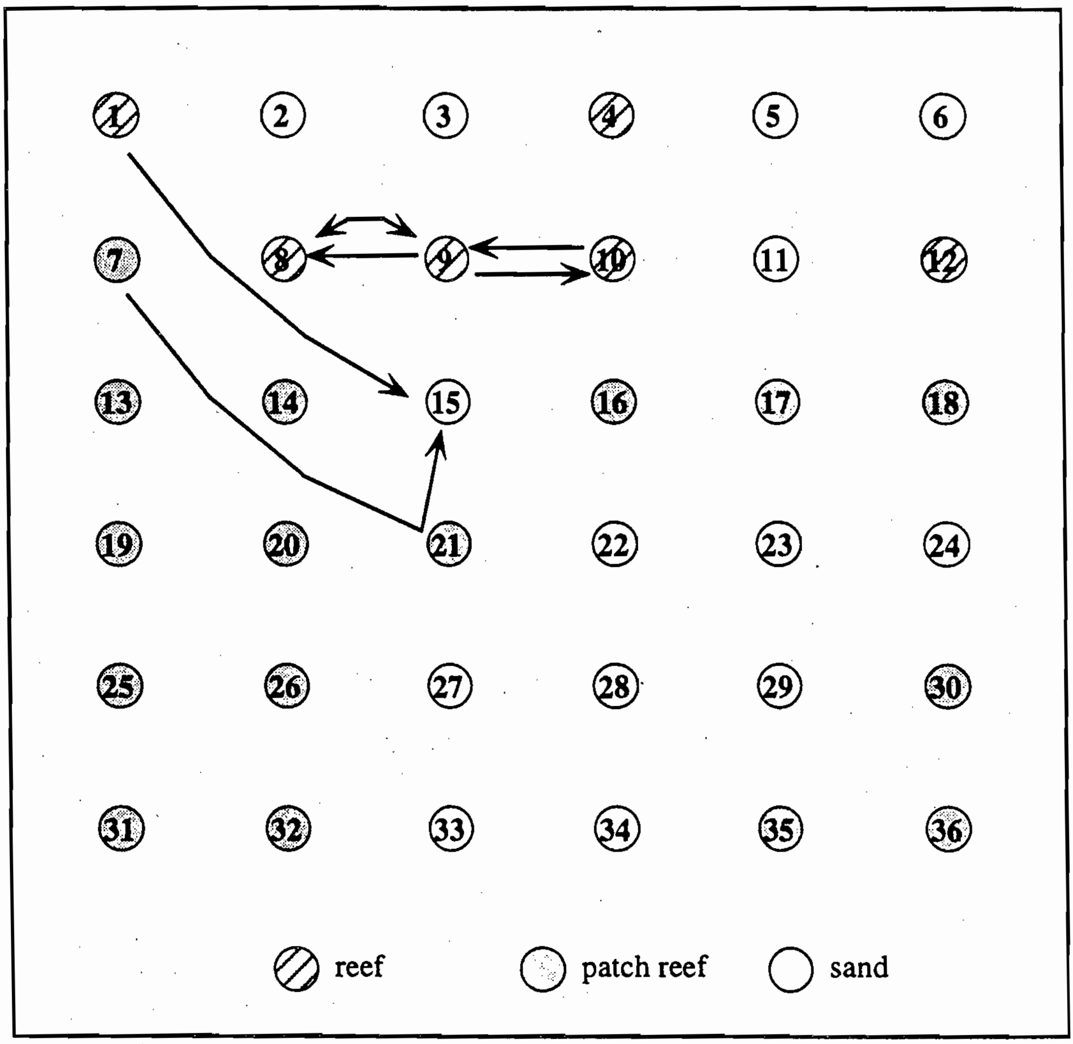

Figure 6.9a: Patterns of movement for *Siganus doliatus* which moved ($n_{(\text{moved})}$ =6, $n_{(\text{not moved})}$ =15) among trapping positions at Loomis, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

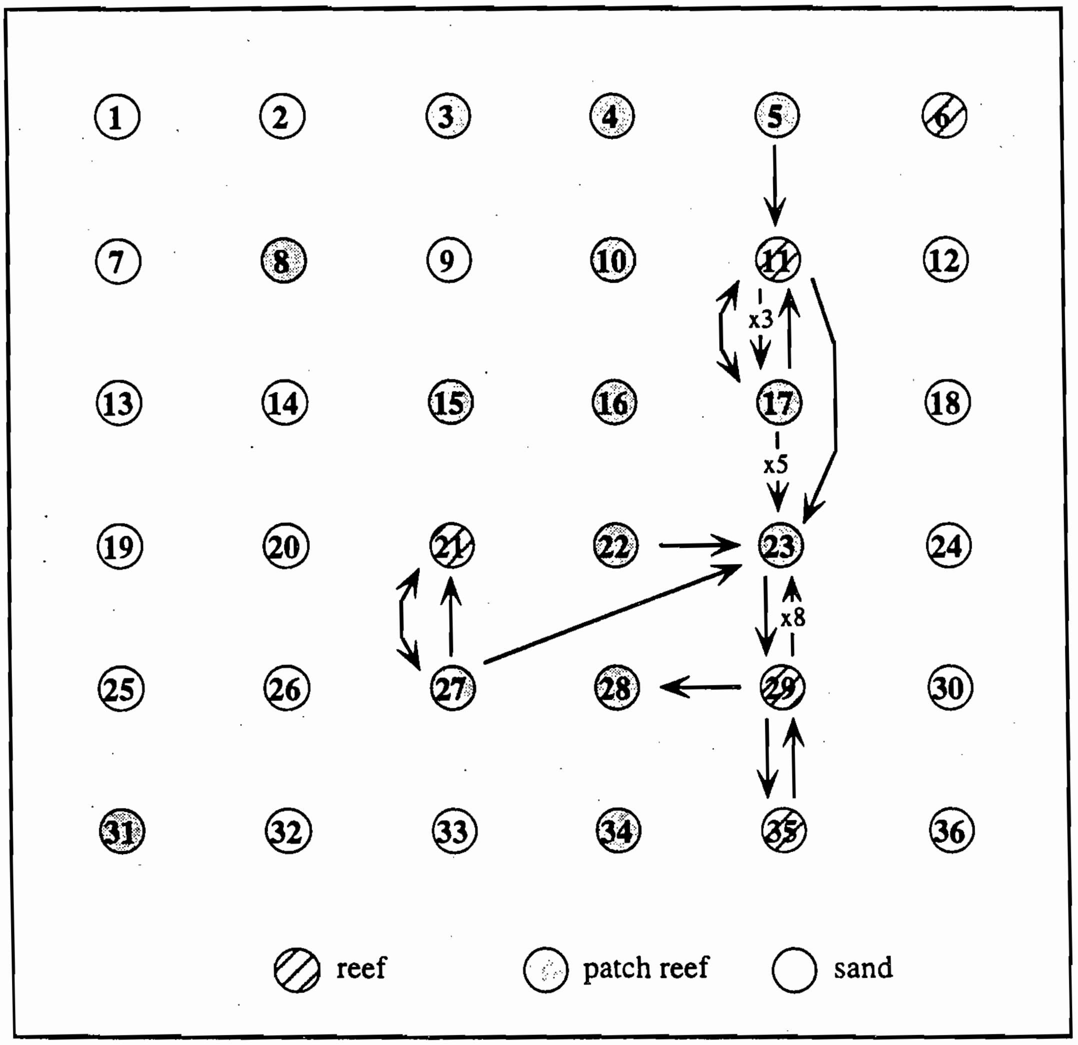

Figure 6.9b: Patterns of movement for *Siganus doliatus* which moved ($n_{(\text{moved})}$ =28, $n_{(\text{not moved})}$ =51) among trapping positions at Mangrove, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

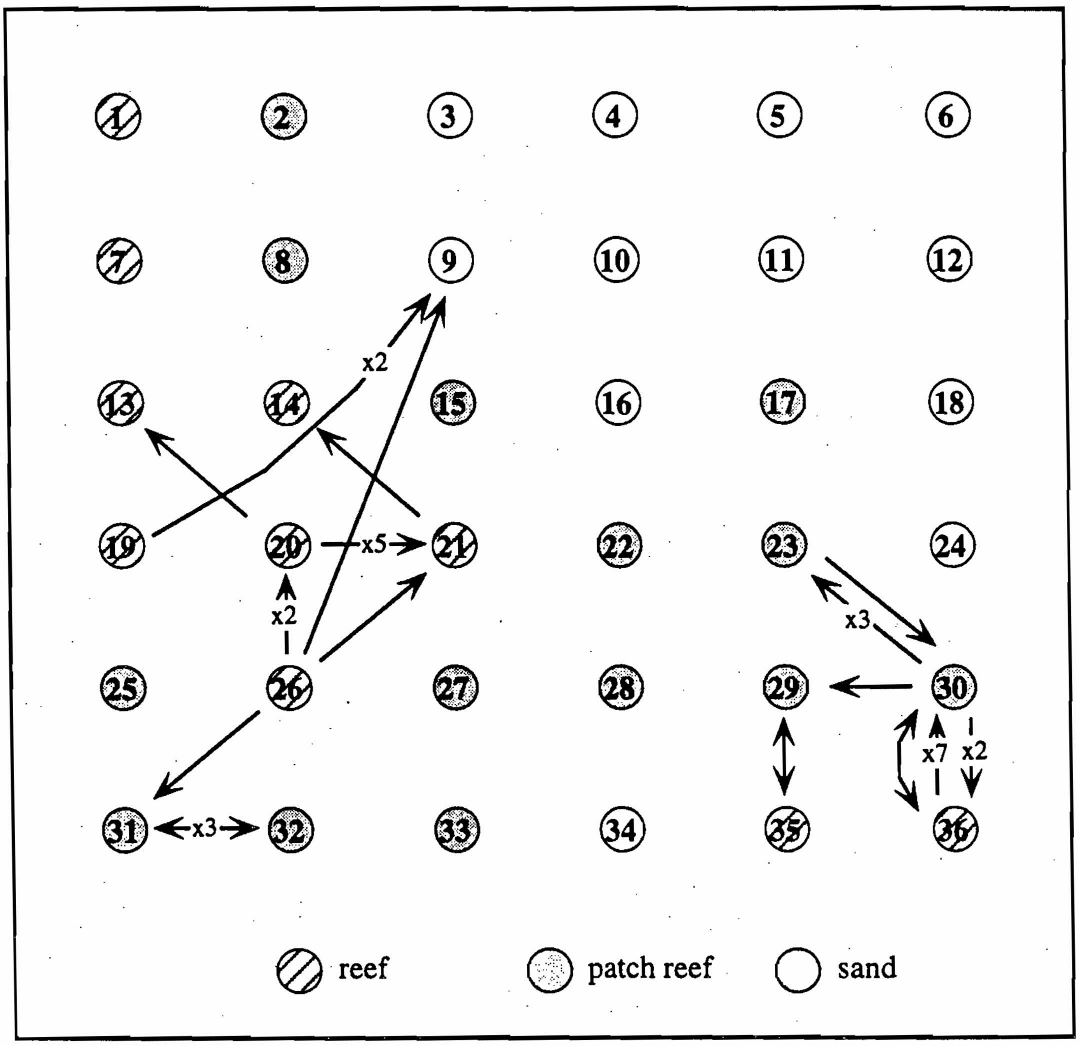

Figure 6.9c: Patterns of movement for *Siganus doliatus* which moved ($n_{(\text{moved})}$ =33, $n_{(\text{not moved})}$ =70) among trapping positions at South, pooled over all trips. Arrows indicate direction of movement, numbers represent number of individuals. The trapping positions are approximately 100 m apart and are shaded according to the three habitat categories.

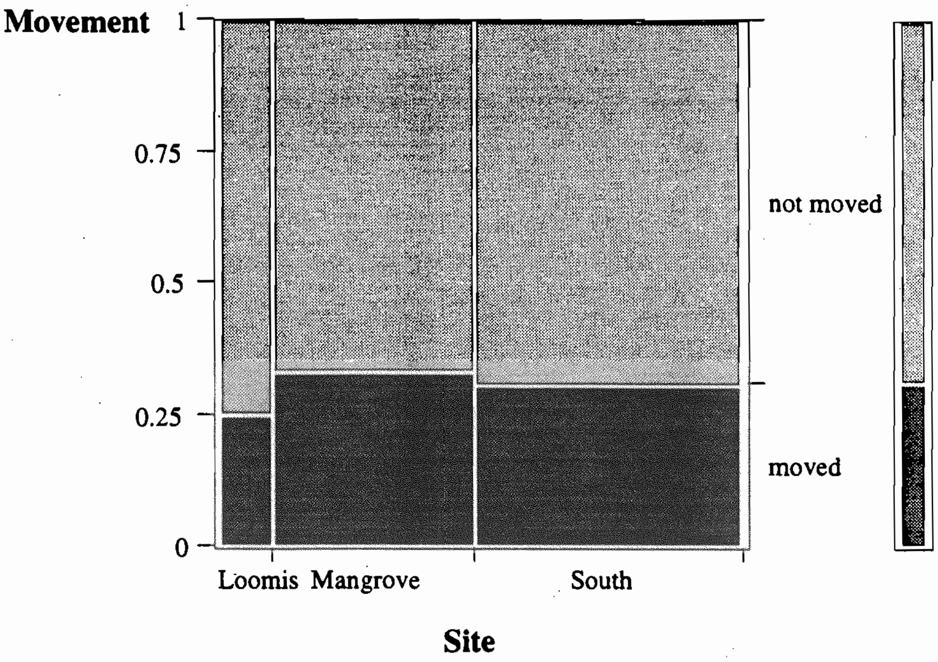

Figure 6.10: Mosaic plot of frequency of moved versus not moved for *Siganus doliatus* for each site. The frequency of movement did not differ significantly among sites. (Likelihood χ^2 = 0.4810, p=0.0.7863).

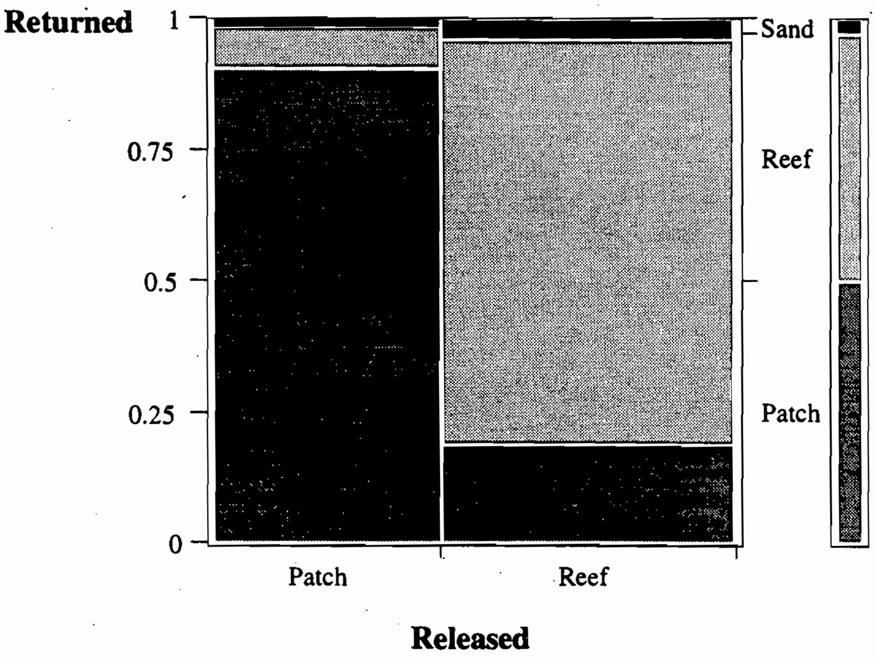

Figure 6.11: Mosaic plot of frequency of movement of *Siganus doliatus* among habitats, pooled over sites, including all releases. There was a significant effect of habitat of release on the frequency of movement among habitats. (Likelihood χ^2 = 110.756, p=0.000).

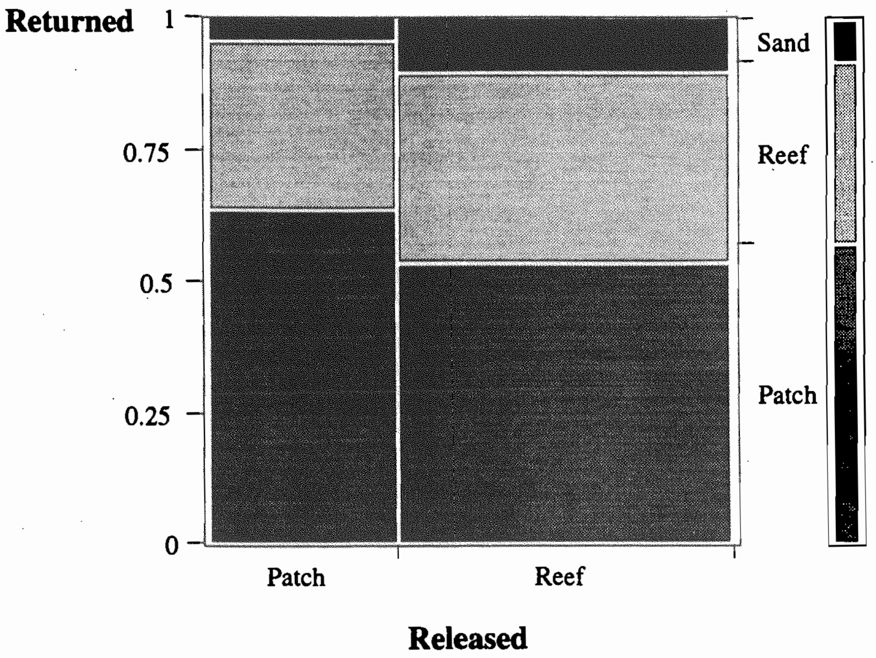

Figure 6.12: Mosaic plot of frequency of movement of *Siganus doliatus* among habitats, pooled over sites, for releases which moved among positions. There effect of habitat of release on frequency of movement among habitats was not significant. (Likelihood $\chi^2 = 8.677$, p=0.0697).

Chapter 7

Species composition and catch per unit effort and size structure of *Plectropomus leopardus* from line fishing

7.1 Introduction

Fishing is one of the major extractive activities on coral reefs. The majority of coral reef fisheries are heavily exploited and many are dangerously over fished (Williams and Munro 1985; Russ 1991; Dugan and Davis 1993b). In the Caribbean, traps, hook and line, gillnets, spears and destructive methods, such as poisons and dynamite, are used to catch a wide variety of reef dwelling species, with approximately 180 species marketed (Munro 1983). A similar situation exists in the Philippines where all of the above mentioned techniques are employed in addition to highly efficient and destructive techniques, such as "muro-ami" drive nets and fish corrals (Alcala and Russ 1990). Harvests consist of a multitude of sizes and species of reef fish with many being caught as juveniles. Hence, fishing may impact directly on a broad range of species through increased total mortality (increased fishing mortality) and indirectly through habitat destruction and shifts in community composition.

In comparison, the reef fish stocks on the Great Barrier Reef (GBR), Australia, are relatively lightly fished (Munro 1987; Dugan and Davis 1993a) and generally exploited by a single type of gear, with hook and line being the predominant method of fishing. The use of traps, nets or longlines to take reef fish is prohibited and spear fishing is limited to recreational use (GBRMPA 1992). The commercial sector of the Reef Line Fishery (RLF) landed on the order of 2000 -3000 mt of reef fish annually between 1989 and 1990 (Trainor 1991). The majority (54%) of the reef based catch is the highly valued coral trout, mostly *Plectropomus leopardus* and to a lesser extent *P.laevis* and *P.maculatus*, although significant catches of sweetlip emperor (*Lethrinus miniatus*) and red emperor (*Lutjanus sebae*) (22% collectively) are taken also (Trainor 1991). A range of species, mainly serranids, lutjanids and lethrinids, comprise the remainder of the reef fish catch which is generally categorised as *"mixed reef fish"* and not identified to a species level (Trainor 1991).

The GBR supports a large and rapidly expanding recreational small boat fleet and a charter boat fishing industry (90 registered vessels). As in the commercial fishery, coral trout is the primary target species of both the small boat fleet and the charter fishery. The recreational small boat fleet has increased an estimated 63%, from 14,887 to 24,300 boats, over the past 10 years (Williams and Russ 1994). Estimates of annual catch by the small boat fleet are uncertain and range from 6600 mt in 1980 (Driml *et al* 1982) to 3500-4530 mt in 1990 (Blamey and Hundloe 1991). There has been considerable concern recently over the perceived decline in the state of the reef fish stocks on the GBR, the rapid expansion of the recreational small boat fleet and the potential for increase in the commercial fleet from latent effort (Gwynne 1991). This concern prompted a review of the data available for the fishery (Williams and Russ 1994) and its management (Gwynne 1991) which resulted in new size limits for 36 common species, recreational bag limits for major target species, a ceiling on the total number of commercial line endorsements and the creation of a specific Reef Line Endorsement for the commercial fishery (QFMA 1993).

Monitoring the abundance and distribution of exploited fish stocks is a fundamental aspect of stock assessment (Hilborn and Walters 1992). In many reef fisheries comparisons of relative abundance of target species over space and time and between fished and unfished areas have relied on estimates of relative abundance obtained using underwater visual counts (*eg* Bell 1983; Russ 1985, 1989; McCormick and Choat 1987; Russ and Alcala 1989; Alcala and Russ, 1990; Cole *et al* 1990; Polunin and Roberts, 1993, 1994). On the GBR the majority of information on the relative abundance and distribution of fished species such as *P.leopardus* has been obtained using UVC techniques also (*eg.* Craik 1981; Ayling and Ayling 1983 a&b; 1984 a&b; 1986; 1992). These studies have provided valuable information on the distribution and relative abundance of *P.leopardus* across the large range of spatial scales which occur on the GBR, provided evidence for the effects of fishing on target species and have been reviewed in detail by Williams and Russ (1994). However, comprehensive stock assessment requires a survey technique(s) which may be used over the entire habitat range occupied by the target species (Hilborn and Walters 1992).

In this respect the major disadvantage of UVC techniques for assessing monitoring reef fish stocks is that it is not possible to routinely survey habitats deeper than 15m. Furthermore, the total area surveyed is often small in comparison to the total area occupied by the resource, the total sample sizes from an individual reef are often small in comparison to estimated population size, many common species of exploited reef fish are not surveyed adequately (Williams 1991; Williams and Russ 1994) and surveys are expensive as highly trained personnel are required. Accordingly, the need for alternative survey methods for monitoring the status of reef fish stocks has been cited as a priority for reef fish research. (Ralston *et al* 1986; Richards and Schnute 1986; Matlock *et al* 1990; Walters and Sainsbury 1990; Williams 1991).

Catch per unit effort (CPUE), from the fishery or from research surveys, is the most commonly used index of abundance used in fisheries stock assessment (Paloheimo and Dickie 1964; Bannerot and Austin 1983; Collie and Sissenwine 1983; Gulland 1988; Hilborn and Walter 1992) and methods of analyses for CPUE data are extensive and well developed (Gavaris 1980; Kimura 1981; Quinn 1985; Richards 1987,1994; Richards and Schnute 1986; 1992; Large 1992; Swartzman 1992). Hence, CPUE data from line fishing is the obvious alternative to UVC techniques for obtaining an index of relative abundance and for measuring the response of reef fish populations to different levels of fishing pressure. However, as with all sampling techniques, it has disadvantages. The most serious from a stock assessment point of view being variation in catchability over space, time and stock density, resulting in CPUE not being directly proportional to abundance (McCall 1976; Winters and Wheeler 1985; Beinssen 1989a; Shardlow 1993). Despite this, CPUE data from line fishing has several advantages over UVC techniques. It is possible to sample over the entire depth range of the resource, a large proportion of the reef area may be sampled and, with the use of skilled fishers, total sample sizes per reef are usually large. Furthermore, it is possible to obtain information on the age and sex structure of the population from the catch, which is not possible with visual techniques (Matlock *et al* 1991).

This chapter describes the species composition of the catch and the catch per unit effort and size structure of *P. leopardus* obtained during a large-scale tagging programme in the Cairns Section of the Great Barrier Reef Marine Park (GBRMP) (see Chapter 8). The objective was to identify the major sources of temporal and spatial variation in species composition of the catch and CPUE and size structure of the *P. leopardus* from line fishing, which could be used in the design of future research surveys and in analysis of CPUE data from reef line fisheries.

7.2 Methods

7.2.1 Study site

The study was done on a cluster of 5 coral reefs (Beaver, Taylor, Farquharson, 17-060/061 (Little Potter) and Potter Reefs) adjacent to the southern boundary of the Cairns Section of the GBRMP (Figure 7.1). The estimated shortest distances between adjacent reefs within the cluster ranged from 200m, between Beaver and Taylor reefs, to 1500 m, between Farquharson and Little Potter reefs (Figure 7.1). These reefs have been zoned Fisheries Experimental reefs for the purposes of the GBRMPA Effects of Fishing Programme (EoFP), following the revision of the Cairns Section zoning plan in 1993, with Beaver reef closed to fishing and the other reefs open to line and spear-fishing (GBRMPA 1993) (Figure 7.1).

7.2.2 Sampling by line-fishing

Fish were caught by commercial line-fishers using 80 lb (36 kg) handlines rigged with a running sinker, an 8 or 9/O hook and baited with a whole Western Australian pilchard (*Sardinops neopilchardus*). Fishing was done from 4.1 m aluminium dories, with one fisher and one tagger per dory, and also from one commercial mother vessel, with two fishers and one or two taggers.

For convenience, any combination of vessel, fishers and taggers will hereafter be referred to as 'dory' and the process of a dory anchoring and fishing will be defined as a 'hang'. In order to distribute the effort of each dory evenly within defined spatial strata, minimum (10 min) and maximum (30 min) hang times were set. The location, depth and start and finish times of each hang were recorded onto prepared data sheets and maps.

7.2.3 Sampling protocol

The perimeter of each reef was divided into a series of blocks, approximately 2 - 2.5 km long, which were used to distribute the sampling effort as evenly as possible around the reef. The number of blocks varied between reefs according to the area of the reef and the amount of "fishable" habitat in each area (Figure 7.2). The boundaries of the blocks were buoyed on the initial tagging exercise (April 1992) and their location mapped and recorded using Global Positioning System (GPS). Following the second tag-recovery exercise (September 1992), prominent reef features were used to delineate the blocks as the process of deploying the buoys required too much time which could otherwise be used for sampling.

The number of dories and total sampling effort varied between trips, however the sampling protocol was the same. Teams of 2-3 dories were assigned to a block which they fished for a "session" (morning/afternoon; average duration = 4hr). In order to distribute the effort evenly within blocks, dories commenced fishing at opposite ends of the blocks and fished towards each other dividing their effort between deep (25-30 m) and shallow (1-5m) hangs. A total of two or 3 blocks were sampled during a session, although this varied between reefs and according to the total number of dories on each trip.

Generally the blocks within each reef were fished sequentially as this minimised travelling time and therefore maximised sampling effort. However, following the initial tagging exercise and on a suggestion made by the commercial fishers, the order in which blocks were fished was timed to coincide with the 'run on' tide. The 'run on' side of a reef is the side where the tide is pushing up onto the reef from the deeper off-reef water. Conversely, the 'run off' side of a reef is the side where the tide is flowing off the top of the reef into the deeper reef slope water. The 'run off' side of a reef generally becomes the 'run on' side when the tide reverses. The fishers believe there is a substantial difference in catch rates between the 'run on' and 'run off' tides with CPUE being higher on the 'run on' side. Therefore, it was decided to stratify the sampling effort with respect to tide in order to maximise catch per unit effort (CPUE) and reduce variation due to tidal status.

7.2.4 Sampling Schedule and Distribution of Effort

Five sampling trips were done over the duration of the study. The number of fishers and duration of each trip is given in Table 7.1. The April 1992 trip was done during neap tides whilst the latter four trips were done during either new moon or full moon spring tides. In April 1992 and 1993, it was not possible to fish the exposed areas (SE) of any of the reefs, with the exception of Beaver Reef, due to prevailing sea conditions. This resulted in the total effort for each reef during these trips being distributed amongst the back reef blocks (Table 2). In September 1992 and October 1993 all blocks of all reefs were fished, except for block 5 at Beaver reef in October 1993 (Table 7.2). The sampling effort for the April 1993 trip was reduced by more than 1.5 days due to mechanical breakdowns to both charter and fishing vessels and, as a result, Little Potter reef was not fished at all and only one 4 h session was done at Farquharson reef.

The distribution of the sampling effort for the February 1994 trip differed from the previous trips. Rather than distributing the total effort evenly between the 5 reefs, the effort was concentrated in those areas where there was the greatest difference between the level of inter-reef movement of *P.leopardus* indicated previously by the public and research returns (Table 7.2 and see Chapter 8). However, the back reef blocks of all reefs were fished to maintain the sampling series for comparison of CPUE among back reef blocks across all reefs.

7.2.5 Analysis

Catch Composition

The effects of trip, reef and species on catch composition was tested using three dimensional contingency tables (Zar 1984), where rows were species (*P.leopardus, Cephalopholis cyanostigma, Lutjanus bohar, L.carponotatus, Lethrinus atkinsoni, L.miniatus* and Others), columns reefs (Beaver, Farquharson, Little Potter, Potter and Taylor Reefs) and tiers trips (April 1992=a, September 1992=b, April 1993=c, October 1993=d and February 1994=e). Results from the contingency table analysis are illustrated as mosaic plots (SAS 1989), where the proportion of the column filled by a species represents its relative contribution to the total for that column, and the width of the column is proportional to the sample size for that column relative to the other columns in the analysis. Correspondence analyses of species by trip and species by reef were used to illustrate potential relationships among these categories.

Catch per unit effort

Catch Per Unit Effort (CPUE) data were analysed using a hang by a dory as a replicate, with units of line hours (line h^{-1}). This measure of effort includes the time between setting and hauling of the anchor only. It provides the best standardised unit of effort as it does not include travelling or search time, which tend to vary among fishers, reefs and trips. Patterns in CPUE of *P.leopardus* among trips, reefs and blocks are presented as mean CPUE (fish/line h^{-1}) with standard errors.

The effects of trip, reef and block on mean CPUE of *P.leopardus* were tested with a three-way mixed model ANOVA, with trip and reef as crossed, fixed factors and block, as a random factor, nested within reef. Block includes the confounded effect of dory, as all dories did not fish all blocks on all trips. However, as there was considerable turnover of fishers during the course of the study and fishers were not systematically allocated to blocks, a consistent bias due to combinations of blocks and dories is considered unlikely.

Size structure

Size structure data are presented as length frequency histograms by trip by reef for *P.leopardus* only. The effects of trip, reef and block on mean length of *P.leopardus* were tested with a three-way mixed model ANOVA, with trip and reef as crossed, fixed factors and block, a random factor, nested within reef.

Due to the unbalanced number of blocks fished on each reef for each trip, only the following data were used in the ANOVA's of CPUE and length of *P.leopardus*: TRIPS: a, b, d, e (trip c was omitted as the distribution of effort was severely restricted and cannot be considered representative); REEFS: all reefs were included, with the exception of Little Potter as it only had one back reef block; BLOCKS: only back reef blocks. These omissions resulted in a more balanced data set for the analyses. All data were tested for normality (D'Agostino 1971 a&b; In Zar 1984) and homoscedacity (Bartlett 1937; In Zar 1984) prior to performing the analyses and transformed accordingly ($x' = \log_{10}(x+1)$). Where transformation failed to improve the distribution of the data, analysis were performed on the untransformed data.

7.3 Results

7.3.1 Catch Composition

A total of 8,043 fish of 61 species from 11 families were caught over the five trips. Catch was dominated by three families; Serranidae, Lutjanidae and Lethrinidae, which accounted for more than 97% of the total catch in numbers. Six species, *Plectropomus leopardus* (57%), *Cephalopholis cyanostigma* (12%), *Lutjanus bohar* (3%), *L.carponotatus* (6%), *Lethrinus atkinsoni* (4%) and *L.miniatus* (3%) dominated the catch (85% of total catch in number). Other common, but less abundant species included: *Epinephelus merra, E.quoyanus, E.fuscoguttatus, Plectropomus laevis, Lutjanus sebae, L.russelli, L.vitta, Symphorus nemataphorus, Lethrinus semicinctus* and *L.*sp.2.

The general pattern of catch composition among reefs and trips was similar, with *P.leopardus* dominant on all reefs, followed by *C.cyanostigma, Lutjanus carponotatus* and *Lethrinus atkinsoni*. (Tables 7.3 and 7.4). The rank of *Lutjanus bohar* and *Lethrinus miniatus* alternated between 5 and 6 among reefs (Tables 7.3 and 7.4). However, despite this general pattern, there was a significant effect of trip on species composition ($\chi^2_{0.05;24}=248.45$, $p<0.0001$) (Figure 7.3). Correspondence analysis suggested that this may have been due to an increase in the occurrence of *P.leopardus* in the catch in September 1992(b) and October 1993(d), while there were proportionally more *C.cyanostigma, Lutjanus carponotatus* and *Lethrinus atkinsoni* during the April 1992(a), 1993(c) and February 1994(e) (Figure 7.3 & 7.4).

There was a significant effect of reef on the frequency of occurrence of each species in the total catch also ($\chi^2_{0.05;24}=216.328$, $p < 0.0001$) (Figure 7.5). Correspondence analysis suggested this may have been due to *C.cyanostigma,* and to a lesser extent *Lutjanus bohar,* comprising a greater percentage of the catch at Potter and Taylor reefs while *Lutjanus carponotatus* and *Lethrinus atkinsoni* were proportionally more abundant at Beaver Reef (Figure 7.5 & 7.6).

7.3.2 Catch per unit effort

Effect of TRIP

Trip had a significant effect on the CPUE of *P.leopardus* ($F_{0.05;3,8}=27.94$; $p=0.0001$) and accounted for 8.42 % of the total variation. There was a significant interaction between trip and block (reef) also ($F_{0.05;23,1424}=1.66$; $p=0.0253$) (Table 7.5). The interaction effect explained a small proportion of the variation relative to the effect of trip (Table 7.6). Mean CPUE for

P.leopardus was significantly higher in September 1992, October 1993 and February 1994 than in April 1992 (Tukey's HSD test $p<0.05$). The highest mean CPUE for *P.leopardus* occurred in September 1992 and October 1993, which corresponded to the peak in the *P.leopardus* spawning season, while the lowest CPUE occurred during April 1992, February 1994 (Figure 7.7) and, to a lesser extent, April 1993 (which was not included in the ANOVA).

Effect of REEF

Mean CPUE for *P.leopardus* did not vary significantly among reefs ($F_{0.05;3,8}=0.13$; $p=0.9412$) (Table 7.5). Although CPUE for *P.leopardus* was generally higher on Beaver reef, it was not significantly different from the other reefs. Catch per unit effort for *P.leopardus* was consistently higher on Beaver, Farquharson and Little Potter (which was not included in the ANOVA) reefs and lowest on Taylor and Potter reefs (Figure 7.7).

Effect of BLOCK

There was a significant effect of block on mean CPUE for *P.leopardus* ($F_{0.05;8,1424}=2.53$; $p=0.0097$) and a significant interaction between trip and block ($F_{0.05;23,1424}=1.66$; $p=0.0253$) (Table 7.5). The effect of block results from CPUE at block 1 of Beaver Reef being higher than CPUE at block 4 on all trips (Tukey's HSD test $p<0.05$). The trip*block interaction is likely to be due to the significantly higher CPUE in block 3 of Taylor Reef (Tukey's HSD test $p<0.05$) and block 8 of Farquharson Reef (Tukey's HSD test $p<0.05$) than the other blocks within each reef during trip d and CPUE in block 2 of Potter Reef being significantly higher than block 3 during all trips except trip d trips (Tukey's HSD test $p<0.05$) (Figure 7.8). There were no other significant differences among blocks within reefs.

Catch per unit effort, and particularly total catch, of *P.leopardus* was generally higher in the back reef blocks of all reefs with the exception of Beaver reef (Appendix 2a). This was most likely due to the difference in the efficiency of the fishers (or gear) between the two reef locations rather than a real difference in the relative abundance of *P.leopardus*. The fishers tended to have greater difficulty finding and correctly anchoring for suitable hangs on the steep reef front slopes of Potter, Farquharson and Taylor reefs and, as a result spent more time searching, did fewer hangs and had a higher percentage of zero catch hangs. The fact that CPUE and total catch of *P.leopardus* on the reef fronts increased on trip d suggests that the fishers may have learned to fish the reef fronts more effectively relative to trip b (Appendix 2a)

7.3.3 Size structure

Effect of TRIP

The mean length of *P.leopardus* decreased significantly over the 22 months of the study ($F_{0.05;3,8}=5.17$; $p=0.0070$) (Table 7.6). Although mean length of *P.leopardus* was not significantly different between April and September 1992, it decreased significantly from September 1992 to October 1993 and again from October 1993 to February 1994 (Tukey's HSD test, $p<0.05$) (Figure 7.9). This last decrease was most evident at Farquharson and Taylor reefs (Figure 7.9).

Effect of REEF

Mean length of *P.leopardus* varied significantly among reefs ($F_{0.05;3,8}=5.44$; $p=0.0247$) (Table 7.6). It was significantly greater on Taylor reef than all other reefs (Tukey's HSD test $p<0.05$) (Figure 7.9). Farquharson and Potter reefs had significantly larger mean length than Beaver reef (Tukey's HSD test $p<0.05$) , but were not different from each other (Tukey's HSD test $p>0.05$) (Figure 7.9). Mean length of *P.leopardus* at Beaver reef was significantly lower than all other reefs (Tukey's HSD test $p<0.05$) (Figure 7.9). Although not included in the ANOVA, the pattern in mean length at Little Potter reef was similar to Beaver reef, with mean length decreasing monotonically over trips (Figure 7.9)

Effect of BLOCK

Mean length of *P.leopardus* varied significantly among blocks within reefs ($F_{0.05;8,2230}=0.0041$; $p=0.0041$) and there was a significant interaction between trip and block also ($F_{0.05;25,2230}=1.62$; $p=0.0311$) (Table 7.6). There was no clear pattern of mean length among blocks (Figures 7.10).

Length frequency distribution of *P.leopardus*

It is evident that the lower mean length at Beaver reef is the result of a high proportion of small (325 mm and 375 mm) size classes of *P.leopardus*, which have recently been recruited to the line fishery, and relatively few large individuals (575 mm or larger) (Figure 7.11). In contrast, Taylor reef has a higher proportion of large *P.leopardus* (with the largest individuals caught during the study caught at Taylor Reef) and fewer individuals in the smaller size classes relative to Beaver Reef (Figure 7.11). As a result the modal size class at Beaver reef (375 mm for all trips) was generally smaller than for Taylor reef, which alternates between the 375 mm and 425 mm size classes (Figure 7.11).

At Farquharson reef, it was apparent that the dramatic reduction in mean length between trip d and trip e was due to the substantial reduction in the proportion of medium (475-525 mm) and large (greater than 575 mm) size classes, with the modal size class being 325 mm in February 1994 (Figure 7.12). This pattern was not evident at Little Potter or Potter Reefs to the same extent, with a modal size class of 375 mm at Little Potter Reef and 375 or 425 mm at Potter Reef for most of trips (Figure 7.12 and 7.13).

7.4 Discussion

The complexity of coral reef fisheries is often cited as one of the main impediments to their effective management (Munro 1983; PDT 1990; Russ 1991). A wide variety of species and trophic groups are harvested with a range of gears and the landed product is distributed through numerous small locations in a variety of forms. In many tropical reef fisheries this makes the collection of reliable catch and effort data extremely problematic (Huntsmen *et al* 1978; Munro 1983; Huntsmen 1987). There are few published accounts of catch statistics from the Great Barrier Reef line fishery (Beinssen 1989 a&b, 1990; Trainor 1991). With the exception of the major target species, several species are generally grouped into common retail marketing categories, such as “Mixed Reef A” which may include several species of lutjanid, lethrinid and serranid (Trainor 1991). This is a common situation in multispecies fisheries, and coral reef fisheries in particular (Munro 1983; PDT 1990), that makes it difficult to estimate the relative contribution of each species to the total catch (Richards 1994) and, therefore, the potential impact of the fishery on the broader reef fish community (Russ 1991). This chapter has presented detailed information on the species composition, CPUE and size distribution of hand-line catches from five reefs over a period of approximately 2 years. The characteristics of catches of reef fish from hand-line fishing and the factors affecting their variation are examined below.

Although a large number of species are caught in tropical reef fisheries, generally a few species dominate the catch by number and weight (Munro 1974,1983; Blanc 1988; Dalzell and Aini 1987; Koslow et al 1988; Beinssen 1989a,1990; Desurmont 1989; Whitelaw et al 1991). In this study a total of 61 species were caught. However, six species accounted for over eighty-five percent of the catch (by number). Catch composition from deep water hand-line fisheries in the Hawaiian and Marina Islands exhibit similar patterns. Polovina (1986b) recorded a total of 30 species during an extensive survey of deep water bottom fish resources of the Marianas Islands. Yet, five species of deep water snapper, *Pristipomoides zonatus*, *P.auricilla P.flavipinnis*, *Etelis* *carbunculus* and *E.coruscans*, collectively comprised 79% (by number) of the total catch of 7,621 fish. In a survey of Johnston Atoll, Ralston *et al* (1986) caught 133 fish of 10 species, of which 58% were two species, *Pristipomoides filamentosus* and *P.zonatus*. Munro (1983b) presented similar results from hand line surveys of the shallow reefs and oceanic banks surrounding Jamaica. A total of 3,478 fish of 52 species were caught from five depth zones ranging from 10 to 250 m. While the relative contribution of the eleven most common species varied between depth zones, generally 5 to 6 species accounted for more than 70 percent of the catch in each zone. These examples and the results from this study illustrate the general pattern that a few high level predators dominate the catches of tropical hand-line fisheries. This suggests that resources for catch monitoring systems and research should be prioritised by identifying and focussing on the dominant species in catch rather than attempting to cover the complete range of species caught in the fishery (Beinssen, 1989a).

The composition and frequency of occurrence of species dominating catches of hand-line fisheries tend to differ among locations within the same fishery. For example, *Plectropomus leopardus* (34%), *Lutjanus adetii* (24%), *Lethrinus miniatus* (12%) and *Epinephelus fasciatus* (13%) dominated the catch during the opening of Boult Reef, in the southern GBR (Beinssen 1989a). In contrast, at Heron Island, only 40 kilometres to the north of Boult Reef, the dominant species were the same, but their relative contribution to the total catch was different: *Lethrinus miniatus* (26%), *Epinephelus fasciatus* (22%), *Plectropomus leopardus* (16%) and *Lutjanus adetii* (13%) (Beinssen 1989 b). Polovina also (1986b) found significant differences in the composition of hand-line catches among the different types of islands and regions of the Marianas Islands. He used cluster analysis to group the 22 locations sampled into clusters based on their catch composition. The resulting three clusters differed in the relative contribution of the five dominant species of deep water snapper. *Pristipomoides flavipinnis* was more common in the southern region, sea mounts had the highest proportion of the 2 *Etelis* species and the northern region was dominated by *P. zonatus* and *P.auricilla*. The pattern among reefs in this study was similar to that found by Beinssen (1989 a&b), with only a few species, about six, dominating the catch at each reef. *Plectropomus leopardus* and *Lethrinus miniatus*, however, were the only dominant species that were common to the two studies. Furthermore, their proportion of the total catch (by number) differed substantially from Beinssen's studies on the southern GBR. This demonstrates that the dominant species and their relative contribution line catches may vary widely among regions within the fishery.

The frequency of occurrence of the six dominant species in this study was found to vary significantly among reefs and trips also. The effect of trip appeared to reflect an increase in the proportion of *P.leopardus* in the catch during September 1992 and October 1993, which coincided with the peak of the spawning season of *P.leopardus*. This is more likely to be the result of an increase in the catchability of *P.leopardus* when fish are aggregated to spawn, rather than a real increase in total population size. Catchability of *P.leopardus* is likely to have increased as a result of the aggregated distribution of fish, in locations which can be efficiently exploited by fishers, and due to an increase in feeding activity of the fish associated with spawning (Johannes and Squire 1988; Samoilys and Squire 1994). Increases in catch rates during the spawning season occur in many fisheries (Pauly and Tsukayama 1987; Colin 1992; Kailola *et al* 1993). This is commonly the result of an increase in catchability due to the change in the distribution and behaviour of the spawning population.

The species composition of the catch was found to vary among reefs also. Potter and Taylor Reefs had a higher proportion of *Cephalopholis cyanostigma* and *Lutjanus bohar* than the other reefs, while Beaver (and to a lesser extent, Little Potter and Farquharson Reefs) had higher percentages of *Lethrinus miniatus*, *L.atkinsoni* and *L.carponotatus*. This could be interpreted as an increase in the proportion of by-catch (*C.cyanostigma* and *L.bohar*) at Taylor and Potter reefs in response to higher fishing pressure on *P.leopardus*. Differences in the species composition of catches among locations have been suggested to be the result of different fishing histories in other tropical reef fisheries (Munro, 1983; Polovina 1986b; Koslow *et al* 1988). This hypothesis is speculative, in this case, in the absence of replication of the "unfished" level. Furthermore, the overall percentage of *C.cyanostigma* appears to vary more over trips than among reefs, with low percentages of *C.cyanostigma* associated with the trips done in the spawning season of *P.leopardus*. It is equally likely that the observed differences in the frequency of occurrence of *C.cyanostigma* and *P.leopardus* among reefs reflect differences in the catchability of *P.leopardus*, rather than real differences in the abundance of the two species. Polovina (1986a) has provided a theoretical framework and empirical example of how interactions between species may influence CPUE and catch composition from a deep water hand-line fishery. Similar interactions between of *P.leopardus* and *C.cyanostigma*, resulting in systematic variation in catchability, could explain the observed pattern in CPUE among reefs and trips. Additional information on the on-site catch dynamics and independent estimates of abundance are required to determine if the relative abundance of other species influences the catchability of primary and secondary target species of hand-line fisheries.

The percentage of *P.leopardus* in the catches during this study was considerably higher than that reported by Beinssen (1989a and b) from the Capricorn Bunker Section of the GBR and by Trainor (1991) for the GBR commercial line fishery (39%, after excluding the pelagic Spanish mackerel, *Scomberomorus commerson*). This highlights the importance of *P.leopardus* in the line fishery, particularly in the northern sectors of the GBR, where it is the most important species targetted by both the commercial and recreational reef fisheries. In contrast, *L.miniatus* which is the second most common species in the GBR commercial line fishery (Trainor, 1991), formed only a small percentage of the total catch from the five reefs in this study. This is due to the restricted distribution of *L.miniatus* on the GBR, where it is found in greatest abundance between Cardwell and Shoalwater Bay (Trainor 1991). The study area was located at the northern extreme of this range.

The available information on catch composition from tropical, hand-line fisheries demonstrates that, although a large number of species are caught, the majority of the catch comprises a few dominant species, and that the composition of these dominant species is likely to vary significantly among regions, locations, reefs and depths. Furthermore, the fact that the dominant species of line fisheries vary considerably among reefs and regions, highlights the need for species level identification of catch, so that species most likely to be affected by the fishery may be identified for future research. Regional variation in species composition will also be important to consider in the interpretation of catch and effort data and the development of management strategies, as primary target species and, therefore the fishing practices of the fishers, may vary considerably among regions (Hilborn and Ledbetter 1979,1985; Hilborn and Walters 1992).

Catch and effort statistics (CPUE) are the most commonly used index of relative abundance or stock size in fisheries stock assessment (Paloheimo and Dickie 1964; Bannerot and Austin 1983; Collie and Sissenwine 1983; Gulland 1988; Hilborn and Walter 1992). The use of CPUE as an index of abundance generally assumes that catch rates are directly proportional to relative stock size. However, there are numerous examples where CPUE has been shown not to be directly proportional to abundance (MacCall 1976; Bannerot and Austin 1983; Winters and Wheeler 1985; Beinssen 1989a; Shardlow 1993). A number of mechanisms have been identified that explain why the relationship between CPUE and abundance should not be directly proportional to abundance. These include, among others, schooling behaviour of the fish, on-site catch dynamics (Gulland 1964; Cook and Beddington 1985; Hilborn and Walters 1992), weather and sea conditions (Richards and Schnute 1986) and fleet dynamics (Hilborn and Ledbetter 1979,1985). In multispecies fisheries such as tropical reef fisheries, interactions among species and shifts in targeting by fishers will also affect the relationship between CPUE and relative stock size (Polovina 1986a; Richards 1994).

Despite these well known limitations, CPUE is still the only index of abundance used in many fisheries stock assessments (Hilborn and Walters 1992). This is largely due to a lack of alternative techniques which may be routinely used to estimate abundance. Underwater fish counts by divers on SCUBA is the most widely used alternative for reef fish populations (*eg* Bell

1983; Russ 1985, 1989; McCormick and Choat 1987; Russ and Alcala 1989; Alcala and Russ, 1990; Cole *et al* 1990; Polunin and Roberts, 1993, 1994). However, routine fish counts on SCUBA are limited to less than 15 m depth. Consequently, large proportion of reef fish stocks are not able to be effectively surveyed with visual census techniques.

Manned submersibles have been used to overcome the depth limitations of SCUBA to assess reef fish stocks in deeper reef waters (Colin 1974; Uzmann *et al* 1977; Parker and Ross 1986; Ralston *et al* 1986; Richards and Schnute 1986; Matlock *et al* 1991). However, the amount of submersible time required to provide sufficiently precise estimates of density from routine surveys is likely to be prohibitive (Richards and Schnute 1986). Furthermore, fish counts from submersibles are subject to the same biases as underwater visual surveys on SCUBA, such as underestimation of numbers of individuals and species (Sale and Douglas 1981; Parker and Ross 1985) and behavioural responses of fish to the diver/submersible which may bias estimates of density (Ralston et al 1986). Hence, while submersibles may be useful to examine the relationship between CPUE and estimated density, CPUE from the fishery or from surveys, is likely to remain the most widely used index of abundance for reef fish stocks at depths below routine SCUBA limits (Richards and Schnute 1986). Studies of the mechanistic relationship between CPUE and visually estimated density should, therefore, be a priority (Richards and Schnute 1986; Hilborn and Walters 1992).

The CPUE data for *P.leopardus* collected in this study have provided some valuable information on factors affecting the variation in catch rates from hand-line fishing among trips and reefs. Catch per unit effort of *P.leopardus* varied significantly among trips and blocks within reefs but not among reefs. The significant effect of trip, associated with trips done during the spawning season of *P.leopardus*, demonstrates that CPUE may vary considerably within years. The higher CPUE during the spawning season is likely to be the result of an increase in catchability which is a common feature in fisheries where spawning aggregations are targeted (*eg* Francis 1992), and has been documented for other *Plectropomus* species and large epinephiline groupers which aggregate to spawn (Johannes 1981; 1988; Shapiro 1987; Johannes and Squire 1988; Colin 1992). This has important implications for the use of aggregate (annual) catch and effort data from the fishery. Targeting of aggregations by fishermen, during the spawning season, may result in annual CPUE remaining high even though the total stock size is declining. Such a relationship between CPUE and abundance, known as *hyperstability*, is common in fisheries where spawning aggregations are targeted (Hilborn and Walters 1992). The significant temporal variation in CPUE found in this study and the widespread occurrence of spawning aggregations in many species of reef fish suggest that the use of annual aggregate CPUE data for stock assessment of reef fish populations may be misleading and therefore inappropriate.

In contrast to the substantial variation in CPUE among trips, CPUE of *P.leopardus* did not vary significantly among reefs in this study, even though one of the reefs (Beaver) had been closed to fishing for eight years. Although CPUE was generally higher on Beaver Reef, the difference was not significant and the proportion of variation explained by reef in the ANOVA was small (0.05%), especially in comparison to the temporal variation due to trip (8.42%). This suggests there is little difference in the relative abundance of *P.leopardus* among the five reefs. This is supported by estimates of density of *P.leopardus* from visual census for Beaver and Potter Reef, made just prior to the first tagging exercise (trip a), which did not detect a significant difference in the mean density of *P.leopardus* between the two reefs (Ayling and Ayling, 1992).

The significant effect of block and the interaction between trip and block indicates that CPUE of *P.leopardus* varies significantly within reefs and this effect varies over time. This highlights the need to stratify sampling programmes among the various temporal scales which are likely to influence CPUE (*eg.* tidal state, lunar cycle and season) as well as spatial scales within reefs (*eg.* front /back, deep/shallow). For example, experience gained from the commercial fishers over the course of this project suggests that fishing the different sides of a reef when the tide is running on to the reef (see 7.2.3) may result in a significantly higher CPUE relative to the "run off" tide in the same location. This effect is likely to be the result of temporal variation in the catchability of *P.leopardus*, possibly related to feeding behaviour, and the fishing practices of the fishermen, rather than variation in actual abundance. However, the important point is that by stratifying the sampling temporally, as well as spatially, it may be possible to remove a large part of the variation from estimates of relative abundance. This will apply equally to alternative sampling methods such as traps and UVC techniques.

The results of the CPUE analysis demonstrate that CPUE of *P.leopardus* varied significantly among trips and blocks within reefs. However, how accurately CPUE from line fishing reflects actual abundance is not clear. There is considerable evidence to suggest that the relationship should not be expected to be one of direct proportion (MacCall 1976; Bannerot and Austin 1983; Winters and Wheeler 1985; Beinssen 1989a; Shardlow 1993). However, there have been few studies of the relationship between CPUE, catchability and abundance for reef line fisheries.

Polovina (1986) suggested that catchability was directly proportional to abundance for two species of deep-water snapper but inversely proportional to the abundance of the dominant species for a less common species. However, he did not have an independent estimate of abundance with which to directly compare his estimates of population size from the depletion exercise. Beinssen (1989a) found CPUE to be nonlinearly related to abundance in a depletion experiment done at Boult Reef in the southern Great Barrier Reef. He suggested that the pattern of declining CPUE was related to the fraction of the population which was in "feeding phase" being removed, rather than the total population. Hence, the population estimate from the depletion experiment was an estimate of the feeding population. A second study by Beinssen (1989b) demonstrated that catchability of *P.leopardus* was considerably higher in an area protected from fishing compared to an adjacent area in which fishing was permitted. The difference in catchability was found to increase with fishing effort.

There is considerable evidence that catchability varies over space and time and with exposure to fishing effort. Therefore, it seems unlikely that CPUE from line fishing will be directly proportional to abundance. This is not to say that CPUE may not be a useful index of abundance. It has many advantages over visual surveys (possible to survey all depths; catch available for age/sex structure *etc*) and the potential biases associated with spatial and temporal variation in catchability ("*sightability*") apply equally to visual census techniques. The effects of time of the day, tidal state or visability conditions on estimates of abundance from visual surveys and how they interact with true abundance have rarely (Sale and Douglas 1981) been quantified for visual surveys but are real sources of potential bias. A more thorough understanding of the relationship between CPUE from line fishing and abundance and its power to detect changes in abundance due to fishing pressure is required if it is to be used with confidence to monitor the status of reef fish stocks (Bannerot and Austin 1983; Richards and Schnute 1986; Walters and Hilborn 1992; Shardlow 1993). This would best be achieved through studies in which the power of available sampling techniques (underwater fish counts, fish traps, line fishing, video techniques) to detect a known change in abundance is compared over a range of abundances and detailed examination of the mechanics of the capture process of the different sampling gears (*eg* Shardlow 1993). In addition, a thorough understanding of the on-site catch processes and fleet dynamics of the fishery will be essential to relate the results of these studies to the analysis of catch and effort statistics from the fishery (Hilborn and Ledbetter 1979, 1985; Hilborn and Walters 1987, 1992).

The mean length of *P.leopardus* decreased monotonically over the course of this study. This decline was particularly evident at Farquharson Reef on the final trip, where large reductions in the proportion of fish in the larger size classes resulted in a 40 mm decrease in mean length. In the absence of size-at-age data and replicated unfished reefs, it is not possible to determine whether this effect is the result of fishing or the influence of a strong cohort entering, or leaving, the population. The high individual variability in growth rates (Ferreira and Russ 1994; Chapter 4 this study) and longevity of *P.leopardus*(Ferreira and Russ 1994) suggests that the relative proportion of cohorts in the population are not likely to be evident from length frequency distributions from catch data (Ferreira and Russ in press; Russ et al 1995). This stresses the essential nature of age-structured data in stock assessment.

The interpretation of the observed pattern is further complicated by the fact that the effect is equally evident for Beaver Reef, which is theoretically unfished (but see Chapter 8), as it is for the other open reefs and that the mean length of *P.leopardus* on Beaver Reef was significantly lower than the other reefs. A higher level of recruitment at Beaver Reef would explain the higher proportion of *P.leopardus* in the smaller size classes and a high level of infringement may explain the low proportion of fish in the larger size classes. However, a higher level of recruitment to Beaver Reef would be contrary to current theory relating the protection status of the reef (Closed/Open to fishing) to the relative level of recruitment it receives. There is evidence to suggest that the level of recruitment of 0+ *P.leopardus* is higher on reefs that are open to fishing than on reefs which are closed to fishing (Ayling *et al* 1991). The length frequency data indicates that the proportion of individuals in the 350-400 mm size class, considered to be fully recruited to the fishery, is generally greater on Beaver Reef. However, the causes of the observed patterns in size structure of *P.leopardus* will only be resolved with the availability of age-structure information at each reef over time and replication of "unfished" reefs.

Variation in size and age structure within reefs has important implications for the design of sampling programmes which aim to obtain representative samples of population structure. If there is significant variation in the size, age or sex structure within a reef it will be necessary to stratify the sampling accordingly. The significant effect of block and the interaction between trip and block for the mean length of *P.leopardus* demonstrates that mean size differs among blocks within reefs and that these differences may not be constant over time. This implies that samples taken from different locations within a reef at different times may provide significantly different estimates of mean size and size structure, even when there may have been no change in the overall size structure of the population on the reef. This emphasises the need for sampling programmes to include within-reef stratification in order to obtain representative estimates of population structures for individual reefs.

This chapter has examined the factors affecting catches of reef fish from five reefs on five occasions over a two year period. The dominance of a few species of high level predator appears to be a common feature of catches in tropical line fisheries. This suggests the impact of fishing will be most direct on these species and research should be focussed on obtaining a comprehensive understanding of their population dynamics and how they respond to fishing pressure, rather than spreading the same research effort over the entire range of species which occur in the catch. The significant temporal and spatial variation in CPUE and size of

P. leopardus within and among reefs highlights the natural levels of variability present in tropical reef fish stocks. The results of this chapter suggest that sampling studies which include within-reef and within-year strata will be required to identify the mechanisms responsible for the observed patterns in population structure. The value of such sampling studies to the management of the fisheries would be enhanced considerably if they are coupled with studies of the fleet dynamics of the fishery and how the distribution of fishing effort relates to catch rates and abundance.

Table 7.1: Starting date, duration, number of dories and tidal state for each research sampling trip.

Trip	Commenced	Duration (d)	No. Dories	Tide
a	1 April 1992	10	10	neap
b	23 September 1992	6	8	spring
c	16 April 1993	6	8	spring
d	22 October 1993	6	6	spring
e	9 February 1994	6	6	spring

Table 7.2: Distribution of sampling effort (n = number of "hangs") among trips, reefs and blocks (back reef blocks (B) and front reef blocks (F)). Trips are April 1992 (a), September 1992 (b), April 1993 (c), October 1993 (d), February 1994 (e). Block numbers correspond to those given in Figure 7.2.

		a	b	c	d	e
Reef	**blk**	**n**	**n**	**n**	**n**	**n**
Beaver	1B	28	18	41	5	29
	2F	25	21	8	16	13
	3F	45	18	24	22	37
	4B	55	18	9	14	55
	5B	26	20	10	-	-
	6B	47	16	45	21	14
	Reef	226	111	137	78	148
Taylor	1B	34	18	46	19	17
	2B	59	21	27	20	13
	3B	52	27	17	9	68
	4F	-	17	-	20	38
	5F	-	8	-	8	-
	6F	-	19	-	9	-
	Reef	145	110	90	85	136
Farquharson	1B	53	13	16	20	20
	2B	-	23	-	17	22
	3B	-	23	-	11	-
	4F	-	3	-	9	-
	5F	-	3	-	14	-
	6F	-	3	-	11	-
	7F	-	25	-	11	-
	8B	71	17	-	23	4
	9B	78	11	8	30	23
	Reef	202	121	24	146	69
Little Potter	1B	73	54	-	40	63
	2F	-	41	-	37	36
	Reef	73	95	-	77	99
Potter	1B	43	26	25	12	-
	2B	102	31	34	22	23
	3B	62	38	25	21	51
	4F	-	6	-	28	25
	5F	-	22	-	12	-
	6F	-	16	-	11	-
	Reef	207	139	84	106	99

Table 7.3: Response profiles of dominant taxa by trip from contingency table analysis: April (a) and September (b) 1992, April (c) and October (d) 1993 and February (e) 1994. Data are proportion of catch by numbers.

Species	a	b	c	d	e	All
Cephelopholis cyanostigma	0.1332	0.0735	0.1548	0.0942	0.1498	0.1181
Plectropomus leopardus	0.5407	0.6300	0.5423	0.6140	0.5009	0.5671
Lutjanus bohar	0.0273	0.0359	0.0278	0.0235	0.0303	0.0291
L.carponotatus	0.0560	0.0405	0.0624	0.0638	0.0749	0.0587
Lethrinus atkinsoni	0.0426	0.0393	0.0290	0.0211	0.0681	0.0412
L.miniatus	0.0389	0.0479	0.0323	0.0347	0.0062	0.0327
Others	0.1614	0.1328	0.1514	0.1487	0.1697	0.1532
Total	2162	1754	898	1614	1615	8043

Table 7.4: Response profiles of catch composition by reef from contingency table analysis: Beaver (b), Farquharson (f), Little Potter (lp), Potter (p) and Taylor (t). Data are proportion of catch by numbers.

Species	b	f	lp	p	t	All
Cephelopholis cyanostigma	0.0823	0.1133	0.1203	0.1419	0.1489	0.1181
Plectropomus leopardus	0.5642	0.5762	0.6086	0.5529	0.5506	0.5671
Lutjanus bohar	0.0239	0.0392	0.0204	0.0309	0.0298	0.0291
L.carponotatus	0.0827	0.0597	0.0612	0.0392	0.0417	0.0587
Lethrinus atkinsoni	0.0584	0.0342	0.0387	0.0392	0.0265	0.0412
L.miniatus	0.0496	0.0355	0.0418	0.0196	0.0132	0.0327
Others	0.1389	0.1419	0.1091	0.1764	0.1893	0.1532
Total	2260	1607	981	1684	1511	8043

Table 7.5: Results of 3-way mixed model ANOVA for effect of trip, reef and block on mean CPUE of *P.leopardus*. Includes data from back reef blocks of Beaver, Taylor, Farquharson and Potter Reefs and trips a, b, d, e only (see text). $\alpha = 0.05$, data were $\log_{10}(x+1)$ transformed.

Source	DF	Type III SS	MS	F ratio	Pr>F	Sign.	% var
Corrected total	1470	1614.86					
TRIP	3	136.00	45.33	27.94	0.0001	***	8.42
REEF	3	0.95	0.31	0.13	0.9412		0.05
BLOCK(REEF)	8	19.78	2.47	2.53	0.0097	***	1.22
TRIP*REEF	9	10.95	1.22	0.75	0.6615		0.68
TRIP*BLOCK(REEF)	23	37.31	1.62	1.66	0.0253	*	2.30
Residual	1424	1388.94	0.98				85.98

Table 7.6: Results of 3-way mixed model ANOVA for effect of trip, reef and block on the mean length to caudal fork of *P.leopardus*. Includes data from back reef blocks of Beaver, Taylor, Farquharson and Potter Reefs and trips a, b, d, e only (see text). Data were untransformed, $\alpha = 0.05$.

Source	DF	Type III SS	MS	F ratio	Pr>F	Sign.	% var
Corrected total	2276	11180341.25					
TRIP	3	114682.82	38227.61	5.17	0.0070	**	1.03
REEF	3	209492.92	69830.97	5.44	0.0247	*	1.87
BLOCK(REEF)	8	102720.73	12840.09	2.82	0.0041	**	0.92
TRIP*REEF	9	98975.55	10997.28	1.49	0.2108	ns	0.09
TRIP*BLOCK(REEF)	23	169938.27	7388.62	1.62	0.0311	*	1.90
Residual	2230	10155975.26	4554.25				90.84

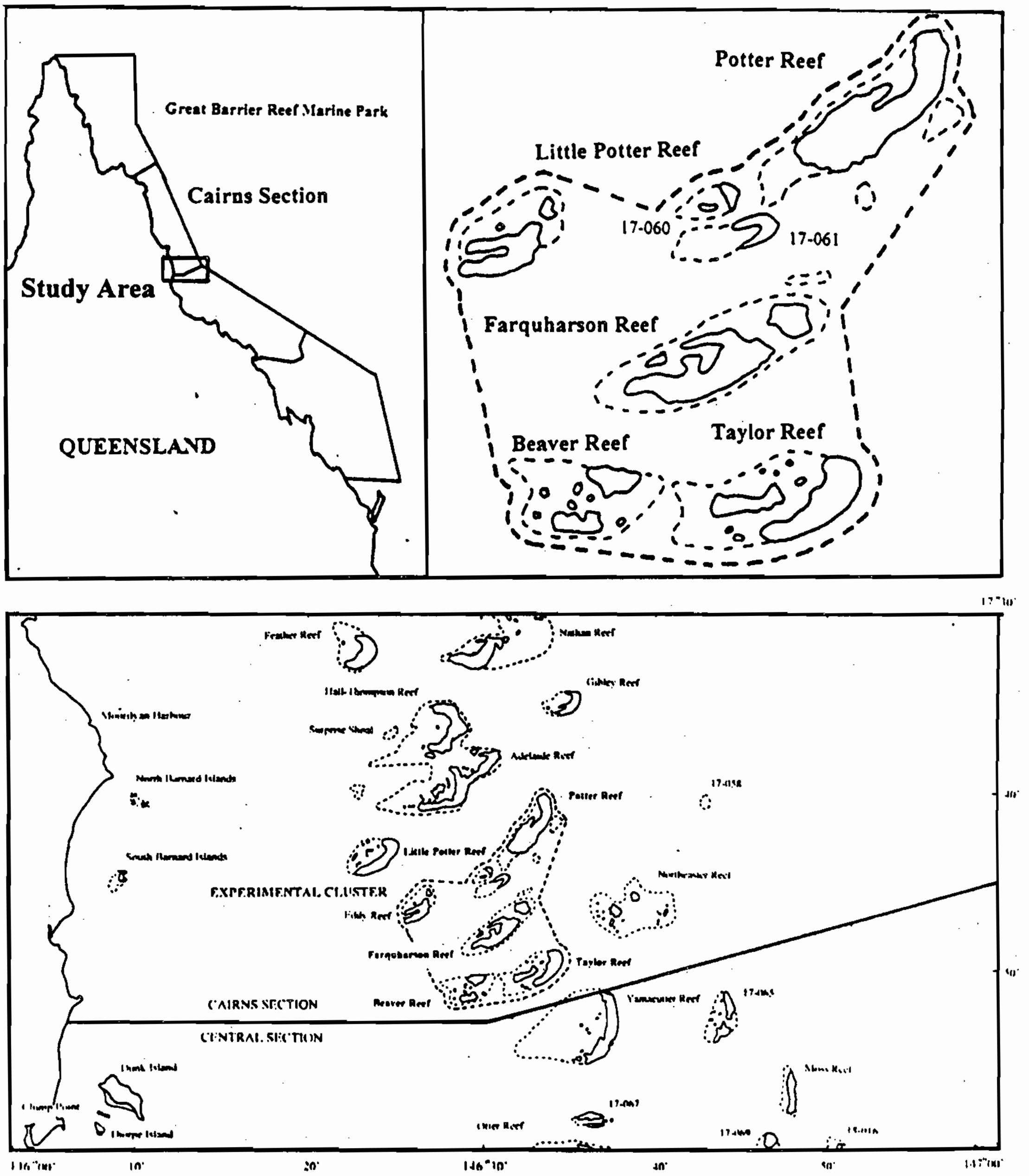

Figure 7.1: Location of study area and study reefs for the large-scale movement study on the Great Barrier Reef.

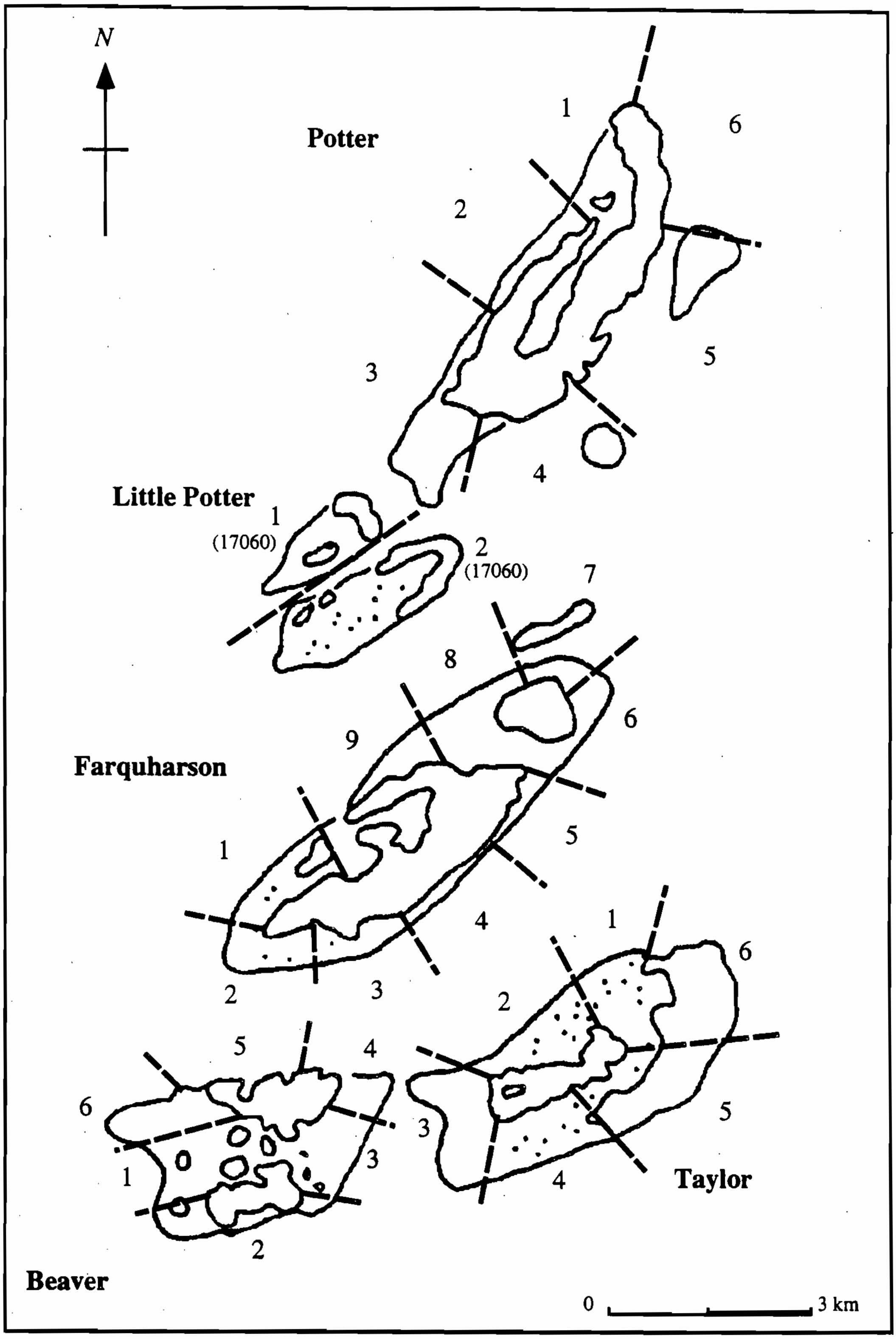

Figure 7.2: Location of sampling blocks within each reef of the study area for the large-scale movement study.

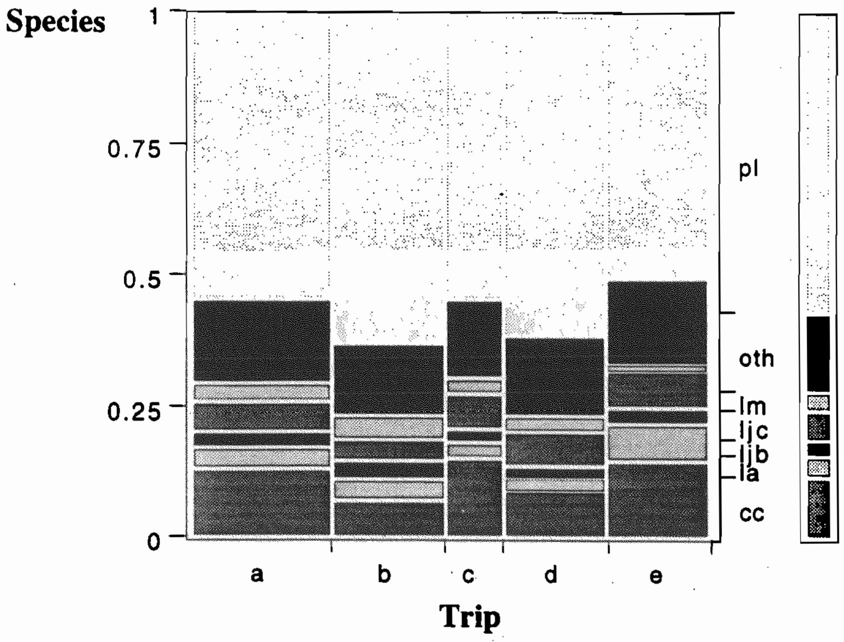

Figure 7.3: Mosaic plot of species compositon of catch by trip. The species are *Cephalopholis cyanostigma* (cc), *Plectropomus leopardus* (pl), *Lutjanus bohar* (ljb), *L.carponotatus* (ljc), *Lethrinus atkinsoni* (la), *L.miniatus* (lm), and Others (oth). Trips are April 1992 (a), September 1992 (b), April 1993 (c), October 1993 (d) and February 1994 (e).

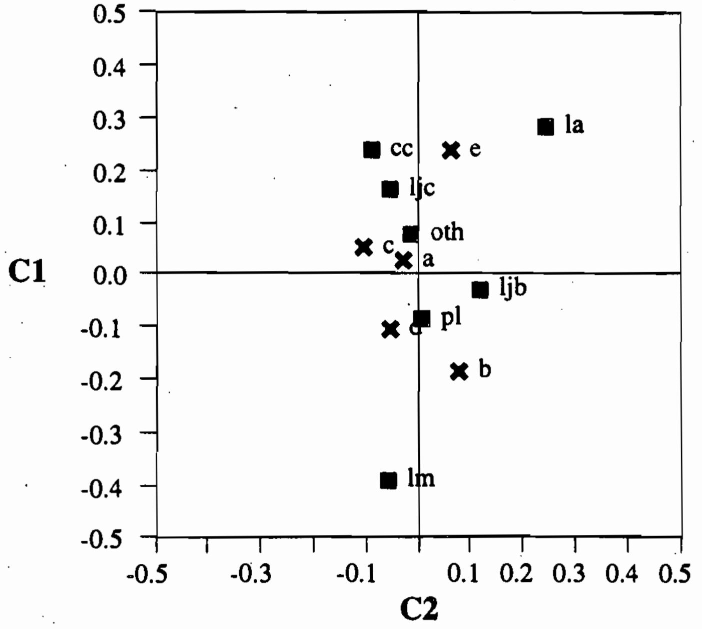

Figure 7.4: Correspondence analysis of species compositon of catch by trip. The first two axes accounted for 90.2% of the total inertia, C1 (75.8%) and C2 (14.4%). The species are *Cephalopholis cyanostigma* (cc), *Plectropomus leopardus* (pl), *Lutjanus bohar* (ljb), *L.carponotatus* (ljc), *Lethrinus atkinsoni* (la), *L.miniatus* (lm), and Others (oth). Trips are April 1992(a), September 1992 (b), April 1993 (c), October 1993 (d) and February 1994 (e).

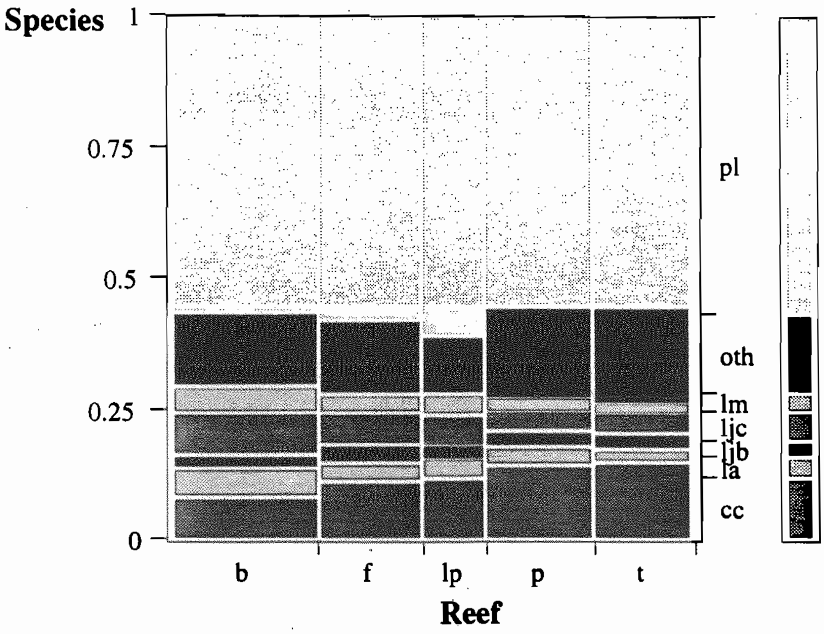

Figure 7.5: Mosaic plot of species compositon of catch by reef. The species are *Cephalopholis cyanostigma* (cc), *Plectropomus leopardus* (pl), *Lutjanus bohar* (ljb), *L.carponotatus* (ljc), *Lethrinus atkinsoni* (la), *L.miniatus* (lm), and Others (oth). Reefs are Beaver (b), Taylor (t), Farquharson (f), Little Potter (lp) and Potter (p) Reefs.

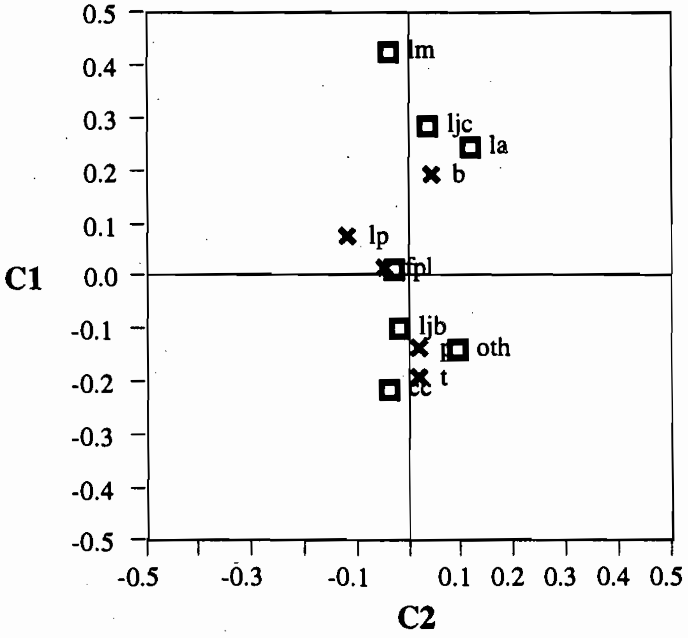

Figure 7.6: Correspondence analysis of species compositon of catch by reef. The first two axis accounted for 90.2% of the total inertia, C1 (75.8%) and C2 (14.4%). The species are *Cephalopholis cyanostigma* (cc), *Plectropomus leopardus* (pl), *Lutjanus bohar* (ljb), *L.carponotatus* (ljc), *Lethrinus atkinsoni* (la), *L.miniatus* (lm), and Others (oth). Reefs are Beaver (b), Taylor (t), Farquharson (f), Little Potter (lp) and Potter (p) Reefs.

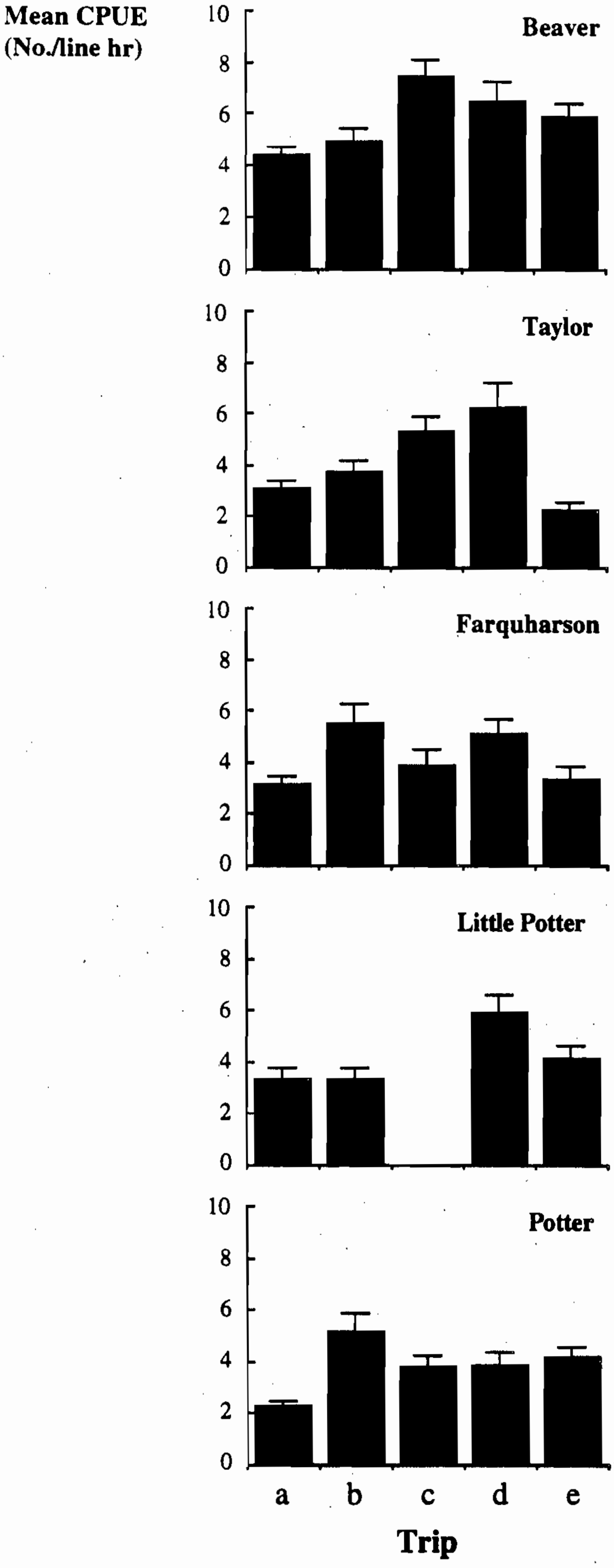

Figure 7.7: Mean CPUE (No./line hr) for *Plectropomus leopardus* by reef and trip for the large-scale study. Trips are April 1992 (a), September 1992(b), April 1993 (c), October 1993 (d) and February 1994 (e). Data from April 1993 (c) were not included in ANOVA for CPUE (see text). Data are untransformed. Error bars are standard errors. Sample sizes are given in Appendix 2a.

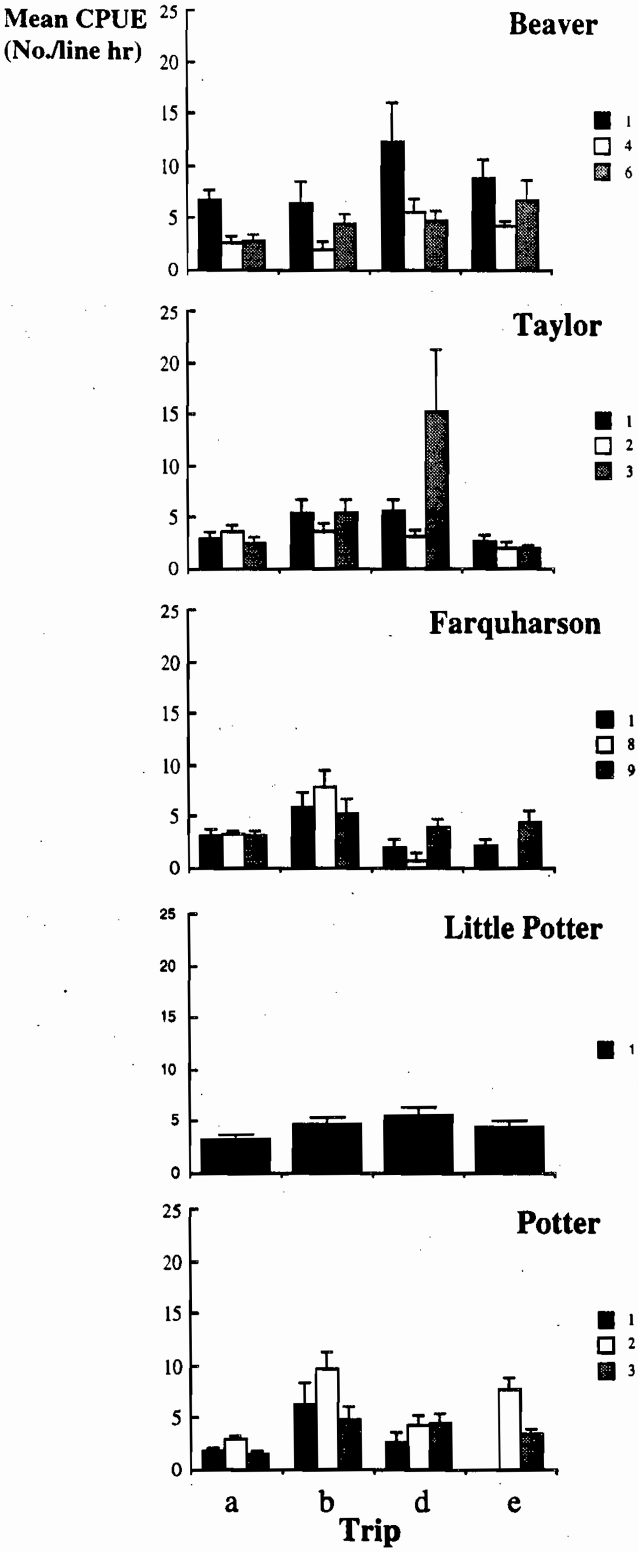

Figure 7.8: Mean CPUE (No./line hr) for *Plectropomus leopardus* by trip, reef and block, for back reef blocks only from the large-scale study. Block numbers correspond to those in Figure 7.2. Trips are April 1992 (a), September 1992 (b), October 1993 (d) and February 1994 (e). Data from April 1993 (c) were not included in ANOVA for CPUE (see text). Data are untransformed. Error bars are standard errors. Sample sizes are given in appendix 2a.

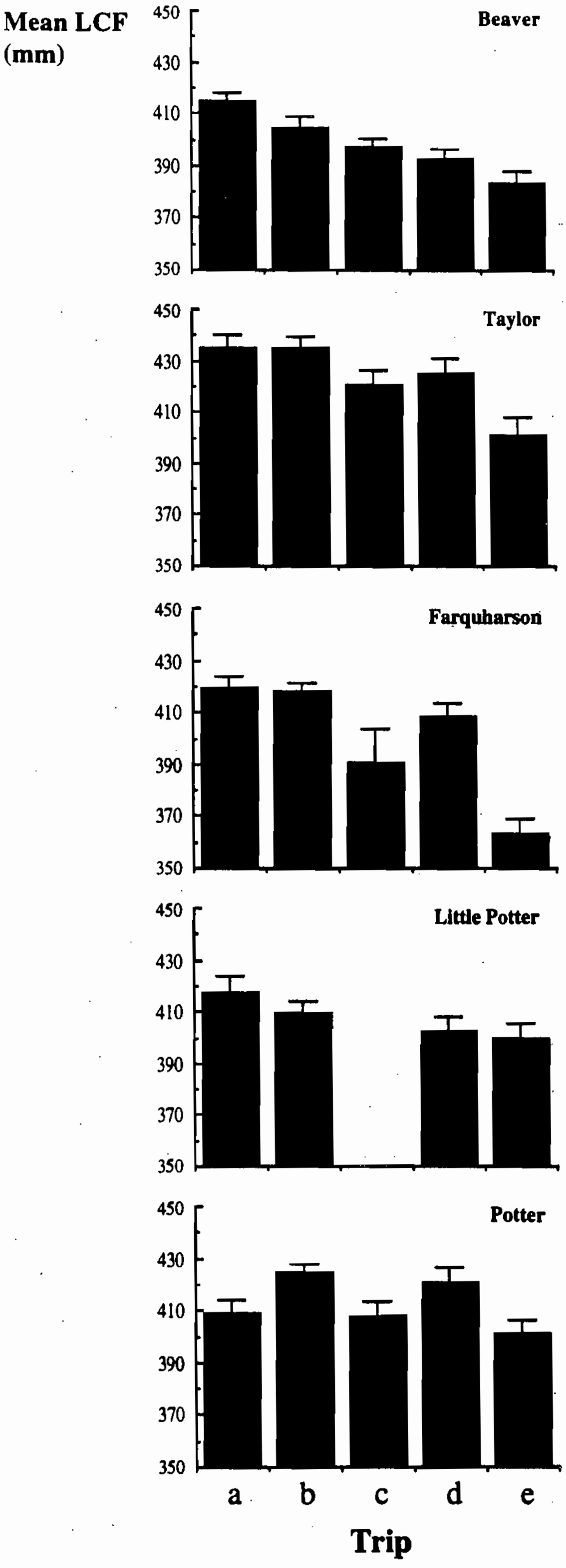

Figure 7.9: Mean length to caudal fork (mm) for *Plectropomus leopardus* by trip and reef for the large-scale study. Trips are April 1992 (a), September 1992 (b), October 1993 (d) and February 1994 (e). Data from April 1993 (c) were not included in ANOVA for mean size (see text). Error bars are standard errors. Sample sizes are given in Appendix 2b.

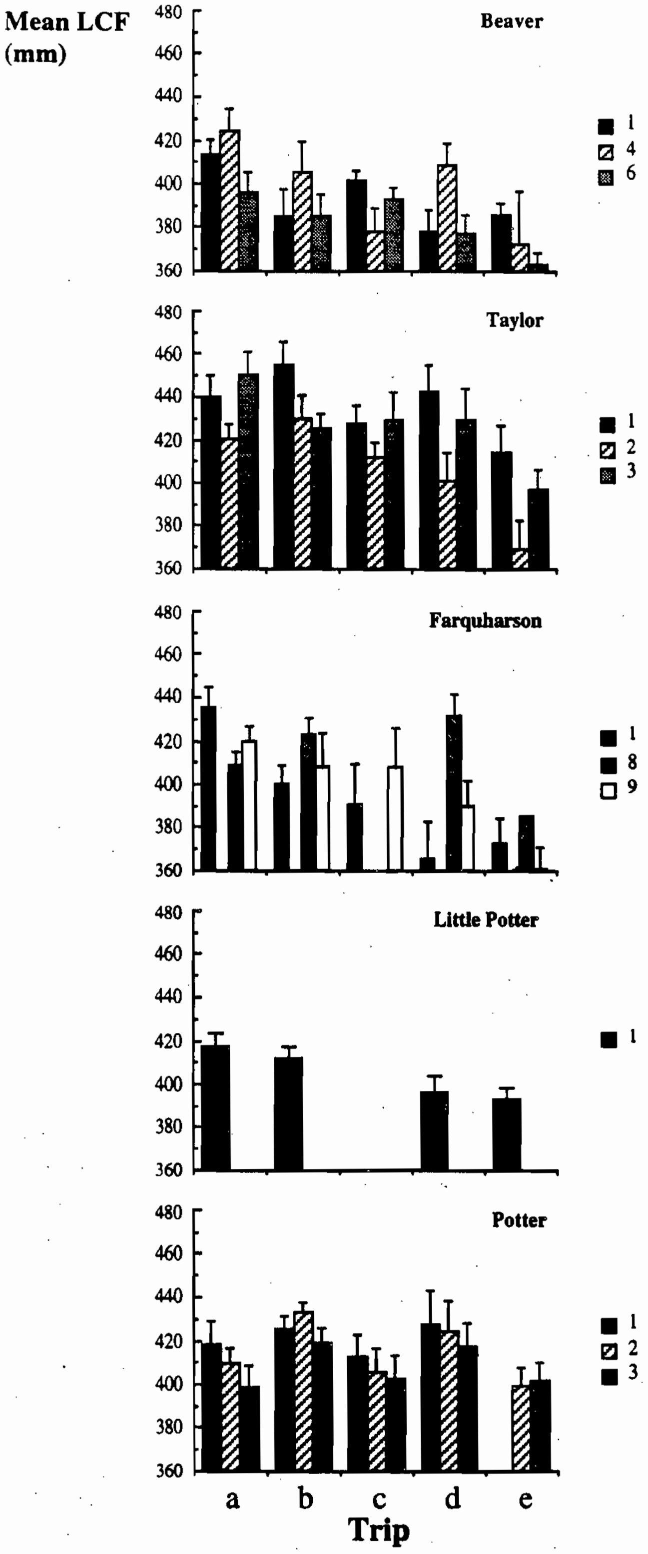

Figure 7.10: Mean length to caudal fork (mm) for *Plectropomus leopardus* by trip, reef and block for the large-scale study. Only those blocks used in the ANOVA of mean length are presented(see text). Block numbers correspond to those in Figure 7.2. Trips are April 1992 (a), September 1992 (b), October 1993 (d) and February 1994 (e). Data from April 1993 (c) were not included in ANOVA for mean length (see text). Error bars are standard errors. Sample sizes are given in appendix 2b.

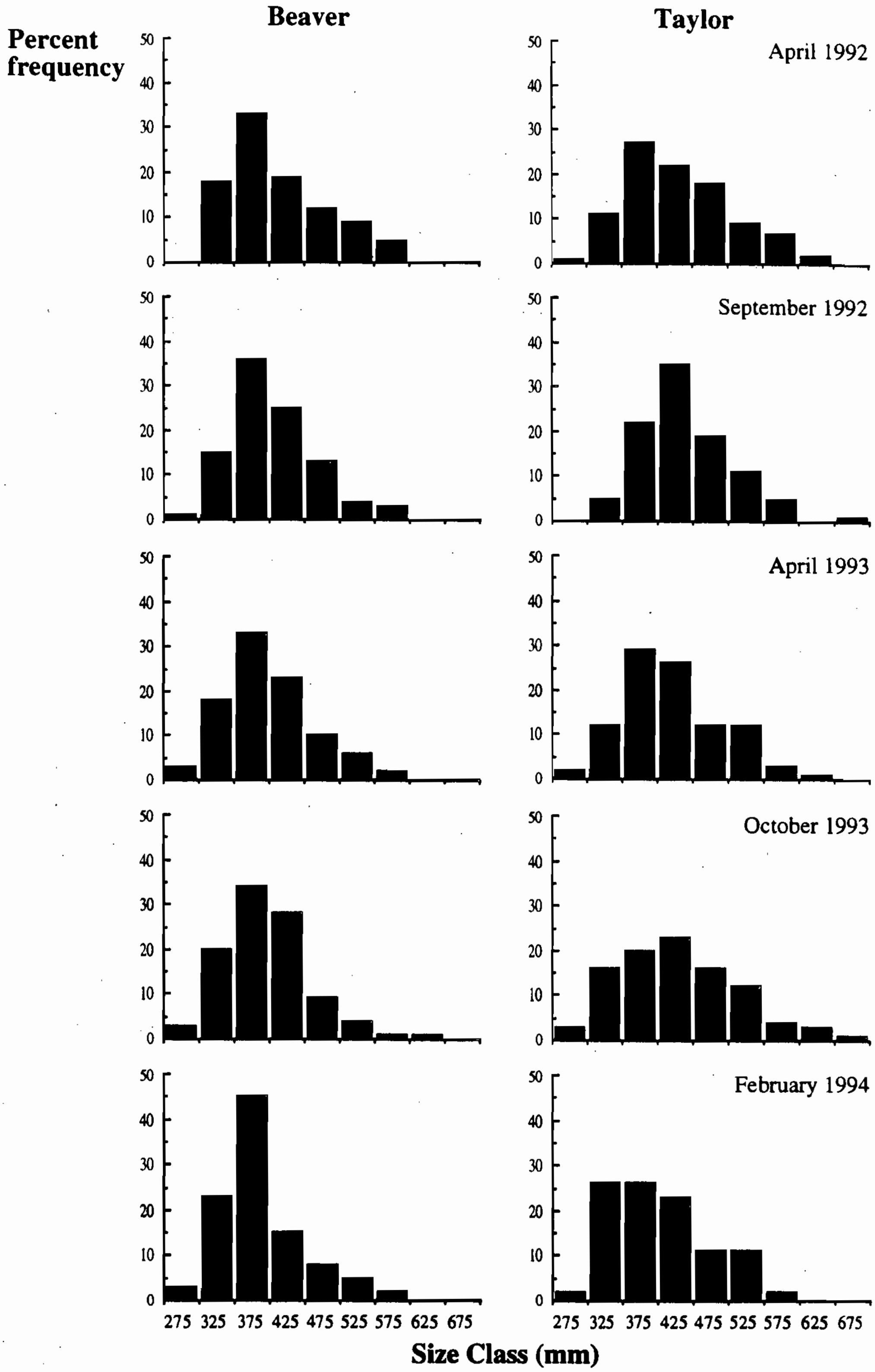

Figure 7.11: Length (LCF) frequency distributions for *Plectropomus leopardus* at Beaver and Taylor Reefs by trip (all blocks) from the large-scale study. Size classes are 50 mm. The mid-point of each size class is given. Trips are April 1992 (a), September 1992 (b), April 1993 (c), October 1993 (d) and February 1994 (e). Sample sizes are given in Appendix 2b. Data from April 1993 (c) were not included in ANOVA for mean length (see text).

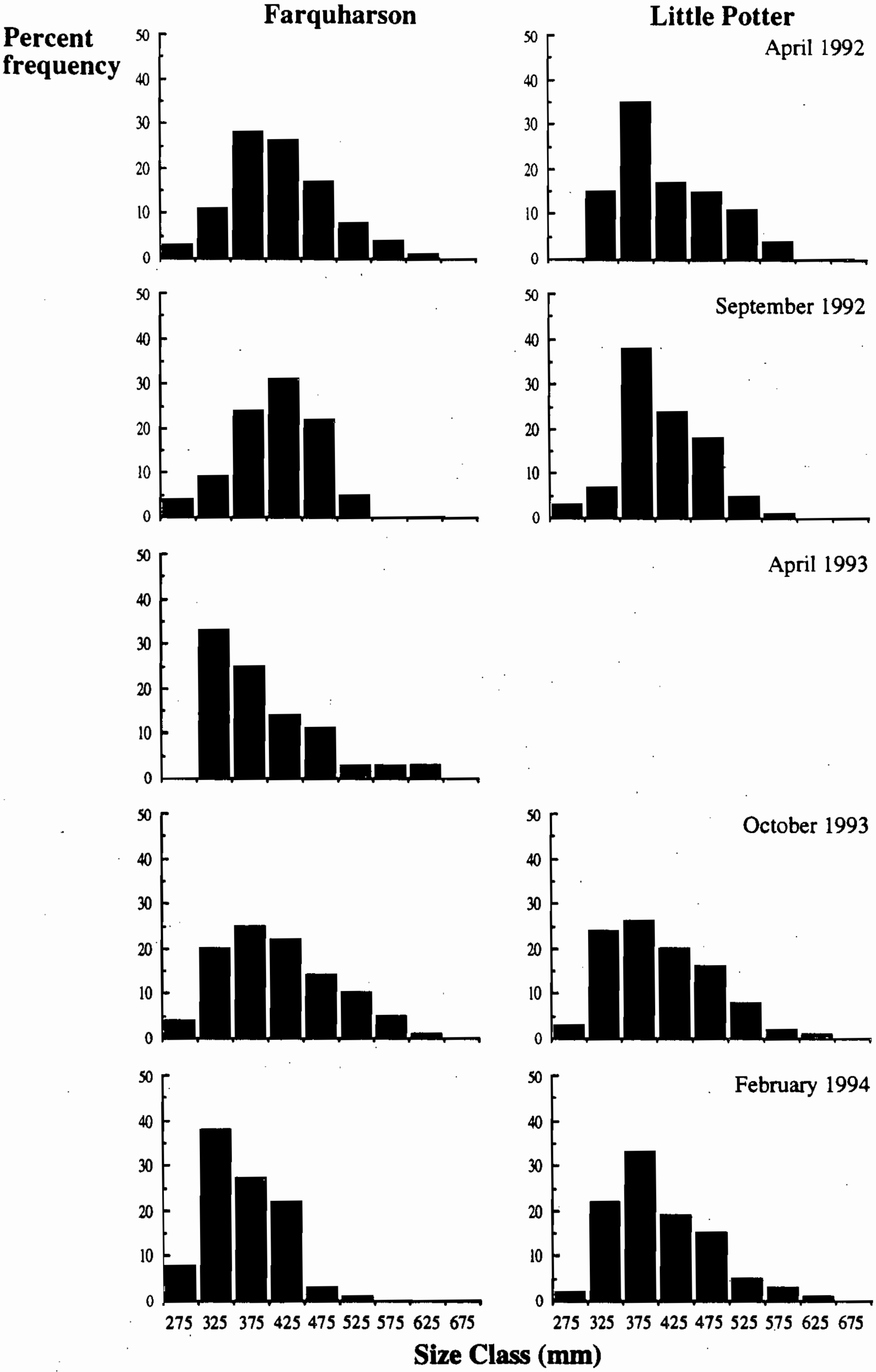

Figure 7.12: Length (LCF) frequency distributions for *Plectropomus leopardus* at Farquharson and Little Potter Reefs by trip (all blocks)from the large-scale study. Size classes are 50 mm. The mid-point of each size class is given. Trips are April 1992 (a), September 1992 (b), April 1993 (c), October 1993 (d) and February 1994 (e). Sample sizes are given in Appendix 2b. Data from April 1993 (c) were not included in ANOVA for mean length (see text).

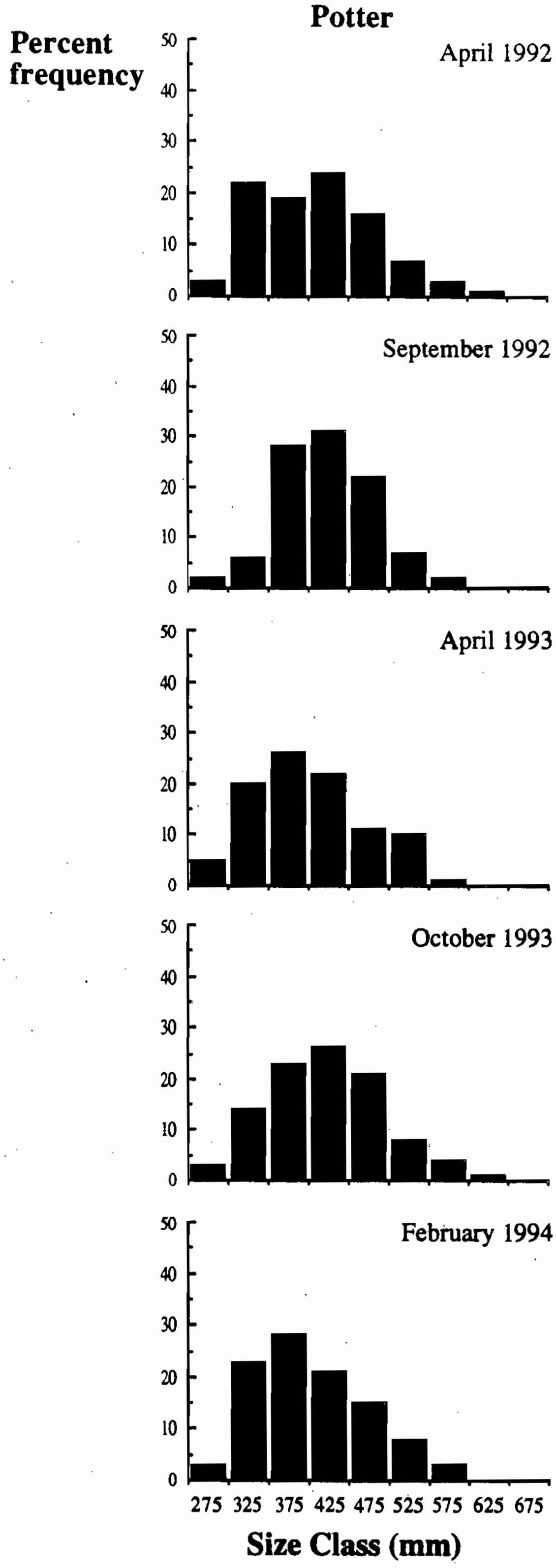

Figure 7.13: Length (LCF) frequency distributions for *Plectropomus leopardus* at Potter Reef by trip (all blocks) from the large-scale study. Size classes are 50 mm. The mid-point of each size class is given. Trips are April 1992 (a), September 1992 (b), April 1993 (c), October 1993 (d) and February 1994 (e). Sample sizes are given in Appendix 2b. Data from April 1993 (c) were not included in ANOVA for mean length (see text).

Chapter 8

Large-scale patterns of movement of *Plectropomus leopardus* within and among coral reefs on the Great Barrier Reef

8.1 Introduction

The use of permanent spatial closures, or Marine Fisheries Reserves (MFR), as a management technique for coral reef fisheries has recently received substantial attention (Davis 1989; Alcala and Russ 1990; PDT 1990; Roberts and Polunin 1991,1993; DeMartini 1993; Dugan and Davis 1993a; Russ *et al* 1993). Marine refugia have often been invoked when more conventional techniques, such as effort or gear restrictions, have failed to achieve the desired management objectives, particularly in regions where the fisheries are subject to intense and unmanageable fishing pressure (*eg* Alcala and Russ 1990; PDT 1990). In other cases, such as the Great Barrier Reef Marine Park (GBRMPA), Australia, fisheries refugia have been used to separate potentially conflicting uses of the coral reef environment and its limited resources (*eg*. extractive and non-extractive activities such as fishing and SCUBA diving, respectively). Furthermore, the relative ease with which spatial boundaries may be defined in coral reef systems and their apparent isolation from each other, has prompted several authors to suggest that individual coral reefs may be ideal experimental units for manipulative experiments to investigate the effects of fishing on fish communities (Walters and Hilborn 1976, 1978; Walters 1986; Sainsbury 1988; Russ 1991; Hilborn and Walters 1992; Williams and Russ 1994).

A fundamental assumption underlying the use of spatial closures to fishing as a management technique is that there is limited exchange among individual spatial strata, in this case individual coral reefs (Walters and Sainsbury 1990; Polacheck 1990; Caddy 1993; DeMartini 1993; Russ *et al* 1993). There are two potential sources of exchange among spatial strata; larval dispersal, and immigration or emigration of post-settlement fishes. A large proportion of reef fish produce planktonic larvae which spend protracted periods in the plankton (Ehrlich 1975; Doherty and Williams 1988; Doherty 1991). In the light of the common perception of coral reef fish as sedentary animals, whose movements may generally be measured in the order of 10's to 100's of meters (Roberts and Polunin 1991; Sale 1991), this suggests that individual reefs may act as local sub-populations of the stock (Carr and Reed 1993). As such, MFR may be a particularly suitable management strategy for reef fish because of the potential for protected populations enhance production outside the reserve through the supply of recruits (Davis 1989; PDT 1990; Fairweather 1991; Roberts and Polunin 1991; Russ 1991; DeMartini 1993; Russ *et al* 1993). The degree of movement between spatial strata (fished/unfished) is an important consideration in the design of effective MFR for two reasons. Firstly, movement of individuals from MFR to fished areas may directly enhance fisheries production as these individuals will have been protected from fishing for some period of their lives and, therefore, theoretically have grown to a larger size before being harvested. Under certain conditions this "leakage" from the MFR to the fished area may result in an overall increase in yield per recruit (Y/R), although simulation studies suggest the magnitude of the increase is likely to be small (Polacheck 1990; DeMartini 1993; Russ *et al* 1993). More importantly, the effectiveness of MFR to protect the spawning stock of a species will largely depend on the extent of movement of the species in relation to the size of the MFR. If the level of movement across reserve boundaries is high, or there is compensatory emigration between the MFR and the fished area(s) the effectiveness of the MFR to enhance spawning stock biomass per recruit (SSB/R) may be compromised (DeMartini 1993). Clearly, the extent of movement of exploited species among spatial strata is an important consideration in the design of MFR.

There is relatively little quantitative information available on the degree to which species of reef fish commonly targeted by fisheries move between individual coral reefs (PDT 1990; Roberts and Polunin 1991; DeMartini 1993; Dugan and Davis 1993b). A general feature of previous studies of movement of reef fish has been that releases have been concentrated at few point locations, the distribution of recapture effort is often unknown and the majority of the returns are recaptured shortly after release by the public in close proximity to the release site (Moe 1966; Beaumariage 1969; Fable 1980; Holt and Arnold 1982; Buxton and Allen 1989, cited in Roberts and Polunin 1991). While the majority of recaptures from these studies have not moved far from the site of release, there are many examples of large scale movements (5-100's of km) of individual fish. These have generally come from fish which have been at liberty for considerably longer than average (Bardach 1958; Randall 1961; Moe 1967; Ansley and Harris 1981; Colin 1992). Furthermore, the existence of spawning aggregations, particularly by large epinephiline groupers, has been well documented (Johannes 1978; 1983; 1988; Shapiro 1987; Johannes and Squire 1988; Colin 1992; Samoilys and Squire 1994) which suggest individuals of these species are at least moving substaintial distances within individual reefs. Thus, the data available suggests that there is the potential for some species of large reef fish to move substantial distances within and among individual reefs. The important questions are "What proportion of the population move within and among reefs, and at what rate(s) do these fish move?".

In 1989 the Great Barrier Reef Marine Park Authority (GBRMPA) commissioned a study to develop and compare alternative experimental designs for a large-scale manipulative experiment to investigate the effects of line and trawl fishing on the reef fish assemblages of the Great Barrier Reef (GBR). The proposed design, which incorporated line fishing treatments applied at a level of individual reefs, assumed that the fish assemblages of individual reefs are independent (Walters and Sainsbury 1990). Given the equivocal nature of the present information on the extent of inter-reef movement by large reef fish, they recommended that a tagging study, designed to estimate the extent of movement of target species among individual reefs, should be a priority of future research (Walters and Sainsbury 1990). This chapter presents the results of such a tagging study.

The main objective of this research was to determine the extent to which large reef fish, principally the common coral trout, *Plectropomus leopardus*, moved among individual coral reefs. This was achieved through a tagging study done on five mid-shelf platform reefs in the Cairns Section of the GBRMP, Australia (Figure 7.1), from April 1992 to February 1994. The specific aims of the study were to determine whether *P.leopardus* moved between the five study reefs and, if so, what proportion of the population of an individual reef the observed level of movement represented. It was also of interest to examine whether there was a seasonal pattern of movement associated with the reproductive activity of *P.leopardus*, as they are known to form spawning aggregations on the GBR (Johannes and Squire 1988; Samoilys and Squire 1994).

This study differed from previous studies of movement of reef fish in two ways. Where logistically feasible, the tagging effort was spread across the entire area of each of the five reefs sampled rather than at discrete tagging locations. This resulted in the tagged fish being distributed across a large proportion of the area each reef. Secondly, returns were obtained from subsequent research tag-recovery exercises as well as from the recreational and commercial fishing communities. This meant that, at least for the research returns, the distribution of recapture effort was known. Secondly, it provided two independent data sources to estimate inter-reef movement which could be used to interpret potential biases in the tag return data.

8.2 Methods

8.2.1 Study site, sampling protocol and schedule, distribution of effort and tagging methods

The study site, sampling protocol and schedule and distribution of tagging effort have been described in Chapter 7 (sections 7.2.1 to 7.2.4). The details of the tags used and the tagging methods have been given in Chapter 5 (section 5.2.1).

8.2.2 Analysis

The return data were separated into two categories; i) those recaptured during the research tag-recovery exercises (research) and; ii) those returned by commercial and recreational fishers (public). This provides an indication of the reliability of the public returns. Furthermore, the more detailed data on location of recapture available from the research returns meant that movements among blocks within reefs could also be examined. Research returns were standardised by recapture effort for comparison of rate of return among reefs. Both research and public returns were standardised by releases for comparison of percent returns among trips, reef and sources of returns. Within-trip returns have been excluded from all estimates of movement.

Movement among reefs was expressed as the percentage of recaptures returned from a reef other than the one on which the fish were released. If the tagged population is assumed to be representative of the population as a whole, then this provides an estimate of the proportion of the population of each reef moving among reefs. The effect of reef on frequency of inter-reef movement of *P.leopardus* , for public returns, and inter-block movement, for research returns, were tested using 2-way contingency tables (Zar, 1984) in *JMP 2.0* (SAS 1989).

8.3 Results

8.3.1 Distribution of releases

A total of 4,627 *P.leopardus* were released over five trips, with totals of 1541, 777, 856, 558 and 895 released on Beaver, Taylor, Farquharson, Little Potter and Potter, respectively (Table 8.1). Although the distribution of releases among trips, reefs and blocks is not even, 30-60 *P.leopardus* were released in each back reef block at each reef, with the exception of Farquharson Reef during trips c and e, Little Potter during trip c and Taylor during trip e (Table 8.1).

The low number of releases in the front reef blocks of Taylor, Farquharson and Potter Reefs was due to their inaccessibility during trips a and c and the very low catches when it was possible to fish them (Table 8.1), rather than lack of effort (Table 8.2). Although the effort in line hours in the front reef blocks was lower than the back reef blocks during trips b and d, the actual sampling effort in numbers of dories and time spent in each block was approximately equal. The discrepancy in line hours is due to the difficulty the fishers had in finding “fishable hangs” on the steep front reef slopes of Potter, Taylor and Farquharson reefs. As a result they spent more time searching for hangs than fishing in the front reef blocks.

8.3.2 Distribution of tag returns

Distribution of research returns

A total of 143 returns of *P.leopardus* were obtained during the four research tag-recovery exercises. One hundred and thirty of these were recaptured between trips (Table 8.3) and 13 within trips. Fish recaptured within the same trip have been excluded from estimates of inter- or intra-reef movement as it was considered that their movements immediately following tagging may not be representative. The majority of the research returns came from Beaver (43) and Potter Reefs (37), with fewer recaptured at Taylor (17), Farquharson (16) and Little Potter Reefs (17) (Table 8.3). Two research returns of *P.leopardus* were excluded from the estimates of inter-reef movement due to insufficient recovery data. Only five other species were recaptured during the research recovery exercises, for a total of 22 returns (Table 8.4).

At Beaver Reef *P.leopardus* were returned from all blocks (Table 8.3), with the majority (77%) from blocks 1,3 and 6. In contrast, at Taylor, Farquharson, Little Potter and Potter Reefs the majority of *P.leopardus* were returned from the back reef blocks (Table 8.3). This is likely to be due to the lower number of releases and effort in the front reef blocks at these reefs (Tables 8.1 and 8.2). Potter reef had the second highest number of returns (37) with the majority (78%) returned from blocks 2 and 3 (Table 8.3).

The overall rate of return (no. returns/effort) of *P.leopardus* was highest at Beaver (0.18), Potter (0.17) and Little Potter Reefs (0.16), while at Farquharson (0.08) and Taylor Reefs (0.09) the rate of return was less than half that at Beaver (Table 8.5). The rate of return varied considerably among trips and reefs. However, there was a consistent increase across reefs during trip e, indicating that the targeting of the sampling effort at specific blocks, to increase the rate of return, had been effective (Table 8.5).

Distribution of public returns

Tags from a total of 300 fish were returned from the public (to February 1994) which included 282 *P.leopardus*. Of these, 273 were accompanied by sufficient information to be used to estimate inter-reef movement. The distribution of these returns among reefs and trips was relatively even, with a maximum of 81 returns from Taylor reef and a minimum of 51 from Little Potter reef (Table 8.6).

Percent returns of *P.leopardus* by trip by reef

The percentage of *P.leopardus* returned during the research exercises ranged from 0.2% at Farquharson Reef on trip c to 5.4% at Potter on trip b (Table 8.7). In general, the percentage of returns was highest on the first recovery exercise (trip b), due to the low number of releases relative to the number of recaptures. Somewhat surprisingly, the number of returns on the subsequent recovery exercises did not increase, despite the considerable increase in the number of releases. Consequently, the overall percent of recaptures decreased, with the exception of the final recovery exercise (Table 8.7).

The percentage of tags returned by the pubic ranged from zero at Beaver Reef (which was to be expected as Beaver Reef is closed to fishing) and Potter reef (April-October 1993) to nearly 15% at Potter Reef between April 1992 and September 1992 (Table 8.7). Generally, percent returns of *P.leopardus* from the public were higher on Potter, Little Potter and Taylor Reefs (Table 8.7). In a similar pattern to that of the research returns, the percent returns from the public decreased with time (Table 8.7).

8.3.3 Patterns of movement among reefs from research returns

One of the 128 research returns of *P.leopardus* (0.78%) had moved between reefs (Table 8.8). This represented 5.9% of the *P.leopardus* returned from Taylor Reef during the research recovery exercises. The *P.leopardus* was tagged in block 3 of Taylor Reef and was recaptured in block 3 of Beaver Reef (Figure 7.2). The remaining 99.2% of *P.leopardus* were recaptured on the reef where they were released (Table 8.8).

Fifty-three *P.leopardus* were recaptured during the final research recovery exercise. The distribution of recapture effort during this final exercise was deliberately focussed in areas where the majority of the returns from the public that provided evidence of inter-reef movement had been caught (*ie* the channels between Beaver and Taylor Reefs and Potter and Little Potter Reefs). All of the 53 returns were recaptured on the same reef where they were released. Of the 13 *P.leopardus* returned from the blocks between Beaver and Taylor Reef 100% were returned from their reef of release as were all the returns from Potter and Little Potter Reefs. The 22 recaptures of species other than *P.leopardus*, were all returned from the reef on which they were released also (Table 8.4). Thus, from the results of the research recovery exercises, it appears that inter-reef movement of *P.leopardus* is very low, with only one occurrence of inter-reef movement out of 140 returns. This represents less than one percent of the tagged population of *P.leopardus* overall and less than 6% of the tagged population of *P.leopardus* for Taylor Reef. Furthermore, the same appears to be the case for the other species of reef fish recaptured from the research recovery exercises, although the number of recaptures were very low.

8.3.4 Patterns of movement among reefs from public returns

The pattern of inter-reef movement of *P.leopardus* from the public returns differed markedly from that of the research returns (Table 8.9). Thirty-seven percent of the *P.leopardus* returned by the public were returned from a reef other than the reef at which they were released (Table 8.10). This included 43 *P.leopardus* which had been released on Beaver Reef and were returned from other reefs. The majority (70%) were returned from Taylor Reef. However, returns of fish which had been released on Beaver Reef were obtained from Farquharson, Little Potter and Potter Reefs also (Table 8.9). It is worthy of note that of the total inter-reef movements from Beaver Reef, 80% of the *P.leopardus* were released in 2 blocks (blocks 3 and 4) directly adjacent to Taylor Reef.

Although the percentage of inter-reef movements from the other reefs were lower than from Beaver, they were considerably higher than the estimates from the research returns. Twenty-two percent, 12% and 15% of the returns released on Taylor, Farquharson and Little Potter Reefs, respectively, were returned from other reefs (Table 8.10). Potter reef had the second highest percentage of inter-reef movements (40%) with 36 *P.leopardus* returned from other reefs (Table 8.9 and 8.10). The difference in frequency of inter-reef movement among these four reefs was significant ($\chi^2_{3,226}$= 17.907; p=0.0005), with Potter Reef having a significantly higher frequency of movement than Taylor, Farquharson and Little Potter Reefs. Ninety-five percent of the inter-reef movements from Potter Reef were released in blocks 1 (39%) and 2 (56%). Beaver Reef was excluded from the analysis as it was not possible to correctly weight the inter-reef movements by fish returned from Beaver Reef.

The majority of the inter-reef movements indicated by the public returns were to the first adjacent reef from the reef of release. However, the pattern of inter-reef movement is not indicative of a random diffusion process. Generally there was a higher percentage of moment to the 3rd adjacent reef from the reef of release (Table 8.11). The majority of these movements were to, or from, Potter Reef (Table 8.9 and 8.11).

There were 5 returns of *P.leopardus* by the public from reefs not included in the study area; 2 from Potter Reef reported as being caught on Nathan Reef (to the north of Adelaide Reef), 2 from Farquharson Reef reported as being caught at Adelaide Reef and a third from Farquharson

Reef returned from unnamed shoal located between Farquharson and Little Potter Reefs (see Figure 7.1 for locations of reefs).

The pattern of movement of *P.leopardus* from two of the major sources of public returns, source A (27%) and source B (17%) are presented in Table 8.12 and 8.13. In both cases the percentage of inter-reef movements is high, 37% and 55%, respectively. In the case of source A, 85% of the inter-reef movements were from Beaver Reef, with the majority to Taylor Reef (Table 8.12). One hundred percent of these returns had been released in blocks 2, 3 and 4 of Beaver Reef which are immediately adjacent to Taylor Reef. In contrast, 81% of the inter-reef movements from source B were from Potter Reef, with one movement from Beaver to Farquharson reef (Table 8.13). All the inter-reef movements from Potter Reef had been released in blocks 1 and 2 of Potter Reef, with the majority released in block 2.

8.3.5 Patterns of movement within reefs from research returns

The majority (65%) of *P.leopardus* were returned from their block of release (Table 8.14). However, there was a varying degree of movement among blocks at all reefs (Table 8.14), with the frequency of inter-block movement at Farquharson Reef being significantly different than at the other reefs ($\chi^2_{12,111}$=23.193; p=0.0261). This was due to the higher frequency of movement to the first adjacent block, mostly between blocks 1 and 2, at Farquharson Reef (Table 8.14).

8.4 Discussion

The degree of movement of post-settlement fishes among management units, such as individual coral reefs, is important in determining the effectiveness of Marine Fisheries Reserves (MFR) to enhance yield per recruit (Y\R) and spawning stock biomass per recruit (SSB\R) of reef fisheries (Polacheck 1990, DeMartini 1993; Russ *et al* 1993). It is also important in assessing the validity of considering individual reefs as independent replicates in large-scale adaptive management experiments designed to examine the response of reef fish populations to varying levels of fishing pressure (Walters and Sainsbury 1990). The results from the research returns in this study indicate that, under the present conditions, the level of movement by *P.leopardus* among reefs is low (<1% of research returns). However, the level of movement among spatial strata within reefs was high (average of 35% of returns were recaptured from another strata). This suggests that, for *P.leopardus*, individual reefs are the minimum appropriate spatial unit for management of reef fisheries. The effectiveness of partial reef closures (which are common on the GBR and in the Philippines) to protect spawning stock biomass is likely to be reduced due to the higher level of exchange among spatial strata within reefs (DeMartini 1993). More practically, given the greater difficulty in accurately defining "on the water" management boundaries within individual reefs (particularly for non-fringing reefs) (PDT 1990), suggests that the use of larger management units (individual reefs, or groups of reefs) may be more effective in reducing incidental or deliberate fishing in areas closed to fishing.

Patterns of movement among reefs

Individual coral reefs potentially represent an ideal unit for spatial closures to fishing and for adaptive management experiments investigating the effects of fishing on multispecies fish stocks (Hilborn and Walters 1978; Russ 1985, 1989, 1991; Walters and Sainsbury 1990; PDT 1990; Roberts and Polunin 1991). However, the use of individual coral reefs as management, or experimental units assumes that the dynamics of the population on one reef is independent of another, and therefore, that the rate of movement of adult fish among reefs is low (Walters and Sainsbury 1990).

There are few studies which have directly examined the degree of inter-reef or large-scale movement of reef fish (Roberts and Polunin 1991; Dugan and Davis 1993b). The majority of studies of movement of reef fish have been confined to a single reef (or section of reef) and inferences about movement on spatial scales larger than those covered by the study have been made on the basis of isolated returns from the public (Bardach 1958; Randall 1961; Beinssen 1989a; Buxton and Allen 1989, cited in Roberts and Polunin 1991; Holland *et al* 1993). The degree of large-scale movement of a variety of reef associated fishes was one of the objectives of a series of tagging studies in the Gulf of Mexico (Moe 1966, 1967; Beaumariage 1969; Fable 1980; Holt and Arnold 1982). The majority of fish recaptured during these studies were returned within a short period (30 to 60 days) following release and provided little evidence of movement from the release sites. There were, however, several examples of large-scale movements by Gag Grouper, *Mycteroperca microlepis*, (range 7 to 15 nautical miles) and Red Snapper, *Lutjanus campechanus* (range 20 to 150 nautical miles) which had been at liberty for longer periods (29 to

1,225 days). Unfortunately, the highly aggregated distribution of releases and the lack of any information on the distribution of recapture effort make it impossible to infer what proportion of the population may move to the extent indicated by these returns (Hilborn 1990; Schwarz and Arnason 1990; Sheridan and Castro Melendez 1990). These studies nevertheless provided direct evidence of the potential for movement among reefs by large reef fish.

Reef-specific estimates of the distribution of fishing effort by the public were not available for the present study. Information on the distribution of commercial effort is available from a compulsory logbook system. However, the finest grid-scale in the logbook system is large enough to include more than one of the reefs involved in this study. The difficulty in obtaining estimates of the distribution of fishing effort within the study area was the primary motivation for the structured research tag-recovery exercises. These exercises provided tag recoveries for which the location of capture and the amount of fishing effort were accurately known. The returns from these trips indicated that *P.leopardus* can move between reefs. However, the level of movement between reef was very low with less than 1% of the tagged population moving between reefs. Furthermore, there was no evidence of movement from the reef theoretically closed to fishing (Beaver Reef) to the nearest adjacent fished reefs (Taylor Reef <200m; Farquharson Reef <1.5 km; Figure 7.2), or any other reef sampled in the research exercises. On the basis of these returns, it appears that movement of *P.leopardus* among reefs, under the study conditions, is very low. This tentatively suggests that post-settlement reef fish on individual platform reefs represent local subpopulations, which are unlikely to interact with subpopulations on adjacent reefs by movement of adults, and that the major connection among subpopulations is likely to be via dispersal of pelagic larvae (Roughgarden and Iwasa 1986; Doherty and Williams 1988; Pulliam 1988; Doherty 1991; Fairweather 1991; Carr and Reed 1993).

The negligible level of movement of *P.leopardus* among reefs suggests that individual reefs may validly be considered as independent experimental units in adaptive management experiments. Coral reefs have often been suggested to represent an ideal experimental unit to investigate the effect of varying levels of fishing pressure on multispecies fish stocks (Walters and Hilborn 1976, 1978; Walters 1986; Sainsbury 1988; Russ 1991; Hilborn and Walters 1992). This implicitly assumes that the exploited populations on individual reefs are independent, *ie*, there is limited exchange of adults between reefs. Walters and Sainsbury (1990) considered a range of experimental design options for a large-scale adaptive management experiment to investigate the effects of line and trawl fishing on reef fish stocks on the GBR. On the basis of these simulations, they suggested that a rate of post-settlement movement among reefs of greater than 25%/annum would be likely to confound the proposed linefishing treatment regime. The results from this study indicate that, under the present conditions, the level of movement of *P. leopardus* among reefs is considerably less than this estimated maximum and that adult populations on adjacent reefs may considered independent.

It should be stressed that the differences in relative abundance (CPUE) and size structure among reefs was low and variable among reefs and trips within the five reefs studied (see Chapter 7). Importantly, there was no significant difference in CPUE between the reef closed to fishing (Beaver Reef) and the other reefs. Thus, the results of this study must be interpreted in light of the small variation in abundance of *P. leopardus* among reefs, as measured by CPUE from linefishing. It is possible that with greater contrast among reefs the level of inter-reef movement may increase. Such compensatory movement in response to density gradients in abundance would result in a net movement of fishes from higher density (MFR) to lower density (fished) areas. Depending on the fishing pressure outside the MFR, the area of the MFR and the rate of emigration, compensatory emigration could negate the protection of spawning stock offered by the MFR (DeMartini 1993). While this does not appear to be the case in this study, it may be cause for concern in regions, such as the Philippines and the Caribbean, where fishing pressure is considerably higher than on the GBR (Munro 1987; Alcala 1988; Koslow 1988; Alcala and Russ 1990; Russ 1991; Dugan and Davis 1993a; Polunin and Roberts 1993).

There was a marked contrast in the degree of movement of *P. leopardus* among reefs from the research recovery exercises and the returns from the public. The majority of movement indicated by the public returns was from Beaver Reef (closed to fishing) to Taylor Reef and from Potter Reef to Little Potter Reef. This contradictory pattern in the two sources of returns, high levels of inter-reef movement from the public returns and no inter-reef movement from the research returns, prompted the redistribution of sampling effort on the last research recovery exercise. The recaptures of *P. leopardus* obtained during that final exercise confirmed the results of the previous research recovery exercises. All *P. leopardus* returned were recaptured on the same reef of release. The most likely explanations for the observed difference in the returns from the public and the research recovery exercise are inaccurate reporting of capture location and deliberate infringement. The implications of these alternatives for the design and effectiveness of MFR and for adaptive management experiements are discussed below (*Infringements*).

Infringement cannot explain the level of inter-reef movement of *P.leopardus* to and from Potter reef indicated by the public returns as Potter Reef is open to fishing. It is possible that movement is real and, due to the temporal scale of the research recovery exercises, it was not evident in the research returns. Migration of fish to spawning aggregations at Potter Reef could explain the observed pattern of movement. This is supported circumstantially by the increase in CPUE in particular blocks at Potter reef during the spawning season (Chapter 7) and the occurrence of fish in spawning condition in the catches during September 1992, which indicate that spawning aggregations of *P.leopardus* do occur at Potter Reef. However, the increase in CPUE may be as equally well explained by an increase in catchability of *P.leopardus* during the spawning, rather than an increase in absolute abundance on Potter Reef (see discussion Chapter 7). Furthermore, 100% of the *P.leopardus* returns recaptured from Potter and Little Potter reefs during the final research recovery exercise were recaptured from their reef of release. Although this does not demonstrate conclusively that inter-reef movement does not occur, it does suggest that if *P.leopardus* move between reefs to spawn, individuals return to the same reef following spawning. Recent research on the spawning behaviour of *P.leopardus* indicates that there are multiple aggregation sites within a reef (Samoilys and Squire 1994; Brown 1994). This suggests that in contrast to some other epinepheline groupers (*eg Epinephelus striatus*) which undergo large spawning migrations to a few aggregation sites (Colin 1992), movement of *P.leopardus* to spawning aggregations may be confined within individual reefs.

Patterns of movement within reefs

Although the majority of *P.leopardus* were recaptured in their block of release, there were significant levels of inter-block movement and the extent of this movement varied significantly among reefs. This supports the results from the small scale study at Lizard Island and the earlier findings of Samoilys (1986) and Beinssen (1989 a,b) that *P.leopardus* moves considerably within individual reefs. Samoilys (1986) recorded movements ranging from 400m to 7.5 km for 12 *P.leopardus* (20% of total number of re-sighting) resighted outside the main study area. Beinssen (1989a) observed that at Boult Reef 10% of the *P.leopardus* were returned from outside their block of release (approximately 2.5 km linear distance) after a period of 90 days. In a more detailed study of the movement of several species of large reef fish across a Marine Park B/A zoning boundary at Heron Island, Beinssen (1989b) found that approximately 29% of *P.leopardus* had moved from their block of release (500m linear distance) after 3-4 weeks at liberty and that this dispersion appeared to continue with time (Beinssen 1990).

The estimates of movement within reefs from this study demonstrate that there was significant movement of *P.leopardus* among blocks within reefs with an average of 26 % of research returns recaptured outside their block of release. The proportion of fish moving among blocks and the distances travelled were greatest on Farquharson, Potter and Taylor Reefs where the movement appeared to be associated with fish moving to, or from, spawning aggregation sites. The greatest distance travelled was approximately 4 km on Potter Reef. Aggregations of *P.leopardus*, identified by exceptionally high CPUE and fish in spawning condition, were commonly associated with deep (>15 m) coral bombies located on, or along, the reef edge where they were exposed to strong tidal currents. Such conditions are consistent with aggregation sites described for *P.leopardus* elsewhere on the GBR and for other species of epinepheline groupers (Johannes 1988; Johannes and Squire 1988; Colin 1992; Samoilys and Squire 1994).

The use of partial reef closures to protect part of an individual reef or a section of continuous fringing reef is widespread in tropical and temperate reef fisheries (Bell 1983; Russ 1985; Buxton and Smale 1989; Davis 1989; Alcala and Russ 1990; Cole *et al* 1990; Polunin and Roberts 1993; Roberts and Polunin 1993). Within the Great Barrier Reef Marine Park (GBRMP) there are numerous examples of partial reef closures which are commonly referred to as "*split zoning*". DeMartini (1993) modelled the potential effect of movement across reserve boundaries on the effectiveness of MFR to increase yield per recruit and spawning stock biomass per recruit of reef fishes. His extensive simulations suggested that high rates of exchange across reserve boundaries could potentially negate the protective effect of the reserve, particularly if the size of the reserve was small in relation to the size of the fished area. The relatively high levels of movement within reefs found in this study suggest that these *split zoning* may not successfully protect the spawning stock of *P.leopardus* in the area closed to fishing.

This situation may be exacerbated if spawning sites are not included within the protected area because *P.leopardus* and other large serranids are particularly vulnerable to line fishing when aggregated, like many other species of large reef fish (Johannes and Squire, 1988; Collins 1992).

It may also be inferred from the results of this study that there will be a degree of incidental infringement in the closed area unless the zoning boundaries can be clearly identified by fishers (see below). While this may be possible on fringing reefs and coral cays, where land marks can be used to define management boundaries, it is generally not possible on individual platfom reefs.

Infringements

A major result of this study was the marked contrast between the estimates of inter-reef movement from the research recovery exercises and from the public returns. A large part of this disparity appears to be the result of some anglers fishing at Beaver Reef and subsequently reporting the capture from another location. This is supported by the results of the final research recovery exercise which deliberately targeted areas within the cluster where the majority of the reported movements had occurred (*ie.* the channel between Beaver and Taylor Reefs) and found no evidence of inter-reef movement.

Incidental and deliberate infringement may explain the apparent misreporting of capture location for fish actually caught on Beaver Reef:. The channel separating Beaver and Taylor Reefs is less than 200 m wide at the closest point of each reef and both reefs are characterised by long, tapered shoals which extend for over a kilometre from the main reef complex (Figure 7.2). This makes it difficult to determine where one reef ends and the other begins. Consequently, incidental infringements may occur as a result of fishers being unsure of where the exact management boundary lies. This suggests it may be more effective to select isolated reefs for MFR to avoid confusion about the location of management boundaries. This scenario applies equally, or even more so, to individual reefs which include "*split zoning*" such as those on the GBR, the Philippines (Russ 1985; Alcala and Russ 1990), and the Caribbean (Polunin and Roberts 1993).

It is also possible that certain fishers may deliberately and intensively fish the protected reef in the form of infrequent pulse fishing [1]. This form of infringement is likely to have a significant impact on the stock and should be of considerable concern not only to managers, but also to scientists wanting to use MFR as controls for manipulative experiments examining the effects of

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[1] This explanation is supported circumstantially by the lack of a significant difference in CPUE or size structure between Beaver Reef (closed to fishing) and the other reefs in the study (Chapter 7), and by reports from the local fishing community that Beaver Reef is regularly fished due to its proximity to Taylor Reef.

fishing on reef fish stocks (Walters and Sainsbury 1990). If all the returns from source A (Table 8.12) from Beaver Reef were actually caught on Beaver, a total of approximately 844 *P.leopardus* would have been caught to obtain the 23 returns. If all the public returns from Beaver Reef are included, this estimate increases to 1,578 *P.leopardus*. This is likely to represent a significant proportion of the *P.leopardus* population on Beaver reef. For example, Beinssen (1989a) estimated the total population size of *P.leopardus* on a small reef (4.5 x 3.0 km) in the southern GBR to be 8613 (SE = 873). This suggests the estimated level of infringement at Beaver Reef is substantial and could possibly negate the positive effects of MFR protection. As a consequence, manipulative experiments investigating the effects of different levels of fishing effort on coral reefs may need to consider MFR as a low fishing pressure level rather than a control for no fishing unless public compliance with management is high.

It may be possible to resolve the discrepancy between the public and research returns by increasing the frequency and intensity of the research recovery exercises to obtain a greater number of returns at the different stages of the *P.leopardus* spawning cycle, as suggested by Davies (1992). However, this is likely to be prohibitively expensive on the scale that would be required. An alternative is to study the behaviour of the of the recreational and commercial fishers in order to understand the important sources of bias and inaccuracy in the information provided with the public tag returns. This would not only increase the value of the tag returns from the public but also provide information on the temporal and spatial distribution of fishing effort and a valuable opportunity to develop a cooperative relationship between the fishing community, scientists and managers.

Conclusions

This research was one of the first attempts to implement a structured tag-recovery study of sufficient spatial and temporal scale to directly estimate the extent to which large reef fish, such as *P.leopardus*, move between and within individual coral reefs. It has demonstrated that the present level of movement of *P.leopardus* among reefs is negligible and is not sufficient to undermine the use of individual coral reefs as MFR or as independent replicates in adaptive management experiments. However, as the contrast in relative abundance and size structure among reefs in the study was low (see Chapter 7), caution should be taken in applying these results more generally. The potential for compensatory movement from MFR to fished areas, in the situation where fishing pressure outside the MFR is high and the contrast in abundance between the MFR and the fished area is large, is yet to be directly investigated for reef fish (but see Alcala and Russ 1990; Russ and Alcala unpublished manuscript). In contrast to inter-reef movement, the level of movement of *P.leopardus* within reefs was found to be considerable. This supports the results of early studies and suggests that the use of partial reef closures within individual reefs may not effectively protect *P.leopardus* within the areas closed to fishing, due to the level of movement across these boundaries.

Table 8.1: Number of *P.leoparus* tagged and released by trip by reef by block. Block numbers correspond to those in Figure 7.2.

	Block	**a**	**b**	**c**	**d**	**e**	**Total**
Beaver	1B	86	26	141	22	104	379
	2F	46	52	46	35	19	198
	3F	146	48	42	48	77	361
	4B	54	16	20	45	69	204
	5B	29	24	21	-	-	74
	6B	54	27	161	39	44	325
	Total	**415**	**193**	**431**	**189**	**313**	**1541**
Taylor	1B	48	47	65	44	13	217
	2B	78	33	71	23	7	212
	3B	60	56	31	29	44	220
	4F	-	14	-	44	29	87
	5F	-	3	-	14	-	17
	6F	-	14	-	10	-	24
	Total	**186**	**167**	**167**	**164**	**93**	**777**
Farquharson	1B	101	32	17	14	12	176
	2B	-	74	-	37	23	134
	3F	-	7	-	9	-	16
	4F	-	1	-	19	-	20
	5F	-	2	-	18	-	20
	6F	-	1	-	27	-	28
	7F	-	57	-	15	-	72
	8B	67	66	-	63	1	197
	9B	80	21	14	46	32	193
	Total	**248**	**261**	**31**	**248**	**68**	**856**
Little Potter	1B	102	115	-	98	104	419
	2F	-	28	-	70	41	139
	Total	**102**	**143**	**0**	**168**	**145**	**558**
Potter	1B	43	70	51	14		178
	2B	105	128	35	32	71	371
	3B	36	56	35	38	60	225
	4F	-	12	-	50	22	84
	5F	-	13	-	13	-	26
	6F	-	2	-	9	-	11
	Total	**184**	**281**	**121**	**156**	**153**	**895**
Cluster	**Total**	**1135**	**1045**	**750**	**925**	**772**	**4627**

Table 8.2: Distribution of sampling effort (line hrs) among blocks within reefs by trip. B=back, F=front. Block numbers correspond to those in Figure 7.2.

	Block	a	b	c	d	e	Total
Beaver	1B	12.02	4.88	15.57	1.73	9.90	44.10
	2F	9.28	7.12	2.57	4.48	3.22	26.67
	3F	17.45	5.95	8.98	6.87	11.23	50.48
	4B	16.65	5.73	2.98	5.03	14.57	44.97
	5B	8.73	6.32	2.97	-	-	18.02
	6B	14.53	5.42	18.75	7.22	5.43	51.35
	Total	**78.67**	**35.42**	**51.82**	**25.33**	**44.35**	**235.58**
Taylor	1B	12.73	7.15	13.25	7.38	4.68	45.20
	2B	21.33	6.93	11.33	6.30	2.97	48.87
	3B	19.40	8.75	5.92	2.67	18.03	54.77
	4F	-	6.77	-	7.03	9.67	23.47
	5F	-	3.47	-	2.50	-	5.97
	6F	-	4.93	-	3.80	-	8.73
	Total	**53.47**	**38.00**	**30.50**	**29.68**	**35.35**	**187.00**
Farquharson	1B	28.70	5.93	-	5.12	5.05	44.80
	2B	-	8.22	4.88	5.67	5.43	50.67
	3B	-	5.48	-	3.00	-	29.33
	4F	-	0.83	-	2.70	-	3.53
	5F	-	2.18	-	4.10	-	6.28
	6F	-	1.50	-	3.30	-	4.80
	7F	-	12.55	-	3.28	-	15.83
	8B	26.47	6.98	-	6.87	0.95	14.80
	9B	20.85	3.80	2.53	9.45	5.73	21.52
	Total	**76.02**	**47.48**	**7.42**	**43.48**	**17.17**	**191.57**
Little Potter	1	25.78	11.43	0.00	14.65	19.45	71.32
	2	0.00	13.63	0.00	11.35	9.00	33.98
	Total	**25.78**	**25.07**	**0.00**	**26.00**	**28.40**	**105.25**
Potter	1B	15.28	9.77	8.47	4.20	-	37.72
	2B	34.55	11.52	10.95	7.00	7.82	71.83
	3B	21.12	12.27	8.53	8.22	14.75	64.88
	4F	-	2.83	-	8.85	7.15	18.83
	5F	-	8.95	-	3.83	-	12.78
	6F	-	4.08	-	3.05	-	7.13
	Total	**70.95**	**49.42**	**27.95**	**35.15**	**29.72**	**213.18**
Cluster	**Total**	**304.88**	**195.38**	**117.68**	**159.65**	**154.98**	**932.58**

Table 8.3: Distribution of research returns by trip, reef and block. Block numbers correspond to those in Figure 7.2.

	Block	**b**	**c**	**d**	**e**	**Total**
Beaver	1B	0	0	0	10	10
	2F	1	2	2	0	5
	3F	6	3	1	6	16
	4B	0	1	0	2	3
	5B	2	0	0	0	2
	6B	1	4	2	0	7
	Total	**10**	**10**	**5**	**18**	**43**
Taylor	1B	0	3	1	0	4
	2B	0	3	1	0	4
	3B	1	1	1	4	7
	4F	0	0	0	1	1
	5F	0	0	1	0	1
	6F	0	0	0	0	0
	Total	**1**	**7**	**4**	**5**	**17**
Farquharson	1B	5	0	0	0	5
	2B	4	-	0	1	5
	3F	0	-	0	-	0
	4F	0	-	0	-	0
	5F	0	-	0	-	0
	6F	0	-	1	-	1
	7F	0	-	0	-	0
	8B	1	-	1	0	2
	9B	1	1	0	1	3
	Total	**11**	**1**	**2**	**2**	**16**
Little Pottler	1B	3	-	1	10	14
	2F	0	-	0	3	3
	Total	**3**	**0**	**1**	**13**	**17**
Potter	1B	4	3	0	-	7
	2B	4	3	2	9	18
	3B	2	4	0	5	11
	4F	0	-	0	1	1
	5F	0	-	0	-	0
	6F	0	-	0	-	0
	Total	**10**	**10**	**2**	**15**	**37**
Cluster	**Total**	**35**	**28**	**14**	**53**	**130**

Table 8.4: Research returns of species other than *P.leopardus*, with total number of returns, number returned from the block of release and the number returned from the reef of release.

Species	No. returned	Block of release	Reef of release
Anyperidon leucogrammicus	2	1	2
Cephalopholis cyanostigma	7	4	7
Lutjanus bohar	2	2	2
L.carponotatus	4	2	4
Lethrinus miniatus	7	6	7
Total	22	15	22

Table 8.5: Research recaptures of *P.leopardus* standardised by sampling effort (line hrs) by trip and reef.

	b	c	d	e	Total
Beaver	0.28	0.19	0.20	0.41	0.18
Taylor	0.03	0.23	0.13	0.14	0.09
Farquharson	0.23	0.13	0.05	0.12	0.08
Little Potter	0.12	-	0.04	0.46	0.16
Potter	0.20	0.36	0.06	0.50	0.17
Total	0.18	0.24	0.09	0.34	0.14

Table 8.6: Distribution of public tag returns of *P.leopardus* by time period and reef.

Reef/Time period	Apr'92-Sept'92	Sept'92-Apr'93	Apr'93-Sept'93	Sept'93-Feb'94	Total
Beaver	0	0	0	0	**0**
Taylor	26	9	22	24	**81**
Farquharson	17	20	18	14	**69**
Little Potter	13	18	18	2	**51**
Potter	27	27	0	22	**76**
Others	2	1	2	0	**5**
Total	**85**	**75**	**60**	**62**	**282**

Table 8.7: The rate of tag return of *P.leopardus* from each reef by the public and from the research recovery trips, expressed as a percent of the culmulative total *P.leopardus* released at each reef.

Reef/Time period	Source	Apr'92-Sept'92	Sept'92-Apr'93	Apr'93-Oct'93	Oct'93-Feb'94
Beaver	Res	2.41	1.64	0.48	1.47
	Pub	0.00	0.00	0.00	0.00
Taylor	Res	0.54	1.98	0.77	0.73
	Pub	13.98	2.55	4.23	3.51
Farquharson	Res	4.44	0.20	0.37	0.25
	Pub	6.85	3.93	3.33	1.78
Little Potter	Res	2.94	-	0.41	3.15
	Pub	12.75	7.35	7.35	0.48
Potter	Res	5.43	2.15	0.34	2.02
	Pub	14.67	5.81	0.00	2.96
Total	**Res**	**3.08**	**1.28**	**0.48**	**1.37**
	Pub	**7.49**	**3.44**	**2.05**	**1.61**

Table 8.8: Pattern of inter-reef movement of *P.leopardus* from research returns. Includes *P.leopardus* which were recaptured among trips only: i.e recaptures within the same trip have been excluded.

	Returned						
Released	Beaver	Taylor	F'harson	L'Potter	Potter	Other	Total
Beaver	**41**	0	0	0	0	0	**41**
Taylor	1	**17**	0	0	0	0	**18**
Farquharson	0	0	**16**	0	0	0	**16**
Little Potter	0	0	0	**16**	0	0	**16**
Potter	0	0	0	0	**37**	0	**37**
Total	**42**	**17**	**16**	**16**	**37**	**0**	**128**

Table 8.9: Pattern of inter-reef movement of *P.leopardus* from public returns.

	Returned						
Released	Beaver	Taylor	F'harson	L'Potter	Potter	Other	Total
Beaver	**0**	30	6	1	6	0	**43**
Taylor	0	**38**	5	0	6	0	**49**
Farquharson	0	0	**46**	0	3	3	**52**
Little Potter	0	1	1	**33**	4	0	**39**
Potter	0	10	5	19	**54**	2	**90**
Total	**0**	**79**	**63**	**53**	**73**	**5**	**273**

Table 8.10: Number and percentage of *P.leopardus* which moved from their reef of release for research and public returns by reef. * note that it is not possible to weight the public returns of fish released at Beaver Reef.

	Research		Public	
Reef	**#**	**%**	**#**	**%**
Beaver	0	0	43	100 *
Taylor	1	5.88	11	22.45
Farquharson	0	0	6	11.54
Little Potter	0	0	6	15.38
Potter	0	0	36	40.00
Total	**1**	**0.78**	**102**	**37.36**

Table 8.11: Percentage of inter-reef movements of *P.leopardus* from public returns to 1st, 2nd and 3rd adjacent reef from reef of release.

Reef	**1st**	**2nd**	**3rd**
Beaver	84	2	14
Taylor	45	0	55
Farquharson	0	50	50
Little Potter	83	17	0
Potter	53	14	33
No. of returns	**64**	**10**	**26**

Table 8.12: Pattern of inter-reef movement of *P.leopardus* from returns from public source A.

	Returned					
Released	Beaver	Taylor	F'harson	L'Potter	Potter	Total
Beaver	**0**	19	0	0	4	**23**
Taylor	0	**1**	0	0	0	**1**
Farquharson	0	0	**0**	0	2	**2**
Little Potter	0	0	0	**31**	1	**32**
Potter	0	1	0	0	**14**	**15**
Total	**0**	**21**	**0**	**31**	**21**	**73**

Table 8.13: Pattern of inter-reef movement of *P. leopardus* from returns from public source B.

	Returned					
Released	Beaver	Taylor	F'harson	L'Potter	Potter	Total
Beaver	**0**	0	1	0	0	**1**
Taylor	0	**14**	3	0	0	**17**
Farquharson	0	0	**7**	0	0	**7**
Little Potter	0	1	0	**0**	0	**1**
Potter	0	3	0	18	**0**	**21**
Total	**0**	**18**	**11**	**18**	**0**	**47**

Table 8.14: Response profiles from 5x4 contingency table analysis of frequency of inter-block movement of *P.leopardus* from research returns. Includes *P.leopardus* which were recaptured among trips only: i.e recaptures within the same trip have been excluded.

	Number of blocks moved				
Reef	**0**	**1**	**2**	**3**	**Total**
Beaver	0.68	0.17	0.12	0.02	**41**
Taylor	0.61	0.39	0.0	0.00	**18**
Farquharson	0.31	0.44	0.19	0.06	**16**
Little Potter	0.68	0.29	0.03	0.00	**16**
Potter	0.69	0.29	0.05	0.00	**35**
Total	**0.65**	**0.26**	**0.07**	**0.02**	**126**

Chapter 9

Implications for management and future research

9. Implications for management and future research

The level of fishing pressure on coral reef fisheries around the world is increasing. In many areas there is an urgent need for immediate management decisions if the stocks and the fisheries are to be sustained (Munro and Williams 1985; PDT 1990; Russ 1991). The complex nature of coral reef fish stocks and the fisheries which exploit them make stock assessment and management by traditional single species/single fishery models difficult, if not impossible, under present circumstances (PDT 1990). Coral reef fisheries generally target a number of species and in most fisheries a range of gears are used (Munro 1983; Alcala 1988; PDT 1990; Russ 1991). Catches are landed at numerous locations and marketed through a variety of outlets ranging from artisinal markets to international export operations. Consequently, time series of catch and effort data for the whole fishery, a principle requirement of most stock assessment models, are rarely available even for the major target species for coral reef fisheries (Munro 1987; PDT 1990).

The paucity of information for formal stock assessment and the failure of assessments based on these techniques in many fisheries has resulted in substantial interest in the use of area closures, such as Marine Fisheries Refugia (MFR), as a management technique for temperate and tropical reef fish (PDT 1990; Roberts and Polunin 1991; Russ 1991; DeMartini 1993; Dugan and Davis 1993a; Polunin and Roberts 1993; Russ *et al* 1993). However, to date there is little empirical evidence available with which to assess the likely effectiveness of MFR (Roberts and Polunin 1991; Dugan and Davis 1993). Information on the degree of movement of adult fishes across MFR boundaries has been cited as essential to evaluating MFR as a fisheries management tool (Polacheck 1990; Roberts and Polunin 1991; Russ 1991; DeMartini 1993; Dugan and Davis 1993; Russ *et al* 1993). This thesis has focussed on the patterns of movement of three species of coral reef fish within and among various spatial scales commonly found on coral reefs. In addition, information on the patterns of growth, mortality and the factors affecting their distribution were obtained. The implications of these results are discussed below in the context of directions for future research on coral reef fish population dynamics and the potential effectiveness of MFR for managing tropical reef fisheries.

Until relatively recently coral reef were generally regarded as being characterised as fast growing, short life-span and high mortality (Ferreira and Russ 1994). This arose from the perception that tropical reef fish could not be aged by conventional aging techniques, such as the reading of otoliths or scales, and the presence of relatively few modes in the length frequency distributions of samples of many species. However, recent studies have shown that it is possible to age a wide range of coral reef fish by reading annuli in whole or sectioned otoliths. The large majority of these studies have found coral reef fish to have considerably greater longevity than previously considered. Importantly, the longevity of a species does not appear to be related to its maximum size. For example, studies on the Great Barrier Reef (GBR) have shown that a small damsel fish, *Pomacentrus molaccensis*, (Fowler 1990) may have a longevity comparable to a large serranid, *Plectropomus leopardus* (Ferreira and Russ 1994). Greater longevity combined with high variation in individual growth rates and, therefore, size at age suggests that length is unlikely to be a good proxy for age in tropical reef fish. The results of the otolith readings for *L.carponotatus* from this study support this pattern as do the results of recent aging studies of smaller tropical lutjanids (Newman 1995; Sheaves 1995) and acanthurids (Howard Choat, Dept Marine Biology, James Cook University, personal communication; Anthony Hart, Victorian Institute of Marine Science, unpublished data). The greater longevity and high variability in size at age of many species of coral reef fish stresses the need for age-based estimates of growth and mortality parameters.

While aging of tropical reef fish by sectioning otoliths is possible for many species, it is time consuming, expensive and requires a degree of training and technology which is not currently available in many tropical countries (Csirke *et al* 1987; Gulland 1987; Munro 1987). Reading of whole otoliths requires less preparation, and therefore expense, although there is a tendency for readings of whole otoliths to underestimate age relative to sectioned otoliths in the older age classes (Boehlert 1985; Ferreira and Russ 1994; Chapter 4 this study). However, older age classes are likely to represent a small proportion of the samples, particularly in heavily fished populations, therefore the proportion of otoliths requiring sectioning may be low. Otolith weight has been shown to be a good indicator of age in a variety of species of tropical and temperate fish (Boehlert 1985; Fletcher 1991; Ferreira and Russ 1994; Newman 1995; Chapter 4 this study). It represents a potential technique for obtaining age-based estimates of growth, mortality and longevity, without the expense associated with sectioning otoliths or the training and interpretational problems of reading otoliths, which has been underutilised to date in tropical reef fisheries biology. A comprehensive comparison of population parameters, such as growth, mortality and longevity, derived from these different techniques should be a priority for future research in coral reef biology. Such a study should include a range of species and samples from several populations in different regions to provide greater generality and to account for potential variation in the relationship between otolith weight and age among regions.

Tagging studies are widely used in fisheries biology to estimate population parameters, including rates of growth and mortality (Parker *et al* 1990), particularly for species which cannot be aged (eg many of the tunas). The use of tagging studies to estimate growth or mortality assumes that the capture and tagging process and the physical presence of the tag do not affect the growth or mortality rate of tagged fish (Jones 1976). Tagging has been shown to affect growth rates (eg Saunders and Allen 1967) and it is likely that there will be some effect no matter what type of tag or capture method are used. Futhermore, the size of fish which can be tagged with conventional external anchor tags reduces the size range from which growth estimates can be made. The lack of information for smaller size classes and the high variability in individual growth rates is likely to result in negatively biased estimates of growth rates from tagging studies (Sainsbury 1980; Francis 1988). The large amounts of time, effort and expense involved in estimating growth rates from tagging and the potential sources of biases strongly suggests that age-based estimates of growth parameters will be a less biased and more cost-effective alternative.

The effect of capture, tagging and carrying a tag (s) on survival of tagged individuals is of critical concern when using tagging studies to estimate mortality rates (Burnham *et al* 1987). As with the effect of tagging on growth rates, there is almost certainly going to be some effect of capture and tagging on the survivorship of tagged individuals. It is a question of how large is the effect. In this regard absolute estimates of mortality from tagging studies are likely to over-estimate the true rate. However, there are often situations in which the key question is not the absolute estimate of mortality but the relative difference in mortality over time or space (Burnham et al 1987; Lebreton et al 1992). In these circumstances multiple capture-recapture experiments potentially represent one of the most powerful techniques for directly studying patterns in mortality among populations and over time (Vetter 1988; Lebreton et al 1992). This study provided one of the first applications of this methodology to the study of reef fish population dynamics. The results were limited by the relatively low recapture rates and the duration of the study which resulted in imprecise estimates of capture probabilities and, hence, imprecise estimates of survivorship. Despite these limitations the data suggested that survivorship may vary among habitats. Given the evidence for within population and regional variation in mortality in other fish stocks (Vetter

1988), further investigation of patterns of mortality among the various spatial scales found in reef systems seem more than warranted.

In order to be effective from a fisheries perspective, MFR must produce a net export of fisheries production equal to, or greater than, the production lost due to the closure of the reserve area to fishing (Dugan and Davis 1993). This may occur either by the export of post-settlement juveniles or adults, or by the dispersal of pelagic larvae. The former assumes that as biomass and density accrues in the reserve a proportion of that biomass will move into the fished area and be caught, and that this may maintain yield per recruit in the fished area. Simulation studies suggest the effectiveness of MFR to maintain yields or spawning stock biomass will depend on the rates of transfer between the reserve and fished area, the size of the reserve, and the growth and natural mortality rates and exploitation schedules of the species (Polacheck 1990; DeMartini 1993). The information on movement of three species of coral reef fish gained from this study and previous studies of movement would suggest that rates of transfer will differ dramatically among species. As a result what is an optimal reserve size in terms of maximising yield per recruit for a large relatively mobile serranid, such as *P.leopardus*, is likely to be sub-optimal for more sedentary species such as *L.carponotatus* and *S.doliatus*. Furthermore, gains in yield per recruit are likely to be lower than reported in the simulation studies if reef fish are generally longer lived as recent age determinations suggest. The movement information from this study would suggest that any gains in yield per recruit for coral reef fish as a result of MFR are likely to be very localised, on a scale of a few hundred meters to a few kilometers, and confined to within an individual reef.

Potentially of greater importance is the possibility that rates of transfer between the reserve and fished areas may be high enough to undermine the protection of the spawning stock within the reserve. The relatively high rates of movement of *P.leopardus* within reefs suggests this could be the case for MFR which involve partial reef closures, such as the split-zonings on the GBR or sectional closures of fringing reefs. In contrast, the low level of movement and high degree of site and habitat fidelity displayed by *S.doliatus* and *L.carponotatus* suggest that partial reef closures may be effective for this type of species if the management boundaries coincide with major habitat demarcations. In light of this information and the greater potential for MFR to augment spawning stock biomass (SSB), relative to yield per recruit, it may be more effective to base MFR design on maximising SSB, at the expense of gains in yield per recruit. This supports DeMartini's conclusion that a single large reserve is likely to be more beneficial than several small reserves of the same total area (The SLOSS concept, single large or several small (Simberloff 1988)), largely due to the higher rates of transfer associated with the smaller reserves

The SLOSS concept is also of value when considering MFR design and the potential impact of fishing infringements within the reserve area. Infringement has been largely ignored in the simulations studies with compliance assumed to be 100% but has been raised as a potential obstacle to MFR (PDT 1990; Russ *et al* 1993). In reality 100% compliance is unlikely to be the case and the information obtained during this study and observations from the Philippines suggest that infringement may have a substantial impact on the reserve populations (Russ and Alcala 1994; Chapter 8 this study). Caddy (1993) provided a useful illustration of the potential relationship between infringement, the need for enforcement and the period of time following closure in the context of rotational harvesting strategies. The likelihood of infringement would be low initially but increase with time since closure as biomass accrued within the protected areas and the incentive to infringe increased. A similar model may be applied to MFR. However, the need for enforcement is going to remain high as the reserve is permanently closed to fishing. In the case of a rotational harvesting system the need for enforcement is periodically relieved when areas are re-opened to fishing (Caddy 1993). In practice the success of MFR as a management strategy for reef fish, or any other fisheries resource, will rely heavily on the support of the entire fishing community for the concept and their compliance with the areal closures. If this support is not forthcoming then the cost of enforcing the closures may be very high. These costs would be reduced and the effectiveness of the enforcement increased if a few large areas were designated as MFR rather than several small areas of a similar total area.

A growing number of studies have demonstrated that many species of coral reef fish are much longer lived than previously considered. This information should be incorporated into simulation studies to re-assess the potential of MFR in light of the different growth, mortality reproduction and longevity parameters it implies. The greatest potential for MFR to maintain or enhance fisheries production appears to be by the production and export of larvae from the reserve to fished areas. However, there is very little empirical information available on the reproductive output from reserve populations or the relationship between reproductive success and population size (Dugan and Davis 1993b). A knowledge of the reproductive potential and spawning behaviour of protected populations and the fate of the larvae produced will be critical information to design appropriately sized and located MFR and should be a priority of future research.

This study has provided valuable quantitative information on the patterns of movement of three species of coral reef fish among several spatial scales found on coral reefs. It has shown that the extent of movement within coral reefs varies among species and habitats and that partial reef closures may not be effective for *P. leopardus*, which moved considerably within individual reefs. However, the extent of movement by *P. leopardus* between reefs was negligible and this suggests that for this species MFR should be designed at a scale of individual reefs or larger. This would ensure the protection of spawning stock biomass and reduce the potential for infringement. However, it must be stressed that these results were obtained from an area where the contrast in abundance, and potentially fishing effort, was not large between reefs. Therefore, it is not possible to conclude that compensatory movement will not occur in the presence of strong contrasts in abundance and fishing pressure between MFR and fished areas. Determining whether this does occur should be a priority of future research of MFR, and should be incorporated into monitoring programmes of MFR effectiveness.

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Appendices

Appendix 1: Catch composition by family, species (by number) and site pooled over all sampling periods for Z-trap catches from the Lizard Island study.

		Loomis		Mangrove		South	
Family	*Species*	Total	%	Total	%	Total	%
Serranidae							
	Cephalopholis cyanostigma	0	0.00	1	0.06	1	0.05
	Cromileptes altivelis	2	0.18	3	0.17	1	0.05
	Epinephelus cyanopodus	0	0.00	2	0.11	0	0.00
	E. corallicola	0	0.00	0	0.00	0	0.00
	E. fuscoguttatus	4	0.37	2	0.11	0	0.00
	E. howlandi	0	0.00	4	0.23	2	0.11
	E. macrospilos	0	0.00	1	0.06	2	0.11
	E. maculatus	1	0.09	0	0.00	0	0.00
	E. merra	6	0.55	0	0.00	9	0.48
	E. polyphekadion	0	0.00	7	0.40	3	0.16
	E. quoyanus	4	0.37	8	0.45	5	0.27
	E. tauvina	0	0.00	4	0.23	3	0.16
	E. malabaricus	13	1.19	4	0.23	12	0.64
	E. ongus	0	0.00	0	0.00	2	0.11
	Plectropomus laevis	1	0.09	1	0.06	0	0.00
	P. leopardus	62	5.70	15	0.85	23	1.23
	P. maculatus	2	0.18	3	0.17	1	0.05
Total Serranidae		95	8.73	55	3.11	64	3.44
Total no. species	17	9		13		12	
Lutjanidae							
	Lutjanus bohar	2	0.18	1	0.06	2	0.11
	L. carponotatus	122	11.21	179	10.11	207	11.11
	L. fulviflamma	128	11.76	139	7.85	112	6.01
	L. fulvus	3	0.28	1	0.06	1	0.05
	L. gibbus	0	0.00	0	0.00	7	0.38
	L. malabaricus	0	0.00	0	0.00	1	0.05
	L. russelli	13	1.19	29	1.64	12	0.64
	L. quinquelineatus	3	0.28	7	0.40	9	0.48
	Symphorus nematophorus	3	0.28	2	0.11	3	0.16
Total Lutjanidae		274	25.18	358	20.21	354	19.00
Total no. species	9	7		7		9	
Lethrinidae							
	Gymnocranius grandoculis	0	0.00	0	0.00	2	0.11
	Lethrinus atkinsoni	31	2.85	15	0.85	34	1.83
	L. harak	7	0.64	9	0.51	9	0.48
	L. lentjan	9	0.83	26	1.47	37	1.99
	L. nebulosus	38	3.49	50	2.82	64	3.44
	L. obsoletus	8	0.74	11	0.62	27	1.45
	L. olivaceus	0	0.00	1	0.06	1	0.05
	L. ornatus	0	0.00	1	0.06	0	0.00
	L. rubrioperculatus	0	0.00	0	0.00	4	0.21
	L. semicinctus	4	0.37	4	0.23	22	1.18
Total Lethrinidae		97	8.92	117	6.61	200	10.74
Total no. species	10	6		8		9	

		Loomis		**Mangrove**		**South**	
Family	*Species*	Total	%	Total	%	Total	%
Nemipteridae							
	Scolopsis affinis	0	0.00	0	0.00	1	0.05
	S. bilineatus	2	0.18	6	0.34	30	1.61
	S. lineatus	0	0.00	3	0.17	1	0.05
	S. margaritifer	0	0.00	18	1.02	24	1.29
	S. monogramma	33	3.03	65	3.67	12	0.64
	S. sp	0	0.00	2	0.11	0	0.00
Total Nemipteridae		35	3.22	94	5.31	68	3.65
Total no. species	6	2		5		5	
Haemulidae							
	Diagramma pictum	46	4.23	97	5.48	14	0.75
	Plectorhinchus celebicus	37	3.40	37	2.09	14	0.75
	P. chaetodonoides	0	0.00	0	0.00	2	0.11
	P. diagrammus	1	0.09	2	0.11	1	0.05
	P. flavomaculatus	0	0.00	0	0.00	3	0.16
	P. goldmanni	19	1.75	6	0.34	7	0.38
	P. obscurum	0	0.00	0	0.00	1	0.05
Total Haemulidae		103	9.47	142	8.02	42	2.25
Total no. species	7	4		4		7	
Siganidae							
	Siganus argenteus	10	0.92	57	3.22	31	1.66
	S. corallinus	3	0.28	67	3.78	21	1.13
	S. doliatus	107	9.83	428	24.17	677	36.34
	S. fuscescens	8	0.74	12	0.68	14	0.75
	S. lineatus	105	9.65	22	1.24	37	1.99
	S. puellus	9	0.83	35	1.98	49	2.63
	S. punctatissimus	0	0.00	14	0.79	23	1.23
	S. punctatus	70	6.43	118	6.66	64	3.44
Total Siganidae		312	28.68	753	42.52	916	49.17
Total no. species	8	7		8		8	
Acanthuridae							
	Acanthurus blochii	6	0.55	2	0.11	2	0.11
	A. dussumieri	5	0.46	29	1.64	5	0.27
	A. mata	2	0.18	0	0.00	0	0.00
	A. nigricauda	1	0.09	5	0.28	1	0.05
	A. xanthopterus	33	3.03	86	4.86	27	1.45
	C. striatus	0	0.00	0	0.00	2	0.11
	Ctenochaetus binotatus	0	0.00	1	0.06	0	0.00
	Zebrasoma veliferum	1	0.09	2	0.11	5	0.27
	Naso annulatus	26	2.39	5	0.28	14	0.75
	N. brevirostris	2	0.18	0	0.00	8	0.43
	N. tuberosus	10	0.92	0	0.00	0	0.00
Total Acanthuridae		86	7.90	130	7.34	64	3.44
Total no. species	11	9		7		9	
Scaridae							
	Scarus flavipectoralis	0	0.00	0	0.00	4	0.21
	S. ghobban	3	0.28	0	0.00	0	0.00

		Loomis		**Mangrove**		**South**	
Family	*Species*	Total	%	Total	%	Total	%
	S. gibbus	0	0.00	0	0.00	1	0.05
	S. niger	0	0.00	0	0.00	1	0.05
	S. psittacus	3	0.28	0	0.00	0	0.00
	S. rivulatus	0	0.00	0	0.00	2	0.11
	S. schlegeli	0	0.00	0	0.00	36	1.93
Total Scaridae		6	0.55	0	0.00	44	2.36
Total no. species	2	2		0		5	
Chaetodontidae							
	Chaetodon aureofasciatus	0	0.00	0	0.00	4	0.21
	C. auriga	12	1.10	1	0.06	12	0.64
	C. melannotus	0	0.00	0	0.00	1	0.05
	C. rainfordi	0	0.00	0	0.00	2	0.11
	C. unimaculatus	0	0.00	0	0.00	0	0.00
	Chelmon rostratus	0	0.00	0	0.00	2	0.11
Total Chaetodontidae		12	1.10	1	0.06	21	1.13
Total no. species	6	1		1		5	
Labridae							
	Cheilinus chlorourus	17	1.56	19	1.07	13	0.70
	C. fasciatus	0	0.00	7	0.40	1	0.05
	Choerodon anchorago	0	0.00	1	0.06	6	0.32
	C. fasciatus	0	0.00	0	0.00	4	0.21
	C. schoenleinii	5	0.46	2	0.11	1	0.05
	Epibulus insidiator	0	0.00	0	0.00	3	0.16
	Hemigymnus melapterus	1	0.09	0	0.00	5	0.27
	Hologymnosus doliatus	1	0.09	0	0.00	1	0.05
Total Labridae		24	2.21	29	1.64	34	1.83
Total no. species	8	4		4		8	
Pomacentridae							
	Dischistodus perspicullatus	5	0.46	59	3.33	6	0.32
	Abudefduf bengalensis	1	0.09	0	0.00	15	0.81
	A. sexfasciatus	0	0.00	0	0.00	0	0.00
	A. septemfasciatus	0	0.00	0	0.00	9	0.48
	Hemiglyphidodon plagiometopon	2	0.18	8	0.45	3	0.16
	Neoglyphidodon melas	3	0.28	0	0.00	1	0.05
Total Pomacentridae		11	1.01	67	3.78	34	1.83
Total no. species	6	4		2		5	
Mullidae							
	Mulloides flavolineatus	0	0.00	0	0.00	1	0.05
	Parupeneus barberinus	0	0.00	3	0.17	2	0.11
	P. ciliatus	1	0.09	0	0.00	4	0.21
	P. indicus	2	0.18	0	0.00	0	0.00
	P. mutifasciatus	2	0.18	0	0.00	5	0.27
	P. trifasciatus	0	0.00	0	0.00	0	0.00
Total Mullidae		5	0.46	3	0.17	12	0.64
Total no. species	6	3		1		4	

		Loomis		**Mangrove**		**South**	
Family	*Species*	Total	%	Total	%	Total	%
Pomacanthidae							
	Pomacanthus semicirculatus	1	0.09	0	0.00	0	0.00
	P. sexstriatus	7	0.64	5	0.28	1	0.05
Total Pomacanthidae		8	0.74	5	0.28	1	0.05
Total no. species	2	2		1		1	
Tetradontidae							
	Arothron hispidus	10	0.92	8	0.45	1	0.05
	A. mappa	0	0.00	0	0.00	0	0.00
	A. nigropunctatus	1	0.09	2	0.11	0	0.00
Total Tetradontidae		11	1.01	10	0.56	1	0.05
Total no. species	3	2		2		1	
Ostracidae							
	Ostracion cubicus	4	0.37	1	0.06	0	0.00
Total Ostracidae		4	0.37	1	0.06	0	0.00
Total no. species	1	1		1		0	
Holocentridae							
	Sargocentron spiniferum	4	0.37	4	0.23	9	0.48
Total Holocentridae		4	0.37	4	0.23	9	0.48
Total no. species	1	1		1		1	
Echeneidae							
	Echeneis naucrates	0	0.00	9	0.51	0	0.00
Total Echenidae		0	0.00	9	0.51	0	0.00
Total no. species	1	0		1		0	
Carangidae							
	Caranx ignobilis	0	0.00	0	0.00	1	0.05
Total Carangidae		0	0.00	0	0.00	1	0.05
Total no. species	1	0		0		1	
Ephipidae							
	Platax tiera	0	0.00	0	0.00	1	0.00
Total Ephipidae		0.	0.00	0	0.00	0	0.00
Total no. species	1	0		0		1	
Kyphosidae							
	Kyphosus cinerascens	1	0.09	0	0.00	0	0.00
Total Kyphosidae		1	0.09	0	0.00	0	0.00
Total no. species	1	1		0		0	
Elasmobranchs							
	Nebrius ferrugineus	0	0.00	0	0.00	1	0.05
	Trianodon obesus	0	0.00	2	0.11	2	0.11
Total Elasmobranchs		0	0.00	2	0.11	2	0.11
Total no. species	2	0		2		2	
Grand Total	**4,736**	**1088**		**1780**		**1868**	
Total no. species	**109**	**65**		**68**		**93**	

Appendix 2a: Distribution of CPUE of *P.leoparus* (no.line^{-1}h^{-1}) among blocks within reefs by trip. Data are sample sizes, means and standard errors by block. B = back reef block, F = front reef block. Block numbers correspond to those in Figure 7.2.

		a			b			c			d			e		
Reef	**blk**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**
Beaver	**1B**	28	6.74	0.95	18	6.41	2.10	41	7.78	1.30	5	12.22	3.39	29	8.88	1.71
	2F	25	4.78	0.86	21	6.26	1.22	8	12.69	5.57	16	5.90	1.51	13	6.29	2.14
	3F	45	7.21	0.93	18	6.71	1.56	24	4.53	1.08	22	7.67	2.13	37	5.52	0.91
	4B	55	2.65	0.54	18	2.01	0.76	9	6.65	1.58	14	5.62	1.36	55	4.20	0.59
	5B	26	2.70	0.80	20	3.34	0.81	10	6.08	2.58	-	-	-	-	-	-
	6B	47	2.85	0.64	16	4.40	0.92	45	8.20	0.96	21	4.77	0.98	14	6.78	1.78
	Reef	**226**	**4.35**	**0.60**	**111**	**4.92**	**0.55**	**137**	**7.44**	**0.67**	**78**	**6.45**	**0.80**	**148**	**5.87**	**0.53**
Taylor	**1B**	34	2.92	0.66	18	5.43	1.30	46	4.40	0.70	19	5.56	1.16	17	2.53	0.74
	2B	59	3.62	0.58	21	3.57	0.90	27	5.90	1.22	20	3.06	0.74	13	1.94	0.72
	3B	52	2.52	0.50	27	5.39	1.33	17	6.60	1.64	9	15.16	5.78	68	1.95	0.37
	4F	-	-	-	17	1.92	0.52	-	-	-	20	7.67	1.86	38	2.73	0.68
	5F	-	-	-	8	0.98	0.54	-	-	-	8	6.77	3.59	-	-	-
	6F	-	-	-	19	2.56	1.08	-	-	-	9	2.14	1.31	-	-	-
	Reef	**145**	**3.06**	**0.33**	**110**	**3.45**	**0.19**	**90**	**5.26**	**0.60**	**85**	**6.24**	**0.94**	**136**	**2.24**	**0.29**
F'harson	**1B**	53	3.12	0.60	13	5.82	1.66	16	3.42	0.67	20	2.01	0.69	20	2.06	0.63
	2B	-	-	-	23	9.39	3.14	-	-	-	17	5.86	1.17	22	3.84	0.99
	3B	-	-	-	23	1.60	1.06	-	-	-	11	2.44	1.05	-	-	-
	4F	-	-	-	3	0.80	0.80	-	-	-	9	7.36	1.23	-	-	-
	5F	-	-	-	3	1.17	0.60	-	-	-	14	4.07	1.63	-	-	-
	6F	-	-	-	3	1.11	1.11	-	-	-	11	7.95	3.03	-	-	-
	7F	-	-	-	25	5.59	1.13	-	-	-	11	3.46	1.31	-	-	-
	8B	71	3.24	0.42	17	7.83	1.71	-	-	-	23	9.07	2.65	4	0.71	0.71
	9B	78	3.11	0.46	11	5.22	1.36	8	4.83	1.38	30	3.99	0.79	23	4.48	1.07
	Reef	**202**	**3.16**	**0.28**	**121**	**5.06**	**0.72**	**24**	**3.89**	**0.64**	**146**	**5.09**	**0.59**	**69**	**3.36**	**0.52**
L' Potter	**1B**	73	3.33	0.45	54	4.71	0.69	-	-	-	40	5.52	0.85	63	4.41	0.69
	2F	-	-	-	41	1.60	0.35	-	-	-	37	6.32	1.04	36	3.60	0.78
	Reef	**73**	**3.33**	**0.45**	**95**	**3.40**	**0.45**	**-**	**-**	**-**	**77**	**5.90**	**0.66**	**99**	**4.15**	**0.52**
Potter	**1B**	43	1.78	0.39	26	6.18	2.14	25	5.34	1.02	12	2.67	0.85	-	-	-
	2B	102	2.93	0.39	31	9.71	1.49	34	2.93	0.62	22	4.17	1.09	23	7.62	1.13
	3B	62	1.50	0.29	38	4.73	1.24	25	3.33	0.65	21	4.45	1.02	51	3.36	0.53
	4F	-	-	-	6	5.62	3.30	-	-	-	28	4.92	1.27	25	2.58	0.56
	5F	-	-	-	22	1.57	0.56	-	-	-	12	2.71	1.17	-	-	-
	6F	-	-	-	16	0.63	0.44	-	-	-	11	2.19	0.92	-	-	-
	Reef	**207**	**2.26**	**0.45**	**139**	**4.84**	**0.65**	**84**	**3.77**	**0.45**	**106**	**3.88**	**0.49**	**99**	**4.15**	**0.44**

Appendix 2b: Distribution of mean length to caudal fork of *P.leoparus* (mm) among blocks within reefs by trip. Data are sample sizes, means and standard errors by block. B=back reef block, F=front reef block. Block numbers correspond to those in Figure 7.2.

		a			b			c			d			e		
Reef		**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**	**n**	**Mn**	**SE**
Beaver	**1B**	87	413	7.63	27	385	12.00	143	401	5.08	22	378	10.28	102	386	5.77
	2F	47	405	10.49	51	409	7.72	54	393	8.64	35	383	9.67	17	425	16.33
	3F	148	427	6.07	51	419	8.00	44	419	10.85	51	401	8.09	3	418	26.30
	4B	56	424	10.17	16	405	14.67	21	378	11.02	44	409	10.04	10	373	24.53
	5B	21	377	11.85	24	407	13.83	23	384	10.34	-	-	-	-	-	-
	6B	53	396	9.62	28	385	10.65	160	393	4.92	40	377	8.69	45	363	5.64
	Reef	**412**	**414**	**3.60**	**197**	**404**	**4.24**	**445**	**397**	**2.95**	**192**	**392**	**4.28**	**177**	**384**	**4.36**
Taylor	**1B**	49	440	9.83	49	455	10.69	68	427	9.00	48	442	12.67	21	414	13.29
	2B	82	420	7.31	34	430	10.30	75	411	7.39	25	401	13.56	12	369	13.15
	3B	63	450	10.82	58	425	7.26	34	429	13.47	31	429	15.36	49	397	9.48
	4F	-	-	-	14	421	14.62	-	-	-	46	405	11.57	27	413	16.46
	5F	-	-	-	3	440	25.06	-	-	-	15	456	20.82	-	-	-
	6F	-	-	-	15	429	16.22	-	-	-	11	435	21.17	-	-	-
	Reef	**194**	**435**	**5.37**	**173**	**435**	**4.83**	**177**	**421**	**5.35**	**176**	**425**	**6.19**	**109**	**401**	**6.67**
F'harson	**1B**	68	436	8.86	37	400	8.65	19	391	18.79	16	365	17.55	15	372	12.18
	2B	-	-	-	86	425	4.75	-	-	-	46	414	12.84	24	359	10.67
	3F	-	-	-	8	352	20.98	-	-	-	9	372	27.73	-	-	-
	4F	-	-	-	1	375		-	-	-	19	414	14.54	-	-	-
	5F	-	-	-	2	403	28.50	-	-	-	18	417	14.68	-	-	-
	6F	-	-	-	1	413		-	-	-	31	417	12.13	-	-	-
	7F	-	-	-	61	428	7.53	-	-	-	15	381	20.75	-	-	-
	8B	104	408	6.69	71	422	7.99	-	-	-	65	431	9.75	1	385	-
	9B	83	420	7.50	21	408	15.71	14	408	18.34	46	390	11.38	33	361	9.90
	Reef	**255**	**419**	**4.40**	**288**	**418**	**3.45**	**36**	**391**	**12.91**	**265**	**408**	**4.80**	**73**	**363**	**6.21**
L' Potter	**1B**	104	417	6.77	120	412	5.21	-	-	-	101	396	7.60	109	393	5.68
	2F	-	-	-	31	401	8.69	-	-	-	73	411	7.88	42	418	12.13
	Reef	**104**	**417**	**6.81**	**151**	**410**	**4.52**	**-**	**-**	**-**	**174**	**402**	**5.54**	**151**	**400**	**5.39**
Potter	**1B**	39	418	11.31	70	425	6.52	56	412	10.38	14	428	15.88	-	-	-
	2B	106	410	6.96	131	433	5.42	40	406	11.09	32	424	14.03	74	399	8.50
	3B	43	398	10.33	56	419	6.69	42	402	10.61	40	418	11.04	61	401	8.91
	4F	-	-	-	12	410	18.19	-	-	-	51	420	9.78	23	405	11.37
	5F	-	-	-	13	387	10.92	-	-	-	13	409	18.22	-	-	-
	6F	-	-	-	2	367	0.50	-	-	-	9	433	10.84	-	-	-
	Reef	**188**	**409**	**5.16**	**284**	**425**	**3.43**	**138**	**407**	**6.19**	**159**	**421**	**5.45**	**158**	**401**	**5.50**