Inter- and intra-habitat movement patterns and population dynamics of small reef fishes of commercial and recreational significance

Thesis submitted by

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This work is dedicated to my wife,

Teresa,

and to our children,

Aaron, Judith and Thea

to whom I owe so much...

... fisheries science will not advance much further

unless management becomes experimental ...

If we wait much longer,

many decisions will have been made by default,

the consequences of which may be hard to undo.

P.A. Larkin 1978

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

(Vincent V. Hilomen)

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ABSTRACT

This research examined smaller reef fishes of commercial and recreational fishing significance (i.e. snappers, emperors and groupers) on the Great Barrier Reef (GBR), Australia. Four questions of importance to reef fish ecology and reef fisheries science were addressed. These were *i*) identification of patterns of distribution and abundance; *ii*) quantification of local patterns of inter- and intra-habitat movements of post-settlement reef fishes in six habitat types in a lagoon; and for *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*, *iii*) the estimation of age, growth and mortality rates and *iv*) estimation of size and age at first sexual maturity.

Antillean Z-traps were used to determine patterns of distribution and abundance of reef fishes in six types of habitat in a lagoon at Lizard Island, GBR. The habitats were *i*) deep sand away from reefs (DSAR), *ii*) deep sand near reefs (DSNR), *iii*) rubble areas (RUBB), *iv*) slopes of reefs (SLOP), *v*) shallow sand near reefs (SSNR) and *vi*) tops of reefs (TOPS). Variations in catch composition and abundance between day and night soaks in these 6 habitats were measured on 7 sampling occasions over a period of 30 months. Data were analyzed using a 3-way fixed ANOVA model (factors were 7 sampling occasions, 6 habitat types and 2 soak times). Habitat types and soak time were the most important factors in explaining variation in catch composition and abundance for most species of reef fish. In general, abundance and species richness were significantly higher at the TOPS and SLOP habitats and lower in the SSNR and DSAR habitats. The DSNR and RUBB habitats had intermediate numbers of species and individuals. DSNR and RUBB habitats were more similar to TOPS and SLOP habitats in terms of species composition than to SSNR and DSAR but were more similar to SSNR and DSAR in terms of abundances. Overall, more individuals and species were caught during night than day in all habitats except in TOPS. The abundances of many lutjanids and lethrinids were higher at night than day in sandy habitats (DSNR, DSAR and SSNR). The abundances of apogonids and holocentrids were higher at night than day in reefal habitats (TOPS and SLOP). In contrast, the abundances of pomacentrids and labrids were significantly higher during the day than at night in reefal habitats.

A TWo-way INdicator SPecies ANalysis (TWINSPAN) on the catch information (120 species by 84 samples of 6 replicate traps; i.e. 7 sampling times by 6 habitat types by 2 soak times) revealed two distinct fish assemblages associated with a) reefal and rubble, and b) sandy habitats. These assemblages changed over a diel period with each of the two 'habitat-based' assemblages showing a distinct day and night fish composition. The nocturnal fish assemblage in sandy habitats further differentiated into two groups, one near and the other away from reefs.

The results indicated the importance of habitats in the local distribution of reef fishes. The present study confirms the significance of habitats as a source of shelter and food resources for reef fishes. The shifts in fish composition between day and night suggested differential movement patterns of fishes from hiding places to feeding areas. Many of the lutjanids, apogonids and holocentrids hid whilst pomacentrids and labrids foraged in reefal habitats by day. By night, pomacentrids and labrids sought shelter whilst apogonids and holocentrids foraged within reefal habitats. Some lutjanids moved to sandy habitats near reefs, while others moved further away from reefs at night to forage. The sandy habitat appeared depauperate during the day but many species, particularly *Lutjanus fulviflamma*, *Lethrinus lentjan* and *L. nebulosus*, frequented this habitat at night.

A mark-recapture technique was used to determine levels and patterns of movement within and between habitat types for lutjanids, lethrinids and serranids. Distances moved were categorized in intervals of 30 m, based on the minimum distance between deployed traps. Results showed that 74% of movements (n=286) were within and 26% were between habitats. These fishes exhibited strong habitat fidelity except in the shallow TOPS habitat, and a high propensity for short distance movements of 30-60 m. Movements within habitats greater than 100 m comprised 20% of the total and only 5% of movements were greater than 500 m. Movements between habitats greater than 100 m comprised 42% of the total and only 5% of movements were greater than 500 m. Large distance movements (100-1500 m) across vast expanses of deep sand were recorded for some reef species (e.g. *Lethrinus nebulosus*, *Lutjanus carponotatus*, and *L. fulviflamma*), but were rare. *Lethrinus nebulosus* appeared to move larger distances than the other species. The number of movements during the night was significantly

higher in SLOP and DSNR habitats than during the day but the distances moved did not differ between night and day. These findings are relevant to the design and location of marine reserves as management tools in coral reef fisheries. Knowledge of movement patterns of reef fish is essential in measuring flux rates of reef fishes across reserve boundaries to adjacent fished areas.

Mark-recapture and aquarium experiments combined with tetracycline (OTC) injection were used to validate the periodicity of opaque bands in sectioned otoliths of *Lutjanus fulviflamma*, *Lethrinus harak*, and *L. lentjan*. Three experiments were conducted on a total of 57 fishes covering a wide range of ages and sizes. Of these, 10 *Lutjanus fulviflamma*, 8 *Lethrinus harak* and 15 *L. lentjan* survived long enough to provide useful information. Results showed an opaque band outside the tetracycline mark and well below the otolith margin in sectioned otoliths of specimens surviving more than a year after OTC treatment (3 of 10 *Lutjanus fulviflamma* and 3 of 15 *Lethrinus lentjan*) or for those which survived from July to March (2 *L. lentjan*). In the case of *Lethrinus harak* no specimen survived more than a year post OTC treatment. The periodicity of formation of opaque bands in otoliths of *L. harak* was assessed indirectly by examination of the distance between the OTC mark and the otolith margin. This distance represented a known period of otolith growth. It corresponded to a fraction of the distance between any two consecutive opaque bands in older fishes (after the third band). This fraction was proportional to the survival period of fish after OTC injection and suggested that the distance between two consecutive opaque bands was roughly equivalent to a year's growth (in 4 of 8 *L. harak*). This suggests that the opaque bands in *L. harak* were formed once each year. Thus, the opaque bands in sectioned otoliths of *Lutjanus fulviflamma*, *Lethrinus lentjan* and *L. harak* were confirmed to be annuli and were determined to be laid down during the months of August to December at Lizard Island, GBR.

Age determination of fishes based on the validated counts of opaque bands in sectioned otoliths showed a high percentage of agreement and a low index of average percentage error (IAPE) among readers, demonstrating the technique to be highly reliable, precise and accurate. Estimates of von Bertalanffy growth parameters (L_∞ (mm FL), K and t_0, respectively, ± SE) obtained using the above method were 246.3 (±3.5), 0.261 (±0.037)

and -4.377 (±0.640) for *Lutjanus fulviflamma* (n=176), 285.0 (±5.0), 0.313 (±0.050) and -3.159 (±0.567) for *Lethrinus harak* (n=132) and 307.2 (±6.8), 0.345 (±0.047) and -2.202 (±0.290) for *L. lentjan* (n=117). Maximum age observed for *Lutjanus fulviflamma* was 17 years, 15 years for *Lethrinus harak* and 14 years for *L. lentjan*. Estimates of natural mortality rate (M ±SE) from age-based catch curves were 0.231 (±0.035) for *Lutjanus fulviflamma*, 0.381 (±0.097) for *Lethrinus harak* and 0.305 (±0.078) for *L. lentjan*. Thus, these three species were long lived, slow growing (but with an initial phase of rapid growth) and had low rates of natural mortality. This information has important implications to the management of the fishery of these species in the future. Their life history characteristics imply that they may be vulnerable to intense exploitation.

Histological examination was performed on gonads of *Lethrinus harak* (n=131), *L. lentjan* (n=96) and *Lutjanus fulviflamma* (n=94; females only) to assess stages of oocyte development. Age and size at first sexual maturity for the 3 species were determined as where 50% of samples in an age or size class attained maturity. Results showed that *Lethrinus harak* reached sexual maturity at 2 years of age and at a size of 220-229 mm FL, *L. lentjan* at 3 years and 250-259 mm FL and *Lutjanus fulviflamma* at 2-3 years and 200-209 mm FL. The presence of an ovarian lumen, brown bodies, the lobed arrangement of spermatogonia, the thicker gonad wall of younger males, and the female biased sex-ratios at younger ages and at smaller sizes were evidence consistent with protogynous hermaphroditism for *Lethrinus harak* and *L. lentjan*. *Lutjanus fulviflamma* was gonochoristic This information forms an important basis for setting legal minimum size limits for these species on the GBR.

The information gained in this study is highly relevant to coral reef fisheries management. The data on movement patterns of reef fishes are particularly useful in testing the utility of marine reserves as a management option. The information on the life history characteristics of *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan* provide the first data for these species on the GBR. This research stresses the need for age-based methods of estimating important life history characteristics of other species in the future.

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Chapter 1. GENERAL INTRODUCTION

1.1 INTRODUCTION

The levels of fishing mortality on reef fishes, particularly in most developing nations, have reached dangerous levels, with the limit to "wild" marine fisheries catches reached many years ago (FAO 1994). This is reflected in the continuing decline of stock abundances as fishing effort is increased (Richards and Megrey 1994). This is particularly true in reef areas near population centers in developing nations where fish are often a main source of animal protein (Carpenter 1977, Munro 1983a, Alcala and Gomez 1985) and fishing is the main source of income and employment (e.g. Russ 1991, McManus *et al.* 1992). The stocks of larger favored predatory species such as groupers, lutjanids and lethrinids in many reef areas of developing nations are precariously low, and likely to be recruitment overfished (Munro 1996). Even in developed nations such as in southeast USA, stocks of reef fish are as low as 5-10% of the original spawning stock (Plan Development Team (PDT) 1990). In some cases, unabated intense fishing has resulted in changes of reef fish communities to less desirable species combinations (i.e. ecosystem overfishing) (e.g. Russ 1991, Jennings and Lock 1996, McManus *in press*). Koslow *et al.* (1988) found that 15 years of increasing fishing effort reduced fish communities in the Pedro Cays, Jamaica dominated by lutjanids and scarids to ones dominated by boxfishes, pufferfishes and squirrelfishes. Even a short period of intense fishing (e.g. 18 months) drastically altered densities of more favored species and significantly changed community structure of reef fishes (Russ and Alcala 1989). Russ (1991) and Jennings and Lock (1996) reviewed coral reef fisheries and provided evaluations of the effects of fishing on coral reef fishes.

The degraded state of coral reef fishery resources in most developing countries has largely been attributed to rapid human population growth and widespread poverty (Carpenter 1977, Yap and Gomez 1985, Pauly 1988, Russ 1991, McManus *in press*). Generally, there are too many users and not enough resources. This has led to a steadily increasing fishing effort such that reef fishery resources are near collapse. In many situations, small scale fishermen resort to wholesale resource destruction in an effort to maintain incomes without regard to future generations (Pauly 1988, Russ 1991). This declining state of reef fisheries in developing countries can be placed in check if effort is drastically reduced (e.g. McManus 1996) and novel approaches to coral reef fisheries management such as establishment of spatial reef refuges are installed (e.g. Bohnsack 1996, Russ 1996). McManus (1996) proposed that, as a general guideline, a 60% reduction in effort (usually number of fishers) will bring maximum economic yield (MEY). Spatial reef refuges (marine reserves) may be one of the few management options available to maintain levels of spawning stock biomass necessary to sustain reef fisheries (PDT 1990, Bohnsack 1996, Russ and Alcala 1996b, Russ 1996).

Coral reef fisheries in developed nations, such as Australia, generally inflict far less fishing mortality on most species of reef fish. The fisheries on the Great Barrier Reef (GBR), Australia use one fishing gear (hook and line) to target 5 to 10 species of large serranids, lutjanids and lethrinids. This line fishery does take a considerable number of species as "by catch" (e.g. 72 species reported in QFMA 1996). This still constitutes a very small percentage of the 1500 species of reef fish on the GBR. However, this situation is changing rapidly. The expansion of the 'live reef fish' trade to Asia means that a much wider variety of reef fish will soon be targeted (QFMA 1996).

This study focuses on the biology of smaller coral reef fishes of commercial and recreational fishing significance (i.e. snappers, emperors and groupers) which comprise a 20-30% "by catch" of the line fishery on the GBR (Trainor 1991). This group of fish, collectively referred to as 'other reef fishes' or 'mixed reef species' in the catch data, constitute 18 of 24 lutjanid species, 18 of 20 lethrinid species and 19 of 25 serranid species. These species are defined by the Queensland Fisheries Management Authority (QFMA) as part of the demersal line fishery on the GBR (QFMA 1996). As such, the contribution of individual species to the catch is difficult to assess. The present study

provides important information on the local distribution and movement patterns of several of these species and makes estimates of the fundamental life history characteristics of age and longevity, growth, mortality and age and size at first sexual maturity of three important "by catch" species (*Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*).

On the GBR, five stakeholder groups use the tropical coral reef resources. These are the commercial fishers, recreational fishers, indigenous fishers, charter fishing boat operators and the passive users of fish stocks (QFMA 1996). The first two have the largest impact on the reef fishery resources of the GBR. Estimates of catches from the commercial reef-line fishery in Queensland indicate an increasing level of harvest on the GBR between 1966/67 and 1990, although it was widely acknowledged that catch estimates before 1988 were underestimates (Williams and Russ 1994). Reliable catch records for the commercial fishers became available in 1988. The total commercial reef catch landed from various sources in Queensland increased by more than 50% from 1815 mt in 1988 to 2791 mt in 1990 (Table 12 in Williams and Russ 1994). Similarly, the commercial reef catch for coral trout (*Plectropomus leopardus*) increased by 32% from 1016 mt in 1988 to 1490 in 1990 (Table 12 in Williams and Russ 1994). The estimated landings of red emperors (*Lutjanus sebae*) and red throat emperors (*Lethrinus miniatus*), and 'other reef fishes' from the same area increased by more than 60% from 799 mt in 1988 to 1301 mt in 1990 (Table 12 in Williams and Russ 1994). It is important to note that the catches of 'other reef fishes' increased by 50% between 1989 and 1990 and have since remained relatively consistent up to 1994 (Mapstone *et al.* 1996). Information on catch and fishing effort for the line fishery prior to 1988 was limited. In a descriptive study of the commercial reef line fishery, Mapstone *et al.* (1996) reported that the overall effort on red throat emperor and 'other reef species' had remained fairly stable between 1989 and 1994.

Recreational fishing on the GBR is favorite pastime among many Australians and various public reef activities have increased steadily over the past two decades. Blamey and Hundloe (1991) estimated a large proportion (68%) of private motor boats visit and fish the 300,000 km^2 GBR marine park. This represented about 24,300 private motor boats and comparisons with a study a decade earlier suggested that the number of boat

owners who fished at sea had increased by 56% in the Rockhampton region, 89% in the Mackay region, 47% in the Townsville region and 73% in the Cairns region (QFMA 1996). In 1990, the total catch of the small-boat recreational fleet on the GBR was estimated at 3500-4300 mt of reef fish and pelagics (Blamey and Hundloe 1991), although others speculated that the catch could be 3 to 4 times that of the commercial line fishery (Williams and Russ 1994). Although a new comprehensive data collection system is currently in place (QFMA 1996), limited data on catch composition and effort are available from this recreational group (e.g. Higgs 1993). There is evidence however, that the current level of exploitation on the GBR has resulted in localized depletion of favored species such as the coral trout (*Plectropomus leopardus* -Serranidae) and red throat emperor (*Lethrinus miniatus* -Lethrinidae) in areas close to population centers (Ayling and Ayling 1985).

The current level of exploitation on the GBR and elsewhere in Australia is expected to increase in the future. On the GBR, the significance of the small lutjanids, lethrinids and groupers is anticipated to increase when the fishery expands, as effort on presently favored stocks (e.g. *P. leopardus*, *Lutjanus sebae*, *L. malabaricus*, *L. erythropterus*, *Lethrinus miniatus*, *L. nebulosus*) increases further and markets for pan-sized and live fish develop (Williams and Russ 1994). A strong possibility for increased fishing pressure on the tropical coral reef species on the GBR exists as more commercial fishermen could shift into the reef line fishery from the trawl fisheries, and as the private small boat fleet increases further in the future. These pose a major concern to efforts at sustaining a viable fishery and must be addressed appropriately and immediately.

1.2 INFORMATION GAPS

Despite the current level of exploitation of reef fish species on the GBR and the alarming state of the coral reef fisheries in most developing countries, little is known about the distribution and abundance, the habitats and the fundamental life history characteristics of many exploited reef fishes (Kailola *et al.* 1993, Williams and Russ

1994, Polunin and Roberts 1996). A detailed review of the critical information gaps for these species on the GBR was provided by Williams and Russ (1994). Available information on distributions and habitats of many of lutjanid, lethrinid and serranid species is incomplete and at best broadly descriptive. Data on distributions of juvenile fish and distribution and abundance of fish below the limits of routine SCUBA surveys are lacking on the GBR.

At present, information on age, growth and mortality rates exist only for 6 of 24 species of lutjanid, 2 of 20 species of lethrinid and 2 of 4 species of *Plectropomus* on the GBR (Williams and Russ 1994). Information on age, growth and mortality of *Lutjanus sebae*, *L. malabaricus* and *L. erythropterus* was supplied by McPherson and Squire (1992), for *L. russelli* by Sheaves (1995a), for *L. carponotatus* by Davies (1995), for *L. adetii* and *L. quinquelineatus* by Newman *et al.* (1996a), for *Lethrinus miniatus* by Walker (1975) and Brown *et al.* 1994, for *L. nebulosus* by McPherson *et al.* (1988), for *Plectropomus maculatus* by Ferreira and Russ (1992) and for *P. leopardus* by Ferreira and Russ (1994). Estimates of growth and mortality rates exist for several species known to occur on the GBR from studies conducted elsewhere. These studies varied in the methods used to estimate growth and mortality parameters (e.g. otoliths, length frequency, vertebra; Tables 9 and 10 in Williams and Russ 1994).

Similarly, information on reproductive biology of many targeted species on the GBR is limited. Critical information on size and age at first sexual maturity is available for 4 of 20 species of lethrinid (*Lethrinus miniatus*, *L. nebulosus*, *L. semicinctus* and *Lethrinus* sp.2) (Walker 1975, Brown *et al.* 1994, G.R. Russ, J. Higgs and B.P. Ferreira unpubl. data) and 2 of 4 species of *Plectropomus* (*P. leopardus* (Goeden 1978, Ferreira 1995) and *P. maculatus* (Ferreira 1993b)) on the GBR. Similar data for lutjanids on the GBR exist for 3 of 24 species of lutjanid (*Lutjanus sebae*, *L. malabaricus* and *L. erythropterus*) (McPherson *et al.* 1992). Data for sexual patterns of 8 species of lethrinid on the GBR exist but are incomplete (Young and Martin 1982) while all serranids that have been studied in detail elsewhere have been protogynous hermaphrodites (Shapiro 1987). In the GBR, information on sexual patterns exist for *P. leopardus* (Goeden 1978, Ferreira 1995) and *P. maculatus* (Ferreira 1993b). The seasonality of spawning activity

of three species of lutjanid (same as above) on the GBR is provided by McPherson *et al.* 1992. All lutjanid species are believed to be gonochoristic (see Grimes 1987).

1.3 THE IMPORTANCE OF DISTRIBUTION AND ABUNDANCE, HABITATS, AND LIFE HISTORY CHARACTERISTICS

Basic information on distribution, abundance and life histories are important for resource management and for achieving sustainable use of these renewable resources. Rosenberg *et al.* (1993) stressed that sustainable use of renewable resources is attainable primarily because there is a sound theoretical and empirical basis for it. For example, the knowledge that these exploited species undergo a two-stage life cycle means larval dispersal (Leis 1987, 1991) and settlement of fish (Victor 1991) are important mechanisms affecting the dynamics of these resources. Information on how they disperse, where they go and the duration of larval stages has strong implications to the management of stocks. Knowledge of the distributions and types of habitat used by juvenile and adult fish may improve the understanding and significance of nearshore habitats and reef areas. This information is critical when fish begin to recruit to the fishery. Chapter 3 of this thesis provides data on the local distribution of adult individuals in 6 different habitat types in a lagoon.

Life history characteristics such as age, growth and mortality rates together with knowledge of reproduction form the backbone of population dynamics. In fisheries science, it is critical to determine age and longevity of fish using methods that are reliable. When ages of individuals in a population are known, the number of individuals in each age class (population age structure) provides a picture of the status of that population. The method of age determination is the key to reliable estimates of growth and mortality rates. Age determination of fish by validated counts of opaque bands in sectioned otoliths have proven to be highly reliable (e.g. Worthington *et al.* 1995, Newman *et al.* 1996a). Estimates of growth and mortality rates based on validated age-determination techniques provide more reliable information for stock assessment (Russ

1991, Williams and Russ 1994). These estimates are key elements in analytical models used to predict potential yields of stocks. Chapter 5 of the present study determines the age of three important species on the GBR by validated counts of opaque bands in sectioned otoliths. Parameters of growth and mortality rates were estimated by age-based methods.

Knowledge of the reproductive biology of exploited populations is an essential part of management (Sadovy 1996). Age and size at first sexual maturity are important parameters in stock assessment. Estimates of these parameters form the basis for setting legal minimum size limits for captured fish. Other important aspects of reproduction are sexual patterns and patterns of spawning behavior. Identifying the type of sexual pattern of an exploited population helps managers devise appropriate management plans for the fishery. For example, the protection of the larger-sized fish in protogynous populations is important in order to maintain a viable female to male population ratio (Bannerot *et al.* 1987, Sadovy 1996). Additionally, knowledge of spawning behavior and the location of spawning aggregation sites may help in protecting an important activity of the population if these areas are closed during the spawning season. In the present study, Chapter 6 examines the age and size at first sexual maturity and provides an initial description of the sexual pattern of three important species.

1.4 THE CONCEPT OF MARINE RESERVES

A number of factors makes practical management of coral reef fisheries difficult and complicated. These are a) the large number of targeted species, b) the large number of fishing gears used, c) the large number of sites where catch could be landed, d) the fact that fishers are often poor with few employment alternatives, e) the high degree of complexity of biological interactions and f) different and often conflicting objectives of users (PDT 1990, Russ 1991). The large number of species in the fisheries invariably involves a diverse range of life history characteristics, many of which are poorly understood. The large number of gears used by subsistence fishers and the numerous

small landing sites spread over a large geographic area make collection of basic catch and effort data complicated, expensive and often impractical. The degree of understanding of biological interactions between reef species is still limited (Sale 1991). The conflict of interest among users (maximizing income whilst fishing at sustainable levels) often leads to a breakdown of management (e.g. Russ and Alcala 1994). The rapid human population growth and widespread poverty exacerbate the situation in many developing countries. All of the above contribute to the general lack of success of conventional management of coral reef fisheries worldwide.

The sheer complexity of coral reef fisheries has made many of the traditional management practices impractical. Under such circumstances the idea of marine reserves as a potential management tool is popular (PDT 1990, Alcala and Russ 1990, Dugan and Davis 1993a, DeMartini 1993, Bohnsack 1993, 1996, Russ and Alcala 1994). Marine reserves were first implemented in the 1930's in Florida (PDT 1990). These are areas of the marine environment protected from various forms of human exploitation, principally fishing (Davis and Dodrill 1980, Roberts and Polunin 1991, Carr and Reed 1993, Russ and Alcala 1996b). Recently, the use of marine reserves has been advocated in the management of coral reef fisheries (Alcala 1988, PDT 1990, Polacheck 1990, Carr and Reed 1993, DeMartini 1993, Dugan and Davis 1993a, Russ and Alcala 1994, 1996a and b). Much of the enthusiasm for the concept of marine reserves can be drawn from the potential benefits they offer. The major potential benefits are:

- the protection of a critical minimum spawning stock biomass from depletion by the fishery (e.g. PDT 1990, Carr and Reed 1993, Dugan and Davis 1993a, Russ and Alcala 1996b),

- ensured recruitment supply to fished areas (e.g. PDT 1990, Dugan and Davis 1993a, Russ and Alcala 1996a and b) via larval dispersal (e.g. Doherty and Williams 1988, Doherty 1991, Leis 1991, Victor 1991),

- possible maintenance or enhancement of yields in adjacent fished areas by movements of adults (i.e. post-settlement movement) (e.g Alcala and Russ 1990, Attwood and Bennett 1994, Russ and Alcala 1996a, Zeller and Russ submitted MS).

PDT (1990), Dugan and Davis (1993a) and Bohnsack (1996) list many other benefits. Among these are insurance against management failure, simplified enforcement, increased management flexibility, and maintenance of population and community diversity. All of these potential benefits add to the appeal of marine reserves in the management of coral reef fisheries, particularly in developing countries.

Two of the drawbacks of marine reserves are that they remove a certain proportion of the stocks from the fisheries and the fact that their ability to achieve the goals above remains virtually untested. Testing the benefits of marine reserves may take some time as changes will not likely be detected in the short term (Dugan and Davis 1993a). This is due to the life history characteristics of many reef fishes, particularly the relatively recent recognition that many may be long-lived, slow growing (but with a phase of rapid growth during the first 2-3 years) and with a low rate of natural mortality (e.g. Fowler 1990b, Fowler and Doherty 1992, Choat and Axe 1996, Choat *et al.* 1996, Newman *et al.* 1996a, Chapter 5 this study).

However, evidence indicates that abundance and size of target species increase within marine reserves (e.g. Bennett and Attwood 1991, Russ and Alcala 1996b). Simulations by DeMartini (1993) showed that maximum gains in spawning stock biomass per recruit (SSB/R) were possible for 'surgeonfish' type life histories, characterized as fast-growing, medium sized and relatively vagile reef fish. For the larger bodied 'jack' type species, characterized as slow growing, long lived and vagile, gains in SSB/R were only attainable with large reserves and low fishing mortality. It is worthwhile to note that these simulations corroborate findings of Polacheck (1990) and Russ *et al.* (1993) showing that marine reserves will increase yield per recruit under high levels of fishing mortality and high rates of transfer. These findings require further study.

To date there is no empirical evidence to show that the reproductive output of the protected spawning stock increases in marine reserves, nor has evidence of enhanced recruitment supply to fished areas from marine reserves been documented. However, movement of adults from reserves to fished areas, with subsequent impacts on adjacent fisheries, has been shown by Alcala and Russ (1990), Attwood and Bennett (1994) and Russ and Alcala (1996a). However, proper documentation of such effects require

measurement of flux rates of fish across reserve boundaries. This requires quantification of movement patterns of reef fish.

Recently, the significance of movements of fishes to population dynamics and to fisheries has become increasingly emphasized (e.g. Robertson 1988, Hestbeck *et al.* 1991, Hilborn 1990, Hilborn et al. 1990, Schwarz and Arnason 1990, Hilborn and Walters 1992, Schwarz *et al.* 1993, Schweigert and Schwarz. 1993). A good understanding of movement patterns of reef fishes is essential in the context of use of marine reserves as management tools for coral reef fisheries (e.g. Alcala and Russ 1990, PDT 1990, Roberts and Polunin 1991, DeMartini 1993, Russ and Alcala 1996a and b). Information about movement of reef fishes will aid in design of and in the testing of the benefits of marine reserves, particularly any enhancement of yield in adjacent fished areas by the 'spillover' effect (Russ and Alcala 1996a). In many developing countries a clear demonstration of directed movement of reef fish from reserves to adjacent fished areas is important to help gain support of the local community in the establishment of marine reserves (Russ and Alcala 1996a). Chapter 3 of the present study examines local inter- and intra-habitat movement patterns of several species of reef fish and makes estimates of distances moved.

1.5 SPECIFIC OBJECTIVES OF THE THESIS

This thesis investigates the biology of smaller members of the Lutjanidae, Lethrinidae and Serranidae. The study aims to provide some of the first quantitative data on levels of local movement patterns of lutjanids, lethrinids and serranids, and to examine spatial and temporal (diel and on scales of several months) patterns of distribution and abundance of reef fishes in six different habitat types in the Lizard Island lagoon on the GBR. It also aims to provide the first estimates of age and longevity, growth and mortality rates, and age and size at first sexual maturation of *Lutjanus*

fulviflamma, *Lethrinus harak* and *L. lentjan* on the GBR. The specific objectives of this thesis are:

- To describe patterns of distribution and abundance of reef fishes in specific habitats within a coral reef lagoon and to determine the temporal (diel and several-months scales) variability in these patterns;
- To determine inter- and intra-habitat movement patterns of lutjanids, lethrinids and serranids and to estimate distances moved;
- To estimate age and longevity, growth and mortality rates of *L. fulviflamma*, *L. harak* and *L. lentjan* using validated age-based techniques; and
- To estimate age and size at first sexual maturation of *L. fulviflamma*, *L. harak* and *L. lentjan*.

Chapter 2. EXPERIMENTAL DESIGN AND METHODS

2.1 INTRODUCTION

This chapter describes the general field methods used in this work. It details a capture-mark-recapture study used in the assessment of patterns of distribution and movements of small reef fishes. Modified Antillean Z-traps were utilized as sampling devices. Crossland (1976) found that Z-traps were more efficient than rectangular and cylindrical traps in terms of catch rates and composition. Trapping is a non-destructive sampling technique well suited to demographic studies of fishes (e.g. Sheaves 1992, Davies 1995 Newman *et al.* 1996a and b, this study). These traps were utilized to sample six different habitat types at Lizard Island lagoon on 7 occasions over a period of 30 months. Using this technique, it was possible to determine habitat preferences of reef fishes, inter and intra-habitat and diel movement patterns, distribution and abundance, catch rates and catch composition, as well as study age determination and growth patterns of the target fishes. Specific laboratory and analytical methods relating to a data chapter are described within that chapter.

2.2 THE STUDY SITE

This study was conducted at Lizard Island (latitude 14° 40' S, longitude 145° 28'), northern Great Barrier Reef (GBR), Australia. Lizard Island is located approximately 30 km from the east coast of northern Queensland and falls under the category of a mid-shelf reef of the GBR (Fig. 2.1). The study area included the lagoon enclosed by two neighboring islands Palfrey and South, and nearby reefal, rubble and shallow sandy areas. Lizard island is influenced by southeast trade winds, which blow

at 15 to 25 knots during May to October, with variable winds alternating with calm periods during the remainder of the year (Vail 1988). The lagoon is relatively protected from the prevailing SE trade winds by a fringing reef running along South island to Bird islet (Fig. 2.1). Tides are semi-diurnal and have a diurnal inequality with a maximum spring tide amplitude of about 3.0 m (Pichon and Morrisey 1981). Almost all year round, trapping work was possible in the lagoon.

A total of nine sampling trips were made between October 1993 and July 1996. Seven of these were intensive sampling trips to determine habitat preferences, inter-habitat and diel movement patterns, catch rates and catch composition, and distribution and abundance of reef fishes, and collect samples for age, growth and mortality, and age and size at first sexual maturity studies. The two other trips were made to conduct a pilot study to locate types of habitat and trial the traps, and to establish an age validation experiment.

2.3 HABITAT TYPES

The study was carried out in a rectangular area approximately 2 km^2, with sides from Mangrove Beach (MB) to Lizard Head (LH) in the northeast, and from Lizard Head to South Island in the southeast, then from South Island to Palfrey Island in the southwest and from Palfrey Island to Mangrove Beach (Fig. 2.2). This area has been protected from fishing since 1983 (Davies 1995). From a pilot study, 6 types of habitat were identified based on attributes of the benthic substratum and depth, which were likely to be important to diel movements of lutjanids and lethrinids (see Chapter 4). These habitats were *i*) deep sand away from consolidated or patch reefs (DSAR), *ii*) deep sand near consolidated reefs (DSNR), *iii*) shallow sand near consolidated reefs (SSNR), *iv*) top portions of consolidated and patch reefs (TOPS), *v*) slopes of consolidated reefs (SLOP), and *vi*) rubble areas (RUBB). All of these habitats were within a single zone (i.e. the lagoon). The locations and a schematic diagram of these habitats are presented in Figures 2.2 and 2.3, respectively.

The reefal areas were essentially lagoonal consolidated patch reefs bordering the lagoon (Fig. 2.2). The habitats TOPS, DSNR and SLOP were located close to these reefal areas. The habitat DSAR was essentially located in the lagoon proper (Fig. 2.2). The habitat RUBB was close to Palfrey and South islands and was part of the shallow portions of the lagoonal patch reefs emanating from these two islands (Fig. 2.2). The habitat SSNR was located behind the reef flat between South and Bird island (Fig. 2.2).

In the lagoon, two locations were identified for the DSAR habitat. These were at the central (blue) lagoon and southwest of Trawler Beach (TB) (Fig. 2.2). These areas were relatively deep (10-15 m) and the benthic substratum was chiefly sand, devoid of any major underwater structures. This habitat was at least 150 m away from any reef structure (Fig. 2.3).

The DSNR habitats were located at the deep edge of lagoonal patch reefs facing towards the lagoon (Fig. 2.2). This habitat type occupied a narrow band located near (within 5-10m) reefal structures (Fig. 2.3) of Palfrey Island and Mangrove Beach (MB) to Trawler Beach (TB) (Fig. 2.2). The depth of this habitat ranged 7-12 m and the benthic substratum was entirely sand.

RUBB habitats were located at two sites close to Palfrey and South islands (Fig. 2.2). These were shallow sites of about 1-3 m deep with almost a flat substratum (Fig. 2.3). Benthos comprised mainly coral rubble, dead corals, dead corals with algae, macroalgae, sand, and occasionally small live corals (<0.5 m diameter) of the massive growth form. During neap tides, some portions of this habitat type were exposed.

SLOP habitats were located on the bombies at the channel between Bird Islet and Lizard Head (Fig. 2.2). This habitat was limited to slopes where the degree of inclination did not exceed 45° (to allow traps to sit in a stable manner) (Fig. 2.3). The depth ranged from 3-6 m. A wide variety of benthic substrata ranging from branching, tabulate and massive corals to dead corals and sand, was present here. Coral cover ranged from 10-80%, generally averaging 30-50%.

SSNR habitats were located along the back fringes of the reef flat between Bird Islet and South Island, facing the blue lagoon (Fig. 2.2). This habitat type occupied a narrow band close (within 3-5m) to patch reefs (Fig. 2.3) which were usually made up of massive *Porites* and branching corals. This habitat was shallow (2-4 m) and the substratum was almost entirely sand.

The habitat TOPS was located directly at the tops of consolidated reef structures (Fig. 2.3) of Palfrey Island, Mangrove Beach, Trawler Beach and portions of Bird Islet (Fig. 2.2). Reefal structures were usually made up of massive to digitate coral growth forms of *Porites*, *Pavona*, *Favia* and *Favites* spp. Coral cover ranged from 20-80%, generally averaging 30-60%. The depth ranged from 1-2 m. Trapping was impossible in this habitat during tides of less than 0.80 m.

During sampling, traps were positioned at least 150 m away from any reef structures at DSAR habitats; 2-3 m away from reef structures at DSNR and SSNR habitats; directly on top of reefs at TOPS habitats (about 1-2 m behind a crest); among rubble, dead corals and sand at RUBB habitats; and on slopes of reefs at SLOP habitats. On any sampling day, traps were at least 30 m away from each other within a group of replicates, with more than 200 m between groups (see below). Amongst the habitats at Lizard Island lagoon, TOPS and DSNR were proximal to each other. In many locations, the distances separating TOPS and DSNR were less than 15 m (Figs. 2.2-3). It was difficult to locate a SLOP habitat with a gentle inclination (<45°) adjacent to TOPS and DSNR and large enough to sample efficiently in the lagoon (i.e. to allow a radius of field of capture of traps which did not overlap, see below).

2.4 SAMPLING DESIGN

2.4.1 Trap Design

Except for 3 slight modifications and improvements, the basic design of the traps used in this study followed that of an Antillean Z-trap used by Sheaves (1992).

Figure 2.4 shows the design of the trap. The frame of the trap was made of light 8 mm mild steel bars while two corrugated 12 mm bars were used to reinforce the base. The heavier bars also acted as a weight which ensured that the trap landed in an upright position when it was deployed/thrown from a boat. An additional door was constructed diagonally opposite a second door on the trap to allow faster and convenient removal of fish during trap work. A bait pot attachment made from a 4-inch shark clip was also added to the trap to reduce the re-baiting time.

A trap was 1.80m long, 1.04 m wide and 0.60 m high and was covered by a 12.5 mm square galvanized mesh wire (Fig. 2.4). Mesh was attached to the frame using 0.8 mm gauge galvanized tie wires and reinforced with 1.2 mm bag ties. Two straight funnels, 375 mm in length, were used in each trap, positioned at the longer side diagonally opposite each other (Fig. 2.4). The funnel design was a simple tapering shape with an elliptical outer aperture of 420 x 200 mm and an elliptical inner aperture of 250 x 150 mm. Doors were attached using 3/8 inch hexagonal nuts as hinges and were locked by an iron bolt sliding downwards along the door frame on fixed 5/8 inch hexagonal nuts. These doors proved to be convenient and reduced the time of processing the catch by almost a third (see Section 2.4.3). Construction of each trap took about 24 man-hours. Each trap weighed approximately 15 kg. A total of 20 traps were constructed (which included 2 spare traps).

Traps were baited with about 350g (8-9 pcs.) of commercial West Australian pilchards (*Sardinops neopilchardus*) placed inside a bait pot made of 90 mm diameter PVC tube (Fig. 2.4). Each pot was 250 mm long with 5-6 20 mm horizontal rectangular slots on either side (the same as those used by Davies 1995). Bait pots were hung from the roof in the center of the trap.

In between sampling trips, traps were removed from the water, cleaned and rinsed in fresh water before being stored in an open yard at the LIRS. This practice extended the longevity of the mesh and avoided growth of algae and other fouling organisms that could have introduced variability in the efficiency of fishing of traps (sensu Davies 1995).

During the course of the study, many traps required small repairs to the mesh. Such repairs were done on the boat by stitching mesh patches onto holes using tie wires. On two separate occasions it was necessary to replace a large portion of mesh damaged by a large fish. In these cases, repairs were made at the research station. During such occasions, spare traps replaced damaged traps, maintaining equal sample sizes throughout the study (see below).

2.4.2 Deployment, Setting and Hauling of Traps

Traps were deployed and set using a 4.1 m motorised aluminum dinghy. The boat was positioned at a grid-location chosen randomly within a habitat before a trap was thrown over the side. For habitats DSNR, SLOP and SSNR, traps were thrown in a manner such that one of the funnels faced a reef structure. After deployment, traps were checked to ensure they were sitting in a stable position. An 8-inch round buoy attached to the trap by a 15 m x 36 mm nylon rope marked its position. Traps within a habitat were at least 30 m from each other to avoid overlapping of the capture field radius of adjacent traps and to ensure statistical independence (Miller 1975, Eggers *et al.* 1982, Miller and Hunte 1987, Recksiek *et al.* 1991, Sheaves 1992, Arena *et al.* 1994, Davies 1995). Locations and positions of traps were marked on maps.

After each soak set (see below), traps were hauled by hand from the boat. Fish were removed from the trap immediately and placed unto nally bins (650 x 400 x 400 mm) filled with fresh seawater.

2.4.3 Processing of the Catch

After removing fish from a trap, any fish with an embolism was treated by pricking the swim bladder with a hypodermic needle to relieve air pressure. The point of insertion of the needle was about 10 mm behind the base of the pectoral fin. This procedure was carried out on the fish in the water (in the nally bin). Embolisms were not very common and in most cases, the fishes recovered.

All fish were identified to species level whenever possible and their numbers counted. The soak period and location of each capture were recorded. Identification of species followed Allen (1985) for Lutjanidae, Carpenter and Allen (1989) for Lethrinidae and Randall *et al.* (1990) for all other species.

Additional information such as fork (FL) and standard (SL) lengths for study species (Serranidae, Lutjanidae, Lethrinidae and common species of Haemulidae) were measured to the nearest mm on a 1 m measuring board. A wet towel was used to handle the fish, keeping their bodies moist and shielding their eyes to keep them calm. Each of these fish were then tagged using standard T-bar anchor tags. *Lutjanus fulviflamma*, *L. quinquelineatus* and fishes in the genus *Lethrinus* were given the appropriate dosages of 50 mg ml^{-1} oxy-tetracycline solution. Details of tagging and administration of tetracycline are described in Section 2.4.5 (below). All data were recorded onto prepared data sheets of waterproof paper. All fishes were returned to the same spot where they were caught.

Recaptured individuals were re-measured, their location of capture recorded and then released in the same manner as described above. Individuals injected with tetracycline that had been in the field for at least 8 months were brought to the research station and kept alive in an aquarium as long as possible.

The processing time for a trap catch varied depending on the number and type of fish, and the weather conditions. On average, it took about 5 minutes to complete the processing of the catch of a trap.

2.4.4 Sampling Method and Schedule

For each trip, habitats were scheduled in random order for sampling. In each habitat, a day and a night set of 4 replicate groups of 6 traps were deployed on randomly chosen grid-positions. In this study, a replicate consisted of a string of 6 traps and 6 traps was considered as a sampling unit. On any trapping day, a total of 18 traps were used simultaneously, except during the first sampling trip (March 1994)

when only 12 traps were available. On the first trip, all 12 traps were used to sample one randomly selected habitat each trapping day and were relocated to another habitat the next trapping day. During the first trip, no habitat was sampled for two consecutive days. From the second to the last sampling trip, 18 traps were allocated to 3 randomly chosen habitats each day and relocated to another 3 habitats the next day until all habitats were completely sampled (see Table 2.1).

Positions of the traps were at least 30 m apart within a group (see above) and at least 200 m distance between groups (i.e. habitats) to ensure statistical independence. For a day set, traps were deployed between 0630 and 0900 hours and were hauled from 1600 to 1830 hours in the same sequence as they were deployed. This fixed the period of day soak on average to about 9.5 hrs. All captured fishes were placed into a nally bin containing fresh sea water for processing (see above). The trap was then rebaited and relocated to another randomly chosen position (at least 30 m away from previous locations of any traps) within a habitat for the night set which was hauled at 0630-0900 hours the next day. This set the period of night soak on average at 14.5 hrs. Following processing of the catch in the morning, the traps were transferred to the next set of 3 habitats in the same manner as described above. A set of 18 traps took about 2-2.5 hrs to lift and process. This was repeated over 8-9 trapping days (12-13 days in the case of the first sampling trip) until all habitats were sampled once. No habitat was sampled on more than two consecutive days except for four cases when tides were very low and deep habitats had to be sampled on 3 consecutive days. Even during these instances, positions and traps were allocated randomly in these habitats (see below). This design permitted estimates of day and night catch composition, as well as an estimation of diurnal movement patterns of fish.

A 3-way factorial fixed Analysis of Variance (ANOVA) design was followed in this study (Underwood 1981). This design (Table 2.1) tested variations in catch rates for numbers of species (total species richness) and individuals (abundances) within and between sampling time (trips), habitat types and soak times. Field samplings were conducted on March 5-20, 1994, October 3-21, 1994, March 4-21, 1995, June 27 - July 9, 1995, October 12-26, 1995, March 8-19, 1996 and July 17-30, 1996. Trapping was

always conducted 2 days or more after and before a full moon to minimize effects of maximum illumination on traps during night soaks, particularly in shallow habitats.

A problem with randomly scheduling the sampling of habitats was the tide. There were a number of occasions when a schedule for a habitat, particularly shallow habitats (RUBB, SSNR and TOPS), had to be postponed until the tide was high enough to ensure that traps were not exposed at any time. In these situations, traps were assigned randomly to deeper habitats. As a result, some habitats during some trips had more than 4 replicate groups in some soak sets. These occasions were as follows: DSAR -October 1994: day soaks (DT) 6 replicate groups (RG's), night soaks (NT) 6 RG's; DSNR -March 1994: NT 6 RG's, October 1994: DT 6 RG's, NT 6 RG's; SLOP -October 1994: DT 6 RG's, NT 6 RG's; and SSNR -July 1995: NT 5 RG's.

A complete sampling exercise for a typical trip involved a total of 288 trap hauls from 48 soak sets (i.e. each soak set is a replicate). For the entire study, a total of 351 soak sets comprising 2,106 trap hauls was conducted.

After each sampling exercise, additional trapping effort with longer soak periods (24, 36, 48 hrs) was done to increase numbers of tagged fish available for the movement study. This extra trapping effort was distributed over all habitats.

2.4.5 Tagging Method

All species of *Lethrinus*, *Lutjanus*, *Plectropomus*, *Epinephelus*, *Cephalopholis* and *Diagramma* greater than 120 mm FL were tagged using standard T-bar anchor (TBA) tags as part of a Mark-Release-Recapture (MRR) program. The tags permitted quantification of diurnal and longer term patterns of movement of snappers, emperors and groupers within and between habitats. These tags were manufactured by Hallprint®, yellow in color, individually numbered and printed with "JCU-MB" (for James Cook University -Marine Biology) and a contact telephone number.

The tags were inserted carefully with an applicator gun (Monarch 3030) at an angle to the left dorsal side of the fish below the second or third dorsal spine. The tags

pierced the dorsal musculature and passed between pterygiophores. Checks were done to ensure that the 'T' portion of the tag was securely locked between pterygiophores. A new tag was applied in cases where tags were not properly attached. Fishes that were injected with tetracycline (see below) were tagged twice for ease of identification. The second tag was inserted about 15 mm behind the first.

2.4.6 Marking by Tetracycline

Individuals of *Lethrinus atkinsoni, L. harak, L. lentjan, L. ornatus, L. semicinctus, Lutjanus fulviflamma* and *L. quinquelineatus* captured in traps were injected with oxy-tetracycline, with a prescribed dosage of 50 mg kg^{-1} bodyweight (Beamish and McFarlane 1987). A 50 mg ml^{-1} tetracycline solution (in sterile NaCl 0.9% as solvent) was used in order not to bloat the gut cavity of fish. The solution was administered just below the pectoral fin into the gut cavity using a 1 ml sterile syringe. Tetracycline injection was carried out for purposes of validating the periodicity of growth increments in the otoliths (e.g. Ferreira and Russ 1992, 1994, Newman et al. 1996a).

2.4.7 Basic Assumptions in Tagging, Tetracycline Marking and Trapping

Two basic assumptions were made in the analyses and interpretation of results. The first assumption was that tagging, marking with tetracycline and trapping had no effect on the growth, behavior and movement of fish. Secondly, all fish had equal probabilities of capture and that each fish acted independently (Schwarz and Arnason 1990). These are major assumptions because it is well known that tagging causes injuries, affects behavior and in some cases, retards growth and increases mortality (e.g. McFarlane and Beamish 1990, Manire and Gruber 1991, Scheirer and Coble 1991, McAllister *et al.* 1992). The effect of tagging, injecting tetracycline and trapping on growth, behavior and movement is difficult to test. However, care in the processing of catch, proper tagging and injection of tetracycline can keep injuries to low levels.

The second assumption requires complete and random mixing between marked and unmarked individuals. Mixing can be expected for reef fishes on a scale of individual reefs or parts thereof (Appeldoorn 1996).

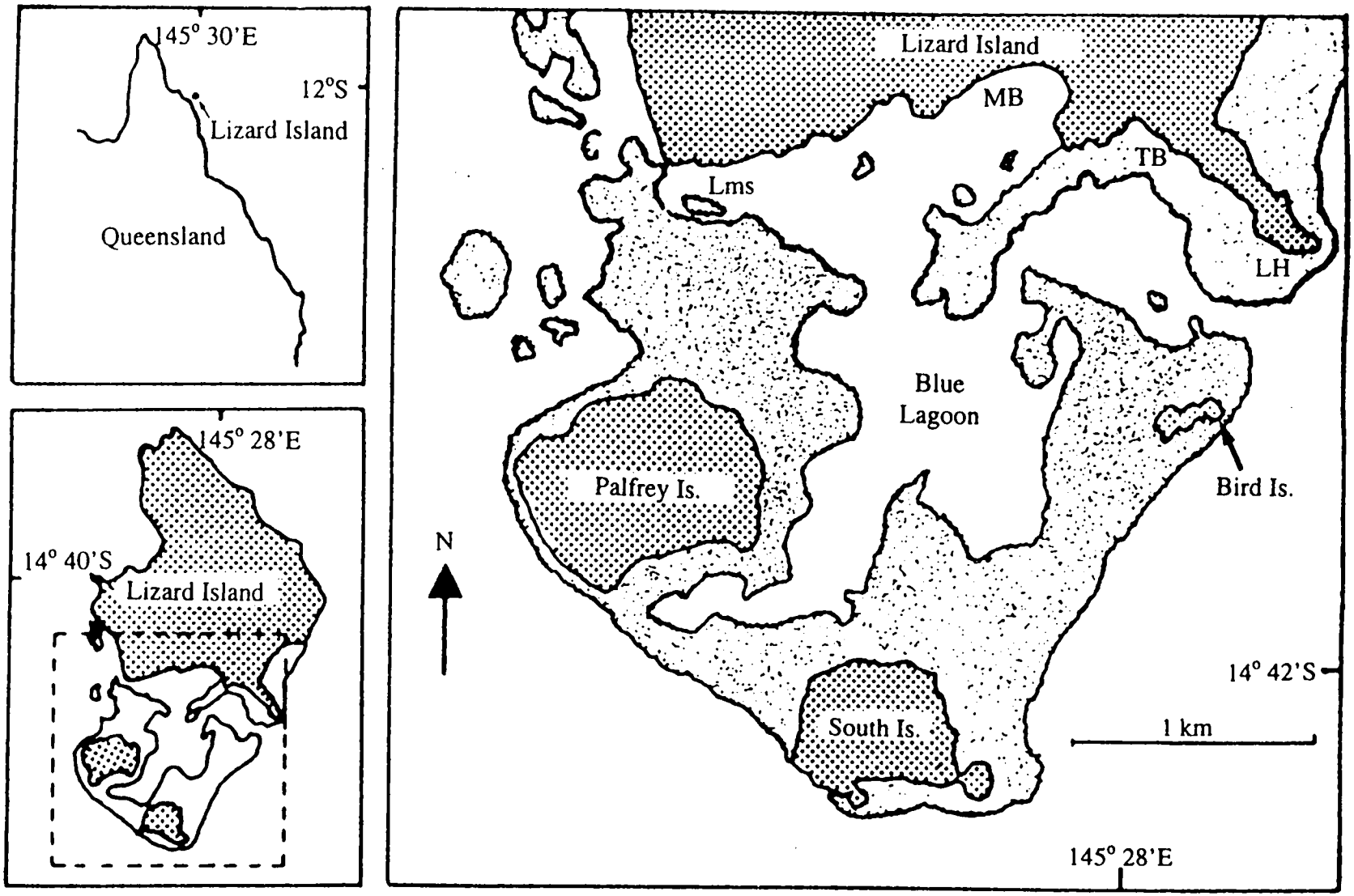


Figure 2.1. Location map of Lizard Island, Great Barrier Reef, Australia. Lms -Loomis Beach, MB -Mangrove Beach, TB -Trawler Beach and LH -Lizard Head. Adapted and modified from Pichon and Morrisey (1981).

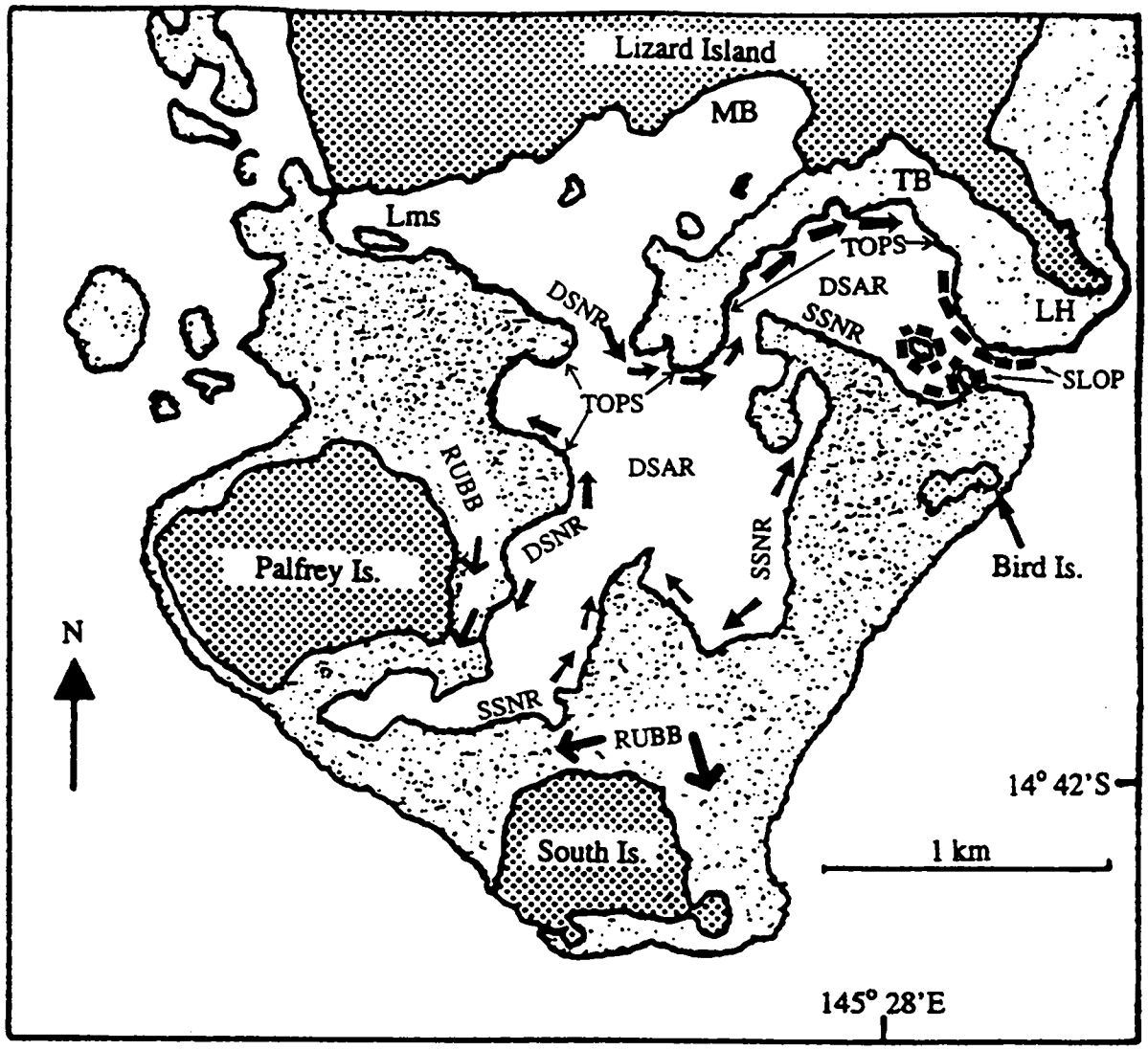


Figure 2.2. Location of the 6 habitat types in Lizard Island lagoon. Arrows outline the general area of the habitat. See Section 2.3 for explanation. Codes for types of habitat are DSAR -deep sand away from reefs, DSNR -deep sand near reefs, RUBB -rubble areas, SLOP -slopes of reefs, SSNR -shallow sand near reefs and TOPS -tops of reefs. Lms -Loomis Beach, MB -Mangrove Beach, TB -Trawler Beach and LH -Lizard Head. Adapted and modified from Pichon and Morrisey (1981).

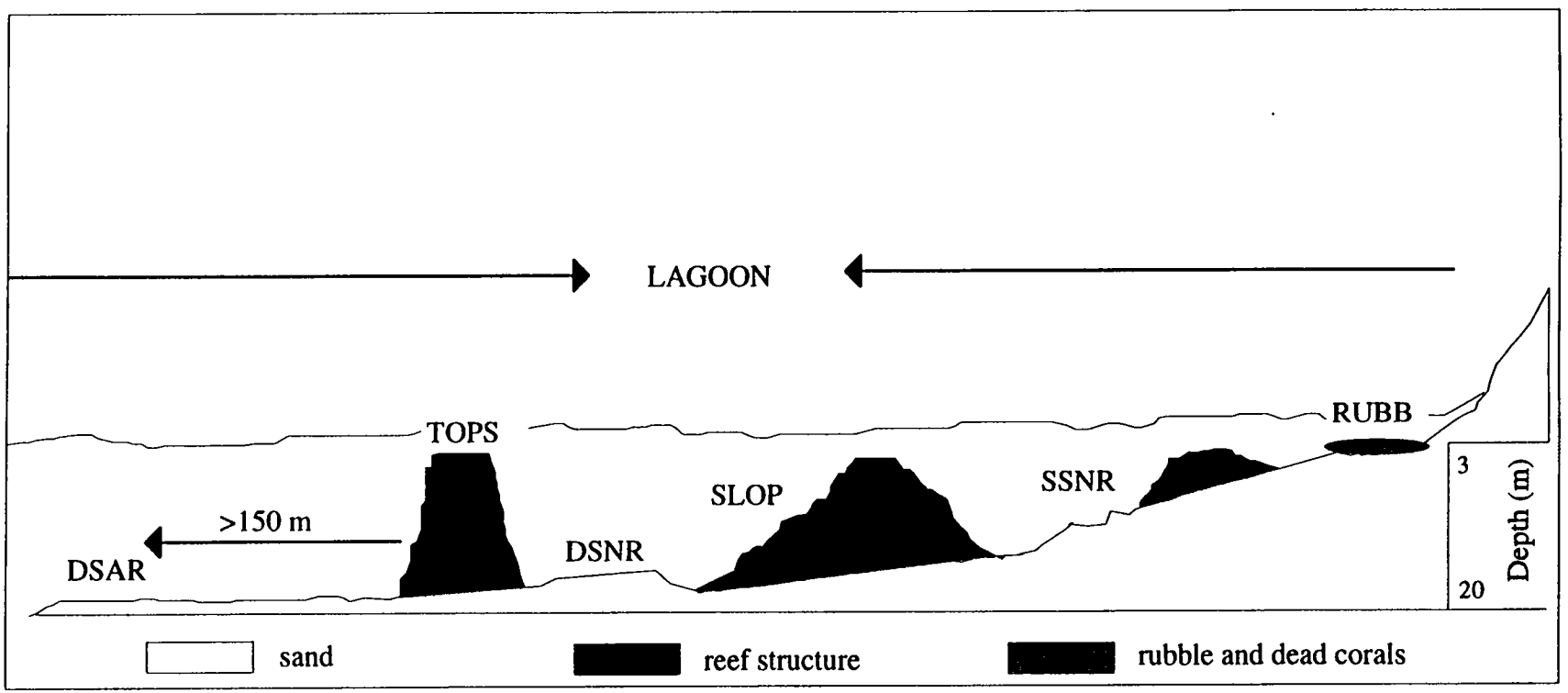


Figure 2.3. Schematic diagram of relative locations of 6 habitat types in Lizard Island lagoon, GBR. Habitat codes are DSAR -deep sand away from reefs, DSNR -deep sand near reefs, RUBB -rubble areas, SLOP -slopes of reefs, SSNR -shallow sand near reefs and TOPS -tops of reefs.

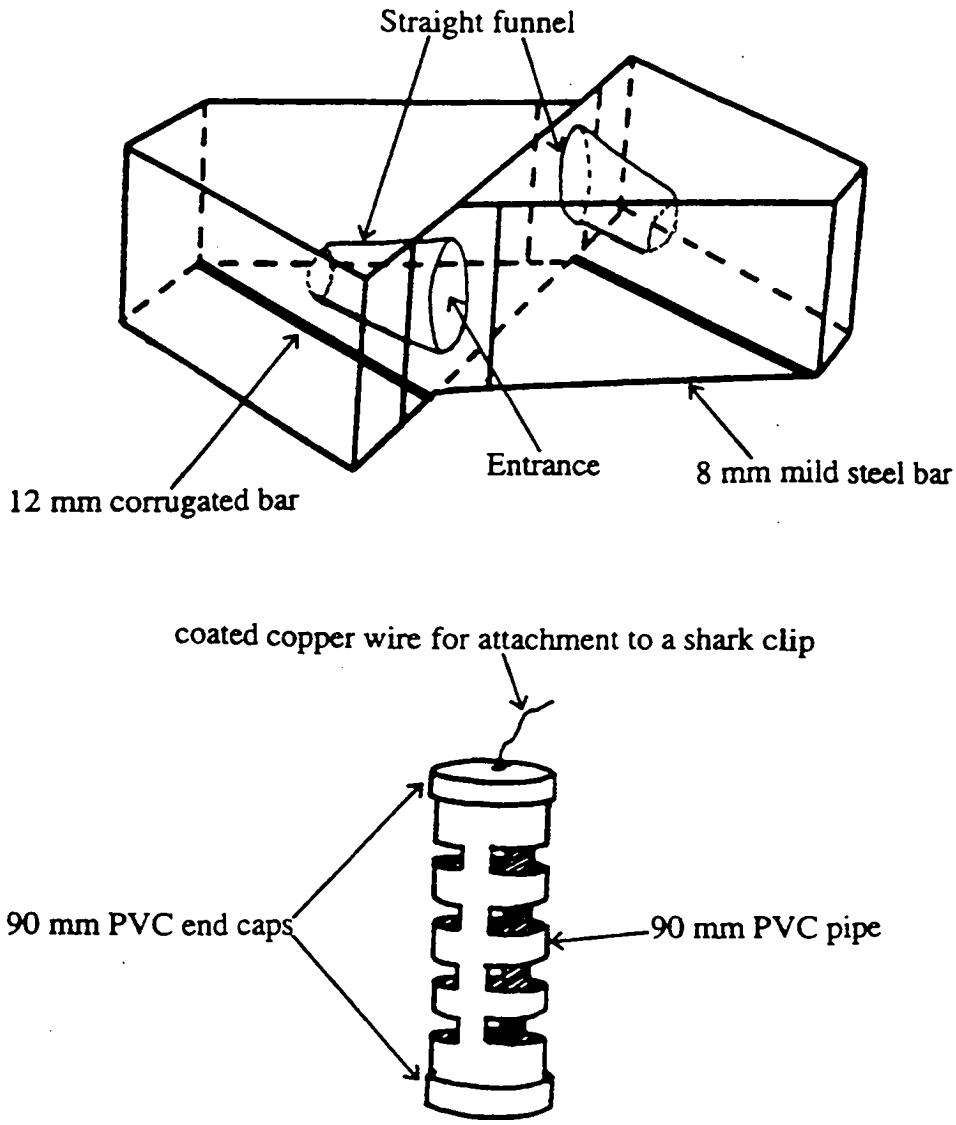


Figure 2.4. Schematic diagram of a Z-trap (top) and a bait pot (below) used in the study. A 12.5 mm square galvanized mesh wire was used to cover the frame of the trap. Adapted and modified from Davies (1995).

Table 2.1. Sampling design for the fish trapping study at Lizard Island lagoon, GBR. Codes for habitat types are: DSAR -deep sand away from reefs, DSNR -deep sand near reefs, RUBB -rubble areas, SLOP -slopes of reefs, SSNR -shallow sand near reefs, and TOPS -tops of reefs.

Factors	Type	Levels	
Sampling time	Fixed	7	Mar '94, Oct '94, Mar '95, Jul '95, Oct '95, Mar '96 and Jul '96
Habitat type	Fixed	6	DSAR, DSNR, RUBB, SLOP, SSNR and TOPS
Soak time	Fixed	2	Day soak (DT) and Night soak (NT)
Replicates		4	4-6 (mostly 4) groups of 6 traps

Chapter 3: DIEL PATTERNS OF DISTRIBUTION AND HABITAT ASSOCIATIONS OF REEF FISHES IN A LAGOON

3.1 INTRODUCTION

Variation in the distribution and abundance of species in space and time is a key concern of ecology. Explaining this variation is a major challenge in studies of community structure of reef fishes (Talbot *et al.* 1978, Sale 1980, 1991, Anderson *et al.* 1981). Studies investigating large spatial scale variation (100's kms across) in the distribution and abundance of reef fishes on the Great Barrier Reef (GBR) have demonstrated significant cross continental shelf variation in species composition and abundance (Anderson *et al.* 1981, Williams 1982, Williams and Hatcher 1983, Russ 1984a and b, Newman and Williams 1996, Newman *et. al.* 1997). Fish community structure varies significantly between cross shelf locations (inshore, mid-shelf and outershelf) with mid-shelf reefs having the highest number of species, inshore reefs lowest and outershelf reefs intermediate (Williams and Hatcher 1983). Similar observations were made for herbivorous fishes (Russ 1984a and b) and lutjanids, lethrinids and serranids (Newman and Williams 1996, Newman *et al.* 1997).

Studies looking at variation on a smaller spatial scale (100's of m to several kms) have demonstrated significant differences within and between adjacent reefs or zones in reefs. For example, Waldner and Robertson (1980) and Bouchon-Navaro *et al.* (1985) showed that the variation in fish species richness and abundance was explained largely by differences in type and quantity of benthic substratum, whereas McManus *et al.* (1981), Roberts and Ormond (1987) and Fowler (1990a) presented data showing weak or no relationship between benthic cover and fish species richness and abundance. Many of the studies of within-zone (between habitat) distributions have tended to concentrate on smaller and more site-attached species (e.g. Pomacentridae), the distribution of which has often been defined by substratum type or physical relief (Williams 1991).

Most of these studies have assessed patterns of distribution, abundance and community structure using underwater visual census methods (UVC) (e.g. Williams 1982, Russ 1984a and b, Bouchon-Navaro et al. 1985, Fowler 1990a, Newman *et al.* 1997) and small quantitative explosive charges (e.g Talbot and Goldman 1972, Williams and Hatcher 1983). Both methods are limited to day time sampling. Thus, only diurnal fishes were censused. Until recently, the use of fish traps has been confined to trap catch-dynamics (e.g. Eggers *et al.* 1982, Miller and Hunte 1987, Arena *et al.* 1994) and assessment of fisheries stocks (e.g. Ferry and Kohler 1987, Koslow et al. 1988, Recksiek *et al.* 1991, Cyr and Sainte-Marie 1995, Eklund and Targett 1991, Rakitin and Kramer 1996). To date, there appears to have been only 4 published studies have employed fish traps to investigate patterns of fish distribution and abundance on the GBR region. Two of these studies investigated small-scale (between-habitat) distribution patterns of fish in tropical estuaries (Sheaves 1992, 1996). The third looked at cross shelf variation in abundance of lutjanids and lethrinids in the central GBR (Newman and Williams 1996), and the fourth investigated variability of population structure of two species of lutjanid among reefs in the central GBR (Newman *et al.* 1996b).

The work described in this chapter used fish traps to assess fish distribution and abundance patterns, and to a certain extent, movement patterns between 6 habitat types in a coral reef lagoon. The use of fish traps has advantages over visual census. First, it allows both day and night sampling. Second, diel movement patterns between habitat types of larger, more mobile, as well as the smaller, site-attached species, can be estimated. Williams (1991) stressed the paucity of such information in an extensive review of within-reef patterns of distribution and abundance of reef fish. Lastly, trapping allows subsequent use of mark-release-recapture (MRR) techniques and limited destructive sampling for demographic studies. Major weaknesses of fish traps are the potentially limited vulnerability of certain fishes to the gear and the difficulties of relating trap catches to absolute *in situ* abundances.

The objectives of this chapter are two-fold.

1. To describe spatial patterns of distribution and relative abundance of reef fishes in specific habitats within a coral reef lagoon.

2. To determine temporal (diel and several-months scales) variability in the spatial patterns. The spatial and temporal patterns will be assessed with regard to potential movement of fishes (both mobile and site-attached species) within and between habitats.

3.2 MATERIALS AND METHODS

The data used in this chapter were from catch information of 2,106 trap hauls comprising 351 replicates each of 6 traps. Details of the study site, habitat types, sampling design, and field methods were described in Chapter 2. Briefly, the catch data was collected from 2 soak periods (day and night time) at 6 different habitat types in Lizard Island lagoon on 7 occasions over a 30 month period.

3.2.1 Analysis of Data

Numerical abundance information and number of species of fish were pooled within replicates prior to analysis. In this study, a replicate consisted of a string of 6 traps (see Section 2.4.4) each separated by at least 30 m. This reduced the chance of zero catches for a replicate and consequently reduced cell variances (*sensu* Sheaves 1992 and see Koslow *et al.* 1988). Differences in lengths of soak periods for day and night were standardized, and abundances and number of species were expressed as units per 8 hr soak. Standardization across differences in lengths of soak period followed the formula, $x_{std} = x * (\text{mean soak time})^{-1} * 8$ hrs; where x was fish abundance or number of species and mean soak time for day soaks was 9.5 hrs and 14.5 hrs for night soaks. In the text and graphical presentations, means were expressed as units of number of species or abundance per string of 6 traps per 8 hr soak, hereafter abbreviated to units per replicate.

A matrix of 120 species by 84 samples was constructed. This included all fish captured and their abundances in the 84 samples. Each of the 84 samples contained pooled species-abundance information from 4-6 replicates (mostly 4 replicates) within each of 6 habitat types for each of 2 soak times in each of 7 sampling times (6 x 2 x 7 = 84 samples). This matrix was subjected to a hierarchical classification analysis to facilitate recognition of patterns and relationships, and to investigate the structure of reef fish assemblages (Gauch 1982). The computer program TWo-way INdicator SPecies ANalysis (TWINSPAN) (Hill 1979) was used. This is a polythetic divisive classification technique based on the reciprocal averaging method. The data was first ordinated using reciprocal averaging and species that characterized the extremes of the reciprocal averaging axis were emphasized in order to polarize the samples, and the samples were then divided into two clusters by breaking the ordination near its middle (Gauch and Whittaker 1981). Each of the resulting clusters was further refined by a reclassification using species with the maximum value (obtained from a weighting index) for indicating poles of the ordination axis. This division process was repeated on a resulting cluster to produce two more clusters, and so on, until each cluster had no more than a specified number of members (i.e. samples). A corresponding ordered sample-species table was produced from which a dendrogram was constructed using the sequences of divisions as integral levels of average distances between clusters of samples (Gauch 1982). Clusters located close to each other are most similar. The program orders the sequence of samples in a cluster to place similar samples near each other. In the analysis, a 5 cut level option of 0, 2, 5, 10 and 50 was found to be most stable (i.e. no significant changes in the patterns despite exclusion of a few outlier samples or rarer species). The fact that stability could be achieved indicated some level of fidelity from the data at these cut levels. A 5 cut level option translates abundances to 5 corresponding scores of 0, 1, 2, 3 and 4 (e.g. Table 3.3). In the cut level option used above, species absent in a sample were assigned a score of 0, species with abundances between 0 and 2 a score of 1, between 2 and 5 a score of 2, between 5 and 10 a score of 3, and between 10 and 50 a score of 4.

Species were assigned to one of six broad trophic categories (piscivore, benthic predator, planktivore, corallivore, herbivore and scavenger) on the basis of available literature records on gut contents (Hiatt and Strassburg 1960, Talbot and Goldman

1972, Hobson 1974, Williams and Hatcher 1983, Sano *et al.* 1984, Thresher and Colin 1986, Randall *et al.* 1990, Myers 1991). For species with no existing dietary information available, the assignment of a trophic category was made based on the external morphology (sensu Thresher and Colin 1986), personal observations in the field and on known diets of related species.

These six trophic categories (above) were relatively broad such that the category 'herbivores' included detritivores in addition to algal grazers. 'Planktivores' were species that take planktonic materials and included many of the omnivorous zooplanktivores. The category 'corallivore' covered fishes that consume both hard and soft corals. 'Piscivores' had a principal diet of fish but may also take some invertebrates. The 'benthic predators' were those, which live mainly on benthic dwelling invertebrates such as crabs, crustaceans, bivalves and polychaete worms. 'Scavengers' were those that feed on scraps of food materials.

Variation in catch rates with sampling time, habitat type and soak time were analyzed using a 3-way analysis of variance (ANOVA). Catch rates were expressed in terms of both species richness and numerical abundance. ANOVAs were carried out on all fish for the variable species richness, and on 17 data sets for the variable catch abundance. The 17 data sets were all fish, 4 trophic groups (benthic predators, piscivores, planktivores and herbivores), the 7 most abundant families (Pomacentridae, Lutjanidae, Apogonidae, Lethrinidae, Labridae, Serranidae and Holocentridae) and 5 abundant species (*Lutjanus carponotatus*, *L. fulviflamma*, *L. quinquelineatus*, *Lethrinus nebulosus* and *Cephalopholis cyanostigma*). The 3 factors (sampling time, habitat type and soak time) were fixed factors (Underwood 1981). Before proceeding with the ANOVA, the data were examined for homogeneity of variance (α=0.05) using Cochran's C-test (Winer *et al.* 1991), for normality using plots of means against variances (Day and Quinn 1989) and residual plots (Sokal and Rohlf 1981). Tests indicated that data transformation ($\log_{10}(x+1)$) was necessary for the variable catch abundance for all 17 data sets. The transformed data passed Cochran's C-test at α=0.01. The plots of means against variances and the residual plots detected no extreme non-normality of the transformed data. To guard against the chance of a Type

I error, analysis of variance was conducted at a more conservative significance level of α=0.01.

Unplanned multiple comparison procedure (UMCP) of means was carried out using Tukey's Honest Significant Difference (HSD) method to distinguish between levels of factors that were significantly different (Day and Quinn 1989). All means in text and graphical presentations were back transformed to the original scale. All error bars were expressed as 95% confidence limits (Sokal and Rohlf 1981).

A preliminary test was done to detect whether the use of fewer traps (12 instead of 18 traps) and the extended trapping period (12 instead of 8 days) in March 1994 (see Section 2.4.4) affected the overall results of the classification and the ANOVAs. This test showed that the overall results remained consistent with and without the first level of the factor sampling time (March 1994).

3.3 RESULTS

3.3.1 Catch Composition and Abundance

Trends in total catch

A total of 2388 fish in 119 species and 27 families were recorded during the course of study. The species and their corresponding numerical abundances over time, across the six habitat types and soak times are given in Appendices A, B and C, respectively. The most species rich families in the samples were Apogonidae (n=26 species), Pomacentridae (n=19), Lutjanidae (n=11), Lethrinidae (n=9), Serranidae (n=8), Holocentridae (n=7) and Labridae (n=5) (Appendix A). The other 20 families accounted for 34 species. The target species in this study (lutjanids, lethrinids and serranids), important to commercial and recreational fishing activities, comprised nearly 25% of the species (n=28).

The ten most numerically dominant species were the snapper *Lutjanus carponotatus* (spanish flag fish) which accounted for more than 14% of the total catch, the damselfish *Amblyglyphidodon curacao* (9.6%), the damselfish *Acanthochromis*

polyacanthus (8.3%), the cardinalfish *Apogon bandanensis* (6.6%), the moon wrasse *Thalassoma lunare* (6.2%), the five-lined snapper *Lutjanus quinquelineatus* (4.6%), the cardinalfish *Apogon compressus* (3.4%), the spangled emperor *Lethrinus nebulosus* (3.2%), the soldierfish *Myripristis murdjan* (3.1%) and the blue-spotted rock cod *Cephalopholis cyanostigma* (2.8%) (Appendix A). The 28 target species (4 of which were in the 10 most abundant species above) accounted for nearly 35% of the total catch. Other notable target species captured in relatively large numbers were *Lutjanus fulviflamma* (2.3%), *Lethrinus semicinctus* (2.2%) and *L. atkinsoni* (1%).

The total catch was dominated by very few species. Six species (5% of species) accounted for 50% of the numerical catch and more than 95% of the total catch accounted for by less than 42% (n=50) of the species (Fig. 3.1). The contribution of each of the other 69 species was on average about 0.07%.

Most species caught in the traps were thus rare. More than 43% of the species were caught only once in 7 sampling times and about 15% only twice in the 7 sampling times (Fig. 3.2a). Ten percent were captured 3 times in 7 sampling times (Fig. 3.2a). The number of species caught once in any of the sampling times (n=52) was 3 times more than those common in all sampling times (n=16) (Fig. 3.2a). Only 2 species were captured at 6 sampling times, 9 species at 5 sampling times and 9 species at any 4 of 7 sampling times.

A similar trend was observed with respect to the occurrence of species in habitat types (Fig. 3.2b). Nearly half of the species (n=56) were unique to any one habitat type, while only 3% (n=4) were common to all habitats (Fig. 3.2b). More than one fifth of the species (n=26) were common to any two habitat types, 13% (n=16) to any 3 habitat types, 4% (n=5) to any 4 and 11% (n=13) to any 5. The number of species unique to a habitat type was 14 times higher than the number of species common to all habitat types.

Comparing between soak times, there were 4 times more species caught during night soaks only (49%, n=59) than day soaks only (12%, n=14) (Fig. 3.2c). Nearly 40% (n=47) of the species were common to both soak times.

In terms of families, the catch was dominated by 7 families which together comprised nearly 92% of the total (Appendix A). The damselfishes (Pomacentridae) and the snappers (Lutjanidae) were the most numerous (Fig. 3.3a) with 570 and 556 individuals captured, respectively. Their abundance was nearly 3 times the combined total of 20 other families. The cardinalfishes (Apogonidae) ranked third, followed by the wrasses (Labridae), emperors (Lethrinidae), groupers (Serranidae) and squirrelfishes (Holocentridae) (Fig. 3.3a). The abundance alone of either the wrasses or the emperors was almost equal to the combined abundance of the 20 other families.

The most numerically abundant members of the Pomacentridae were *Amblyglyphidodon curacao* and *Acanthochromis polyacanthus* which together comprised nearly 75% of all damselfishes (Appendix B). The dominant species of Lutjanidae were *Lutjanus carponotatus*, *L. quinquelineatus* and *L. fulviflamma* which together made up over 90% of all snappers. *Apogon bandanensis*, *A. compressus* and *Fowleria* sp. "1" comprised more than 60% of all apogonids. Among the emperors, *Lethrinus nebulosus*, *L. semicinctus*, *L. atkinsoni*, and *L. lentjan* were the most numerous, totalling more than 90% of individuals. *Thalassoma lunare* and *Choerodon fasciatus* made up more than 97% the total number of labrids, while *Cephalopholis cyanostigma* and *Plectropomus leopardus* together totalled nearly 80% of the serranid individuals. *Myripristis murdjan* and *Sargocentron spiniferum* were the most important holocentrids, comprising nearly 95% of their numbers.

The percentage distribution of catch abundances of these families varied across habitat types (Fig. 3.3b). Four families (Lutjanidae, Apogonidae, Lethrinidae and Holocentridae) were distributed in all 6 habitat types with a preference for 2-3 habitat types. For example, more than 75% of all lutjanids were caught in habitats TOPS (tops of reefs), SLOP (slopes of reefs) and DSNR (deep sand near reefs) in approximately equal proportions, while the majority of the lethrinids (72%) were trapped at DSAR (deep sand away from reefs), RUBB (rubble areas) and SLOP (Fig. 3.3b). Similarly, more than 90% of the holocentrids were recorded from 3 habitat types (SLOP, DSNR and TOPS) and the majority of the cardinalfishes (62%) came from TOPS and SSNR (shallow sand near reefs). In contrast, 3 families (Pomacentridae, Labridae and Serranidae) occurred in all habitat types except DSAR, but with at least half their total

recorded from a single habitat type only (Fig. 3.3b). For example, more than half of the pomacentrids and labrids were captured at the TOPS and SLOP habitats, respectively. The vast majority of serranid individuals (70%) were caught on the SLOP. Numbers of lutjanids and lethrinids were relatively high in all 6 habitat types (except TOPS for lethrinids) while serranids were relatively limited to coralline habitats (i.e. SLOP and TOPS) (Fig. 3.3b).

Catch abundances varied also between day and night soaks for various families. More lutjanids, apogonids and lethrinids were caught at night (Fig.3.3c). Holocentrids were trapped only at night. Ninety-five per cent of all apogonids and about 60% of all lutjanids and lethrinids were caught at night (Fig. 3.3c). The opposite trend was observed for the damselfishes and wrasses. Nearly 80% of the pomacentrids and wrasses were trapped during the day soaks (Fig. 3.3c). For serranids, the catch between day and night was about even.

Three categories dominated the trophic composition of the catch in terms of number of species (Table 3.1). One third of the species captured were planktivores, 30% were benthic predators, and 21% were piscivores. Herbivores comprised nearly 11% of all species captured while corallivores made up less than 5%. A single species comprised the scavenger category. This was the remora *Echeneis naucrates*.

Amongst the planktivores, more than half of the species captured were apogonids and a quarter were pomacentrids (Table 3.1). All of the species of apogonids classified as planktivores were omnivorous zooplanktivores. The benthic predators were mainly lutjanids, lethrinids and labrids while piscivores consisted of all of the serranids plus a few of the lutjanids and apogonids (Table 3.1). More than 61% of the herbivores were pomacentrids.

In terms of numerical abundances, the benthic predators and planktivores dominated the total catch (Table 3.2). The former comprised more than 45% of individuals, while the latter made up 32%. The herbivores accounted for 11% of individuals and the piscivores 9%. The corallivores and scavengers comprised less than 2% of the individuals in the total catch. The main bulk of the benthic predators were trapped in the SLOP, DSNR and TOPS and their numbers were of moderate

levels in the 3 other habitat types (Table 3.2). A large proportion of the planktivores were captured at the TOPS habitat and very few were found in the DSAR (Table 3.2). The other 4 habitats had moderate numbers of planktivores. The piscivores were most numerous in the coralline habitats (SLOP and TOPS) and in the SSNR (Table 3.2). Few were caught in the other 3 habitats. Nearly 80% of all herbivores were caught in the TOPS and SLOP and very few in the SSNR, DSNR and RUBB. No herbivores were recorded in the DSAR.

Trends between sampling times (trips)

The mean catch rate for all fish varied from 2.1 to 4.7 fish per replicate (i.e. 6 traps combined) among sampling times (Fig. 3.4a). Catch rates were highest in each year during March (late summer) and lowest during July (winter). Catch rates during October (early summers) were of an intermediate level. The highest mean catch rate recorded in March 1996 (4.7 fish per replicate) was more than twice that of the lowest catch rate recorded in July 1995.

The mean catch rates for the 7 most abundant families over time are shown in Figure 3.5a-g. No family followed the same trend noted above for total catch rate. However, the highest and lowest mean catch rate occurred in summer (March or October) and winter (July), respectively, for all families except for the apogonids and holocentrids. The apogonids (Fig. 3.5c) and holocentrids (Fig. 3.5g), both recorded their highest and lowest catch rates in summer (March 1995 and March 1994, and March 1996 and October 1994, respectively). In the case of the pomacentrids (Fig. 3.5a), the highest and lowest catch rates occurred in March 1994 and July 1996, respectively; for lutjanids (Fig. 3.5b), March 1996 and July 1995; for Lethrinids (Fig. 3.5d), March 1996 and July 1996; for labrids (Fig. 3.5e), October 1995 and July 1996; and for serranids (Fig. 3.5f), October 1994 and July 1996.

The mean catch rates for all families remained fairly constant over time except for the pomacentrids, lutjanids and apogonids (Fig. 3.5). For these families, mean catch rates were much higher in some sampling times. For example, more pomacentrids were trapped during the first 2 sampling times (March and October 1994) than during other times (Fig. 3.5a). Similarly, a big increase in the mean catch

rate was observed in March 1996 for the lutjanids (Fig. 3.5b) but the means for all other trips remained similar. For the apogonids, the mean catch rate in March 1995 was much higher than the means of the other times.

Trends across habitat types

Across habitat types (Fig. 3.4b), the mean catch rate for all fish combined ranged from 1.7 fish per replicate at deep sand away from reefs (DSAR) to 7.1 fish per replicate at the tops of reefs (TOPS). The two highest catch rates were recorded from the two habitats with relatively high coral cover, the tops of reefs (TOPS), the slopes of reefs (SLOP) (Fig. 3.4b). Deep sand away from reefs (DSNR) close to good coral cover, had intermediate catch rates (Fig. 3.4b). Shallow sand near reefs (SSNR), rubble areas (RUBB) and deep sand away from reefs (DSAR) all had low catch rates (Fig. 3.4b) that were about 3 to 4 times less than recorded at the SLOP and TOPS habitats. Catch rate in the DSNR (2.8 fish per replicate) was 1.5 times higher than catch rates at RUBB, SSNR and DSAR, but 2 to 2.5 times less than those recorded on the SLOP and TOPS, respectively.

The composition of catches varied across the six habitat types (Fig. 3.6). The 7 most numerically abundant families were represented in all habitat types except at DSAR. The labrids and serranids were totally absent while the pomacentrids and holocentrids were rare at DSAR (Fig. 3.6f). In 3 habitats, some families were also rare. These were the lethrinids at the TOPS (Fig. 3.6a), serranids and holocentrids at the RUBB (Fig. 3.6d), and labrids, serranids and holocentrids at the SSNR (Fig. 3.6e). The 7 families were only well represented in the SLOP and DSNR habitats (Figs. 3.6b and c, respectively).

The catch rates at the TOPS habitats consisted mainly of pomacentrids, although lutjanids, apogonids and labrids were also common (Fig. 3.6a). The mean catch rate for the pomacentrids (1.9 fish per replicate) was almost twice that of lutjanids and 10 times higher than that of the serranids.

In the SLOP habitats, lutjanids were the most common fish caught followed by the pomacentrids, labrids and serranids (Fig. 3.6b). The mean catch rates of the

pomacentrids, labrids and serranids differed little from each other and were at least 1.5 times less than that for the lutjanids. The lethrinids had a relatively high catch rate of similar magnitude to that of the apogonids and holocentrids. The mean catch rate of the lutjanids was 3 times higher than that of the lethrinids, apogonids and holocentrids.

The lutjanids clearly dominated the catch at the DSNR habitat (Fig. 3.6c) with a mean catch rate (1.10 fish per replicate) 4 times higher than the second ranking family (apogonids). The mean catch rate of 4 families (apogonids, pomacentrids, holocentrids and lethrinids) was similar while labrids and serranids had the lowest catch rate among the 7 families.

There was no clearly dominant group in catches from RUBB habitats (Fig. 3.6d). The catch was distributed evenly across 5 families (pomacentrids, lutjanids, apogonids, lethrinids and labrids). The mean catch rate for all of these families was approximately equal.

Four families formed the main component of the catch at the SSNR habitat (Fig. 3.6e). Apogonids and lutjanids comprised the majority of the catch. The pomacentrids and lethrinids had similar but lower catch rates. At the DSAR habitat (Fig. 3.6f), lutjanids, lethrinids and apogonids were common in the catch with the first two being the most numerous.

Trends between day and night soaks

More fish were trapped during the night than the day soaks (Fig. 3.4c). The mean catch rate for all fish during the night (3.4 fish per replicate) was 1.3 times that of the day soaks. This pattern was observed for all but three of the seven most abundant families (Fig. 3.7). Two of these families, the pomacentrids and labrids, had higher mean catch rates during the day soaks (by factors of 2.5 and 3, respectively) than the night soaks, while the serranids had approximately equal catch rates for both soak times.

Holocentrids were never caught during the day (Fig. 3.7). There were 21 times more apogonids, 2 times more lethrinids and 1.7 times more lutjanids caught during the night than the day soaks.

3.3.2 Spatial and Temporal Patterns of Fish Assemblages

A classification analysis was carried out to investigate the general pattern of spatial and temporal variation of the fish assemblages sampled by traps (Fig. 3.8). One sample, SSNRDTO95 (a day soak in the shallow sand near reef in October 1995), had no catch and was omitted from the analysis. The remaining 83 samples grouped into 3 main clusters (A, B and C in Fig. 3.8). The analysis clearly differentiated fish assemblages based on habitat type and soak time. It did not differentiate fish assemblages based on sampling time (trips). The first split of the data set placed all samples from day time soaks at the sandy habitats in cluster C (Fig. 3.8) distinct from samples in the reefal, near reefal and rubble habitats (A), and the samples from sandy habitats during night time soaks (B). The next division placed the vast majority of samples from the reefal, near reefal and rubble habitats (Cluster A) distinct from the samples in the sandy habitats during night time soaks (Cluster B).

The samples in cluster A divided further based on soak time. All but 2 samples from day soaks grouped to form cluster A1 (labelled as 'day time soaks' in Fig. 3.8). All but 2 samples from night soaks grouped to form cluster A2 (labelled as 'night time soaks').

Samples in cluster 'B' were separated based on proximity to a reef (Fig. 3.8). All samples collected from near reefs grouped together to form cluster B1 and all samples collected away from reefs were contained in cluster B2.

To a lesser extent, the analysis differentiated finer details of habitat types but did not differentiate between depths. Although the clear distinction between habitat types was based on type of substratum (i.e. coralline and sandy), there was indication that specific habitat types such as TOPS, SLOP and RUBB were differentiated. For example, in cluster A1, a small group of RUBB samples subsequently separated (Fig. 3.8). This separation of the RUBB habitat reflected the known habits of the 2 indicator species, *Pomacentrus chrysurus* and *Lethrinus semicinctus* (Fig. 3.8). Additionally,

the habitat SLOP appeared to be a distinct group from TOPS and DSNR in the last division in cluster A2 (Fig. 3.8). A similar pattern was observed in cluster A1.

Species common and evenly distributed in samples on one side of a division but rare or absent on the other are termed indicator species (also known as diagnostic species) for those samples. The indicator species for each level of division are shown in Figure 3.8. Samples from cluster C (sandy habitats/day time soaks) were characterized by the remora *Echeneis naucrates* (a scavenger), while 4 reef species indicated the other end of the RA axis (for clusters A and B together: *Amblyglyphidodon curacao*, *Lutjanus carponotatus*, *Thalassoma lunare* and *Lutjanus fulviflamma*) (Fig. 3.8). Reefal, near reefal and rubble habitats (cluster A) were characterized by *Amblyglyphidodon curacao*, *Lutjanus carponotatus* and *Thalassoma lunare*, while sandy habitats/night time soaks (cluster B) were identified by *Lethrinus nebulosus* and *Lutjanus quinquelineatus* (Fig. 3.8).

The day time soaks (cluster A1) in reefal, near reefal and rubble habitats were characterized by *Acanthochromis polyacanthus* and *Thalassoma lunare*. The night time soaks (cluster A2) for the same habitats were characterized by 3 apogonids (*Apogon bandanensis*, *A. compressus* and *Fowleria* sp. '1') and 2 holocentrids (*Myripristis murdjan* and *Sargocentron spiniferum*) (Fig. 3.8). The near reefs (cluster B1) of the sandy/night time habitats were distinguished by *Lutjanus carponotatus* and *Myripristis murdjan*, and those 'away from reefs' (cluster B2) by *Lutjanus fulviflamma* and *Lethrinus lentjan* (Fig. 3.8).

Table 3.3 is an ordered table of species by samples giving an indicative list of species representing each cluster in Figure 3.8. Only the top 50 species by numerical abundance were included in this table. They are displayed as ordered by the program TWINSPAN (Hill 1979). The strength of associations of the species to their respective clusters reflected their catch abundances in samples identified in those clusters. For example, the first 35 species (from species no. 1 *Aeoliscus strigatus* (coded as AEO STRI) to no. 35 *Myripristis murdjan* (MYR MURD) in Table 3.3) were strongly associated with 60 samples (39 to 68 in Table 3.3) contained in cluster A (reefal, near reefal and rubble habitats in Fig. 3.8). Note that the abundance scores of these 35

species were much higher in samples 39 to 68 (Table 3.3) than in 23 samples from sandy habitats (02 to 01 in Table 3.3). For example, *Acanthochromis polyacanthus* (species no.5 (ACA POLY)), *Amblyglyphidodon curacao* (no.6 (AMB CURA)), *Thalassoma lunare* (no.20 (THA LUNA)) and *Lutjanus carponotatus* (no.33 (LUT CARP)) had abundance scores indicating stronger preference for habitats characterized in cluster A than those in the sandy habitats. In some instances, some species such as *Acanthochromis polyacanthus* (species no.5), *Amblyglyphidodon curacao* (no.6) and *Thalassoma lunare* (no.20), which were very abundant on reefal habitats, were virtually absent in sandy habitats (as indicated by dash lines in 23 samples (02 to 01) under sandy habitats in Table 3.3).

Fourteen species (from species no.33 *Lutjanus carponotatus* (LUT CARP) to no.46 *Lethrinus nebulosus* (LET NEBU) in Table 3.3) characterized cluster B: 'sandy habitats/night time soaks' (Fig. 3.8). The higher abundance scores of these 14 species tended towards samples identified in cluster B (16 samples from 02 to 58 in Table 3.3). In particular abundance scores of *Lutjanus quinquelineatus* (species no.45 (LUT QUIN)) and *Lethrinus nebulosus* (no.46 (LET NEBU)) were consistently in intermediate levels in samples of cluster B (Table 3.3).

Four species (from species no.47 *Gnathonodon speciosus* (GNA SPEC) to no.50 *Scolopsis bilineatus* (SCO BILI) in Table 3.3) preferred samples in cluster C: 'sandy habitats/day time soaks (Fig. 3.8). These 4 species had high abundance scores in samples identified as cluster C (7 samples from 03 to 01 in Table 1). In particular, the abundance score of *Echeneis naucrates* (species no.49 (ECH NAUC) in Table 1) was consistently high in these samples.

In general, of the top 50 species listed in Table 3.3, 32 species (from no.1 *Aeoliscus strigatus* (AEO STRI) to no.32 *Cheilodipterus quinquelineatus* (CHE QUIN)) were fishes highly associated with reefal habitats. Six were considered ubiquitous (from species no.33 *Lutjanus carponotatus* (LUT CARP) to no.38 *L. bohar* (LUT BOHA)) as their abundance scores were spread over both major clusters (i.e. by habitat), and 12 (from species no.39 *Lutjanus russelli* (LUT RUSS) to no.50 *Scolopsis bilineatus* (SCO BILI)) were highly associated with sandy habitats (Table 3.3).

Indicative lists of species associated with the smaller groupings (clusters A1, A2, B1 and B2 in Fig. 3.8) can also be inferred from Table 3.3. Within the reefal, near reefal and rubble habitat samples (cluster A in Fig. 3.8), twenty species beginning with *Aeoliscus strigatus* (species no.1 (AEO STRI)) to *Thalassoma lunare* (no.20 (THA LUNA)) distinguished day time soaks (cluster A1 in Fig. 3.8 or 28 samples (17 to 76) in Table 3.3) from night time soaks (cluster A2 in Fig. 3.8 or 28 samples (22 to 68) in Table 3.3). The night soaks (cluster A2) were characterized by twelve species (from species no.21 *Amblyglyphidodon leucogaster* (AMB LEUC) to no.32 *Cheilodipterus quinquelineatus* (CHE QUIN), Table 3.3). This grouping consisted principally of 5 apogonids, 2 muraenids and a holocentrid.

Within cluster B ('sandy habitats/night time soaks' in Fig. 3.8), eight species (from no.33 *Lutjanus carponotatus* (LUT CARP) to no.40 *Diagramma pictum* (DIA PICT) in Table 3.3) characterized samples from near reefs (cluster B1 in Fig. 8 or 6 samples (02 to 63) in Table 3.3). Six species (from no.41 *Lethrinus lentjan* (LET LENT) to no. 46 *Lethrinus nebulosus* (LET NEBU), Table 3.3) were associated with the samples away from reefs (cluster B2 in Fig. 8 or 10 samples (06 to 58) in Table 3.3). This group included *Lutjanus fulviflamma* (no.42 (LUT FULV)) nearly 50% of which were captured during night time in sandy habitats away from reefs.

3.3.3 Variation in Catch Rates

Summaries of 3-way ANOVAs are reported in Table 3.4 for total species richness and Table 3.5 for numbers of all fish, numbers within 4 trophic groups, numbers in the top 7 families, and numbers in 5 selected species. In all 18 analyses (Tables 3.4 and 3.5), 20 first order interactions were significant (see Table 3.6 also).

In the analysis for numbers of Apogonidae, a significant second order interaction (Time *x* Habitat *x* Soak time) was detected ($p<0.01$). An inspection of the mean square (MS) values for Apogonidae indicated that the interaction was very strongly driven by the factor soak time (Table 3.5h). Nearly two thirds of the total variability was explained by this factor alone. To make data interpretation more simple

and consistent across all variates, the significance level was set at $\alpha = 0.001$ for Apogonidae.

A summary of the significant effects ($p<0.01$) from the 18 ANOVAs is given in Table 3.6. Two of the analyses had 2 significant main effects only. Another 2 had one significant main effect only. Two resulted in a significant main and a first order interaction. Six had a significant first order interaction and another 6 had 2 significant first order interactions.

Summaries of the results of the unplanned multiple comparisons (Tukey's HSD method) are presented below each plot of means for significant effects ($p<0.01$) in Figures 3.9 to 3.34. These summaries often show clear relationships, although a number of inevitably complex and ambiguous relationships existed, particularly in analyses where interactions were significant. In the text, emphasis was given to the salient points and the main trends.

Number of species (species richness)

All fish

Two first order interactions, Time *x* Habitat and Habitat *x* Soak time, were significant ($p<0.001$ and $p<0.01$, respectively) in the variation in catch rates for total species richness (Table 3.4). The effect of habitat type at each sampling time (Fig. 3.9) indicated a general trend for more species to be caught in habitats SLOP and TOPS (the two habitats with high live coral cover) than in other habitats, especially in early summer (October). In March 1994, the mean species richness at the SLOP (4.5 species per replicate) was significantly higher (3-5 times) than in the DSAR, DSNR, RUBB and SSNR. In October 1995, the mean number of species caught in the SLOP (3.9 per replicate) was 4-6 times higher than in the same four habitats. In addition, there were 9 times more species in the SLOP (2.8 per replicate) than in the RUBB in July 1995. The same trend was true for the habitat TOPS (Fig. 3.9). There was 3-4 times more species at the TOPS (3.6 per replicate) than in the DSAR and DSNR in March 1994. In October 1994, both SLOP and TOPS (3.9 and 3.8 species per replicate, respectively) had 3-7 times more species than any of the habitats DSAR, RUBB and SSNR. In

March 1995, March 1996 and July 1996 no significant difference in species richness was observed amongst the habitats.

Conversely, the effect of sampling time on each habitat type remained fairly consistent in most habitat types except in the SLOP and RUBB (Fig. 3.9). In the SLOP habitat, significantly more species (2 times) were recorded in March 1994 and October 1995 (4.5 and 4.4 species per replicate, respectively) than in July 1996. For the habitat RUBB, there were 7 times more species in March 1996 (3.1 per replicate) than in July 1995.

A simpler picture was seen in the second interaction (Fig. 3.10). There was no significant variation in the mean number of species caught between day and night soaks for all habitat types. However, the effect of habitat type on species richness differed between soak periods. During the day soaks there was significantly more species (2-4 times) at the SLOP and TOPS (3.1 and 3.3 per replicate, respectively) than in the other four habitats (Fig. 3.10). During the night soaks, significantly more species (1.5-2.5 times) were trapped at the SLOP (3.8 per replicate) than in RUBB, DSAR, DSNR and SSNR, while the TOPS (2.8 species per replicate) had significantly more species (by a factor of 2) than in RUBB and DSAR (Fig. 3.10).

Number of individuals (catch abundance)

All fish

The analysis of the mean number of all fish resulted in two significant first order interactions. These were Time *x* Habitat and Habitat *x* Soak time ($p< 0.001$ and $p<0.0001$, respectively) (Table 3.5a). In the first interaction, the effect of habitat types was more evident than the effect of sampling times (Fig. 3.11).

The mean number of fish captured in TOPS and SLOP (the two habitats with high live coral cover) were significantly higher than in many of the other habitats in most of the sampling times, especially during early summers (October) (Fig. 3.11). The mean catch rates in the TOPS and SLOP (8.44 and 8.80 fish per replicate, respectively) were nearly 5-7 times higher than in the DSNR and DSAR in March 1994. In July 1995, the means in the TOPS and SLOP (4.17 and 4.63 fish per

replicate, respectively) were 16-18 times higher than in the RUBB. In October 1994 there was 6-25 times more fish in the TOPS (10.43 fish per replicate) than in the DSAR, RUBB and SSNR, and 5-15 times more fish in the SLOP (6.41 fish per replicate) than in the DSAR and SSNR. Similarly in October 1995 the means at TOPS and SLOP (7.13 and 6.75 fish per replicate, respectively) were 6-7 times more than in the RUBB and SSNR (Fig. 3.11). The number of fishes caught in all habitats did not differ on the other 3 occasions (March 1995, 1996 and July 1996).

The effect of sampling time on habitat types was observed only at the habitat RUBB (Fig. 3.11). In this habitat, there were 13-20 times more fish caught in March 1995 and 1996 (3.28 and 5.15 fish per replicate, respectively) than in July 1995.

The effect of soak time was significant in the two deep sandy habitats (DSNR and DSAR) only (Fig. 3.12). In these two habitats, the number of fish trapped during the night soaks (3.85 and 2.55 fish per replicate, respectively) was twice that in day soaks.

The effect of habitat type was similar in each soak time. During the day soaks, there were 2-8 times more fish caught at the habitats TOPS and SLOP (8.78 and 4.74 fish per replicate, respectively) than in the other four habitats (Fig. 3.12). At night there was 2-4 times less fish in the SSNR, RUBB and DSAR than in TOPS and SLOP (5.67 and 6.12 fish per replicate, respectively). In addition, significantly less fish were trapped in the habitat RUBB (1.62 fish per replicate) than in the DSNR (3.85 fish per replicate).

Benthic predators

The Time *x* Habitat and Habitat *x* Soak time interactions were significant ($p<0.001$ and $p<0.0001$, respectively; Table 3.5b). The effect of habitat was significant in October 1994, July 1995 and October 1995 (Fig. 3.13). At all other times, the mean numbers of fish per replicate in all the habitats did not differ significantly (Fig. 3.13). In October 1994, significantly more benthic predators (17 times) were caught in the SLOP (3 fish per replicate) than in SSNR. In July 1995, the mean number of benthic predators in the SLOP (3.88 fish per replicate) was significantly higher (7-24 times)

than in the TOPS and RUBB. In October 1995, there were 6-18 times more benthic predators trapped in the SLOP (4.62 fish per replicate) than in the DSAR, RUBB and SSNR. In addition, 12 times more benthic predators were captured in the TOPS (3.01 fish per replicate) than in the RUBB.

The effect of sampling time in each habitat type was not significant except in the DSNR (Fig. 3.13). In this habitat, the mean number of benthic predators in March 1996 (4.48 fish per replicate) was significantly higher (7-8 times) than in March 1994 and July 1995.

The effect of soak time was significant only in the DSAR habitat (Fig. 3.14). In this habitat, significantly more benthic predators (5 times) were caught during night (1.94 fish per replicate) than day. There was no significant difference in the number of benthic predators caught between day and night in the other 5 habitats (Fig. 3.14).

The effect of habitat type was significant in both soak periods (Fig. 3.14). During the day soaks, the mean number of benthic predators in the TOPS and SLOP (2.58 and 2.47 fish per replicate, respectively) were significantly higher (2-7 times) than in the other 4 habitats. A complex picture was observed for the night soaks. The mean number of benthic predators in the SLOP (3 fish per replicate) was significantly higher (2-4 times) than in the TOPS, SSNR and RUBB (Fig.3.14). Similarly, benthic predators were significantly higher (2-3 times) in the DSNR (2.27 fish per replicate) than in the SSNR and RUBB, and significantly more in the DSAR (1.94 fish) than in the RUBB (Fig. 3.14).

Piscivores

Habitat type was the only significant factor influencing the variation in catch abundances for piscivores ($p < 0.0001$; Table 3.5c). The mean number of piscivores was significantly higher (2-11 times) in the SLOP (0.76 fish per replicate) than in the other 5 habitats and significantly higher (2-5 times) in the TOPS (0.38 fish per replicate) than in the DSNR, RUBB and DSAR (Fig. 3.15).

Planktivores

There was a significant main effect of soak time and a first order Time *x* Habitat interaction on planktivore abundance ($p < 0.001$ for both; Table 3.5d). The mean number of planktivores during night soaks (0.89 fish per replicate) was significantly higher (by a factor of 2) than the day soaks (Fig. 3.16).

The effect of habitat type was significant during March 1994 and October 1994 (Fig. 3.17). In March 1994, there were 10-55 times more planktivores in the TOPS (mean of 3.41 fish per replicate) than in the DSAR, DSNR and SSNR. In October 1994, the mean number of planktivores in the TOPS (5.60 fish per replicate) was significantly higher (8-93 times) than in the other 5 habitats.

The effect of sampling time was significant only in the TOPS and RUBB habitats (Fig. 3.17). In the TOPS, there was 7 times more planktivores in October 1994 (mean of 5.60 fish per replicate) than in March 1995. Mean abundance in the RUBB in March 1995 (2.35 fish per replicate) was significantly higher than in July 1995.

Herbivores

The factors sampling time and habitat type affected catch abundances of herbivores significantly ($p < 0.001$ and $p < 0.0001$, respectively; Table 3.5e). The mean number of herbivores in March 1994 and October 1994 (0.47 and 0.51 fish per replicate, respectively) was significantly higher (3-4 times) than in October 1995 and July 1996 (Fig. 3.18a). The mean number of herbivores in the TOPS (1.02 fish per replicate) was at least twice that of the other 5 habitats (Fig. 3.18b). In addition, the mean in the SLOP (0.43 fish per replicate) was 3 times more than in the DSNR and DSAR.

Pomacentridae (damselfishes)

Time *x* Habitat and Habitat *x* Soak time interactions were significant for numbers of pomacentrids ($p<0.001$ and $p<0.0001$, respectively Table 3.5f). The effect of habitat on pomacentrid abundance was significant in March 1994, October 1994 and

March 1996 (late and early summers) (Fig. 3.19). During these occasions, significantly more pomacentrids were caught in the TOPS and SLOP than in many of the other habitats. In March 1994, the mean numbers caught in the TOPS (3.70 fish per replicate) was 7-30 times more than in the SSNR, RUBB, DSNR and DSAR. No pomacentrid was recorded in the habitat DSAR at any time. Significantly more pomacentrids (5-35 times) were caught in the TOPS (3.53 fish per replicate) than in the RUBB, DSNR and SSNR in October 1994, and 19-30 times more on TOPS (2.47 fish per replicate) than in the SSNR and DSNR in March 1996. Similarly, nearly 25 times more pomacentrids were trapped in the SLOP (2.92 fish per replicate) than in the DSNR in March 1994, and 20 times more in the SLOP (1.98 fish per replicate) than in the SSNR in October 1994.

The effect of sampling time was significant only in the habitat SLOP (Fig. 3.19). In this habitat, there was 12-20 times more damselfishes caught in March 1994 (2.92 fish per replicate) than in March 1995, July 1995 and July 1996, and 14 times more in October 1994 (1.98 fish per replicate) than in July 1995.

The effect of soak time was significant only in the habitat TOPS (Fig. 3.20) where 4.5 times more damselfishes were caught during the day (3.65 fish per replicate) than night soaks. Significantly more pomacentrids (4-12 times) were caught in the TOPS (3.65 fish per replicate) than in all other habitats during the day soaks (no pomacentrid was ever caught at the DSAR during a day soak) (Fig. 3.20). At night, there was significantly more pomacentrids (40-50 times) trapped at the TOPS and SLOP (0.79 and 0.64 fish per replicate, respectively) than at the DSAR.

Lutjanidae (snappers)

The Time *x* Habitat and Habitat *x* Soak time interactions were significant in the catch abundance of snappers ($p<0.01$ and $p<0.001$, respectively Table 3.5g). In October 1995, there were 11-13 times more snappers trapped in the TOPS and SLOP (1.98 and 2.12 fish per replicate) than in the RUBB and SSNR (Fig. 3.21). There were 5-6 times more snappers entering the traps in the DSNR (3.29 fish per replicate) than

in the DSAR and SSNR in March 1996. In July 1995, there were significantly more snappers caught in the habitat SLOP (1.73 fish per replicate) than in the RUBB habitat. In the habitat TOPS, there was significantly more snappers (10 times) caught in March 1996 (2.74 fish per replicate) than in July 1995. In the habitat DSNR, 4-6 times more snappers were recorded in March 1996 (3.29 fish per replicate) than in March 1994, March 1995 and July 1995.

The effect of soak time was significant in the 2 deep sandy habitats only (DSNR and DSAR; Fig. 3.22). For both these habitats, more snappers were trapped during the night than the day soaks. In the habitat DSNR, 3 times more snappers was trapped during the night soaks (1.76 fish per replicate) than the day soaks. In DSAR, 6 times more snappers were caught during the night soaks (0.84 fish per replicate) than day soaks.

During the day, 4-9 times more snappers were trapped in the TOPS and SLOP (1.31 and 1.02 fish per replicate, respectively) than in the DSAR, RUBB and SSNR (Fig. 3.22). At night, 2 to 4 times more snappers were caught in the DSNR (1.76 fish per replicate) than in the RUBB SSNR, DSAR, and TOPS. In addition, 3 times more snappers were caught in the SLOP (1.37 fish per replicate) than in the RUBB and SSNR for the same soak time.

Apogonidae (cardinalfishes)

The mean catch rates for the apogonids differed significantly over sampling time ($p<0.001$; Table 3.5h). There was 2-3 times more cardinalfishes in March 1995 (0.76 fish per replicate) than in all other sampling times except in October 1994 (Fig. 3.23).

There was a significant interaction between Habitat and Soak time ($p<0.0001$; Table 3.5h). In the TOPS, SLOP and SSNR habitats, there were significantly more cardinalfishes caught during the night than day soaks (Fig. 3.24). In the TOPS habitat, 17 times more apogonids was recorded at night (1.85 fish per replicate) than during the day. In the SSNR habitat, 30 times more were caught during the night (1.17 fish per replicate) than the day. In the habitat SLOP, the mean of 0.90 fish per replicate during

the night soaks was higher than the day soaks (no apogonid was trapped during the day soaks in this habitat).

The catch rates for apogonids did not differ between habitat types during the day. At night, 2 to 7 times more apogonids were caught at the TOPS (1.85 fish per replicate) than in all other habitats except SSNR (Fig. 3.24). SSNR (1.17 fish per replicate) had 2-4 times more cardinalfishes than RUBB and DSAR, while SLOP (0.90 fish per replicate) had 3 times more than in the DSAR.

Lethrinidae (emperors)

The catch rates for the emperors did not vary significantly over sampling time (Table 3.5i). However, a significant Habitat *x* Soak time interaction was detected for this group ($p<0.01$ Table 3.5i). The effect of soak time was significant only for the habitat DSAR (Fig. 3.25). In this habitat, the mean number of emperors caught during night time (0.67 fish per replicate) was 6 times higher than the day time. The catch rates did not differ between habitats during the day. At night, the habitat DSAR had 3-22 times more lethrinids (mean of 0.67 fish per replicate) than in the TOPS and DSNR. The SLOP had 13 times more emperorfishes (0.41 fish per replicate) than the TOPS.

Labridae (wrasses)

Two significant interactions were observed in the analysis for the number of labrids (Table 3.5j). These were Time *x* Habitat and Habitat *x* Soak time ($p<0.01$ and $p<0.0001$, respectively). The effect of habitat was significant on 2 occasions (October 1994 and October 1995; Fig. 3.26). During the 2 occasions, significantly more labrids were recorded in the SLOP and TOPS than in the other four habitats. In October 1994, there was 6 times more labrids in the SLOP (1.36 fish per replicate) than in the DSNR (no labrids were caught in the RUBB, SSNR and DSAR during this time). In October 1995, the wrasses caught in the SLOP and TOPS (1.18 and 1.27 fishes per replicate, respectively) were 14-16 times more abundant than in the RUBB (no labrid was caught in the DSNR, SSNR and DSAR during this time).

The effect of sampling time was significant in only 2 habitats (TOPS and SLOP; Fig. 3.26). The number of wrasses caught in March 1994 and July 1995 in the

TOPS was 10-15 times less than in October 1995 (1.27 fish per replicate) (Fig. 3.26). In the SLOP habitat, significantly more labrids were caught in October 1994 and October 1995 (1.36 and 1.18 fishes per replicate, respectively) than in July 1996.

The number of labrids caught during the day in the TOPS and SLOP habitats were significantly greater than night soaks (Fig. 3.27). In the TOPS the mean for the day soaks (0.80 fish per replicate) was 6 times higher than for the night soaks. Similarly, the mean for the day soaks (1.08 fish per replicate) in the SLOP was 3 times higher than the night soaks. During the day soaks, there was 3-13 times more labrids caught in the TOPS and SLOP (0.80 and 1.08 fish per replicate, respectively) than in the other four habitats (Fig. 3.27). In the night soaks only SLOP had significantly higher catch rates than DSAR. No labrid was recorded in the habitat DSAR.

Serranidae (trouts and groupers)

Habitat type was the only significant factor affecting catch rates of the serranids ($p<0.0001$; Table 3.5k). The catch rates did not differ significantly through time nor between soak times. The number of serranids caught in the SLOP (0.67 fish per replicate) was 3-41 times higher than in the other 5 habitats (Fig. 3.28). The habitat TOPS had the second highest mean catch rate (0.19 fish per replicate), 10-11 times higher than in the RUBB and SSNR. No groupers were caught in the DSAR.

Holocentridae (soldier or squirrelfishes)

A significant Habitat *x* Soak time interaction was present for the analysis of holocentrid catch rates ($p<0.0001$; Table 3.5l). Catch rates were significantly higher at night than day soaks in 3 habitats (TOPS, SLOP and DSNR) (Fig. 3.29). No holocentrids were caught during the day in any of the 6 habitats. During night soaks, the number of holocentrids trapped in the TOPS (0.33 fish per replicate), SLOP (0.55 fish per replicate) and DSNR (0.52 fish per replicate) was significantly more (5-17 times) than in the RUBB, SSNR and DSAR.

Lutjanus carponotatus (spanish flag snapper)

The catch rates of *Lutjanus carponotatus* showed a significant Time *x* Habitat interaction ($p<0.0001$; Table 3.5m). In July 1995, the mean number of *L. carponotatus* (1.50 fish per replicate) caught in the SLOP was significantly higher than in all other habitats except DSNR (Fig. 3.30). This catch rate (SLOP) was 7-9 times higher than in the TOPS, SSNR and RUBB. No *L. carponotatus* were caught in the DSAR at any sampling time nor soak time. In October 1995, the mean catch rates in the SLOP and TOPS (1.82 and 1.60 fish per replicate, respectively), were significantly higher than in the SSNR, RUBB and DSAR. These catch rates in SLOP and TOPS were about 3-15 times higher than in SSNR and RUBB. The mean catch rates at the TOPS and DSNR in March 1996 (2.66 and 2.32 fish per replicate, respectively) were about 4-12 times higher than in the SSNR and RUBB.

In the TOPS habitat, the mean catch in March 1996 (2.66 fish per replicate) was significantly higher (4-16 times) than in March 1994, October 1994 and July 1995 (Fig. 3.30). The mean in October 1995 (1.60 fish per replicate) was 9 times higher than in July 1995. The mean catch rate in the SLOP habitat in October 1995 (1.82 fish per replicate) was significantly higher (5 times) than in October 1994. Similarly, the mean catch rate in the DSNR in March 1996 (2.32 fish per replicate) was 4-23 times greater than at all other sampling times except July 1996.

Lutjanus fulviflamma (black-spot snapper)

There was a significant Habitat *x* Soak time effect on the catch rate of *Lutjanus fulviflamma* ($p<0.0001$; Table 3.5n). Catch rates between day and night time did not differ in all habitats except in the DSAR. The mean catch rate in the DSAR at night (0.38 fish per replicate) was significantly higher (17 times) than in the day (Fig. 3.31). Additionally, catch rates between habitats did not differ during the day. At night the mean catch rate in the DSAR (0.38 fish per replicate) was significantly higher (6-12 times) than in the other 5 habitats (Fig. 3.31).

Lutjanus quinquelineatus (5-lined seaperch snapper)

There was a significant Habitat *x* Soak time effect on the catch rate of *Lutjanus quinquelineatus* ($p<0.0001$; Table 3.5o). The mean catch rates were significantly

higher at night than day in SLOP, DSNR and DSAR (Fig. 3.32). Virtually no *L. quinquelineatus* were recorded during day soaks in all habitats except in the DSAR. The mean catch rate at night in the DSAR (0.35 fish per replicate) was 16 times higher than in the day. Catch rates between habitats did not differ during the day. At night, the mean catch rate in the DSNR of 0.75 fish per replicate was 2-9 times higher than in the DSAR, SLOP and SSNR. No fish was trapped in the RUBB and TOPS. In addition, the mean in the DSAR (0.35 fish per replicate) was 4 times higher than in the SSNR.

Lethrinus nebulosus (spangled emperor)

There was a significant Habitat *x* Soak time effect on the catch rates of *Lethrinus nebulosus* ($p<0.01$; Table 3.5p). The effect of soak time was significant only in the SSNR and DSAR (Fig. 3.33). In both habitats, the mean catch rates during the night soaks (0.23 and 0.38 fish per replicate, respectively) were higher than the day soaks by factors of 11 and 4, respectively. The effect of habitat types on the soak times was only evident during the night soaks. During night soaks, the mean catch rate in the DSAR (0.38 fish per replicate) was 7-21 times higher that in the TOPS, SLOP and RUBB. The mean catch rate in the SSNR (0.23 fish per replicate) was 12 times higher than in the SLOP.

Cephalopholis cyanostigma (blue-spotted rockcod)

Habitat and Soak time affected the catch rates of *Cephalopholis cyanostigma* significantly ($p<0.0001$ and $p<0.01$, respectively; Table 3.5q). Significantly more fish were caught in the SLOP than in the other 5 habitats (Fig. 3.34a). The mean in the SLOP (0.36 fish per replicate) was 4-18 higher than in TOPS, DSNR and SSNR. No fish was recorded in the RUBB and DSAR. The mean catch rate during the night soaks (0.10 fish) was significantly greater (by a factor of 2) than the day soaks (Fig. 3.34b).

3.4 DISCUSSION

The aims of this chapter were to describe diel patterns of distribution of reef fishes in specific habitat types based on catches from fish traps, and to identify factors that are important in the spatial and temporal distribution of fishes. This study specifically investigated variations between 6 habitat types within a lagoon (single reef zone) at day and night on 7 different occasions. This work complements the studies on diel variability of trap catch rates (Newman and Williams 1995) and cross shelf variations of lutjanids and lethrinids in the central GBR (Newman and Williams 1996).

The catch data profile clearly suggests a limitation in the scope of the study. This work is limited to the dominant species captured by the traps and by the biases of the gear as a sampling device. The bias of the traps to attract fish is assumed to be consistent across all factors (i.e. sampling time, habitat types and soak time). Cappo and Brown (1996) assessed how traps operate and identified bait effects, fish behavior and trap design as the 3 most important factors to affect effectiveness of traps as sampling devices. Several studies (e.g. Munro 1974, Newman 1990) have shown the presence of bait affected little the overall catch rates of traps but significantly influenced catch composition over long soaks (in the order of days). Behavioral factors such as conspecific attraction, the need to seek shelter, curiosity, thigmotropic associations, presence or absence of predators and random movements have been suggested to affect entry of fish to traps (Munro 1974, Newman 1990). Conspecific attraction enhances ingress (Munro 1974, Davies 1989). For example, the aggregating nature of many benthic predators (e.g. lutjanids and lethrinids), planktivores (e.g. *Acanthochromis polyacanthus*) and herbivores (e.g. *Amblyglyphidodon curacao*) may explain their high abundances (n=1090, 771 and 267, respectively) in overall trap catches obtained in this study. The high abundances of planktivores and herbivores in trap catches in this study were consistent with those obtained by Davies (1989), Newman (1990) and Davies (1995). It was highly likely that conspecific attraction, the need to shelter and curiosity may explain entry of planktivores and herbivores to traps, particularly on shallow reef environments (<20m). The variation in catch rates of these trophic groups in time (day or night) and in types of habitats are discussed below (see Section 3.4.2 and 3.4.3). Additionally, Cappo and Brown (1996) noted that serranids

(piscivores) entered traps to feed on captives and ignored the bait. They further reported that a significantly lower mean time of arrival of piscivores at the trap in instances when small fish ('pickers') initially fed on the bait suggests piscivores were attracted to captives rather than bait. Moreover, Munro (1974) reported that the maximum catch size for Antillean Z traps is reached in 7-10 days. The observation that piscivores feed on captives rather than the bait, the longer time to reach maximum catch size for this particular trap design and the shorter soaks (<20 hrs) may explain the moderate abundances of piscivores (n=220) in the overall trap catches obtained in this study.

Another assumption is that only fishes active during a particular time in a habitat type are likely to be captured. This is in general agreement with the findings of Parrish (1982) in the Caribbean. The major reason for a fish not to be trapped in a habitat should be inactivity at that time. This is demonstrated by the data on holocentrids and most apogonids. They were trapped only during night at some reefal habitats. This does not suggest in any way their absence in these habitats during the day. They hide to sleep during the day in ledges and crevices and forage for food at night (Chave 1978, Hobson *et al.* 1981). This verifies the known habits of these fishes as nocturnally active (Hiatt and Strassburg 1960, Hobson 1974, Luckhurst and Luckhurst 1978b, Randall *et al.* 1990).

Despite the limitations of the sampling technique, the study collected substantial information on at least 50 species. These were mainly the medium sized (200-250 mm TL) benthic predators (mostly *Lutjanus* and *Lethrinus* spp.), small (<100 mm TL) omnivorous zooplanktivores (e.g. *A. polyacanthus* and most apogonids), the herbivores (predominantly *A. curacao*) and medium sized (200-300 mm TL) piscivores (mostly serranids). The major results of this study can be summarized as follows:

1. Two distinct fish assemblages were identified to occur within the lagoon based on broad habitat types (mainly substratum type). These two assemblages were those fishes a) highly associated with reefal and rubble habitats and another which were b) highly associated with sandy habitats.

2. More importantly, these assemblages changed over a diel period. Each of the two 'habitat-based' assemblages (in 1 above) had a distinct day and a night composition. The nocturnal assemblage in the sandy habitats further differentiated based on proximity to a reef with distinct near reef and away from reef fish assemblages.

3. The major components of variability in species catch composition and abundance were habitat type and soak time. The factor sampling time affected catch rates significantly in only 2 of 18 analyses and was interacted with the factor habitat type on another 8 occasions (i.e. interactions involving the factor sampling time). In these 8 interactions, the contribution of the factor habitat type to the variation was far greater than that of the factor time, as indicated by the higher mean square values (MS) of the former.

3.4.1 Temporal Patterns (Sampling time)

There was no dramatic temporal pattern of distribution and abundance of fishes in Lizard Island lagoon. The classification analysis grouped samples largely on the basis of habitat type and soak time. Only catch rates of apogonids and herbivores showed significant changes over time which were not confounded with other factors. However, the best catch rates in March for all fish combined, March and October for pomacentrids and March for lutjanids and apogonids suggested seasonal influence, albeit weak. The catch rates for the other groups remained relatively constant over time. The observed high catch rates of fishes during March and October can be partly explained by the greater fish activity during the warmer times of the year, making them more likely to be captured in traps. Fowler (1990a) provided a similar explanation for the observed seasonal changes in the abundance of some butterflyfishes. This, however, could not account for the relatively constant catch rates of the other groups. Another possible explanation for this temporal variability was chance catches, particularly for schooling fish. Large catches occurred by chance a number of times for apogonids (*Apogon bandanensis*, *A. compressus*) and pomacentrids (*Acanthochromis polyacanthus*, *Amblyglyphidodon curacao* and *Chromis viridis*).

3.4.2 Spatial Patterns (Habitat types)

The fish assemblages sampled by traps in Lizard Island lagoon were dominated numerically by pomacentrids, lutjanids, apogonids, labrids, lethrinids, serranids and holocentrids. Three of these, lutjanids, lethrinids and serranids, are major target or by catch species of commercial and recreational line fisheries and were subjects of further study in later chapters.

The habitat TOPS was characterized by high catch rates of pomacentrids, lutjanids, apogonids, planktivores and benthic predators, while labrids, serranids, holocentrids, piscivores and herbivores occurred in moderate numbers. Very few lethrinids were captured in this habitat. Five species, *Amblyglyphidodon curacao, Acanthochromis polyacanthus, Lutjanus carponotatus, Apogon bandanensis*, and *A. compressus*, were highly associated with the habitat TOPS as they were consistently captured in high numbers. *Thalassoma lunare, Epinephelus merra* and *Myripristis murdjan* were trapped in moderate numbers in this habitat. This habitat had a high live coral cover relative to all other habitats except the SLOP habitat.

Six groups, lutjanids, pomacentrids, labrids, serranids, benthic predators and piscivores, displayed a strong association with the habitat SLOP. Moderate numbers of lethrinids, apogonids, holocentrids and herbivores also characterized SLOP habitats. The species *Amblyglyphidodon curacao, Lutjanus carponotatus, L. quinquelineatus, Fowleria* sp. '1', *Lethrinus semicinctus, L. atkinsoni, Thalassoma lunare, Choerodon fasciatus, Cephalopholis cyanostigma, Plectropomus leopardus* and *Sargocentron spiniferum* showed high preference for this habitat.

In the DSNR, the lutjanids and benthic predators were the most characteristic groups. *Lutjanus quinquelineatus*, *L. carponotatus* and *Myripristis murdjan* had a strong preference for this habitat. The habitat RUBB was characterized by moderate numbers of pomacentrids, lutjanids, apogonids, lethrinids and labrids, and very low catch rates of serranids and holocentrids. RUBB appeared to be a good settlement habitat for many fish as most of the juvenile fishes of *Lutjanus gibbus*, *Lethrinus semicinctus* and *Neoglyphidodon melas*, and all of the adults and juveniles of *Pomacentrus chrysurus* were captured in this habitat.

The SSNR habitat was characterized by moderate to low catches of pomacentrids, lutjanids, apogonids and lethrinids. Labrids, serranids and holocentrids were virtually absent in the SSNR. Moderate numbers of *Lethrinus nebulosus* and *Apogon cookii* were consistently captured in this habitat. The DSAR habitat was characterized by moderate to low catches of lutjanids, apogonids and lethrinids. Five species, *Echeneis naucrates*, *Lutjanus fulviflamma*, *Lethrinus lentjan* and *Rhabdamia gracilis* characterized the DSAR habitat.

The spatial distribution of the fish assemblage in the lagoon was determined by habitat types broadly differentiated into two types -reefal and sandy. There were generally more species and higher numbers of fish caught in the reefal than the sandy habitats. The TOPS and SLOP habitats were the most similar and were characterized by high species richness and abundance. These two habitats had the highest catch rates for five of the most dominant families (pomacentrids, lutjanids, apogonids, serranids and holocentrids). TOPS and SLOP were the preferred habitat of more than two thirds of the total species. The most abundant of these were *Amblyglyphidodon curacao, Lutjanus carponotatus, Thalassoma lunare* and *Myripristis murdjan.* All except the last species were indicator species for reefal, near reefal and rubble habitats (cluster A in Fig. 3.8).

In contrast, the sandy habitats SSNR and DSAR were the most depauperate in terms of fish abundance and species richness. A total of 46 and 26 species were recorded for SSNR and DSAR, respectively, many of which were rare species (i.e. those which were captured only once). SSNR and DSAR (together with RUBB) had the lowest catch rates. Moderate numbers of lutjanids, apogonids and lethrinids were common to both habitats. Only *Lethrinus nebulosus* and *Lutjanus fulviflamma* were consistently captured in these two habitats. These two species were indicator species for the sandy habitats (cluster B and B2, respectively).

DSNR and RUBB appeared intermediate habitats with moderate numbers of species and individuals. DSNR and RUBB were more similar to TOPS and SLOP in terms of fish faunal composition than to SSNR and DSAR but were more similar to SSNR and DSAR in terms of catch rates than to TOPS and SLOP. Species similar to

DSNR and RUBB, and TOPS and SLOP included *Lutjanus carponotatus, L. quinquelineatus, Apogon bandanensis, Acanthochromis polyacanthus* and *Thalassoma lunare*. The species similar to DSNR and RUBB and SSNR and DSAR were *Lutjanus fulviflamma* and *Lethrinus nebulosus*.

The general results of the ANOVAs support the observed spatial distribution of the fish assemblages in the lagoon. The factor habitat type affected numbers of herbivores, piscivores and serranids significantly. The abundances of these fish groups were higher in reefal habitats (TOPS and SLOP) than in sandy habitats (SSNR and DSAR). The factor habitat type interacted significantly with sampling time on 8 occasions (for total species richness of all fish, numbers of all fish, benthic predators, planktivores, pomacentrids, lutjanids, labrids and *Lutjanus carponotatus*) and with soak time on 12 occasions (for total species richness of all fish, numbers of all fish, benthic predators, pomacentrids, lutjanids, labrids, apogonids, lethrinids, holocentrids, *Lutjanus fulviflamma, L. quinquelineatus* and *Lethrinus nebulosus*) (Table 3.6). The variation in numbers of fish species and individuals between habitats was larger and more important than sampling time in all 8 interactions. In the other 12 significant interactions (between habitat type and soak time), the variation in numbers of fish species and individuals due to habitat was larger and more important than soak time for the total species richness of all fish, numbers of all fish and for benthic predators. Variation in numbers of fish species and individuals due to soak time was larger and more important than habitat for abundance of apogonids, lethrinids, holocentrids, *Lutjanus fulviflamma, L. quinquelineatus* and *Lethrinus nebulosus*. Habitat and soak time were equally important in their effects on abundance of pomacentrids, lutjanids and labrids. In these 20 instances, habitat TOPS and SLOP had generally higher numbers of fish species and individuals (and DSNR for the lutjanids) than the other 4 habitats.

The type of substratum appeared largely responsible for the observed differences in the spatial patterns of distribution and abundance of fish. Unfortunately, no benthic data were collected from each habitat to relate with fish composition and abundance. The habitats were chosen based on broad substratum categories such that each of the habitats were distinctly different (e.g. sandy (SSNR, DSAR and DSNR) vs.

reefal (TOPS and SLOP) and rubble areas). These broad habitat categories were thought to be likely important to diel movements of lutjanids and lethrinids in the study area. Within each broad category, depth and/or location from a potential refuge point distinguished a habitat. For example among the sandy habitats, SSNR was different from DSNR based on depth. DSAR differed from SSNR based on depth and distance from a reef structure. DSNR was different from DSAR based on the distance from a reef structure. In the reefal habitats, TOPS were habitats with high live coral cover located on tops of bombies distinct from SLOP habitats, also with high coral cover, located on the slopes of patch reefs. RUBB was obviously different from sandy and reefal habitats in that the substratum was chiefly dead coral rubble. Thus, the benthic substrata fell clearly into 3 categories (live coral cover, rubble, and sand) and detailed quantitative data on the benthos would not have assisted the differentiation of the fish communities substantially.

Gladfelter and Gladfelter (1978) were among the first to point out that structurally similar habitats support similar fish fauna. Habitat characteristics such as live coral cover and structural heterogeneity of the substratum may explain the similar, more diverse and abundant fish assemblages in the TOPS and SLOP habitats of coral patch reefs compared to the less species rich and less abundant fish assemblages in the sandy habitats SSNR, DSNR and DSAR. Sheaves (1996) showed distinct differences in catch composition and abundance of fish in traps in 4 different habitats in a tropical estuary, with habitats of higher structural heterogeneity (i.e. snag habitats) having higher catch rates than clear habitats. Similarly, Davies (1995) reported consistently higher catch rates for *Lutjanus carponotatus*, *Siganus doliatus* and *Plectropomus leopardus* in reef habitats than in sandy habitats. The present study contrasts with that of Parrish (1982) who found no difference in catch rates of traps between reef and sand flat habitats in a Puerto Rican reef. The longer soak period used in his study may possibly explain this difference.

The overall spatial distribution of reef fishes found in this study is consistent with a number of studies that investigated fish distributions in adjacent reef zones, both for site-attached and relatively mobile species. Talbot and Goldman (1972) reported distinct reef fish assemblages related to different substratum characteristics in various

zones of One Tree Reef, GBR. Itzkowitz (1977) found that type and quantity of substratum determined distribution, movement, behavior and territoriality of damselfishes in a Jamaican reef. Waldner and Robertson (1980) observed significant differences in the distribution of 7 Caribbean damselfishes in 6 different habitat types, suggesting differential substratum utilization. Similarly, Carpenter *et al.* (1981) found that fish abundance was correlated with greater complexity of the type of substratum, and that fish abundance was negatively correlated with the percentage cover of sand. Jennings *et al.* (1996) reported that a significant proportion of the variance in biomass of 3 genera of reef fishes (*Chaetodon*, *Scarus* and *Parupeneus*) was explained by habitat variables, largely by coral and sand cover. In another study, Bell and Galzin (1984) found that species richness and density of reef fish was proportional to live coral cover. More importantly, they demonstrated that small changes in coral cover produced significant changes in these parameters. Similarly, Hart *et al.* (1996) found a positive correlation between densities of herbivorous fishes and live coral cover. A number of studies, however, reported little or no significant relationship between fish species richness and abundance, and coral cover (e.g. McManus 1981, Roberts and Ormond 1987, Fowler 1990a).

Other factors influencing distribution and abundance of reef fishes include physical characteristics of habitats such as topographic complexity (Luckhurst and Luckhurst 1978a, Carpenter *et al.* 1981), exposure to wave energy (Williams 1982), varying degrees of embayment (Horikoshi 1987, Hilomen and Gomez 1988), food availability (Thresher 1983a), water quality and current flow (e.g. Thresher 1983b), availability of hiding places (de Boer 1978, Roberts and Ormond 1987, Caley and St. John 1996), and biological interactions such as competition (Smith and Tyler 1972, 1973, Connell 1975, Anderson *et al.* 1981), predation (Zaret 1980, Sih *et al.* 1985, Hixon and Beets 1989, 1993), and recruitment (Doherty and Williams 1988, Doherty 1991, Doherty and Fowler 1994, Caley *et al.* 1996). Williams (1991) reviewed potential processes causing patterns of within-reef distribution of coral reef fishes. He points out that within a zone, selection of habitat appears to be a major process determining the substratum type and depth distribution of many small, site-attached damselfishes within reefs (e.g. Sweatman 1983). Correlations found between numbers of species and individuals and abundance of shelter sites for *Chromis cyanea* (De Boer

1978) and a reef fish assemblage in the Caribbean (Hixon and Beets 1993) support this point. In contrast, Caley and St. John (1996) did not observe habitat selection in fish settling onto artificial refuges. Pre-settlement processes such as larval distribution and supply and patterns of larval settlement were suggested to be important in explaining much of the variability of the distribution of many butterflyfishes (Fowler 1990a) and wrasses (Eckert 1985). The possible influence of differential mortality rates due to predation may play an important role (Jones 1991, Hixon 1991, Hixon and Beets 1993, Caley *et al.* 1996) but this needs to be explored. Interference competition may play a minor role (Doherty and Williams 1988), although a more extensive review of literature by Caley and St. John. (1996) has shown more examples of such processes.

The spatial distribution of recreationally and commercially important groups such as serranids, lutjanids and lethrinids is of direct practical interest to fisheries. The coralline, sloping habitats were the most important for serranids, particularly *Cephalopholis cyanostigma*, while practically all habitat types were important for lutjanids and lethrinids. Shpigel and Fishelson (1989 a and b) found similar results for a number of *Cephalopholis spp.* in the Red Sea. Reefal habitats and sandy habitats near reefal structures were important for *Lutjanus carponotatus* and *L. quinquelineatus* while *L. fulviflamma* and *Lethrinus nebulosus* preferred the sandy habitats at night. Davies (1995) also observed higher catch rates of *Lutjanus carponotatus* in reefal habitats than in sandy habitats, and the reverse for *L. fulviflamma.* Such results may assist to predict potential catch composition from a rough assessment of habitat types.

The present study suggests that spatial variation within a zone is more distinct than temporal variation. This is in general agreement with the findings of Choat *et al.* (1988) and Fowler (1990a), emphasizing the greater importance of spatial variation than temporal fluctuations in reef fish communities.

3.4.3 Diel Patterns (Day and night fish assemblages)

Most studies of patterns of within-reef distribution and abundance of reef fishes (e.g. Williams 1982, Russ 1984a, b, Hilomen and Gomez 1988, Letournier 1996a, b, Newman and Williams 1996b) have ignored potential diel effects on fish assemblages. The present study demonstrates a distinct diel change-over in species composition and abundance within two broad habitat types in Lizard Island lagoon. Each of the reefal and sandy habitats had a distinct diurnal and nocturnal fish assemblage. The nocturnal fish assemblage in the sandy habitats further differentiated into a group near and another group away from reef structures.

Within each diel fish assemblage, the general spatial patterns were preserved. There were more numbers of species and individuals in the reefal habitats than in the sandy habitats for both diurnal and nocturnal assemblages. Diurnal assemblages were characterized by the significantly higher abundances of pomacentrids and labrids in the reefal habitats, and a general paucity of abundances in the sandy habitats. Nocturnal assemblages had significantly higher abundances of planktivores, serranids, holocentrids and apogonids in reefal habitats than in the sandy habitats. More benthic predators, especially lutjanids and lethrinids composed the nocturnal fish assemblage in the sandy than in the reefal habitats.

The difference between the diurnal and nocturnal fish assemblages in reefal habitats was reflected not in total numbers of species and individuals but in species composition. The diurnal fish group dominated by pomacentrids and labrids was replaced by nocturnal planktivores, serranids, holocentrids, and apogonids. The diurnal assemblage was characterized by *Acanthochromis polyacanthus* and *Thalassoma lunare*, while *Apogon bandanensis*, *A. compressus*, *Fowleria* 'sp.1', *Myripristis murdjan* and *Sargocentron spiniferum* distinguished the nocturnal assemblage. Abundances of *Lutjanus quinquelineatus* and *Cephalopholis cyanostigma* were significantly higher during night than day in sloping reefal habitats.

The nocturnal fish assemblage had significantly more fish than the diurnal assemblage in the sandy habitats. The omnivorous/planktivorous cardinalfishes were a distinct component of the nocturnal assemblage for shallow sandy habitats while

benthic predators, lutjanids, apogonids, lethrinids, some holocentrids, *Lutjanus fulviflamma*, *L. quinquelineatus*, and *Lethrinus nebulosus* were a distinct component of the night group in deep sandy habitats. The diurnal fish assemblages in sandy habitats were characterized by very poor catches with only *Echeneis naucrates* being trapped consistently. This depauperate fauna by day was replaced by relatively high abundances of benthic predators, mostly lutjanids and lethrinids (*Lethrinus nebulosus Lutjanus fulviflamma* and *L. quinquelineatus*) at night.

Additionally at night, distinct near reef and away from reef assemblages were observed. The nocturnal near reef fish assemblage was composed predominantly of *Lutjanus carponotatus* and *Myripristis murdjan* while the away from reef assemblage consisted mainly of *Lutjanus fulviflamma* and *Lethrinus lentjan*.

The major trophic groups showed some distinct diel patterns. There were significantly more nocturnal planktivores than diurnal planktivores in all six habitat types. This finding is consistent with the more widespread distribution of nocturnal planktivores throughout a reef in contrast to diurnal planktivores that are more abundant near reef edges where currents are stronger (Hobson 1991). The different distribution patterns of these groups appear to follow the distribution of their prey. The relatively bigger prey of nocturnal planktivores are residents of reefs while the transient prey of diurnal planktivores are smaller and tend to concentrate in currents along reef edges (Hobson and Chess 1978).

Numbers of benthic predators remained relatively constant during day and night in all habitats except at deep sand away from reefs (DSAR). At the DSAR, there were significantly more benthic predators at night than day. The higher numbers of benthic predators in the DSAR implies movement of these fishes from daytime hiding sites to feeding areas in the deep sand at night.

The diel shift of fish assemblages within a habitat suggests the possibility of interhabitat movements (Ogden and Buckman 1973, McFarland *et al.* 1979, Helfman *et al.* 1982, Holland *et al.* 1993, Holland *et al.* 1996) and differential feeding activities of fish (Hobson 1972, 1973, 1975, Luckhurst and Luckhurst 1978b, Chave 1978, Hobson et al. 1981). The diurnal feeding regimes described for many pomacentrids

(Hobson 1972, Allen 1975) and labrids (Hobson 1972) in patch reefs and in the water column near coralline structures may have contributed to the high catch rates of these fishes in reefal areas during the day. These diurnal fishes descend to seek shelter in the reef at dusk and remain in hiding until the morning when they begin their day time activities (Hobson 1972).

Nocturnal feeding activities of holocentrids and apogonids are well known (Hobson 1974, Luckhurst and Luckhurst 1978b, Chave 1978). The high nocturnal catch rates of these groups are consistent with the findings of these earlier studies. Movements of these fishes from reefal hiding places by day to nearby sandy habitats (SSNR for apogonids and DSNR for holocentrids) at night were apparently common in this study. Short but well-defined movements from diurnal shelter locations on the reef to night feeding sites have been described elsewhere for nocturnal species such as apogonids (Chave 1978) and holocentrids (Hobson 1972, Luckhurst and Luckhurst 1978).

Movement from a diurnal resting shelter to night feeding areas may largely explain the high catch rates of benthic predators, mostly lutjanids and lethrinids, in sandy habitats. *Lutjanus fulviflamma* had significantly higher catch rates at night than day in the DSAR (Tukey's HSD: NT>DT). During collections of *L. fulviflamma* (for age determination and growth studies; see Chapter 5), it was observed that during the day this fish tends to aggregate in groups of about 70-150 individuals on shallow patch reefs (<7m deep and tens of meters in diameter). Two daytime visual surveys in the DSAR conducted in March 1995 (between trapping periods; 1100-1400 hrs) recorded virtually no large fish during 2 x 30 min swims (on SCUBA). Additionally, trap data indicated that 61% of *L. fulviflamma* caught at night in all habitats were captured in DSAR. These observations suggest that it is very likely that *L. fulviflamma* moves to deep sand tens of meters away from reefal structures to feed on benthic dwelling organisms. This may explain the observation of Davies (1995) of higher catch rates of *L. fulviflamma* in sandy than in reefal habitats. A similar suggestion can be made for *Lutjanus quinquelineatus* (moving from reefal hiding places during the day to DSAR and DSNR during night time) and for *Lethrinus nebulosus* (moving from diurnal resting areas to shallow and deep sandy habitats at night). Studies on feeding habits

have shown that *L. fulviflamma* preys on crabs, shrimps and blenniid and gobiid fish (Sano *et al.* 1984) and *L. nebulosus* preys on a wide variety of molluscs (Jones *et al.* 1992). These prey species are abundant in sandy habitats.

Movement from day time resting sites to night time feeding sites is well documented for the white goatfish *Mulloides flavolineatus* (Holland et al. 1993), adults of grunts (*Haemulon flavolineatum* and *H. plumieri*) (Helfman et al. 1982), juvenile *H. flavolineatum* (Helfman and Schultz 1984) and juvenile grunts (McFarland *et al.* 1979). The reverse, movement from nocturnal resting grounds to day time feeding areas, has been demonstrated for the striped parrotfish *Scarus croicensis* (Ogden and Buckman 1973) and the blue trevally *Caranx melampygus* (Holland *et al.* 1996). These crepuscular movements take place just before evening for the former and just after the morning 'quiet period' for the latter (McFarland *et al.* 1979, Hobson *et al.* 1981). Such behavior apparently serves to minimize predation threats for these animals (Hobson 1973).

This study has demonstrated, by use of fish traps, distinct reefal and sandy and diurnal and nocturnal fish assemblages. Results are in general agreement with documented diel feeding patterns largely generated from visual census data (e.g. Hobson 1973, 1974, Chave 1978, Luckhurst and Luckhurst 1978b, McFarland *et al.* 1979 and Hobson *et al.* 1981). This suggests that traps may be adequate sampling tools for investigating movement and diel distributions of larger and more mobile species, circumventing problems of visual censusing at night. Literature on diel and inter-habitat movement is scant (Williams 1991). Such information on spatial and temporal patterns of within reef distribution and movement are required for better management and utilization of this valuable and renewable fishery resource. The issue of inter- and intra-habitat movement of reef fish in Lizard Island lagoon is addressed specifically in the next chapter of this thesis.

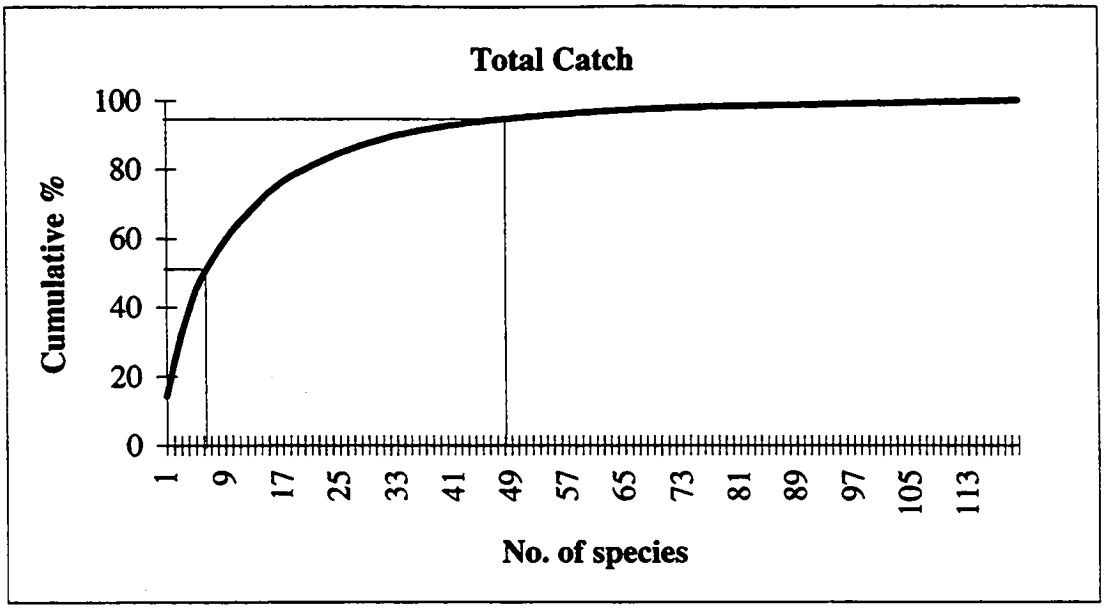


Figure 3.1. Percentage cumulative numerical catch abundances of the 119 species caught in Z-traps in Lizard Island lagoon. Less than 50 species comprised 95% of total catch.

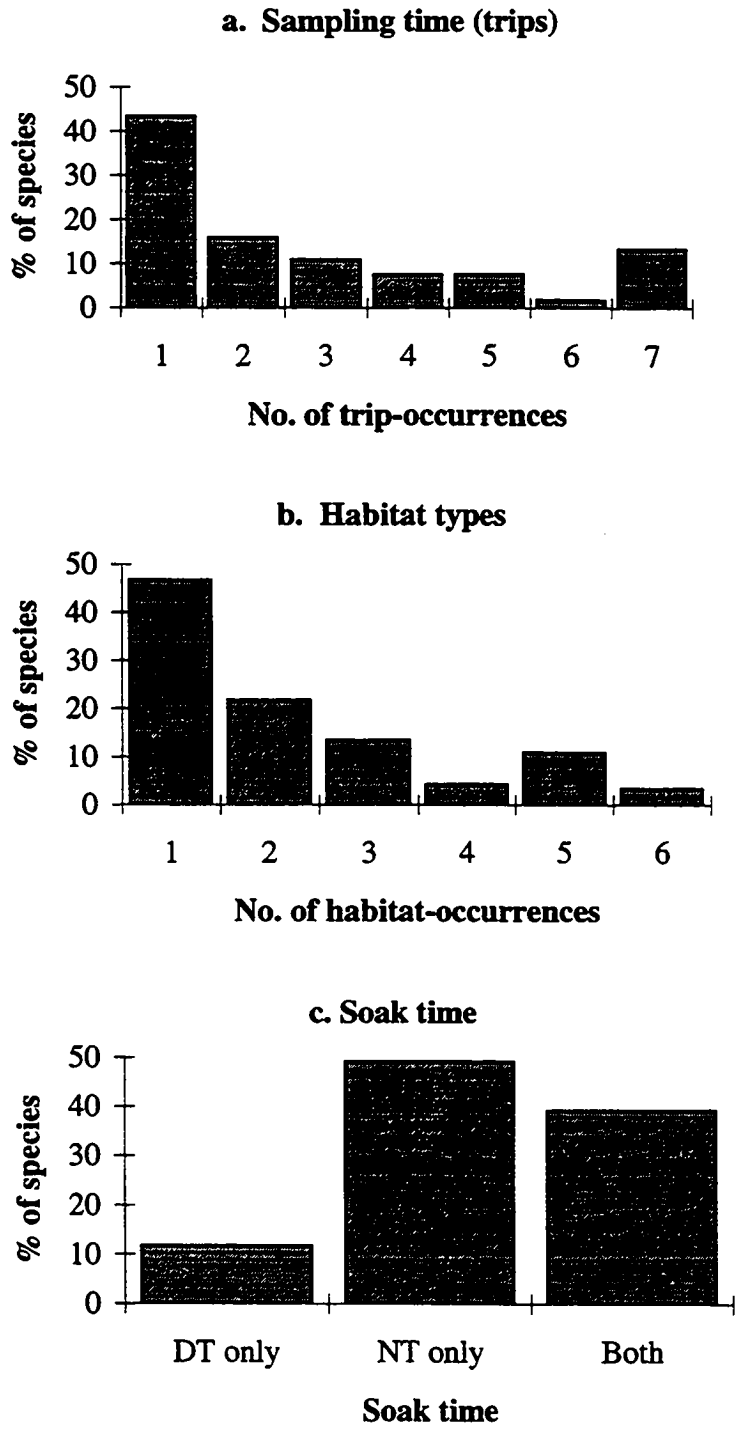


Figure 3.2. Percentage of species occurring in Z-trap catches (a) amongst sampling times (trips), (b) amongst habitat types, and (c) amongst soak times. Codes for soak times NT -night time and DT -day time.

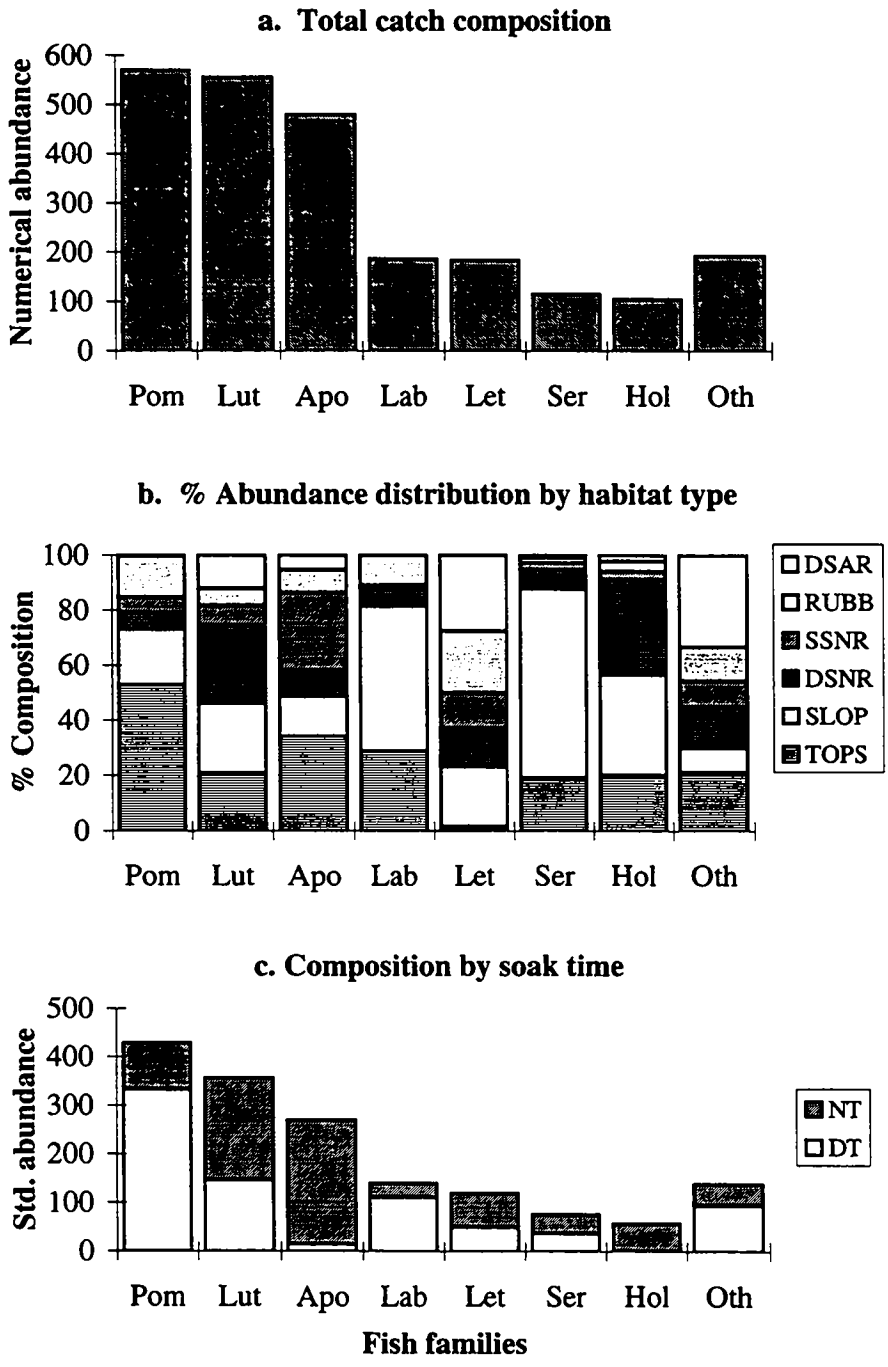


Figure 3.3. Trends in numerical catch data for the 7 most abundant families as (a) total catch composition, (b) % abundance in habitat types, and (c) composition by soak time (abundances standardized across different soak periods). Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near reefs, RUBB -rubble areas, SSNR -shallow sand near reefs and DSAR -deep sand away from reefs; for fish families Pom -Pomacentridae, Lut -Lutjanidae, Apo -Apogonidae, Let -Lethrinidae, Lab -Labridae, Ser -Serranidae, Hol -Holocentridae and Oth -20 other families.

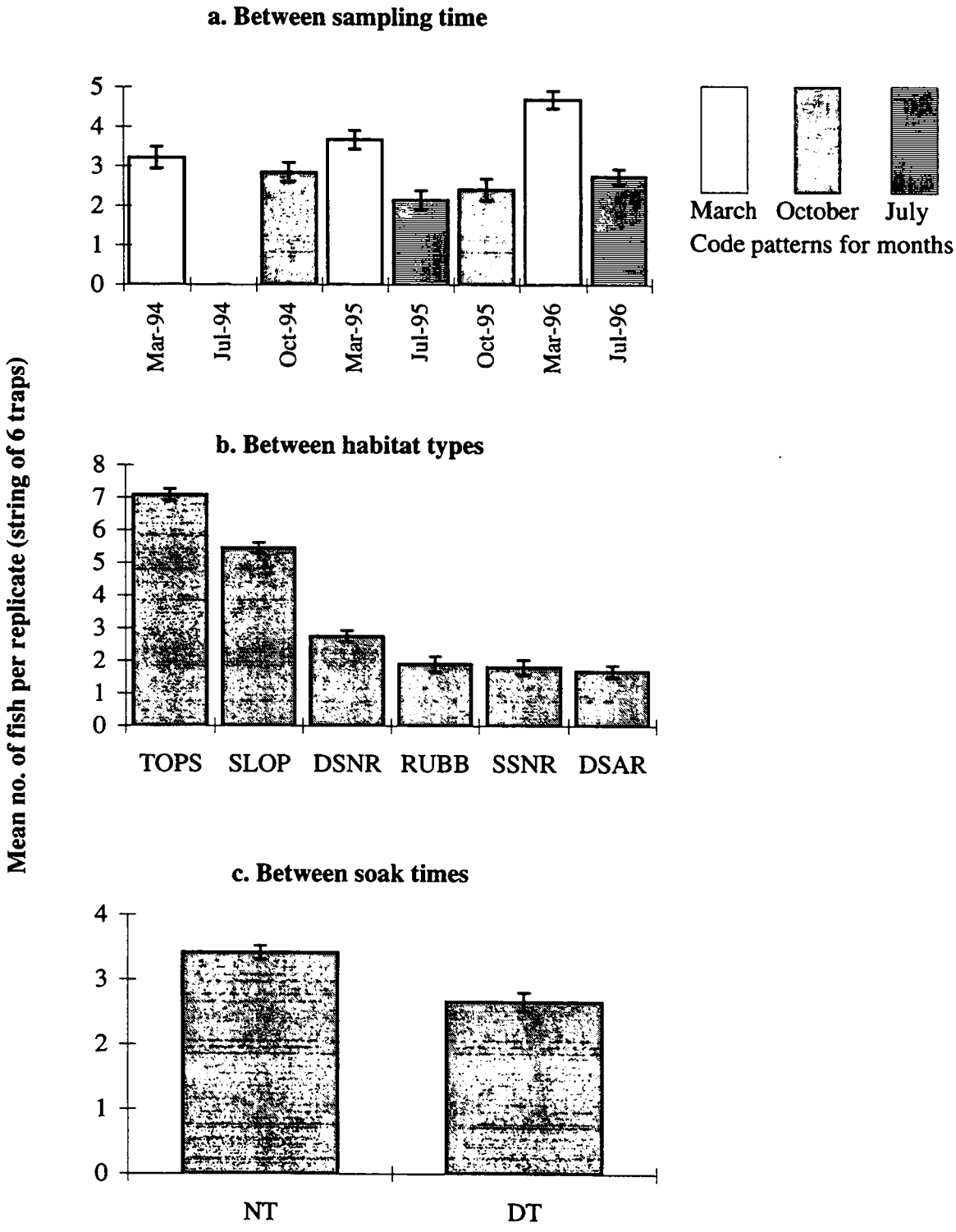


Figure 3.4. Mean number of fish per string of 6 traps (a replicate) between (a) sampling times (trips), (b) habitat types, and (c) soak times. Error bars are 95% confidence limits. No sampling was done in July 1994. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near reefs, RUBB -rubble areas, SSNR -shallow sand near reefs and DSAR -deep sand away from reefs; for soak times NT -night time and DT -day time.

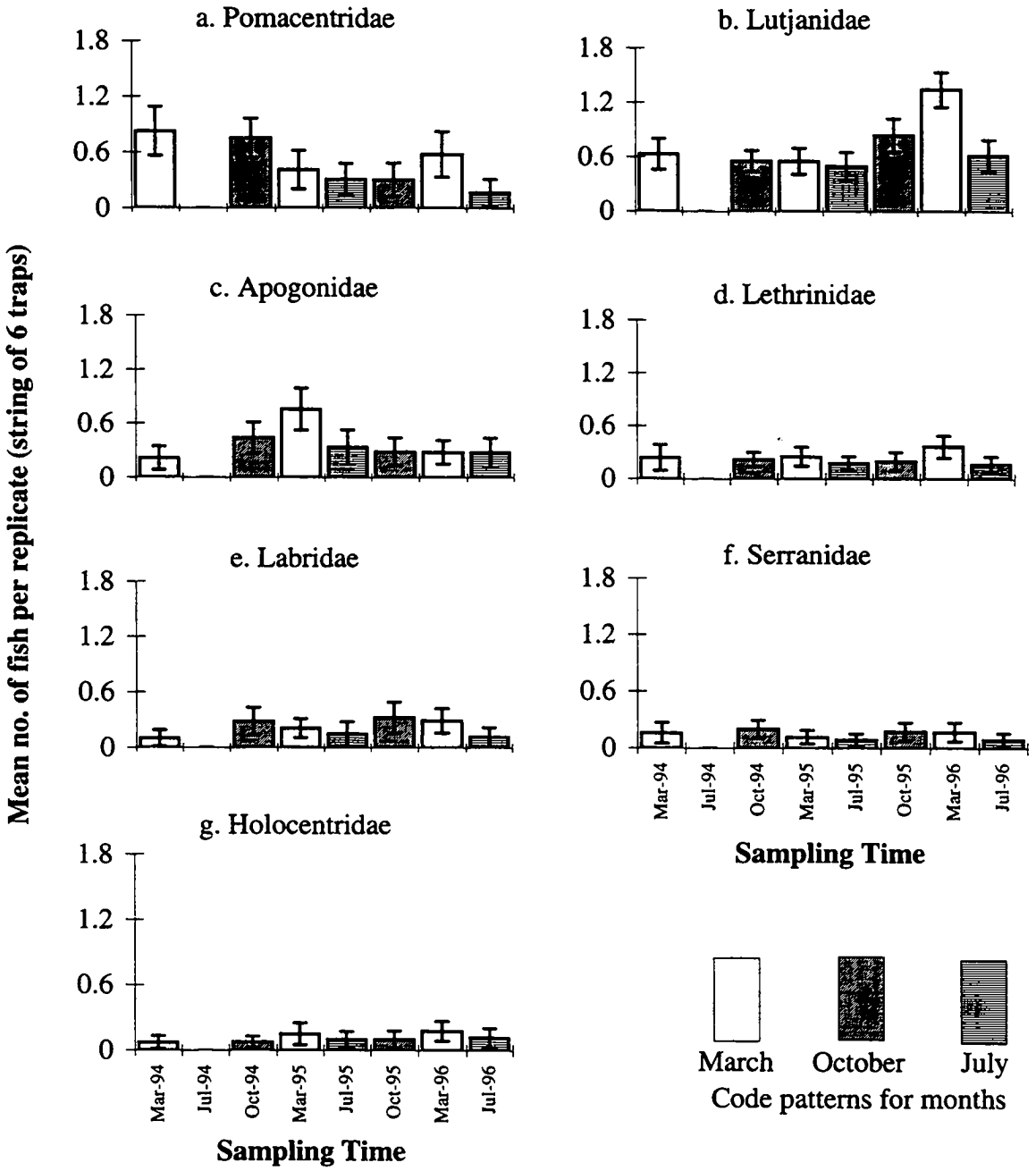


Figure 3.5. Variation in mean catch rate of the 7 most abundant families (**a-g**) over the sampling times. No sampling was done in July 1994. Error bars are 95% confidence limits.

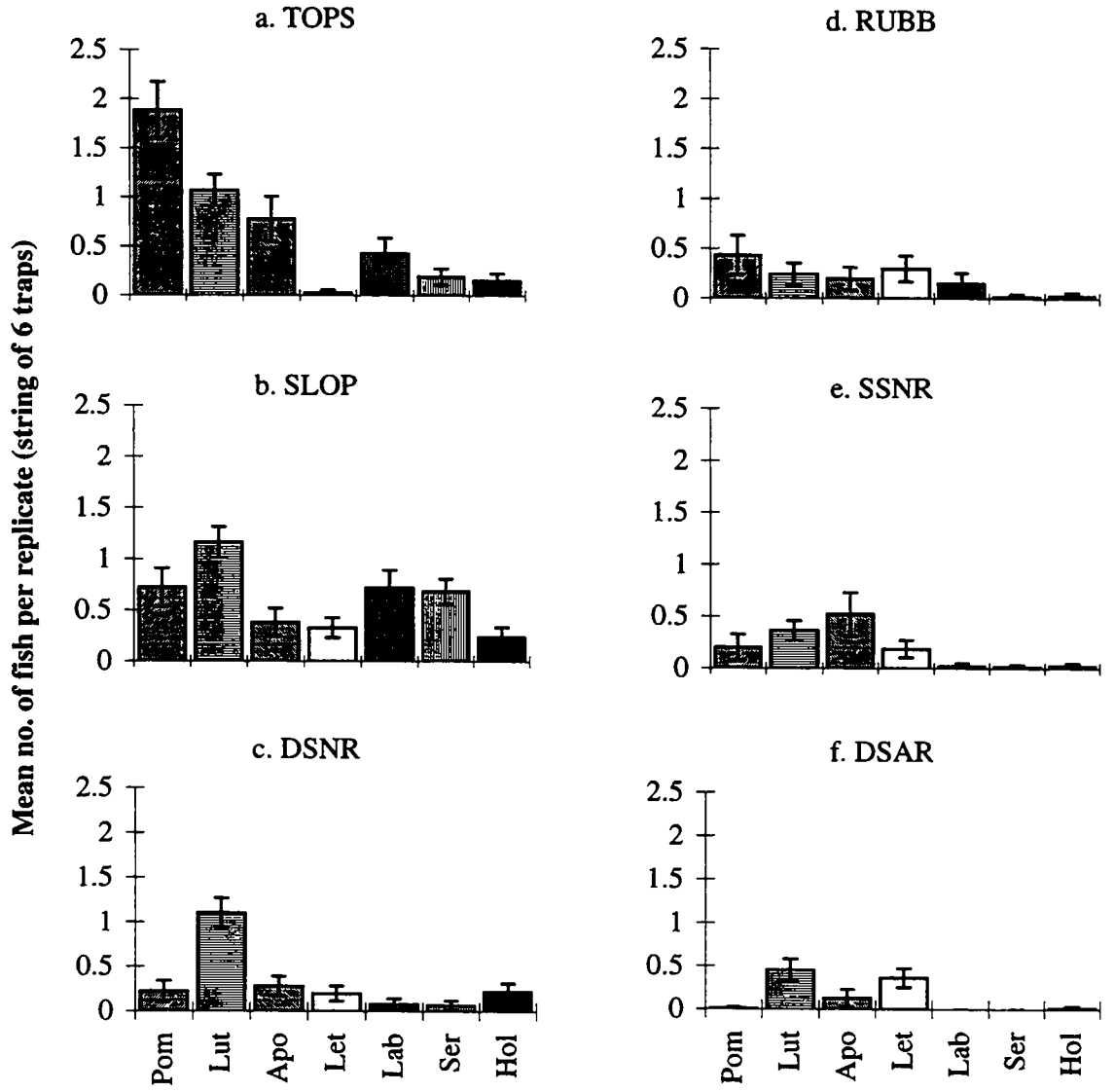


Figure 3.6. A comparison of the mean catch rate of fish in the 7 most abundant families across all habitat types (**a-f**). Error bars are 95% confidence limits. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near reefs, RUBB -rubble areas, SSNR -shallow sand near reefs and DSAR - deep sand away from reefs; for fish families Pom -Pomacentridae, Lut - Lutjanidae, Apo -Apogonidae, Let -Lethrinidae, Lab -Labridae, Ser -Serranidae and Hol -Holocentridae.

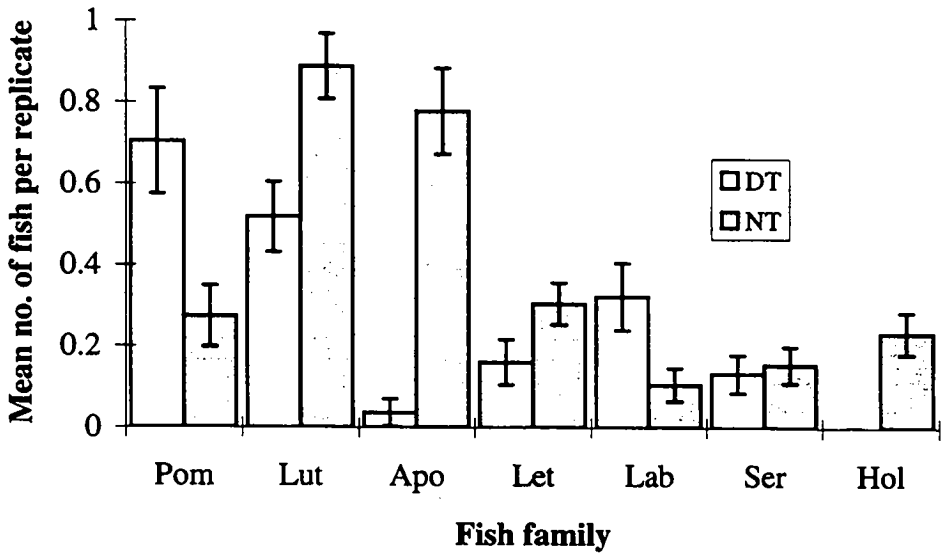


Figure 3.7. A comparison of the mean number of fish per replicate (string of 6 traps) between soak times for each of the 7 most abundant families. Error bars are 95% confidence limits. Codes for fish families are: Pom -Pomacentridae, Lut -Lutjanidae, Apo -Apogonidae, Let -Lethrinidae, Lab -Labridae, Ser -Serranidae and Hol -Holocentridae; for soak time, NT -night time and DT -day time.

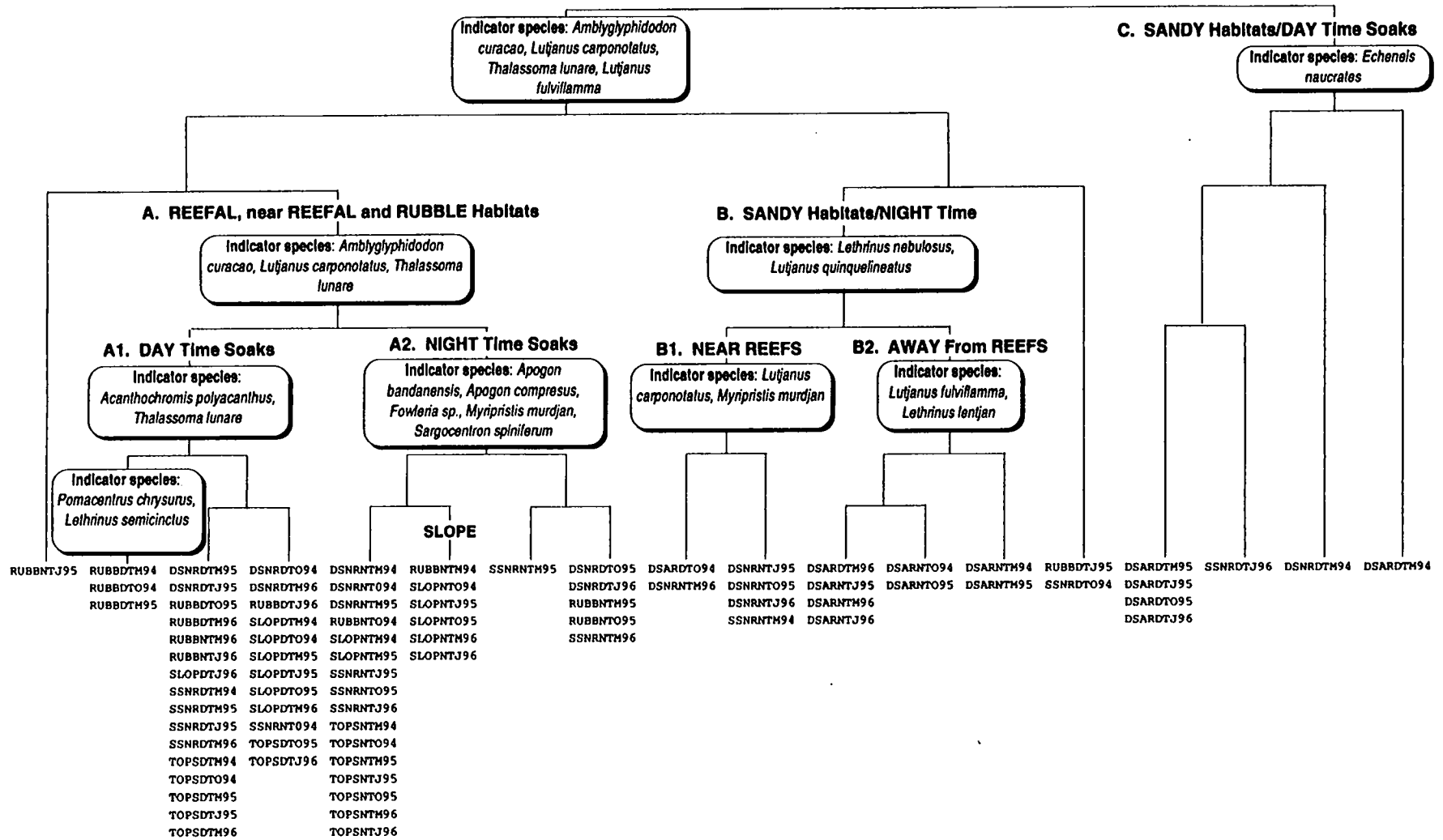
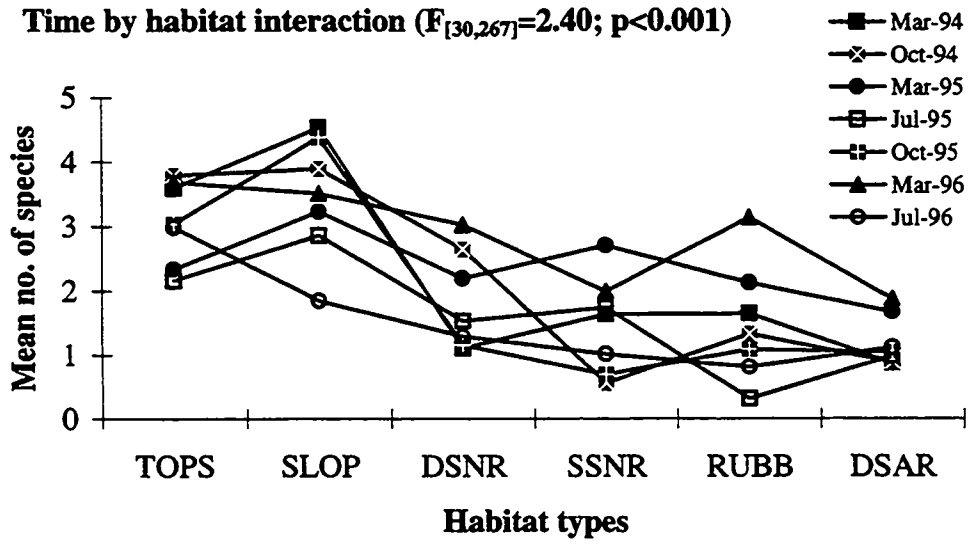


Figure 3.8. Dendrogram of the 84 samples generated by TWo-way INdicator SPecies ANalysis (TWINSPAN). One sample, SSNRDTO95, had no catch and was dropped by the program. Indicator species characterized the poles of the reciprocal average axis for a given level of division. Each sample is coded as HHHHSSMYY for HHHH -habitat type, SS -soak time and MYY for the month and year of sampling. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near reefs, RUBB -rubble areas, SSNR -shallow sand near reefs and DSAR -deep sand away from reefs; for soak times NT -night time and DT -day time; for month and year M94 -March 1994, O94 -October 1994, M95 -March 1995, J95 -July 1995, O95 -October 1995, M96 -March 1996 and J96 -July 1996.



TOTAL SPECIES RICHNESS

Effect of habitat type on sampling time

Time: **Mar 94**
SLOP > RUBB, SSNR, DSAR, DSNR
TOPS > DSAR, DSNR
SLOP, TOPS, RUBB, SSNR, DSAR, DSNR

Time: **Oct 94**
SLOP, TOPS > DSAR, RUBB, SSNR
SLOP, TOPS, DSNR, DSAR, RUBB, SSNR

Time: **Mar 95**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 95**
SLOP> RUBB
SLOP, TOPS, DSNR, DSAR, SSNR, RUBB

Time: **Oct 95**
SLOP > DSAR, DSNR, SSNR, RUBB
SLOP, TOPS, DSAR, DSNR, SSNR, RUBB

Time: **Mar 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Effect of sampling time on habitat type

Habitat: **TOPS**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **SLOP**
Mar 94, Oct 95 > Jul 96
Mar 94, Oct 95, Oct 94, Mar 95, Jul 95, Mar 96, Jul 96

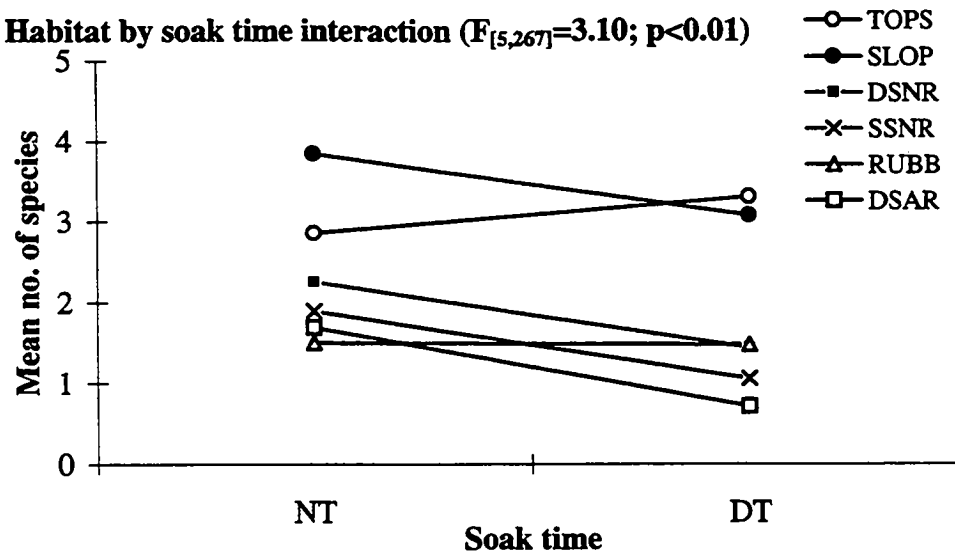
Habitat: **DSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 96 > Jul 95
Mar 96, Mar 95, Oct 94, Oct 95, Mar 94, Jul 96, Jul 95

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.9. Plot of total species richness of all fish for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.



TOTAL SPECIES RICHNESS

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

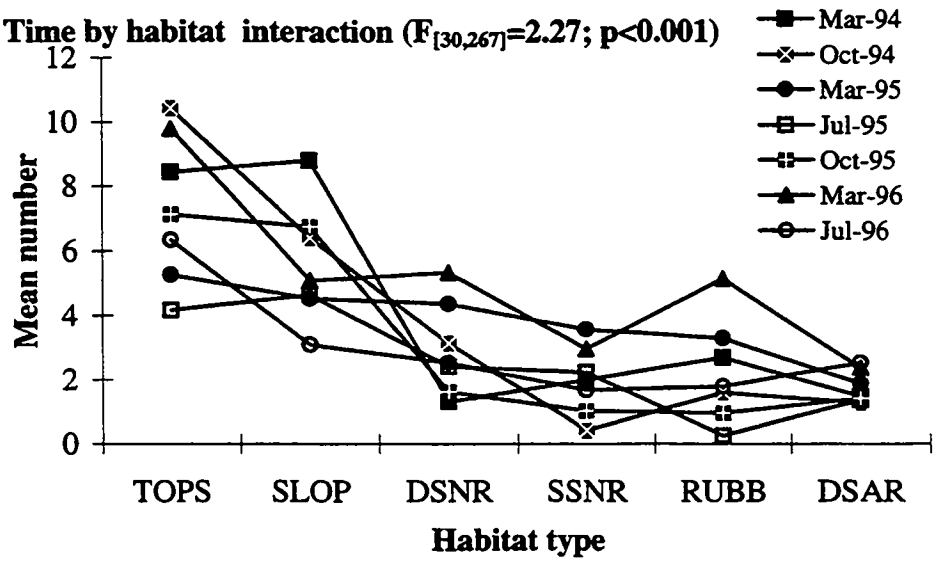
Habitat: **DSAR**
NT, DT

Effect of habitat type on soak time

Soak: **DT**
SLOP, TOPS, > DSNR, RUBB, DSAR, SSNR

Soak: **NT**
SLOP > RUBB, DSAR, DSNR, SSNR
TOPS > RUBB, DSAR
SLOP, TOPS, DSNR, SSNR, DSAR, RUBB

Figure 3.10. Plot of mean total species richness for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.



ALL FISH

Effect of habitat type on sampling time

Time: **Mar 94**
TOPS, SLOP > DSAR, DSNR
TOPS, SLOP, RUBB, SSNR, DSAR, DSNR

Time: **Oct 94**
TOPS > DSAR, RUBB, SSNR
SLOP > DSAR, SSNR
TOPS, SLOP, DSNR, DSAR, RUBB, SSNR

Time: **Mar 95**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 95**
TOPS, SLOP> RUBB
TOPS, SLOP, DSNR, DSAR, SSNR, RUBB

Time: **Oct 95**
TOPS > DSAR, RUBB, SSNR
SLOP > RUBB, SSNR
TOPS, SLOP, DSNR, DSAR, SSNR, RUBB

Time: **Mar 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Effect of sampling time on habitat type

Habitat: **TOPS**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **SLOP**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

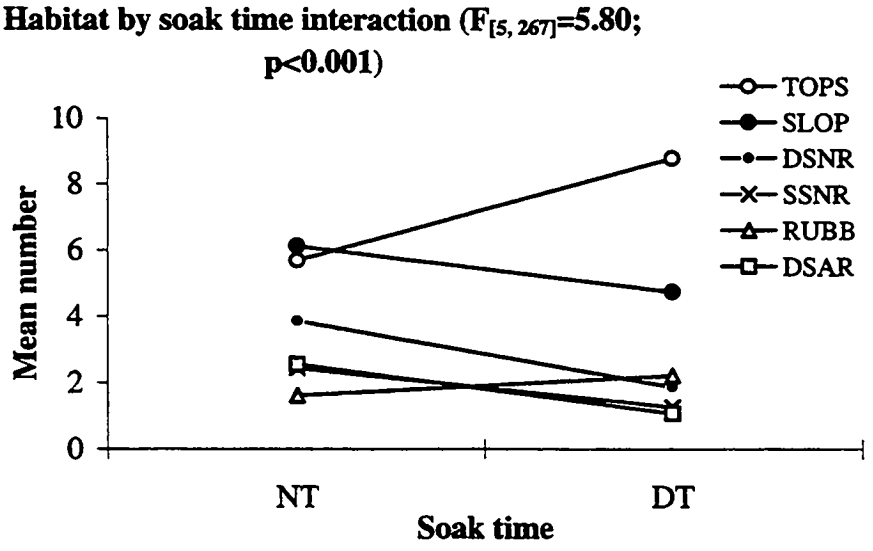
Habitat: **DSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 95, Mar 96 > Jul 95
Mar 95, Mar 96, Oct 94, Oct 95, Mar 94, Jul 96, Jul 95

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.11. Plot of mean number of fish for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.



ALL FISH

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT > DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

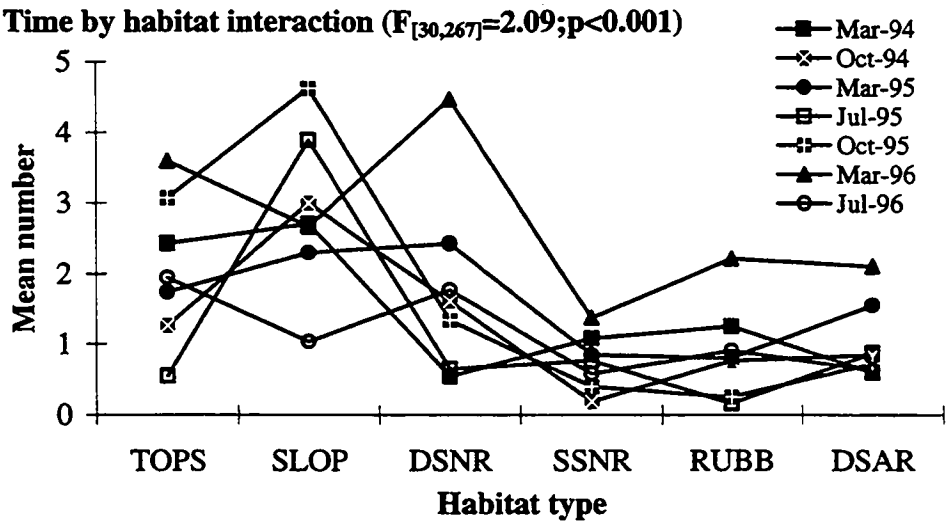
Habitat: **DSAR**
NT > DT

Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP > DSNR, RUBB, DSAR, SSNR

Soak: **NT**
TOPS, SLOP > SSNR, RUBB, DSAR
DSNR > RUBB
TOPS, SLOP, DSNR, SSNR, DSAR, RUBB

Figure 3.12. Plot of mean number of fish for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

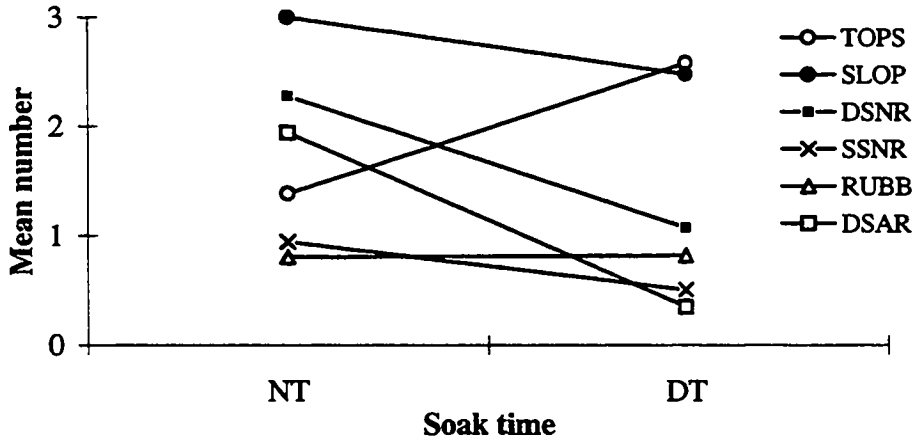


BENTHIC PREDATORS

Effect of habitat type on sampling time	Effect of sampling time on habitat type
Time: **Mar 94**	Habitat: **TOPS**
TOPS, SLOP, RUBB, SSNR, DSAR, DSNR	Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96
Time: **Oct 94**	Habitat: **SLOP**
SLOP > SSNR	Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96
SLOP, TOPS, DSNR, DSAR, RUBB, SSNR	
Time: **Mar 95**	Habitat: **DSNR**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR	Mar 96 > Mar 94, Jul 95
	Mar 96, Oct 94, Mar 95, Jul 96, Oct 95, Mar 94, Jul 95
Time: **Jul 95**	Habitat: **SSNR**
SLOP> TOPS, RUBB	Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96
SLOP, DSNR, DSAR, SSNR, TOPS, RUBB	
Time: **Oct 95**	Habitat: **RUBB**
SLOP > DSAR, RUBB, SSNR	Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96
TOPS > RUBB	
SLOP, TOPS, DSNR, DSAR, SSNR, RUBB	
Time: **Mar 96**	Habitat: **DSAR**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR	Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96
Time: **Jul 96**	
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR	

Figure 3.13. Plot of mean number of benthic predators for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS - tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

Habitat by soak time interaction ($F_{[5,267]}$=7.32; p<0.001)



BENTHIC PREDATORS

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

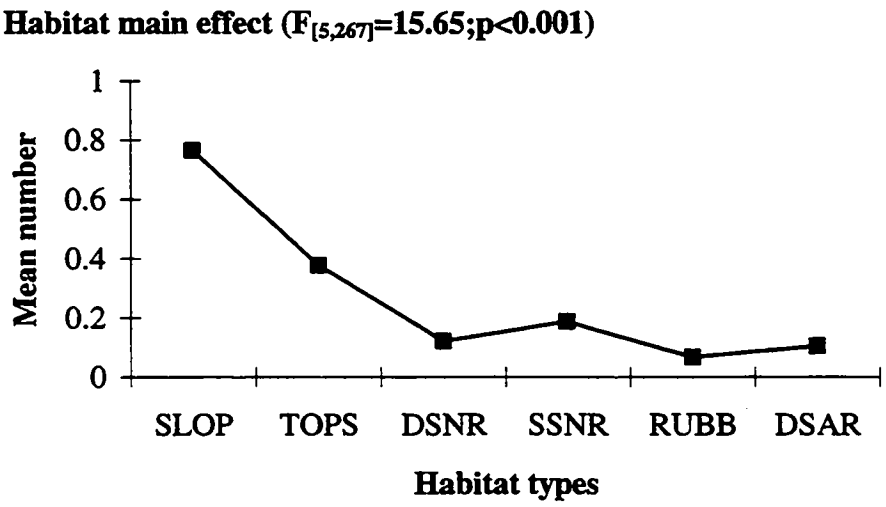
Habitat: **DSAR**
NT > DT

Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP > DSNR, RUBB, DSAR, SSNR

Soak: **NT**
SLOP > TOPS, SSNR, RUBB
DSNR > SSNR, RUBB
DSAR > RUBB
SLOP, DSNR, DSAR, TOPS, SSNR, RUBB

Figure 3.14. Plot of mean number of benthic predators for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS - tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

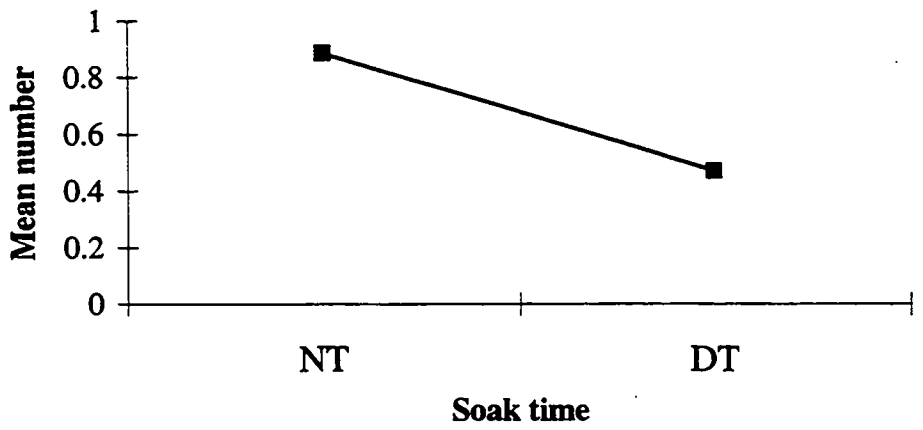


PISCIVORES

SLOP > TOPS, SSNR, DSNR, RUBB, DSAR

TOPS > DSNR, RUBB, DSAR

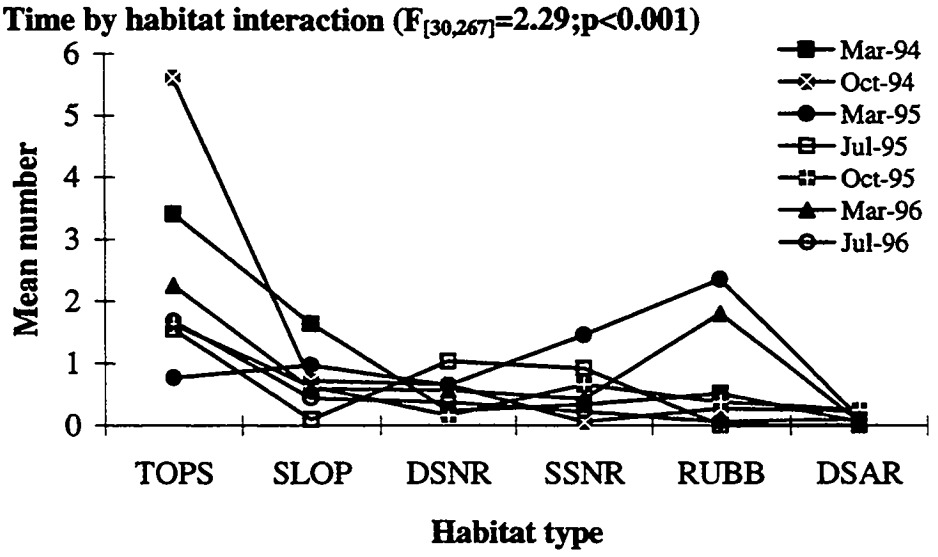
Figure 3.15. Plot of mean number of piscivores for the factor habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.



PLANKTIVORES

NT > DT

Figure 3.16. Plot of mean number of planktivores for the factor soak time. Number of planktivores was significantly higher during the night soaks (NT) than the day soaks (DT).



PLANKTIVORES

Effect of habitat type on sampling time

Time: **Mar 94**
TOPS > DSAR, DSNR, SSNR
TOPS, SLOP, RUBB, DSAR, DSNR, SSNR

Time: **Oct 94**
TOPS > SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Mar 95**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 95**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Oct 95**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Mar 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Time: **Jul 96**
TOPS, SLOP, DSAR, DSNR, RUBB, SSNR

Effect of sampling time on habitat type

Habitat: **TOPS**
Oct 94 > Mar 95
Oct 94, Mar 94, Jul 95, Oct 95, Mar 96, Jul 96, Mar 95

Habitat: **SLOP**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

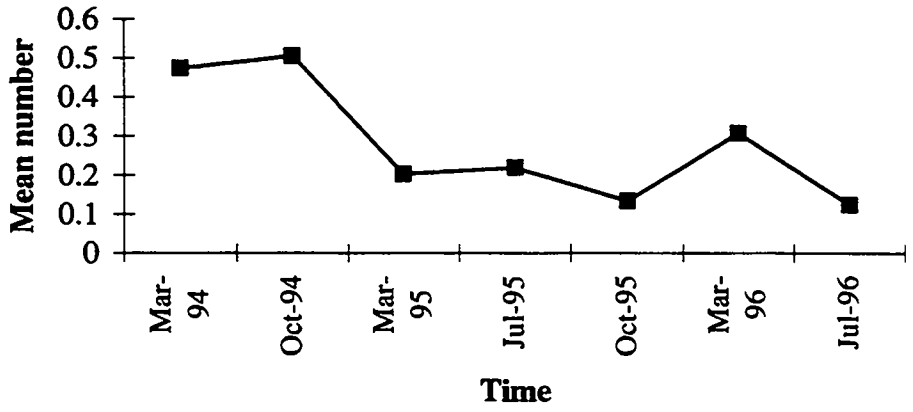
Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 95 > Jul 95
Mar 95, Oct 94, Mar 94, Jul 96, Oct 95, Mar 96, Jul 95

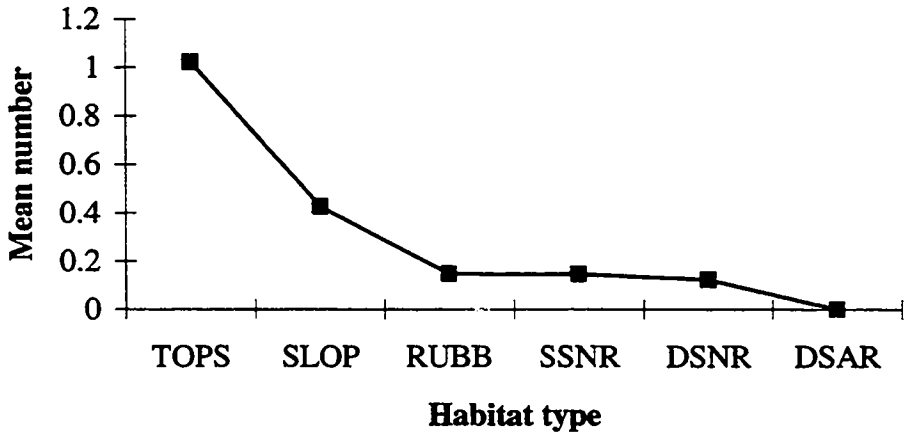
Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.17. Plot of mean number of planktivores for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

a. Time main effect ($F_{[6,267]}$=4.02;p<0.001)



b. Habitat main effect ($F_{[5,267]}$=20.51;p<0.001)



HERBIVORES

a. Time main effect:

Mar 94, Oct 94 > Oct 95, Jul 96

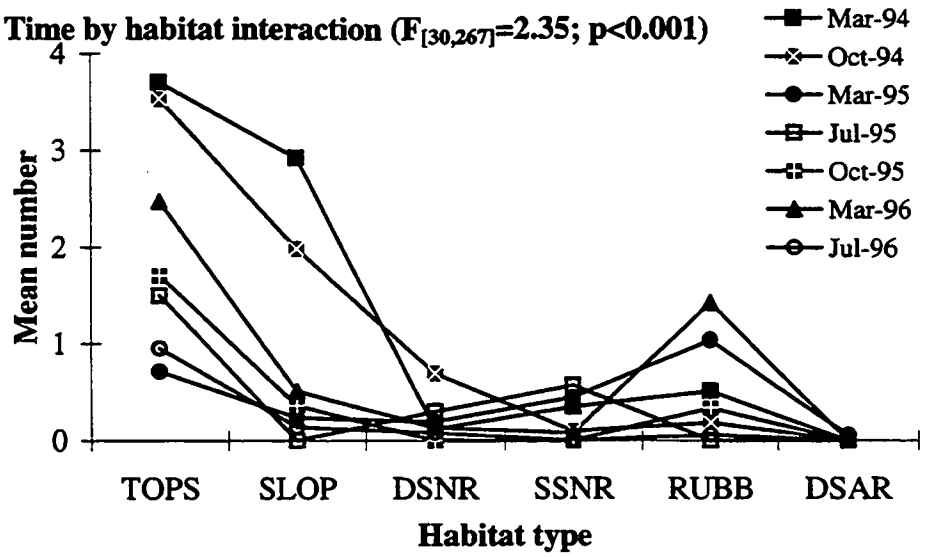
Mar 94, Oct 94, Mar 95, Jul 95, Mar 96, Oct 95, Jul 96

b. Habitat type main effect:

TOPS > SLOP, RUBB, SSNR, DSNR, DSAR

SLOP > DSNR, DSAR

Figure 3.18. Plot of mean number of herbivores for the main effects of factors (a) sampling time and (b) habitat type. A summary of multiple comparison of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR - deep sand near from reefs, SSNR -shallow sand near reefs, RUBB - rubble areas and DSAR -deep sand away from reefs.



POMACENTRIDAE

Effect of habitat type on sampling time

Time: **Mar 94**
TOPS > SSNR, RUBB, DSNR, DSAR
SLOP > DSNR, DSAR
TOPS, SLOP, SSNR, RUBB, DSNR, DSAR

Time: **Oct 94**
TOPS > RUBB, DSNR, SSNR, DSAR
SLOP > SSNR, DSAR
TOPS, SLOP, RUBB, DSNR, SSNR, DSAR

Time: **Mar 95**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Jul 95**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Oct 95**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Mar 96**
TOPS > SSNR, DSNR, DSAR
TOPS, SLOP, RUBB, SSNR, DSNR, DSAR

Time: **Jul 96**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Effect of sampling time on habitat type

Habitat: **TOPS**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **SLOP**
Mar 94 > Mar 95, Jul 95, Jul 96
Oct 94 > Jul 95
Mar 94, Oct 94, Oct 95, Mar 96, Mar 95, Jul 96, Jul 95

Habitat: **DSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

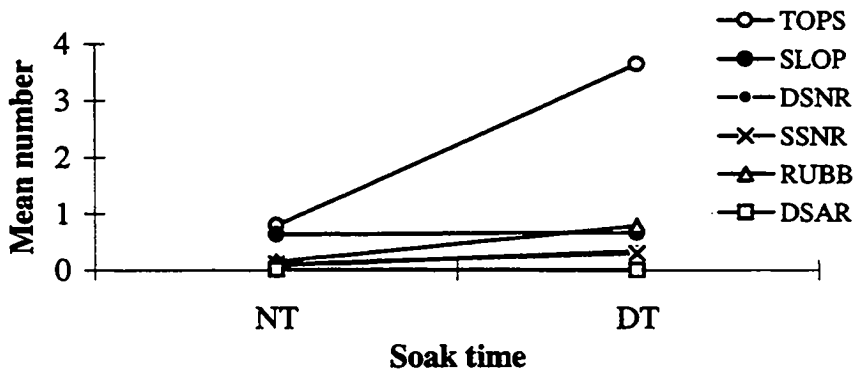
Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.19. Plot of mean number of Pomacentridae for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

Habitat by soak time interaction ($F_{[5,267]}$=6.08; p<0.001)



POMACENTRIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
DT > NT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

Habitat: **DSAR**
NT, DT

Effect of habitat type on soak time

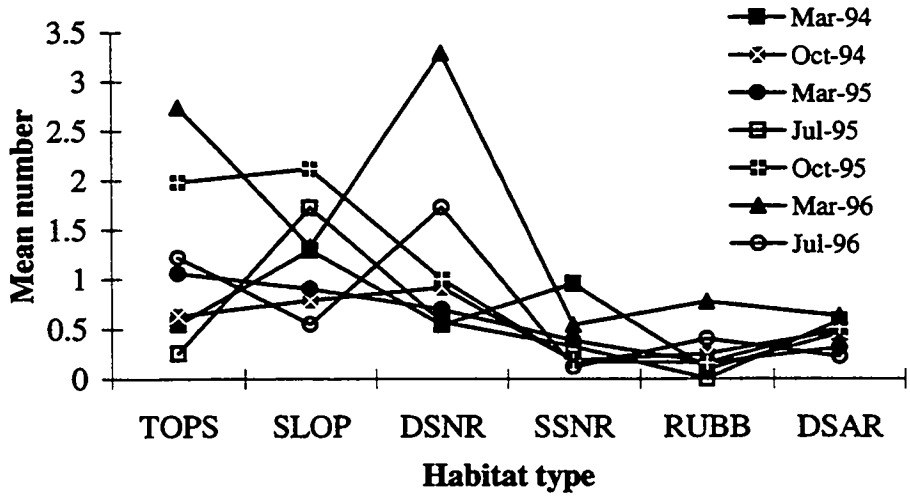
Soak: **DT**
TOPS > RUBB, SLOP, SSNR, DSNR, DSAR

RUBB, SLOP > DSAR

Soak: **NT**
TOPS, SLOP > DSAR
TOPS, SLOP, RUBB, SSNR, DSNR, DSAR

Figure 3.20. Plot of mean number of Pomacentridae for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT - night time and DT -day time.

Time by habitat interaction ($F_{[30,267]}$=2.10; p<0.01)



LUTJANIDAE

Effect of habitat type on sampling time

Time: **Mar 94**
DSNR, TOPS, SLOP, DSAR, RUBB, SSNR

Time: **Oct 94**
DSNR, TOPS, SLOP, DSAR, RUBB, SSNR

Time: **Mar 95**
DSNR, TOPS, SLOP, DSAR, RUBB, SSNR

Time: **Jul 95**
SLOP > RUBB
SLOP, DSNR, TOPS, SSNR, DSAR, RUBB

Time: **Oct 95**
TOPS, SLOP > RUBB, SSNR
TOPS, SLOP, DSNR, DSAR, RUBB, SSNR

Time: **Mar 96**
DSNR > DSAR, SSNR
DSNR, TOPS, SLOP, RUBB, DSAR, SSNR

Time: **Jul 96**
DSNR, TOPS, SLOP, DSAR, RUBB, SSNR

Effect of sampling time on habitat type

Habitat: **TOPS**
Mar 96 > Jul 95
Mar 96, Mar 94, Oct 94, Mar 95, Oct 95, Jul 96, Jul 95

Habitat: **SLOP**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSNR**
Mar 96 > Mar 94, Mar 95, Jul 95
Mar 96, Oct 94, Oct 95, Jul 96, Mar 94, Mar 95, Jul 95

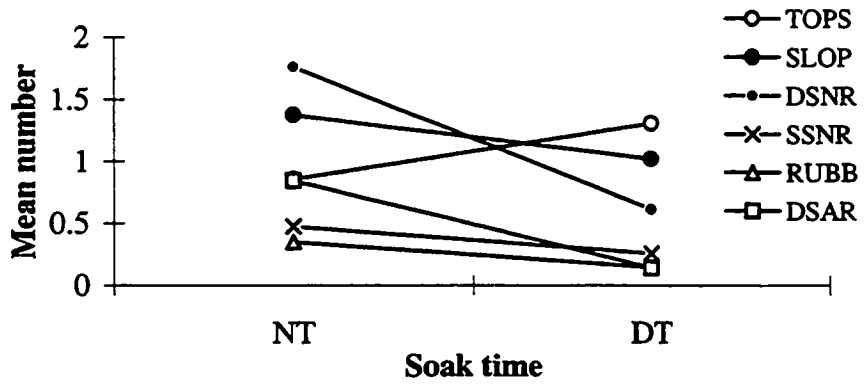
Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.21. Plot of mean number of Lutjanidae (snappers) for the factors sampling time and habitat type. A summary of multiple comparison of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR deep sand near from reefs, SSNR -shallow sand near reefs, RUBB - rubble areas and DSAR -deep sand away from reefs.

Habitat by soak time interaction ($F_{[5,267]}$=5.06; p<0.001)



LUTJANIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT > DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

Habitat: **DSAR**
NT > DT

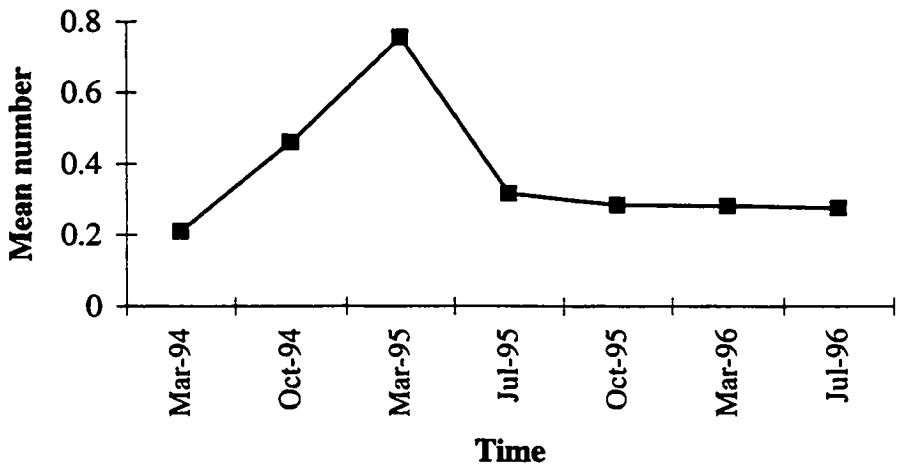
Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP > DSAR, RUBB, SSNR
TOPS, SLOP, DSNR, DSAR, RUBB, SSNR

Soak: **NT**
DSNR > RUBB, SSNR, DSAR, TOPS
SLOP > RUBB, SSNR
DSNR, SLOP, TOPS, DSAR, RUBB, SSNR

Figure 3.22. Plot of mean number of Lutjanidae (snappers) for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Time main effect ($F_{[6,267]}$=3.88; p<0.001)

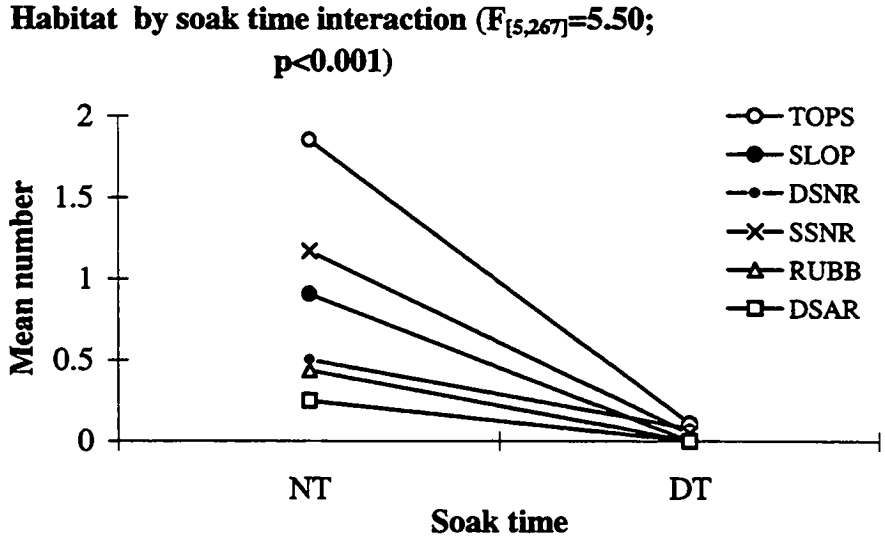


APOGONIDAE

Mar 95 > Mar 94, Jul 95, Oct 95, Mar 96, Jul 96

Mar 95, Oct 94, Mar 94, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.23. Plot of mean number of Apogonidae for the main effect of factor sampling time. A summary of multiple comparison of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference.



APOGONIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
NT > DT

Habitat: **SLOP**
NT > DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT > DT

Habitat: **DSAR**
NT, DT

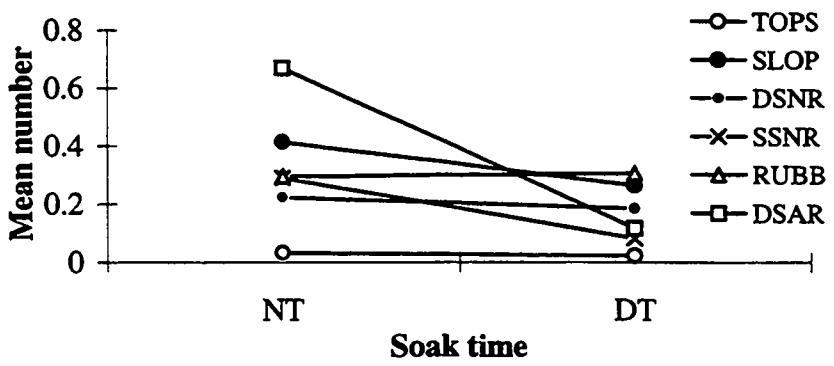
Effect of habitat type on soak time

Soak: **DT**
DSAR, SLOP, RUBB, SSNR, DSNR, TOPS

Soak: **NT**
TOPS > SLOP, RUBB, DSAR, DSNR
SSNR > RUBB, DSAR
SLOP > DSAR
TOPS, SSNR, SLOP, DSNR, RUBB, DSAR

Figure 3.24. Plot of mean number of Apogonidae for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Habitat by soak time interaction ($F_{[5,267]}$=3.30; p<0.001)



LETHRINIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

Habitat: **DSAR**
NT > DT

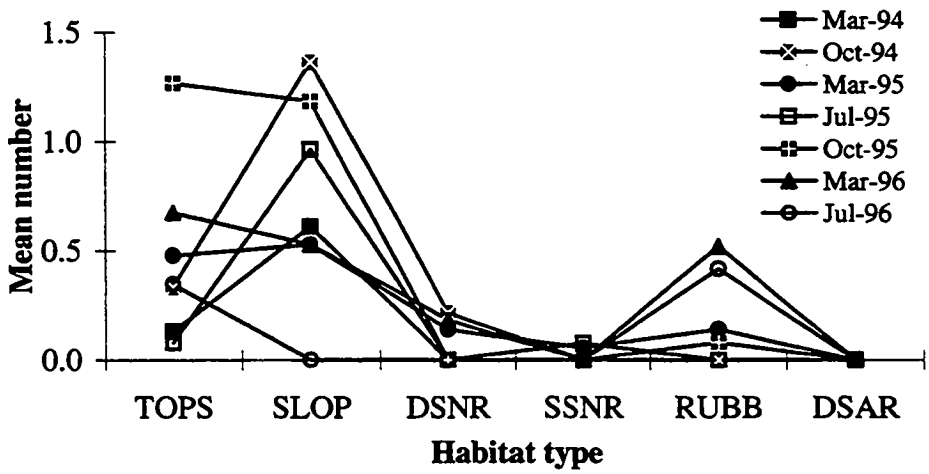
Effect of habitat type on soak time

Soak: **DT**
DSAR, SLOP, RUBB, SSNR, DSNR, TOPS

Soak: **NT**
DSAR > TOPS, DSNR
SLOP > TOPS
DSAR, SLOP, RUBB, SSNR, DSNR, TOPS

Figure 3.25. Plot of mean number of Lethrinidae (emperors) for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Time by habitat interaction ($F_{[30,267]}$=2.09; p<0.01)



LABRIDAE

Effect of habitat type on sampling time

Time: **Mar 94**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Oct 94**
SLOP > RUBB, DSNR, SSNR, DSAR
SLOP, TOPS, RUBB, DSNR, SSNR, DSAR

Time: **Mar 95**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Jul 95**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Oct 95**
SLOP, TOPS > RUBB, DSNR, SSNR, DSAR

Time: **Mar 96**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Time: **Jul 96**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Effect of sampling time on habitat type

Habitat: **TOPS**
Oct 95 > Mar 94, Jul 95
Oct 95, Oct 94, Mar 95, Mar 96, Jul 96, Mar 94, Jul 95

Habitat: **SLOP**
Oct 94, Oct 95 > Jul 96
Oct 94, Oct 95, Mar 94, Mar 95, Jul 95, Mar 96, Jul 96

Habitat: **DSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

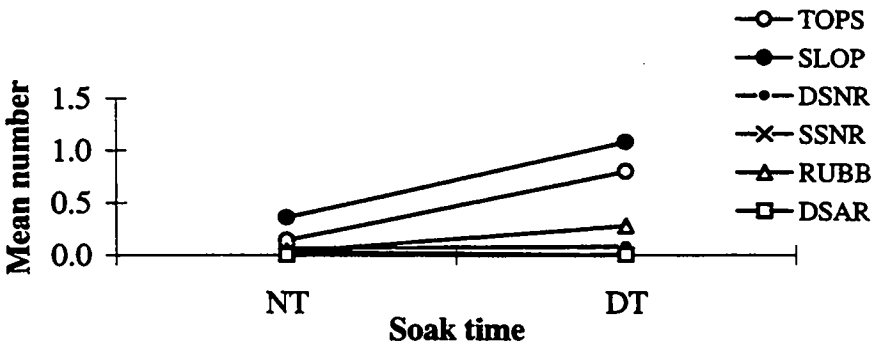
Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.26. Plot of mean number of Labridae for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

Habitat by soak time interaction ($F_{[5,267]}$=5.64; p<0.001)



LABRIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
DT > NT

Habitat: **SLOP**
DT > NT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

Habitat: **DSAR**
NT, DT

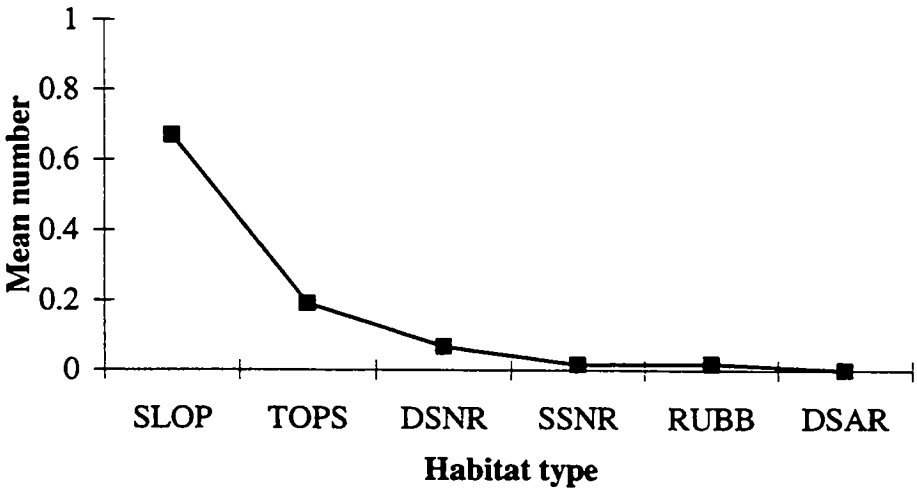
Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP > RUBB, DSNR, SSNR, DSAR

Soak: **NT**
SLOP > DSAR
SLOP, TOPS, RUBB, DSNR, SSNR, DSAR

Figure 3.27. Plot of mean number of Labridae for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Habitat main effect ($F_{[5,267]}$=36.60; p<0.001)

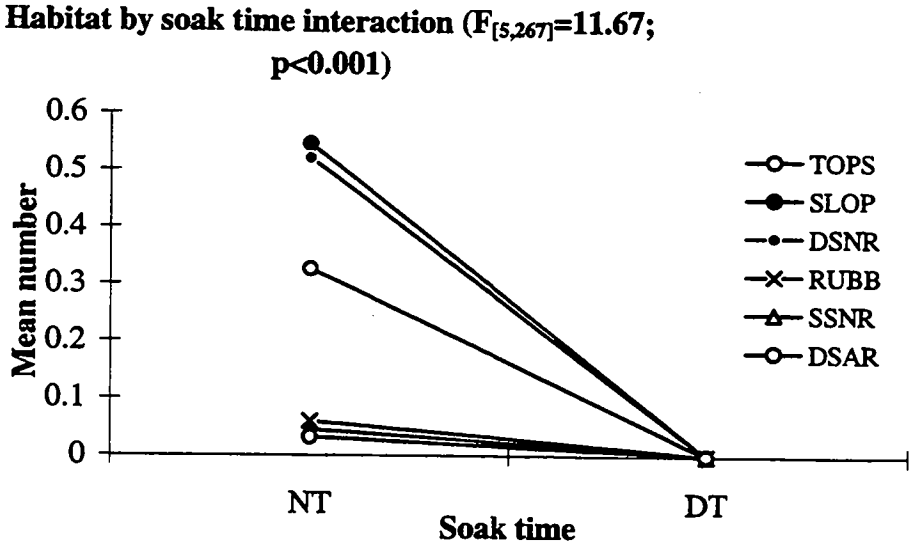


SERRANIDAE

SLOP > TOPS, DSNR, RUBB, SSNR, DSAR

TOPS > RUBB, SSNR, DSAR

Figure 3.28. Plot of mean number of Serranidae (groupers) for the main effect of factor habitat type. A summary of multiple comparison of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.



HOLOCENTRIDAE

Effect of soak time on habitat type

Habitat: **TOPS**
NT > DT

Habitat: **SLOP**
NT > DT

Habitat: **DSNR**
NT > DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT, DT

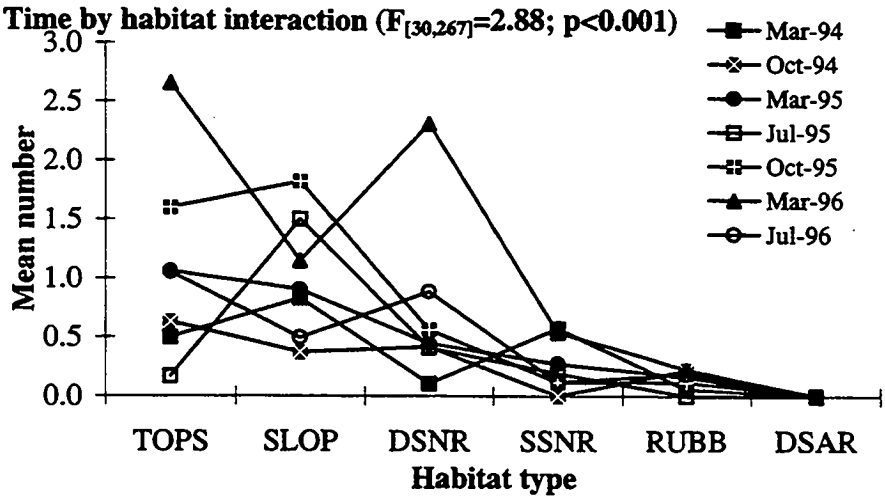
Habitat: **DSAR**
NT, DT

Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Soak: **NT**
TOPS, SLOP, DSNR > RUBB, SSNR, DSAR

Figure 3.29. Plot of mean number of Holocentridae for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.



Lutjanus carponotatus

Effect of habitat type on sampling time

Time: **Mar 94**
TOPS, DSNR, SLOP, SSNR, RUBB, DSAR

Time: **Oct 94**
TOPS, DSNR, SLOP, SSNR, RUBB, DSAR

Time: **Mar 95**
TOPS, DSNR, SLOP, SSNR, RUBB, DSAR

Time: **Jul 95**
SLOP > TOPS, SSNR, RUBB, DSAR
SLOP, DSNR, TOPS, SSNR, RUBB, DSAR

Time: **Oct 95**
TOPS, SLOP > SSNR, RUBB, DSAR
TOPS, SLOP, DSNR, SSNR, RUBB, DSAR

Time: **Mar 96**
TOPS, DSNR > SSNR, RUBB, DSAR
SLOP> DSAR
TOPS, DSNR, SLOP, SSNR, RUBB, DSAR

Time: **Jul 96**
TOPS, DSNR, SLOP, SSNR, RUBB, DSAR

Effect of sampling time on habitat type

Habitat: **TOPS**
Mar 96 > Mar 94, Oct 94, Jul 95
Oct 95 > Jul 95
Mar 96, Oct 95, Jul 96, Mar 95, Mar 94, Oct 94, Jul 95

Habitat: **SLOP**
Oct 95 > Oct 94
Oct 95, Mar 94, Mar 95, Jul 95, Mar 96, Jul 96, Oct 94

Habitat: **DSNR**
Mar 96 > Mar 94, Oct 94, Mar 95, Jul 95, Oct 95
Mar 96, Jul 96, Mar 94, Oct 94, Mar 95, Jul 95, Oct 95

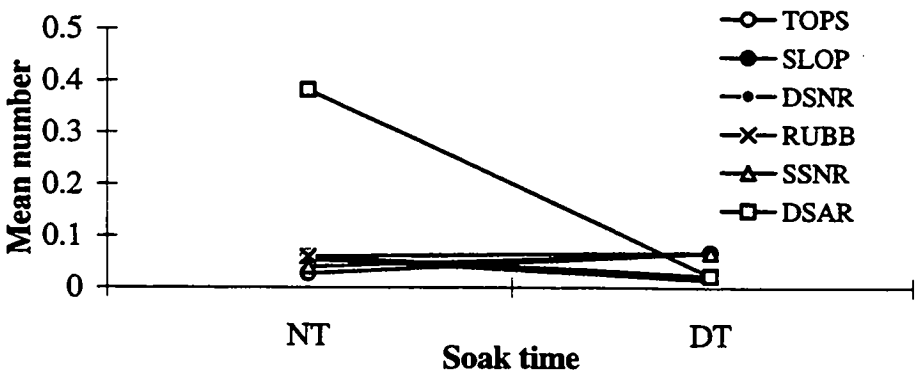
Habitat: **SSNR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **RUBB**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Habitat: **DSAR**
Mar 94, Oct 94, Mar 95, Jul 95, Oct 95, Mar 96, Jul 96

Figure 3.30. Plot of mean number of *Lutjanus carponotatus* for the factors sampling time and habitat type. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

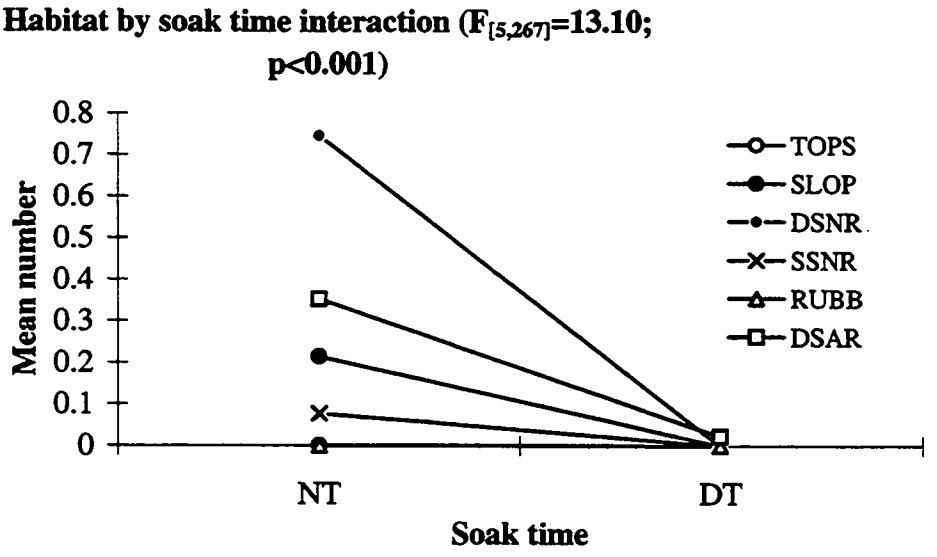
Habitat by soak time interaction ($F_{[5,267]}$=6.80; p<0.001)



Lutjanus fulviflamma

Effect of soak time on habitat type	Effect of habitat type on soak time
Habitat: **TOPS**	Soak: **DT**
NT, DT	TOPS, SLOP, DSNR, RUBB, SSNR, DSAR
Habitat: **SLOP**	
NT, DT	
Habitat: **DSNR**	Soak: **NT**
NT, DT	DSAR > TOPS, SLOP, DSNR, RUBB, SSNR
Habitat: **RUBB**	
NT, DT	
Habitat: **SSNR**	
NT, DT	
Habitat: **DSAR**	
NT > DT	

Figure 3.31. Plot of mean number of *Lutjanus fulviflamma* for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.



Lutjanus quinquelineatus

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT
Habitat: **SLOP**
NT > DT
Habitat: **DSNR**
NT > DT
Habitat: **RUBB**
NT, DT
Habitat: **SSNR**
NT, DT
Habitat: **DSAR**
NT > DT

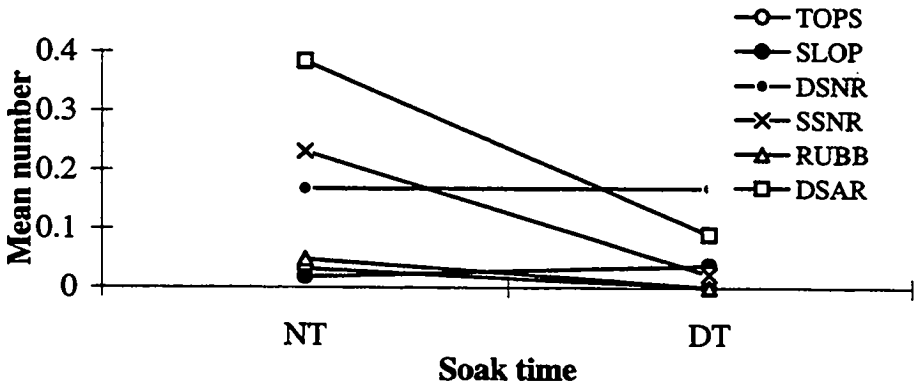
Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

Soak: **NT**
DSNR > DSAR, SLOP, SSNR, RUBB, TOPS
DSAR > SSNR, RUBB, TOPS

Figure 3.32. Plot of mean number of *Lutjanus quinquelineatus* for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Habitat by soak time interaction ($F_{[5,267]}$=3.76; p<0.01)



Lethrinus nebulosus

Effect of soak time on habitat type

Habitat: **TOPS**
NT, DT

Habitat: **SLOP**
NT, DT

Habitat: **DSNR**
NT, DT

Habitat: **RUBB**
NT, DT

Habitat: **SSNR**
NT > DT

Habitat: **DSAR**
NT > DT

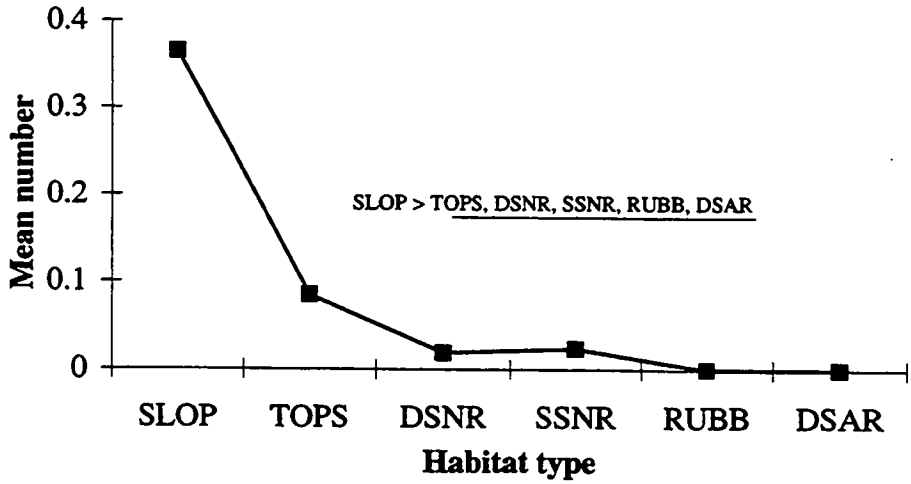
Effect of habitat type on soak time

Soak: **DT**
TOPS, SLOP, DSNR, RUBB, SSNR, DSAR

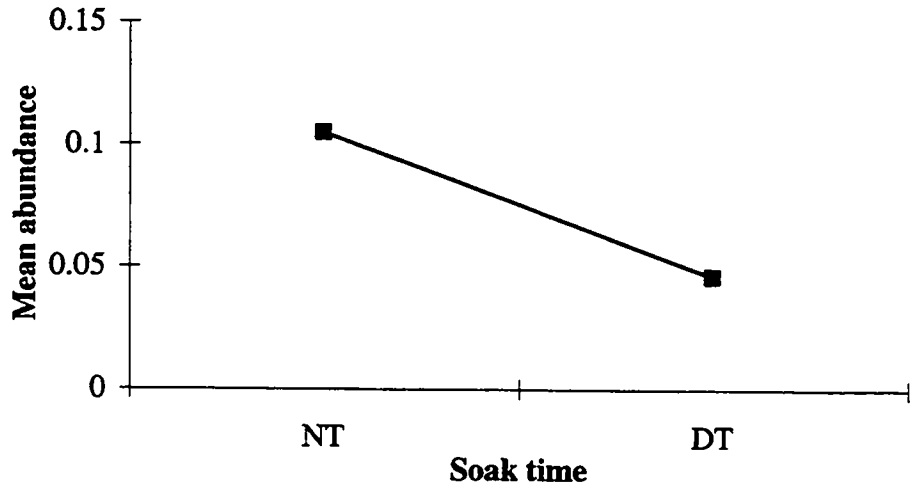
Soak: **NT**
DSAR > SLOP, TOPS, RUBB
SSNR > SLOP
DSAR, SSNR, DSNR, TOPS, RUBB, SLOP

Figure 3.33. Plot of mean number of *Lethrinus nebulosus* for the factors habitat type and soak time. A summary of multiple comparisons of means is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

a. Habitat main effect ($F_{[5,267]}$=30.11; p<0.001)



b. Soak time main effect ($F_{[1,267]}$=9.1; p<0.01)



Cephalopholis cyanostigma

Figure 3.34. Plot of mean number of *Cephalopholis cyanostigma* for the main effects of factors (a) habitat type and (b) soak time. Means were compared and a summary for (a) is supplied (Tukey's HSD method). Means of items joined by a line indicate no significant difference. Codes for habitat types are: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near from reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; soak times NT -night time and DT -day time.

Table 3.1. Number of species within broad trophic categories for the 7 most abundant families. Codes of trophic categories: BP -benthic predators, PI -piscivores, PL -planktivores, H -herbivores, C -corallivores, S -scavengers.

	TROPHIC CATEGORIES							
Families	**BP**	**PI**	**PL**	**H**	**C**	**S**	**Totals**	**%**
Pomacentridae	0	0	10	8	1	0	**19**	15.97
Lutjanidae	8	3	0	0	0	0	**11**	9.24
Apogonidae	1	2	23	0	0	0	**26**	21.85
Lethrinidae	9	0	0	0	0	0	**9**	7.56
Labridae	5	0	0	0	0	0	**5**	4.20
Serranidae	0	8	0	0	0	0	**8**	6.72
Holocentridae	4	0	3	0	0	0	**7**	5.88
Others (20 fam.)	9	12	3	5	4	1	**34**	28.57
Totals	**36**	**25**	**39**	**13**	**5**	**1**	**119**	
%	30.25	21.01	32.77	10.92	4.20	0.84		

Table 3.2. Total number of individuals classified into broad trophic categories for catches in 6 habitat types and two soak times *(italized type face).* Numbers for soak times were standardized for differences in soak periods. Codes for trophic categories: BP -benthic predators, PI -piscivores, PL -planktivores, H -herbivores, C -corallivores, S -scavengers; for habitat types: TOPS -tops of reef, SLOP -slopes of reef, DSNR -deep sand near reefs, SSNR -shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs; for soak times: NT -night time and DT -day time.

	TROPHIC CATEGORIES					
	BP	**PI**	**PL**	**H**	**C**	**S**
Habitat types						
TOPS	**211**	**44**	**332**	**132**	**3**	**0**
NT	*49*	*14*	*96*	*34*	*1*	*0*
DT	*103*	*15*	*133*	*60*	*2*	*0*
SLOP	**317**	**91**	**103**	**81**	**5**	**1**
NT	*104*	*31*	*44*	*32*	*2*	*0*
DT	*109*	*29*	*20*	*19*	*1*	*1*
DSNR	**227**	**16**	**82**	**18**	**0**	**3**
NT	*90*	*5*	*38*	*4*	*0*	*0*
DT	*54*	*6*	*12*	*9*	*0*	*3*
SSNR	**85**	**42**	**111**	**19**	**0**	**2**
NT	*34*	*21*	*54*	*3*	*0*	*0*
DT	*20*	*3*	*12*	*11*	*0*	*2*
RUBB	**105**	**7**	**117**	**17**	**6**	**0**
NT	*28*	*2*	*25*	*4*	*1*	*0*
DT	*45*	*3*	*61*	*8*	*4*	*0*
DSAR	**145**	**20**	**26**	**0**	**0**	**20**
NT	*68*	*3*	*14*	*0*	*0*	*4*
DT	*19*	*13*	*0*	*0*	*0*	*11*
TOTALS	**1090**	**220**	**771**	**267**	**14**	**26**
NT	*373*	*76*	*271*	*77*	*4*	*4*
DT	*350*	*69*	*238*	*107*	*7*	*17*
% of Totals	45.64	9.21	32.29	11.18	0.59	1.09

Table 3.3. An ordered species by samples table output by TWo-way INdicator SPecies ANalysis (TWINSPAN) for the top 50 species and 84 samples (one sample, SSNRDTO95, had no catch and was dropped by the program TWINSPAN). Each column of numbers and dash '-' lines represents a sample coded by the first 2 rows of numbers and read from top to bottom. Each number or dash line in a column is a correspondence score of the species for that sample. A correspondence score of 0-4 indicates abundance of the species (0 appearing as a dash line) for that particular sample. Groupings of samples follow from Figure 8. Codes for species are listed in Appendix C.

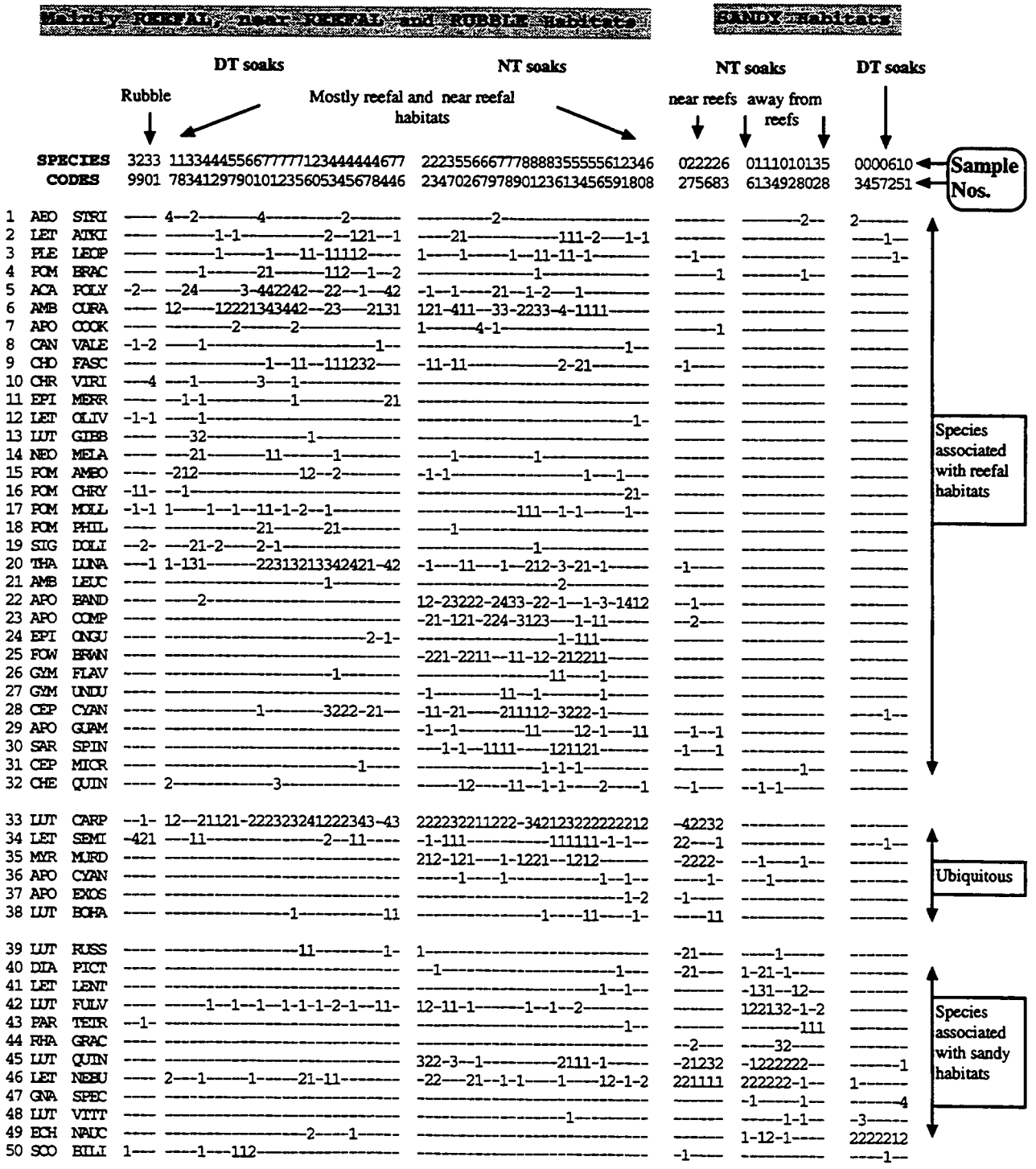


Table 3.4. Summary of a 3-factor analysis of variance for the variate total species richness (number of species). Numbers were standardized across differences in soak period. Significance levels are: ns = $p>0.01$; * = $0.01>p>0.001$; ** = $0.001>p>0.0001$; *** = $p<0.0001$.

Source of Variation	df	MS	F	p
Time (T)	6	10.7404	7.124	***
Habitat type (H)	5	51.5912	34.222	***
Soak time (S)	1	21.2495	14.095	**
TxH	30	3.6249	2.404	**
TxS	6	2.7511	1.825	ns
HxS	5	4.6737	3.100	*
TxHxS	30	1.6438	1.090	ns
Residual	267	1.5076		

Table 3.5. Summaries of 3-factor analyses of variance for the variates numbers of all fish, numbers within 4 broad trophic groups, numbers in the top 7 families and numbers within selected species. Abundances were standardized across different soak periods. Data were transformed to $\log_{10}(x+1)$ and α-level set to 0.01. Significance levels are: ns = $p>0.01$; * = $0.01>p>0.001$; ** = $0.001>p>0.0001$; *** = $p<0.0001$. [1]α-level set to 0.001; see Section 3.3.3 for explanation.

	a. ALL FISH				b. BENTHIC PREDATORS			
Source of Variation	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
Sampling time (T)	6	0.3725	5.241	***	6	0.3936	6.468	***
Habitat type (H)	5	2.3717	33.367	***	5	1.0192	16.750	***
Soak time (S)	1	0.5523	7.770	**	1	0.6768	11.123	**
TxH	30	0.1613	2.270	**	30	0.1271	2.089	**
TxS	6	0.0893	1.257	ns	6	0.0319	0.524	ns
HxS	5	0.4126	5.805	***	5	0.4453	7.317	***
TxHxS	30	0.1153	1.622	ns	30	0.0577	0.949	ns
Residual	267	0.0711			267	0.0608		

	c. PISCIVORES				d. PLANKTIVORES			
Source of Variation	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
Sampling time (T)	6	0.2554	0.989	ns	6	0.1282	1.850	ns
Habitat type (H)	5	0.4040	15.649	***	5	1.2538	18.089	***
Soak time (S)	1	0.0215	0.834	ns	1	1.0143	14.634	**
TxH	30	0.0258	1.000	ns	30	0.1585	2.287	**
TxS	6	0.0253	0.979	ns	6	0.1105	1.595	ns
HxS	5	0.0189	0.732	ns	5	0.1432	2.066	ns
TxHxS	30	0.0252	0.975	ns	30	0.0845	1.221	ns
Residual	267	0.0258			267	0.0693		

	e. HERBIVORES				f. POMACENTRIDAE			
Source of Variation	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
Sampling time (T)	6	0.1357	4.017	**	6	0.2781	4.873	***
Habitat type (H)	5	0.6931	20.514	***	5	1.4886	26.080	***
Soak time (S)	1	0.1293	3.828	ns	1	1.4204	24.886	***
TxH	30	0.0522	1.546	ns	30	0.1344	2.355	**
TxS	6	0.0201	0.595	ns	6	0.0571	1.000	ns
HxS	5	0.0771	2.283	ns	5	0.3474	6.086	***
TxHxS	30	0.0283	0.837	ns	30	0.0391	0.685	ns
Residual	267	0.0338			267	0.0571		

	g. LUTJANIDAE				h. APOGONIDAE[1]			
Source of Variation	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
Sampling time (T)	6	0.2335	5.858	***	6	0.1473	3.880	**
Habitat type (H)	5	0.6975	17.499	***	5	0.3052	8.038	***
Soak time (S)	1	0.7525	18.880	***	1	4.7426	124.899	***
TxH	30	0.0839	2.105	*	30	0.0599	1.577	ns
TxS	6	0.0242	0.608	ns	6	0.0567	1.493	ns
HxS	5	0.2018	5.064	**	5	0.2090	5.504	***
TxHxS	30	0.2886	0.724	ns	30	0.0688	1.811	ns
Residual	267	0.0399			267	0.0380		

Table 3.5 con't.

i. LETHRINIDAE

Source of Variation	df	MS	F	p
Sampling time (T)	6	0.0278	1.398	ns
Habitat type (H)	5	0.1189	5.988	***
Soak time (S)	1	0.2378	11.974	**
TxH	30	0.0343	1.725	ns
TxS	6	0.0444	2.234	ns
HxS	5	0.0655	3.300	*
TxHxS	30	0.0269	1.354	ns
Residual	267	0.0199		

j. LABRIDAE

df	MS	F	p
6	0.0472	2.008	ns
5	0.4825	20.534	***
1	0.5243	22.314	***
30	0.0492	2.096	*
6	0.0063	0.269	ns
5	0.1326	5.643	***
30	0.0316	1.345	ns
267	0.0235		

k. SERRANIDAE

Source of Variation	df	MS	F	p
Sampling time (T)	6	0.0128	1.089	ns
Habitat type (H)	5	0.4306	36.605	***
Soak time (S)	1	0.0065	0.556	ns
TxH	30	0.0131	1.116	ns
TxS	6	0.0084	0.716	ns
HxS	5	0.0015	0.130	ns
TxHxS	30	0.0079	0.668	ns
Residual	267	0.0118		

l. HOLOCENTRIDAE

df	MS	F	p
6	0.0120	1.397	ns
5	0.1004	11.670	***
1	0.7317	85.096	***
30	0.0094	1.088	ns
6	0.0120	1.397	ns
5	0.1004	11.670	***
30	0.0094	1.088	ns
267	0.0086		

m. Lutjanus carponotatus

Source of Variation	df	MS	F	p
Sampling time (T)	6	0.1971	7.546	***
Habitat type (H)	5	0.9080	34.767	***
Soak time (S)	1	0.0305	1.167	ns
TxH	30	0.0751	2.875	***
TxS	6	0.0216	0.827	ns
HxS	5	0.0444	1.700	ns
TxHxS	30	0.0216	0.826	ns
Residual	267	0.0261		

n. Lutjanus fulviflamma

df	MS	F	p
6	0.0123	1.890	ns
5	0.0302	4.464	**
1	0.0415	6.367	ns
30	0.0098	1.504	ns
6	0.0059	0.900	ns
5	0.0443	6.801	***
30	0.0071	1.097	ns
267	0.0065		

o. Lutjanus quinquelineatus

Source of Variation	df	MS	F	p
Sampling time (T)	6	0.0248	2.571	ns
Habitat type (H)	5	0.1319	13.648	***
Soak time (S)	1	0.5536	57.271	***
TxH	30	0.0077	0.797	ns
TxS	6	0.0174	1.796	ns
HxS	5	0.1267	13.104	***
TxHxS	30	0.0068	0.706	ns
Residual	267	0.0097		

p. Lethrinus nebulosus

df	MS	F	p
6	0.0149	1.805	ns
5	0.0706	8.569	***
1	0.1066	12.947	**
30	0.0109	1.323	ns
6	0.0091	1.102	ns
5	0.0309	3.756	*
30	0.0083	1.006	ns
267	0.0082		

q. Cephalopholis cyanostigma

Source of Variation	df	MS	F	p
Sampling time (T)	6	0.0057	1.066	ns
Habitat type (H)	5	0.1609	30.112	***
Soak time (S)	1	0.0486	9.096	*
TxH	30	0.0090	1.675	ns
TxS	6	0.0085	1.596	ns
HxS	5	0.0117	2.185	ns
TxHxS	30	0.0060	1.128	ns
Residual	267	0.0053		

Table 3.6. Summary of significant effects ($p<0.01$) from 18 ANOVAs (Tables 3.4 and 3.5). Codes for factors are T -sampling time, H -habitat types and S -soak times.

Variate	Data set	Factors with significant effects
Number	Herbivores	T and H
Number	*Cephalopholis cyanostigma*	H and S
Number	Piscivores	H
Number	Serranidae	H
Number	Apogonidae	T and H x S
Number	Planktivores	S and T x H
Number	*Lutjanus carponotatus*	T x H
Number	Lethrinidae	H x S
Number	Holocentridae	H x S
Number	*Lutjanus fulviflamma*	H x S
Number	*Lutjanus quinquelineatus*	H x S
Number	*Lethrinus nebulosus*	H x S
Total sp. richness	All fish	T x H and H x S
Number	All fish	T x H and H x S
Number	Benthic predators	T x H and H x S
Number	Pomacentridae	T x H and H x S
Number	Lutjanidae	T x H and H x S
Number	Labridae	T x H and H x S

Chapter 4: INTER- AND INTRA-HABITAT MOVEMENT PATTERNS OF SMALL REEF FISHES

4.1 INTRODUCTION

The concept of marine reserves as a fisheries management tool has gained wide advocacy over recent years (e.g. Plan Development Team (PDT) 1990, Bohnsack 1993, DeMartini 1993, Man *et al.* 1995, Russ 1996, Russ and Alcala 1996a and b) largely because of a growing concern that current management practices (e.g. gear restrictions, catch quotas and seasonal closures) are not preventing declining catches and in some cases, the failure of fisheries (Carr and Reed 1993, Dugan and Davis 1993a). Marine reserves are areas protected from any form of human exploitation, often located adjacent to fished areas (DeMartini 1993, Russ and Alcala 1996b). The purpose of marine reserves is simple. They create a haven within which a critical minimum spawning stock biomass is protected. Thus, marine reserves can potentially prevent recruitment and growth overfishing (e.g. Alcala and Russ 1990, Polacheck 1990, Russ 1991, Roberts and Polunin 1991, Dugan and Davis 1993a). This ensures recruitment supply to fished areas through larval dispersal and permits the possibility of enhancement or maintenance of yields in fished areas close to reserves by possible movement of adults ('spillover' effect) (e.g. PDT 1990, Alcala and Russ 1990, Roberts and Polunin 1991, Bohnsack 1993, Russ 1996). Although there is a need to assess recruitment benefits from marine reserves, the general consensus from the fisheries point of view is that marine reserves provide larval recruits to exploited areas, as suggested by Davis and Dodrill (1980) for the spiny lobster *Panulirus argus* in Florida. Plan Development Team (1990) pointed out that the fecundity of fish increases substantially with fish size. Thus, when a spawning stock is protected, increasing the density, average age and average size of fish, the potential for recruitment benefits is great. However, Russ and Alcala (1996a) pointed out that if such recruitment benefits

occur, they will tend to apply at a larger spatial scale, since larvae may disperse great distances. In the Philippines, this point and the fact that most community-based managers and local village folk assume immediate local benefits from a marine reserve, mean that it is potentially difficult to convince them to support and maintain a marine reserve in their area (Russ and Alcala 1996a).

The second mechanism by which potential yields in exploited reef areas adjacent to marine reserves may be enhanced is movement of adult fish ('spillover' effect). Movement of target species from a reserve to adjacent fished areas has been shown for lobsters (Davis and Dodrill 1989), shrimps (Gitschlag 1986) and the surf-zone fish *Coracinos capensis* (galjoen) (Attwood and Bennett 1994). Until recently, practically no empirical data existed on movement of coral reef fish between reserves and nearby exploited areas. Alcala and Russ (1990) attributed the maintenance of high yields in areas adjacent to reserves to the emigration of adult fishes from the reserve to non-reserve area in Sumilon Island, Philippines. Russ and Alcala (1996a) reported circumstantial evidence suggesting export of biomass of adults of large predatory reef fishes from a reserve to an adjacent fished site using underwater visual census monitoring of fish densities. Zeller and Russ (submitted MS) used ultrasonic telemetry to track movements of coral trout, *Plectropomus leopardus,* and demonstrated crossings of reserve boundaries of up to 30 times a month.

To fully evaluate the benefits of marine reserves in the context of flux rates of fishes from reserves to adjacent fished areas, there is a need for a better understanding of fish movement patterns, not only for big target species but also for the small, commercial reef fishes such as many lutjanids and lethrinids. In many developing countries such as the Philippines, these small lutjanids and lethrinids form a major part of the municipal fishery yield comprising about 10-15% of the total fishery production (Carpenter 1977, Murdy and Ferraris 1980, Alcala 1981, McManus 1988). Aside from the widespread notion that most small coral reef fishes (e.g. pomacentrids) are strongly site-attached and thus move little, virtually nothing is known about the patterns of movement of many reef fishes, particularly the small predatory fish such as lutjanids and lethrinids (Williams 1991). Several studies have noted that most fish movements are related to feeding (e.g. Hobson 1973, 1991), ontogenetic habitat preferences (e.g.

Bryant *et al.* 1989) and spawning (e.g. Johannes 1978, Robertson 1983, Shapiro 1987, Funicelli *et al.* 1989, Zeller submitted MS). However, there is a general absence of data on the "background" levels of movement of reef fishes in the published literature (Robertson 1988, Roberts and Polunin 1991 but see Zeller *in press*). An understanding of movement patterns of reef fishes is critical in choosing locations and deciding upon sizes and boundary positions of marine reserves. In a tagging study Davies (1995) described movement patterns of three species of reef fish at three spatial scales (among sites, among habitats within sites and among trapping positions within habitats) in the Lizard Island lagoon. He observed that *P. leopardus* regularly moved among trapping positions and across habitat types while very few movements from the habitat of release were exhibited by *Lutjanus carponotatus* and *Siganus doliatus*.

The present study focuses on local patterns of inter- and intra-habitat movement of small reef fishes. This study investigates the frequency of movement of reef fishes within and between habitats and estimates the range of distances moved. The specific objectives of the study are:

1. To compare levels of movement of reef fishes (expressed as frequencies and probabilities) within and between six types of habitat and between day and night.

2. To estimate distances moved by reef fishes within and between habitats and between day and night.

4.2 MATERIALS AND METHODS

A capture-mark-recapture technique described in Section 2.4 was used to assess patterns of inter- and intra-habitat movement of small reef fishes in the Lizard Island lagoon. Briefly, modified Antillean Z-traps were used in a multiple capture-recapture study in six habitat types in the lagoon on 7 sampling occasions over a period of 30

months. These habitats were deep sand away from reefs (DSAR), deep sand near reefs (DSNR), rubble areas (RUBB), slopes of reefs (SLOP), shallow sand near reefs (SSNR) and tops of reefs (TOPS). The locations and descriptions of these habitats are given in Section 2.3.

Traps were positioned at least 30 m away from each other within a habitat and at least 200 m away from each group of 6 replicate traps (i.e. the minimum distance between any 2 habitats during simultaneous sampling). When traps were relocated within a habitat after a set (day/night soak), the traps were positioned at least 30 m from the previous trapping positions. Locations and relative positions of traps were marked on a map. It was assumed that each recapture constituted a movement since traps were moved by at least 30 m during each set. All recaptures from the sampling program in Chapter 3 and additional trapping effort using longer soak times were used in the analysis. In comparing movement between day and night, recaptures from longer soaks were excluded because the period when the fish entered the trap could not be determined. Information on a previous capture of a fish was known based on the tag returns. This information included date and time (e.g. day/night), and location of release in a habitat type and length measurements of the fish.

The number of releases in each of the six habitat types over the seven sampling trips depended on the catch. This resulted in uneven sample sizes of releases across habitats and sampling times. Thus, movement was assessed only as probabilities of movement within and between habitats. Probabilities of movement (between two habitats) were essentially percentages of movement from habitat A to B based on the total number of movements in A and computed as:

$$Pr_{A \to B} = K_B/M_A,$$

where K_B was the total number of recaptures in habitat type B released from A, and M_A was the total number of recoveries in all habitats from releases in A. Similarly, probabilities of within habitat movement were computed as:

$$Pr_{A \to A} = K_A/M_A,$$

where K_A was the total number of recoveries in habitat A from releases in A. Tables of probabilities of movement were constructed for all species combined and for 10 individual species.

A movement was assumed to have occurred at night when a tagged fish was recovered in the morning following a late afternoon soak. A day movement was assumed when a tagged fish was recovered in the late afternoon following an early morning soak. The number of day and night movements within and between habitats was tested against an equal binomial proportion using a Chi-square (χ^2) one-sample test (1 degree of freedom, 0.05 level of significance) (Snedecor and Cochran 1967). The null hypothesis (H_o) was that the number of movements of fish was equal between day and night (i.e. p=q=0.50). The number of recoveries at day (d) and night (n) were compared for all species combined and for *L. carponotatus*. There was insufficient data for other comparisons. Applying χ^2 tests on a total number of movements (M = d+n) less than 6 was considered unwise (Zar 1984).

Although this study was not designed specifically to investigate distances of movement of reef fishes *per se*, the sampling method in Section 2.4.4 permitted a semi-quantification of distances moved in intervals of 30 m. Distance movements were estimated from the location of last release (as determined from the trap number and position of the previous capture) to present recovery. Since the marks on a map indicated only relative positions of traps, distance movements were categorized in intervals of 30 m. A recovery in an adjacent trap position was considered a 30 m movement, two adjacent trap positions 60 m and so on. The distances of large movements (most often between habitats) were estimated by plotting a straight line between point of release and recapture on a nautical chart. Estimates of large distance movements were to the nearest 100 m. Percentage frequencies of distances moved, in intervals of 30 m, were constructed for all species combined, *Lutjanus carponotatus*, *L. quinquelineatus*, *Plectropomus leopardus*, *Cephalopholis cyanostigma*, *Lethrinus atkinsoni*, *Lutjanus fulviflamma*, and *Lethrinus nebulosus*. The frequency of distances moved within and between habitats and between day and night were estimated for all species combined and *L. carponotatus*. There was insufficient data for other species

for comparisons of within and between habitat movements or between day and night movements.

The frequency distributions of distances moved were tested for non-parametric goodness of fit to a normal distribution for all species combined, *L. carponotatus*, *L. quinquelineatus*, *P. leopardus*, *C. cyanostigma* and *L. atkinsoni*. Such tests were not performed on *L. fulviflamma* and *L. nebulosus* due to lack of data in many consecutive distance classes. The Kolmogorov-Smirnov (K-S) test was used since it has greater power than the G- or chi-square tests for continuous frequency distributions and is especially advantageous with small sample sizes (Sokal and Rohlf 1981). In addition, the tables of K-S tests are conservative (Lilliefors 1967), thus, the probability of rejecting a null hypothesis was smaller.

Frequency distributions of the number of distance movements within and between habitats and between day and night for all species combined and for *L. carponotatus* were compared and subjected to a non-parametric Kolmogorov-Smirnov (K-S) two-sample test. The null hypothesis was that the distributions of the two samples (i.e. frequency of distance movements within and between habitats and between day and night) were similar in terms of statistics of location (central tendency), dispersion, skewness and other measures. The K-S two-sample test is sensitive to differences in such statistical measures of distributions (Sokal and Rohlf 1981). All calculations were made using the software STATISTICA Release 5.0 (StatSoft, Inc. 1995).

4.3 RESULTS

A total of 995 fish in 32 species from five families were tagged and released (Table 4.1). Five species, *Lutjanus carponotatus* (30%), *L. quinquelineatus* (17%), *L. fulviflamma* (7%), *Lethrinus nebulosus* (14%) and *Cephalopholis cyanostigma* (9%)

comprised nearly 80% of the fish released. There were 142 single returns recorded, with an overall recapture rate of approximately 14.3% (Table 4.1). More than half of the returns (56%) were *L. carponotatus*, which had the highest recapture rate (26%), of species with at least 50 tagged fish (Table 4.1). Other species with high recapture rates and at least 50 tagged fish were *L. fulviflamma* and *C. cyanostigma* (11% for both), *L. nebulosus* (7%), then *L. quinquelineatus* (6%) (Table 4.1).

The number of fish released varied over time (Tables 4.2a-k). In general, releases during the month of July were lower than in the months of March and October, reflecting variations in catch rates (see Chapter 3). Recoveries were generally high within the first to sixth month after release for *L. carponotatus* (Table 4.2b), and moderate for *L. nebulosus* (Table 4.2c), *L. quinquelineatus* (Table 4.2d) and *C. cyanostigma* (Table 4.2e). The number of recoveries declined rapidly beyond six months at large for all these species. For other species (Tables 4.2f-k), the number of releases and returns were low. The longest period of liberty of recaptures was 22 months for *L. carponotatus* (n=2, tagged in October 1994 and recaptured in July 1996) (Table 4.2b) and *L. semicinctus* (n=1; Table 4.2k), 20 months for *L. atkinsoni* (n=1; Table 4.2j), 18 months for *L. nebulosus* (n=1; Table 4.2c) and *L. russelli* (n=1; Table 4.2h), and 13 months for *L. quinquelineatus* (n=1; Table 4.2d), *C. cyanostigma* (n=5; Table 4.2e), *L. fulviflamma* (n=3; Table 4.2f) and *P. leopardus* (n=1; Table 4.2g).

The total numbers released in each habitat varied over time for all species combined (Table 4.3a) and for each of the 10 species (Tables 4.3b-k). Except for *L. nebulosus* (Table 4.3c), *L. fulviflamma* (Table 4.3e) and *D. pictum* (Table 4.3i), the number of releases (R) was generally lower in DSAR than in any other habitat. The number of releases (R) was generally higher in the habitats TOPS, SLOP and DSNR than in the other three habitats for most species (Table 4.3). This was due to the patterns of catch composition and abundance in these habitats (see Chapter 3). The rates of recapture for all species combined was highest in TOPS (22.8%), moderate in DSNR, SLOP and SSNR (14-17%) and lowest in DSAR and RUBB (5-7%) (Table 4.3a). The recovery rate of *L. carponotatus* was consistently high in TOPS, SLOP and DSNR (27-30%), moderate in SSNR (19%) and low in RUBB (5%) (Table 4.3b). The recapture rate for *L. nebulosus* was highest in SSNR (14.8%) and moderate in DSAR,

DSNR and RUBB (5-8%) (Table 4.3c). The rate of recapture for *L. quinquelineatus* was about 8% in SSNR and DSNR and below 4% in SLOP and DSAR (Table 4.3g). All recaptures for *L. semicinctus* were observed in RUBB and SLOP habitats (Table 4.3f), while all *D. pictum* recaptures were in deep sandy habitats (DSAR and DSNR; Table 4.3i). *Cephalopholis cyanostigma* and *L. atkinsoni* were recaptured only in the SLOP habitat, with almost the same recapture rates (14 and 15%, respectively; Tables 4.3j and k). The unusually high recapture rates of *P. leopardus* in habitats DSNR and TOPS reflect the small numbers of releases in these habitats (Table 4.3d). The same was observed for *L. fulviflamma* in habitat SLOP (Table 4.3e) and for *L. russelli* in DSAR (Table 4.3h). The rates of recapture in the DSAR and SSNR for *L. fulviflamma* (Table 4.3e), in DSNR for *L. russelli* (Table 4.3h) and in SLOP for *P. leopardus* (Table 4.3d) were more moderate.

Of the total 142 returns, 87 were recaptured once and 55 individuals were recaptured from two to 17 times (Table 4.4). The single and multiple recoveries totalled 286 movement records (each recapture was considered a movement). Of these movements, more than two thirds were for *L. carponotatus* (Table 4.4). Four species, *C. cyanostigma*, *P. leopardus*, *L. quinquelineatus* and *L. nebulosus* had less than 20 recorded movements while the remaining species had less than 10 movement records (Table 4.4). Nearly two thirds of movements (64%) were recorded within 0-30 days of release (re-releases included), 24% within 90-160 days, 6% after 161-230, 5% after 231-370 and 2% after more than 370 days (Table 4.5). Overall, between 77-93% of the total movements were recorded within 5 months of release or re-release.

4.3.1. Probabilities of Inter- and Intra-Habitat Movement

All species combined

The number of movements within habitats was significantly higher than between habitats (χ^2=61.850, df=1, p<0.01). Nearly 74% of movements (total n=286) were within habitats and 26% were between habitats. Movements of fish between habitats were recorded from DSAR to SLOP, DSNR to DSAR, DSNR to RUBB,

DSNR to SSNR, DSNR to TOPS, SLOP to DSAR, SLOP to RUBB, SSNR to DSNR, TOPS to DSNR and TOPS to SSNR (Table 4.6a). Except for movements from TOPS to DSNR (Pr=0.71) and DSNR to TOPS (Pr=0.32), the probability of between habitat movement was low ($0.01 \leq Pr \leq 0.10$; Table 4.6a). Movement of fish in DSAR, RUBB, SLOP and SSNR was almost entirely within habitat ($0.90 \leq Pr \leq 1.00$; Table 4.6a). Fish released in these habitats were recovered in the same habitat more than 90% of the time. The probability of movement of fish from TOPS to DSNR was significantly higher than movements within TOPS ($\chi^2=11.500$, df=1, $p<0.01$) (Table 4.6a). The probability of movement from DSNR to TOPS did not differ significantly from within DSNR ($\chi 2=0.0755$, df=1, $p>0.05$) (Table 4.6a).

The relatively higher number of movements from TOPS to DSNR and DSNR to TOPS than for any other between habitat movements is attributed to the close proximity of these two habitats (vertical distance of 8-10 m) at Lizard Island lagoon (see Section 2.3 and Figs. 2.2-3). The majority of the fish exchanges between TOPS and DSNR occurred at the reefal areas in Palfrey Island and Mangrove beach (Fig. 2.2).

Lutjanus carponotatus

The number of movements within habitats was significantly higher than between habitats for *L. carponotatus* ($\chi^2=16.922$, df=1, $p<0.01$). Sixty-five percent of movements of *L. carponotatus* were within and 35% between habitats. Movement of *L. carponotatus* between habitats was recorded from DSAR to SLOP, DSNR to SSNR, DSNR to TOPS, SLOP to DSAR, SSNR to DSNR, TOPS to DSNR and TOPS to SSNR (Table 4.6b). Except for movements between DSNR to TOPS (Pr=0.46) and TOPS to DSNR (Pr=0.70), probabilities of between habitat movements were low ($0.02 \leq Pr \leq 0.10$) (Table 4.6b). The probability of movement of *L. carponotatus* from TOPS to DSNR was significantly higher than within TOPS ($\chi^2=9.302$, df=1, $p<0.01$) (Table 4.6b). The probability of movement of *L. carponotatus* from DSNR to TOPS did not significantly differ from that within DSNR ($\chi^2=0.0755$, df=1, $p>0.05$) (Table 4.6b). A single movement of *L. carponotatus* was recorded from DSAR to SLOP, while 2 movements from SLOP to DSAR were noted (Table 4.6b). All fish recorded

moving between SLOP and DSAR habitats were originally tagged and released in the SLOP habitat.

Almost all movements of *L. carponotatus* in SLOP, SSNR and RUBB were within habitat ($0.90 \leq Pr \leq 1.00$; Table 4.6b). One within habitat movement of *L. carponotatus* was observed in RUBB and none in DSAR.

Lethrinus nebulosus

Only 13 movements were recorded for *L. nebulosus*. Of these, only 1 was between habitats (DSNR to DSAR; Table 4.6c). The rest were within habitats DSAR, RUBB, SSNR and RUBB.

Plectropomus leopardus

A total of 16 movements were recorded for *P. leopardus*. Six of these were between habitat movements. These were from DSNR to TOPS, SLOP to RUBB and TOPS to DSNR (Table 4.6d). The movements of *P. leopardus* from DSNR to TOPS (n=2) and TOPS to DSNR (n=3) were recorded for 3 fish. All but one of these fish were initially tagged in DSNR. The majority of the 10 within habitat movements of *P. leopardus* occurred in DSNR and SLOP.

Other species

All but one of the observed movements of *L. fulviflamma* were within habitat (in DSAR, SLOP, SSNR and DSNR; Table 4.6e). The single between habitat movement of *L. fulviflamma* was from DSNR to TOPS (Table 4.6e). Similarly, all but one movement of *L. semicinctus* was within habitat (within RUBB and SLOP; Table 4.6f). The between habitat movement of *L. semicinctus* was from DSNR to RUBB. All movements observed for *L. quinquelineatus*, *L. russelli*, *D. pictum*, *C. cyanostigma* and *L. atkinsoni* were within habitat (Tables 4.6g-k). Within habitat movement was observed for *L. quinquelineatus* in all habitats except in RUBB and TOPS (Table 4.6g). Movements within habitats were recorded for *L. russelli* in DSAR, DSNR and SSNR (Table 4.6h), in DSAR and DSNR for *D. pictum* (Table 4.6i), and in SLOP for

C. cyanostigma (Table 4.6j) and *L. atkinsoni* (Table 4.6k). The latter 2 species displayed very strong habitat fidelity for the SLOP habitat.

Day and night movements

Of the 286 individual movements, 45% were night movements, 26% were day movements and 29% were undetermined (i.e. recaptured during soaks covering both day and night periods). Overall, the total number of night movements was significantly higher (by a factor of 1.7) than in the day (χ^2=13.005, p<0.01, df=1).

For all species combined, the number of within habitat movements did not differ between day and night in all habitats except in DSNR and SLOP (Table 4.7a). Although the number of night movements in SSNR was higher than those in the day for all species combined, this ratio was not significant (χ^2=1.500, df=1, p>0.05) (Table 4.7a). Similarly, the number of movements in TOPS during the day did not differ significantly from the number at night for all species combined (χ^2=0.000, df=1, p>0.05) (Table 4.7a). In DSNR and SLOP, the number of movements during the night was significantly higher than during the day for all species combined (χ^2=7.500 and 4.102, respectively; p<0.05, df=1 for both) (Table 4.7a).

The number of movements from DSNR to TOPS and TOPS to DSNR did not differ between day and night for all species combined (χ^2=0.160 and 0.893, respectively; p>0.05, df=1 for both) (Table 4.7a). All other movements from DSNR to SSNR (n=1), SSNR to DSNR (n=2) and TOPS to SSNR (n=1) occurred during night time, while movements from DSAR to SLOP (n=1) and DSNR to RUBB (n=1) occurred during the day for all species combined (Table 4.7a).

For *L. carponotatus*, the number of movements within habitats did not differ between day and night in DSNR (χ^2=1.562, df=1, p>0.05), SLOP (χ^2=0.417, df=1, p>0.05) and TOPS (χ^2=0.000, df=1, p>0.05) (Table 4.7b). All movements within RUBB (n=1) and SSNR (n=1) occurred during night for *L. carponotatus* (Table 4.7b). The number of movements between habitats from DSNR to TOPS and TOPS to DSNR did not differ between day and night for *L. carponotatus* (χ^2=0.045 and 0.346, respectively; p>0.05, df=1 for both) (Table 4.7b). All other movements of *L.*

carponotatus from DSAR to SLOP (n=1) and DSNR to SSNR (n=1) occurred during the day, while those from SSNR to DSNR (n=2) and TOPS to SSNR (n=1) occurred at night (Table 4.7b).

4.3.2 Distances Moved

The percentage frequencies of distances moved were highly biased toward short distance movements (30 to 60 m) for all species combined (K-S d=0.318; p<0.01) (Fig. 4.1a), *L. carponotatus* (K-S d=0.267; p<0.01) (Fig. 4.1b), *P. leopardus* (K-S d=0.421; p<0.01) (Fig. 4.1c) and *C. cyanostigma* (K-S d=0.376; p<0.05) (Fig. 4.1d). *Lutjanus quinquelineatus* showed the same bias for short distance movements but not significantly so (K-S d=0.285; p<0.20) (Fig. 4.1e) probably due to a small sample size. The same bias toward short distance movement was observed for *L. atkinsoni* (Fig. 4.1f) though the distribution did not differ significantly from normal (K-S d=0.272; p>0.20). Similarly, more than 60% of movements of *L. fulviflamma* were in the range of 30 and 60 m (Fig. 4.1g). In contrast, *L. nebulosus* showed a tendency towards longer distance movement (>500 m; Fig. 4.1h). This larger distance movement (>500 m) constituted more than 60% of the total movements recorded for *L. nebulosus.*

The distances moved by the combined species ranged between 30 to 1500 m (Fig. 4.1a), 30 to 750 m for *L. carponotatus* (Fig. 4.1b), 30 to 1500 m for *P. leopardus* (Fig. 4.1c), 30 to 120 m for *C. cyanostigma* (Fig. 4.1d), 30 to 150 m for *L. quinquelineatus* (Fig. 4.1e), 30 to 90 m for *L. atkinsoni* (Fig. 4.1f), 30 to 500 m for *L. fulviflamma* (Fig. 4.1g) and 60 to 1000 m for *L. nebulosus* (Fig. 4.1h). Overall, more than 60% of the total movements were in the range of 30 to 60 m, while only 5% comprised movements greater than 500 m.

Within and between habitats

The range of movements within a habitat (30 to 1000 m; Fig. 4.2a) was similar to the range of movements between habitats (30 to 1500 m; Fig. 4.2b) for all species combined. The number of movements in each distance category within and between

habitats were both biased toward short distances for all species combined (K-S d=0.323, Fig. 4.2a and K-S d=0.324, Fig. 4.2b, respectively; $p<0.01$ for both). Distance movements greater than 100 m comprised 20% of total movements within and 42% between habitats, while movements greater than 500 m represented 5% of both within and between habitat movements for all species combined. However, the proportion of movements for each distance category within habitats was significantly different than between habitats for all species combined (K-S two-sample test: D_{min} = -0.014, D_{max}= 0.229, $p<0.01$).

The range of distances moved between habitats (30 to 750 m; Fig. 4.3b) was twice that of within habitats (30 to 300 m; Fig. 4.3a) for *L. carponotatus*. The frequency of distances moved within and between habitats by *L. carponotatus* were both biased toward short distances (K-S d=0.301, Fig. 4.3a and K-S d=0.294, Fig. 4.3b, respectively; $p<0.01$ for both). Distance movements greater than 100 m comprised 17% of movements within and 40% of movements between habitats, while movements greater than 500 m were not observed within and constituted about 4% of between habitat movements of *L. carponotatus*. The proportion of movements observed for *L. carponotatus* for each distance category within habitats was significantly different from that between habitats (K-S two sample test: D_{min}= -0.000, D_{max}= 0.249, $p<0.01$).

A high of 17 movements was observed for one *L. carponotatus* (fish 15676; 237 mm FL) over an 18-month period. This fish was initially tagged and released in the TOPS habitat at Mangrove Beach (Position 1 in Fig. 4.4) in October 1994. In March 1995 (135 days later) it was recaptured approximately 120 m away from the point of previous release. Over the next 18 days it was again recaptured 5 times within the general area of position 1 in Figure 4.4. Three of the 5 movements were from TOPS to DSNR and 2 were from DSNR to TOPS, covering distances estimated between 30 and 60 m. In July 1995 (160 days from previous release) it was recovered in SSNR near Bird Islet (Position 2 in Fig. 4.4) about 750 m away from the previous point of release, across a large expanse of deep (8-12 m) sand. Three days later it was recaptured in DSNR near Mangrove Beach (Position 3 in Fig. 4.4) covering approximately the same distance of 750 m. In October 1995 (104 days from previous release), it was again recaptured in the general vicinity of position 3 in Figure 4.4.

Over the next 8 days it was recovered twice moving between TOPS and DSNR over distances estimated at 30 to 60 m. In March 1996, (142 days after previous release), it was again recovered in the general vicinity of position 3 (Fig. 4.4) about 60 m away from previous point of release. Over the next 10 days, it was recaptured 4 more times traversing between TOPS and DSNR over distances of approximately 30 to 60 m. It was recovered for the last time 2 days later in DSNR (Position 4 in Fig. 4.4) about 150 m away from it's previous point of release.

Another *L. carponotatus* (fish 16526; 241 mm FL) was recorded to move 15 times over a period of 13 months (July 1995 to July 1996). All but two of the 15 movements were within the SLOP habitat over distances of about 30 to 120 m. In October 1995 (108 days from initial release) a movement from SLOP to DSAR, covering a distance of about 120 m, was recorded. In March 1996 (140 days after previous release) it was recaptured back in SLOP about 60 m from the point of previous release. Another lutjanid, *L. russelli* (fish 16539: 277 mm FL), demonstrated a large distance movement covering approximately 1000 m across shallow sand (3-5 m) from SSNR near Palfrey to the same habitat at Loomis (Positions 5 to 6 in Fig. 4.4). This movement occurred over a period of 117 days after release.

Other examples of large movements within a habitat were observed for two individuals of *L. nebulosus*. The first (fish 15648; 415 mm FL) was initially tagged and released in a RUBB habitat in October 1994 (Position 1 in Fig. 4.5). In March 1995 (135 days after initial release), it was recovered about180 m away from point of release in the same habitat (Position 2 in Fig. 4.5). Six days later it was recaptured in the same habitat (Position 3 in Fig. 4.5) some 500 m away. The other *L. nebulosus* (fish 15649; 435 mm FL) was tagged and released in a SSNR habitat near South Island in October 1994 (Position 4 in Fig. 4.5). In March 1995 (146 days after initial release), it was recaptured in the same habitat near Bird Islet about 500 m away from point of release (Position 5 in Fig. 4.5). In July 1995 (116 days after previous release), it was recovered in SSNR between Bird Islet and South Island about 500 m away from point of last release (Position 6 in Fig. 4.5). In March 1996 (250 days after previous release), it was recaptured for the last time in SSNR near South Island (Position 7 in Fig. 4.5) about 1000 m from point of previous release. Another large movement was exhibited

by a coral trout, *P. leopardus* (fish 15403; 568 mm FL). This fish was tagged in SLOP at Trawler beach in March 1994 (Position 8 in Fig. 4.5). A year later (367 days after release), it was recovered in the RUBB in South Island (Position 9 in Fig. 4.5) approximately 1500 m away from point of release.

Day and night movements

The range of distances moved during night (30 to 1000 m; Fig. 4.6b) was twice that recorded during the day (30 to 500 m; Fig. 4.6a) for all species combined. The frequency of movement in each distance category during day and night favored the short distances for all species combined (K-S d=0.265, Fig. 4.6a and K-S d=0.329, Fig. 4.6b; $p<0.01$ for both). Distance movements greater than 100 m constituted 26% of total movements during the day and 27% at night, while movements greater than or equal to 500 m were 3 and 4%, respectively, for all species combined. The proportions of movements in each distance category did not differ significantly between day and night for all species combined (K-S two sample test: D_{min}= -0.039, D_{max}= 0.063, $p>0.20$).

For *L. carponotatus*, the range of night movement (30 to 750 m; Fig. 4.7b) was twice that recorded during the day (30 to 270 m; Fig. 4.7a). The number of movements in each distance category during day and night were both biased toward short distances (K-S d=0.272, Fig. 4.7a and K-S d=0.281, Fig. 4.7b; $p<0.01$ for both). Distance movements greater than 100 m constituted 24% of movements during the day and 32% during the night. Movements greater than 500 m were not recorded during the day and represented 4% of movements at night. The proportions of movements in each distance category did not differ significantly between day and night for *L. carponotatus* (K-S two sample test: D_{min}= -0.072, D_{max}= 0.039, $p>0.20$).

4.4. DISCUSSION

The high rates of recapture provided this study with information on movement patterns of reef fish within and between habitats, and partitioned this into day and night movements in the lagoon of Lizard Island. This resulted from sustained tagging and recovery effort over 30 months. Multiple recaptures of several individuals indicate a lack of independence for some observations, but multiple recoveries provided a larger number of observations over longer time periods of liberty. Single and multiple recaptures allowed the tracking of movement patterns of fish and an assessment of the mobility of fish within and between habitat types, factors of potential importance to fisheries biologists (Hilborn 1990). Hilborn *et al.* (1990) point out that patterns of fish movement are usually not clearly discerned unless mark recovery data, especially multiple recoveries, are available. Multiple recaptures stem from a tendency of reef fish to re-enter traps. Such observations have been made in previous trapping/tagging studies (e.g. Bardach 1958, Randall 1961, 1963, Recksiek *et al.* 1991, Sheaves 1993, Davies 1995).

The generally high rates of recapture of reef fish were consistent with those obtained by Davies (1995) in the same general study area, particularly for *L. carponotatus* (Davies 22%; this study 26%). Recksiek *et al.* (1991) obtained higher recapture rates in Puerto Rico for four species of reef fish (34%: 101 of 272), most likely due to the fixed positions of traps and longer soak times used in their study. In contrast, reported recapture rates were low in tagging studies in Texas (4.9-5.6%: Fable Jr. 1980), Florida (0.3-2.8%: Funicelli *et al.* 1989; 1.6-9.4%: Bryant *et al.* 1989) and South Africa (2.6%: Buxton and Allen (1989) as cited in Russ and Alcala 1996a).

Two of the major points from this study were:

1. There was strong habitat fidelity among all study species in all habitats except in the habitat TOPS. A significant movement from the TOPS to DSNR was observed for *L. carponotatus*.

2. All study species, except perhaps *L. nebulosus*, generally moved short distances (scales of 30-60 m) most of the time. This propensity to move short rather than long

distances was observed within and between habitats, and between day and night observations. Thus:

i) Distances moved between habitats were significantly larger than those moved within habitats for all species combined and for *L. carponotatus*. The proportion of movements in each distance category was significantly different within and between habitats for all species combined and for *L. carponotatus* (shapes of curves in Fig. 4.2a and b, and Fig. 4.3a and b differ even when corrected for sample size).

ii) Distances moved did not differ significantly during night and day. The proportion of movements in each distance category did not differ significantly between day and night for all species combined nor for *L. carponotatus*. However, significantly more night than day movements were observed in SLOP and DSNR habitats for all species combined.

iii) Some species (e.g. *L. carponotatus* and *L. fulviflamma*) may move distances of 100's of meters across vast expanses of deep sand, but this type of movement is rare. *Lethrinus nebulosus* appeared to move larger distances (>500 m) than other species. Large distance movements (>500 m) were more probable at night and across sand, for all species combined and for *L. carponotatus*.

4.4.4 Habitat Fidelity

A strong habitat fidelity was observed for *L. carponotatus* in the SLOP and SSNR habitats. However, *L. carponotatus* released in the TOPS habitat was more likely to be recovered in the DSNR. The observed movements of *L. carponotatus* from TOPS to DSNR may suggest a small scale migration pattern to DSNR, a habitat likely to support abundant benthic prey. Furthermore, these two habitats are often in close proximity in Lizard Island lagoon, separated by a vertical distance of only 8-10 m in the study area (see Figs. 2.2-3 in Chapter 2). A preliminary examination of gut contents of *L. carponotatus* indicated a preference for benthic invertebrates, mainly

crustaceans, and fish (unpubl. data). Benthic crustaceans are abundant in sandy habitats.

Lutjanus carponotatus appeared active during day and night. The number of movements recorded did not differ significantly between these two periods. This was consistent with the finding in Chapter 3 that abundances of *L. carponotatus* did not differ significantly between day and night in reefal areas. Preliminary results of a bait experiment conducted from 0530-1930 hrs with traps being hauled and emptied every 3 hrs, suggested that *L. carponotatus* appeared to be active most of the day. It is not known if *L. carponotatus* have peak hours of feeding activity.

The data for other species, although of limited extent, provided important information on movement patterns. *Lethrinus nebulosus*, *Lutjanus russelli* and *Diagramma pictum* displayed strong fidelity with sandy habitats near reefs. *Plectropomus leopardus*, *Lutjanus fulviflamma*, *L. quinquelineatus*, *Lethrinus semicinctus*, *L. atkinsoni*, and *Cephalopholis cyanostigma* displayed strong affinity with reefal habitats. Movements of these species out of their associated habitats were rare. However for *L. fulviflamma* (and to a lesser extent *L. quinquelineatus*), there was a strong suggestion of movement from reefal resting areas to feeding areas in deep sand away from reefs at night (see Section 3.4.3). Two species in particular, *C. cyanostigma* and *L. atkinsoni*, showed marked fidelity with the SLOP habitat.

Habitat fidelity has been noted for *L. carponotatus*, *Siganus doliatus* and *P. leopardus* at Lizard Island (Davies 1995, Zeller 1997). Davies (1995) found that fish were recovered in the same position and habitat of release 68% of the time for *L. carponotatus* and 69% of the time for *S. doliatus* in reef and patch reef habitats. Similarly, Zeller (1997) demonstrated that *P. leopardus* stayed within their home range, and mostly on hard bottom reef substratum, most of the time. *Epinephelus coioides*, *E. malabaricus* and *L. russelli* were observed to move little between habitats in an estuary in northeastern Australia (Sheaves 1993). Tagging studies elsewhere also support the idea of high habitat fidelity of reef fish (Bardach 1958, Randall 1961, 1963, Recksiek *et al.* 1991). Bardach (1958) found chaetodontids, *Epinephelus guttatus*, *E. striatus* and *Haemulon sciurus* moved very little in a hectare of reef in Bermuda.

Randall (1961, 1963) obtained almost all recoveries of *Acanthurus bahianus* and *H. plumieri* from the same five tagging locations on a single reef in the Virgin Islands. The high recapture rates for *A. bahianus*, *H. plumieri*, *Sparisoma aurofrenatum* and *S. chrysopterum* from the same tagging location (reef area ~600 m^2) in Puerto Rico led Recksiek *et al.* (1991) to conclude that most reef fishes were non-migratory.

4.4.2 Propensity for Short Distance Movement

All study species except *Lethrinus nebulosus* exhibited a propensity for short distance movement of the order of 10's to about 60 m. *Lethrinus nebulosus* often exhibited much larger distance movements of the order of 100's up to 1000 m in sandy habitats. The propensity for short distance movements observed in this study was consistent with those recorded for *Epinephelus coioides*, *E. malabaricus* and *Lutjanus russelli* in a tropical estuary (Sheaves 1993). Sheaves (1993) noted that more than 70% of tag recoveries were within 40 m of the release point and less than 13% of returns were more than 240 m from sites of previous release. The propensity for short distance movements is consistent with high habitat fidelity of reef fishes.

The data for all species combined and for *L. carponotatus* demonstrated that short distance movements were the rule, regardless of the type of habitat (within and between habitats) or time (day or night). The result for all species combined should be treated with caution. Not all species demonstrated movement between habitats and many species demonstrated few day and night movements. Moreover, there was a difference in the proportion of distances moved within and between habitats, with more movements observed in the larger distance categories (range of 10's up to 150 m and >500 m) for between habitat movement. The scale of movement within (30-60 m) and between (30-500 m) habitats were small relative to the size of most habitats in the study area. Any two habitats were often separated by considerable distances, except that the TOPS and DSNR were usually separated by vertical distances of only 5-8 m on many bombies in the study area. During sampling, care was exercised to maintain at least a 200 m separation when these two particular habitats were sampled simultaneously.

Few studies have examined small scale movement patterns of reef fishes in detail. The main purpose of many tagging studies has often been to investigate growth and mortality of fishes (e.g. Kirkwood 1983, Francis 1988, Francis *et al.* 1992, Xiao 1994, You-Gan *et al.* 1995), estimate population size (e.g. Nichols 1992), estimate the degree of interaction or discreteness of fish stocks (Clay 1990, Hilborn 1990) and measure large scale migration and movement patterns (e.g. Funicelli *et al.* 1989, Kallio-Nyberg and Ikonen 1991, Attwood and Bennett 1994). Many of the earlier studies of migration and movement presented raw data by drawing arrows from points of release to locations of recoveries (e.g. Funicelli *et al.* 1989). Until recently, there has been very little formal statistical analysis of movement data (Hilborn 1990). Several workers have proposed using maximum likelihood estimators to analyze movement data derived from tag-recovery data (Hilborn 1990, Schwarz and Arnason 1990, Schwarz *et al.* 1993, Schweigert and Schwarz 1993, Xiao 1996). A main goal of such studies was to describe how movement and migration may impact population dynamics in two spatially distinct locations. Schwarz and Arnason (1990) recognized three migration mechanisms and proposed three models based on the fidelity of fish to tagging and recovery areas. The complete fidelity model proposed by Schwarz and Arnason (1990) may be useful in future studies of reef fish movement. In the case of the present study, the lack of systematic and uniform effort to recover fish in ways similar to that made by Davies (1995), would seriously violate an assumption of this model. In Davies (1995), the sites were divided into permanent trapping grids and traps were randomly positioned in rows of six traps which sequentially sampled the area. The focus in the present study was mainly on the patterns and 'background' levels of movement of reef fishes within and between habitats (the frequency of interaction) at both day and night over a relatively small area. This study was interested in estimates of distances moved within a local area. Short distance movements, such as most of those recorded in this study, are thought not likely to impact local population density significantly. Despite the difference in the methods used in this study and that of Davies (1995), the conclusions were consistent and provide empirical data which support the idea that reef fishes are strongly site-attached. The major results from this study provide heuristic insights important to reef fishery biologists (see below).

Large distance movements

Large distance movements observed for *Lutjanus carponotatus*, *L. russelli*, and *Plectropomus leopardus* were rare in this study, but appeared common for *Lethrinus nebulosus*. More data is required to better understand the local movement patterns of *L. nebulosus*.

In tagging studies such as this, there was no way of knowing the precise trajectories and distances a fish had moved over long periods of recovery. All but one of the large distance movements occurred after more than 100 days since release. The estimated 750 m movements from DSNR to SSNR and SSNR to DSNR observed for *L. carponotatus* were likely to have been made directly over deep sand. A better way of tracking movement was demonstrated by Zeller (1997) for coral trouts. He implanted transmitters into the gut cavity of fish and followed them over extended periods of time. This method is expensive and also may not be appropriate for small reef fish unless miniaturization of transmitters becomes available.

Large distance movements of fish may be rare, but other studies have observed such movements of reef fish. Fable Jr. (1980) reported recoveries of 2 (235 and 245 mm FL) of 793 small vermilion snappers (*Rhomboplites aurorubens*) and 1 (280 mm FL) of 299 red snappers (*Lutjanus campechanus*) in locations 5-10 km away from points of release after 160-170 days. These distances are 5 to 10 times those observed in this study for fish of similar size. Little is known about these rare, large distance movements except that it is noted to happen in a small proportion of tagged individuals. Roberts and Polunin (1991) suggested the possibility of genetic disposition of some individuals within a population for long distance movement.

4.4.3 Relevance to Marine Fisheries Reserves

An important basis for establishing marine reserves are their potential to maintain or even enhance fisheries yield by protecting a critical spawning biomass to ensure recruitment supply via larval dispersal, and allow fish to grow to larger sizes

and then move to adjacent fished areas (Russ and Alcala 1996a). The results of this study have direct implications for the potential movement of adult fish to adjacent fished areas. The small distances moved by fish imply that the 'spillover' effect may be limited, but it also implies that protection from fishing, if effective, should lead to biomass buildup (not much 'leakage') and thus, marine reserves should be effective in protecting spawning stock to enhance/maintain recruitment.

Designs and locations of marine reserves should consider that small predatory coral reef fish, such as lutjanids and lethrinids, are likely to be highly habitat attached, with movement on scales of 10's of m only, with occasional movements on scales of 100's of m. This study has shown that about 19% of fish movements within a habitat were in the range of a few 100's up to 500 m. The possibility of establishing marine reserves on portions of contiguous reef with uniform habitat quality should be explored. The location of the protected portion within the reef could be critical. Factors such as edge to area ratio, edge permeability and the relative quality of habitat inside and outside of reserve will likely influence flux rates across reserve boundaries (Buechner 1987, Stamps *et al.* 1987).

There is a possibility that the high habitat fidelity and propensity for short distance movements found in this study may be limited to reefs where fishing pressure is low. In regions where fishing pressure is intense, movement patterns may be influenced by strong density gradients from unfished to fished areas. It will be of interest to investigate movement patterns of fish along differential gradients of fish density. The argument of whether different fish population densities trigger net movement towards a low density area depend on many factors and remains to be resolved. Tagging studies looking at flux rates of smaller predatory fishes crossing reserve boundaries could assess whether there is a net movement toward adjacent exploited areas. Russ and Alcala (1996a) and Zeller and Russ (submitted MS) provided evidence of movement of large predatory coral reef fish between reserve and adjacent exploited areas.

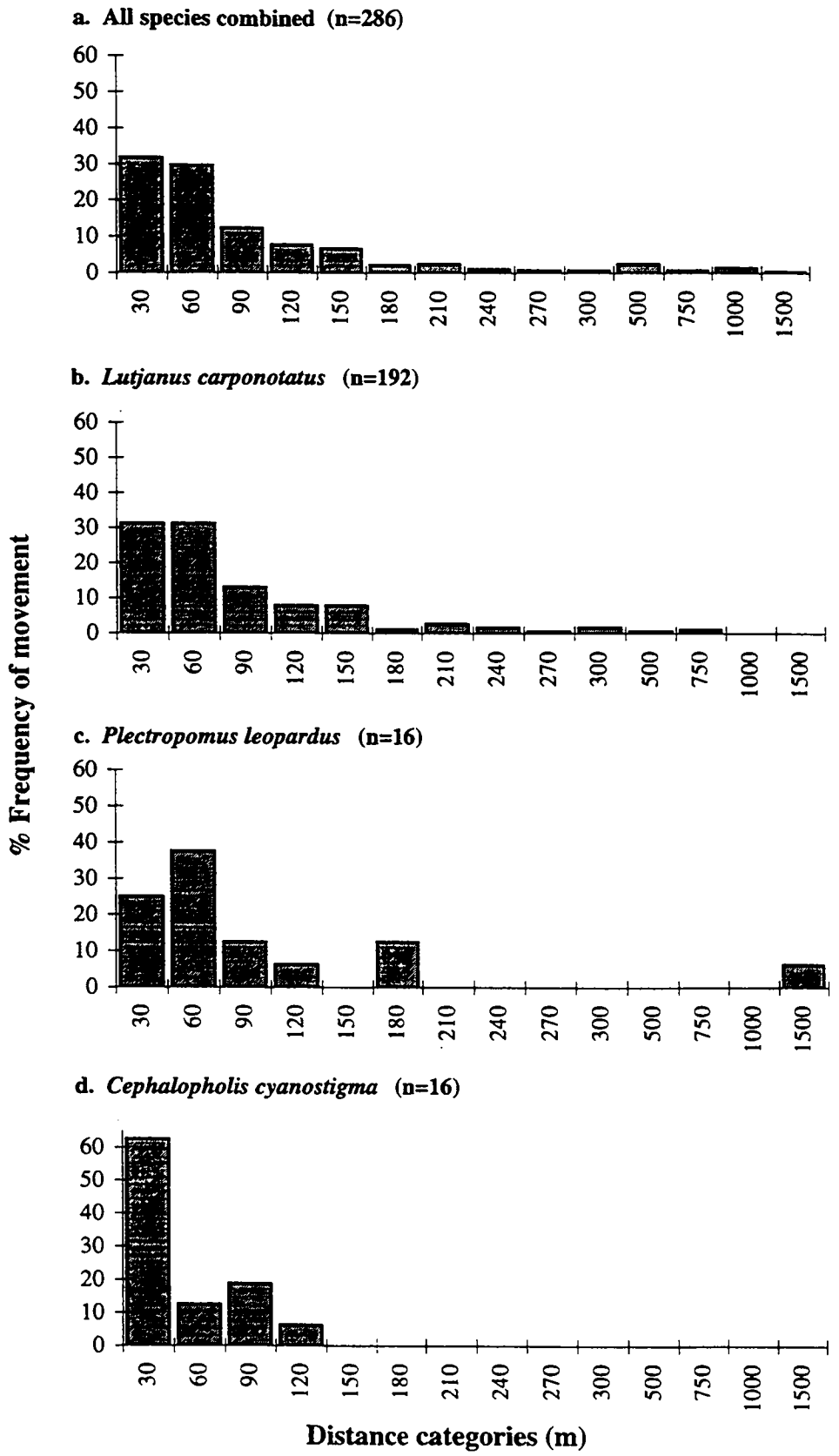


Figure 4.1. Percentage frequency of distances moved by all species combined (a) and 7 species (b-h) in Lizard Island lagoon, GBR.

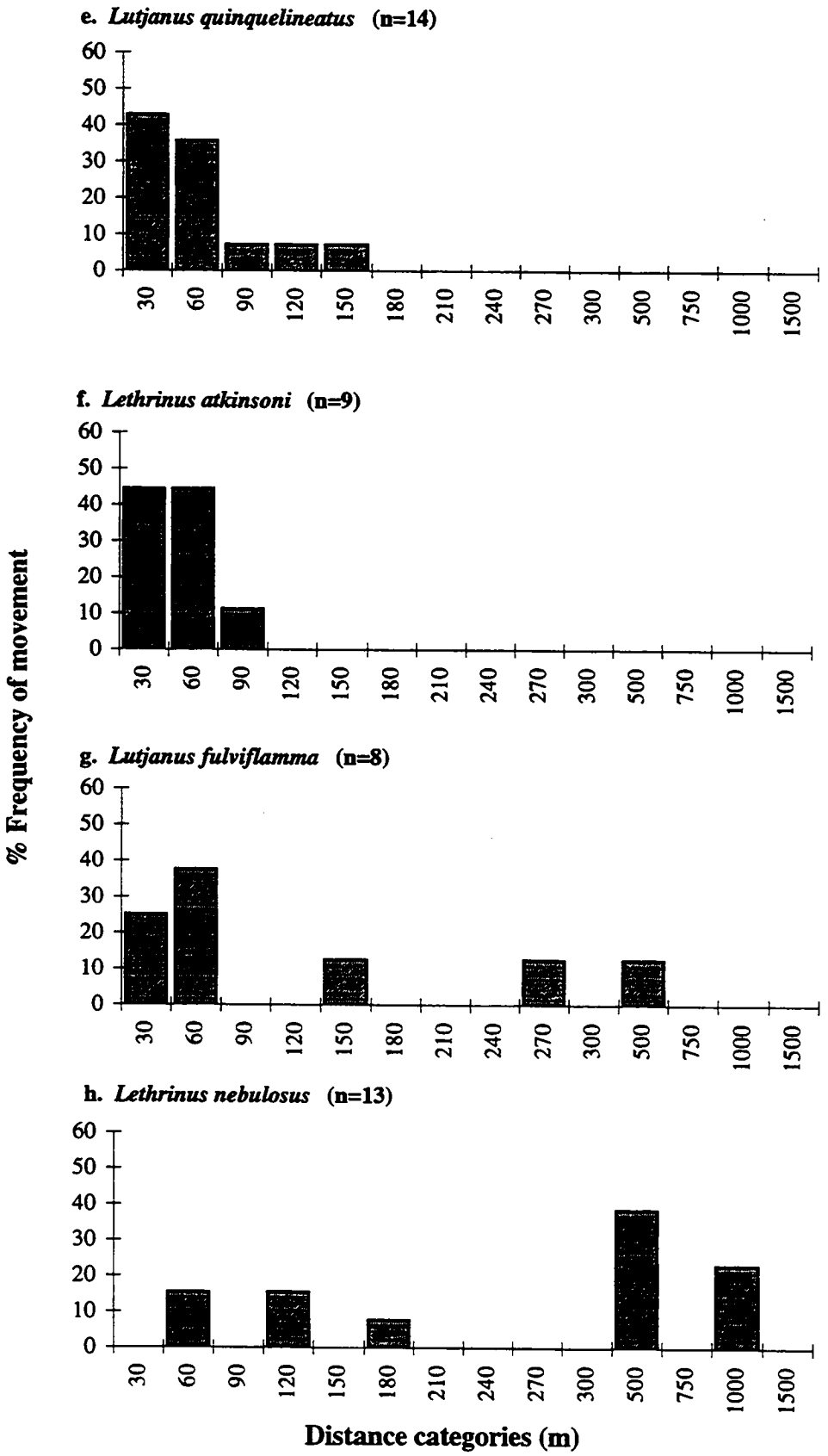


Figure 4.1. con't.

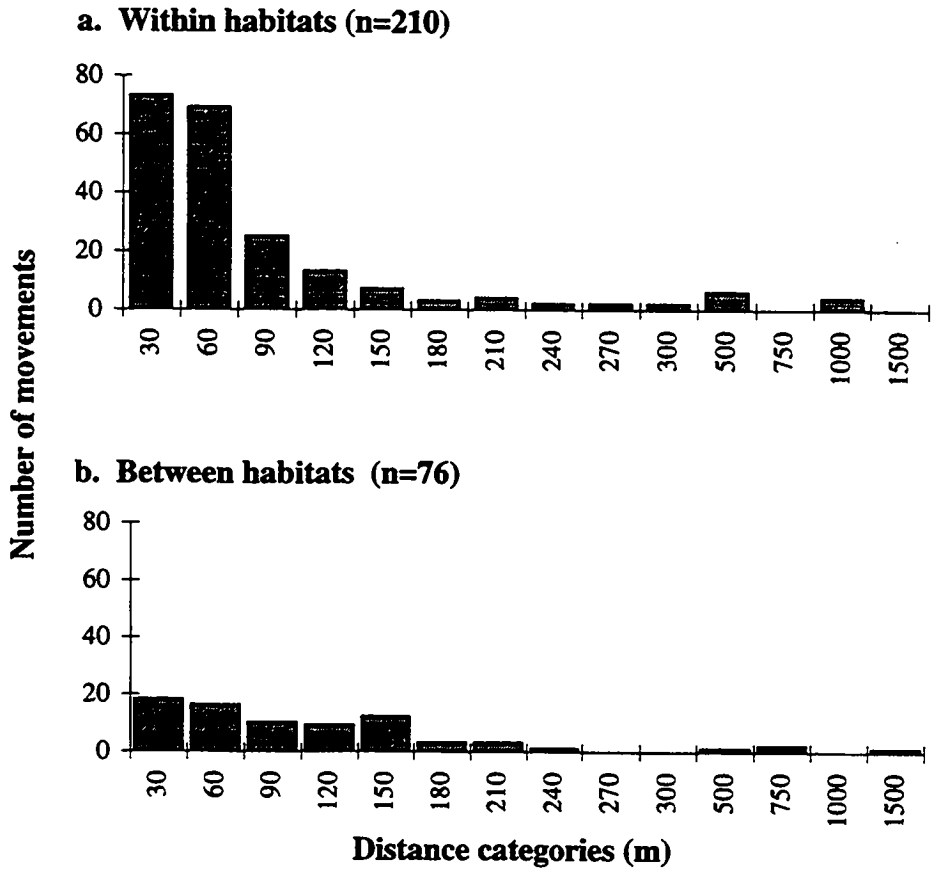


Figure 4.2. Number of fish movements in categories of distance moved (a) within and (b) between habitats for all species combined.

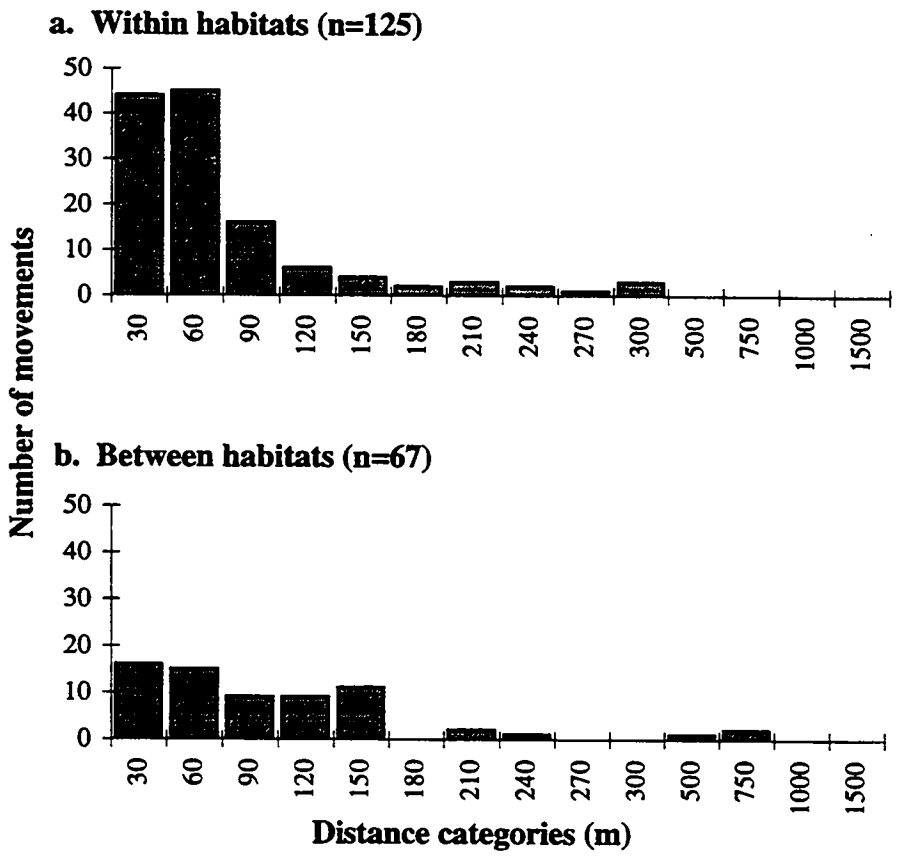


Figure 4.3. Number of fish movements in categories of distance moved (a) within and (b) between habitats for *Lutjanus carponotatus*.

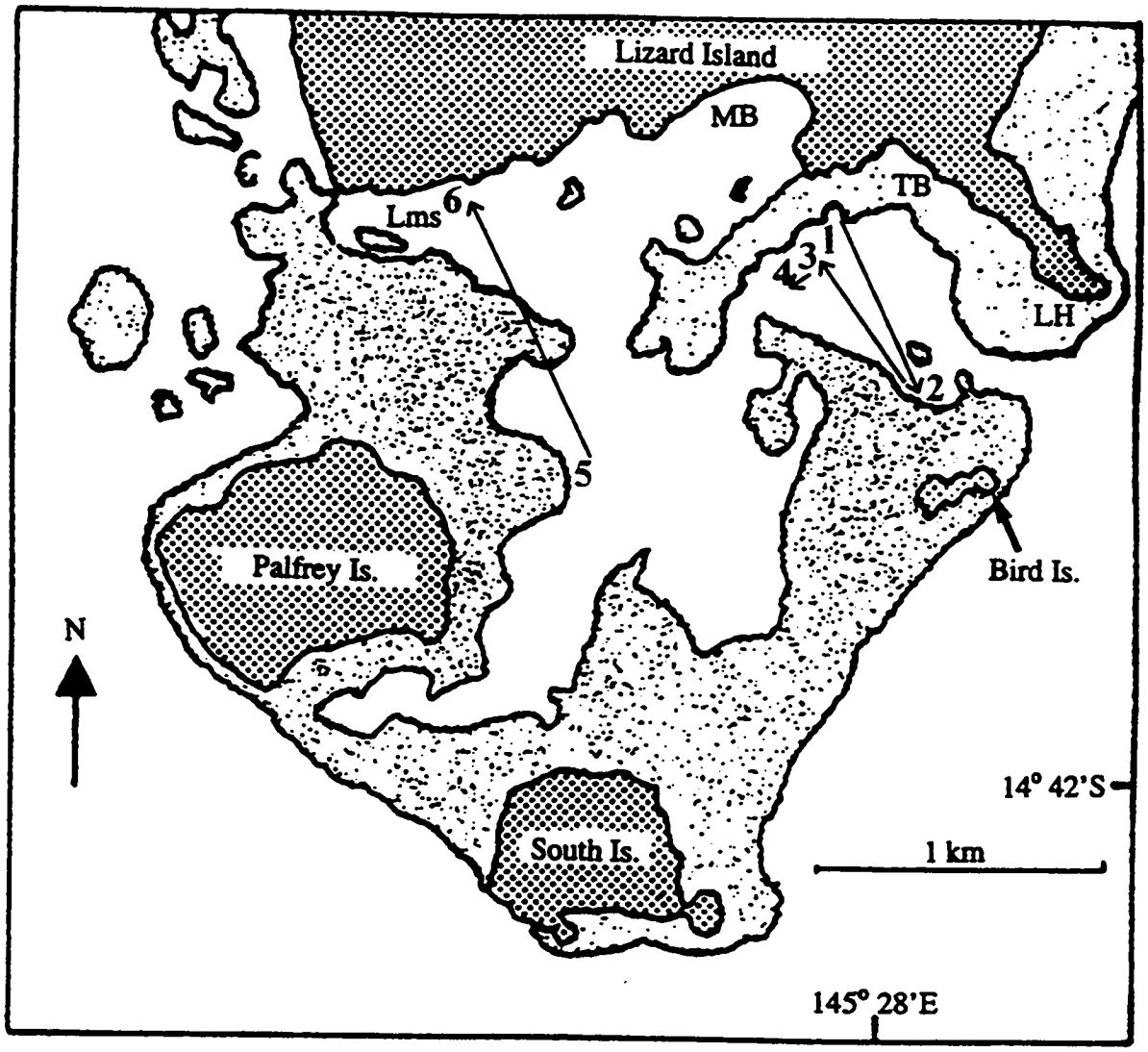


Figure 4.4. Movements of an *L. carponotatus* (fish 15676) (positions 1-4) and an *L. russelli* (fish 16539) (positions 5-6).

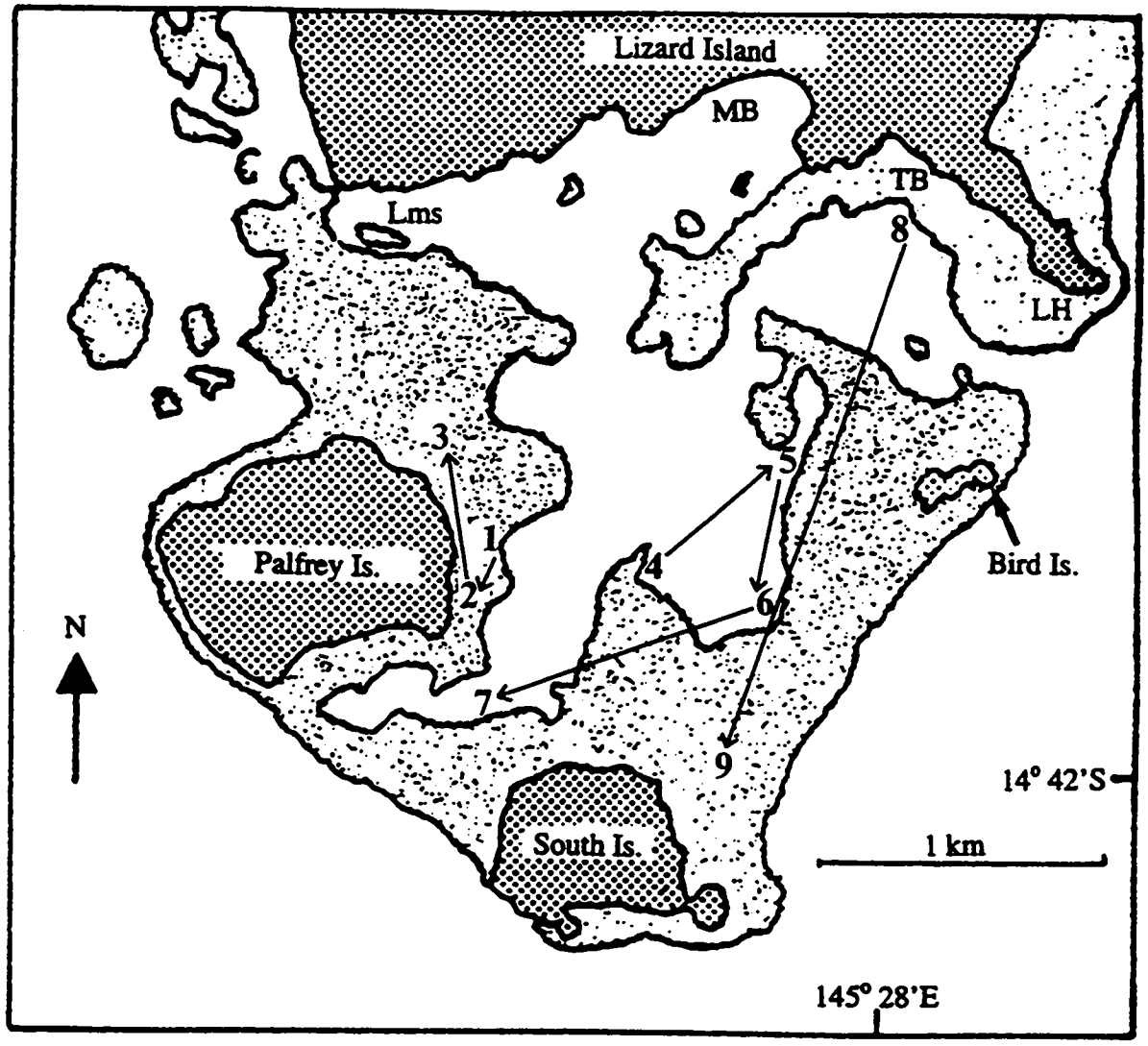


Figure 4.5. Movements of two *L. nebulosus* (fish 15648; positions 1-3 and fish 15649; positions 4-7) and a *P. leopardus* (fish 15403; positions 8-9).

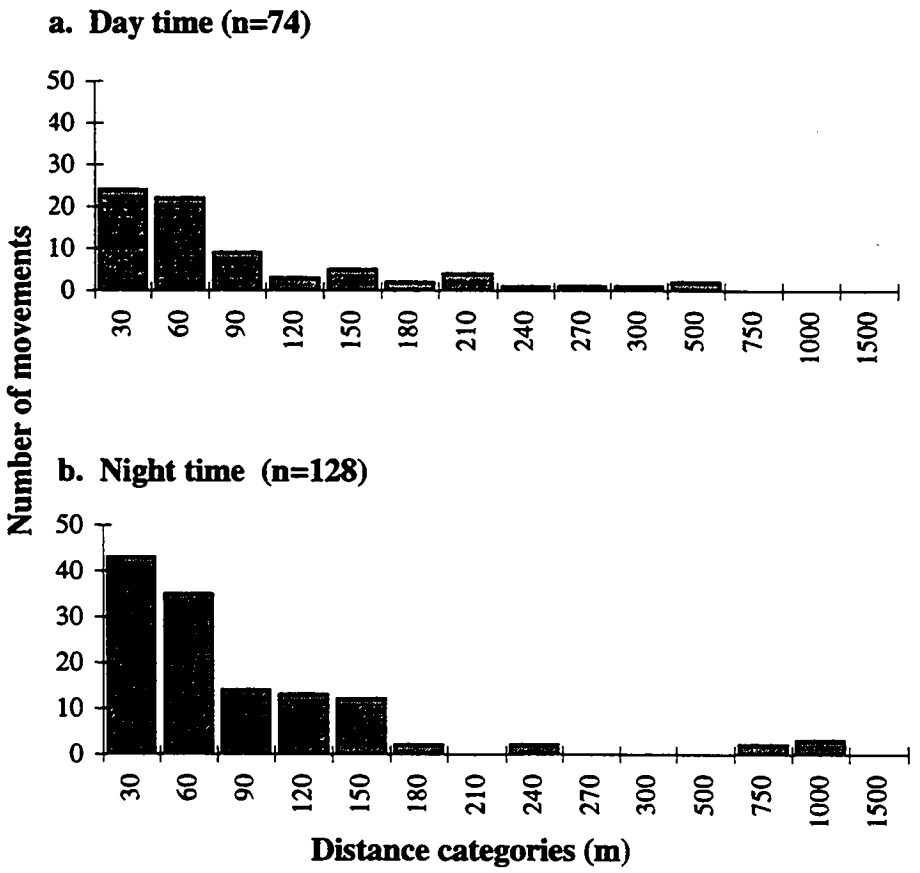


Figure 4.6. Number of fish movements in categories of distance moved by (a) day and (b) night for all species combined.

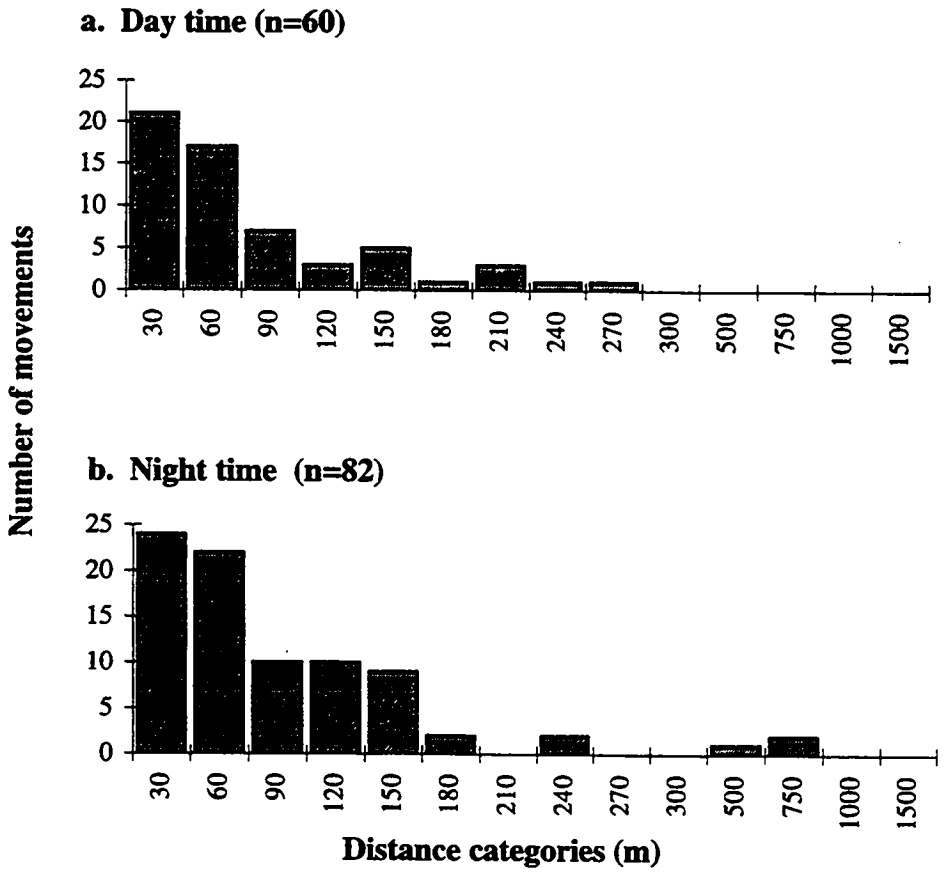


Figure 4.7. Number of fish movements in categories of distance moved by (a) day and (b) night for *L. carponotatus*

Table 4.1. Summary of total releases, returns and recapture rates of species in a mark-recapture study in Lizard Island lagoon, GBR from March 1994 to July 1996. Multiple recoveries were counted once here.

Family	Species		Total Releases (R)	Total Returns (K)	Recapture Rate (%)
Lutjanidae	*Lutjanus carponotatus*		304	80	26.32
	Lutjanus quinquelineatus		170	10	5.88
	Lutjanus fulviflamma		72	8	11.11
	Lutjanus russelli		23	4	17.39
	Lutjanus vitta		10	0	
	Lutjanus bohar		6	0	
	Lutjanus fulvus		3	1	33.33
	Symphorus nematophorus		3	0	
	Lutjanus gibbus		1	0	
	Lutjanus lemniscatus		1	0	
	Lutjanus monostigma		1	0	
		Total	594	103	17.34
Lethrinidae	*Lethrinus nebulosus*		135	10	7.41
	Lethrinus semicinctus		30	4	13.33
	Lethrinus atkinsoni		29	3	10.34
	Lethrinus lentjan		8	0	
	Lethrinus olivaceus		3	0	
	Lethrinus ornatus		2	0	
	Lethrinus obsoletus		1	0	
	Lethrinus variegatus		1	0	
		Total	209	17	8.13
Serranidae	*Cephalopholis cyanostigma*		90	10	11.11
	Plectropomus leopardus		26	7	26.92
	Epinephelus merra		15	0	
	Epinephelus ongus		12	1	8.33
	Cephalopholis microdon		6	0	
	Epinephelus malabaricus		4	0	
	Cephalopholis boenack		3	0	
	Epinephelus fuscoguttatus		3	0	
	Epinephelus hexagonatus		2	0	
		Total	161	18	11.18
Haemulidae	*Diagramma pictum*		28	4	14.29
	Plectorhynchus chaetodontoides		1	0	
		Total	29	4	13.79
Others			2	0	
		TOTAL	**995**	**142**	**14.27**

Table 4.2. Summary of number of releases (R) and returns (K) in sampling times (T) in the Lizard Island lagoon for all combined species (a) and for 10 individual species (b-k). Multiple returns within a sampling time were counted once.

a. All species combined

		Returns (K) in						
Releases in Time (T)	**No. of release (R)**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	143	2	14	4	1	2	0	0
Oct-94	190		11	16	8	8	6	4
Mar-95	142			12	2	6	5	1
Jul-95	95				10	18	1	1
Oct-95	176					12	3	0
Mar-96	178						18	8
Jul-96	71							10
Total	995	6	28	34	22	46	33	24

b. *Lutjanus carponotatus*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	36	0	4	0	0	1	0	0
Oct-94	38		6	6	3	3	3	2
Mar-95	54			11	2	3	2	1
Jul-95	28				9	8	1	1
Oct-95	54					11	0	0
Mar-96	69						14	6
Jul-96	25							8
Total	304	0	10	17	14	26	20	18

c. *Lethrinus nebulosus*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	1	0	0	0	0	0	0	0
Oct-94	38		0	4	2	0	1	0
Mar-95	17			0	0	1	0	0
Jul-95	17				0	2	0	0
Oct-95	28					0	1	0
Mar-96	27						0	0
Jul-96	7							1
Total	135	0	0	4	2	3	2	1

Table 4.2 con't.

d. *Lutjanus quinquelineatus*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	60	0	4	1	0	0	0	0
Oct-94	28		1	0	0	0	0	0
Mar-95	18			1	0	0	0	0
Jul-95	7				0	2	0	0
Oct-95	23					0	1	0
Mar-96	19						0	1
Jul-96	15							0
Total	170	0	5	2	0	2	1	1

e. *Cephalopholis cyanostigma*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	13	1	1	1	0	0	0	0
Oct-94	31		1	2	1	1	0	0
Mar-95	18			1	0	1	3	0
Jul-95	7				0	1	0	0
Oct-95	8					0	0	0
Mar-96	9						0	0
Jul-96	4							0
Total	90	1	2	4	1	3	3	0

f. *Lutjanus fulviflamma*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	5	0	0	0	0	0	0	0
Oct-94	19		1	1	1	3	0	0
Mar-95	2			0	0	0	0	0
Jul-95	12				1	1	0	0
Oct-95	21					0	0	0
Mar-96	11						0	0
Jul-96	2							0
Total	72	0	1	1	2	4	0	0

g. *Plectropomus leopardus*		Returns (K) in						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	4	1	3	1	0	0	0	0
Oct-94	7		1	2	1	0	0	0
Mar-95	5			0	0	0	0	0
Jul-95	3				0	1	0	0
Oct-95	2					0	1	0
Mar-96	3						0	1
Jul-96	2							0
Total	26	1	4	3	1	1	1	1

Table 4.2 con't.

h. *Lutjanus russelli*		**Returns (K) in**						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	5	0	0	0	0	0	0	0
Oct-94	3		0	0	0	0	1	0
Mar-95	1			0	0	0	0	0
Jul-95	5				0	2	0	0
Oct-95	4					0	0	0
Mar-96	5						1	0
Jul-96	0							0
Total	23	0	0	0	0	2	2	0

i. *Diagramma pictum*		**Returns (K) in**						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	0	0	0	0	0	0	0	0
Oct-94	1		0	0	0	0	0	0
Mar-95	0			0	0	0	0	0
Jul-95	2				0	0	0	0
Oct-95	8					1	0	0
Mar-96	15						3	0
Jul-96	2							0
Total	28	0	0	0	0	1	3	0

j. *Lethrinus atkinsoni*		**Returns (K) in**						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	6	0	2	1	1	1	0	0
Oct-94	4		0	0	0	0	0	0
Mar-95	6			0	0	0	0	0
Jul-95	2				0	0	0	0
Oct-95	3					0	0	0
Mar-96	2						0	0
Jul-96	6							1
Total	29	0	2	1	1	1	0	1

k. *Lethrinus semicinctus*		**Returns (K) in**						
T	**R**	**Mar-94**	**Oct-94**	**Mar-95**	**Jul-95**	**Oct-95**	**Mar-96**	**Jul-96**
Mar-94	2	0	0	0	0	0	0	0
Oct-94	5		1	1	0	0	1	1
Mar-95	6			0	0	1	0	1
Jul-95	1				0	0	0	0
Oct-95	6					0	0	0
Mar-96	8						0	0
Jul-96	2							0
Total	30	0	1	1	0	1	1	2

Table 4.3. Summary of the number of releases (R) and single returns (K) in each habitat and recapture rates for all species combined (a) and 10 individual species (b-k).

HABITAT	Total Releases (R)	Total Single Returns (K)	Recapture Rate (K/R*100)
a. All species combined			
DSAR	175	10	5.71
DSNR	259	37	14.29
RUBB	60	4	6.67
SLOP	256	45	17.58
SSNR	118	17	14.41
TOPS	127	29	22.83
b. *Lutjanus carponotatus*			
DSAR	0	0	-
DSNR	73	20	27.40
RUBB	19	1	5.26
SLOP	82	24	29.27
SSNR	37	7	18.92
TOPS	93	28	30.11
c. *Lethrinus nebulosus*			
DSAR	48	3	6.25
DSNR	41	2	4.88
RUBB	13	1	7.69
SLOP	5	0	-
SSNR	27	4	14.81
TOPS	1	0	-
d. *Plectropomus leopardus*			
DSAR	0	0	-
DSNR	8	4	50.00
RUBB	1	0	-
SLOP	13	2	15.38
SSNR	1	0	-
TOPS	3	1	33.33
e. *Lutjanus fulviflamma*			
DSAR	39	2	5.13
DSNR	9	2	22.22
RUBB	2	0	0.00
SLOP	5	2	40.00
SSNR	13	2	15.38
TOPS	4	0	0.00
f. *Lethrinus semicinctus*			
DSAR	4	0	0.00
DSNR	5	0	0.00
RUBB	9	2	22.22
SLOP	11	2	18.18
SSNR	1	0	0.00
TOPS	0		-
g. *Lutjanus quinquelineatus*			
DSAR	43	1	2.33
DSNR	88	7	7.95
RUBB	0		-
SLOP	27	1	3.70
SSNR	12	1	8.33
TOPS	0		-
h. *Lutjanus russelli*			
DSAR	2	1	50.00
DSNR	13	1	7.69
RUBB	0		-
SLOP	0		-
SSNR	7	2	28.57
TOPS	1	0	0.00
i. *Diagramma pictum*			
DSAR	19	3	15.79
DSNR	7	1	14.29
RUBB	0		-
SLOP	0		-
SSNR	2	0	0.00
TOPS	0		-
j. *Cephalopholis cyanostigma*			
DSAR	0		-
DSNR	4	0	0.00
RUBB	0		-
SLOP	70	10	14.29
SSNR	5	0	0.00
TOPS	11	0	0.00
k. *Lethrinus atkinsoni*			
DSAR	0		-
DSNR	3	0	0.00
RUBB	1	0	0.00
SLOP	20	3	15.00
SSNR	4	0	0.00
TOPS	1	0	0.00

Table 4.4. Frequency of recaptures of the total 142 individual returns (K) in Lizard Island lagoon, GBR. Each recapture was considered a movement. Total number of movements (M) was the total number of movements from K individuals computed as the sum of the products of the frequency of recapture and number of individuals in each category (e.g. for *L. nebulosus* M is 8*1+1*2+1*3 = 13).

		Frequency of recaptures									
Species	**K**	**1**	**2**	**3**	**4**	**5**	**7**	**8**	**15**	**17**	**M**
Lutjanus carponotatus	80	44	14	9	3	5		3	1	1	192
Cephalopholis cyanostigma	10	6	3		1						16
Plectropomus leopardus	7	2	2	2	1						16
Lutjanus quiquelineatus	10	7	2	1							14
Lethrinus nebulosus	10	8	1	1							13
Lethrinus atkinsoni	3	2					1				9
Lutjanus fulviflamma	8	8									8
Lethrinus semicinctus	4	2	2								6
Diagramma pictum	4	3	1								5
Lutjanus russelli	4	4									4
Epinephelus ongus	1		1								2
Lutjanus fulvus	1	1									1
Total	142	87	26	13	5	5	1	3	1	1	**286**

Table 4.5. Records of movement in days after release/re-release of K individuals in Lizard Island lagoon, GBR. Each return (recapture) was considered a movement. M is the total number of movement recorded from K individuals.

		Days after release/re-release					
Species	**K**	**0-30**	**90-160**	**161-230**	**231-370**	**>370**	**M**
Lutjanus carponotatus	80	146	33	6	7		192
Cephalopholis cyanostigma	10	5	5	3	1	2	16
Plectropomus leopardus	7	8	5	2	1		16
Lutjanus quiquelineatus	10	6	5	3			14
Lethrinus nebulosus	10	2	8	1	2		13
Lethrinus atkinsoni	3	5	2	2			9
Lutjanus fulviflamma	8	2	2		2	2	8
Lethrinus semicinctus	4	2	2	1		1	6
Diagramma pictum	4	5					5
Lutjanus russelli	4	1	2			1	4
Epinephelus ongus	1				1	1	2
Lutjanus fulvus	1		1				1
Total		182	65	18	14	7	**286**

Table 4.6. Probability of movements within and between habitats for all combined species (a) and 10 individual species (b-k). M is total number of movements from a habitat. Probability of movement to a habitat was defined as the number of recaptures in that habitat over M. See Section 4.2 for codes of habitat. *χ^2-test significant.

a. All combined species

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	10	*0.90*			*0.10*		
DSNR	81	*0.01*	*0.62*	*0.01*		*0.01*	*0.32*
RUBB	5			*1.00*			
SLOP	109	*0.02*		*0.01*	*0.97*		
SSNR	32		*0.06*			*0.94*	
TOPS	49		*0.71**			*0.06*	*0.22*
Total	286						

b. *Lutjanus carponotatus*

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	1				*1.00*		
DSNR	54		*0.52*			*0.02*	*0.46*
RUBB	1			*1.00*			
SLOP	70	*0.03*			*0.97*		
SSNR	20		*0.10*			*0.90*	
TOPS	46		*0.70**			*0.07*	*0.24*
Total	192						

c. *Lethrinus nebulosus*

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	2	*1.00*					
DSNR	3	*0.33*	*0.67*				
RUBB	2			*1.00*			
SLOP	0						
SSNR	6					*1.00*	
TOPS	0						
Total	13						

Table 4.6. con't.

d. ***Plectropomus leopardus***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	0						
DSNR	7		*0.71*				*0.29*
RUBB	0						
SLOP	6			*0.17*	*0.83*		
SSNR	0						
TOPS	3		*1.00*				
Total	16						

e. ***Lutjanus fulviflamma***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	2	*1.00*					
DSNR	2		*0.50*				*0.50*
RUBB	0						
SLOP	2				*1.00*		
SSNR	2					*1.00*	
TOPS	0						
Total	8						

f. ***Lethrinus semicinctus***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	0						
DSNR	1			*1.00*			
RUBB	2			*1.00*			
SLOP	3				*1.00*		
SSNR	0						
TOPS	0						
Total	6						

g. ***Lutjanus quinquelineatus***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	1	*1.00*					
DSNR	11		*1.00*				
RUBB	0						
SLOP	1				*1.00*		
SSNR	1					*1.00*	
TOPS	0						
Total	14						

Table 4.6 con't.

h. ***Lutjanus russelli***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	1	*1.00*					
DSNR	1		*1.00*				
RUBB	0						
SLOP	0						
SSNR	2					*1.00*	
TOPS	0						
Total	4						

i. ***Diagramma pictum***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	3	*1.00*					
DSNR	2		*1.00*				
RUBB	0						
SLOP	0						
SSNR	0						
TOPS	0						
Total	5						

j. ***Cephalopholis cyanostigma***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	0						
DSNR	0						
RUBB	0						
SLOP	16				*1.00*		
SSNR	0						
TOPS	0						
Total	16						

k. ***Lethrinus atkinsoni***

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	0						
DSNR	0						
RUBB	0						
SLOP	9				*1.00*		
SSNR	0						
TOPS	0						
Total	9						

Table 4.7. Number of day (DT) and night time (NT) movements within and between habitats for all species (a) and *Lutjanus carponotatus* (b). M is number of movements. *χ^2 test significant. See Section 4.2 for codes of habitat.

a. All species combined

		TO:					
FROM:	**Time**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	**DT**	*1*			*1*		
	NT	*4*			*0*		
	Total M	**5**			**1**		
DSNR	**DT**		*7*	*1*		*0*	*11*
	NT		*23**	*0*		*1*	*14*
	Total M		**30**	**1**		**1**	**25**
RUBB	**DT**			*1*			
	NT			*2*			
	Total M			**3**			
SLOP	**DT**				*34*		
	NT				*54**		
	Total M				**88**		
SSNR	**DT**		*0*			*1*	
	NT		*1*			*5*	
	Total M		**1**			**6**	
TOPS	**DT**		*11*			*0*	*6*
	NT		*17*			*1*	*5*
	Total M		**28**			**1**	**11**

b. *Lutjanus carponotatus*

		TO:					
FROM:	**M**	***DSAR***	***DSNR***	***RUBB***	***SLOP***	***SSNR***	***TOPS***
DSAR	**DT**				*1*		
	NT				*0*		
	Total M				**1**		
DSNR	**DT**		*5*			*1*	*10*
	NT		*11*			*0*	*12*
	Total M		**16**			**1**	**25**
RUBB	**DT**			*0*			
	NT			*1*			
	Total M			**1**			
SLOP	**DT**				*27*		
	NT				*33*		
	Total M				**60**		
SSNR	**DT**		*0*			*0*	
	NT		*1*			*1*	
	Total M		**2**			**1**	
TOPS	**DT**		*11*			*0*	*6*
	NT		*15*			*1*	*5*
	Total M		**26**			**1**	**11**

Chapter 5: AGE, GROWTH AND MORTALITY OF *LUTJANUS FULVIFLAMMA* (Forsskål, 1775), *LETHRINUS HARAK* (Forsskål, 1775) AND *L. LENTJAN* (Lacèpéde, 1802)

5.1 INTRODUCTION

A precise and accurate method of age determination is important for an understanding of the status and dynamics of fish stocks (Beamish and McFarlane 1987). Age determination of fishes, though sometimes a difficult task, is an integral component of modern fishery science (Paul 1992). Estimates of growth and mortality rates require an ageing technique (or some proxy of age) that is reliable and accurate. These parameters of growth and mortality are key components in analytical models used to predict potential yields of stocks. Thus, reliable estimates of these parameters can form the basis of proper management and sustainable utilization of renewable fishery resources.

In the recent past, many studies have used length frequency modes (e.g. Foucher and Fournier 1982, contributions in Munro 1983a), scales (e.g. Barnes and Power 1984), vertebrae (e.g. Ferreira and Vooren 1991), whole otoliths (e.g. McPherson *et al.* 1988), sectioned otoliths (e.g. Ferreira and Russ 1992, 1994, Newman *et al.* 1996a, Choat and Axe 1996, Choat *et al.* 1996) and other calcified structures (Bagenal and Tesch 1978) to determine fish age. Of these, length frequency, scales and otoliths are the most commonly used. It is often suggested that it is difficult to determine the age of tropical reef fish (e.g. Munro 1983a). As recently as 1996, in a major review of coral reef fisheries (Polunin and Roberts 1996) it was stated that length frequency analysis was required to estimate important population parameters of reef fish since age determination was difficult or impossible (p. 364 of Polunin *et al.* 1996). However, length frequency analysis often tends to underestimate age due to the

'pile up' effect (i.e. multiple age classes in single length modes as the animals age) (Newman *et al.* 1996a and see also Beamish and McFarlane 1987) and is often inaccurate due to enormous variations in individual growth rates (Sainsbury 1980). Scales are unreliable for long-lived, slow growing species because annuli become generally indistinct near the margin after age of maturity (Beamish and Chilton 1977) and their deciduous nature means that many have to be examined from the one animal. In the case of whole otoliths, the problem of indistinct annuli on the margin can be overcome when they are sectioned and age is determined from the internal banding sequence of alternating translucent and opaque bands (e.g. Ferreira and Russ 1992, 1994, Newman *et al.* 1996a, Choat and Axe 1996, Choat *et al.* 1996). Boehlert (1985) demonstrated that otoliths continue growing on their internal surfaces even when fish approach asymptotic length. Otoliths are thus a superior structure for age determination. Recently, the use of otoliths in age determination of many species of reef fish has been demonstrated successfully in several species of reef fish (e.g. Fowler 1990b, Fowler and Doherty 1992, Ferreira and Russ 1992, 1994, Newman *et al.* 1996a, Choat and Axe 1996, Choat *et al.* 1996). The empirical data supporting the contention that tropical reef fish can have their ages determined are clearly increasing. Thus, the suggestion by Polunin *et al.* (1996) (p. 365) to use length frequency analysis rather than age-based techniques in stock assessment of tropical reef fish is questionable.

In this study the opaque bands in sectioned otoliths of three species of reef fish were validated and ages were determined based on counts of opaque marks in sectioned otoliths. These species were *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*. These are relatively small fish of commercial and recreational fishing significance on the Great Barrier Reef (GBR) and form part of the estimated 20-30% "by catch" of the line fisheries (Trainor 1991). To date there is no information on the age, longevity, growth and mortality of these fishes on the GBR. In the near future, the significance of these smaller lutjanids and lethrinids is likely to increase as the fishery expands, markets develop and fishing effort on major target species increases further (Williams and Russ 1994).

The black-spot snapper, *L. fulviflamma*, is probably the most widely distributed lutjanid on the GBR (Williams and Russ 1994) and considered by Talbot (1960) the

most widely distributed of all lutjanid species in east Africa. The distribution of *L. fulviflamma* includes the Indo-Pacific from Samoa to East Africa, and from Australia northward to the Ryukyu Islands (Allen 1985). It inhabits coral reefs at depths between 3-35 m and juveniles are sometimes found in brackish waters of mangrove estuaries or in lower reaches of freshwater streams (Allen 1985). They feed mainly on crustaceans and fishes (Allen 1985) and form large aggregations in shallow water on the seaward side of reef slopes.

The distribution of the thumb print emperor, *L. harak*, covers the Indian Ocean and western Pacific including the Red Sea, East Africa, Seychelles, Maldives, Sri Lanka, Andamans, Indonesia, the Philippines, southern Japan, northeast Australia, Papua New Guinea, the Caroline Islands, Solomons, Vanuatu, Fiji and Samoa (Carpenter and Allen 1989). On the GBR, the distribution of this species is unknown but has been noted to be extremely abundant at Orpheus and Green Islands (Williams and Russ 1994). It inhabits coastal waters usually associated with shallow sand, coral rubble, mangroves, lagoons, seagrass beds and coral reefs to depths of 50 m (Sato et al. 1984, Carpenter and Allen 1989). It feeds on polychaetes, crustaceans, molluscs, echinoderms and small fishes (Carpenter and Allen 1989). At Lizard Island, *L. harak* was common near rocky-out-crops close to the beach.

The pink-eared emperor, *L. lentjan*, is widely distributed in the Indo-West Pacific including the Red Sea, Arabian Gulf, East Africa to the Ryukus and Tonga (Carpenter and Allen 1989). In Australia, it is commonly found in north Queensland island reefs usually over sandy bottom areas, in deep lagoons and near coral reefs to depths of around 50 m (Williams and Russ 1994). The juveniles and small adults are commonly found in loose aggregations over seagrass beds, in mangrove swamps and in shallow sandy areas, while adults are generally solitary and found in deeper waters (Carpenter and Allen 1989). This species primarily feeds on crustaceans and molluscs but the diet may include echinoderms, polychaetes and fishes (Carpenter and Allen 1989).

The objectives of this study were:

1. To determine ages of fish of the three species using counts of opaque bands in sectioned otoliths and to validate the periodicity of formation of the opaque bands in the otoliths.

2. To determine the suitability of otolith weight as a predictor of age in these species.

3. To estimate growth and mortality rates of the three species based on the ageing technique above (1).

5.2 MATERIALS AND METHODS

5.2.1 Sample Collection

Samples were collected on each field trip to Lizard Island during late mornings and early afternoons of the 8-9 days of the intensive trapping program (see Chapter 3). Collections were made using traps, spear and hook and line in areas outside of the lagoon where studies of distribution and abundance (Chapter 3) and movement of fishes (Chapter 4) were being conducted. A total of 176 *Lutjanus fulviflamma*, 134 *Lethrinus harak* and 121 *L. lentjan* were collected over 30 months. All but 51 *L. lentjan* and 1 *L. fulviflamma* were from Lizard Island. These 52 fishes were taken from reefs off Townsville, Queensland (about 650 km south of Lizard Island) using hook and line (n=13) and traps (n=39). Hook and line samples came from recreational fishers. The trap samples came from research field collections conducted at John Brewer, Lodestone, Rib, Kelso, Cape Upstart and Cleveland Bay near Townsville, Queensland (provided by J. Higgs and S. Newman). All trap samples were collected from depths of 35-40 m, except those in Cleveland Bay.

All size ranges of fish were targeted during collection. Spear fishing provided the opportunity to target size ranges sampled poorly by trap and hook and line. Immediately after collection, fishes were placed in an ice box in the field and frozen in the laboratory. Fishes were thawed before fork length (FL) standard length (SL) and wet body weight (W) were measured. Lengths and weights were measured to the nearest mm using a standard fish measuring board and to the nearest 0.01 gram using an electronic top balance, respectively. Otoliths (sagittae) were carefully removed, cleaned and stored dry in labelled paper envelopes. Gonads were sexed macroscopically when possible, dissected out carefully, weighed (wet weight) and fixed in Formaldehyde-Acetic acid-Calcium Chloride (FAACC) (Winsor 1994) for later study (see Chapter 6). Guts were fixed in 10% sea water buffered formalin (SWF).

5.2.2 Age Validation Experiments

Two approaches were taken to validate the periodicity of annuli in the otoliths of the three species. The first was to release marked fishes in the wild (field validation) and the second involved holding fish in aquaria (validation in aquaria). In the first approach details of the field procedure for administering oxy-tetracycline and marking animals externally were described in Section 2.4.3-6. Validation in aquaria acted as an adjunct to field validation for *L. fulviflamma*, but was necessary for the other 2 species due to the low numbers of captures, releases in the wild and virtually no recaptures (Table 4.1).

A total of 127 fishes were injected with tetracycline: 82 *Lutjanus fulviflamma*, 31 *Lethrinus lentjan* and 14 *L. harak*. The large number of *L. fulviflamma* reflects the large number of captures in traps (Table 4.1). Nearly 75% of these were released in the wild. The other 2 species were rarely caught in traps, even when trapping effort was concentrated in their preferred habitats. For these two species, live animals were collected using hook and line. As wide a range of sizes of fish as possible were used for age validation.

Sixty-one *L. fulviflamma*, 8 *L. lentjan* and 1 *L. harak* were injected with oxy-tetracycline and released in the wild (attempted field validation). Of these, six *L. fulviflamma* were recaptured. None of *L. lentjan* or *L. harak* were recaptured.

The total number of specimens used in the validation in aquaria (including recaptures from the field) in 3 separate attempts was 57: 21 *L. fulviflamma*, 23 *L. lentjan* and 13 *L. harak*. In March 1995, 4 *L. fulviflamma*, 7 *L. lentjan* and 2 *L. harak* were injected with the appropriate dosage of oxytetracycline. These fishes were then placed individually in extra strong plastic bags with O_2-saturated sea water and packed in 2 110-liter ice chest containers. They were transported from Lizard Island to a 1000-liter fiberglass tank at the Sir George Fisher Centre at James Cook University, Townsville Queensland (a distance of approximately 650 kms). Despite the nearly 8 hours of travel, only one fish died. The aquarium was a closed system with a water turnover rate of 8-10 times a day. Artificial shelter was provided in the tank for fishes. Fishes were fed to satiation using a wide variety of food every other morning. Food consisted of deshelled prawns, pieces of pilchards, bivalves and other invertebrates. All leftover pieces of food were taken out of the water after a period of 2 hrs. The aquarium was cleaned and the water was treated with Myxazin® (a broad spectrum anti-bacterial and anti-fungal agent) regularly. This experiment lasted 59 days (late May 1995) after which all fish succumbed to a disease, possibly triggered by the onset of the cold season. In a similar experiment carried out at the Australian Institute of Marine Science in Townsville, a similar large and sudden mortality of fish in aquaria was noted at about the same time of the year (pers. com., M. Cappo).

In October 1995 a second experiment was conducted at the newly constructed open sea water system aquarium at the Lizard Island Research Station (LIRS). This involved 11 *L. fulviflamma*, 9 *L. lentjan* and 3 *L. harak*. Five of the *L. fulviflamma* were field recaptures. Of these, 2 were recaptured more than a year after initial tetracycline injection and the three other fish were recaptured a little over 4 months after injection. Two of the *L. lentjan* were left over from a small pilot study conducted in July 1995 to test if fish injected with tetracycline would survive in small (<600-liter) glass aquaria. Fishes were placed in 3 separate aquaria of different capacities. Twelve fishes (3 species mixed and >200 mm FL) were placed in a 1000 liter fiberglass tank.

Another 6 fishes (*L. fulviflamma* and *L. lentjan* 180<FL<200 mm) and a further 5 (*L. fulviflamma* and *L. lentjan* <180 mm FL) were placed, respectively, in a 600 and a 300-liter glass aquarium with the sides painted black. Care and feeding schedules were the same as those for the first experiment. Water flow rate was regulated to about 7-8 turnovers a day. All 12 fish in the largest tank, 4 in the 600-liter tank and 3 in the 300-liter tank died within the first 46 days. Most died within a week after a water pump failed, coinciding with a very hot day. Crowding and physical stress were the most likely factors responsible for the failure of the experiment. The 4 other fish survived for 4-8 months.

The third experiment was carried out in January 1996 and conducted at LIRS. This final attempt used 6 *L. fulviflamma*, 7 *L. lentjan* and 8 *L. harak*. One of the *L. fulviflamma* was a field recapture 7 months after tetracycline injection. Three *L. lentjan* survived for 14 months while the remainder lived for 3-10 months.

Otoliths and gonads of tetracyclined fishes were processed in the same manner as described above. The sagittae (otoliths) were wrapped and stored in aluminum foil to prevent light from degrading the tetracycline mark. Marked otoliths were examined under a fluorescence microscope in conjunction with transmitted light to simultaneously view fluorescent tetracycline bands and the annuli. Black and white photographs were taken of these specimens. In cases when the tetracycline mark was barely visible in the presence of both light sources, photographs of the same field for the same specimen, using exactly the same settings, were taken with each light source (fluorescent or plain transmitted) to enable the two images to be superimposed and to locate the position of the tetracycline mark relative to the nearest annulus. With transmitted light, annuli appeared as dark bands. In fluorescent light they appeared as white milky (opaque) bands.

5.2.3 Counts of Opaque Bands in Sectioned Otoliths

The age of fish was determined by counting checks or annuli (Wilson *et al.* 1987) in sectioned otoliths. Several recent studies have shown that age can be

underestimated using whole otoliths (see Campana 1984, Fujiwara and Hankin 1988 and Ferreira and Russ 1994). Otoliths were weighed to the nearest 0.001 gram on an electronic top balance before embedding in commercial epoxy resin. The epoxy resin was allowed to stand at room temperature for at least 24 hrs to harden. A transverse section 0.3-0.5 mm thick running through the core of the otolith was made using a low-speed diamond blade saw. Sections were mounted on glass slides with Crystal Bond 509 adhesive and polished with 1000-grade sand paper and 9 μm lapping film. Sections were examined on a black background under a dissecting stereomicroscope at x40 magnification using reflected light from a fiber-optic cold light source. Oil was used to enhance contrast of alternating dark and opaque bands, referred to as annuli (Wilson *et al.* 1987). Annuli were counted in the general area of the sulcus, starting from the nucleus to the proximal margin. When this was not possible (due to the quality of otolith preparation) counts were made on the dorsal or ventral side of the otolith depending upon where the annuli were more distinct. Ages were assigned to fish based on the number of annuli counted in otoliths.

Counting of annuli followed the procedure of Ferreira and Russ (1992). Briefly, two readers (Vincent V. Hilomen and Garry R. Russ) independently counted the annuli. Counts were accepted and used in the analysis when both agreed. When counts differed, the count was repeated independently, generally after a period of 2 weeks and was accepted when the two readers obtained the same count. When there was disagreement on the second count, differences in counts were discussed between readers and the count was accepted only when both readers reached agreement, otherwise the count in question was not included in the analysis. The precision of ring counts (age estimates) for each reader and for combined readers was assessed using the Index Average Percent Error (IAPE) of Beamish and Fournier (1981). In assessing precision of readings for fishes aged 0, there is a possibility that X_j (average age calculated for the *j*th fish) can be zero and renders equation 2, $1/R*\Sigma^{R}_{i=1}| X_{ij}-X_j| /X_j$ (where R is the number of times fish age was read, X_{ij} is the *i*th age determination of the *j*th fish), of Beamish and Fournier (1981) undefined. In cases when $X_j = 0$, the denominator for equation 2 was ignored. In addition, the differences in age estimates for younger fish contribute more to the estimated total-precision measure than do

similar errors for older fish (Anderson *et al.* 1992). In the presentation of estimates of average error for jth fishes (in Tables 5.1-5.3), the estimated error for the *j*th fish with age = 0 was not converted to a percentage.

5.2.4 Analysis of Data

Length-weight relationships were calculated using a power function,

$$W=a*FL^{b};$$

where W is the wet weight (g) of fish, FL is the fork length (mm), a is the multiplicative factor and b ($b > 1$) the exponent. When $b = 3$, weight growth is isometric and allometric when $b \neq 3$ (Pauly 1984). The relationship was determined and parameters 'a' and 'b' estimated using a non-linear least squares estimation procedure. All samples were used except those which were raised in aquaria (i.e fish in the age validation experiments).

The relationships of otolith weight to fish age, fish weight and fish length (fork length) were assessed. The first two relationships were best described by the linear equation,

$$y = mx + b,$$

where otolith weight was the independent variable (x) and fish age or fish weight were the dependent variables (y). The otolith weight to fish length relationship was best described by a power function,

$$y = a*x^{b};$$

where y was fork length (FL in mm), a is a multiplicative factor and b was the exponent ($0 < b < 1$). These relationships were determined using a non-linear, least squares estimation method.

Growth rates of the three species were estimated using the von Bertalanffy growth function (VBGF). Chen *et al.* (1992) have shown that the VBGF describes growth better than polynomial functions. The VBGF is defined as,

$$L_t = L_\infty * (1 - \exp^{-K*(t-t_0)});$$

where L_t is the length of fish at age t, L_∞ is the asymptotic length, K is the growth coefficient that determines the rate of growth towards L_∞, t is age and t_0 is the hypothetical age at which length is zero. The VBGF was fitted to length at age data for each species and for data from male and female samples of *L. fulviflamma* using a non-linear, least-squares estimation procedure. *Lethrinus harak* and *L. lentjan* exhibited a sexual pattern consistent with protogyny (see Chapter 6) and thus, estimating growth parameters for separate sexes was difficult due to the absence of males in the younger age classes.

Estimates of the instantaneous rate of total mortality (Z) were obtained from age frequency distributions of each species using the age-based catch-curve method described by Beverton and Holt (1957), Chapman and Robson (1960) and Ricker (1975). A catch curve for each species was derived by plotting the natural logarithm of the number of fish for each age (N_t) against their corresponding age (t), and Z was estimated from the descending slope, b. Survival rate (S) was calculated using $S = \exp^{-Z}$ (Ricker 1975).

In this study, fishing mortality (F) was considered zero because the site was a marine protected area (Davies 1995) close to the Lizard Island Research Station. Thus, estimates of total mortality rates (Z) were considered as measures of natural mortality rate (M) because Z = M (in Z = M+F) when F is zero.

The mortality rate (M) was calculated across three different age ranges for each species. The mortality estimate with the highest r^2 from among these three was compared with estimates of natural mortality (M) derived from three empirical regression equations used to estimate mortality. These were equations from Pauly (1980), Hoenig (1983) and Ralston (1987). The equation of Pauly (1980) was $\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T$, where L_∞ and K were VBGF

parameters, and T the mean annual water temperature (°C). For the northern GBR (14-16°S) T was 26.6°C (Lough 1994). Hoenig's (1983) equation for fish was ln Z = 1.46 - 1.01 ln t_{max}, where t_{max} was the maximum age in years. Ralston (1987) used the equation M = -0.0666 + 2.52 K, where K was the VBGF growth coefficient. All calculations were made using the software STATISTICA Release 5.0 (StatSoft, Inc. 1995).

5.3 RESULTS

5.3.1 Length and Weight Data

Length frequency distributions

The length frequency distribution of the *Lutjanus fulviflamma* sample was normally distributed (Fig. 5.1a, W=0.972, p>0.05) (Shapiro *et al.* 1968). The *Lethrinus harak* sample was skewed to the left (Fig. 5.1b) while the *L. lentjan* sample appeared bimodal (Fig. 5.1c). The preponderance of larger fish in the *L. harak* sample suggested a bias in sampling by spear, despite attempts to minimize this. The second peak in the size distribution for *L. lentjan* (at 290-300 mm) were mostly fish collected from deeper sites off Townsville.

Individuals of *L. fulviflamma* ranged from 96 to 289 mm, with more than half between 210 to 240 mm fork length (FL) (Fig. 5.1a). *Lethrinus harak* individuals ranged from 89 to 322 mm FL, with the size class 260-270 mm being the most numerous (Fig. 5.1b). *Lethrinus lentjan* individuals ranged between 104 to 337 mm FL. Unlike the other 2 species, a large proportion of the samples of *L. lentjan* were in the smaller size classes (170-180 to 210-220 mm) (Fig. 5.1c).

Length-weight relationships

Wet body weight (ungutted) was related strongly to fork length for all three species ($r^2 > 0.95$) (Fig. 5.2a-c). Values of the exponent *b* for all species were not significantly different from 3 (t-tests, all $p>0.05$, Pauly 1984). This indicated that weight growth for these species was isometric (i.e. weight growth proceeds in the same dimension as the cube of fork length).

5.3.2 Age Validation

After completion of the three experiments the total number of useful specimens was 10 *L. fulviflamma*, 8 *L. harak* and 15 *L. lentjan*. The other 11 *L. fulviflamma*, 5 *L. harak* and 8 *L. lentjan* were 3 years or older and the tetracycline marks in the sectioned otoliths were right at the otolith margins due to a post injection survival period of just 2-4 months. In one case, the tetracycline mark was not visible, perhaps due to an insufficient dosage of tetracycline. For specimens less than 3 years of age, a clear gap between the tetracycline mark and the otolith margin was visible, suggesting relatively fast otolith growth in young fish.

Lutjanus fulviflamma

The periodicity of the formation of annuli in the otoliths of *L. fulviflamma* was determined from 10 fishes ranging in age from 0 to 11 years (Fig. 5.3) and ranging in size from 161 to 254 mm FL. Three of these fishes, 428, 412 and 482, were at liberty post-treatment of oxy-tetracycline (OTC) for 12, 9 and 8 months, respectively, before they were recaptured and retained in aquaria until death. This brought the total period since OTC treatment to nearly 14 months for fishes 428 and 412 and almost 12 months for fish 482. The other 7 fishes were all kept in captivity post OTC injection. Three of these (483, 417 and 416) survived for six months while the rest (420, 485, 484 and 481) lived for 5 months only (Fig. 5.3).

The otoliths of the ten fishes above displayed a clear fluorescent band under UV light (Fig. 5.3). Fishes which lived for at least a year or more post OTC treatment,

had a clear fluorescent mark before the last annulus (fish 428 in Plates 5.1 and 5.2, and fish 482 in Plate 5.3) or sitting on the last complete annulus with another annulus forming close to the margin (fish 412 in Plate 5.4).

Fish 428, a 5 year old *L. fulviflamma*, had its OTC mark (bright glow in Plate 5.1b) just before (i.e. below) the fifth annulus (opaque band). This was determined from a comparison of the locations and positions of annuli in Plates 5.1a (dark bands in transmitted light) and 5.1b (milky white in fluorescent light). An enlargement of the same specimen presented in Plate 5.2 confirmed the position of the OTC mark to be before the fifth annulus. Note that the 5th annulus lay in line with a natural mark (a dark spot on the specimen, indicated by an arrow) which is distinct in Plates 5.2a and b. The OTC mark was clearly positioned below the natural mark which was located approximately at the center of the 5th annulus. In fact, the strong milky white appearance of the 5th annulus in Plate 5.2b could have been influenced by the glow of the OTC mark below it.

Similar observations were noted for fish 482, a 6 year old *L. fulviflamma* (Plate 5.3). In this specimen, the 6th annulus was visible as a faint thin dark line (Plate 5.3a). The distance between the 4th and the 5th annuli was roughly half the distance between the 5th annulus and the otolith margin suggesting that another annulus existed between the 5th annulus and the margin. Moreover, the image of the same specimen under fluorescent light in Plate 5.3b supports this. The OTC mark is clearly seen as a thin bright glow starting at the edge of the sulcus. This mark dissipated into a much wider, dull milky white line resembling the whitish color of an annulus. The thin bright glow (OTC mark) sits at the base of the dull milky white line, the 6th annulus.

In the case of fish 412, an 11+ year old *L. fulviflamma*, the OTC mark was on the 11th annulus, as indicated by a comparison of the positions and locations of annuli in transmitted (Plate 5.4a) and fluorescent light (Plate 5.4b). The distance between the 11th annulus and the margin was almost the same as the distance between any 2 consecutive annuli (i.e. width of translucent bands) from the 7th to the 11th annulus. Since the OTC mark was on the 11th annulus and the distance between the OTC mark and the margin represented a year's growth, then this implies that distances between

consecutive annuli were equivalent to a year's growth. More importantly, if the OTC mark administered a year earlier was on the 11th annulus, then another annulus should be expected after it. This other annulus (12th) is actually present, though incomplete (see arrow in Plate 5.4a).

For fishes which died less than a year after OTC treatment, no annulus was observed after the OTC marks despite a clear gap between the mark and the margin (Fig. 5.3). Evidence from all 10 fish thus support the contention that opaque (milky) bands in sectioned otoliths were laid down once a year (i.e. were annuli).

The time at which an annulus was laid down in otoliths of *L. fulviflamma* appeared to be late winter to late spring (August to December). Fishes that were treated with OTC in July (fish 482) or in October (fishes 412 and 428) and survived at least a year revealed one complete annulus after and close to the OTC mark (Fig. 5.3) suggesting that the opaque band was laid down after July. In fact the OTC mark of fish 412, which was administered in October, sat on the 11th annulus itself (Plate 5.4 and Fig. 5.3).

Thus, the formation of opaque bands (annuli) in sectioned otoliths of *L. fulviflamma* appeared to be during August to December. This is supported further by the positions of OTC marks in fishes that died less than a year after OTC treatment. Those which were marked in January had their fluorescent marks right after or very close to the last annulus (fishes 485, 484 and 483 aged 6, 4 and 2 years old, respectively; Fig. 5.3) indicating that the opaque band was just recently completed. Those treated in July had their OTC mark a clear wide gap after the last annulus (fishes 420, 417 and 416 aged 8, 2 and 1 years old, respectively; Fig. 5.3) suggesting formation of an opaque band some months before. The location of the OTC mark in fish 481 (0+ yr old marked in January) suggested that no opaque band was formed between January and May (Fig. 5.3). All evidence from these fishes was consistent with the suggestion that opaque bands are formed during late winter to late spring (August to December) for *L. fulviflamma*.

Lethrinus harak

The periodicity of annulus formation in otoliths of *L. harak* was determined from 8 fishes ranging in age from 1-12 years (Fig. 5.4) and ranging in size from 184 to 287 mm FL. None of these survived more than 5 months in aquaria. Four fishes (488, 489, 487 and 491 in Fig. 5.4) survived for a little over 4 months. The rest survived between 2 and 3 months.

All sectioned otoliths of the eight fishes displayed clear OTC marks located after or above the last annulus (Fig. 5.4). All OTC marks were located relatively close to the otolith margin due to the short period of survival after OTC injection (Fig. 5.4). Older fish surviving less than 3 months had the OTC mark very close to the otolith margin (e.g. fish 172; Fig. 5.4). In fish surviving a little over 4 months (fish 488, 489, 487 and 491), the location of the OTC mark was well below (i.e. before) the otolith margin (Fig. 5.4). A clear gap between the OTC mark and the otolith margin was obvious under higher magnification. Typical examples of these are presented in Plate 5.5. The OTC mark (bright glow) in the otoliths of fish 488 (Plate 5.5a; an 8 year old) and fish 487 (Plate 5.5b; a 4 year old) was well above the 8th and 4th annulus (milky white band), respectively, and below the otolith margin. The distance between the OTC mark and the otolith margin in fish 488 and 487 represented otolith growth of 4 months (Plate 5.5). This distance was approximately a third of the distance between the 8th and the 7th opaque bands in fish 488 (Plate 5.5a) and between the 4th and 3rd bands in fish 487 (Plate 5.5b). Given that the growth of the otolith in 4 months corresponded roughly to a third of the distance between 2 consecutive opaque bands, it suggests that the distance between the consecutive opaque bands (annuli) represented a year's otolith growth. This suggests that each opaque band was formed once each year for *L. harak*.

The time of annulus formation in otoliths of *L. harak* appeared to be before January and probably well after July. Fishes given OTC treatment in January (fish 488, 489, 490, 487, 486 and 491 in Fig. 5.4) had OTC marks well after the last complete annulus (i.e. OTC mark sits on the translucent band before the otolith margin). The same was true in the otoliths of fishes which were injected in March (fish 172 and 170

in Fig. 5.4). Otoliths of fishes which died in May (172, 488, 489, 487, 491 and 170) had no opaque band after the OTC mark nor close to the otolith margin. Assuming otolith growth to be constant (see Boehlert 1985), back calculating the distance representing 4 months growth (above) places the formation of opaque bands in otoliths of *L. harak* around winter to late spring (i.e. August-December). Note that the distance between any two consecutive annuli after the third annulus appeared to be uniform (see Plate 5.8). Evidence from these 8 fish was consistent with the contention that opaque bands in the otoliths were annuli laid down during winter to late spring for *L. harak.*

Lethrinus lentjan

The determination of annulus formation in the otoliths of *L. lentjan* was based on 15 fishes ranging in age between 0 and 1 year and ranging in length from 160 to 254 mm FL. Three fish (497, 496 and 495) survived for 14 months after tetracycline injection, one fish (494) for 9 months, two fish (325 and 396) for 8 months and the rest from 1-6 months (Fig. 5.5).

Otoliths of each of these 15 fish displayed a clear OTC mark (Fig. 5.5). An example is shown in Plate 5.6. Otoliths of fish surviving more than a year after OTC treatment showed an annulus after the OTC mark (497, 496 and 495 in Fig. 5.5) indicating they were 0+ year old when captured and injected. The first opaque band of these 3 fishes appeared scattered and relatively wide. In many *L. lentjan*, the first annulus appeared as a scattered, wide milky band towards the lateral edge of a sectioned otolith (compare first annulus with other annuli in the sectioned otolith of older fish; Plate 5.9). A distinct opaque band formed after the OTC mark in the otolith of fish 325 in Plate 5.6. Fish 325 was captured and injected in July 1995 and survived for 8 months. The location of the first annulus (line of arrows) was clearly above the OTC mark and well below the otolith margin (Plate 5.6). Thus, annuli appeared to be laid down once a year in the otoliths of *L. lentjan.*

The period of annulus formation in the otoliths of *L. lentjan* appeared to be during late winter to late spring (August to December). This period was determined from the position of the OTC mark relative to the nearest annulus in the otolith and relative to the otolith margin. Otoliths of fishes captured and marked at age 1+ year

old in January (480 and 479) or March (169 and 168) and which survived no longer than 6 months (i.e. not later than July) showed no annulus after the OTC mark (Fig. 5.5). This suggested that their first annulus were formed well before January. Otoliths of fish aged 0+ year old when captured, marked in January and which survived until August (493) or October (494) showed no annulus after the OTC mark (Fig. 5.5). Similarly, otoliths of 0+ year old fish marked in March, which lived for two months (167, 165, 166), showed no annulus after the OTC mark (Fig. 5.5). The otolith of fish 247, a 0+ year old when marked in July 1995 and which survived until a month later, showed the same pattern (Fig. 5.5). In the case of fish 325 and 396, both were captured and marked when they were 0+ year old in July. Both survived until March the following year (8 months) and their otoliths showed an annulus formed some distance after (i.e. above) the OTC mark (Fig. 5.5 and Plate 5.6). This suggested that annuli were laid down after July. Similarly, otoliths of fish marked in January which survived until March the following year (497, 496 and 495) showed an annulus a fair distance after the OTC mark and nearer to the margin (Fig. 5.5). This supports the suggestion that annuli formed after July and before January. Evidence from all 15 fish was consistent with the contention that an opaque band (i.e. annulus) was laid during late winter to late spring (August to December) for *L. lentjan*.

5.3.3 Age Estimation

The sectioned otoliths of the 3 study species showed a pattern of alternating translucent and opaque zones (annulus) for fish greater than 0+ years of age (Plates 5.7-5.9). The recognition of the first annulus was always critical to correct age determination. The first annulus formed a fair distance from the nucleus (Plates 5.7a-c, 5.8a-c and 5.9a-c). The distance between the first and second annulus was greater than the distance between the second and third annulus (Plates 5.7a-c, 5.8a-c and 5.9a-c). Beyond the third annulus, the distances between any two consecutive annuli was fairly uniform and much smaller than the distance between the first and the second, and between the second and third annuli (Plates 5.7a, 5.8a and 5.9a).

Age estimates for *L. fulviflamma* showed a high percentage agreement between readers as well as a high precision (low IAPE) of counts. Both readers agreed 84% of the time. The total-error in precision was only 1.31% (Table 5.1). Agreement in readings across all age groups was high, ranging between 70-100%. Percentage agreement in all age groups was >80% except in age groups 10 and 13 where agreement fell to 70 and 75%, respectively, possibly related to small sample sizes (Table 5.1). All disagreements in the readings, except for one, deviated by only ± 1. The total reading precision error was small, as indicated by a low IAPE (Table 5.1). The perceived higher precision of readings for younger than for older fish (Table 5.1) was likely a property of the precision measure used (see Anderson *et al.* 1992).

For *L. harak*, the agreement between readers was 1.22 times lower than the agreement rate in *L. fulviflamma*. Counts for *L. harak* between the two readers agreed 69% of the time (Table 5.2). The majority of the disagreements in counts deviated by ± 1 (nearly 26%), close to 5% by ± 2 and less than 1% by ± 3 (Table 5.2). Agreement in readings across all age groups was reasonably high (>60%) except for age groups 2 and 4 (both over 55%). The total reading precision error was slightly higher than that in *L. fulviflamma* with an IAPE of 1.8% (Table 5.2).

The agreement between readers in counts of annuli for *L. lentjan* was slightly higher than that for *L. harak*. Counts agreed nearly 72% of the time (Table 5.3) but the range of percentage agreement between age groups varied widely compared with the two other species. Percentage agreement was less than 60% in five age groups (4, 6, 7, 9 and 11) compared with only two age groups for *L. harak* and none for *L. fulviflamma*. This was likely due to the small sample sizes for many age classes. The total reading precision error was highest for *L. lentjan* among the three species at 2.27% (Table 5.3).

The age structures of the samples for the three study species are shown in Figure 5.6. Data for these age structures were derived from the same samples used in Figure 5.1. All age structures differed significantly from normal distributions ($p<0.000$ for all species) and were dominated by 2 or 3 age classes. For example, the *L. fulviflamma* sample was dominated by age classes 1 and 8 (Fig. 5.6a) while age classes

1, 2 and 8 dominated the *L. harak* sample (Fig. 5.6b). In the case of *L. lentjan*, the age structure was strongly skewed to the right, with a preponderance of samples in age classes 0 and 1 (Fig. 5.6c).

The youngest fish for all three species was aged 0+ year while the oldest fish varied with species. It was 17 years for *L. fulviflamma*, 15 for *L. harak* and 14 for *L. lentjan* (Fig. 5.6). The average ages of the *L. fulviflamma*, *L. harak* and *L. lentjan* samples were 5.45, 4.61 and 2.46 years, respectively (Fig. 5.6a-c). These represent average ages of samples from Lizard Island for the former 2 species. The lower average age for *L. lentjan* was likely to be an artefact of sampling. The majority of *L. lentjan* collected from Lizard Island were 0-1 year old (Fig. 5.6c). Many of the older (>2 years of age) and larger (> 250 mm FL) individuals of *L. lentjan* were caught from deeper reefs off Townsville, Queensland by line fishing. This suggests that individuals of this species may shift their distribution to deeper water as they get older.

Relationship of otolith weight to age, fish weight and fish length

Otolith weight was a good predictor of age, fish weight and fish length for the three species (Figs. 5.7, 5.8 and 5.9, respectively). The first two relationships were linear while the third was a power function. Otolith weight was highly correlated with age, accounting more than 87% of the variability in age for the three species (Figs. 5.7a-c). The rate of weight gain of the otolith with age was 4 times higher in *L. lentjan* and three times higher in *L. harak* than in *L. fulviflamma*. This demonstrates that otoliths of *L. lentjan* were bigger than otoliths of *L. harak* and *L. fulviflamma* for a given age.

Similarly, otolith weight explained greater than 80% of the variability in fish weight in all three species (Fig. 5.8a-c). The rate of weight gain of the otolith with fish weight was nearly 1.5 times higher in *L. lentjan* than in *L. fulviflamma*. It was 0.75 times higher in *L. harak* than in *L. fulviflamma*.

Otolith weight predicted fork length (FL) by a power function. Greater than 86% of the variability in FL was explained by otolith weight in all 3 species (Fig.5.9a-c). Initially both variables increased very rapidly until about FL = 200 mm for *L.*

fulviflamma (Fig. 5.9a) and *L. lentjan* (Fig. 5.9c) and FL = 250 mm for *L. harak* (Fig. 5.9b) before slowing down to almost a linear positive slope. Based on the trajectory of the line, otoliths seem to add on weight even when FL changed little at larger sizes.

5.3.4 Growth Models

von Bertalanffy Growth Function (VBGF)

The length at age data for the three study species fitted the VBGF reasonably well (r^2 was 0.751, 0.745 and 0.835 for *L. fulviflamma* (both sexes combined), *L. harak* and *L. lentjan*, respectively) (Fig. 5.10a-c and Table 5.4). Growth during the first 2 years in all three species was very rapid before slowing down over the next 2 years, resulting in an extended period of little change in size (FL). *Lutjanus fulviflamma*, *L. harak* and *L. lentjan* reached 81, 80 and 76% of their respective L_∞ in the first two years and almost 90% of their L_∞ after the fourth year. Observed maximum ages for samples of *L. fulviflamma*, *L. harak* and *L. lentjan* were 17, 15 and 14 years, respectively (Tables 5.1-3).

The growth of male *L. fulviflamma* was described by the von Bertalanffy Growth Function $L_t = 240.435 * (1 - \exp^{-0.230 * (t + 5.670)})$ (Fig. 5.10a). The growth of female *L. fulviflamma* was similar, but they reached a larger size than the males and was described by $L_t = 253.262 * (1 - \exp^{-0.236 * (t + 4.698)})$ (Fig. 5.10a). The growth of *L. fulviflamma* for both sexes combined was $L_t = 246.310 * (1 - \exp^{-0.261 * (t + 4.377)})$ (Fig. 5.10a). The growth models for *L. harak* and *L. lentjan* were $L_t = 284.994 * (1 - \exp^{-0.313 * (t + 3.159)})$ (Fig. 5.10b) and $L_t = 307.200 * (1 - \exp^{-0.345 * (t + 2.202)})$ (Fig. 5.10c), respectively. Amongst the three species, L_∞ was 1.25 times higher in *L. lentjan* and 1.16 times higher in *L. harak* than in *L. fulviflamma* (Table 5.4). The K for *L. lentjan* was 1.1-1.3 times higher than the K of the other two species (Table 5.4). The K for *L. harak* and *L. fulviflamma* differed little (Table 5.4). This suggested that individuals of *L. lentjan* were the largest and reached L_∞ fastest amongst the three species.

5.3.4 Mortality Rates

Instantaneous rates of mortality (M) tended to increase with the inclusion of a more restricted age range for the catch curve regression (Fig. 5.11-13). The best estimates of M (as indicated by the highest r^2 values) were from more restricted age ranges. For example, in *L. fulviflamma*, M was 0.166 (± 0.035) from 1-15 years old (r^2 = 0.636) (Fig. 5.11a). This increased to 0.194 (± 0.033) for ages ranging from 4-14 years (r^2 = 0.791) (Fig. 5.11b) and to 0.231 (± 0.035) for 4-15 years old (r^2 = 0.813) (Fig. 5.11c). Similarly for *L. harak*, M was 0.210 (± 0.053) for 1-13 years old (r^2 = 0.587) (Fig. 5.12a), 0.239 (± 0.080) for 4-13 years of age (r^2 = 0.525) (Fig. 5.12b) and 0.381 (± 0.097) for ages 6-13 years (r^2 = 0.719) (Fig. 5.12c). For *L. lentjan*, M was 0.128 (± 0.050) for 1-14 years old (r^2 = 0.358) (Fig. 5.13a), 0.184 (± 0.089) for 8-14 years of age (r^2 = 0.457) (Fig. 5.13b) and 0.305 (± 0.078) for 9-14 years old (r^2 = 0.792) (Fig. 5.13c).

The best estimates of natural mortality rate for populations of *L. fulviflamma*, *L. harak* and *L. lentjan* at Lizard Island, GBR were 0.231 (± 0.035), 0.381 (± 0.097) and 0.305 (± 0.078) for age ranges 4-15, 6-13 and 9-14 years, respectively. These exponential rates of mortality correspond to survivorship rates of 79.4, 68.3 and 73.7% for *L. fulviflamma*, *L. harak* and *L. lentjan*, respectively (Table 5.5). The Hoenig (1980) formula predicted values of M for *L. fulviflamma* and *L. lentjan* very close to the estimates of the present study (Table 5.5). This estimate of M was 0.065 times higher for *L. fulviflamma* and only 0.017 times lower for *L. lentjan* but 1.37 times lower for *L. harak* than estimates of this study (Table 5.5). These estimates of M for all species except *L. harak* fall within the S.E. range of the estimates of the present study. In contrast, the estimates of mortality rates in this study were much lower than predictions from the empirical formula of Pauly (1980) for *L. fulviflamma* and *L. lentjan*. The Pauly formula's estimate was 1.74 and 1.50 times higher (and were outside the S.E. range) than the estimates of M obtained in the present study for *L. fulviflamma* and *L. lentjan*, respectively (Table 5.5). This estimate of M for *L. harak* fell within the S.E. range of the estimate of the present study. The Ralston formula's

estimate of M for *L. fulviflamma* was 2.52 times higher than that obtained in the present study and was outside the S.E. range (Table 5.5). This equation was valid only for lutjanids and groupers.

5.4 DISCUSSION

5.4.1 Analysis and Interpretation of Otoliths

This study provides estimates of growth and mortality rates based on age-validated counts of annuli in sectioned otoliths of *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*. The combination of field (mark-recapture) and aquarium techniques confirmed opaque bands in sectioned otoliths of these species were annuli laid down in late winter to late spring (August to December). The results were robust since the validation involved a wide range of ages and sizes of fish. Even in cases where fish did not survive more than a year after OTC injection (e.g. *L. harak*), the amount of otolith growth during a known period (represented by the distance between the OTC mark and the otolith margin) was roughly equivalent to the appropriate fraction of a year's growth relative to the distance between consecutive opaque bands. More importantly, the locations of the OTC mark in sectioned otoliths were consistent with the contention that the opaque bands were annuli. These observations are further supported by similar validation studies on 31 species, most of which are reef fishes. Opaque bands in sectioned otoliths have been validated to be annuli in *Anoplopoma fimbria* (Beamish *et al.* 1983); *Plectropomus maculatus* (Ferreira and Russ 1992); *Pomacentrus moluccensis* and *P. wardi* (Fowler 1990b, Fowler and Doherty 1992); *Pagrus auratus* (Francis *et al.* 1992, Ferrell *et al.* 1992); *Scarus schlegeli* (Lou 1992b); *Plectropomus leopardus* (Ferreira and Russ 1994); *Lutjanus carponotatus* (Davies 1995); *Epinephelus malabaricus, E. coioides*, *Lutjanus argentimaculatus* and *L. russelli* (Sheaves 1995); *Lutjanus adetii* and *L. quinquelineatus* (Newman *et al.* 1996a); *Acanthurus lineatus*, *A. olivaceus*, *Ctenochaetus striatus* and *Zebrasoma*

scopas (Choat and Axe 1996), *Chlorurus sordidus*, *Scarus frenatus*, *S. niger* and *S. rivulatus* (Choat *et al.* 1996), and *Lutjanus sebae*, *L. erythropterus* and *L. malabaricus*, *L. johnii*, *L. argentimaculatus*, *L. carponotatus*, *L. vitta*, *L. rivulatus*, *L. bohar*, *L. gibbus* and *L. monostigma* (Cappo *et al.* in prep.). This evidence strengthens the contention that the opaque bands in sectioned otoliths observed in this study are annuli. The validation and the high precision and agreement in counting of opaque bands make sectioned otoliths a highly reliable method for age determination of *Lutjanus* and *Lethrinus* species.

Similar studies in places closer to the equator have shown consistent results. Mamauag (1997) found opaque bands in sectioned otoliths of *Plectropomus leopardus* in Palawan, Philippines were reasonably discernable and annuli. Age determination studies on *Nemipterus* spp. in Kavieng, Papua New Guinea by M. Chapau also indicated that opaque bands in sectioned otoliths were discernable and laid once a year (G. Russ, pers. com.). This plethora of evidence strongly indicates that counts of opaque bands in sectioned otoliths are reliable techniques for age determination of reef fish in the tropics.

Fowler and Doherty (1992) set three criteria for otoliths to be a good age determination tool. These were: *i*) they must display an internal structure of increments, *ii*) this structure must be relatable to a regular time scale and *iii*) the otoliths must grow through out the lives of the fish at a perceptible rate. Sections of the otoliths from the three species displayed a sequence of distinct alternating opaque and translucent zones (Plates 5.7-5.9). These zones were interpretable, fulfilling the first criterion.

The periodicity of formation of opaque bands was demonstrated to be annual by the validation study, implying that the distance between any two consecutive opaque bands represented otolith growth in one year. This evidence showed that the sequence of alternating opaque and translucent zones in sectioned otoliths of the three species can be related to a regular time scale, thus satisfying the second criterion.

The decreasing distances between consecutive opaque bands from the first to the fourth annulus reflected a rapidly decreasing otolith growth rate during the first 4

years. The generally uniform distance between consecutive opaque bands after the fourth band indicated a slow, constant otolith growth after the fourth year. This growth of the otolith appears to mirror the somatic growth of fish, but displays continuous addition of crystals on the internal surface of the sagitta (otolith) as the fish ages (Boehlert 1985). The trajectories of plots of otolith weight and FL (Fig. 5.9) and otolith weight and fish age (Fig. 5.7) support the contention that otoliths grow throughout the life of fish despite an asymptotic growth curve in length. This satisfies the third criterion set by Fowler and Doherty (1992). This property of otoliths makes them a superior recorder of age in fishes.

The prevailing perception in the early to mid 1980's was that it was not easily possible to determine ages of tropical reef fishes because hard structures (e.g. otoliths) of these fish did not contain annuli that could be easily interpreted to provide estimates of age. The large numbers of studies in the 1990's (above) provided empirical data to show that this perception was wrong. Age determination studies have provided unequivocal evidence that many reef fish live longer, have square growth curves and have lower natural mortality rates (see below) than previously assumed. The present study has produced results consistent with this.

The opaque bands in the otoliths of the three species appeared to be formed during late winter to late spring (August to December), coinciding with low water temperature. This period is consistent with that of the formation of opaque bands in the otoliths of other species on the GBR. Doherty and Fowler (1992) found that opaque bands in otoliths of *Pomacentrus moluccensis* and *P. wardi* formed during September to December. Similarly, Ferreira and Russ (1992) and Ferreira and Russ (1994) observed that annuli in otoliths of *Plectropomus maculatus* and *P. leopardus*, respectively, formed in August to September. The opaque bands in otoliths of four species of acanthurid (Choat and Axe 1996) and of four species of scarid (Choat *et al.* 1996) were laid down in the early austral summer (about November to December). Newman *et al.* (1996a) showed that the opaque bands in otoliths of *Lutjanus adetii* and *L. quinquelineatus* were laid down during June to August. Loubens (1978) suggested that the appearance of annuli was correlated with a change in water temperature. Ferrell *et al.* (1992) reported that otolith growth in *Pagrus auratus* was least in winter

and greatest in spring and summer. Ralston and Williams (1989) attributed the formation of annual marks in otoliths of a deep-water lutjanids to the seasonal temperature minimum. Other studies however, have attributed formation of opaque bands to reproductive activity and condition of fish (e.g. McPherson *et al.* 1988). This seems unlikely to apply in this study as opaque bands were present in otoliths of individuals that have not previously spawned (see Chapter 6; also McPherson and Squire 1992). Newman *et al.* (1996a) however, suggested that the cues for annulus formation may be correlated with other factors that initiate spawning cycles in mature individuals.

Otolith weight was found to be a good predictor of fish age for the three species in this study. This was consistent with the findings of Worthington *et al.* (1994) for *Pomacentrus moluccensis* and *P. wardi*, and with the results of Newman *et al.* (1996a) for *Lutjanus adetii* and *L. quinquelineatus*. A strong correlation between otolith weight and fish age was demonstrated for these species. The advantage of otolith weight over otolith length or width is the continued deposition of aragonite crystals on the internal surface of the otolith (Boehlert 1985), thus the increase in weight as the fish ages. This may also explain the strong linear relationship of otolith weight to fish weight and the power relationship of otolith weight to fish length (FL) found in this study.

The demonstration of a strong correlation between otolith weight and fish age in a number of species (e.g. *Sebastes pinniger* and *S. diploproa* in Boehlert 1985, *Sardinops sagax neopilchardus* in Fletcher 1993, *P. moluccensis* and *P. wardi* in Worthington *et al.* 1994, *L. adetii* and *L. quinquelineatus* in Newman *et al.* 1996a, and *L. fulviflamma*, *L. harak* and *L. lentjan* in this study) provides a potential technique for a rapid assessment of age, growth and mortality estimates of fishes, in contrast to the more involved process of sectioning and reading otoliths (see also Pawson 1990, Worthington *et al.* 1994, 1995).

Assuming that most age classes were sampled equally well in this study, and that post-settlement mortality rates were relatively stable, the age structures of samples showed some suggestion of previous years of good recruitment of the three species at

Lizard Island. For example, the dominance of age classes 1 and 8 for *L. fulviflamma* suggested events of good recruitment at Lizard Island one and eight years before the sampling (i.e. in 1994 and 1987). A similar observation suggests good recruitment of *L. harak* in 1994, 1993 and 1987. For *L. lentjan*, good recruitment appeared to occur in 1995 and 1994. The pattern of recruitment of the three species in the lagoon was not constant from year to year but showed distinct interannual fluctuation. Ferreira and Russ (1995) demonstrated a similar phenomenon for populations of *Plectropomus leopardus* on four reefs of the GBR. Although the sample sizes were relatively small, this present study suggests a useful method for monitoring strengths of year classes important in the management of fishery resources. One of the strongest advantages of determining the age of fish is that strong cohorts can be detected in the population age structure and followed over time if yearly sampling is conducted (Russ *et al.* 1996). This is one of the fundamental reasons why Russ *et al.* (1996) strongly advocate the use of reliable age determination techniques in fisheries research over other methods which are unlikely to detect and track strong cohorts in fish populations (e.g. length frequency analysis). Representative age structures give managers a clear picture of the age status of stocks. Knowledge of the strength of recruitment to a fishery detected early on in age structures may give management ample time to plan strategies to avert fishery failures and possibly sustain yields.

5.4.2 Growth Models

The growth rates of *L. fulviflamma*, *L. harak* and *L. lentjan* were similar although they attained their L_∞ at slightly different rates. With potential maximum longevities exceeding 10 years, the growth of the three species is considered slow. However, the initial 2 years of growth of the three species was very rapid. More than 76% of their maximum lengths were attained in the first 2 years. After this period, growth declined and length virtually ceased to increase (i.e. they approached asymptotic length) at about 6-7 years for *L. fulviflamma* and *L. harak* and at about 5-6 years for *L. lentjan*. Newman *et al.* (1996a) reported that *Lutjanus adetii* and *L. quinquelineatus* approached their asymptotic lengths at around 5 years (but could live

to 35 years) while Matthews and Samuel (1985) showed that *L. malabaricus* approached asymptotic length at around 7-8 years (and could live at least 15-20 years). Manooch (1987) reviewed growth of lutjanids and concluded that these fish are long lived and slow growing.

The females of *L. fulviflamma* were slightly larger than males in the older age classes. This is consistent with the findings of Grimes (1987) who reported that, in general, female lutjanids tended to be more prevalent than males in the larger size classes. This finding is at variance with those of McPherson and Squire (1992) for *L. sebae* and *L. malabaricus*, Newman et al. (1996a) for *L. adetii* and *L. quinquelineatus*, and Davis and West (1992) for *L. vittus*.

The large variation in length for a given age and the reduced growth in length after the fourth year for the three species indicated that length was a poor predictor of age. The length of a young fish (e.g. 2-3 years old) may be the same as the length of a very old fish (e.g. a 10 year old) (Fig. 5.10). Thus, age determination by length frequency analysis will be unreliable, since the lengths of younger and older fish overlap substantially (see also Beamish and McFarlane 1987). When this happens the assumption that modal progressions in length distributions represent progressions of year classes is likely to be invalid.

Estimates of growth parameters vary with the different methods used to estimate them. The estimates of K for *L. harak* from length frequency analysis in Fiji (Dalzell *et al.* 1989) were higher than estimates from sectioned otoliths in this study (Table 5.6). Estimates of L_∞ and K for *L. fulviflamma* were similar to those of Loubens (1980b) in New Caledonia who used whole and cracked otoliths (Table 5.6). Furthermore, the estimates of growth parameters (L_∞ and K) for *L. lentjan* from sectioned otoliths in this study and in the New Caledonia study (Loubens 1980b) were similar (Table 5.6). Estimates of K using scales for *L. lentjan* in India (Toor 1964b) differed substantially with those from the Gulf of Aden (Aldonov and Druzhinin 1979) (Table 5.6). Toor (1964b) used scales and appeared to underestimate the maximum age of *L. lentjan* in India substantially (Table 5.6). In a study of the lingcod, *Ophiodon elongatus*, Beamish and Chilton (1977) found that use of scales underestimated the age

of older fish by as much as half. Similarly, Newman *et al.* (1996a) found length frequency analysis underestimated actual age of two lutjanid species because there was a lack of clear length modes in the length distribution. When age is underestimated, growth rate, mortality rate and production are overestimated. This study demonstrates that *L. fulviflamma*, *L. harak* and *L. lentjan* are slow growing but with an initial phase of rapid growth and with longevities well in excess of 10 years.

5.4.3 Mortality rates

The estimates of instantaneous rates of natural mortality (M) in this study were generally lower than the estimates from the Pauly (1980) formula for all three species and from the Ralston (1987) formula for *L. fulviflamma*. When Pauly's (1980) empirical formula was used to derive M in other studies (e.g. Loubens 1980b, Dalzell *et al.* 1989, Toor 1964b, Carpenter and Allen 1989), they were also substantially higher than those obtained in the present study (Table 5.6). Agger *et al.* (1973) have shown that when M is overestimated, fishing mortality (F) is generally underestimated, leading to overestimates of potential yield of fish stocks. This could lead to overexploitation and serious consequences for the fisheries. The application of the Pauly (1980) and Ralston (1987) empirical formulae for estimating M should be used with caution. Newman *et al.* (1996a) reached a similar conclusion in a study of mortality rates of *L. adetii* and *L. quinquelineatus*. In contrast, Hoenig's (1983) equation predicted values very close to estimates of M for *L. fulviflamma* and *L. lentjan* obtained in this study, but provided a more conservative estimate for *L. harak* than in the present study. Hoenig's (1983) equation appears to be a good first approximation of M for lutjanids and lethrinids in unfished areas, and probably also for other species.

The estimates of M for the three study species may not be representative of populations GBR-wide. The small sample sizes and the bias of the samples towards young fish in the Lizard Island lagoon limit the general applicability of the results. The lower estimates of M for other lutjanid species in deeper waters of the GBR (e.g. 0.235 and 0.154 for *Lutjanus adetii* and *L. quinquelineatus*, respectively, in Newman *et al.*

1996a) may indicate a lack of large and old fish in samples in the present study. There is circumstantial evidence that fish move to deeper water as they age. Carpenter and Allen (1989) record that adults of *L. lentjan* are generally solitary and found in deeper waters.

This study has demonstrated that counts of opaque bands in sectioned otoliths are a highly reliable and accurate technique of age determination (high precision and low IAPE). Age structures are very important tools in fisheries science and should be made a routine component of the assessment and management of reef fisheries. Growth and mortality rates are estimated more reliably from age-based techniques. The present study has described growth and mortality characteristics of *L. fulviflamma*, *L. harak* and *L. lentjan* by such methods. Information gained from this study has important implications to the management of the reef line fishery on the GBR. These species are slow growing, long lived and have low natural mortality rates despite their relatively small size. These life history characteristics suggest slow accumulation of biomass, making these species highly vulnerable to over-exploitation. Ages and sizes at first reproduction and, where applicable, sex change are also important life history characteristics. These are estimated for the three study species in the next chapter of this thesis.

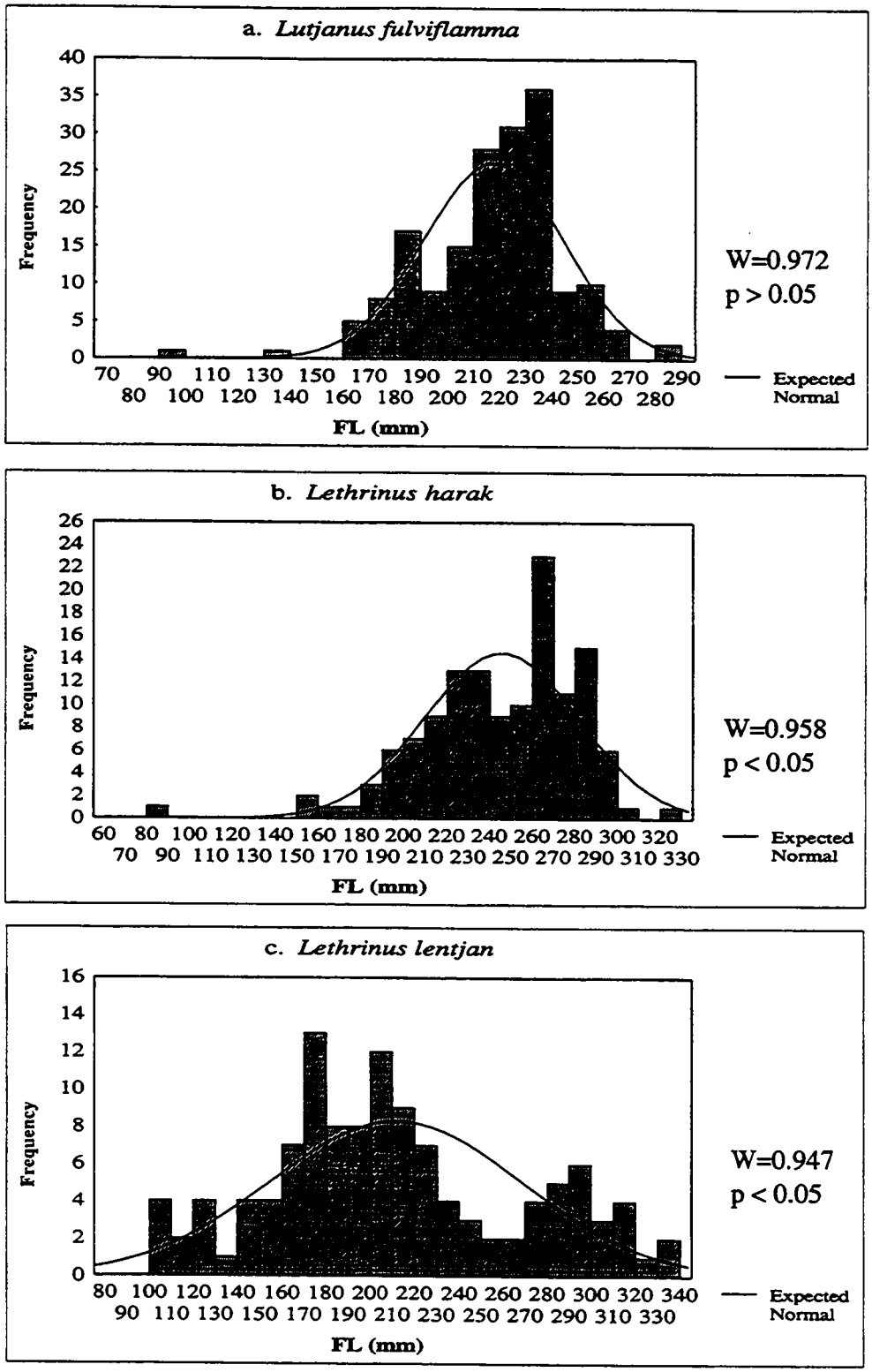


Figure 5.1. Length frequency distributions of (a) *Lutjanus fulviflamma* (n=176), (b) *Lethrinus harak* (n=132) and (c) *Lethrinus lentjan* (n=117). Shapiro-Wilk's test for normality (W) indicated that only (a) was normally distributed.

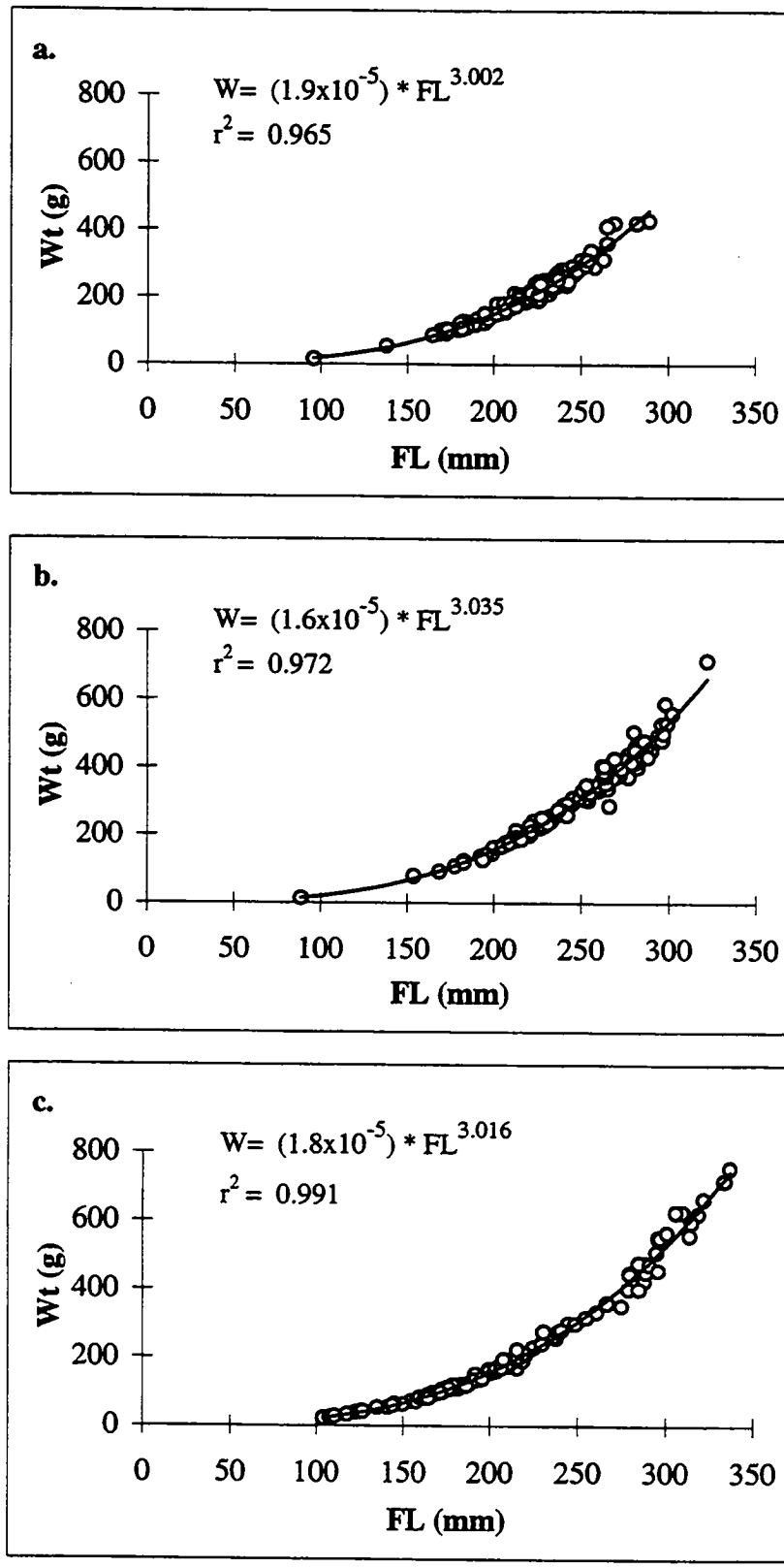


Figure 5.2. Length-weight relationships of *Lutjanus fulviflamma* (n=155), *Lethrinus harak* (n=121) and *Lethrinus lentjan* (n=103). The value of the exponent *b* was not significantly different from 3, indicating isometric weight growth for all three species.

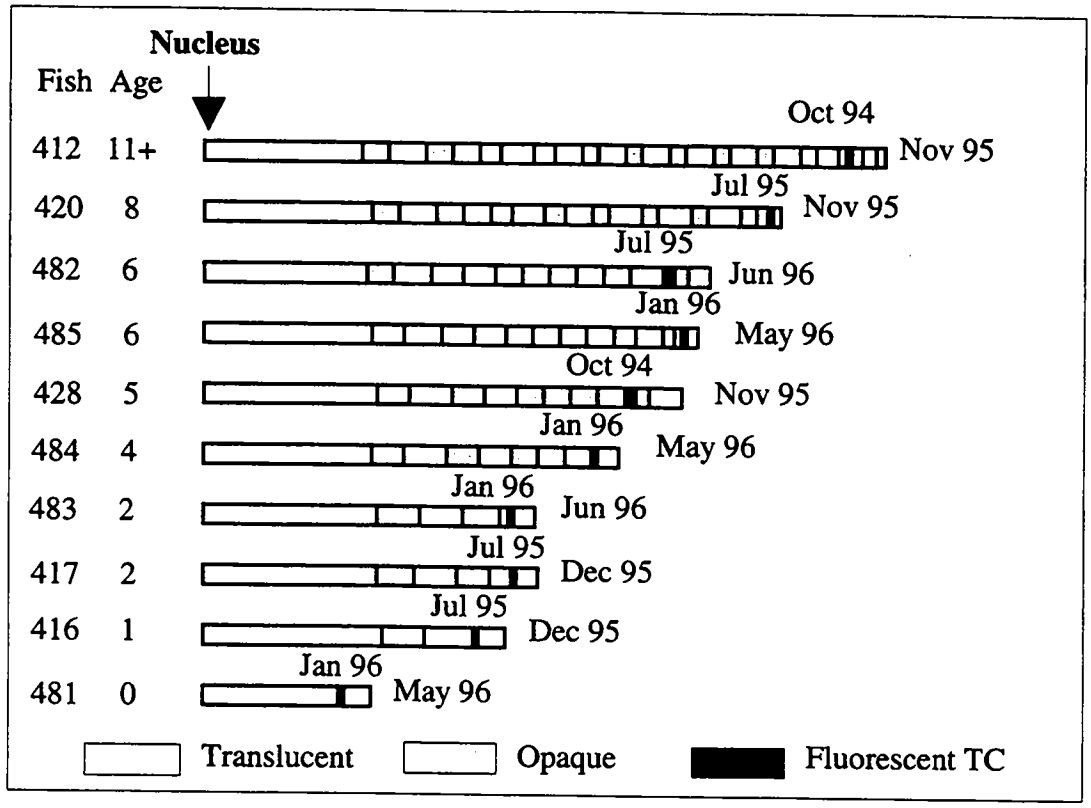


Figure 5.3. Diagrammatic representation of the relative positions of translucent and opaque (annuli) bands and flourescent marks (oxy-tetracycline (OTC)) in sectioned otoliths of OTC-treated specimens of *Lutjanus fulviflamma*. Distances between translucent and opaque bands are indicative and do not represent actual distances. Dates above the bar show the time a fish was treated with oxy-tetracycline. The dates at the end of each bar show the time of death. Fishes 412, 482 and 428 were 8, 9 and 12 months at liberty, respectively, before recapture and were then retained in aquaria until death. The others were all raised in aquaria after OTC treatment. Note OTC marks on fishes 412, 482 and 428 sit on or just before the last full annulus as shown in Plates 5.1-4.

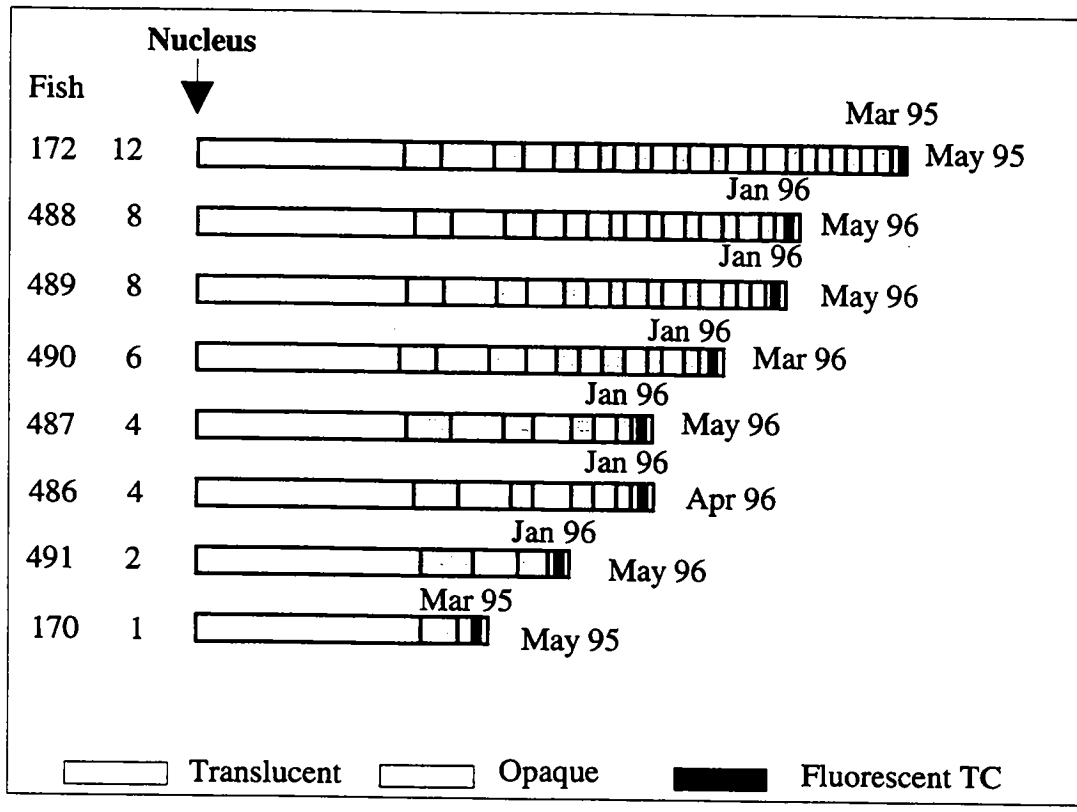


Figure 5.4. Diagrammatic representation of the relative positions of translucent and opaque (annuli) bands and flouresent marks (oxy-tetracycline (OTC)) in sectioned otoliths of OTC-treated specimens of *Lethrinus harak*. Distances between translucent and opaque bands are indicative and do not represent actual distances. Dates above the bar show the time a fish was treated with oxy-tetracycline. The dates at the end of each bar show the time of death. All fishes were raised in aquaria. None survived more than 5 months. All OTC marks lie after and close to the last annuli, suggesting formation of the annulus was before January. See text and Plate 5.5 for explanation.

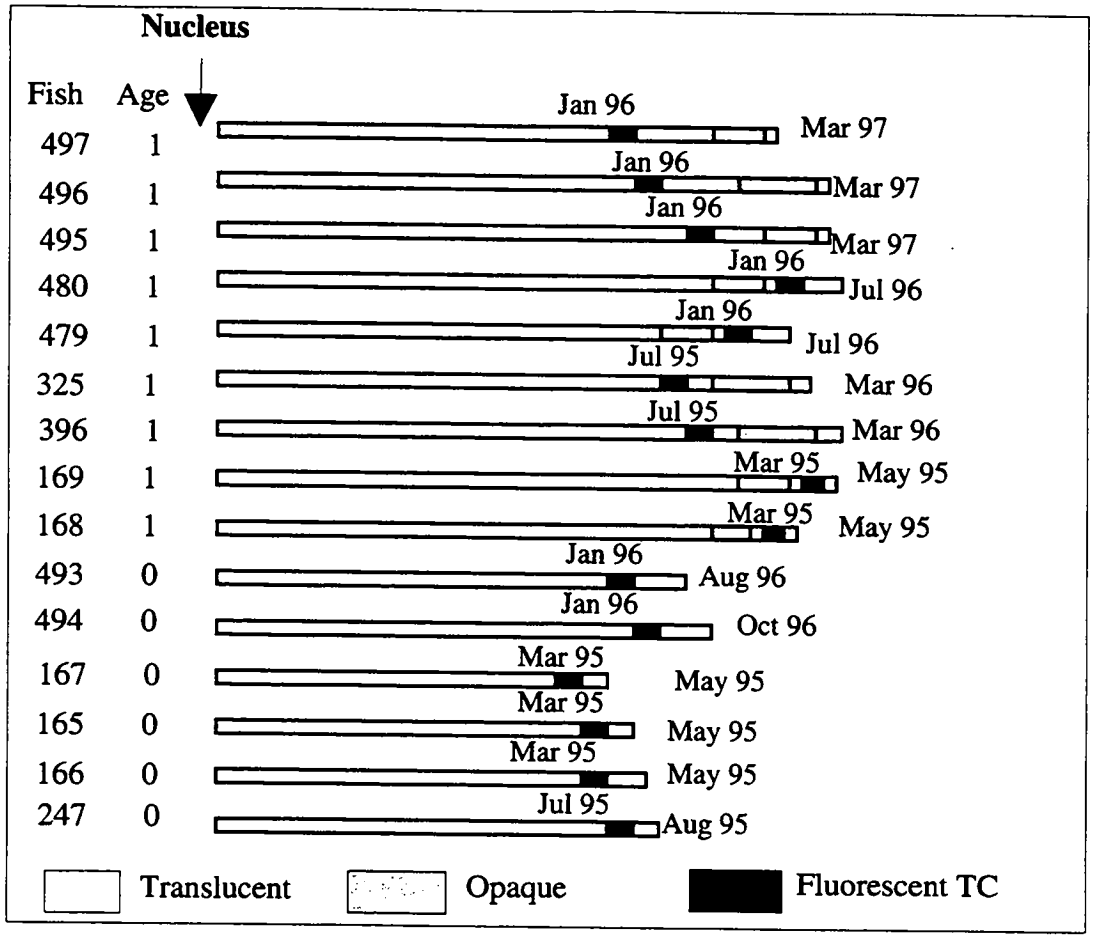
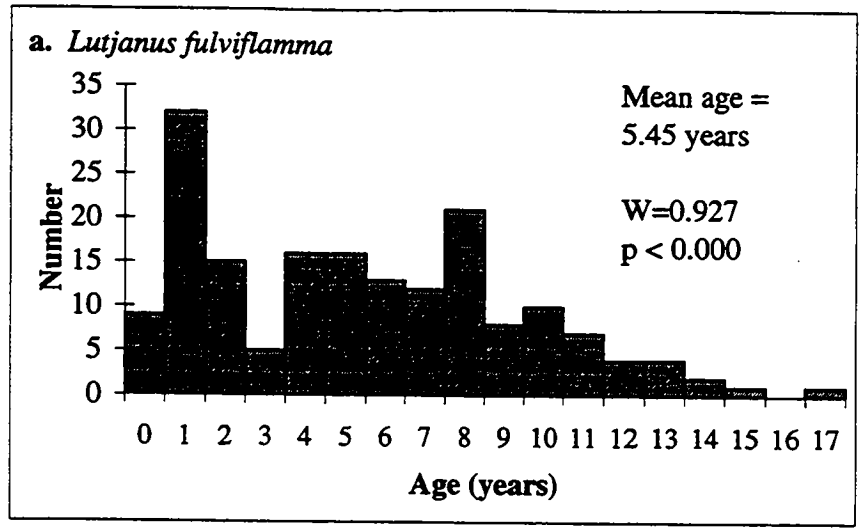
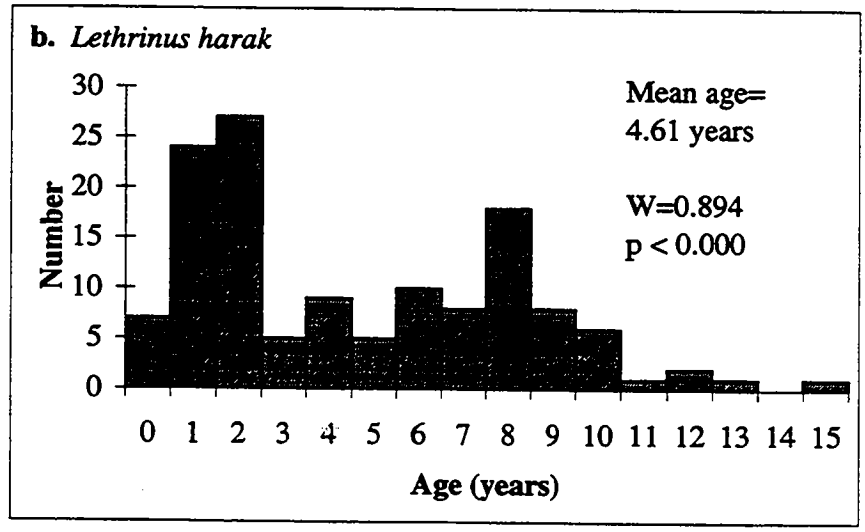
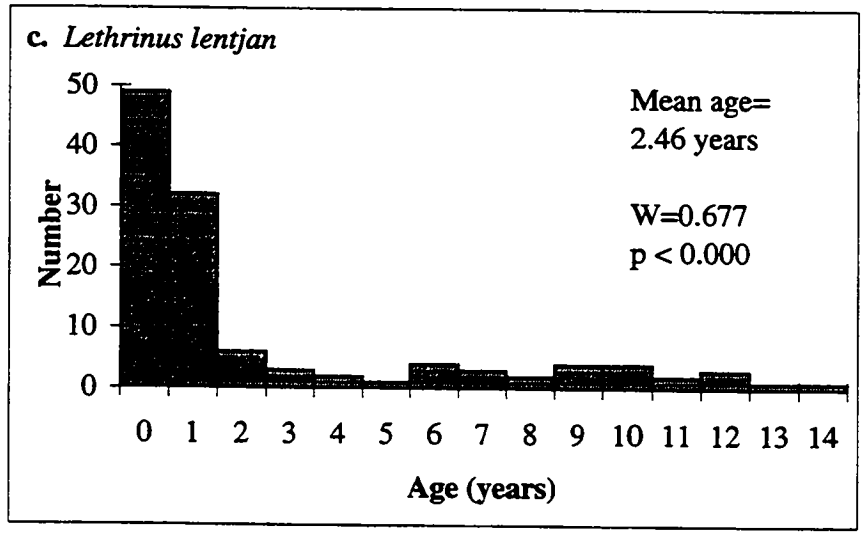


Figure 5.5. Diagrammatic representation of the relative positions of translucent and opaque (annuli) bands and flourescent marks (oxy-tetracycline (OTC)) in sectioned otoliths of OTC-treated specimens of *Lethrinus lentjan*. Distances between translucent and opaque bands are indicative and do not represent actual distances. Dates above the bar show the time a fish was treated with oxy-tetracycline. The dates at the end of each bar show the time of death. All fishes were raised in aquaria. Three fish (497, 496 and 495 survived 14 months after OTC injection. All but four fish (480, 479, 169 and 168) were 0+ yr old at the time of OTC treatment. See text and Plate 5.6 for explanation.







Firgure 5.6. Age frequency distributions of the same data sets as in Figure 5.1. Age was based on validated counts of annuli in sectioned otoliths. Shapiro-Wilk's tests for normality (W) showed that all distributions differed significantly from normal.

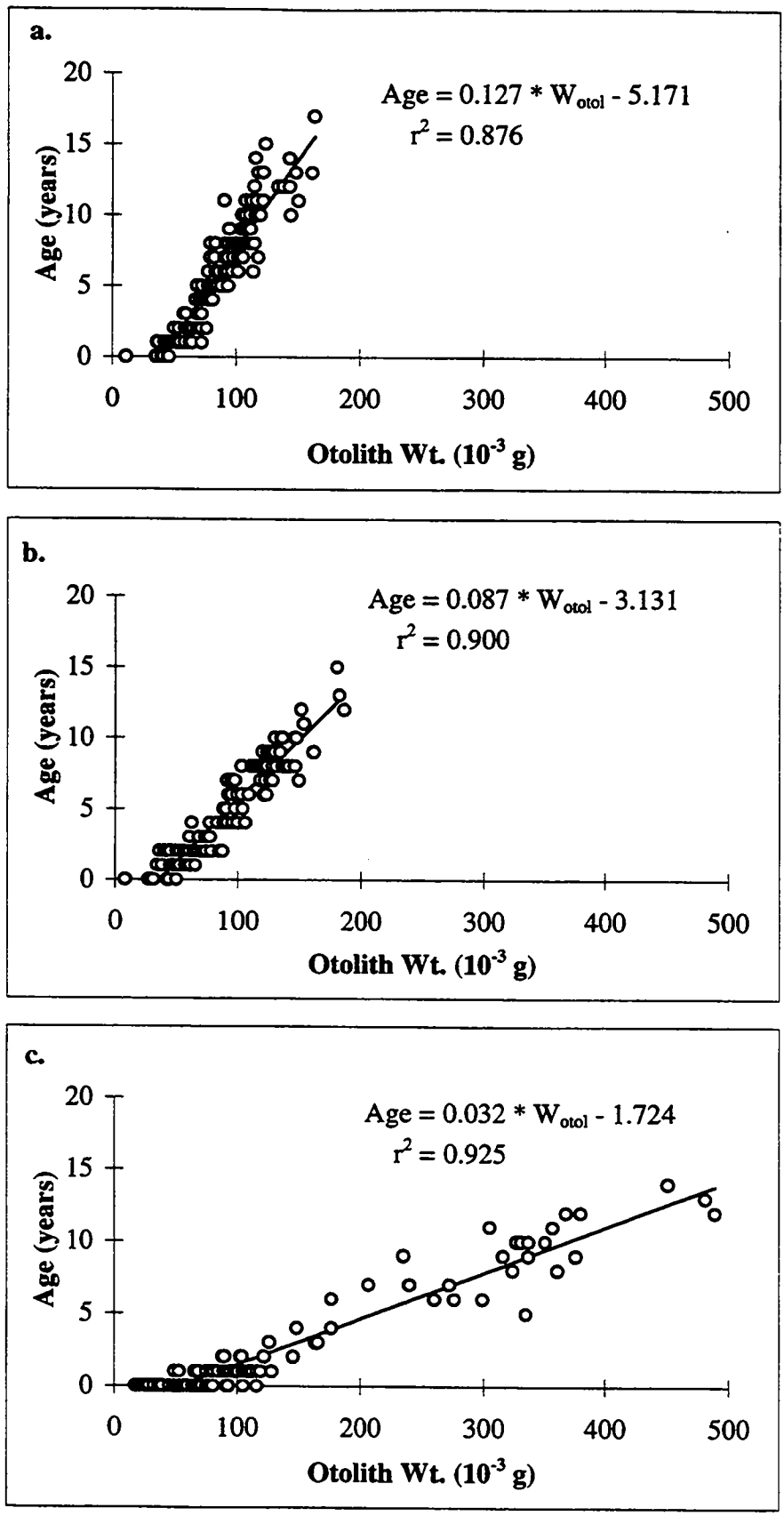


Figure 5.7. Otolith weight- fish age relationships for (a) *Lutjanus fulviflamma* (n=176), (b) *Lethrinus harak* (n=128) and (c) *Lethrinus lentjan* (n=117).

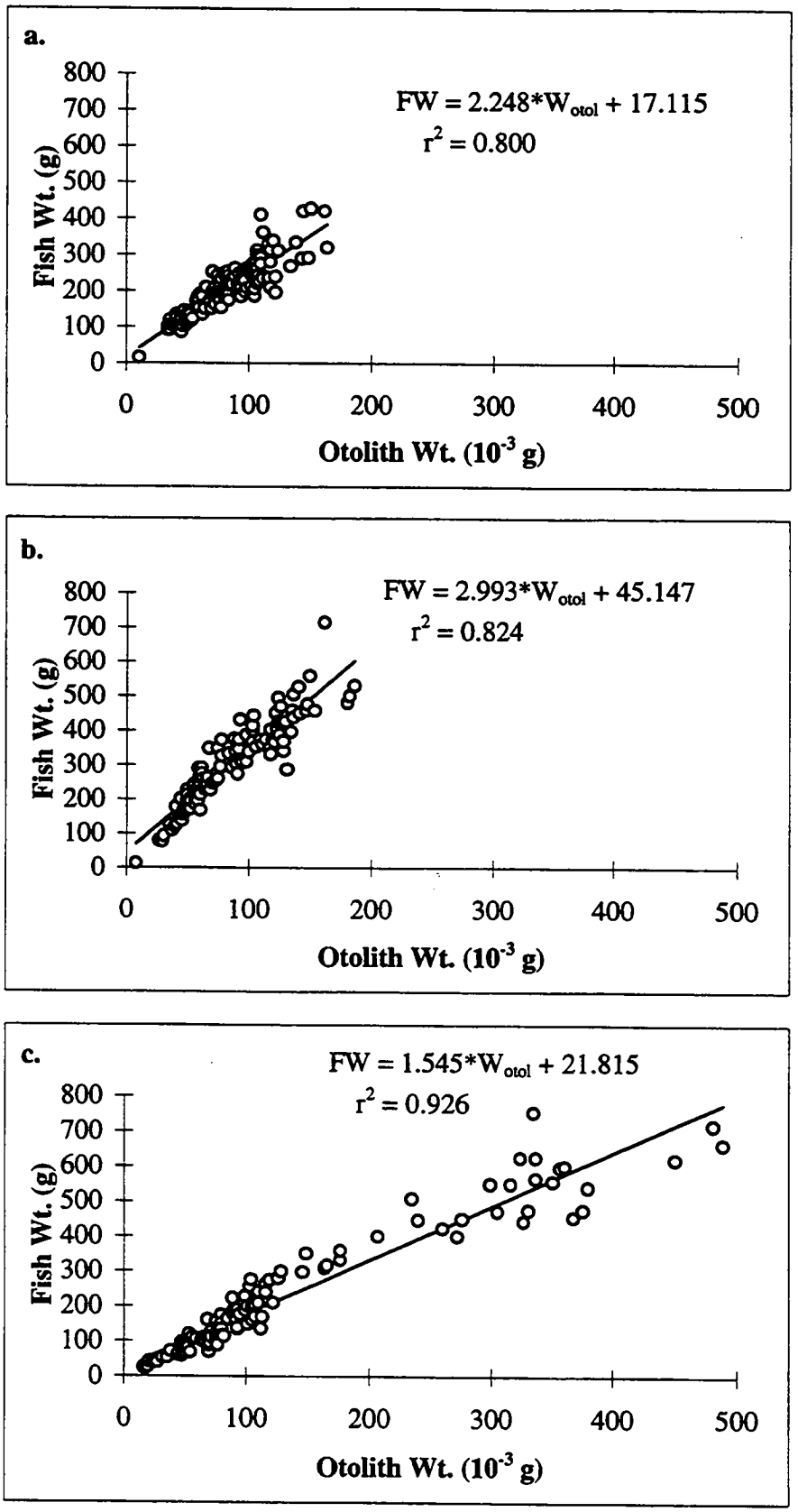


Figure 5.8. Otolith weight-fish weight (FW) relationships for (a) *Lutjanus fulviflamma* (n=155), (b) *Lethrinus harak* (n=119) and (c) *Lethrinus lentjan* (n=117).

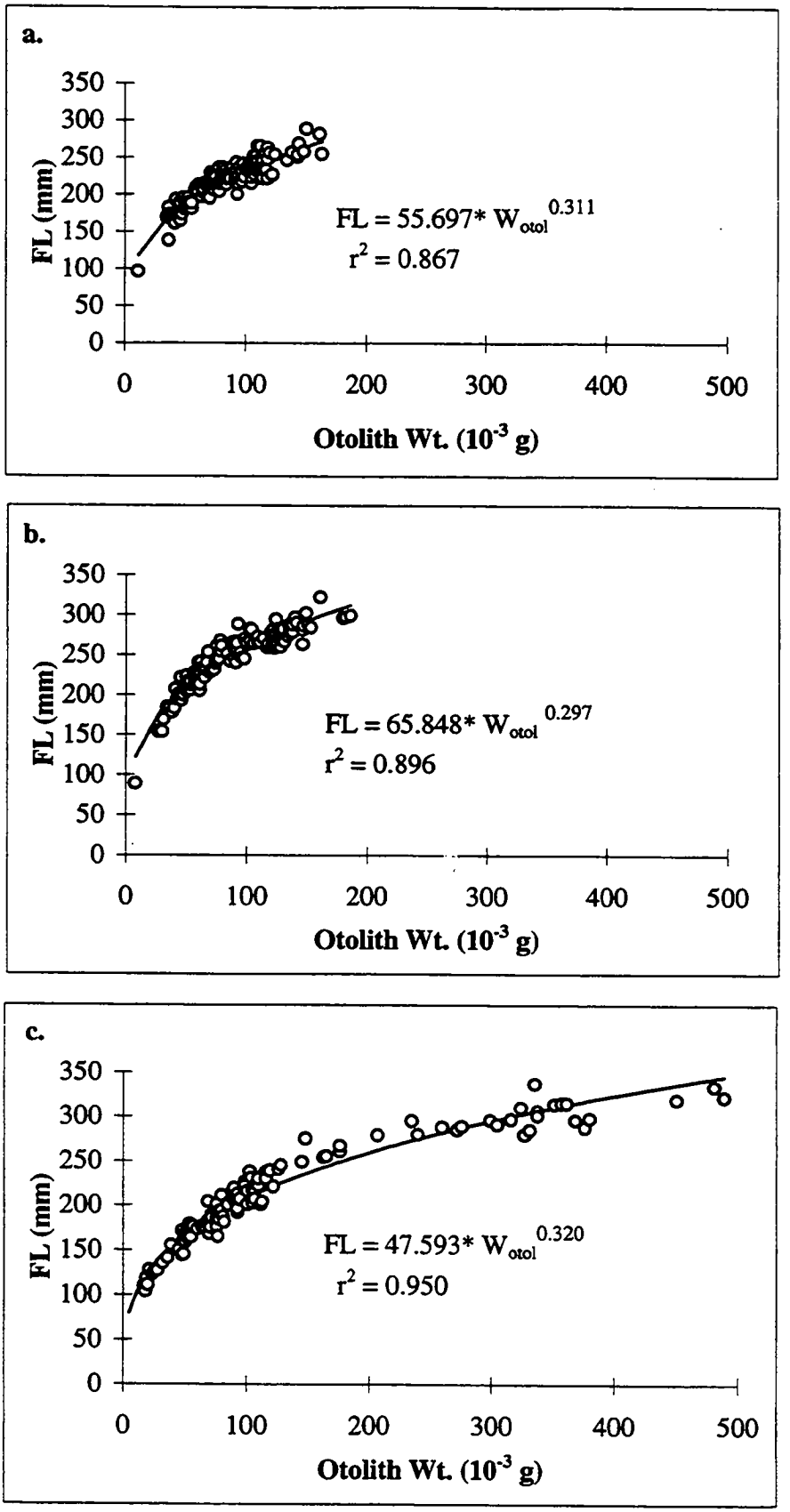


Figure 5.9. Otolith weight - fish length (in mm FL) relationships for (a) *Lutjanus fulviflamma* (n=176), (b) *Lethrinus harak* (n=129) and (c) *Lethrinus lentjan* (n=117).

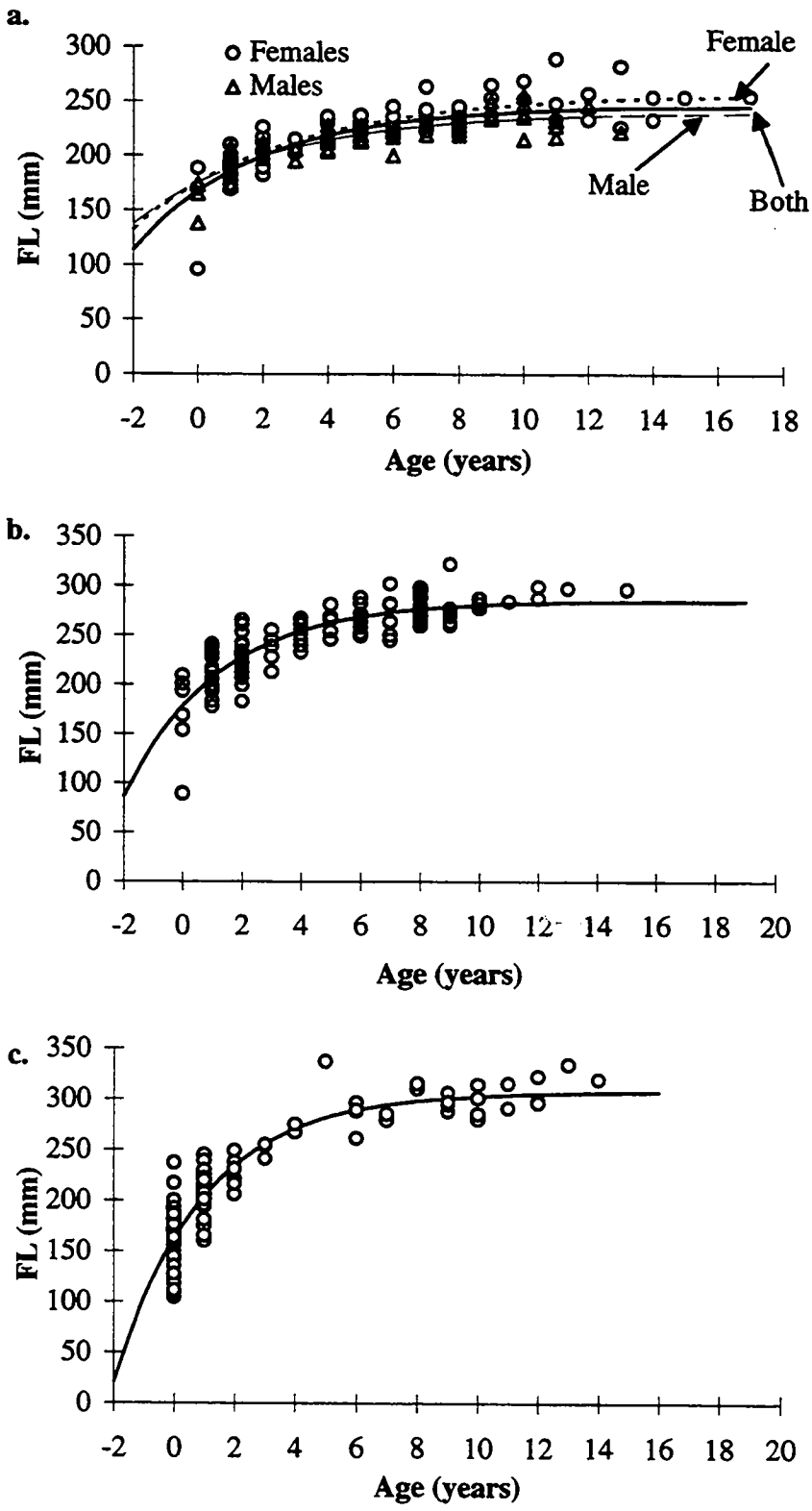


Figure 5.10. The von Bertalanffy growth curve fitted to length at age data of (a) male (n=69), female (n=94) and both sexes combined (n=163) for *Lutjanus fulviflamma*, (b) *Lethrinus harak* (n=132) and (c) *Lethrinus lentjan* (n=117). Estimates of VBGF growth parameters are presented in Table 5.4.

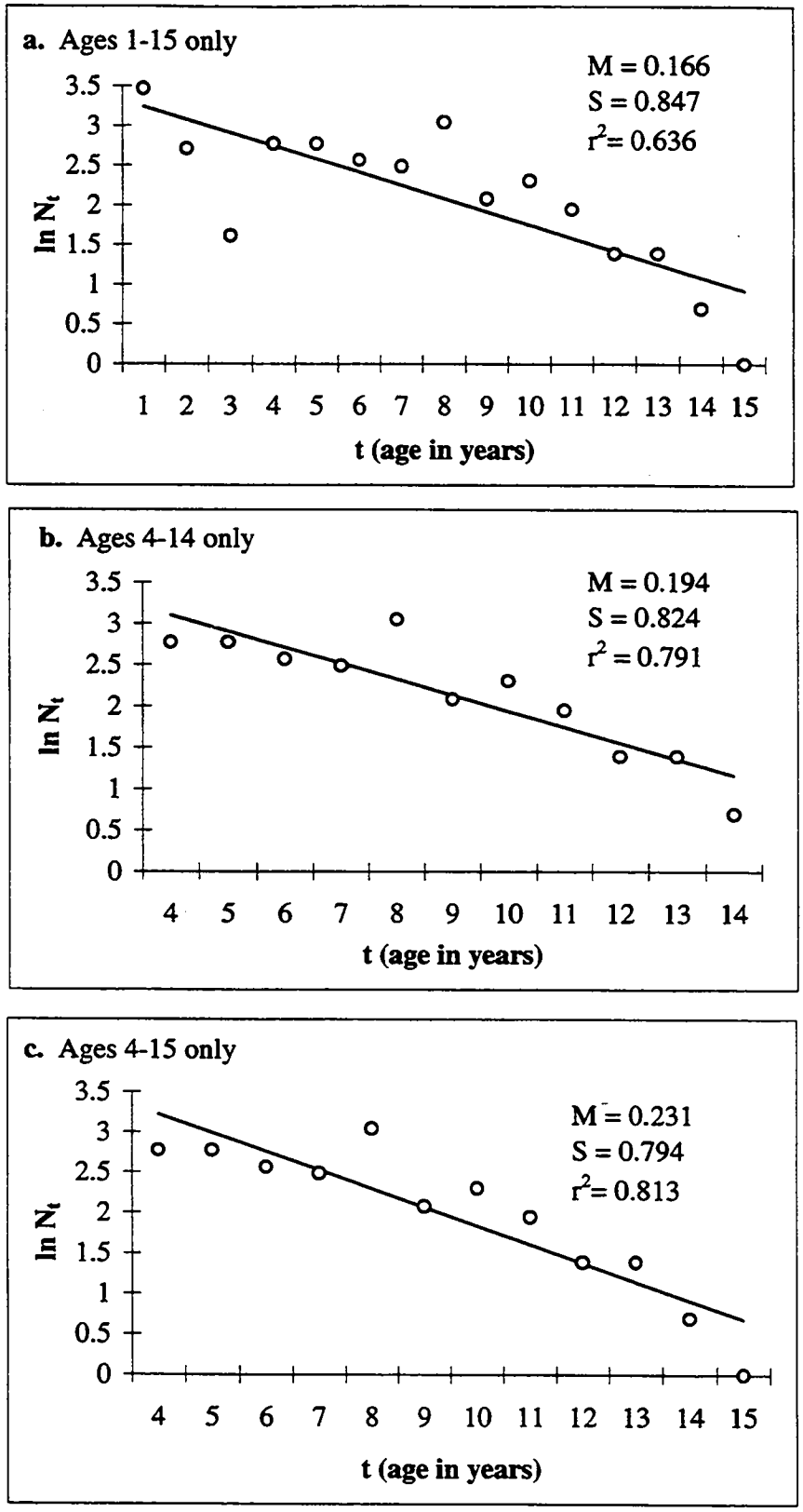


Figure 5.11. Instantaneous rates of mortality (M) and survivorship (S) for different age ranges (a-c) of *Lutjanus fulviflamma* as estimated from age-based catch-curves.

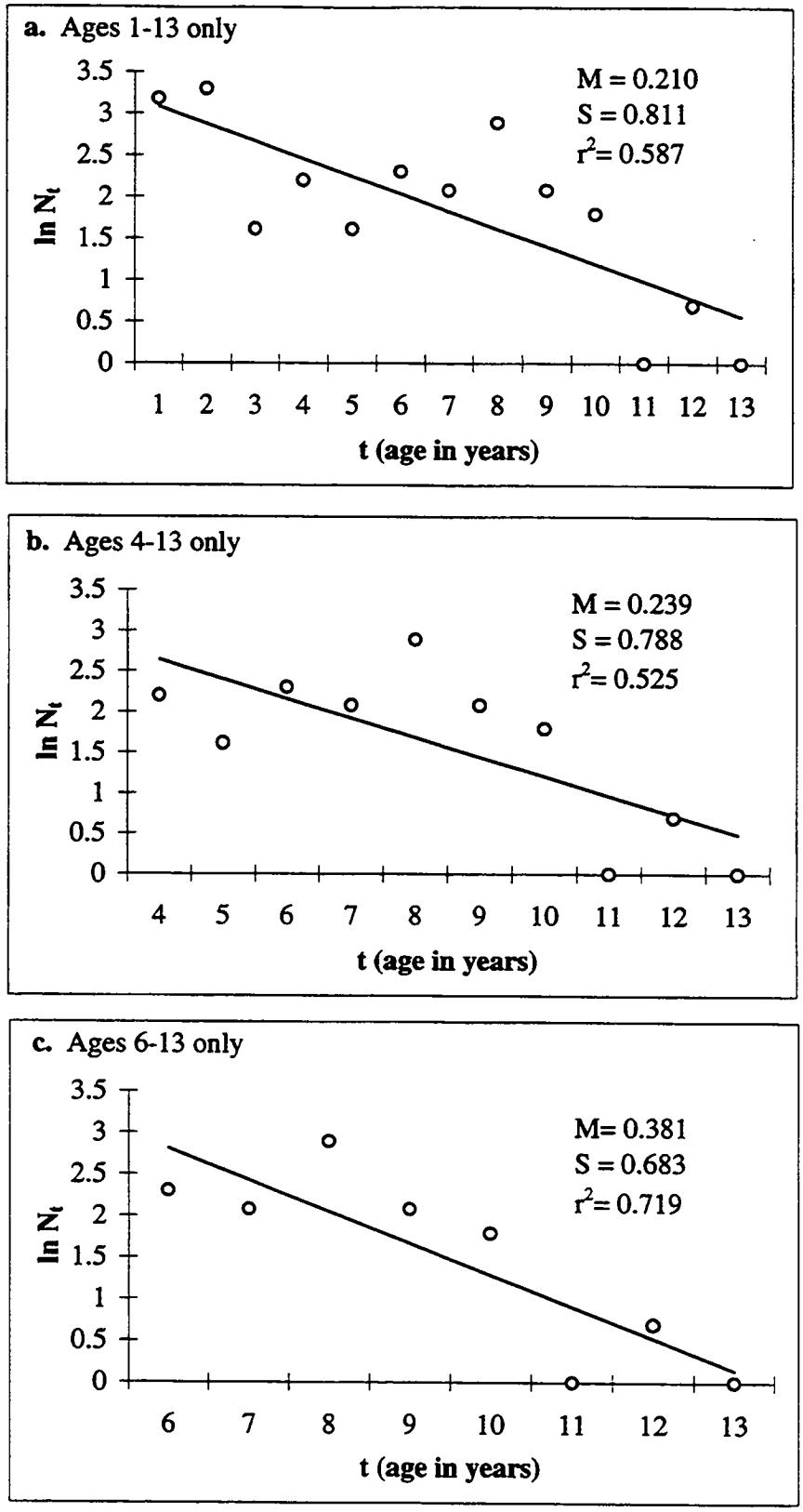


Figure 5.12. Instantaneous rates of mortality (M) and survivorship (S) for different age ranges (a-c) of *Lethrinus harak* as estimated from age-based catch-curves.

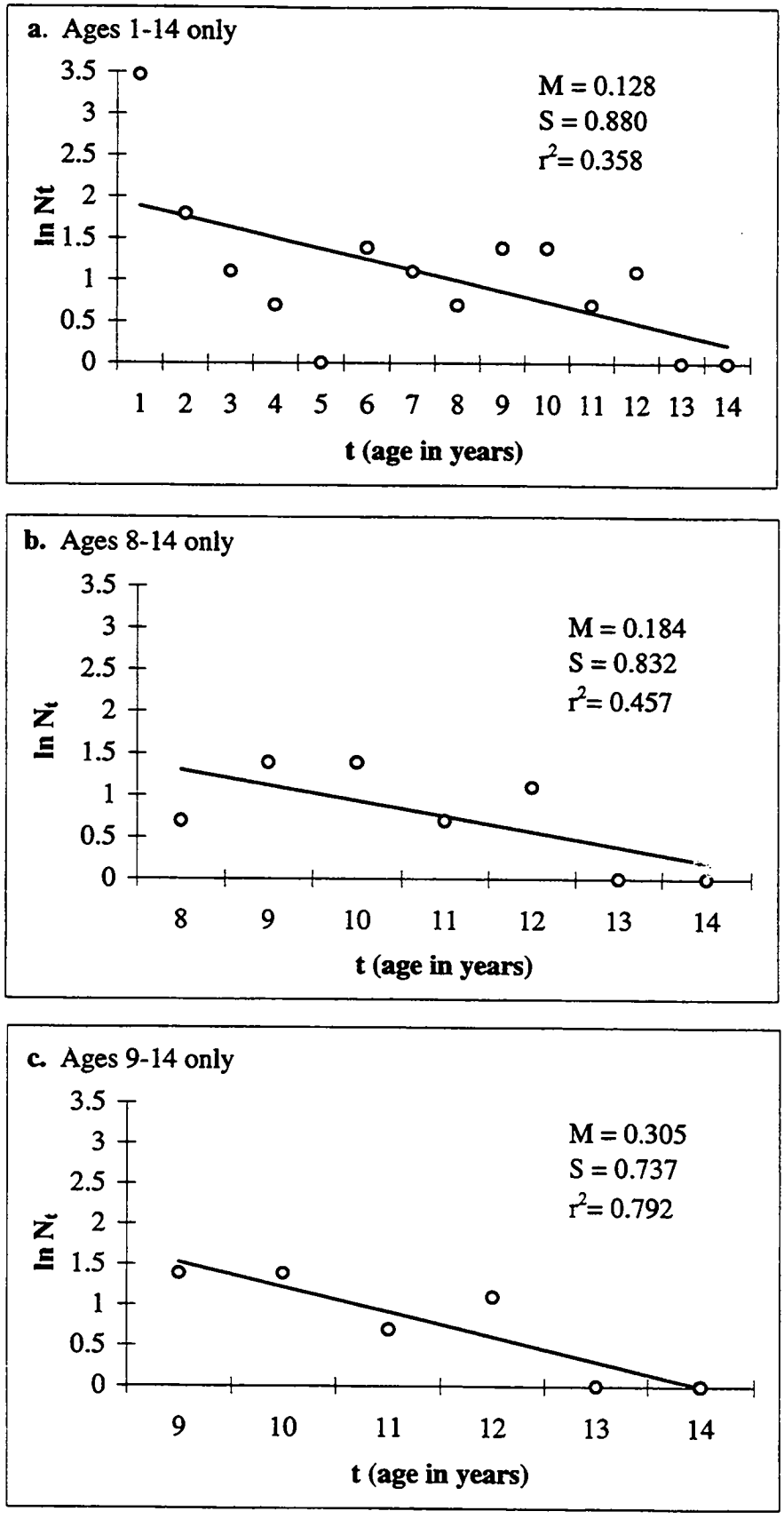


Figure 5.13. Instantaneous rates of mortality (M) and survivorship (S) for different age ranges (a-c) of *Lethrinus lentjan* as estimated from age-based catch-curves.

Table 5.1. Percentage agreement and precision of counts of annuli between 2 readers for *Lutjanus fulviflamma*. Precision was based on IAPE of Beamish and Fournier (1981). * not expressed as percentage.

	PERCENTAGE AGREEMENT Deviation in Counts					PRECISION Average Percentage Error		
Agreed Count	N	0	±1	±2	% Agreement	Reader 1	Reader 2	1 and 2
0	9	8	1		88.89	0.00	1.78*	1.89*
1	32	27	5		84.38	18.74	12.50	15.63
2	15	13	2		86.67	0.00	6.67	3.33
3	5	4	1		80.00	11.43	0.00	6.21
4	16	13	3		81.25	2.98	3.13	3.05
5	16	14	2		87.50	2.37	2.37	2.37
6	13	11	2		84.62	2.40	2.34	1.28
7	12	10	2		83.33	2.21	2.16	1.19
8	21	17	4		80.95	1.19	2.13	1.69
9	8	7	1		87.50	2.46	0.00	1.31
10	10	7	2	1	70.00	1.82	3.76	2.00
11	7	6	1		85.71	0.00	2.26	1.21
12	4	4			100.00	0.00	0.00	0.00
13	4	3	1		75.00	2.94	0.00	1.70
14	2	2			100.00	0.00	0.00	0.00
15	1	1			100.00	0.00	0.00	0.00
16	0							
17	1	1			100.00	0.00	0.00	0.00
Total	176	148	27	1				
% Total		84.09	15.34	0.57	**IAPE=**	**0.28**	**0.94**	**1.31**

Table 5.2. Percentage agreement and precision of counts of annuli between 2 readers for *Lethrinus harak*. Precision was based on IAPE of Beamish and Fournier (1981). * not expressed as percentage.

	PERCENTAGE AGREEMENT Deviation in Counts						PRECISION Average Percentage Error		
Agreed Count	N	0	±1	±2	±3	% Agreement	Reader 1	Reader 2	1 and 2
0	7	5	2			71.43	1.71*	1.71*	1.71*
1	24	19	5			79.17	7.67	16.67	11.99
2	27	15	8	3	1	55.56	24.93	16.76	18.14
3	5	4	1			80.00	0.00	11.43	6.21
4	9	5	3	1		55.56	9.15	10.21	7.98
5	5	3	2			60.00	6.15	6.15	6.15
6	10	7	2	1		70.00	3.05	7.62	4.59
7	8	5	3			62.50	3.18	3.57	3.38
8	18	12	6			66.67	2.64	2.64	2.64
9	8	6	1	1		75.00	0.00	6.00	3.57
10	6	5	1			83.33	2.82	0.00	1.54
11	1	1				100.00	0.00	0.00	0.00
12	2	2				100.00	0.00	0.00	0.00
13	1	1				100.00	0.00	0.00	0.00
14	0								
15	1	1				100.00	0.00	0.00	0.00
Total	132	91	34	6	1				
% Total		68.94	25.76	4.55	0.76	**IAPE=**	**1.75**	**1.91**	**1.80**

Table 5.3. Percentage agreement and precision of counts of annuli between 2 readers for *Lethrinus lentjan*. Precision was based on IAPE of Beamish and Fournier (1981). * not expressed as percentage.

	PERCENTAGE AGREEMENT					PRECISION		
		Deviation in Counts				Average Percentage Error		
Agreed Count	N	0	±1	±2	% Agreement	Reader 1	Reader 2	1 and 2
0	49	37	12		75.51	1.92*	1.59*	1.76*
1	32	24	8		75.00	15.54	25.00	17.61
2	6	4	1	1	66.67	26.67	23.81	16.67
3	3	3			100.00	16.67	0.00	9.80
4	2	1	1		50.00	0.00	14.29	10.00
5	1	1			100.00	0.00	0.00	0.00
6	4	1	2	1	25.00	7.14	11.11	12.50
7	3	1	1	1	33.33	14.04	6.06	8.94
8	2	2			100.00	0.00	0.00	0.00
9	4	2	2		50.00	4.29	4.29	4.29
10	4	3		1	75.00	7.89	0.00	4.49
11	2	1	1		50.00	4.76	0.00	3.49
12	3	2	1		66.67	3.81	0.00	2.35
13	1	1			100.00	0.00	0.00	0.00
14	1	1			100.00	0.00	0.00	0.00
Total	117	84	29	4				
% Total		71.79	24.79	3.42	**IAPE=**	**2.50**	**2.08**	**2.27**

Table 5.4. Estimates of von Bertalanffy growth parameters (±S.E.) for the three species. *Lethrinus harak* and *L. lentjan* exhibited a sexual pattern consistent with protogyny and separating growth parameters of males and females was difficult due to the absence of males in younger age classes.

Species	L_∞ (FL in mm)	K	t_0(yr)	n	r^2
Lutjanus fulviflamma					
MALE	240.435 ± 5.079	0.230 ± 0.051	-5.670 ± 1.230	69	0.782
FEMALE	253.262 ± 5.190	0.236 ± 0.044	-4.698 ± 0.887	94	0.781
BOTH SEXES	246.312 ± 3.507	0.261 ± 0.037	-4.377 ± 0.640	176	0.751
Lethrinus harak	284.994 ± 4.980	0.313 ± 0.050	-3.159 ± 0.567	132	0.745
Lethrinus lentjan	307.200 ± 6.766	0.345 ± 0.047	-2.202 ± 0.290	117	0.835

Table 5.5. Comparative estimates of natural mortality (M) and survivorship (S) rates derived from age-based catch curves (this study) and from regression equations of Pauly (1980), Hoenig (1983) and Ralston (1987). Values of M for 'this study' were chosen from the age ranges providing the best fit in the regression (i.e. line with the highest r^2) in Figs. 5.11-13 .

Species	Parameter	Age-based catch curve (this study) (±S.E.)	Pauly estimate	Hoenig estimate	Ralston estimate
Lutjanus fulviflamma 4-15 yr old	M	0.231 (0.035)	0.403	0.246	0.592
	S	79.4%	66.8%	78.2%	55.3%
Lethrinus harak 6-13 yr old	M	0.381 (0.097)	0.435	0.279	_
	S	68.3%	64.7%	75.6%	
Lethrinus lentjan 9-14 yr old	M	0.305 (0.078)	0.454	0.300	_
	S	73.7%	63.5%	74.1%	

Table 5.6. Comparison of estimates of growth parameters of the von Bertalanffy Growth Function (L_∞, K and t_0), maximum age, and mortality parameters derived from different methods for *L. fulviflamma*, *L. harak* and *L. lentjan*.

	Growth Parameters					Mortality Parameters					
Species	L_∞ (mm)	K	t_0(yr)	Maximum Age (yrs)	Method of Growth Determination	Z	M	F	Method of M Determination	Locality	Reference
Lutjanus fulviflamma	246.3 (FL)	0.261	-4.377	17	Otoliths	-	0.231	-	ABCC[1]	Lizard Island, GBR	This study
Lutjanus fulviflamma	248.0 (SL)	0.300	-	23	Otoliths		0.800		Pauly (1980)	New Caledonia	Loubens (1980b)
Lethrinus harak	285.0 (FL)	0.313	-3.159	15	Otoliths	-	0.381	-	ABCC[1]	Lizard Island, GBR	This study
Lethrinus harak	330.0 (SL)	0.490	-	-	Length Frequency	1.60	1.07	0.53	Pauly (1980)	Central Fiji	Dalzell *et al.* (1989)
Lethrinus harak	342.0 (SL)	0.450	-	-	Length Frequency	2.03	1.01	1.02	Pauly (1980)	Western Fiji	Dalzell *et al.* (1989)
Lethrinus harak	339.0 (SL)	0.460	-	-	Length Frequency	1.52	1.03	0.50	Pauly (1980)	Northern Fiji	Dalzell *et al.* (1989)
Lethrinus lentjan	307.2 (FL)	0.345	-2.202	14	Otoliths	-	0.305	-	ABCC[1]	Lizard Island, GBR	This study
Lethrinus lentjan	292.0 (SL)	0.330	-	15	Otoliths	-	0.820	-	Pauly (1980)	New Caledonia	Loubens (1980b)
Lethrinus lentjan	640.0 (TL)	0.270	-	5	Otoliths/Scales	-	0.610	-	Pauly (1980)	India	Toor (1964b)
Lethrinus lentjan	511.0 (TL)	0.170	-	9	-	-	0.420	-	Pauly (1980)	Red Sea	Carpenter & Allen (1989)
Lethrinus lentjan	426.0 (TL)	0.480	-	-	Scales	-	-	-		Gulf of Aden	Aldonov & Druzhinin (1979)

[1]Age-based catch curve

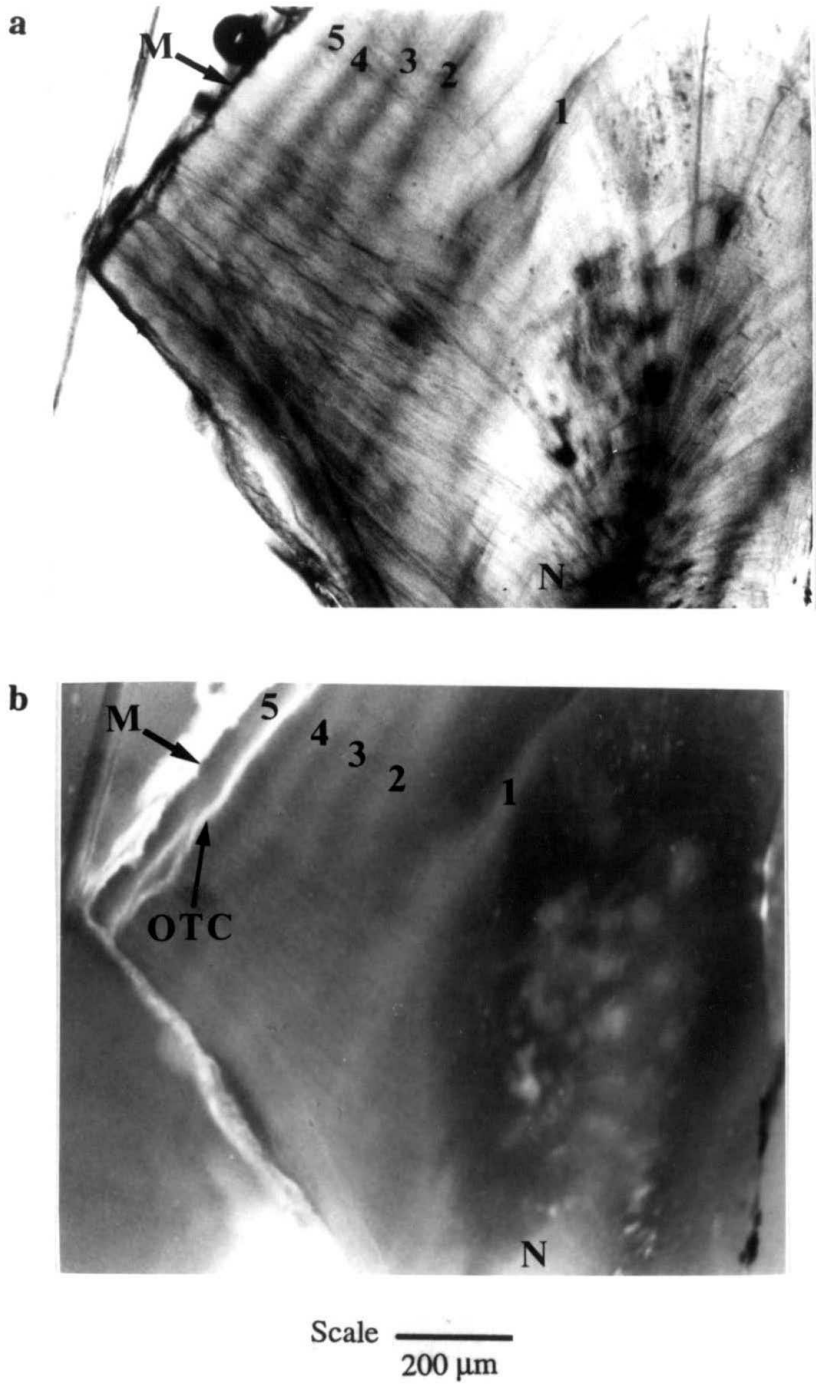


Plate 5.1 Sectioned otolith of specimen 428 (*Lutjanus fulviflamma*) in (a) transmitted and (b) fluorescent light. Opaque bands (1-5) appear dark in transmitted (a) and milky white in fluorescent (b) light. Specimen 428 was 4+ yr old when injected with oxytetracycline (OTC) in October 1994 and survived until November 1995. Note 5 opaque bands in (a) and (b) with the 5th sitting above the OTC mark (see enlargement in Plate 5.2). M = otolith margin; N = nucleus.

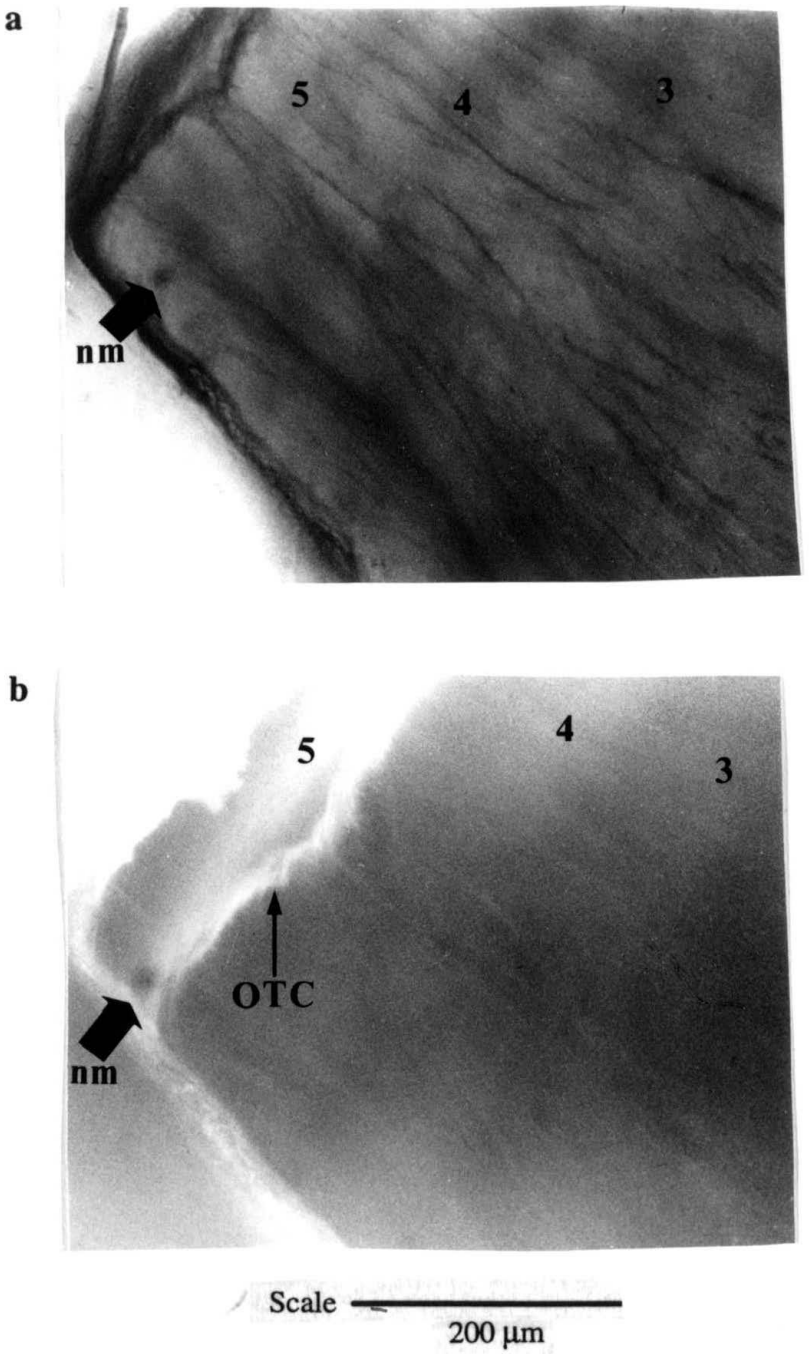


Plate 5.2. Enlarged image of the sectioned otolith of specimen 428 in Plate 5.1 in (a) transmitted and (b) fluorescent light. Note the 5th opaque band in line with a natural mark (nm) in (a) and (b). In (b), note the 5th annulus sitting above the OTC mark.

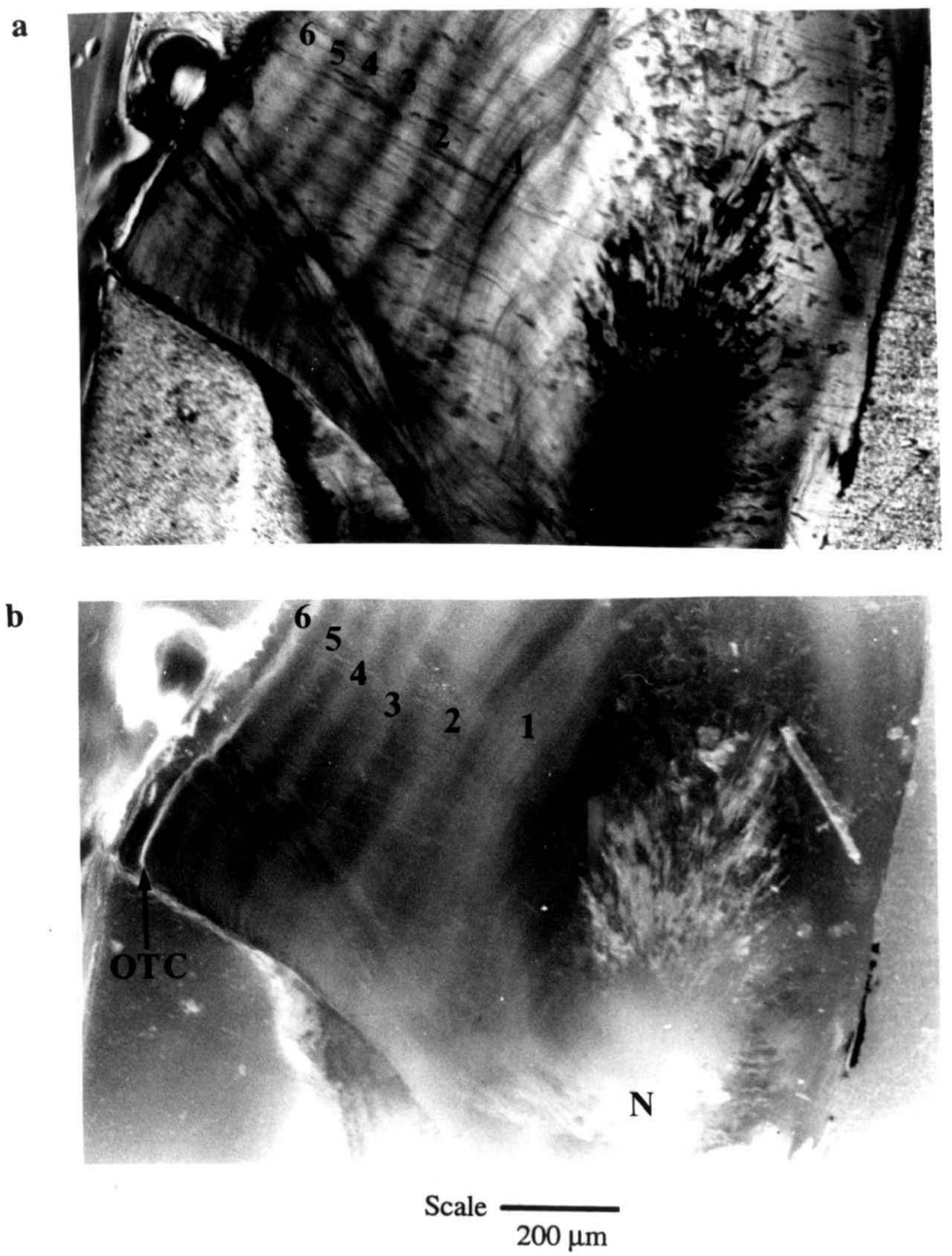


Plate 5.3. Sectioned otolith of specimen 482 (*Lutjanus fulviflamma*) in (a) transmitted and (b) fluorescent light. Specimen 482 was 5+ yr old when injected with OTC in July 1995 and survived until May 1996. Note opaque bands (1-6) in (a) and (b). The 6th in (a) appears as a faint thin dark band. Note that the distance between the 4th and the 5th opaque band in (a) is roughly half the distance between the 5th and the margin suggesting the presence of a 6th band. In (b), the 6th band is clearly visible with the OTC band sitting on it. N = nucleus.

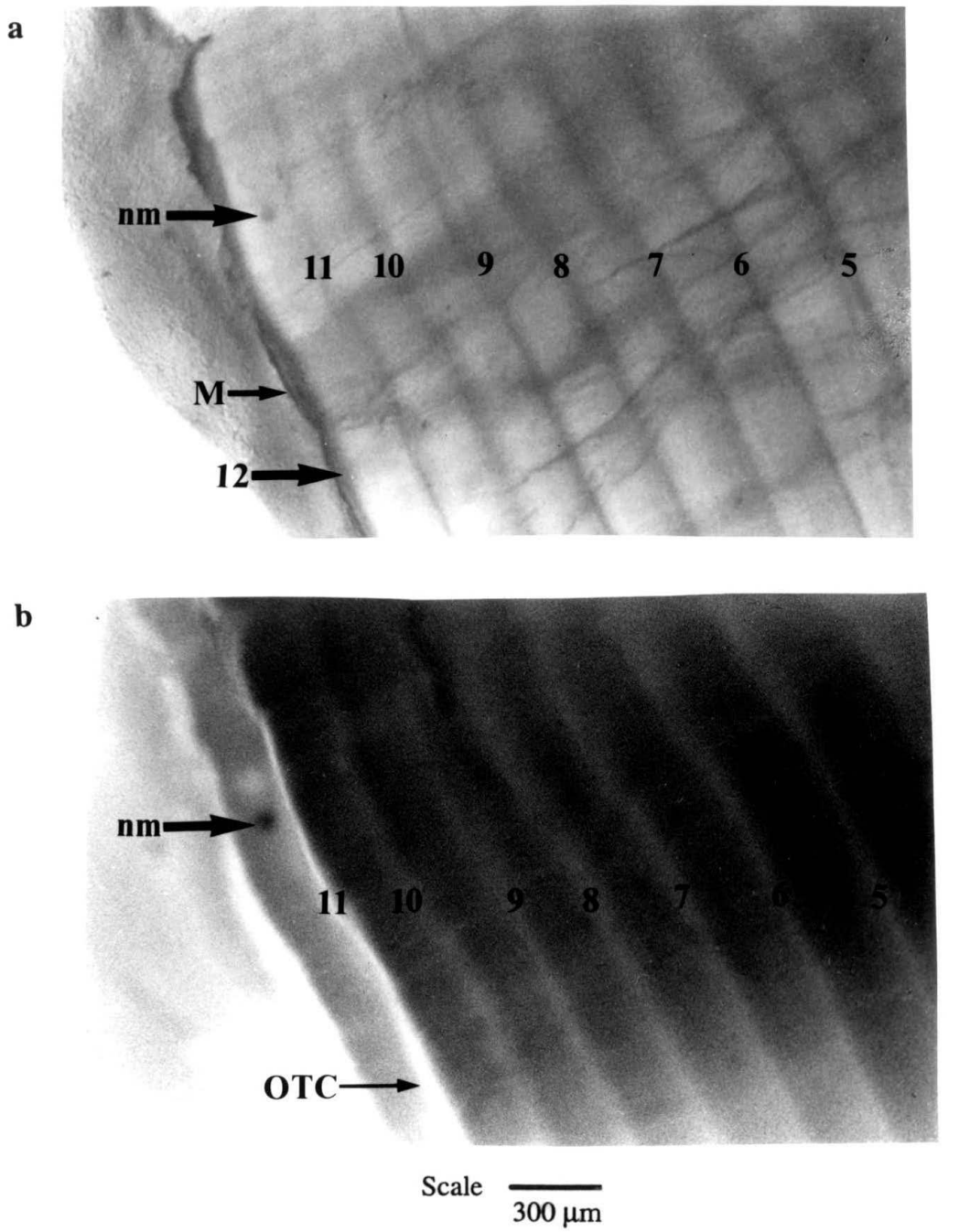


Plate 5.4. Sectioned otolith of specimen 412 (*Lutjanus fulviflamma*) in (a) transmitted and (b) fluorescent light. Specimen 412 was 11 yr old when injected with OTC in October 1994 and survived until November 1995. Note the OTC mark sits on the 11th opaque band in (b) below (i.e. to the right of) a natural mark (nm) which is also visible in (a). A 12th incomplete opaque band is visible close to the margin (M) in (a). Note the almost uniform distances between consecutive opaque bands in (a) and (b).

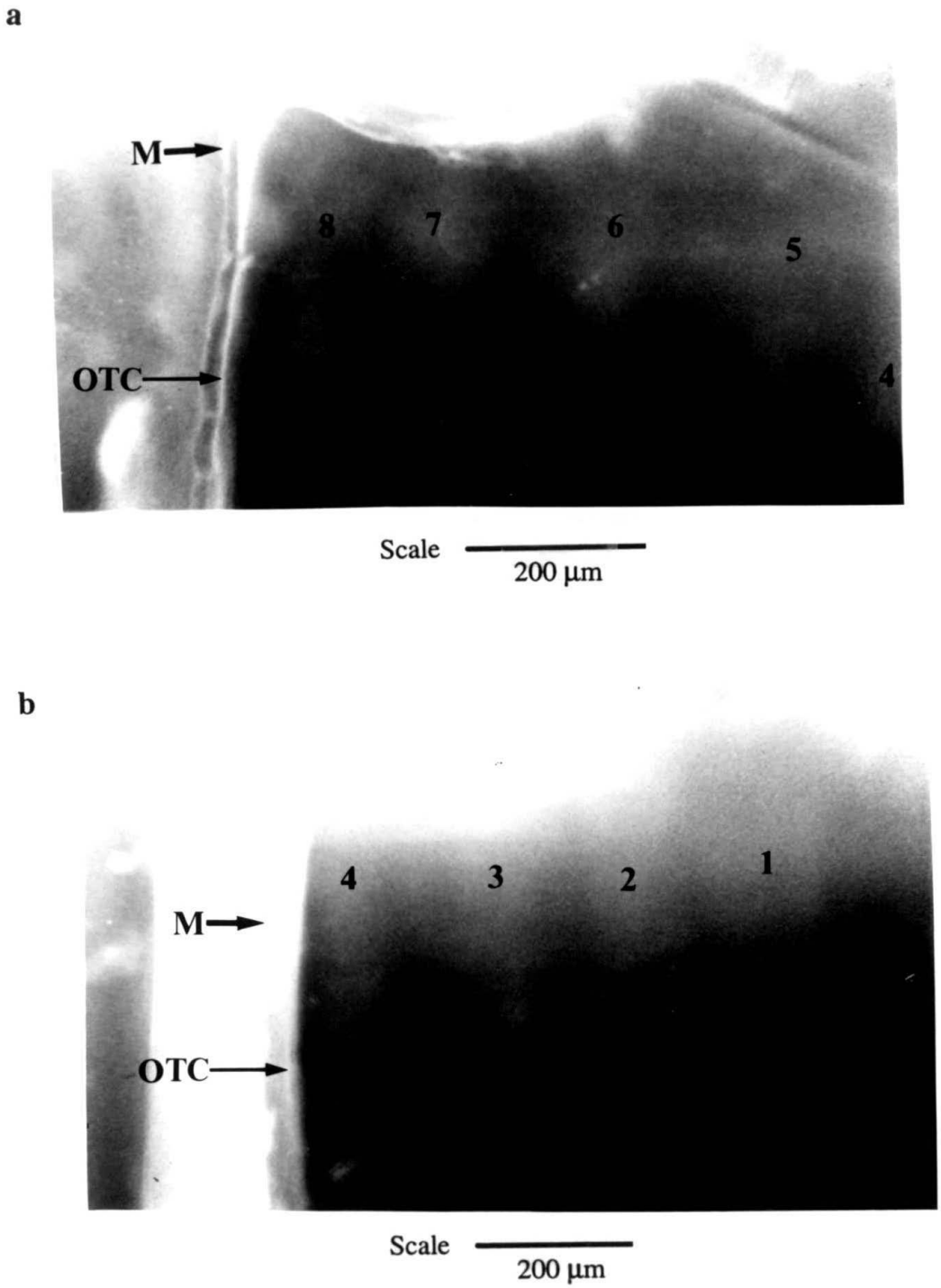


Plate 5.5. Sectioned otoliths of specimens (a) 488 and (b) 487 (both *Lethrinus harak*) under both transmitted and fluorescent light simultaneously. Opaque bands appear as milky white bands. Specimen 488 (a) and 487 (b) were 8 and 4 yrs old, respectively, when injected with OTC in January 1996 and survived until May 1996. Note that the distance between the OTC mark and the otolith margin (M) in (a) and (b), otolith growth equivalent to 4 months, is roughly a third of the distance between the 7th and 8th opaque bands in (a) and the 3rd and 4th in (b), suggesting that the distance between consecutive opaque bands reflects a year's growth.

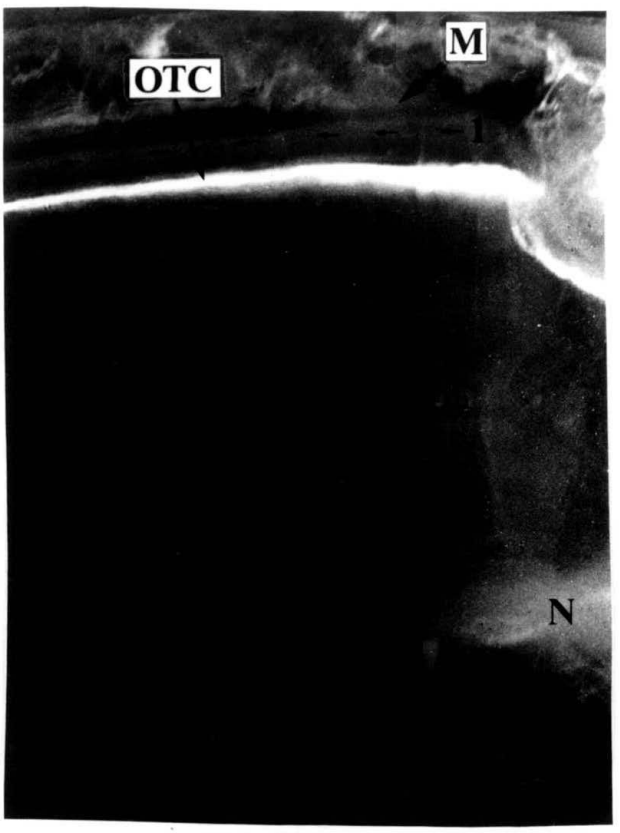


Plate 5.6. Sectioned otolith of specimen 325 (*Lethrinus lentjan*) under both transmitted and fluorescent light simultaneously. Specimen 325 was 0+ yr old when injected with OTC in July 1995 and survived until March 1996. Note the 1st opaque band (traced by small arrows) formed above the OTC mark. N= nucleus; M = otolith margin.

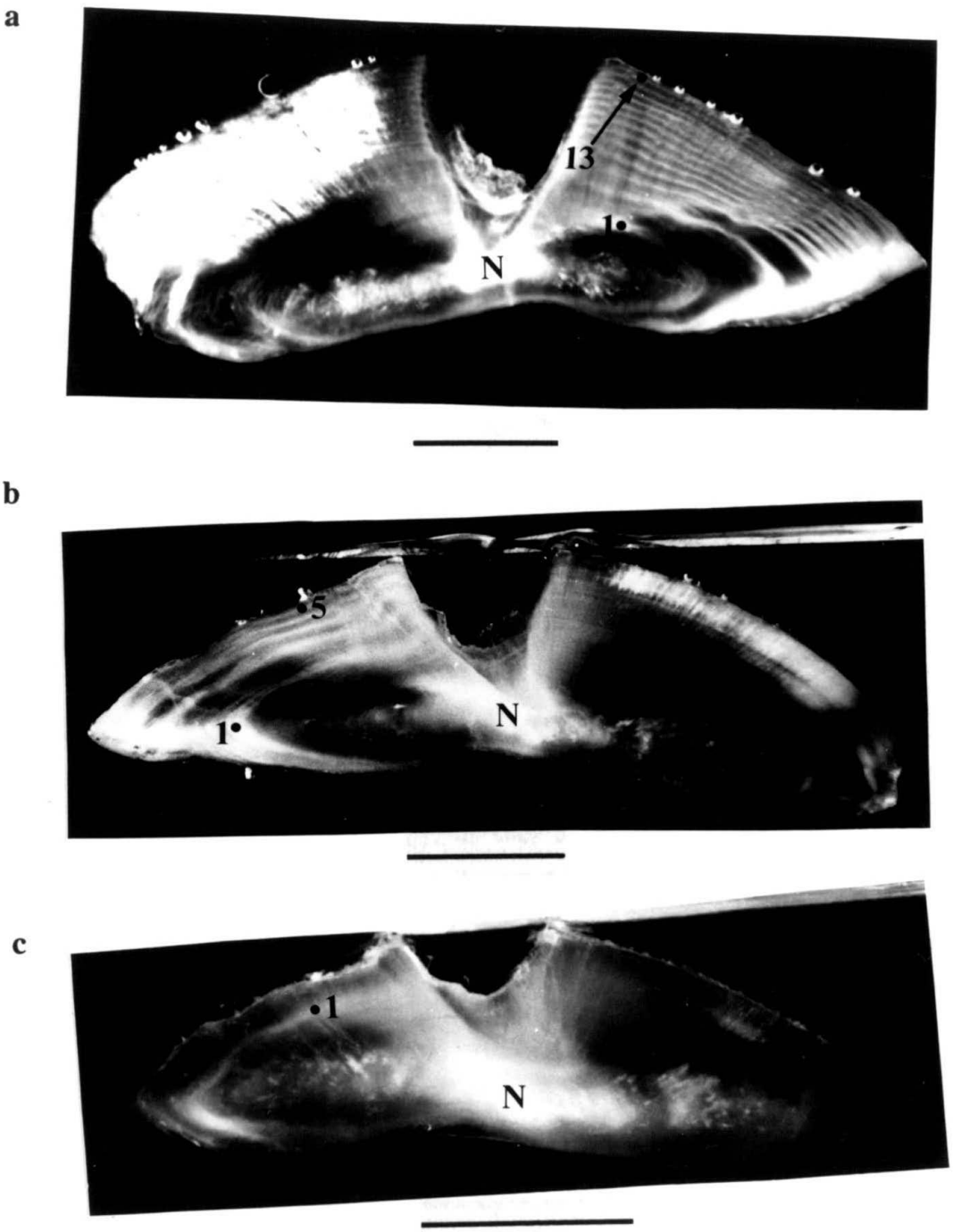


Plate 5.7. Examples of sectioned otoliths of *Lutjanus fulviflamma* under reflected light. Ages of fish in years correspond to counts of opaque bands. Shown are (a) a 13 yr old, (b) a 5 yr old and (c) a 1 yr old specimen. N=nucleus; scale bar = 1 mm.

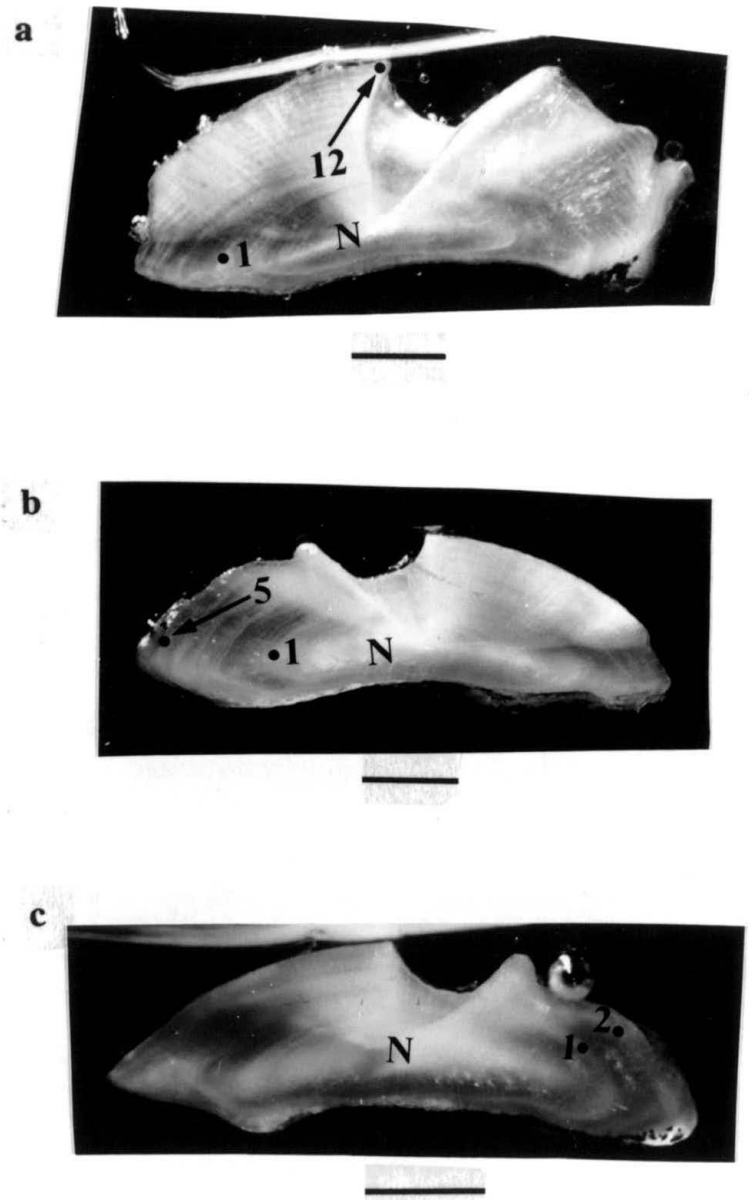


Plate 5.8. Examples of sectioned otoliths of *Lethrinus harak* under reflected light. Ages of fish in years correspond to counts of opaque bands. Shown are (a) a 12 yr old, (b) a 5 yr old and (c) a 2 yr old specimen. N=nucleus; scale bar = 1 mm.

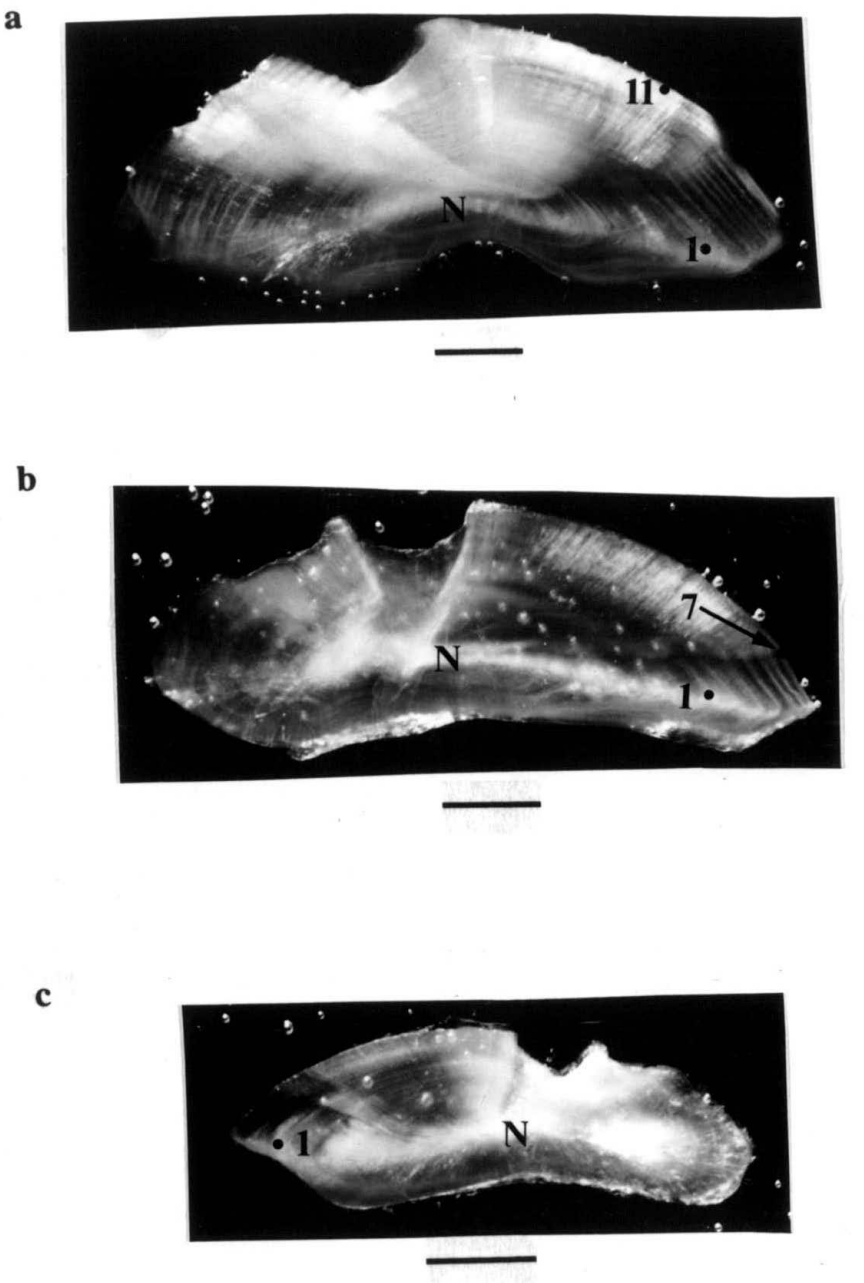


Plate 5.9. Examples of sectioned otoliths of *Lethrinus lentjan* under reflected light. Ages of fish in years correspond to counts of opaque bands. Shown are (a) an 11 yr old, (b) a 7 yr old and (c) a 1 yr old specimen. N=nucleus; scale bar = 1 mm.

Chapter 6: SIZE AND AGE AT FIRST SEXUAL MATURITY OF *LUTJANUS FULVIFLAMMA* (Forsskål, 1775), *LETHRINUS HARAK* (Forsskål, 1775) AND *L. LENTJAN* (Lacèpéde, 1802)

6.1 INTRODUCTION

One of the major problems identified in reef fisheries is the maintenance of a viable spawning stock biomass (Plan Development Team (PDT) 1990). Fishery management agencies often implement legal minimum size limits on fish species to partly address this problem. The basis for this important management practice is a knowledge of the size at first sexual maturity of fish. The objective of this management strategy is to allow fish to spawn at least once before they recruit to the fishery. The determination of the size limit is based on the trade off between maintaining a sufficient proportion of spawning stock biomass per recruit while at the same time attempting to maximize yield per recruit (Hill 1990).

Three species of reef fish, *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan* are included in this study. On the GBR, little is known about the reproductive biology of many lutjanids and lethrinids, including these three species. Information on size at first sexual maturity and seasonality on the GBR exists for only 4 of 20 species of lethrinids (*Lethrinus miniatus*, *L. nebulosus*, *L. semicinctus* and *Lethrinus* sp.2) and 3 of 24 species of lutjanids (*Lutjanus sebae*, *L. malabaricus* and *L. erythropterus*) (Williams and Russ 1994, McPherson *et al.* 1992). Additional information on the type of sexual patterns of lethrinids on the GBR exists for only 8 of 20 species (*Lethrinus nematacanthus* (=*genivittatus*), *L. choerorhynchus* (=*nebulosus* in Carpenter and Allen 1989), *L. lentjan*, *L. variegatus* (=*Lethrinus* sp.2), *L. rubrioperculatus*, *L. chrysostomus* (=*L. miniatus*), *L. nebulosus* and *L. fraenatus* (=*L. laticaudis*) (Young

and Martin 1982; synonyms from Williams and Russ 1994), and 3 of 24 species of lutjanids (same 3 species above (McPherson *et al.* 1992)). Data on age at first sexual maturity is lacking for most of the lutjanids and lethrinids on the GBR.

The primary objectives of this study are:

1. To determine size and age at first sexual maturity of *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*.

2. To describe sexual patterns in these three species.

6.2 MATERIALS AND METHODS

Histological analysis was conducted on gonads removed from fishes used in the age, growth and mortality study (see Chapter 5) to assess stages of oocyte development and to determine sexual maturity. Male and female gonads were distinguishable macroscopically for *L. fulviflamma* but often not for *L. harak* and *L. lentjan*. Male gonads of *L. fulviflamma* displayed the angular configuration typically seen among males in gonochoristic fish populations (J.H. Choat pers. com.). Previous histological studies have not found evidence of hermaphroditism in lutjanids and led Grimes (1987) to conclude that the Lutjanidae are gonochoristic. All gonads for *L. harak* (n=131) and *L. lentjan* (n=96) were processed because of the difficulty in distinguishing females from males. For *L. fulviflamma* only the females (n=94) were included in the histological examination.

Transverse sections from the central portion of each gonad were processed following Winsor (1984). Sections 5µm thick were prepared from each gonad and stained with Mayers Haematoxylin and Youngs eosin-erythrosin (HE stain) (Winsor 1984). Developmental stages of oocytes were adapted from Yamamoto *et al.* (1965), Moe (1969), Ferreira (1993a) and Adams (1996). Oocytes were staged as follows:

Stage 1 (Plates 6.1a, 6.2a and 6.3a) -previtellogenic, small rounded oocytes, dense basophilic cytoplasm (appearing as blue to purple in HE stain); Stage 2 (Plates 6.1a, 6.2a and 6.3a) -similar to stage 1 but nucleolus is conspicuous (chromatin nucleolus stage); Stage 3 (Plates 6.1b, 6.2b and 6.3b) -oocytes relatively larger with a larger nucleus, cytoplasm is strongly basophilic, and lampbrush chromosomes are formed in the nucleus visible under higher magnification; Stage 4 (Plates 6.1b, 6.2b and 6.3b) - differs from previous stage by the general enlargement of oocytes together with signs of cytoplasmic changes indicated by less basophilic substances and formation of "yolk vesicles" or cortical alveoli (Wallace and Selman 1981); Stage 5 (Plates 6.1b, 6.2b and 6.3b) -oocytes with vitellogenin-derived yolk in the cytoplasm (Burton *et al.* 1997) and zonia radiata is well formed. General descriptions of the male gonad followed that of Sadovy and Shapiro (1987) for *L. harak* and *L. lentjan*. Developmental stages of the testes were not described here.

Maturity was determined based on the most advanced oocyte in the gonad. Immature females were those that had not spawned previously. The gonads of immature females were dominated by stage 1 and 2 oocytes and were characterized by a relatively thin gonad wall (Burton *et al.* 1997) and the absence of brown bodies (atrefied vitellogenic oocytes; Sadovy and Shapiro 1987) and post ovulatory follicles. Examples of immature female gonads of *L. fulviflamma*, *L. harak* and *L. lentjan* are shown in Plates 6.1a, 6.2a and 6.3a, respectively. Females in the process of active vitellogenesis (oocytes in stages 3-5) were considered sexually mature. Examples of these are shown in Plates 6.1b, 6.2b and 6.3b for *L. fulviflamma*, *L. harak* and *L. lentjan*, respectively. Gonads of mature resting females were dominated by stage 1 and 2 oocytes (similar to those of immature females) but the presence of brown bodies (Young and Martin 1982, Sadovy and Shapiro 1987), post ovulatory follicles and a relatively thicker gonad wall (Burton *et al.* 1997) were evidence that these fish had spawned previously. The presence of these gonadal structures distinguished mature from immature females even when all oocytes were in developmental stages 1 and 2.

Atretic bodies such as brown bodies were unlikely to occur in virgin females unless they were stressed by captivity or crowding (Polder 1971, Saidapur 1978). Brown bodies in their typical circular form and post ovulatory follicles may

disintegrate through atresia after a period of time. However, traces of lipofuscin (the major component of brown bodies) may remain in the gonad during and after degeneration (Adams 1996). Therefore, additional sections from all gonads with only stage 1 and 2 oocytes were made and stained with Alcian Blue PAS (Periodic Acid Solution) to detect the remnants of atresia and distinguish immature from mature (but resting) gonads. Brown bodies and lipofuscin (products of vitellogenic atresia) stain magenta in color when treated with Alcian Blue PAS (Adams 1996). Examples of an immature gonad and a mature resting gonad stained in Alcian Blue PAS are shown in Plates 6.4a and b, respectively. The presence/absence of lipofuscin was used to supplement the more conventional criteria in distinguishing mature resting females from immature virgin females. A plot of wet weight of gonads with stages 1 and 2 oocytes against fish size (FL in mm) and fish age (years) was used to estimate the critical weight of gonad, fish size and fish age when first sexual maturation began.

The gonadosomatic index (GSI) was computed for each fish as the ratio of gonad wet weight to wet weight of fish multiplied by 100. Samples were grouped according to the three sampling months (March, July and October) possible in the study. Mean monthly GSI was plotted to estimate when gonads increased in weight during the year, suggesting the spawning period for the three species.

The size and age at first maturity of a species was estimated by plotting the percentage of mature and immature female individuals against size (mm in FL) and age (years) classes. The size or age class at maturity was defined as that where more than 50% of the individuals were sexually mature on *proviso* that larger or older classes had higher percentages of sexually mature individuals.

Sex ratios, age and size frequency distributions of both sexes and histological evidence from male gonads were used to detect the type of sexual pattern of the three species. In species suspected to undergo sex reversal, size and age of sex change were estimated based on the overlap zone in the size or age distributions of males and females (Shapiro 1984). Criteria to diagnose hermaphroditism in fishes followed Sadovy and Shapiro (1987).

The mean wet weights of gonads between mature resting females and immature females of *L. fulviflamma* and *L. harak*, and the mean sizes and the mean ages of males and females of each of the three species were compared using t-tests at α=0.05 (Sokal and Rohlf 1981). F-tests for homogeneity of variance (α=0.05) were carried out on each data set prior to t-tests. The data on wet weights of gonads of mature resting females and immature females for *L. fulviflamma* and the sizes of males and females of *L. harak* required data transformation ($\log_{10}$ x). The transformed data passed the F-tests. All calculations were made using the software STATISTICA Release 5.0 (StatSoft, Inc. 1995).

6.3 RESULTS

6.3.1 Histological Examination of Gonads

The appearance of the various stages of oocytes was similar for all three species (Plates 6.1-3). All gonads judged as mature contained all five stages of oocytes with the majority of oocytes in stages 4 or 5 (Plates 6.1b, 6.2b and 6.3b). In many of these, brown bodies were distinctly visible (Plates 6.1b and 6.2b) suggesting previous spawning. Gonads of immature females contained only neatly packed stage 1 and 2 oocytes (Plates 6.1a, 6.2a and 6.3a). In gonads of many of the mature resting females, oocytes in stages 1 and 2 were arranged in a disorganized manner around connective tissues (Plate 6.4b). Lipofuscin occurred in mature resting females as clumps of rounded structures which were magenta in color (Plate 6.4b).

Male gonads of *L. harak* and *L. lentjan* were rounded to oblong in shape. Histological examination revealed evidence of sex reversal. Evidence included the presence of *i*) an ovarian lumen, *ii*) brown bodies, *iii*) lobed spermatogonia, and *iv*) a thick gonadal wall in young males and a thin gonadal wall in old males (Plates 6.5a and b). These structures were verified by J.H. Choat as consistent with the appearance

of secondary males. The structures were compared with three male gonad samples of *L. fulviflamma*. Examination showed that gonads of male *L. fulviflamma* did not exhibit any of the above structures.

Histological examinations showed that of the 94 female *L. fulviflamma*, 68 were mature and 21 immature. For *L. harak*, 39 were determined as males and 92 were females. Of the females, 68 were mature and 24 immature. For *L. lentjan*, 11 were found to be males and 85 were females. Of the females, only 10 were mature and 75 were immature.

6.3.2 Sexual Maturity

The size at first sexual maturity for *L. fulviflamma*, *L. harak* and *L. lentjan* were estimated at 200-209, 220-229 and 250-259 mm FL, respectively (Fig. 6.1a-c). Some female individuals of *L. fulviflamma* may begin to mature at sizes as small as 160-169 mm FL, and conversely, a few may still be immature at sizes as large as 220-229 mm FL (Fig. 6.1a). Females of *L. harak* began to mature at 200-209 (Fig. 6.1b) and around 250 mm FL for *L. lentjan* (Fig. 6.1c).

The age at first sexual maturity was estimated between 2-3 years for *L. fulviflamma* (Fig. 6.2a), 2 years for *L. harak* (Fig. 6.2b) and 3 years for *L. lentjan* (Fig. 6.2c). Some females of *L. fulviflamma* began to mature at 0+ years of age (Fig. 6.2a), while *L. harak* began at 1 year of age (Fig. 6.2b) and *L. lentjan* at 3 years of age (Fig. 6.2c).

Gonads having lipofuscin (i.e. those of mature resting females) were clearly separated from those without lipofuscin (i.e. those of immature females) in plots of gonad weight against fish size (Fig. 6.3) and fish age (Fig. 6.4). The demarcation between weights of gonads with and without lipofuscin was distinct. Gonads with lipofuscin were significantly heavier than those without lipofuscin in *L. fulviflamma* ($t_{0.05[47]} = 8.200$, $p<0.000$) and in *L. harak* ($t_{0.05[32]} = 8.684$, $p<0.000$). The heavier gonads belonged to larger sized (Fig. 6.3) and older fish (Fig. 6.4). This suggests that

females of *L. fulviflamma* begin to mature when their gonads attain a weight of about 0.6-0.7g at a size of a little over 200 mm FL (Fig. 6.3a) and at an age of less than 3 years (Fig. 6.4a). Similarly, female *L. harak* begin to mature when their gonads reach a weight of about 0.8-9g at a size of about 220 mm FL (Fig. 6.3b) and at an age of less than 4 years (Fig. 6.4b). This increase in gonad weight of virgin females is likely to occur around spring (i.e. spawning season, see below).

These estimates of size and age at first sexual maturity based on gonad weights and presence of lipofuscin for *L. fulviflamma* and *L. harak* are within the range of estimates based on plots in Figures 6.1a and b, and 6.2a and b above. The size of the smallest fish with a gonad containing lipofuscin was 213 mm FL for *L. fulviflamma* (Fig. 6.3a) and 246 mm FL for *L. harak* (Fig. 6.3b). Interestingly, these sizes were larger than the upper estimates (209 and 229 mm FL, respectively) of the size at first maturation in the plots in Figures 6.1a and b, suggesting that these individuals have most likely spawned before. Similarly, the youngest fish among those with lipofuscin were 3 and 4 years for *L. fulviflamma* (Fig. 6.4a) and *L. harak* (Fig. 6.4b), respectively. These ages are older than estimates of the age at first sexual maturity obtained using plots in Figures 6.2a and b (2-3 years for *L. fulviflamma* and 2 years for *L. harak*). This strongly suggests that these individuals may have spawned previously. Thus, the presence of lipofuscin in gonads of fish appears to be a reliable indicator of mature resting females. There were insufficient mature resting individuals to do a similar analysis for *L. lentjan*.

Mean GSI increased during October for all three species (Fig. 6.5). The mean GSI increased by a factor of 13 in October for *L. fulviflamma* (Fig. 6.5a), a factor of 2.4 in October for *L. harak* (Fig. 6.5b) and a factor of 2.3 in October for *L. lentjan* (Fig. 6.5c).

6.3.3 Sex Ratios at Size and at Age

The overall male to female ratios for *L. fulviflamma*, *L. harak* and *L. lentjan* were 1:1.36, 1:2.36 and 1:7.73, respectively. Length frequency distributions of males

and females for *L. fulviflamma* showed that both sexes were represented in most size classes, with modes occurring close to the middle of the class ranges (Fig. 6.6a). The distribution of lengths of *L. fulviflamma* almost completely overlapped for each sex. Although the female sample size of *L. fulviflamma* was larger than that of the males in the larger size classes, the mean length of both sexes did not differ significantly (male = 214.5 ± 20.9, female = 221.8 ± 26.2: FL in mm; $t_{0.05[161]} = 1.908$, $p>0.05$).

Females were represented in all size classes of the length frequency distribution of *L. harak* with peaks at three size classes (220-229, 240-249 and 260-269 mm FL) (Fig. 6.6b). The males of *L. harak* first appeared in substantial numbers in the 250-259 mm (FL) size class with a mode at 260-269 mm FL. However, two male individuals were recorded at a lower size class (230-239 mm FL) (Fig. 6.6b). Males of *L. harak* were significantly larger (mean FL = 273.6 ± 15.6 mm) than females (mean FL = 233.3 ± 35.9 mm) ($t_{0.05[129]} = 5.996$, $p<0.000$).

For *L. lentjan*, the distribution of lengths of females was highly biased toward the smaller size classes with peaks at 170-179 and 200-209 mm FL. Males did not start to appear consistently until 280-289 mm (FL) (Fig. 6.6c). The males of *L. lentjan* were significantly larger (mean FL= 296.7 ± 24.2 mm) than the females (mean FL = 204.5 ± 40.7 mm) ($t_{0.05[94]} = 7.334$, $p<0.000$). This result may have been influenced by the small samples of the larger size classes.

Age frequency distributions of males and females of *L. fulviflamma* overlapped substantially (Fig. 6.7a). Both sexes were represented in each age class with a male to female ratio slightly lower than unity in most age classes. Mean age of each sex did not differ significantly (male = 5.3 ± 3.6, female = 5.6 ± 3.9 years) ($t_{0.05[161]} = 0.457$, $p>0.05$).

The age frequency distribution of females of *L. harak* was biased towards the younger age classes (Fig. 6.7b), with a mode at age class 2. Males of *L. harak* did not appear consistently until age class 4, peaking at age class 8. Two male individuals were recorded at ages 1 and 2 years (Fig. 6.7b). The mean age of males of *L. harak*

(7.7 ± 2.6 years) was twice that of females (3.3 ± 2.9 years) ($t_{0.05[129]}$ = 8.033, p<0.000).

The age distribution of female *L. lentjan* was highly biased towards the younger age classes. Males were absent until age class 6 (Fig. 6.7c). The mean age for males of *L. lentjan* was nearly 7 times (9 ± 3.2 years) that of females (1.3 ± 2.4 years) ($t_{0.05[94]}$ = 9.701, p<0.000).

6.4. DISCUSSION

The occurrence of asynchronous stages of oocytes in mature gonads in all of the three species suggested that these species were batch spawners, probably spawning over a protracted reproductive season. Based on the results of the mean GSI's, the spawning period for *L. fulviflamma* probably begins in October and may last for a few months on the GBR. This finding for *L. fulviflamma* was consistent with evidence from histological examinations of gonads of Lutjanidae (Grimes 1987). Based on histological evidence, Grimes (1987) concluded that Lutjanidae were batch spawners. Similarly, evidence from 3 lutjanid species on the GBR showed that spawning periods could last between 5-8 months, with peaks in November-January for *L. sebae* and *L. malabaricus*, and October-November for *L. erythropterus* (McPherson *et al.* 1992).

The spawning period for *Lethrinus harak* and *L. lentjan* may start after October and could last for a few months. This is the first data for spawning seasonality for *L. harak* and *L. lentjan* on the GBR. Little is known about the spawning seasonality for many lethrinids on the GBR (Williams and Russ 1994). In the central GBR (off Townsville region), GSI's of *L. miniatus* peaked in July-August, suggesting that spawning of this species may extend over several months (Walker 1975). In the southern GBR (Swains Reefs and the Capricorn Bunker Group), histological evidence and GSI's of female *L. miniatus* indicated that spawning activity occurred during July

to November with peaks during the latter three months of this period (Brown *et al.* 1994). The GSI's of other lethrinids in the central GBR, such as for *L. nebulosus*, peaked in June to July, *L. semicinctus* in December-January and *Lethrinus* sp.2 in September to October (Walker 1975). This indicates that spawning period for these species on the GBR occurs once a year between June and January. In contrast, Toor (1964a) found that the spawning of *L. lentjan* occurred twice a year during December to February and June to August in India. In Okinawa (Japan), the spawning period of *Lethrinus rubrioperculatus* was longer (April to December) (Ebisawa 1997) than in any of the above lethrinid species on the GBR.

The seasonal spawning pattern observed for the three study species was consistent with those found for other species of fish on the GBR. The spawning period of *Plectropomus maculatus* in the central GBR (Ferreira 1993b) and of *P. leopardus* in the northern and central GBR (Ferreira 1995) occurred during September to November. Doherty (1983) reported that the spawning period of *Pomacentrus flavicauda* and *P. wardi* in the southern GBR was during spring and summer (October-March). Histological evidence from female gonads and GSI's showed that *Scarus rivulatus* and *S. schlegeli* spawn during September to January and May to September, respectively, in the northern GBR (Lou 1992a). Doherty (1991) reviewed fish recruitment and demonstrated a single recruitment peak of most reef fish on the GBR during February to March. Such data is also consistent with a single spawning season late in the calendar year.

6.4.1 Size and Age at First Sexual Maturity

The estimated size at first sexual maturity of 200-209 mm FL (2-3 years) for *L. fulviflamma* at Lizard Island was higher than the estimates Loubens (1980a) and Talbot (1960) obtained for the same species in New Caledonia (172 mm SL) and east Africa (160 mm SL), respectively. This estimate however, was within the size range of what Allen (1985) reported for *L. fulviflamma* (200-250 mm TL; unsourced).

In this study, *L. fulviflamma* attained sexual maturity at roughly 79-82% of its maximum length (ML). This observation differs with that of Grimes (1987) who suggested that, in general, lutjanids reach sexual maturity at approximately 40-50% of their maximum lengths. In New Caledonia, Loubens (1980a) showed that *L. fulviflamma* attained sexual maturity at 60% of its maximum length (ML) while Talbot (1960) reported maturity attained at 73% of ML for the same species in East Africa. Available data for other lutjanids on the GBR indicate that they reach sexual maturation at sizes greater than 50% of their ML. The onset of sexual maturation for *L. sebae* was 548 mm FL or 62% of ML, *L. malabaricus* 576 mm FL or 69% of ML and *L. erythropterus* 485 mm FL or 81% of ML (computed from McPherson *et al.* 1992 and McPherson and Squire 1992). If Grimes (1987) is correct, then the size estimates at first sexual maturity closer to ML for some lutjanids on the GBR tend to imply that sexual maturation is delayed for these lutjanids on the GBR. One of the direct consequences of fishing mortality is a reduction in population density which consequently reduces total reproductive output of a population. Ecological and evolutionary theory suggests that populations tend to respond to such disturbances (Calow 1979). A response to the reduction of population density caused by fishing mortality can be rapid changes in the reproductive strategy in order to maintain evolutionary fitness, and may involve reproduction at a smaller size or younger age. This has been noted in exploited populations of the chinook salmon *Oncorhynchus tshawytscha* (Ricker 1981), the plaice *Pleuronectes platessa* (Horwood et al. 1986) and the spiny lobster *Panulirus marginatus* (DeMartini *et al.* 1992) but has not been documented for reef fishes. An early onset of sexual maturation in terms of size or age may be a consequence of intensely exploited populations. This happens when individuals that mature at larger sizes or older ages are harvested more intensively, leaving the population with spawners that are smaller-sized and younger. A cumulative genetic effect may result in a population in which the average size and age of maturation decreases (e.g. Ricker 1981). The perceived delay in the onset of sexual maturation of some lutjanids on the GBR relative to other areas may be indicative of relatively low levels of fishing mortality.

The estimated size and age at first sexual maturity for *L. harak* (210-229 mm FL at 2 years) may be the first estimate for this species. These estimates are approximately 74-84% of maximum length and 13% of the life span.

In this study, *L. lentjan* reached first sexual maturity at sizes between 250-259 mm FL and at 3 years of age. This size estimate was lower than obtained by Toor (1964a; 300 mm SL) for the same species in India. The size at onset of sexual maturation in the present study was 78-84% of its ML. This was nearly twice the estimate of Toor (1964a; 47% of ML). This disparity should be treated with caution because the maximum length for the *L. lentjan* population could have been underestimated in this study. Toor's (1964a) estimate for age at first sexual maturity for *L. lentjan* (3 years) was the same as obtained in this study.

The estimated sizes at first sexual maturity of *L. harak* and *L. lentjan* in this study were similar to that of *L. rubrioperculatus* in Okinawa (Ebisawa 1997). If the same criteria of sexual maturity in this study were applied to the samples of *L. rubrioperculatus*, this species reached first sexual maturity at approximately 220-229 mm FL (calculated from Table 3 of Ebisawa 1997).

Possible use of lipofuscin

Atresia of unspawned vitellogenic oocytes is well documented and is a common phenomenon in the production of brown bodies. It has been used as evidence for previous vitellogenesis and spawning when found in mature resting females (Sadovy and Shapiro 1987), and for female to male sex reversal when found in testes (Young and Martin 1982). Confusion arises in distinguishing gonads of mature resting from gonads of immature (prespawned) females when brown bodies and similar structures have degenerated. Oocyte atresia has been known to produce lipofuscin (Sadovy and Shapiro 1987, Adams 1996). The staining method (Alcian Blue PAS), used to detect lipofuscin, helped to differentiate between gonads of mature resting and immature females (pers. obs., Adams 1996). The plot of gonad weight against fish size and fish age provided estimates of gonad weight, fish size and fish age at first sexual maturity for *L. fulviflamma* and *L. harak*. These estimates were close to those derived from plots of the percentage of mature individuals against size and age classes. This

method may provide a relatively reliable first approximation of size and age at first sexual maturity, as it reduces subjectivity often associated with detecting mature resting females.

6.4.2 Sexual Patterns

The sexual pattern for *L. harak* and *L. lentjan* appeared consistent with protogynous hermaphroditism. Histological evidence from males of both species showed structures indicating sex reversal. This evidence included the presence of an ovarian lumen, the presence of brown bodies, the lobed arrangement of spermatogonia, and a gonadal wall that was thicker for younger and thinner for older males. These structures, when present in male gonads, suggest that the gonads were formerly functional ovaries (Sadovy and Shapiro 1987).

The above histological findings for *L. harak* and *L. lentjan* were supported by the size and age frequency distributions of each sex, and by the sex ratios of size and age classes. The frequency distributions indicated *i*) that females dominated the smaller size and younger age classes, with virtually no males present in these classes, *ii*) males began to appear in the larger size and older age classes, but did not dominate these classes, and *iii*) the mean size of males was significantly larger than females in both species. These frequency distributions suggested that individuals started life as females and some individuals underwent sex reversal later in life. The size and age at which *L. harak* underwent sex change appeared to be between 250-259 mm FL at around 4 years. The lack of samples in the larger size and older age classes made similar estimation difficult for *L. lentjan*, although a tentative estimate may be 280-289 mm FL at 6 years. This estimate was well within the range of two size classes (253-271 and 289-307 mm (measured length not indicated)) obtained for sex change of *L. lentjan* on the northwest shelf of Australia and in the Gulf of Carpentaria in northeastern Australia, respectively, when males began to appear in the length distributions (Table 1 in Young and Martin 1982).

The male to female ratios for *L. harak* and *L. lentjan* in the present study were far less than unity, indicating a large bias towards females, typical of protogyny. Furthermore, the mean size of males was significantly larger than females for *L. harak* and *L. lentjan*. This result is consistent for many protogynous populations, where males are generally bigger than females within a social unit in which sex change is socially controlled (Shapiro 1984, Sadovy and Shapiro 1987). In some protogynous populations of scarids, males maintain a harem and large size is an advantage in maintaining a harem (Choat pers. com.). The gender switching at a certain size and age range and maintenance of harems of some scarids is thought to be a highly successful reproductive strategy in many perciforms (Shapiro 1984). This type of haremic strategy, at least at the time of spawning, is probably likely to occur in *L. harak* and *L. lentjan*.

Studies of other species of lethrinid support the above observations of a protogynous sexual pattern for *L. harak* and *L. lentjan* in this study. Ebisawa (1997) observed transitional individuals in samples of *L. rubrioperculatus* in Okinawa collected between February and December and concluded that this species exhibited protogynous hermaphroditism. Furthermore, Young and Martin (1982) examined 8 species of Lethrinidae, including *L. lentjan*, and concluded that protogynous hermaphroditism was the typical mode of sexuality amongst lethrinids.

Sadovy and Shapiro (1987) established the criteria to diagnose hermaphroditism in fishes and pointed out that the two strongest lines of evidence for sex change were the observation of transitional individuals and the demonstration of sex change by experimental induction. While the histological evidence, the size and age distributions of each sex and the sex ratios for *L. harak* and *L. lentjan* in this study were consistent with protogyny, this study did not observe transitional individuals. An experiment to induce sex change was beyond the scope of this study.

Lutjanus fulviflamma is gonochoristic. Histological examination of a few male gonads, the sex ratio and the size and age frequency distributions of the sexes indicated that individuals do not undergo sex change. In a review of the reproductive biology of

the Lutjanidae, Grimes (1987) concluded that the sexual pattern of this family is gonochoristic (i.e. there is no histological evidence to the contrary).

The estimates of size and age at first sexual maturity, knowledge of the spawning period and of the type of sexual pattern of these species have strong implications for management of the fishery for these species in the future. For example, to protect a viable spawning stock for these species, legal size limits in open reefs must consider the sizes at first sexual maturity, as well as the sizes at which individuals in protogynous populations begin to reverse sex. At present there are no minimum size nor recreational bag limits for the three species on the GBR. A size limit of 250 mm TL exists for some smaller lutjanids such as *L. adetii*, *L. russelli* and *L. carponotatus*, but none for the smaller lethrinids on the GBR (QFMA 1996). A size limit 10% above the size at first sexual maturity for *L. fulviflamma* might help ensure sufficient spawning stock biomass. This would represent a legal minimum size limit of *L. fulviflamma* of 230 mm FL (which is about 250 mm TL).

In the case of *L. harak* and *L. lentjan*, capture of fish above 260 and 290 mm FL (sizes at which sex reversal apparently begin, respectively) should be avoided. However, there is a need for further study of these two species since these estimates were based on a small sample size. There is a need to compare estimates from different geographic locations on the GBR and elsewhere to better understand this problem. Furthermore, conservative catch limits (e.g. bag limits for recreational fishers) for these three species should be imposed on open reefs until the effects of fishing on the stocks are better understood.

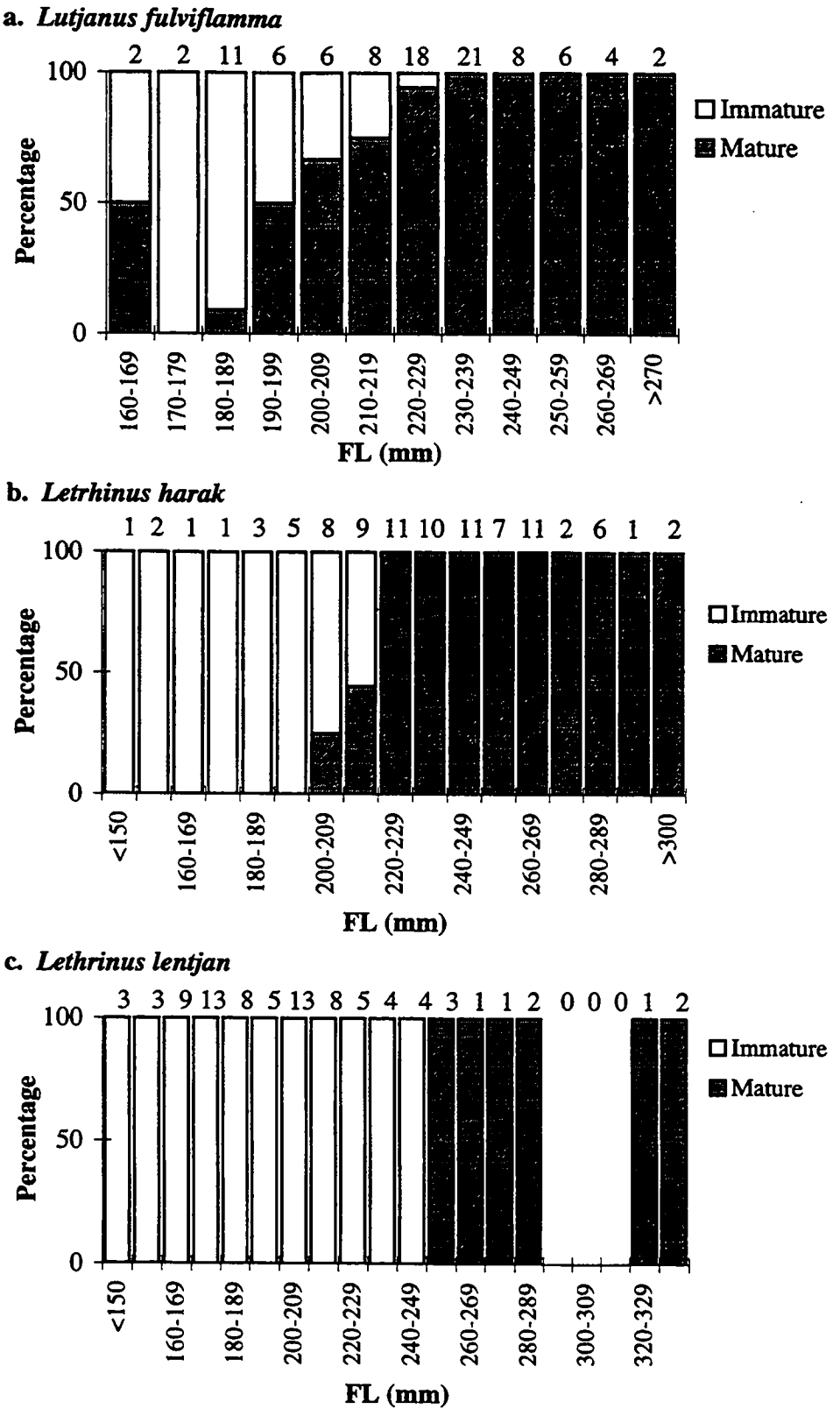


Figure 6.1. Percentages of mature and immature females against fork length (FL) for the 3 species. Sample size for each length class is indicated by the number at the top of the bar.

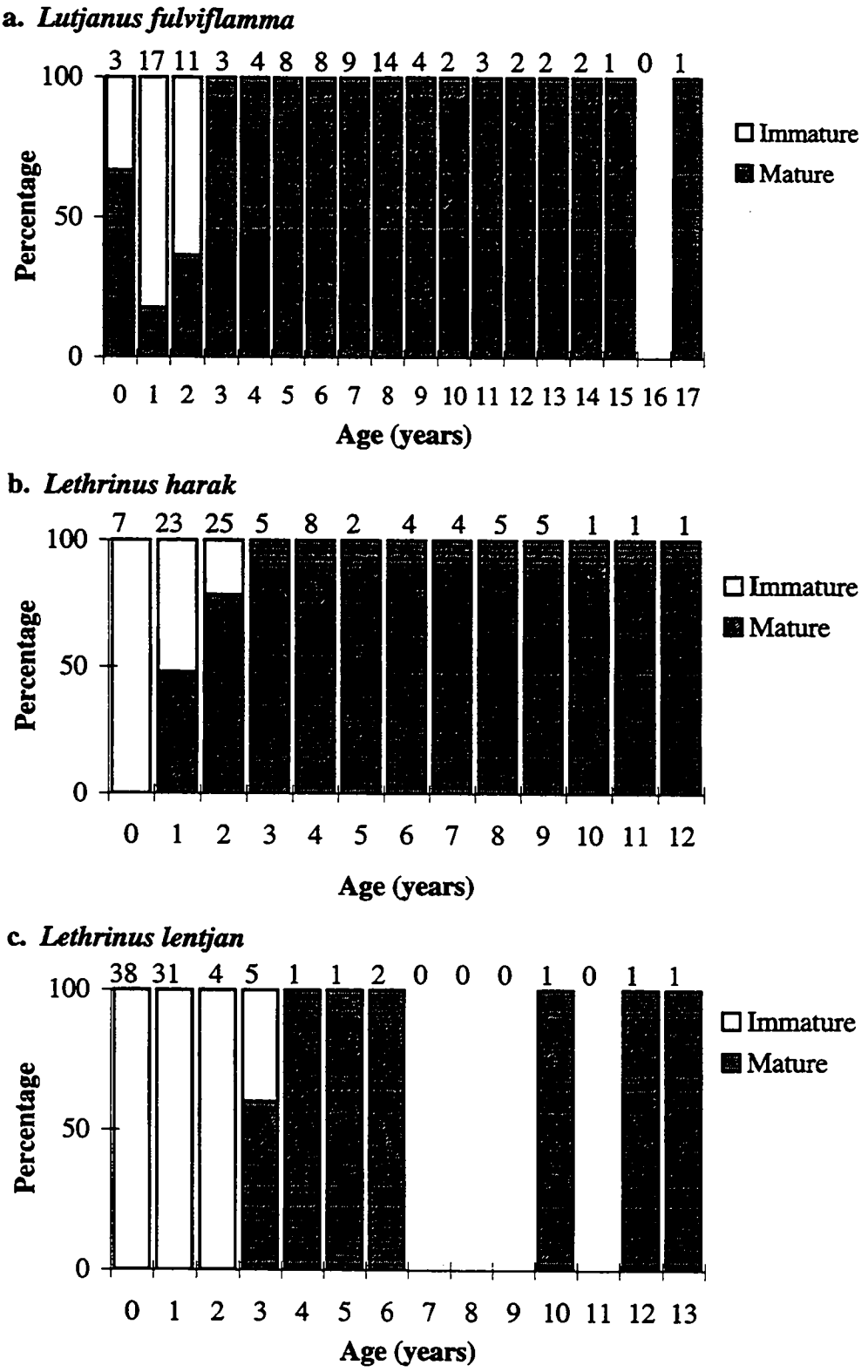
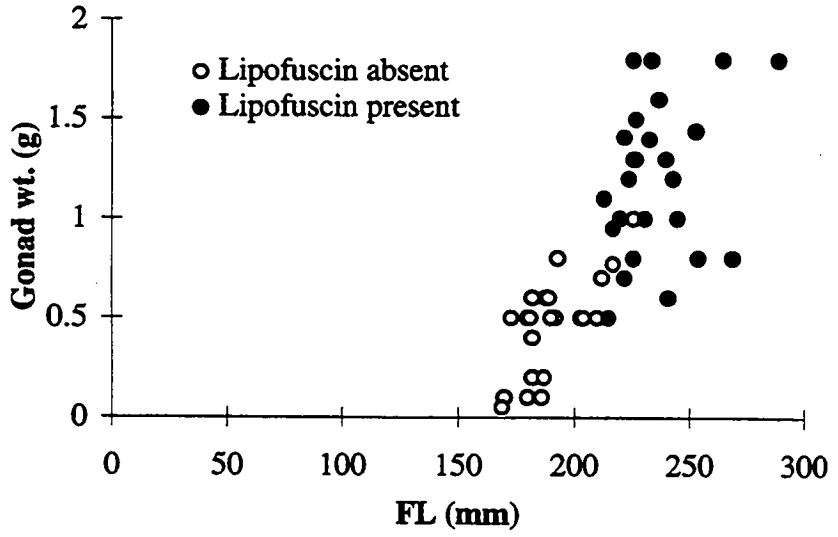


Figure 6.2. Percentages of mature and immature females against ages for the 3 species. Sample size of each age class is indicated by the number at the top of the bar.

a. *Lutjanus fulviflamma*



b. *Lethrinus harak*

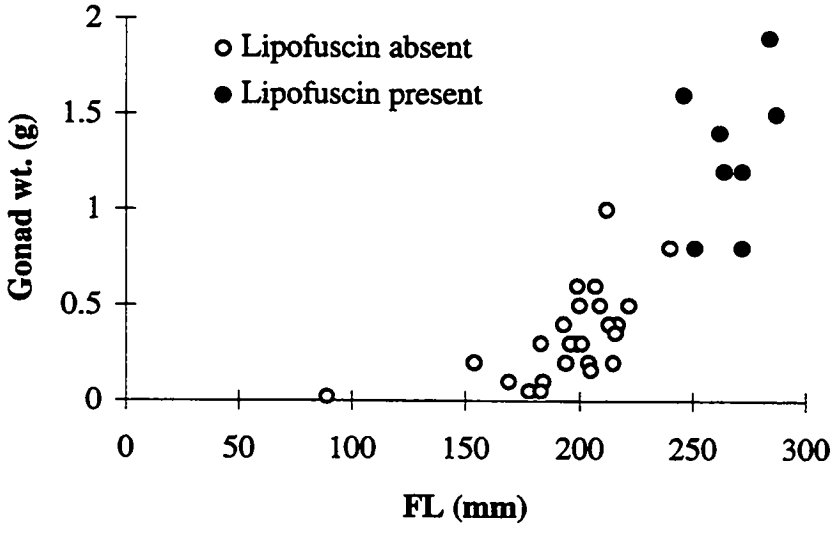
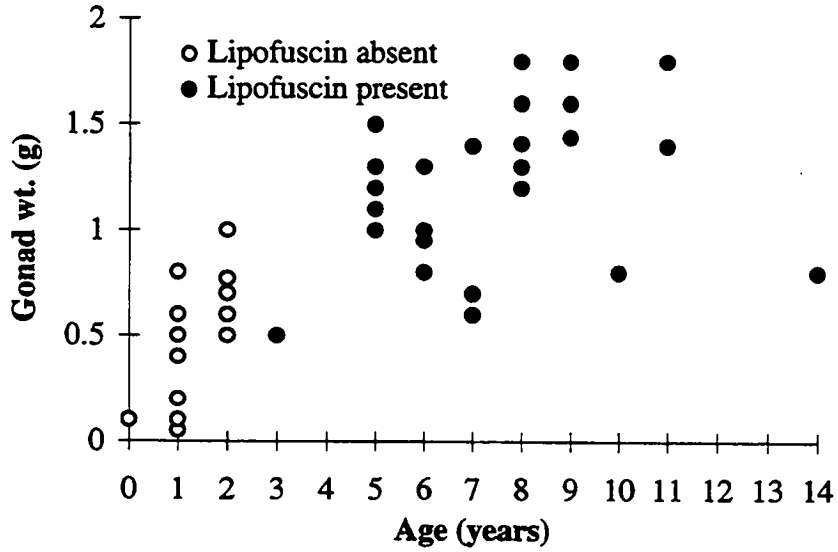


Figure 6.3. Weight of female gonads with stages 1 and 2 oocytes only, plotted against fork length (FL) for (a) *Lutjanus fulviflamma* (n=49) and (b) *Lethrinus harak* (n=34). Gonads of mature resting females (with lipofuscin -the major component of brown bodies) were significantly heavier than unspawned immature gonads for both species (a. $t_{0.05[47]}$ = 8.200 and b. $t_{0.05[32]}$ = 8.684, $p<0.000$ for both).

a. ***Lutjanus fulviflamma***



b. ***Lethrinus harak***

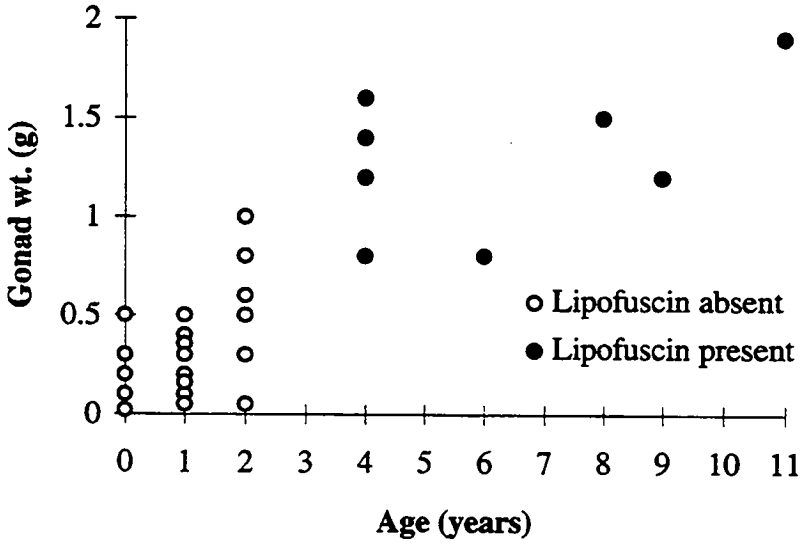
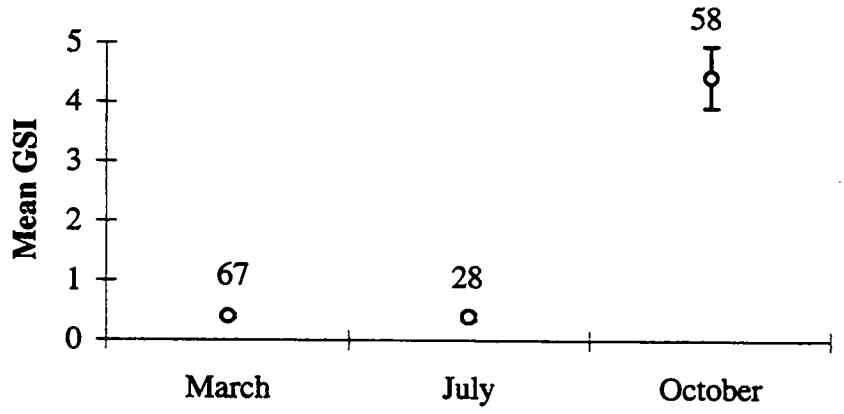
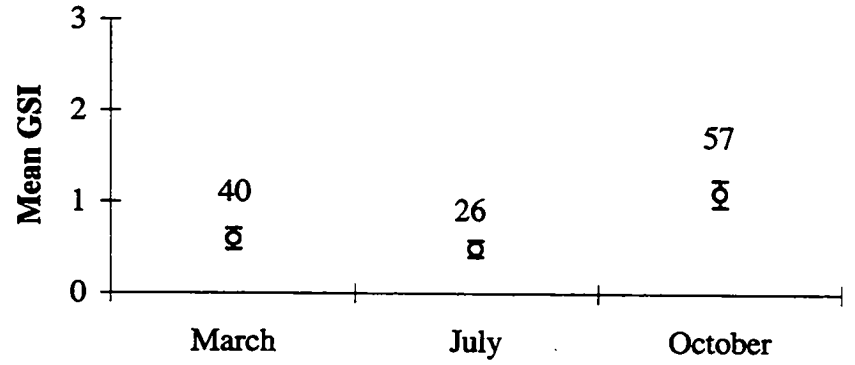


Figure 6.4. Weight of female gonads with stages 1 and 2 oocytes only, plotted against age (years) for (a) *Lutjanus fulviflamma* (n=49) and (b) *Lethrinus harak* (n=34). Gonads of mature resting females (with lipofuscin -a major component of brown bodies) were significantly heavier than unspawned immature gonads for both species (a. $t_{0.05[47]}$ = 8.200 and b. $t_{0.05[32]}$ = 8.684, $p<0.000$ for both) .

a. ***Lutjanus fulviflamma***



b. ***Lethrinus harak***



c. ***Lethrinus lentjan***

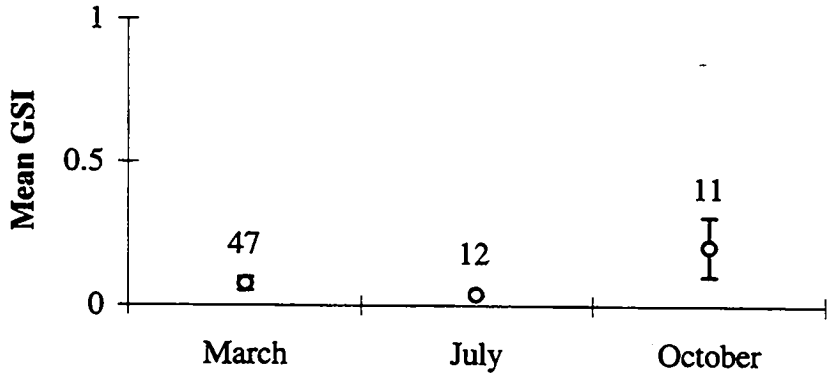
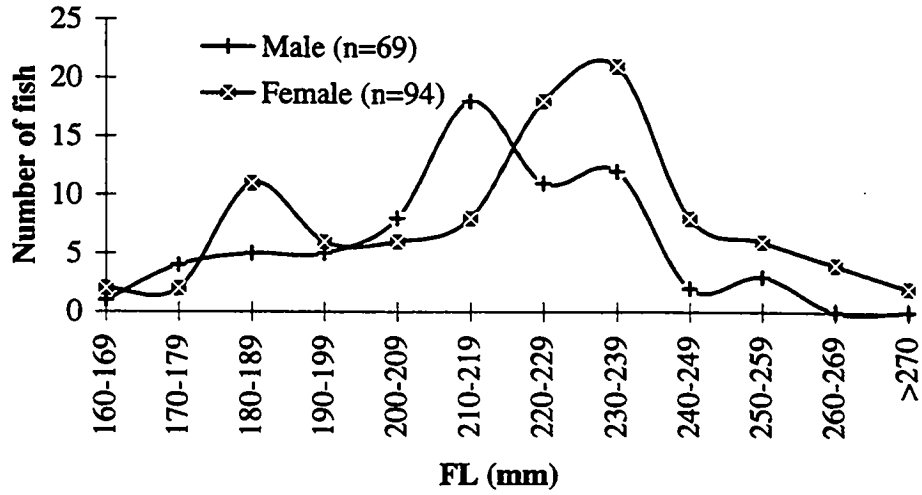
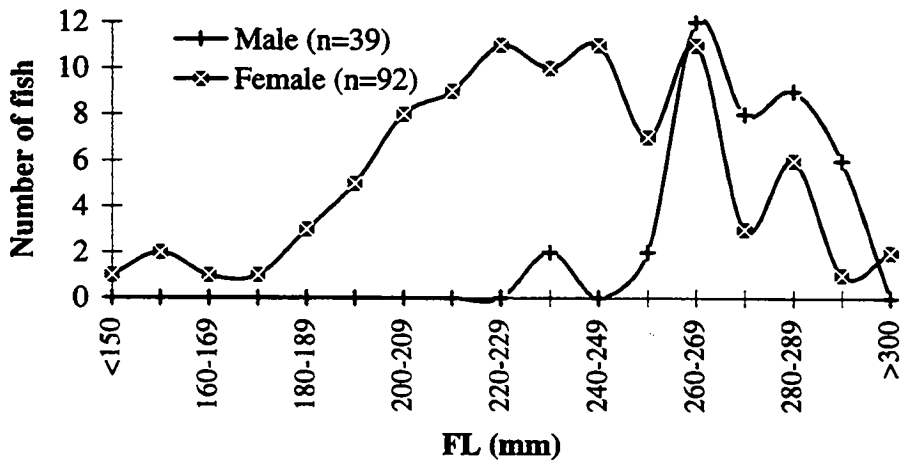


Figure 6.5. Mean gonadosomatic index (GSI) (±S.E.) during sampling times for the three species. There was a consistent increase in mean GSI during the month of October in all three species, suggesting that spawning may begin during the early austral summer. Numbers above data points indicate sample size.

a. ***Lutjanus fulviflamma***



b. ***Lethrinus harak***



c. ***Lethrinus lentjan***

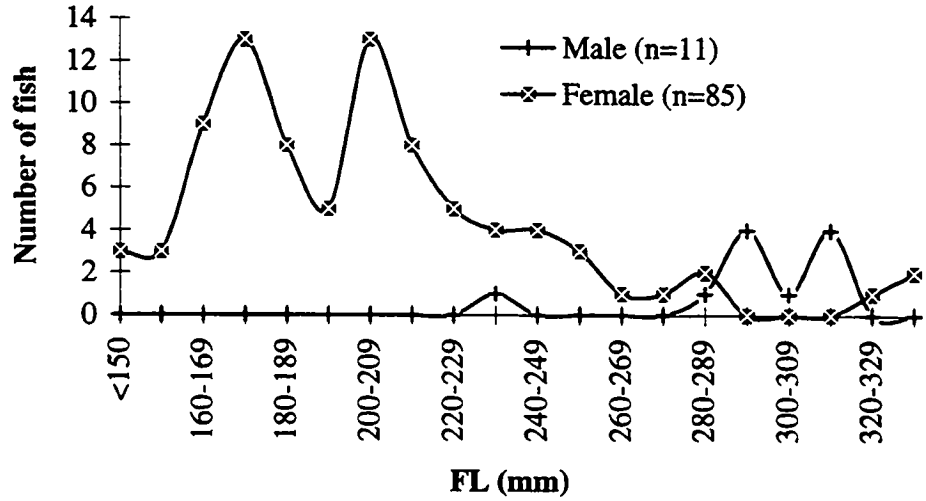
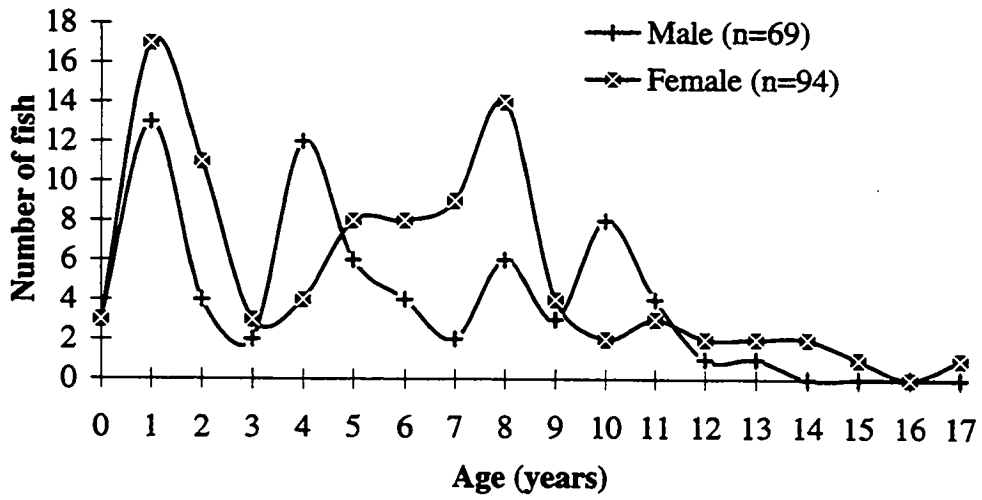
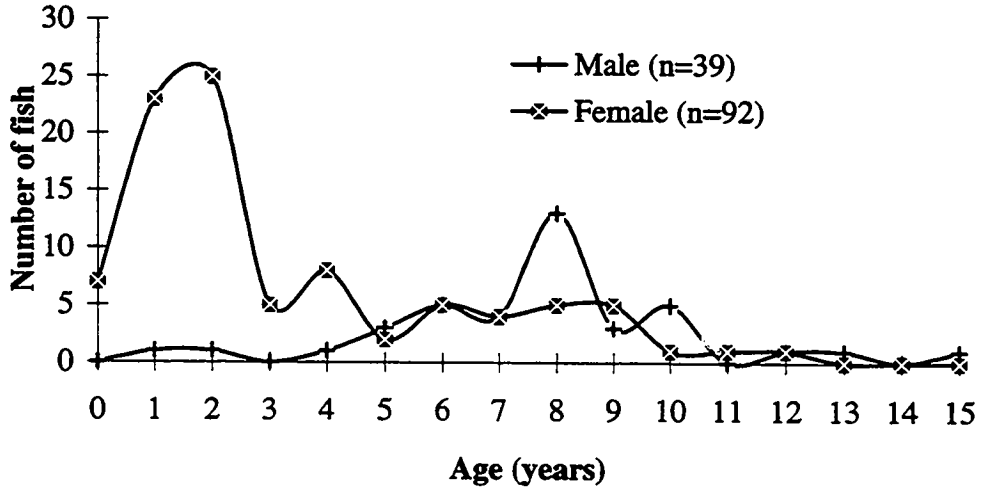


Figure 6.6. Length frequency distribution of males and females of (a) *Lutjanus fulviflamma*, (b) *Lethrinus harak* and (c) *L. lentjan*. FL -fork length.

a. ***Lutjanus fulviflamma***



b. ***Lethrinus harak***



c. ***Lethrinus lentjan***

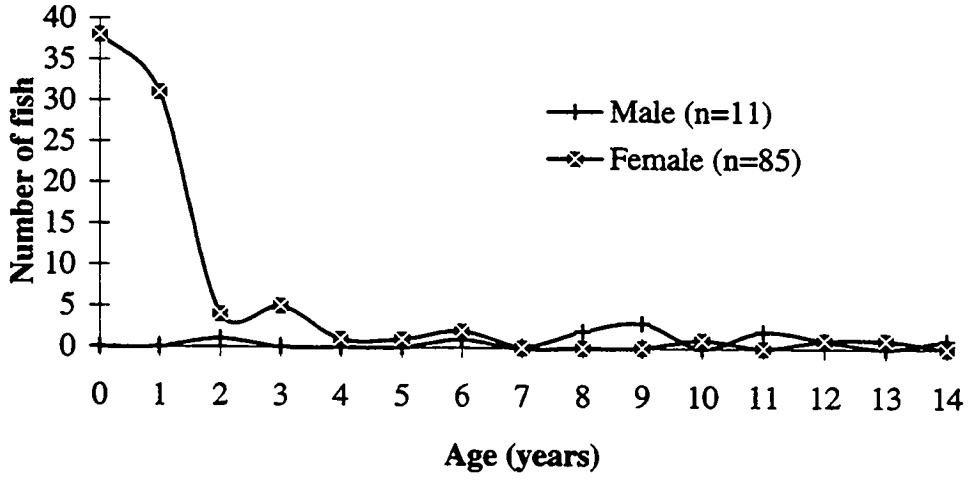


Figure 6.7. Age frequency distribution of males and females of (a) *Lutjanus fulviflamma* , (b) *Lethrinus harak* and (c) *L. lentjan.*

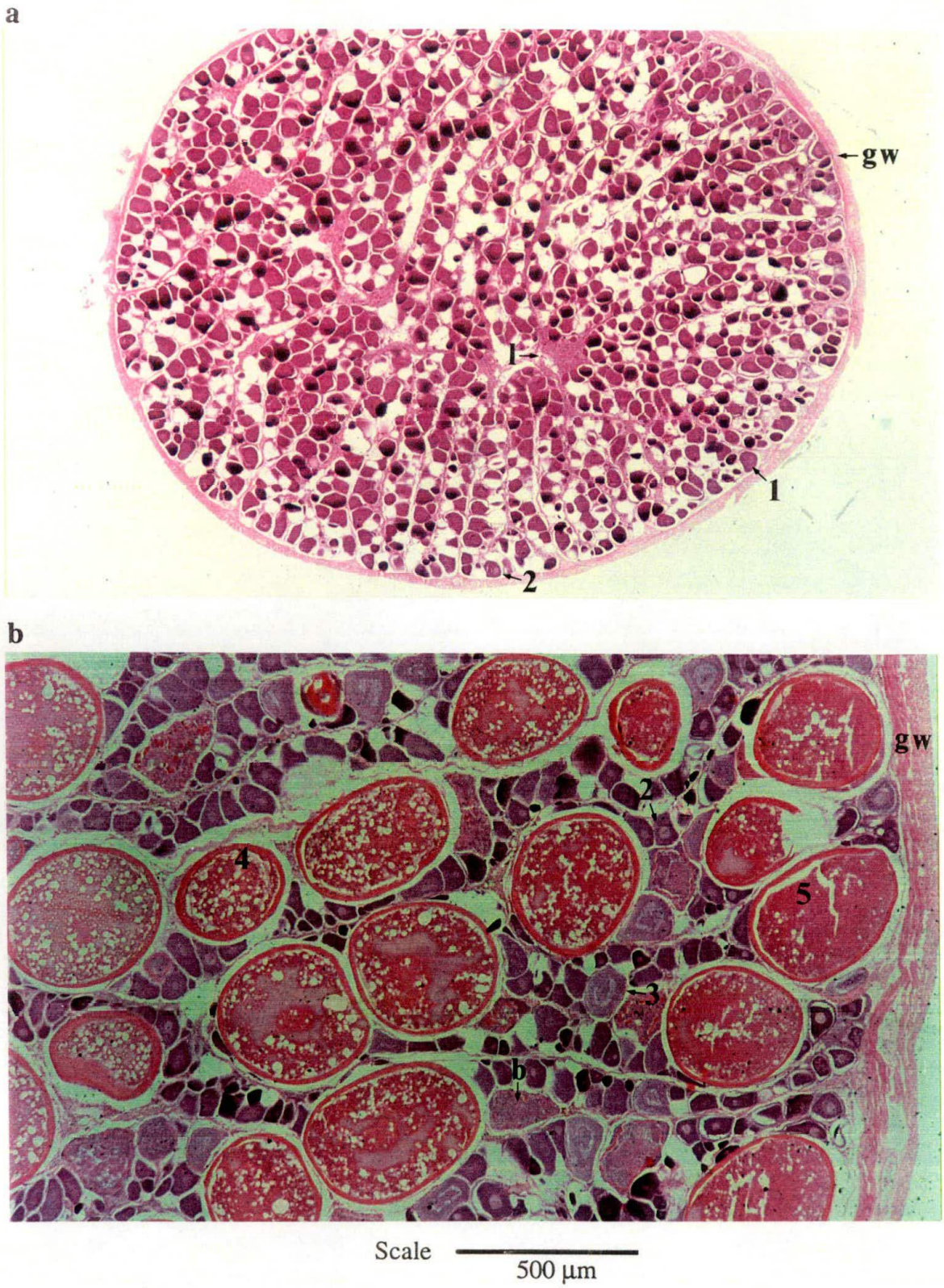


Plate 6.1. Cross sections of (a) an immature and (b) mature female gonad of *Lutjanus fulviflamma* stained in HE. Numbers refer to the stage of oocyte development. Codes are gw = gonad wall, b = brown bodies and l = leach material due to freezing of sample.

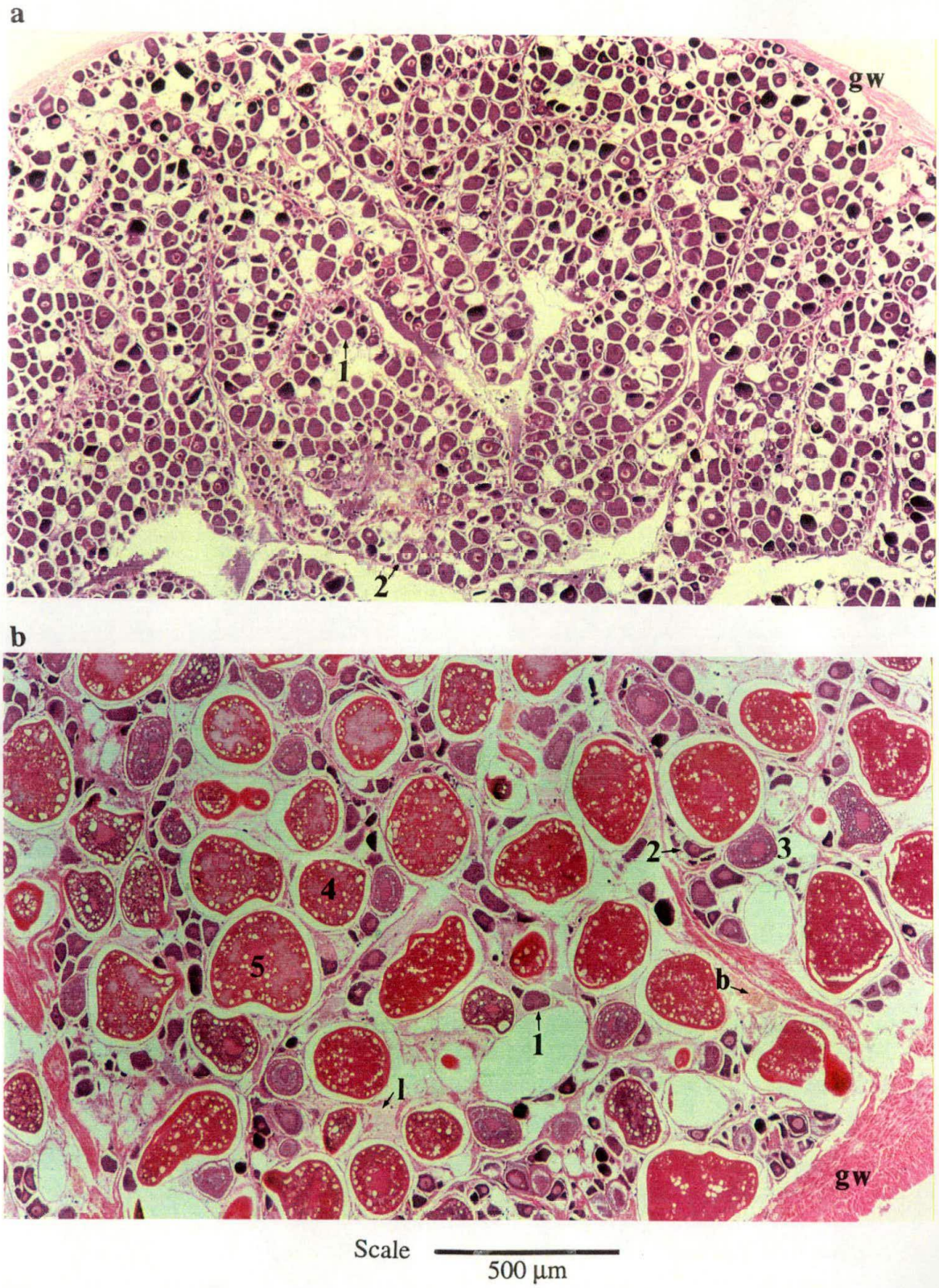


Plate 6.2. Cross sections of (a) an immature and (b) mature female gonad of *Lethrinus harak* stained in HE. Numbers refer to the stage of oocyte development. Codes are gw = gonad wall, b = brown bodies and l = leach material due to freezing of sample.

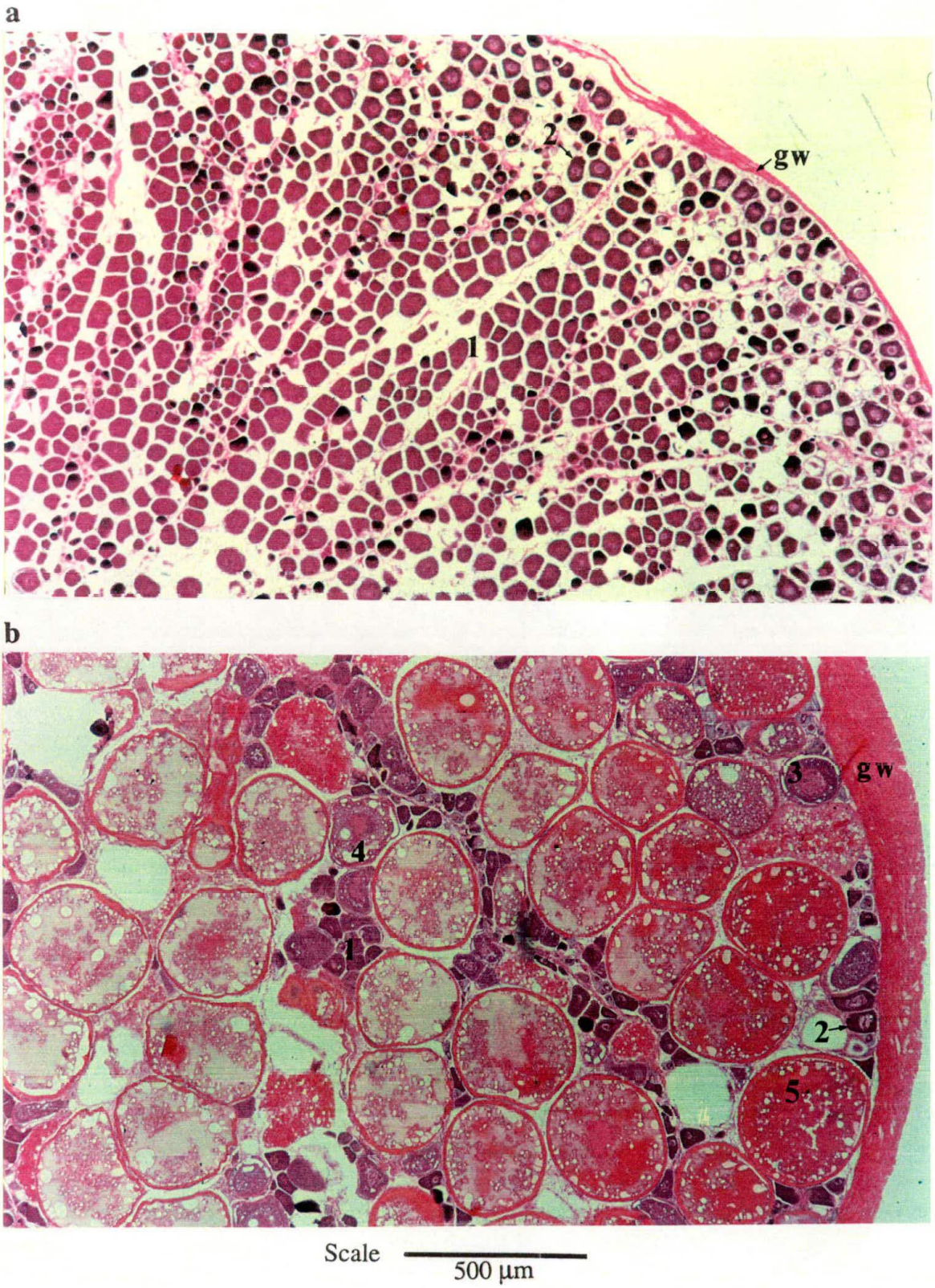


Plate 6.3. Cross sections of (a) an immature and (b) mature female gonad of *Lethrinus lentjan* stained in HE. Numbers refer to the stage of oocyte development. Codes are gw = gonad wall.

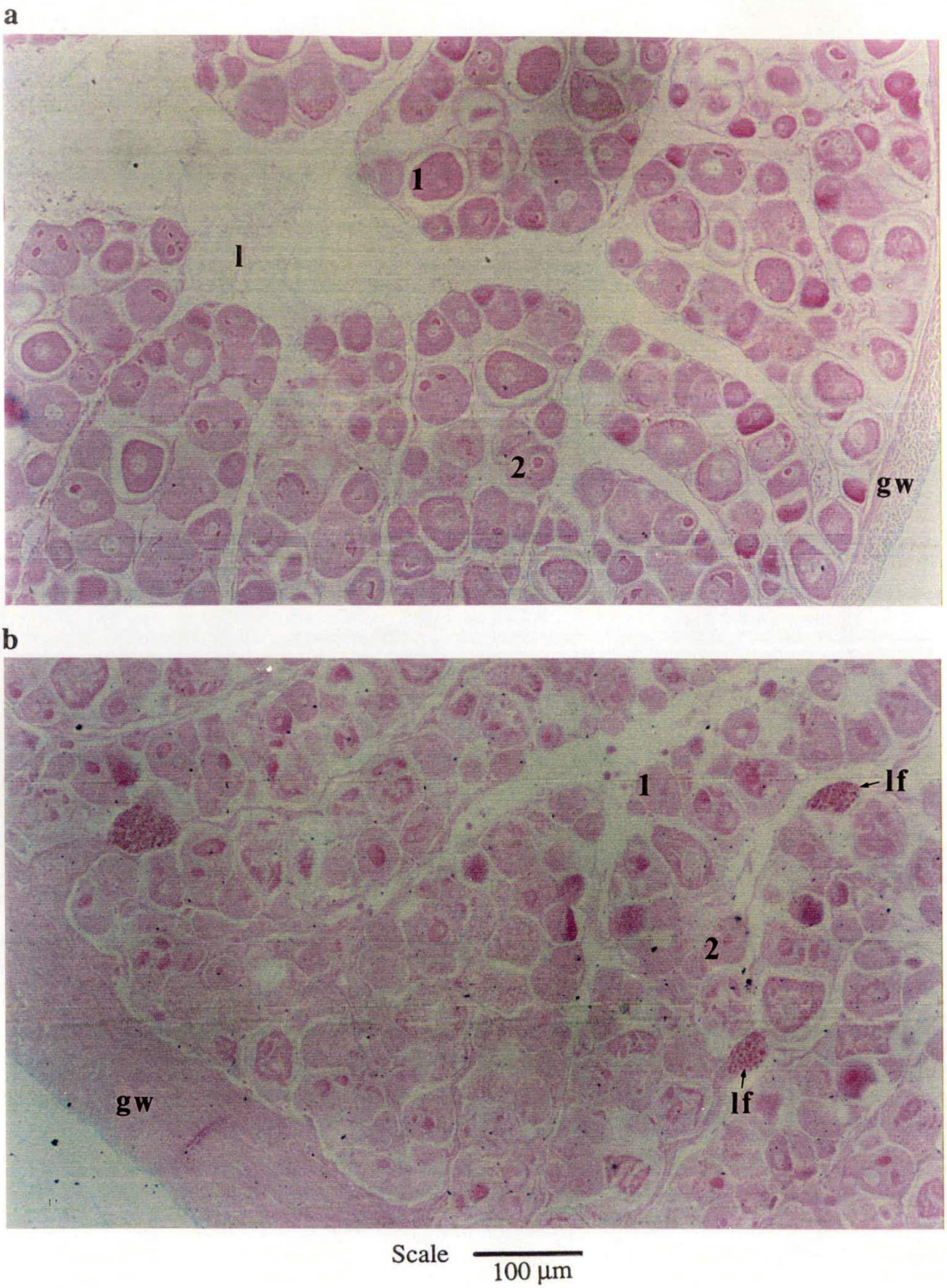


Plate 6.4. Cross sections of (a) immature and (b) mature resting female gonads stained in Alcian Blue PAS. Note the same developmental oocyte stages in both samples. The mature resting gonad in (b) was distinguished from the immature sample in (a) by the presence of lipofuscin (lf). Note the thicker gonad wall (gw) in (b). 'l' = leached material due to freezing of sample.

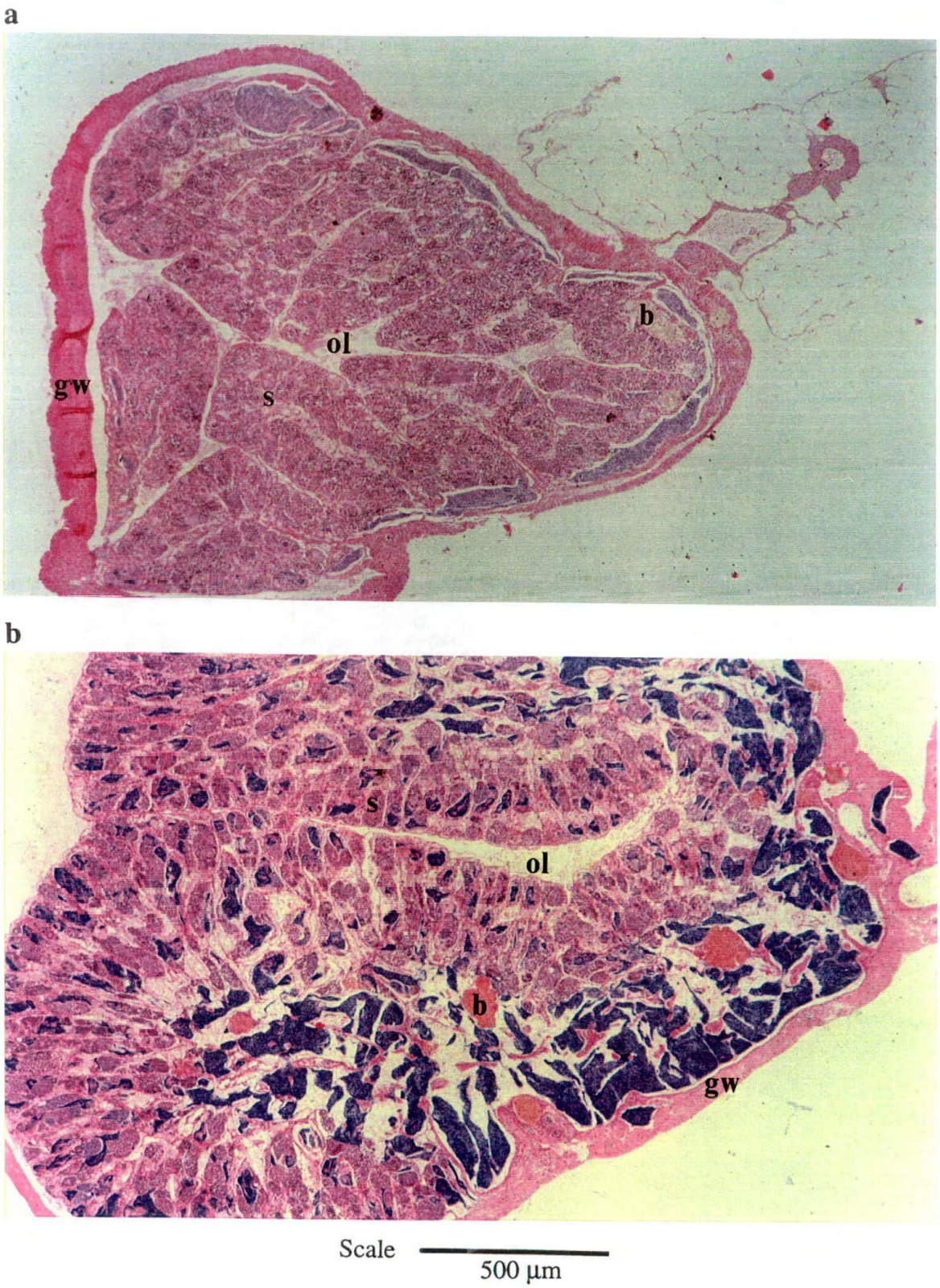


Plate 6.5. Cross section of male gonads of (a) a 2 yr old *Lethrinus harak* and (b) a 14 yr old *L. lentjan*. Note the presence of an ovarian lumen 'ol', brown bodies 'b' and the relatively thicker gonad wall 'gw' in the younger (a) than the older sample in (b). 's' = spermatogonia.

Chapter 7. IMPLICATIONS TO CORAL REEF FISHERIES

7.1 INTRODUCTION

This study collected important baseline information on population dynamics of small commercial and recreationally important fishes of the reef line fishery on the Great Barrier Reef (GBR). Age, growth and mortality rates, and age and size at first sexual maturity of three important "by catch" species (*Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan*) were investigated. These parameters largely determine stock productivity. Estimates of their magnitude and variation provide information on the status of stocks and on potential yield (Russ 1991, Appeldoorn 1996). The study also investigated local movement patterns and factors determining local distribution of coral reef fish, particularly lutjanids, lethrinids and serranids at the Lizard Island lagoon, GBR. This information is important to better understand the ecology of these resources.

On the GBR, catches of reef fish are considerably low (Munro 1987, Dugan and Davis 1993b) in comparison to catches taken in many developing countries, such as the Philippines, where exploitation of reef fishery resources has reached alarming levels (Carpenter 1977, Murdy and Ferraris 1980, McManus 1988, Russ and Alcala 1989, FAO 1994). While small lutjanids and lethrinids currently make up a small but important component of the reef catch on the GBR (Trainor 1991), the rapid expansion of the size of the recreational small boat fleet over the past decade, coupled with developing markets for pan sized fish and live fish will increase the significance of these resources in the near future (Williams and Russ 1994). Faced with this scenario, information on basic life history characteristics, on local patterns of movement and on factors determining distribution and abundance of post-settlement lutjanids and lethrinids have been identified as a priority area of research (Russ 1991, Williams

1991, Williams and Russ 1994). The information gained from this research will be critical to sustainable utilization and management of these renewable fishery resources. The major findings of this study were:

- Local distribution patterns of reef fishes were influenced strongly by habitat type (mainly the type of substratum) and diel period. Distinct fish assemblages occupied reefal and sandy habitats and each of these fish assemblages changed in composition and abundance during day and night.

- The small predatory reef fish (mostly lutjanids and lethrinids) exhibited strong habitat fidelity, with a high propensity for short distance movement. Distances moved were frequently in 30's to 60 m, although they may occasionally move larger distances of up to 500 m within a habitat.

- The age determination of reef fish using validated counts of opaque bands in sectioned otoliths was not only possible but also a highly reliable technique. This technique showed that *Lutjanus fulviflamma*, *Lethrinus harak* and *L. lentjan* were long-lived species with potential maximum life spans in excess of 10 years. They grow rapidly during the first 2 years of life, reaching about 80% of their respective L_∞, after which little growth in length occurs. Rates of natural mortality were low, suggesting that these species are potentially vulnerable to high levels of exploitation.

- Estimates of size and age at first sexual maturity for *L. fulviflamma*, *L. harak* and *L. lentjan* ranged between 74-84% of their L_∞ (i.e. 200-209, 210-229 and 250-259 mm FL, respectively) and between 2-3 years. Based on gonad histology and sex-ratios at age and size, *Lethrinus harak* and *L. lentjan* exhibited a sexual pattern consistent with protogyny. *Lutjanus fulviflamma* was gonochoristic.

The above points have been discussed in their respective chapters. Their implications to management of coral reef fisheries are presented below. This chapter concludes with a section on directions of future research.

7.2 RELEVANCE TO MANAGEMENT OF CORAL REEF FISHERIES

Management options in any fishery generally include limits on total catch, fishing effort, gear restrictions, fishing areas and seasons. The suitability of a management plan is determined by local social, economic and political considerations (Munro 1996). The management of coral reef fisheries is often far more complicated than that of other fisheries. Coral reef fisheries are multispecific, with fishing effort spread among a variety of gears. The collection of basic fisheries data such as catch and effort is made even more difficult because a large number of artisanal fishermen land their catch at a large number of sites over a wide area and effort is often unevenly distributed spatially (Russ 1991, McManus *in press*). This makes traditional management practices such as catch quotas and minimum size limits impractical in many coral reef fisheries.

With a very high level of exploitation of coral reef fisheries by subsistence and small-scale fishermen worldwide (Ruddle 1996), the need to develop more effective management strategies for these resources is urgent. Fairly recently, a number of studies have stressed the merits of marine reserves as a management option (PDT 1990, Bohnsack 1993, DeMartini 1993, Dugan and Davis 1993a, Carr and Reed 1993, Man *et al.* 1995, Bohnsack 1996, Russ and Alcala 1996a and b). Dugan and Davis (1993a) discussed the potential benefits of such an option and enumerated the following hypotheses: target species in reserves will increase a) in abundance, b) in mean size and age, and c) in reproductive output. In addition, marine reserves will d) enhance recruitment inside and outside of the reserve by larval dispersal, e) maintain genetic diversity of stocks and f) enhance fishery yields in adjacent exploited areas by export of adult fish. Furthermore, marine reserves may increase species diversity, habitat complexity and enhance community stability. A more detailed review of these potential benefits is found in PDT (1990) and Bohnsack (1996).

The effectiveness of marine reserves has not yet been fully evaluated. Yield per recruit simulations suggest that such fisheries enhancement effects (d and f above) were possible under certain conditions (Polacheck 1990, Russ *et al.* 1993, DeMartini 1993). To date, very little data are available to assess the effectiveness of marine

reserves in terms of larval export to areas outside of reserves. However, evidence for increases in abundance of target species following closure to fishing has been reported in South Africa (Bennett and Attwood 1991) and in the Philippines (Russ and Alcala 1996b). More importantly, the enhancement of local fishery yield from movement of adults from the reserves to exploited areas has been demonstrated at two Philippine islands (Alcala and Russ 1990, Russ and Alcala 1996a and b) and for *Coracinos capensis* in South Africa (Attwood and Bennett 1994).

The results of the present study on local movement patterns of reef fish has provided useful information for the design and location of marine reserves, particularly in terms of movement of fish from reserves to adjacent fished areas. Design and location of marine reserves are critical if the potential benefits are to be attained (Carr and Reed 1993, Bohnsack 1996). A partial closure of a reef may result in flux rates across boundaries provided that there is a continuum of uniform habitat type across the boundary. Results of the present study demonstrated considerable movement within habitats of up to 150 m for most small lutjanids and lethrinids and up to 500 m for *Lethrinus nebulosus*. On the other hand, if managers wished to restrict fish movements across boundaries, the boundary could include a large expanse of habitat in which probabilities of movement are low (e.g. a wide expanse of sand). A partial closure located centrally on a fringing reef may achieve flux rates at both ends (two boundaries). It is thought that density gradients may influence flux rates across boundaries between closed and open areas (Beverton and Holt 1957). Whether or not there is a net flux to fished areas remains to be tested. This design may well be suited to small fringing reefs such as those in the Philippines. However, the applicability of this design requires rigorous assessment. Two concerns about the design arise. Firstly, transfer rates may be so high that protection of the spawning stock will be undermined. Secondly, boundaries within individual reefs may be difficult to demarcate and may not be respected by reef users. The latter concern will need critical cooperation from the local community.

A total closure of reefs will more likely favor protection of a critical spawning biomass and lead to an increase in abundance, mean size and age of target species in reserve areas (Polacheck 1990, DeMartini 1993, Chapter 4 this study). This approach,

however, may not readily affect nearby fisheries in a positive manner and this may be critical to successful establishment of a cost-effective, community-based marine reserve (Russ and Alcala 1996a). Dugan and Davis (1993a) suggested that experimental testing of marine reserves may take 10-15 years, given that many effects are often not detectable in the short term.

Most management practices, such as imposition of limits on catch and fishing effort rely heavily on current knowledge of stock sizes and fundamental life history characteristics of targeted species. It is essential therefore that data on age, growth and mortality rates, and age and size at first sexual maturation must be accurate. Thus, estimates of population parameters should be based on reliable and validated methods. Of these parameters, age is the most critical, simply because many analytical models in population dynamics incorporate age information. This study acknowledges that age determination of fish using validated counts of annuli in sectioned otoliths is time consuming and requires expertise (Csirke *et al.* 1987, Gulland 1987, Munro 1987). However, the quality of information gained far outweighs the additional effort because the estimate is highly reliable. The present study has demonstrated that age determination was possible and highly reliable for *L. fulviflamma*, *L. harak* and *L. lentjan* and potentially applicable to a wide variety of reef fishes.

In the past 15-20 years, the general perception of coral reef fishes (and tropical fish) was that they were short-lived, fast-growing and had high rates of natural mortality (e.g Thompson and Munro 1983a,b,c, Gaut and Munro 1983, Reeson 1983a and b, Aiken 1983a and b, Munro 1983b, Wyatt 1983). In contrast, results from the present study and an increasing number of others (e.g. Fowler 1990b, Fowler and Doherty 1992, Lou 1992b, Ferreira and Russ 1992, 1994, Newman *et al.* 1996a, Choat and Axe 1996, Choat *et al.* 1996; this study) indicate that these paradigms should be questioned. The perception that reef fish are short lived, fast growing species with high rates of mortality has persisted probably because of the widespread use of length-based methods to estimate growth parameters (see contributions in Munro 1983). These methods often overestimate growth and mortality rates and underestimate age (e.g. compare Hardisty 1961, 1969 and Purvis 1980; and see Beamish and McFarlane 1987, Lai and Gunderson 1987). Furthermore, it has long been believed that age

determination of reef fish was difficult, at best (e.g. contributions in Munro 1983a, Gulland 1987, Pauly and Morgan 1987, Longhurst and Pauly 1987). High estimates of natural mortality result in overestimation of potential yields of fish stocks (Agger *et al.* 1973).

A critical assumption in length-based methods is that modes in length frequency distributions represent age-classes (Munro 1983a, Pauly 1987, Longhurst and Pauly 1987). This assumption must be questioned for most reef fish because validated age techniques have demonstrated large variations in individual growth rates (e.g. Newman et al. 1996a, this study). In many cases, a 2 year old fish can have the same length as a 10 year old. This means a wide overlap in lengths of fish of different ages. This also means that length-frequency analysis is likely unreliable in estimating growth parameters for many species, particularly long-lived species (e.g. Beamish and McFarlane 1987). Length-frequency analysis is useful however, when information about the fast-growing phase of fish is required (Foucher and Fournier 1982), generally during the first 2 years of life.

The assumption that opaque bands in sectioned otoliths were laid down annually was confirmed in age validation experiments (see Chapter 5). Counts of opaque bands in sectioned otoliths should be used routinely as an age determination technique in tropical fisheries (see Russ *et al.* 1996). It could be argued that the cost of such a technique will restrict sample sizes. Worthington *et al.* (1995) caution that when sample size is restricted, the effect of sampling error on age structure may be greater than the effect of ageing error from a less accurate method of age determination. This problem of cost and restricted sample size could be resolved by reading whole otoliths or by measuring otolith weight. Using otolith weight as a proxy of age is more economic but still a more reliable method of age determination (Newman et al. 1996a, this study) than length-based methods, provided that the relationship of otolith weight and age is calibrated for each new sample of fish (Worthington *et al.* 1995).

Knowledge of the reproductive patterns of fish is important to maintain sufficient reproductive output of exploited populations. The age and size at first sexual

maturation of fish represents a significant transition in the life history because it marks the point when individuals begin to contribute to future generations (Sadovy 1996). The age and size at which 50% (or higher) of a sample of fish attain sexual maturity often forms the basis for setting legal minimum limits in size of capture of targeted species. This practice provides fish with a chance to spawn at least once before they recruit to the fishery. Information on age and size at first maturity have far reaching implications. This study provided an estimate of age and size at first sexual maturity for three potentially important fishery species on the GBR. *Lutjanus fulviflamma*, *L. harak* and *L. lentjan* in Lizard Island lagoon (GBR) attain first sexual maturity at a relatively young age (2-3 years) and at sizes close to their maximum lengths (74-84% of L_∞).

Information on the sexual pattern of fish stocks is also of major significance to fishery management, since fishing mortality could potentially disrupt reproduction in an exploited stock (Sadovy 1996). For example, in a protogynous population, removal of the largest individuals could lead to a decline in the proportion of males in the population (Russ 1991). This could reduce the frequency of contact between males and females and compromise their reproductive success (Bannerot *et. al.* 1987). The present study found that the sexual pattern of *L. harak* and *L. lentjan* was consistent with protogyny. Fishery management should examine this information in terms of legal size limits for these fishes on the GBR.

This study showed that types of habitat play a major role in the distribution patterns of post-settlement reef fishes. This result is consistent with many earlier studies. These studies have suggested that distribution patterns on reefs may largely be driven by habitat selection at settlement (Sweatman 1983, 1985, Doherty and Williams 1988, Victor 1991, Williams 1991), differential mortality after settlement (e.g. Hixon 1991, Hixon and Beets 1993) and post-settlement movement (Robertson 1988, Roberts 1996, this study). The day and night changes in the spatial distribution and abundance of fish assemblages appeared to be associated with feeding behavior. These day and night shifts suggest diel movement of fish to feeding areas within a locality (e.g. Hobson 1973, 1975, 1991, Ogden and Buckman 1973, McFarland *et al.* 1979, Helfman *et al.* 1982, Holland *et al.* 1993). The importance of the quality and type of habitats in

determining reef fish distributions relate to the resource requirements of reef fishes (e.g. Choat and Bellwood 1991). Choat and Bellwood (1991) summarized general fish-habitat interactions such as use of reef structure for shelter and as a source of food. These two activities form a link between fish movement and recycling of nutrients within reef systems. Resource requirements of fishes often change with ontogeny and thus, any species may need a wide variety of habitats (e.g. Sale 1991, Carr and Reed 1993). Given the significance of habitats to population dynamics and ecology of reef fishes, management plans for coral reef fisheries should consider the protection of a wide variety of habitats (e.g Carr and Reed 1993, Dugan and Davies 1993).

Finally, effective management of coral reef fisheries must be based upon an understanding of reef ecology, reef fisheries science, and sociocultural and economic conditions of users (McManus 1996). There is now a growing body of evidence that effective management of fishery resources requires local participation (e.g. Alcala 1988, McManus *et al.* 1988, Russ and Alcala 1996a). McManus (1996) provides an excellent evaluation of how collaboration of fishery and social scientists can contribute to the sustainability of fishery resources. Fisheries management plans for coral reefs should be based on scientific data and should be trialed and tested (Walters and Holling 1990). As Larkin (1978) admonished, "...fisheries science will not advance much further unless management becomes experimental ..."

7.3 DIRECTIONS OF FUTURE RESEARCH

Detailed measurements of habitat attributes such as benthic cover was one of the shortcomings of this study. It would have been more informative if the variation in catch rates and catch composition from traps could have been related to more specific habitat attribute/s. However, the study was very successful in identifying assemblages clearly related to reefal and sandy habitats. Extensive data on age/size specific distributions of reef fishes over a wide variety of habitats may improve the understanding of the significance of habitat types to the ontogeny of reef fish. Habitat

shifts related to ontogeny may be key processes affecting local distribution patterns of reef fishes. Williams (1991) stressed the need for rigorous study of the factors determining within reef distributions. In addition, parallel data collection on fish diets and the distribution and abundance of prey of fish such as crustaceans, benthic invertebrates and zooplankton (Hobson 1991) may help elucidate the patterns of distribution and diel movement of reef fishes observed in this study.

The use of underwater visual census (UVC) to estimate reef fish abundance has gained wide acceptance as a tool in stock assessment (e.g. Harmelin-Vivien *et al.* 1985, Fowler 1987, Polunin *et al.* 1996). This technique, however, is generally limited to daylight hours, depths not exceeding 20 m (SCUBA restrictions), requires highly trained personnel and the presence of the observer may affect the behavior of many target species in heavily exploited areas. In view of these drawbacks, the potential use of traps in stock assessment deserves further evaluation. The suitability of this method has been examined for effective area fished (Miller 1975, Miller and Hunte 1987, Eggers *et al.* 1982) but has rarely been tested against independent estimates of abundance such as underwater visual census (UVC) (e.g. Davies 1989). If traps sample target species adequately then they will be a reliable and independent sampling tool that is affordable and requires less highly skilled personnel. The limited resources and logistics in the present study prevented a comparison of daytime catch rates from traps and independent estimates of abundance from UVC.

The effects of tagging and capture by traps on the behavior and growth of fishes should be addressed. This is an important but a difficult task. Many tagging studies (e.g Schwarz and Arnason 1990), including the present one, assumed that such effects on fish are minimal. To date there is little data to support this from coral reefs.

More data is needed not only to assess effectiveness of marine reserves in providing adult individuals to adjacent fished areas, but also to examine and identify patterns of movement to spawning sites. Despite the recognition of a need for data on flux rates of fish across marine reserve boundaries, there is surprisingly little good quantitative data on this subject. In fact, quantitative studies of local movement patterns of reef fishes are relatively rare (e.g. Robertson 1988, Williams 1991, Roberts

1996). Of particular interest is movement of reef fish across a gradient of fish density within a fairly uniform habitat type. Studies of movement can be observational (e.g. Robertson 1988) but generally involve tagging of fish (e.g. Randall 1961, 1963, Davies 1995, this study). It is noteworthy that the present study externally tagged almost a thousand fish over a 30 month period. Despite this amount of effort, substantial information on probabilities of movement within and between habitats was obtained for relatively few species. This emphasizes that movement information useful to fishery managers will require extensive tagging studies, preferably in combination with high technology methods such as ultrasonic telemetry (e.g. Holland *et al.* 1993, 1996, Zeller and Russ submitted MS). Tagging studies with a clearly defined set of objectives and sampling strategies designed to measure flux rates across reserve boundaries should be a priority of future research evaluating the effectiveness of marine reserves.

The present study has demonstrated the successful use of tagging in a multiple capture-recapture trapping program to address levels of movement of small reef fishes within and between habitats. For smaller reef fishes such as pomacentrids and labrids, the use of implant microtags is recommended (Beukers *et al.* 1995). The use of ultrasonic telemetry (Zeller and Russ submitted MS) is an expensive but highly effective method to track movement for larger reef fish.

The collection of basic life history information of exploited populations of reef fishes using age-based methods should also be a priority. At present, information on age, growth and mortality rates and age and size at first sexual maturity exist for much less than half the species of lutjanids and lethrinids on the GBR. Even less information of this type exists for such reef fish in most developing nations.

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Appendix A. Numbers of individuals per species across sampling times pooled over habitat types and soak times for Z-trap catches in Lizard Island lagoon, GBR.

Family	Species	Mar-94	Oct-94	Mar-95	Jul-95	Oct-95	Mar-96	Jul-96	Total	% Comp.
Pomacentridae	*Amblyglyphidodon curacao*	58	71	17	24	16	26	18	230	**9.63**
	Acanthochromis polyacanthus	58	32	3	13	22	60	11	199	**8.33**
	Chromis viridis	10	0	36	0	0	2	0	48	**2.01**
	Pomacentrus moluccensis	3	4	4	3	2	1	1	18	**0.75**
	Pomacentrus amboinensis	0	6	0	2	1	7	1	17	**0.71**
	Pomacentrus brachialis	5	2	4	0	0	3	2	16	**0.67**
	Neoglyphidodon melas	1	2	1	0	0	5	0	9	**0.38**
	Pomacentrus chrysurus	1	1	3	0	2	0	0	7	**0.29**
	Pomacentrus philippinus	5	2	0	0	0	0	0	7	**0.29**
	Amblyglyphidodon leucogaster	1	3	0	0	0	0	0	4	**0.17**
	Dischistodus pseudochrysopoecilus	0	1	1	0	0	1	0	3	**0.13**
	Pomacentrus wardi	0	1	1	0	0	0	1	3	**0.13**
	Dischistodus perspicillatus	0	1	0	0	0	1	0	2	**0.08**
	Dischistodus prosopotaenia	1	1	0	0	0	0	0	2	**0.08**
	Abudefduf whitleyi	0	0	0	0	1	0	0	1	**0.04**
	Chromis agilis	0	0	1	0	0	0	0	1	**0.04**
	Chrysiptera rollandi	0	0	0	0	1	0	0	1	**0.04**
	Hemiglyphidodon plagiometopon	0	1	0	0	0	0	0	1	**0.04**
	Stegastes nigricans	0	0	0	0	0	1	0	1	**0.04**
Lutjanidae	*Lutjanus carponotatus*	33	29	44	35	57	95	46	339	**14.20**
	Lutjanus quinquelineatus	41	15	9	4	14	10	16	109	**4.56**
	Lutjanus fulviflamma	6	20	2	6	11	9	5	59	**2.47**
	Lutjanus gibbus	0	0	0	0	0	12	0	12	**0.50**
	Lutjanus vitta	0	0	1	9	1	0	0	11	**0.46**
	Lutjanus bohar	1	0	0	0	2	3	4	10	**0.42**
	Lutjanus russelli	1	2	0	1	1	4	0	9	**0.38**
	Symphorus nematophorus	1	2	0	0	0	0	0	3	**0.13**
	Lutjanus fulvus	0	0	0	1	0	0	1	2	**0.08**
	Lutjanus monostigma	0	0	0	0	1	0	0	1	**0.04**
	Lutjanus rufolineatus	0	0	1	0	0	0	0	1	**0.04**
Apogonidae	*Apogon bandanensis*	14	40	54	21	5	16	8	158	**6.62**
	Apogon compressus	5	22	8	16	4	5	22	82	**3.43**
	Fowleria sp."1"	0	12	14	6	6	6	9	53	**2.22**
	Apogon cookii	5	0	3	0	30	2	0	40	**1.68**
	Cheilodipterus quinquelineatus	0	2	23	10	0	2	1	38	**1.59**
	Rhabdamia gracilis	0	13	0	4	6	0	0	23	**0.96**
	Apogon guamensis	3	2	1	1	4	7	0	18	**0.75**
	Cheilodipterus macrosoma	0	0	0	15	0	0	0	15	**0.63**
	Apogon cyanosoma	0	1	3	0	0	0	4	8	**0.34**
	Apogon exostigma	0	0	1	0	0	4	0	5	**0.21**
	Apogon sp."3"	0	0	5	0	0	0	0	5	**0.21**
	Apogon aureus	0	0	4	0	0	0	0	4	**0.17**
	Apogon fraenatus	0	0	4	0	0	0	0	4	**0.17**
	Apogon ocellatus	0	4	0	0	0	0	0	4	**0.17**
	Foa brachygramma	0	2	0	1	1	0	0	4	**0.17**
	Apogon fuscus	1	0	2	0	0	0	0	3	**0.13**
	Archaemia melasma	2	0	0	1	0	0	0	3	**0.13**
	Apogon angustatus	2	0	0	0	0	0	0	2	**0.08**
	Apogon doederleini	0	0	1	0	0	0	1	2	**0.08**
	Apogon talboti	1	1	0	0	0	0	0	2	**0.08**
	Archaemia leai	1	1	0	0	0	0	0	2	**0.08**
	Apogon mollucensis	0	1	0	0	0	0	0	1	**0.04**
	Apogon sp."1"	1	0	0	0	0	0	0	1	**0.04**
	Apogon sp."2"	1	0	0	0	0	0	0	1	**0.04**
	Archaemia fucata	1	0	0	0	0	0	0	1	**0.04**
	Foa sp."1"	1	0	0	0	0	0	0	1	**0.04**

Appendix A. con't.

Family	Species	Mar-94	Oct-94	Mar-95	Jul-95	Oct-95	Mar-96	Jul-96	Total	% Comp.
Lethrinidae	*Lethrinus nebulosus*	3	15	10	11	12	18	8	77	**3.22**
	Lethrinus semicinctus	20	9	4	2	4	7	3	49	**2.05**
	Lethrinus atkinsoni	5	2	3	3	4	2	6	25	**1.05**
	Lethrinus lentjan	2	0	7	1	0	11	1	22	**0.92**
	Lethrinus olivaceus	1	0	1	0	1	2	0	5	**0.21**
	Lethrinus variegatus	3	0	0	2	0	0	0	5	**0.21**
	Lethrinus harak	0	0	1	0	0	0	0	1	**0.04**
	Lethrinus obsoletus	0	0	0	0	0	1	0	1	**0.04**
	Lethrinus ornatus	0	0	1	0	0	0	0	1	**0.04**
Labridae	*Thalassoma lunare*	8	42	14	18	30	23	14	149	**6.24**
	Choerodon fasciatus	0	8	3	3	9	6	0	29	**1.21**
	Cheilinus fasciatus	3	0	1	0	0	0	0	4	**0.17**
	Cheilinus chlororus	0	0	0	0	1	0	0	1	**0.04**
	Stethojulis bandanensis	0	0	1	0	0	0	0	1	**0.04**
Serranidae	*Cephalopholis cyanostigma*	13	19	8	6	8	10	4	68	**2.85**
	Plectropomus leopardus	3	5	3	3	2	3	3	22	**0.92**
	Epinephelus ongus	0	1	0	0	3	3	2	9	**0.38**
	Epinephelus merra	0	0	0	0	3	2	1	6	**0.25**
	Cephalopholis microdon	0	1	1	0	2	0	1	5	**0.21**
	Cephalopholis boenack	1	1	0	0	0	0	0	2	**0.08**
	Epinephelus fuscoguttatus	1	1	0	0	0	0	0	2	**0.08**
	Epinephelus malabaricus	1	0	0	0	0	0	0	1	**0.04**
Holocentridae	*Myripristis mudjan*	5	3	17	11	11	16	11	74	**3.10**
	Sargocentron spiniferum	4	7	2	2	2	4	3	24	**1.01**
	Neoniphon sammara	0	1	1	0	0	0	0	2	**0.08**
	Myripristis sp."1"	0	0	1	0	0	0	0	1	**0.04**
	Myripristis violacea	0	0	0	0	0	0	1	1	**0.04**
	Sargocentron sp."1"	0	0	0	0	0	0	1	1	**0.04**
	Sargocentron violaceum	0	0	0	0	0	1	0	1	**0.04**
Blenniidae	*Dasson variabilis*	0	0	0	0	0	0	1	1	**0.04**
	Salarias fasciatus	1	0	0	0	0	0	0	1	**0.04**
Caesionidae	*Caesio cuning*	0	1	0	0	0	0	1	2	**0.08**
	Pterocaesio digramma	0	0	0	0	1	0	0	1	**0.04**
Carangidae	*Carangoides fulvoguttatus*	0	0	1	0	0	0	0	1	**0.04**
	Gnathonodon speciosus	13	0	1	1	0	0	0	15	**0.63**
Centriscidae	*Aeoliscus strigatus*	27	0	25	0	0	2	0	54	**2.26**
Chaetodontidae	*Chaetodon trifasciatus*	2	0	0	0	0	0	0	2	**0.08**
	Chaetodon melannotus	0	0	0	0	0	1	0	1	**0.04**
	Chaetodon plebeius	0	0	0	0	0	1	0	1	**0.04**
Cirrhitidae	*Parapercis tetracantha*	0	2	1	1	0	0	0	4	**0.17**
Echeneidae	*Echeneis naucrates*	4	0	2	3	4	4	9	26	**1.09**
Ephiphidae	*Platax tierra*	0	0	3	0	0	1	0	4	**0.17**
Fistulariidae	*Fistularia commersoni*	0	0	0	1	0	0	0	1	**0.04**
Haemulidae	*Diagramma pictum*	0	0	1	1	2	14	2	20	**0.84**
	Plectorhinchus chaetodontoides	0	0	1	0	0	0	0	1	**0.04**
Leiognathidae	*Leiognathus sp."1"*	0	0	1	0	0	0	0	1	**0.04**

Appendix A. con't.

Family	Species	Mar-94	Oct-94	Mar-95	Jul-95	Oct-95	Mar-96	Jul-96	Total	% Comp.
Monacanthidae	*Oxymonocanthus longirostris*	0	0	0	0	0	0	1	1	**0.04**
Mugiloididae	*Mulloides flavolineatus*	0	0	0	0	0	1	0	1	**0.04**
Muraenidae	*Gymnothorax undulatus*	0	3	3	0	0	1	0	7	**0.29**
	Gymnothorax flavimarginatus	1	2	1	0	0	0	0	4	**0.17**
	Gymnothorax criboris	0	0	0	0	1	0	0	1	**0.04**
	Gymnothorax javanicus	0	0	0	0	0	0	1	1	**0.04**
	Gymnothorax sp."1"	0	0	0	1	0	0	0	1	**0.04**
Nemiteridae	*Scolopsis bilineatus*	0	0	1	2	0	6	1	10	**0.42**
	Scolopsis monogramma	0	0	0	0	0	4	0	4	**0.17**
Scaridae	*Hipposcarus longiceps*	0	1	0	0	0	0	0	1	**0.04**
Siganidae	*Siganus doliatus*	2	3	1	0	0	5	3	14	**0.59**
	Siganus corallinus	0	0	0	0	0	1	0	1	**0.04**
Spyraenidae	*Sphyraena jello*	1	0	0	0	0	0	0	1	**0.04**
Synodontidae	*Synodus variegatus*	0	0	0	1	0	1	0	2	**0.08**
	Saurida gracilis	1	0	0	0	0	0	0	1	**0.04**
Tetraodontidae										
	Arothron hispidus	0	0	0	0	0	1	0	1	**0.04**
	Canthigaster valentinni	1	1	3	0	0	1	0	6	**0.25**

SUMMARY

Family	Mar-94	Oct-94	Mar-95	Jul-95	Oct-95	Mar-96	Jul-96	Total	% Comp.
a. Abundances									
Pomacentridae	143	128	71	42	45	107	34	570	**23.87**
Lutjanidae	83	68	57	56	87	133	72	556	**23.28**
Apogonidae	38	101	123	75	56	42	45	480	**20.10**
Lethrinidae	34	26	27	19	21	41	18	186	**7.79**
Labridae	11	50	19	21	40	29	14	184	**7.71**
Serranidae	19	28	12	9	18	18	11	115	**4.82**
Holocentridae	9	11	21	13	13	21	16	104	**4.36**
Others (20 Fam.)	53	13	45	11	8	44	19	193	**8.08**
Total	390	425	375	246	288	435	229	**2388**	
b. Number of species									
Pomacentridae	10	14	10	4	7	10	6	**19**	**15.97**
Lutjanidae	6	5	5	6	7	6	5	**11**	**9.24**
Apogonidae	13	12	13	9	7	7	6	**26**	**21.85**
Lethrinidae	6	3	7	5	4	6	4	**9**	**7.56**
Labridae	2	2	4	2	3	2	1	**5**	**4.20**
Serranidae	5	6	3	2	5	4	5	**8**	**6.72**
Holocentridae	2	3	4	2	2	3	4	**7**	**5.88**
Others (20 Fam.)	10	7	14	8	4	15	8	**34**	**28.57**
Total	54	52	60	38	39	53	39	**119**	

Appendix B. Percentage composition of species across all habitat types pooled over sampling times and soak periods for Z-trap catches in Lizard Island lagoon, GBR. Code for habitat types are TOPS -tops of reefs, SLOP -slopes of reefs, DSNR -deep sand away from reefs, SSNR - shallow sand near reefs, RUBB -rubble areas and DSAR -deep sand away from reefs.

Family	Species	TOPS	SLOP	DSNR	SSNR	RUBB	DSAR	Total Abund.	Importance value (within family)
Pomacentridae	*Amblyglyphidodon curacao*	53.48	32.61	6.52	7.39	0.00	0.00	230	0.4035
	Acanthochromis polyacanthus	73.37	6.53	3.02	5.03	12.06	0.00	199	0.3491
	Chromis viridis	22.92	0.00	0.00	0.00	77.08	0.00	48	0.0842
	Pomacentrus moluccensis	38.89	16.67	16.67	5.56	22.22	0.00	18	0.0316
	Pomacentrus amboinensis	0.00	23.53	41.18	0.00	35.29	0.00	17	0.0298
	Pomacentrus brachialis	37.50	37.50	0.00	12.50	6.25	6.25	16	0.0281
	Neoglyphidodon melas	33.33	22.22	0.00	0.00	44.44	0.00	9	0.0158
	Pomacentrus chrysurus	0.00	0.00	0.00	0.00	100.00	0.00	7	0.0123
	Pomacentrus philippinus	42.86	57.14	0.00	0.00	0.00	0.00	7	0.0123
	Amblyglyphidodon leucogaster	0.00	100.00	0.00	0.00	0.00	0.00	4	0.0070
	Dischistodus pseudochrysopoecilus	0.00	0.00	0.00	33.33	66.67	0.00	3	0.0053
	Pomacentrus wardi	66.67	33.33	0.00	0.00	0.00	0.00	3	0.0053
	Dischistodus perspicillatus	0.00	50.00	50.00	0.00	0.00	0.00	2	0.0035
	Dischistodus prosopotaenia	0.00	0.00	100.00	0.00	0.00	0.00	2	0.0035
	Abudefduf whitleyi	100.00	0.00	0.00	0.00	0.00	0.00	1	0.0018
	Chromis agilis	0.00	0.00	0.00	0.00	100.00	0.00	1	0.0018
	Chrysiptera rollandi	0.00	100.00	0.00	0.00	0.00	0.00	1	0.0018
	Hemiglyphidodon plagiometopon	0.00	0.00	0.00	100.00	0.00	0.00	1	0.0018
	Stegastes nigricans	0.00	100.00	0.00	0.00	0.00	0.00	1	0.0018
Lutjanidae	*Lutjanus carponotatus*	30.97	30.38	25.37	8.26	5.01	0.00	339	0.6097
	Lutjanus quinquelineatus	0.00	22.94	49.54	4.59	0.00	22.94	109	0.1960
	Lutjanus fulviflamma	8.47	13.56	10.17	10.17	8.47	49.15	59	0.1061
	Lutjanus gibbus	0.00	0.00	8.33	0.00	91.67	0.00	12	0.0216
	Lutjanus vitta	0.00	9.09	0.00	0.00	0.00	90.91	11	0.0198
	Lutjanus bohar	40.00	30.00	10.00	10.00	10.00	0.00	10	0.0180
	Lutjanus russelli	11.11	0.00	77.78	0.00	0.00	11.11	9	0.0162
	Symphorus nematophorus	0.00	66.67	0.00	0.00	0.00	33.33	3	0.0054
	Lutjanus fulvus	0.00	0.00	50.00	50.00	0.00	0.00	2	0.0036
	Lutjanus monostigma	100.00	0.00	0.00	0.00	0.00	0.00	1	0.0018
	Lutjanus rufolineatus	0.00	0.00	0.00	0.00	0.00	100.00	1	0.0018
Apogonidae	*Apogon bandanensis*	43.67	10.13	5.06	20.89	20.25	0.00	158	0.3292
	Apogon compressus	69.51	13.41	9.76	7.32	0.00	0.00	82	0.1708
	Fowleria sp."1"	20.75	47.17	15.09	15.09	1.89	0.00	53	0.1104
	Apogon cookii	7.50	0.00	5.00	87.50	0.00	0.00	40	0.0833
	Cheilodipterus quinquelineatus	28.95	7.89	15.79	42.11	0.00	5.26	38	0.0792
	Rhabdamia gracilis	0.00	0.00	17.39	0.00	0.00	82.61	23	0.0479
	Apogon guamensis	16.67	38.89	16.67	22.22	5.56	0.00	18	0.0375
	Cheilodipterus macrosoma	0.00	0.00	0.00	100.00	0.00	0.00	15	0.0313
	Apogon cyanosoma	12.50	12.50	25.00	12.50	12.50	25.00	8	0.0167
	Apogon exostigma	0.00	0.00	20.00	60.00	20.00	0.00	5	0.0104
	Apogon sp."3"	20.00	0.00	0.00	40.00	40.00	0.00	5	0.0104
	Apogon aureus	0.00	0.00	0.00	100.00	0.00	0.00	4	0.0083
	Apogon fraenatus	0.00	0.00	25.00	75.00	0.00	0.00	4	0.0083
	Apogon ocellatus	75.00	0.00	25.00	0.00	0.00	0.00	4	0.0083
	Foa brachygramma	50.00	50.00	0.00	0.00	0.00	0.00	4	0.0083
	Apogon fuscus	0.00	33.33	33.33	0.00	33.33	0.00	3	0.0063
	Archaemia melasma	0.00	66.67	0.00	33.33	0.00	0.00	3	0.0063
	Apogon angustatus	0.00	0.00	0.00	50.00	0.00	50.00	2	0.0042
	Apogon doederleini	0.00	0.00	0.00	50.00	50.00	0.00	2	0.0042
	Apogon talboti	50.00	0.00	50.00	0.00	0.00	0.00	2	0.0042
	Archaemia leai	50.00	0.00	0.00	50.00	0.00	0.00	2	0.0042
	Apogon mollucensis	0.00	0.00	0.00	0.00	0.00	100.00	1	0.0021
	Apogon sp."1"	0.00	100.00	0.00	0.00	0.00	0.00	1	0.0021
	Apogon sp."2"	0.00	100.00	0.00	0.00	0.00	0.00	1	0.0021
	Archaemia fucata	0.00	0.00	0.00	100.00	0.00	0.00	1	0.0021
	Foa sp."1"	100.00	0.00	0.00	0.00	0.00	0.00	1	0.0021

Appendix B. con't.

Family	Species	TOPS	SLOP	DSNR	SSNR	RUBB	DSAR	Total Abund.	Importance value (within family)
Lethrinidae	*Lethrinus nebulosus*	2.60	5.19	27.27	22.08	3.90	38.96	77	**0.4140**
	Lethrinus semicinctus	0.00	30.61	10.20	4.08	51.02	4.08	49	**0.2634**
	Lethrinus atkinsoni	4.00	80.00	0.00	12.00	4.00	0.00	25	**0.1344**
	Lethrinus lentjan	0.00	0.00	0.00	4.55	9.09	86.36	22	**0.1183**
	Lethrinus olivaceus	0.00	0.00	0.00	0.00	100.00	0.00	5	**0.0269**
	Lethrinus variegatus	0.00	0.00	0.00	0.00	100.00	0.00	5	**0.0269**
	Lethrinus harak	0.00	0.00	0.00	100.00	0.00	0.00	1	**0.0054**
	Lethrinus obsoletus	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.0054**
	Lethrinus ornatus	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0054**
Labridae	*Thalassoma lunare*	34.23	46.31	4.70	2.01	12.75	0.00	149	**0.8098**
	Choerodon fasciatus	6.25	81.25	12.50	0.00	0.00	0.00	32	**0.1739**
	Cheilinus chlororus	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0054**
	Cheilinus fasciatus	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0054**
	Stethojulis bandanensis	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.0054**
Serranidae	*Cephalopholis cyanostigma*	16.18	75.00	4.41	4.41	0.00	0.00	68	**0.5913**
	Plectropomus leopardus	22.73	54.55	22.73	0.00	0.00	0.00	22	**0.1913**
	Epinephelus ongus	11.11	88.89	0.00	0.00	0.00	0.00	9	**0.0783**
	Epinephelus merra	66.67	0.00	0.00	0.00	33.33	0.00	6	**0.0522**
	Cephalopholis microdon	20.00	60.00	0.00	0.00	0.00	20.00	5	**0.0435**
	Cephalopholis boenack	0.00	100.00	0.00	0.00	0.00	0.00	2	**0.0174**
	Epinephelus fuscoguttatus	0.00	100.00	0.00	0.00	0.00	0.00	2	**0.0174**
	Epinephelus malabaricus	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0087**
Holocentridae	*Myripristis mudjan*	20.27	29.73	45.95	1.35	0.00	2.70	74	**0.7115**
	Sargocentron spiniferum	12.50	62.50	4.17	8.33	12.50	0.00	24	**0.2308**
	Neoniphon sammara	50.00	0.00	0.00	0.00	50.00	0.00	2	**0.0192**
	Myripristis sp."1"	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0096**
	Myripristis violacea	100.00	0.00	0.00	0.00	0.00	0.00	1	**0.0096**
	Sargocentron sp."1"	100.00	0.00	0.00	0.00	0.00	0.00	1	**0.0096**
	Sargocentron violaceum	0.00	0.00	100.00	0.00	0.00	0.00	1	**0.0096**
Blenniidae	*Dasson variabilis*	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.5000**
	Salarias fasciatus	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.5000**
Caesionidae	*Caesio cuning*	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.3333**
	Pterocaesio digramma	0.00	100.00	0.00	0.00	0.00	0.00	2	**0.6667**
Carangidae	*Gnathonodon speciosus*	0.00	0.00	0.00	0.00	0.00	100.00	15	**0.9375**
	Carangoides fulvoguttatus	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0625**
Centriscidae	*Aeoliscus strigatus*	50.00	3.70	25.93	0.00	3.70	16.67	54	**1.0000**
Chaetodontidae	*Chaetodon melannotus*	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.2500**
	Chaetodon plebeius	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.2500**
	Chaetodon trifasciatus	0.00	100.00	0.00	0.00	0.00	0.00	2	**0.5000**
Cirrhitidae	*Parapercis tetracantha*	0.00	0.00	0.00	25.00	75.00	0.00	4	**1.0000**
Echeneidae	*Echeneis naucrates*	0.00	3.85	11.54	7.69	0.00	76.92	26	**1.0000**
Ephiphidae	*Platax tierra*	0.00	25.00	0.00	0.00	0.00	75.00	4	**1.0000**
Fistulariidae	*Fistularia commersoni*	0.00	0.00	0.00	0.00	0.00	100.00	1	**1.0000**
Haemulidae	*Diagramma pictum*	0.00	0.00	45.00	0.00	0.00	55.00	20	**0.9524**
	Plectorhinchus chaetodontoides	0.00	0.00	0.00	0.00	0.00	100.00	1	**0.0476**
Leiognathidae	*Leiognathus sp."1"*	0.00	0.00	0.00	0.00	0.00	100.00	1	**1.0000**

Appendix B. con't.

Family	Species	TOPS	SLOP	DSNR	SSNR	RUBB	DSAR	Total Abund.	Importance value (within family)
Monacanthidae	*Oxymonocanthus longirostris*	0.00	0.00	0.00	0.00	100.00	0.00	1	**0.5000**
Mugiloididae	*Mulloides flavolineatus*	0.00	0.00	0.00	0.00	100.00	0.00	1	**1.0000**
Muraenidae	*Gymnothorax undulatus*	57.14	0.00	14.29	28.57	0.00	0.00	7	**0.5000**
	Gymnothorax flavimarginatus	0.00	50.00	0.00	25.00	25.00	0.00	4	**0.2857**
	Gymnothorax criboris	0.00	100.00	0.00	0.00	0.00	0.00	1	**0.0714**
	Gymnothorax javanicus	100.00	0.00	0.00	0.00	0.00	0.00	1	**0.0714**
	Gymnothorax sp."1"	100.00	0.00	0.00	0.00	0.00	0.00	1	**0.0714**
Nemiteridae	*Scolopsis bilineatus*	0.00	0.00	10.00	70.00	20.00	0.00	10	**0.7143**
	Scolopsis monogramma	0.00	0.00	25.00	0.00	0.00	75.00	4	**0.2857**
Scaridae	*Hipposcarus longiceps*	100.00	0.00	0.00	0.00	0.00	0.00	1	**1.00000**
Siganidae	*Siganus doliatus*	35.71	21.43	0.00	0.00	42.86	0.00	14	**0.9333**
	Siganus corallinus	100.00	0.00	0.00	0.00	0.00	0.00	1	**0.0667**
Spyraenidae	*Sphyraena jello*	100.00	0.00	0.00	0.00	0.00	0.00	1	**1.0000**
Synodontidae	*Synodus variegatus*	0.00	0.00	0.00	100.00	0.00	0.00	2	**0.6667**
	Saurida gracilis	0.00	0.00	0.00	100.00	0.00	0.00	1	**0.3333**
Tetraodontidae	*Arothron hispidus*	0.00	0.00	0.00	100.00	0.00	0.00	1	**0.5000**
	Canthigaster valentinni	0.00	0.00	0.00	16.67	83.33	0.00	6	**1.0000**

SUMMARY

	Family		TOPS	SLOP	DSNR	SSNR	RUBB	DSAR	Total Catch (n)
a. Abundances									
	Pomacentridae		52.98	20.18	5.96	5.61	15.09	0.18	**570**
	Lutjanidae		20.86	25.54	28.06	7.37	6.12	12.05	**556**
	Apogonidae		34.17	14.58	9.58	28.13	8.33	5.21	**480**
	Labridae		28.80	52.72	5.98	1.63	10.87	0.00	**186**
	Lethrinidae		1.61	21.51	13.98	12.90	22.58	27.42	**184**
	Serranidae		19.13	68.70	6.96	2.61	1.74	0.87	**115**
	Holocentridae		20.19	36.54	34.62	2.88	3.85	1.92	**104**
	Others (20 Fam.)		21.24	8.81	15.03	9.33	12.44	33.16	**193**
									2388
		Total	30.23	25.04	14.49	10.85	10.55	8.84	
b. Number of species									
	Pomacentridae		8	12	6	6	9	1	**19**
	Lutjanidae		5	6	7	5	4	6	**11**
	Apogonidae		13	12	13	17	8	5	**26**
	Lethrinidae		2	4	2	5	7	3	**9**
	Labridae		2	4	2	1	2	0	**5**
	Serranidae		5	7	2	1	1	1	**8**
	Holocentridae		5	3	3	2	2	1	**7**
	Others (20 Fam.)		8	12	6	9	11	9	**34**
		Total	48	60	41	46	44	26	**119**

Appendix C. Percentage catch of species in day and night soak periods. Catch data were standardized across soak periods and pooled over sampling times and habitat types. Codes for soak time DT -day time and NT -night time.

Family	Species	Species Codes	Total Catch (n)	DT	NT
Pomacentridae	*Acanthochromis polyacanthus*	ACA POLY	162	93.88	6.12
	Amblyglyphidodon curacao	AMB CURA	158	57.04	42.96
	Chromis viridis	CHR VIRI	40	100.00	0.00
	Pomacentrus amboinensis	POM AMBO	13	87.69	12.31
	Pomacentrus moluccensis	POM MOLL	13	65.61	34.39
	Pomacentrus brachialis	POM BRAC	12	77.05	22.95
	Neoglyphidodon melas	NEO MELA	7	75.32	24.68
	Pomacentrus philippinus	POM PHIL	6	90.16	9.84
	Pomacentrus chrysurus	POM CHRY	5	53.37	46.63
	Amblyglyphidodon leucogaster	AMB LEUC	2	33.72	66.28
	Dischistodus pseudochrysopoecilus	DIS PSEU	2	75.32	24.68
	Pomacentrus wardi	POM WARD	2	43.28	56.72
	Dischistodus perspicillatus	DIS PERS	1	60.42	39.58
	Dischistodus prosopotaenia	DIS PROS	1	60.42	39.58
	Abudefduf whitleyi	ABU WHIT	1	100.00	0.00
	Chromis agilis	CHR AGIL	1	100.00	0.00
	Stegastes nigricans	STE NIGR	1	100.00	0.00
	Chrysiptera rollandi	CHR ROLL	1	0.00	100.00
	Hemiglyphidodon plagiometopon	HEM PLAG	1	0.00	100.00
Lutjanidae	*Lutjanus carponotatus*	LUT CARP	226	49.94	50.06
	Lutjanus quinquelineatus	LUT QUIN	60	1.39	98.61
	Lutjanus fulviflamma	LUT FULV	36	30.14	69.86
	Lutjanus gibbus	LUT GIBB	9	75.32	24.68
	Lutjanus vitta	LUT VITT	8	80.28	19.72
	Lutjanus bohar	LUT BOHA	6	39.55	60.45
	Lutjanus russelli	LUT RUSS	6	43.28	56.72
	Symphorus nematophorus	SYM NEMA	2	43.28	56.72
	Lutjanus fulvus	LUT FLVS	1	60.42	39.58
	Lutjanus monostigma	LUT MONO	1	100.00	0.00
	Lutjanus rufolineatus	LUT RUFO	1	0.00	100.00
Apogonidae	*Apogon bandanensis*	APO BAND	87	0.96	99.04
	Apogon compressus	APO COMP	45	0.00	100.00
	Fowleria sp."1"	FOW BRWN	29	0.00	100.00
	Cheilodipterus quinquelineatus	CHE QUIN	24	38.34	61.66
	Apogon cookii	APO COOK	24	17.90	82.10
	Rhabdamia gracilis	RHA GRAC	13	0.00	100.00
	Apogon guamensis	APO GUAM	10	0.00	100.00
	Cheilodipterus macrosoma	CHE MACR	8	0.00	100.00
	Apogon cyanosoma	APO CYAN	4	0.00	100.00
	Apogon exostigma	APO EXOS	3	0.00	100.00
	Apogon sp."3"	APO WHIT	3	0.00	100.00
	Apogon aureus	APO AURE	2	0.00	100.00
	Apogon fraenatus	APO FRAE	2	0.00	100.00
	Apogon ocellatus	APO OCEL	2	0.00	100.00
	Foa brachygramma	FOA BRAC	2	0.00	100.00
	Apogon fuscus	APO FUSC	2	0.00	100.00
	Archaemia melasma	ARC MELA	2	0.00	100.00
	Apogon angustatus	APO ANGU	1	0.00	100.00
	Apogon doederleini	APO DOED	1	0.00	100.00
	Apogon talboti	APO TALB	1	0.00	100.00
	Archaemia leai	ARC LEAI	1	0.00	100.00
	Apogon mollucensis	APO MOLL	1	0.00	100.00
	Apogon sp."1"	APO SP1	1	0.00	100.00
	Apogon sp."2"	APO SP2	1	0.00	100.00
	Archaemia fucata	ARC FUCA	1	0.00	100.00
	Foa sp."1"	FOA SP.	1	0.00	100.00

Appendix C. con't.

Family	Species	Species Codes	Total Catch (n)	DT	NT
Lethrinidae	*Lethrinus nebulosus*	LET NEBU	47	30.19	69.81
	Lethrinus semicinctus	LET SEMI	35	65.20	34.80
	Lethrinus atkinsoni	LET ATKI	17	50.43	49.57
	Lethrinus lentjan	LET LENT	12	0.00	100.00
	Lethrinus variegatus	LET VARI	4	69.60	30.40
	Lethrinus olivaceus	LET OLIV	3	50.43	49.57
	Lethrinus harak	LET HARA	1	0.00	100.00
	Lethrinus obsoletus	LET OBSO	1	0.00	100.00
	Lethrinus ornatus	LET ORNA	1	0.00	100.00
Labridae	*Thalassoma lunare*	THA LUNA	115	83.25	16.75
	Choerodon fasciatus	CHO FASC	23	66.24	33.76
	Cheilinus chlororus	CHE CHLO	1	0.00	100.00
	Cheilinus fasciatus	CHE FASC	1	0.00	100.00
	Stethojulis bandanensis	STE BAND	1	0.00	100.00
Serranidae	*Cephalopholis cyanostigma*	CEP CYAN	44	42.20	57.80
	Plectropomus leopardus	PLE LEOP	15	60.42	39.58
	Epinephelus ongus	EPI ONGU	6	43.28	56.72
	Epinephelus merra	EPI MERR	5	88.41	11.59
	Cephalopholis microdon	CEP MICR	3	27.62	72.38
	Cephalopholis boenack	CEP BOEN	1	60.42	39.58
	Epinephelus fuscoguttatus	EPI FUSC	1	0.00	100.00
	Epinephelus malabaricus	EPI MALA	1	100.00	0.00
Holocentridae	*Myripristis mudjan*	MYR MURD	41	0.00	100.00
	Sargocentron spiniferum	SAR SPIN	13	0.00	100.00
	Neoniphon sammara	NEO SAMM	1	0.00	100.00
	Myripristis sp."1"	MYR SP.	1	0.00	100.00
	Myripristis violacea	MYR VIOL	1	0.00	100.00
	Sargocentron sp."1"	SAR SP1	1	0.00	100.00
	Sargocentron violaceum	SAR VIOL	1	0.00	100.00
Blenniidae	*Dasson variabilis*	DAS VARI	1	0.00	100.00
	Salarias fasciatus	SAL FASC	1	0.00	100.00
Caesionidae	*Caesio cuning*	CAE CUNI	1	0.00	100.00
	Pterocaesio digramma	PTE DIGR	2	0.00	100.00
Carangidae	*Carangoides fulvoguttatus*	CAR FULV	1	100.00	0.00
	Gnathonodon speciosus	GNA SPEC	12	90.84	9.16
Centriscidae	*Aeoliscus strigatus*	AEO STRI	43	87.04	12.96
Chaetodontidae	*Chaetodon trifasciatus*	CHA TRIF	1	0.00	100.00
	Chaetodon plebeius	CHA PLEB	1	100.00	0.00
	Chaetodon melannotus	CHA MELA	1	0.00	100.00
Cirrhitidae	*Parapercis tetracantha*	PAR TETR	3	82.08	17.92
Echeneidae	*Echeneis naucrates*	ECH NAUC	20	80.56	19.44
Ephiphidae	*Platax tierra*	PLA TIER	2	0.00	100.00
Fistulariidae	*Fistularia commersoni*	FIS COMM	1	100.00	0.00
Haemulidae	*Diagramma pictum*	DIA PICT	12	14.50	85.50
	Plectorhinchus chaetodontoides	PLE CHAE	1	0.00	100.00
Leiognathidae	*Leiognathus sp."1"*	SML SLIP	1	100.00	0.00

Appendix C. con't.

Family	Species	Species Codes	Total Catch (n)	DT	NT
Monacanthidae	*Oxymonocanthus longirostris*	OXY LONG	1	100.00	0.00
Mugiloididae	*Mulloides flavolineatus*	MULL FLAV	1	0.00	100.00
Muraenidae	*Gymnothorax undulatus*	GYM UNDU	4	0.00	100.00
	Gymnothorax flavimarginatus	GYM FLAV	2	33.72	66.28
	Gymnothorax criboris	AUST EEL	1	0.00	100.00
	Gymnothorax javanicus	GYM JAVA	1	0.00	100.00
	Gymnothorax sp."1"	GYM SP.	1	0.00	100.00
Nemiteridae	*Scolopsis bilineatus*	SCO BILI	8	78.08	21.92
	Scolopsis monogramma	SCO MONO	2	0.00	100.00
Scaridae	*Hipposcarus longiceps*	SCA HARI	1	0.00	100.00
Siganidae	*Siganus doliatus*	SIG DOLI	11	84.84	15.16
	Siganus corallinus	SIG CORA	1	0.00	100.00
Spyraenidae	*Sphyraena jello*	SPH JELL	1	100.00	0.00
Synodontidae	*Synodus variegatus*	SYN VARI	2	100.00	0.00
	Saurida gracilis	SAU GRAC	1	0.00	100.00
Tetraodontidae	*Arothron hispidus*	ARO THRO	1	100.00	0.00
	Canthigaster valentinni	CAN VALE	4	60.42	39.58

SUMMARY

a. Abundances

Pomacentridae		429	**77.50**	**22.50**
Lutjanidae		357	**40.81**	**59.19**
Apogonidae		270	**5.31**	**94.69**
Lethrinidae		120	**41.49**	**58.51**
Labridae		140	**79.49**	**20.51**
Serranidae		76	**48.61**	**51.39**
Holocentridae		57	**0.00**	**100.00**
Others (20 Fam.)		139	**67.85**	**32.15**
	Total	1588	**49.42**	**50.58**

b. Number of species

Pomacentridae	19	17	15
Lutjanidae	11	10	10
Apogonidae	26	3	26
Lethrinidae	9	5	9
Labridae	5	2	5
Serranidae	8	7	7
Holocentridae	7	0	7
Others (20 Fam.)	34	17	27
Total	119	61	106