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SPATIAL VARIABILITY IN THE DISTRIBUTION, ABUNDANCE, GROWTH, MORTALITY AND AGE STRUCTURES OF TROPICAL SNAPPERS (PISCES : LUTJANIDAE) IN THE CENTRAL GREAT BARRIER REEF, AUSTRALIA.

Thesis submitted by

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at

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This thesis is dedicated to my parents

Raymond John

and

Marie Elizabeth

whom I owe so much.

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Stephen John NEWMAN

January, 1995

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Abstract

The aim of this thesis was to determine the distribution and abundance of the three major families of fishes of commercial and recreational importance in the central Great Barrier Reef (Lutjanidae, Lethrinidae and Serranidae), with particular emphasis on the snappers (Lutjanidae), and to examine the age structures, growth rates and mortality rates of two snappers, *Lutjanus adetii* and *L. quinquelineatus*. Data were collected on distribution and abundance at four spatial scales : cross-continental shelf, among individual reefs, among reef zones within reefs and with depth; and two temporal scales : night versus day and two-monthly intervals over a 12 month period.

Fish traps were used to quantify the distribution and abundance of the Lutjanidae and Lethrinidae on reefs across the central Great Barrier Reef. The assemblages of fishes on inshore reefs were distinctive from those on midshelf and outershelf reefs. There were significantly fewer individuals of the Lutjanidae and Lethrinidae inshore. All species examined displayed significant cross shelf changes in abundance. This variation in abundance was due to an absence or low abundance of individuals at one or more cross shelf locations. Possible causes of these patterns are discussed. The genera *Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus*, *Gnathodentex*, *Gymnocranius*, *Lethrinus* and *Monotaxis* were all characteristic of the shallow shelf waters less than 100m. In contrast, species of the genera *Paracaesio*, *Pristipomoides* and

Wattsia were characteristic of the intermediate depths (100-200m) and the deeper outer reef slope waters in excess of 200m were characterised by species of the genus *Etelis*.

Visual censuses were used to quantify the distribution and abundance of the Lutjanidae, Lethrinidae and Serranidae in three reef zones (windward reef slope, lagoon, leeward back reef slopes) of three reefs on the mid-shelf and three reefs on the outer continental shelf in the central region of the Great Barrier Reef. The assemblages of species of the Lutjanidae, Lethrinidae and Serranidae displayed distinct patterns of distribution and abundance within the shallow waters of the central GBR at three spatial scales : between locations (outershelf and midshelf communities); between reefs (high abundance vs. low abundance reefs); and within reefs (characteristic communities within zones on individual reefs). Significant spatial variability was identified in the abundances of many species and species of the Lutjanidae, Lethrinidae and Serranidae were found to occur in assemblages which were characteristic of major zones (windward reef slopes, lagoons and leeward back reef slopes) and this pattern was consistent within and among shelf locations. Location on the continental shelf accounted for a high proportion of the variation in community structure. The Lutjanidae and Serranidae were more abundant on the midshelf while the Lethrinidae (in particular *Gnathodentex aurolineatus* and *Monotaxis grandoculis*) were more abundant on the outershelf reefs. Additionally, a large proportion of the species recorded were relatively rare within a given zone, reef or location. Care will need to be taken in determining the appropriate spatial scales of sampling in any future experiments (eg. manipulations of fishing pressure) to ensure that the effects of smaller scale spatial differences are not confounded when larger scale comparisons are made.

Spatial and temporal patterns in the distribution and abundance of the Lutjanidae and Lethrinidae were examined among midshelf reefs using a combination of visual censuses and fish traps. Visual censuses were used to survey the shallow water assemblages, while fish traps were used to survey deeper water assemblages below diveable depths. The assemblages of the Lutjanidae and Lethrinidae were found to vary significantly spatially among reefs and between depths and also between diel sampling periods. Significant among reef differences were observed in the shallow water assemblages for both the Lutjanidae and Lethrinidae. The deeper water assemblages of the Lutjanidae and Lethrinidae, sampled by traps varied more between depths and between diel sampling periods than among reefs or over the 12 month sampling period. *Lutjanus carponotatus*, *L. fulviflamma* and *Lethrinus miniatus* were significantly more abundant in the shallow set traps (12-18m), whereas *Lutjanus adetii*, *L. russelli*, *L. sebae*, *L. vitta*, *Gymnocranius audleyi*, *Lethrinus sp.2* and *Abalistes stellaris* were all significantly more abundant in the deep set traps (30-40m). Additionally, *Lutjanus adetii*, *L. fulviflamma*, *L. quinquelineatus*, *L. russelli*, *L. sebae*, *L. vitta* and *Lethrinus miniatus* were all significantly more abundant in night set traps. In contrast, *Lethrinus sp. 2*, *Abalistes stellaris* and *Plectropomus leopardus* were all significantly more abundant in day set traps. The diel variability in trap catches is consistent with what is known of the

feeding behaviour of the species examined. There was seasonal variability in mean species abundance in both visual census counts and trap catch data but significant trends were identified for only two species, *Lethrinus obsoletus* and *Gymnocranius audleyi*. Peaks in mean species abundance occurred generally in the June through September sampling periods.

The age and growth of *Lutjanus adetii* and *L. quinquelineatus* from the central Great Barrier Reef were determined from studies of annuli in sectioned otoliths (sagittae). The periodicity of formation of the annuli (ages) was validated through a field study involving oxytetracycline labelling of tagged fishes. Validation was obtained from tagged fishes which were recaptured after 12 months or more at liberty. This is the first time that the direct validation of ages has been achieved in *Lutjanus* species. A single opaque and translucent zone (viewed under transmitted light) was found to be formed once per year with the opaque band (annulus) formed during the winter months, May - August. Otolith (sagittae) weight was found to be strongly correlated with the age of individuals of both species. There was significant differential growth between the sexes in observed length-at-age and weight-at-age for both *L. adetii* and *L. quinquelineatus*. Males were larger than females in both species. The von Bertalanffy growth functions were as follows :

$$\textit{L. adetii}_{(m)} : L_t = 269.1\ (1 - e^{-0.165\ (t + 6.12)})$$

$$\textit{L. adetii}_{(f)} : L_t = 315.1\ (1 - e^{-0.029\ (t + 40.29)})$$

$$\textit{L. quinquelineatus}_{(m)} : L_t = 214.5\ (1 - e^{-0.2599\ (t + 3.427)})$$

$$\textit{L. quinquelineatus}_{(f)} : L_t = 204.3\ (1 - e^{-0.1664\ (t + 7.552)})$$

The oldest individuals examined were a male *L. adetii* 24 years of age and a female *L. quinquelineatus* 31 years of age. The shape of the growth curve of both of these lutjanid species was initially quite steep over the first few years and then became essentially asymptotic. This form of asymptotic growth curve suggests that curves describing natural mortality as a function of age will also be initially steep (high mortality) and then flatten substantially over the asymptotic growth period (low mortality) before increasing again with senility. This is in contrast to most classical fisheries models which assume that natural mortality (M) is constant and low over a wide range of ages. The annual instantaneous rate of total mortality (Z) was estimated to be 0.300 for *L. adetii*, representing an annual survivorship of approximately 74%. The annual instantaneous rate of total mortality for *L. quinquelineatus* was estimated to be 0.154, representing an annual survivorship of approximately 86%. Regression methods used to produce estimates natural mortality rates such as those of Pauly (1980) and Ralston (1987) were found to produce overestimates of natural mortality for these long lived species and hence underestimate survivorship. Regression methods used to produce estimates of total and natural mortality rates such as those described by Pauly (1980), Hoenig (1983) and Ralston (1987) should be applied with caution. The slow growth, protracted longevity and low natural mortality rates imply that both *L. adetii* and *L. quinquelineatus* are vulnerable to overfishing despite their small size.

There was significant variability in the growth, mortality and age structures of *L. adetii* and *L. quinquelineatus* at the spatial scale of individual

reefs. Significant differences in the mean length, age and weight of both species were observed among reefs independent of the sex of the fish. There were also significant differences in observed weight-at-length among reefs for both species. The age structures of both *L.adetii* and *L. quinquelineatus* were also significantly different among reefs. Peaks in abundance of year classes were variable from reef to reef. Comparisons of the von Bertalanffy growth curves indicated that the pattern of growth in individuals of *L. quinquelineatus* was significantly different among reefs, while the pattern of growth in individuals of *L. adetii* was not significantly different among reefs. However, there were no significant differences in the mean length of the early age classes of either species among reefs. The mortality rates and hence survivorship of both *L. adetii* and *L. quinquelineatus* among reefs were highly variable. It is hypothesised that the varying age structures and mortality rates of both of these species at the spatial scale of individual coral reefs is determined by the non-equilibrial balance of variable recruitment interacting with density independent mortality. Hence the effect of good recruitment years may persist in the age structure of populations over time.

Contents

Chapter 1

Chapter 2

Chapter 7

Chapter 8

List of Illustrations and Figures

List of Tables

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.

Stephen John NEWMAN

January, 1995

Chapter 1

General Introduction

The fishes of the family Lutjanidae are primarily distributed throughout the tropical and subtropical seas of the world from shallow inshore estuarine areas to deep reef areas at depths as great as 500m (Allen, 1985). Adults are commonly associated with hard bottom structure, vertical relief or large epibenthos. The early developmental stages of most species of the Lutjanidae and their distributions are poorly known.

Taxonomy

Despite their abundance and importance as commercial food fishes the taxonomy of the Lutjanidae was poorly understood until the reviews of Allen (1985 : all lutjanid species known to date) and Allen and Talbot (1985 : Indo-Pacific *Lutjanus*) and the synopses of Anderson (1987) and Allen (1987). Pre-1985 substantial taxonomic confusion occurred in the literature, at least in part as a consequence of the similar appearances of many closely related species and the large number of nominal species of Lutjanidae (see Allen, 1985). The common synonyms and misidentifications of *Lutjanus* species known to occur on the Great Barrier Reef were summarised by Williams and Russ (1994). Their summary is extended and expanded to other genera of lutjanids below (Section 1.1). There are currently 103 lutjanid species known worldwide. This includes 40 species of the genus *Lutjanus* in the Indo-West Pacific. The 103 lutjanid species currently recognised differs in two instances from those described by Allen (1985). It includes the recent recognition of *Lutjanus ophuysenii* (Bleeker) as a valid species whose geographic distribution is restricted to the eastern Asian Shelf of the western North Pacific (Iwatsuki *et. al.*, 1993). This species has in the past been confused with *L. vitta* (Quoy and Gaimard) which is widely distributed throughout the Indo-West Pacific region except in the eastern Asian Shelf. Both species however appear to be sympatric in southwestern Taiwan and in the vicinity of Hong Kong (Iwatsuki *et. al.*, 1993). Additionally, *L. ambiguous* (Poey) is no longer considered a valid species, but instead is recognised as a natural intergeneric hybrid of *Ocyurus chrysurus* (Bloch) and *L. synagris* (Linnaeus) (Loftus, 1992; Domeier and Clarke, 1992). Both Loftus (1992) and Domeier and Clarke (1992) also argue that the apparent ease with which *Ocyurus* hybridises with *Lutjanus*, and the paucity of morphological characters differentiating the two genera, indicate that the presently accepted classification needs review and propose that *Ocyurus* should be synonymised with *Lutjanus*.

The Lutjanidae along with the Caesionidae form the superfamily Lutjanoidea and despite a number of generalised percoid characters there is no synapomorphic character that is known to distinguish the Lutjanidae from the other percoid families (Anderson, 1987). The limits and relationships of the Lutjanidae have been analysed by Johnson (1980) and four subfamilies are currently recognised (Apsilinae, Etelinae, Lutjaninae and the Paradicichthyinae). The Lutjanidae are treated as a natural group because of the obvious intermediacy of the Apsilinae between the Etelinae and Lutjaninae which are considered the most advanced groups, with the Paradicichthyinae considered to be the primitive sister group of the Lutjaninae and closely associated to the related family Caesionidae (Johnson, 1980). There are presently 44 species representing nine genera from all four subfamilies of the family Lutjanidae known to occur on the Great Barrier Reef (Lutjaninae : *Lutjanus*, *Macolor*; Etelinae: *Aphareus*, *Aprion*, *Etelis*, *Pristipomoides*; Apsilinae : *Paracaesio*; Paradicichthyinae : *Symphorichthys*, *Symphorus*). The genus *Lutjanus* is by far the most speciose with 25 species recorded to date.

Significance to Fisheries

The worldwide catch of lutjanids in 1991 that was reported to the Food and Agriculture Organisation of the United Nations totalled 70,689 metric tons (mt). The largest nominal catches of lutjanids were in the western central Pacific (Fishing Area 71) and western central Atlantic (Fishing Area 31) regions (Table 1.1). Substantial catches were also recorded from the northwest Pacific (Fishing Area 61) and western Indian Ocean (Fishing Area 51) areas (see Table 1.1). Individual world catch statistics were reported for the following species : *Lutjanus argentimaculatus* 7,708mt; *L. argentiventris* 3,727mt; *L. campechanus* 6.450mt; *L. purpureus* 3,907mt; *L. synagris* 2,691mt; and *Ocyurus chrysurus* 6,728 (FAO, 1993). The total catch of other *Lutjanus* species (excluding those above) worldwide totalled 33,807mt (FAO, 1993). The total catch of lutjanids in Australian waters in 1991 (as reported to the FAO) totalled 128 mt (FAO, 1993). This included 120 mt from the Indian Ocean region and

8 mt from the western Pacific area. The total and individual species catches supplied are frequently underestimates of the real catch of lutjanids worldwide (FAO, 1993).

Table 1.1 : Nominal catches of the Lutjanidae worldwide in 1991 by major fishing areas *.

Fishing Area (Code)	Catch (mt)
Inland waters of Asia (04)	4,698
Western central Atlantic (31)	15,497
Eastern central Atlantic (34)	237
Western Indian Ocean (51)	8,561
Eastern Indian Ocean (57)	1,880
Northwest Pacific (61)	8,851
Northeast Pacific (67)	320
Western central Pacific (71)	28,065
Eastern central Pacific (77)	2,524
Southeast Pacific (87)	56

* source FAO (1993).

In tropical Australian waters lutjanids form a significant proportion of the demersal catch in both the commercial and recreational fisheries. In Western Australia and the Northern Territory, lutjanids are caught by commercial fishermen using demersal and semi-pelagic otter trawls, traps, droplines, and deepwater handlines (Western Australia), while in Queensland they are handlined and also longlined (Kailola *et. al.*, 1993). The northern trawl fishery that operates in the Arafura and Timor Seas of northern Australia principally targets *Lutjanus malabaricus* with an annual total catch of 3,200 tonnes (Anon., 1991b; 1992). Five of the larger species of *Lutjanus* (*L. argentimaculatus*, *L. erythropterus*, *L. johnii*, *L. malabaricus* and *L. sebae*) are of outstanding commercial and recreational importance on the Great

Barrier Reef. Smaller species such as *L. adetii*, *L. carponotatus*, and *L. vitta*, as well as the deeper dwelling *Pristipomoides* species are receiving increasing attention from fishermen and this is reflected in the commercial catches. The total lutjanid catch on the Great Barrier Reef in 1993 was 33,941 kg which was considerably less than the total catch in the preceding years 1992 (55,710 kg) and 1991 (66,596 kg) (CFISH 1993 : Georgina Eliason, personal communication). The commercial catch of lutjanids on the Great Barrier Reef in 1993 was dominated by the "redfish" (*L. sebae*, *L. malabaricus* and *L. erythropterus*) and to a lesser extent the *Pristipomoides* species (see Table 1.2). A summary of the total lutjanid catches on the Great Barrier Reef from 1988 to 1993 are provided in Appendix 2. Queensland fishermen consider the resources of 'redfish' (*Lutjanus sebae*, *L. malabaricus* and *L. erythropterus*) in the Reef Line Fishery are in decline (Gwynne, 1990). However, the catch rates and the size of reef fish caught by the offshore charter boat fleet on the reef since 1963 have remained fairly stable (Williams and Russ, 1994).

Table 1.2 : Commercial catches of individual lutjanid species on the Great Barrier Reef in 1993 **.

Species	Catch (kg)
Lutjanus sebae	15,283
Lutjanus malabaricus	6,691
Pristipomoides species (mixed)	6,400
Lutjanus erythropterus and *L. malabaricus* (mixed)	2,433
Lutjanus argentimaculatus	1,360
Lutjanus adetii and *Lutjanus vitta* (mixed)	1,307
Lutjanus carponotatus	286

** commercial fisheries catch data courtesy of CFISH (1993) : the commercial fisheries database (Georgina Eliason, personal communication).

The Lutjanidae, along with the Lethrinidae and Serranidae, also comprise the majority of demersal fish caught by recreational fishermen on the Great Barrier Reef (Higgs, 1993). The total recreational fishing catch on the Great Barrier reef has been estimated at between 3,500 - 4,300 tonnes per year (Anon., 1993). The average weight of captured fish in the central GBR region alone has increased rapidly since 1988, and this is directly attributable to an increase in the percentage of lutjanids in the catch (Higgs, 1993). Recreational fishermen mainly target *Lutjanus* species, however the deepwater *Pristipomoides* species are caught incidentally as part of the general reef fish catch from outer reef slope waters in depths greater than 50m.

Distributions and Habitats

The Lutjanidae are distributed throughout the tropical seas of the world from scattered rocky reefs on open continental shelves to oceanic insular localities such as atoll reefs. The fishery resources of rocky and coral bottoms, both in coastal and offshore areas, in all tropical oceans are dominated by the lutjanids and serranids with many species attaining a large size.

In the eastern Atlantic (African west coast), there is a lower diversity of lutjanids than elsewhere in the tropics. In this region Fager and Longhurst (1968) analysed the fish community through recurrent group analysis and found the fauna of rocky, deeply submerged reefs and banks in 30-40m principally included *Lutjanus agennes*, *L. fulgens*, *L. goreensis* and *Lethrinus atlanticus*. The lutjanid community was commonly associated with the warm water of the mixed layer and upper thermocline.

In the western Atlantic there is a greater relative area of reef rock and sand habitat and the lutjanid community is relatively more uniform. The Holocene coral reefs along the shelf edge in this region support a well-defined lutjanid community (Longhurst and Pauly, 1987). In 60-70m of water along the shelf off Guiana and northern Brazil a valuable handline fishery exists for *L. campechanus* and *L. buccanella*. On the Campeche Bank, Sauskan and Ryzhov (1977) describe three statistical species associations in which the core group associated with hard sandy grounds is dominated by the lutjanids *Ocyurus chrysurus* and *L. synagris*. In the western tropical and subtropical Atlantic, Longhurst and Pauly (1987) distinguish four assemblages of demersal fishes. The principle one is the lutjanid community, which is found on a fauna of rock, coral and coral sand from Florida to Brazil and which is dominant on the Bahamas, the Antilles and other Caribbean Islands and on the coast from Yucatan to Panama and is represented by 14 lutjanid species, among others.

In the Indo-Pacific region the Lutjanidae are characteristic of hard bottoms of rocky banks with coral heads. Morgans (1964) undertook line fishing surveys of the North Kenya Banks and showed that the above the thermocline, the fish fauna is dominated by the lutjanids, lethrinids and serranids, with *L. rivulatus*, *L. bohar* and *Lethrinus crocineus* each contributing more than 10% of the landed biomass and that below the thermocline *Pristipomoides filamentosus* is one of the most abundant species. Off Mozambique, *L. bohar* dominates a typical rocky bank community of snappers and groupers (Longhurst and Pauly, 1987). Wheeler and Ommaney (1953) performed extensive handline surveys of the Mauritius and Seychelles banks from 15-60m and identified 44 commercially useful demersal species, and most were lutjanids and serranids, with *L. sebae* and *L. obsoletus* comprising more than 75% of individuals. More recent trawl surveys of the Mahe Plateau in 1978 found a typical bank fauna dominated by *L. sebae* and *L. lutjanus* (see Longhurst and Pauly, 1987). Similarly Mees (1992) describes *Pristipomoides filamentosus*, *Aprion virescens* and *L. sebae* as key members of the Seychelles demersal fishery. In the Hawaiian Archipelago demersal fish comprise less than 5% of all landings and the Lutjanidae dominate the landed biomass especially in the shallower areas, with *Pristipomoides sieboldii* and *Aprion virescens* the dominant species (Ralston and Polovina, 1982). Longhurst and Pauly (1987) report that the Wadge Bank (Indian continental shelf) has a similar fauna to the Indian Ocean banks, with 40% of the landed biomass comprising lutjanids, lethrinids and serranids (eg. *L. argentimaculatus*, *L. sebae*, *L. nebulosus*). Similarly, there exists in the South China Sea a sandy ground fauna in 60-90m with warm bottom water in which the Lutjanidae form 49% of the landed biomass and principally includes *L. sebae*, *L. lutjanus*, *L. vitta* and *L. gibbus* (Longhurst and Pauly, 1987). Okera (1982) in an extensive trawl survey of the north Australian continental shelf characterised 6 assemblages of recurrent species groups. The lutjanidae were conspicuous and dominant members of the hard bottom assemblage that included boulders, rocks and reefs at various depths with *L. argentimaculatus*, *L. erythropterus* and *L. russelli* the principle species. The Lutjanidae were also dominant in the midshelf species assemblage over mixed deposits from 60-110m where the principle species were *L. malabaricus* and *L. vitta*.

Purely oceanic insular localities such as atoll reefs are generally characterised by *L. bohar*, *L. fulvus*, *L. gibbus*, *L. kasmira*, *L. monostigma* and *L. rivulatus* as well as species of *Etelis*, *Paracaesio* and *Pristipomoides* (Allen, 1985).

A number of the lutjanid species that are of major commercial importance in the tropical fisheries of the world occur in the deep reef areas of the outer slopes of reefs from depths of 60 to greater than 300 metres. These species have only recently been recorded from the Great Barrier Reef (Kramer *et. al.*, 1994) and remain relatively unfished in these waters (Kramer *et. al.*, 1993).

The deep slope lutjanid communities of the Indo-Pacific region can be generalised into 3 distinct faunal assemblages based upon the depth of capture (Mead, 1979; Sundberg and Richards, 1984; Brouard and Grandperrin, 1985; Allen, 1985; Dalzell and Preston, 1992). There is however, considerable overlap among capture zones by some species. The shallow zone (0-100m) faunal assemblage consists principally of the genus *Lutjanus*, as well as *Aprion*, *Macolor*, *Symphorichthys*, *Symphorus*, and to a lesser extent *Aphareus*. The intermediate zone (100-200m) faunal assemblage is characterised by the *Pristipomoides* and to a lesser extent *Paracaesio*. The deep zone (>200m) faunal assemblage is dominated by the *Etelis* species. Both the *Pristipomoides* and *Etelis* species are commercially important in many areas of the Indo-Pacific region (Allen, 1985; Polovina, 1987; Anonyme, 1989; Dalzell and Preston, 1992).

In tropical estuarine areas lutjanid species are primarily represented by the juveniles and sub-adults of species occurring in the adjacent coastal, shelf and slope waters. The juveniles of at least 19 species of *Lutjanus* have been recorded from mangrove estuaries and the lower reaches of freshwater streams and bays including the Atlantic species *L. agennes*, *L. analis*, *L. apodus*, *L. campechanus*, *L. cyanopterus*, *L. dentatus*, *L. endecacanthus*, *L. goreensis*, *L. griseus*, *L. jocu* and the Indo-Pacific species *L. argentimaculatus*, *L. ehrenbergii*, *L. erythropterus*, *L. fulviflamma*, *L. fulvus*, *L. johnii*, *L. malabaricus*, *L. russelli* and *L. sebae*, while a further 3 species of Indo-Pacific *Lutjanus* (*L. fuscescens*, *L. goldiei* and *L. maxweberi*) are also known to inhabit freshwaters throughout their life history (Allen, 1985).

Age, Growth and Mortality

Lutjanids in general are long lived, slow growing and have relatively low rates of natural mortality. Maximum ages generally exceed 10 years and in some cases may exceed 40 years (*L. malabaricus* - Kuwait : Mathews and Samuel, 1985), with von Bertalanffy growth coefficients (K) usually falling within 0.1 - 0.35 year^{-1} (see reviews by Manooch (1987) and Williams and Russ (1994)). The determination of age and growth in snappers has most frequently been resolved through the analysis of rings formed on calcareous structures rather than by other methods such as length frequency analysis or tag-recapture studies.

Most studies of age and growth of lutjanids in Australian waters have been from the North West Shelf of Australia and the Arafura Sea region (Lai and Liu, 1979; Chen *et. al.*, 1984; Edwards, 1985; Yeh and Chen, 1986; Yeh *et. al.*, 1986; Ju *et. al.*, 1988; Ju *et. al.*, 1989; Liu and Yeh, 1991; Seyama *et. al.*, 1991; Davis and West, 1992) with only two published studies from waters of the Great Barrier Reef (McPherson *et. al.*, 1988; McPherson and Squire, 1992). These studies have concluded that lutjanids in general have relatively slow rates of growth and that maximum ages in general do not exceed 10 years (Seyama *et. al.* (1991) is an exception with an age of 27 years given to a specimen of *L. sebae*), although no studies have conclusively validated aging methodologies. In contrast, Loubens (1980b) in New Caledonia conducted extensive studies on the growth of lutjanids and found that they were particularly long lived. Three species, *L. adetii* (37), *L. bohar* (38), and *L. sebae* (35) were found to live for more than 30 years and a further three species, *Aprion virescens* (26), *L. fulviflamma* (23), and *L. quinquelineatus* (22) were found to live for more than 20 years, while another three species, *L. argentimaculatus* (18), *L. gibbus* (18), and *L. vitta* (12) were found to live for more than 10 years. Similarly, Mathews and Samuel (1985) reported a maximum age of 46 years for *L. malabaricus* in Kuwaiti waters in a major study of over 2000 fish collected monthly over nearly a 3 year period. These studies suggest that, while regional variation may occur, the longevity of snappers in Australian waters might also be expected to exceed 20 years and that the validation of age and growth studies is imperative to provide accurate growth parameters for management purposes.

The relatively low levels of natural mortality that characterise the lutjanids indicate a low natural turnover ratio, with natural mortality in lutjanids arising principally from predation, parasitism and senility (see review of Ralston, 1987). Ralston (1987) concluded that because of the low natural mortality rates and the relatively slow growth rates of lutjanid species they have a limited productive capacity and are thus vulnerable to overfishing.

Reproduction and Early Life History

The Lutjanidae are dioecious (separate sexes) and display no distinct sexual dimorphism. The reproductive pattern is gonochoristic with sex remaining constant throughout their life history following sexual differentiation. There is a paucity of information available on the spawning behaviour of the Lutjanidae (reviewed by Thresher (1984) and Grimes (1987)). Observations of reproductive behaviour and spawning in lutjanids in their natural habitat are known for only one species, *Lutjanus synagris* off southeast Florida (Wiklund, 1969). Other studies of reproductive behaviour and spawning in lutjanids have been of fish in aquaria (eg. *L. campechanus* : Gulf of Mexico, Arnold *et. al.*, 1978; *L. kasmira* : Japan, Suzuki and Hioki (1979); and *L. stellatus* : Japan, Hamamoto *et. al.*, 1992). These studies have provided detailed early life history information regarding spawning behaviour, eggs and larvae. This relative paucity of information on reproduction arises from the logistic constraints associated with protracted underwater observations and the nocturnal activity patterns of most lutjanid species, as well as their occurrence in a wide range of habitats.

On the basis of the above studies, reproductive behaviour of lutjanids is fundamentally similar among different species. Lutjanids are group spawners with either a protracted summer spawning season or a relatively continuous, year-round, spawning pattern with peaks during autumn and spring. Prior to the onset of spawning lutjanids repeat a number of spiral and ascending movements (eg. schooling, searching, nuzzling), with the spawning time occurring during the crepuscular period to about 2 hours after sunset. Species-specific behaviour patterns also occur for example; in *L. kasmira* initial spawning behaviour is among pairs (Suzuki and Hioki, 1979) while in *L. synagris* (Wiklund, 1969) and *L. stellatus* (Hamamoto *et. al.*, 1992) a number of males gather around a single female. During the spawning season nuptial coloration has been observed to occur before the onset of dusk, enabling differentiation of the sexes, with females possessing a lighter coloured body and a swollen abdomen (Wiklund, 1969; Hamamoto *et. al.*, 1992).

Similarly, the early life history of many lutjanid species is unknown or incomplete. Leis (1987) has produced the only review of the early life history of the Lutjanidae, with recent additions by Kojima (1988; in Japanese), Mori (1988; *Lutjanus bohar* and *L. vitta* : in Japanese), Potthoff *et. al.* (1988; *L. campechanus*), Iwatsuki *et. al.* (1989; *L. ehrenbergii*), Soletchnik *et. al.* (1989; *Ocyurus chrysurus*) Iwatsuki *et. al.* (1991; *L. fulviflamma*) and Hamamoto *et. al.* (1992; *L. stellatus*).

Egg size in lutjanids range from 0.65 - 1.02mm, with most occurring between 0.70 - 0.85mm. Most lutjanid larvae have an oil globule which is colourless to slightly yellowish and they range in size from 0.13 - 0.19mm. Fertilised eggs are buoyant and larvae have numerous melanophores present along the ventral edges of the body.

No key to identify the eggs and larvae of lutjanids presently exists. This is due to the large number of unstudied species and the simplified figures and descriptions that are available from those species previously studied. It has been suggested by Hamamoto *et. al.* (1992) that the pattern of melanophore pigmentation, especially the melanophores along the ventral edges of the body, might prove to be a diagnostic feature applicable to differentiate species of *Lutjanus*. Presently unique species diagnostic features of lutjanid larvae have not been described.

Rationale

While broadscale distribution patterns of lutjanids have been described throughout the tropical oceans of the world and are usually associated with hard bottom structure, there have been no quantified studies of the distribution and abundance of the Lutjanidae within the complex matrix of reefs in the Great Barrier Reef region. Basic knowledge of the distribution of fish species of commercial and recreational importance is lacking in the Great Barrier Reef (Williams and Russ, 1994). In particular, there is a general lack of understanding of species distributions below approximately 20m and for no lutjanid species is there a good understanding of its distribution throughout its complete life history.

The development of sampling methodologies (eg. fish traps) to quantify the demersal communities beyond the depths of effective visual (SCUBA) census and the modification and refinement of existing visual census techniques to contend with the schooling behaviour of many *Lutjanus* species will allow the ecology of a variety of these commercially and recreationally significant species to be examined in detail.

The management of important demersal fisheries such as the Lutjanidae in the waters of the Great Barrier Reef is complicated by a lack of accurate landing figures from both the commercial and particularly the recreational fishermen, combined with fluctuating levels of effort, changes in gear types and a rapidly expanding and diverse recreational fishing component. The present status of knowledge relevant to the needs of management for the ecologically sustainable development of lutjanid species in the

Queensland commercial and recreational fisheries have been described as either incomplete or inadequate (Anon., 1991a). A detailed understanding of the biology of the species taken by these fisheries (especially age validation, growth rates and age structures) is essential for effective management.

In addition to the Lutjanidae, the distribution and abundance of the Lethrinidae and Serranidae will also be examined at similar spatial scales. However, the main focal point of this thesis will be on the Lutjanidae.

This study aims to provide some of the first quantitative data on the distribution and abundance, growth, mortality and age structures of the Lutjanidae on the Great Barrier Reef. Detailed analysis of these patterns at a range of spatial and temporal scales will allow us to determine species specific distribution patterns, growth rates and age structures as well as to hypothesise how these may reflect the recruitment and movement patterns of the fish.

This thesis will examine :

- The distribution and abundance patterns of the Lutjanidae and Lethrinidae among reefs along a cross shelf longitudinal gradient;
- The distribution and abundance patterns of the Lutjanidae, Lethrinidae and Serranidae within and among midshelf and outershelf reefs;
- The spatial and temporal distribution and abundance patterns of the Lutjanidae and Lethrinidae within and among midshelf reefs (small scale latitudinal variation);
- The growth, mortality and age structures of two *Lutjanus* species (*L. adetii* and *L. quinquelineatus*) among reefs within the matrix of reefs in the central region of the Great Barrier Reef.

Chapter 2

General Materials and Methods

2.1 Study Area

The study reefs were located within the central section of the Great Barrier Reef (latitudes 18°S to 19°S). A number of studies on the coral reef biota of this region have been undertaken over the last decade [eg. hard corals (Done, 1982); soft corals (Dinesen, 1983); coral dwelling crustacea (Preston and Doherty, 1990; 1994); algal turfs (Scott and Russ, 1987); fish communities (Williams, 1982; 1983; Williams and Hatcher, 1983); herbivorous grazing fishes (Russ, 1984a; 1984b); holothuroids (Hammond *et. al.*, 1985); sponges (Wilkinson and Trott, 1985) and calcified green algae (Drew, 1983)]. The benthic reef communities typically are dominated by the hard corals, and Done (1982) distinguished 17 types of hard coral community in 3 classes across the entire continental shelf and into the Coral Sea. The coral communities within the central Great Barrier Reef display distinct patterns of distribution at both the between reef and cross shelf spatial scales. They can be categorised into various *Acropora* and non-*Acropora* types (Done, 1982). The outershelf reefs are characterised by the *Acropora palifera/humilis* variant coral community and the midshelf reefs are characterised by the *Acropora hyacinthus/splendida* coral communities (Done, 1982). In contrast, the inshore reefs are characterised not only by their relatively small size, but by a relative paucity of the genus *Acropora*, despite some species being locally abundant (Done, 1982). Additionally, a number of benthic communities were present only at the inshore reefs. For example, a *Sargassum* dominated macro-algal community (Phillips Reef) and *Montipora* coral communities (Done, 1982).

The species and community diversity of corals is greatest among the midshelf reefs and is significantly less on the inshore reefs than elsewhere (Done, 1982). The midshelf (M) and outershelf (O) reefs of the Great Barrier Reef have distinct patterns of zonation and can generally be divided into reef slope, reef crest, reef flat, lagoon and back reef zones, whereas the inshore (I) reefs have less distinct patterns of zonation in their structure. The structure of these zones on the midshelf and outershelf reefs are characterised by distinctive coral communities which have been shown to vary significantly at the within reef scale (Done, 1982). The individual reefs sampled during the course of this study include Pandora (I), Rib (M), John Brewer (M), Lodestone (M), Kelso (M), Davies (M), Myrmidon (O), Dip (O) and Bowl (O). The study reefs are their locations are described in detail in each respective chapter.

2.2 Visual Census Technique

The shallow water assemblages of the families Lutjanidae, Lethrinidae and Serranidae were surveyed by a rapid visual census technique similar to that used by Williams (1982; 1986) and Russ (1984a; 1984b). The lutjanid, lethrinid and serranid assemblages were identified to species according to Allen and Talbot

(1985), Allen (1985), Carpenter and Allen (1989), Randall and Heemstra (1991) and Heemstra and Randall (1993). A census dive consisted of a 45 minute swim (using SCUBA) along a reef zone (eg. reef slope, lagoon, back reef) in a relatively uniform direction, swimming in a meandering zig-zag pattern up and down the reef face from the surface to a depth of 10-12m, recording the total number of each target species seen. All individuals within approximately 5m either side of the diver were recorded, and all the target species were censused simultaneously. The 45 minute period was chosen on the basis of preliminary observations and previous studies (eg. Ayling and Ayling, 1992) which noted that the distribution of many of the target species tended to be clumped and often formed large aggregations and thus required large census transects in order to minimise variance heterogeneity. Additionally, because of the cryptic behaviour of some of the target species, all microhabitats encountered (such as ledges and caves) were searched intensively. All data were recorded on prepared census forms containing lists of all target species known to occur on the Great Barrier Reef (from Allen and Talbot, 1985; Allen, 1985; Carpenter and Allen, 1989; Randall and Heemstra, 1991; and Heemstra and Randall, 1993) and all census observations were made by one observer (SJN) to ensure consistency. The average distance covered on a census dive was calculated on the basis of 10 independent census dives, which were all measured using GPS (Global Positioning System) technology. The distance covered by a census dive was approximately 400m in any reef zone, so that the total area censused was approximately 4,000m^2 (400m × 10m). The 10-12m depth limit was dictated by the physiological constraints of an observer doing a number of repetitive dives per day.

2.3 Fish Traps - Design, Equipment and Procedure

The trap design was based on the O or cylindrical shaped trap which is commonly used in the Western Australian snapper fishery of Shark Bay and the demersal trap fishery of the North West Shelf of Australia (Bowen, 1961; Moran and Jenke, 1989; Anon., 1990; Whitelaw *et. al.*, 1991). The design was modified from that described in Anon. (1990) and Whitelaw *et. al.* (1991). Two funnel entrances were used instead of one (thereby increasing the chance of having one entrance facing away from the prevailing current at any one time); and these funnel entrances were reduced from a vertical slit entrance of 900mm height to only a 300mm height × 100mm wide vertical opening in the centre of the vertical wall of the trap (Figure 2.1). The trap entrance had incurving walls which tapered to the opening. The entrances extended approximately 400mm into the trap (see Figure 2.2). The aim of the modified style of entrance funnel was to decrease the egress (escapement) of trapped fish, whilst maintaining the relatively high rates of ingress of fish to the NW shelf style trap.

The traps were cylindrical with a diameter of 1500mm, a height of 900mm, a plan area of approximately 1.8m^2, and a volume of approximately 1.6m^3. Frames were constructed of 10mm diameter steel rod and were covered with galvanised 40mm hexagonal wire mesh. Hauling bridles were attached to each individually numbered trap and the bridle was supported above the trap with the aid of a small polystyrene float. The bridles were attached by nylon rope (8mm) to a surface buoy (25cm longline float) and then with a leader line to a dan buoy (radar pole). Each trap was individually buoyed to allow ease of recovery. Logistically it was not feasible (with regard to both clearance times and the size of traps) to fish more than 12 traps simultaneously at any one time.

The majority of trapping operations were conducted on board the *R.V. Hercules*, a purpose-built aluminium barge. The *R.V. Hercules* is 12.0m long, with a beam of 3.95m and a draft (when loaded with a full complement of 12 traps) of less than 0.5m. The forward deck space of approximately 30m^2 allowed easy storage of twelve 'O' traps. Towards the bow, the *R.V. Hercules* had an electrically driven capstan mounted on a masthead which was used to haul the traps through an L shaped frame over the starboard side onto the side decking, facilitating the easy removal of trapped fish. The traps were released from the starboard side of the research vessel, pulled upright when submerged and then allowed to sink to the substratum. Trap lines and floats were always streamed out to decrease the risk of entanglement and hence loss of traps. Hauling or setting a trap took less than 3 minutes. The catch of each trap was placed in bins of running seawater. Each fish was identified to species according to Allen (1985), Carpenter and Allen (1989) Randall *et. al.* (1990), Randall and Heemstra (1991) and Heemstra and Randall (1993), measured to the nearest millimetre (standard length, length to caudal fork, and body depth), tagged and released.

Traps were baited with Western Australian pilchards (*Sardinops neopilchardus*), which yielded significantly higher catches than other types of bait in a study on the North West Shelf of Australia (Whitelaw *et. al.*, 1991). Each trap was baited with approximately 1kg of mulched pilchards placed in a single crab pot style bait canister (see Figure 2.1). Fresh bait canisters were placed in traps every time that the traps were set. Each bait canister was constructed of 300mm high × 80mm diameter PVC tubing, in which ten, 30mm diameter holes were drilled to allow fish access to the bait and to allow the release of a bait plume. The bait canister was capped at each end with a PVC cap and suspended from the top of the trap, so that it hung suspended in the centre of the trap between the funnel openings (see Figure 2.2).

Traps were set a minimum distance of 50 metres apart and ranged up to a few hundred metres apart in order that the capture field of each trap would not overlap (Eggers *et. al.*, 1982; Davies 1989). This resulted in less competition (overlap) between the capture fields of adjacent traps. Although the extent of the capture field of these traps was not determined in this study, it was considered to be approximately 50m in diameter.

2.4 Tagging Procedures and Rationale

All individuals were measured and tagged on the left side of the body, with the body flattened. Fish were all double tagged with two fine or standard T-bar anchor tags (depending on the size of the fish). Both tags were inserted into the flesh immediately below the dorsal fin. The first tag was situated beneath the 1st and 3rd dorsal spines and the second tag was inserted at the junction between the spinous and soft dorsal fin.

Fish were all injected with terramycin (oxytetracycline hydrochloride, 100mg/ml) before being released. Injection of all species was done with a 1.0ml syringe and 26 gauge (0.45 × 13mm) needle which was inserted under the scales and through the skin into the coelomic cavity in close proximity to the pelvic fin region with a dosage of 0.5ml of oxytetracycline hydrochloride per kg of fish (see McFarlane and Beamish, 1987; Fowler, 1990; Ferreira and Russ, 1992).

The tagging, injection procedure and measurement of fish was conducted as quickly as possible, with fish never out of the water for more than a minute. Thus, stress and handling time were kept to a minimum. Fish which were badly embolised from deep set traps were pierced with a hyperdermic needle behind the pectoral fin (approximately 30mm), through the flesh just below the spine and into the swim bladder in order to facilitate the release of the accumulated gas.

The primary objective of the tagging study was to obtain validated ages from injected fish that had been at large for periods in excess of twelve months and where possible to provide independent estimates of the growth rate of these species.

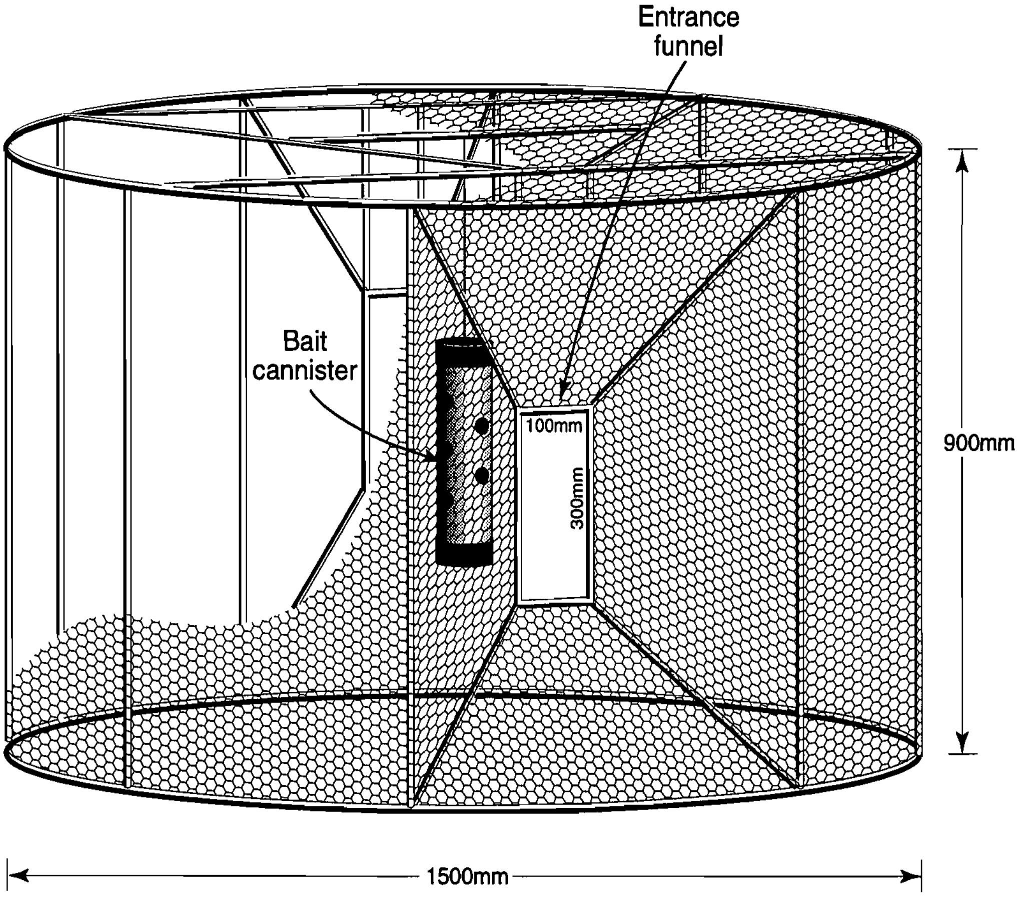

Figure 2.1 : Modified 'O' trap design.

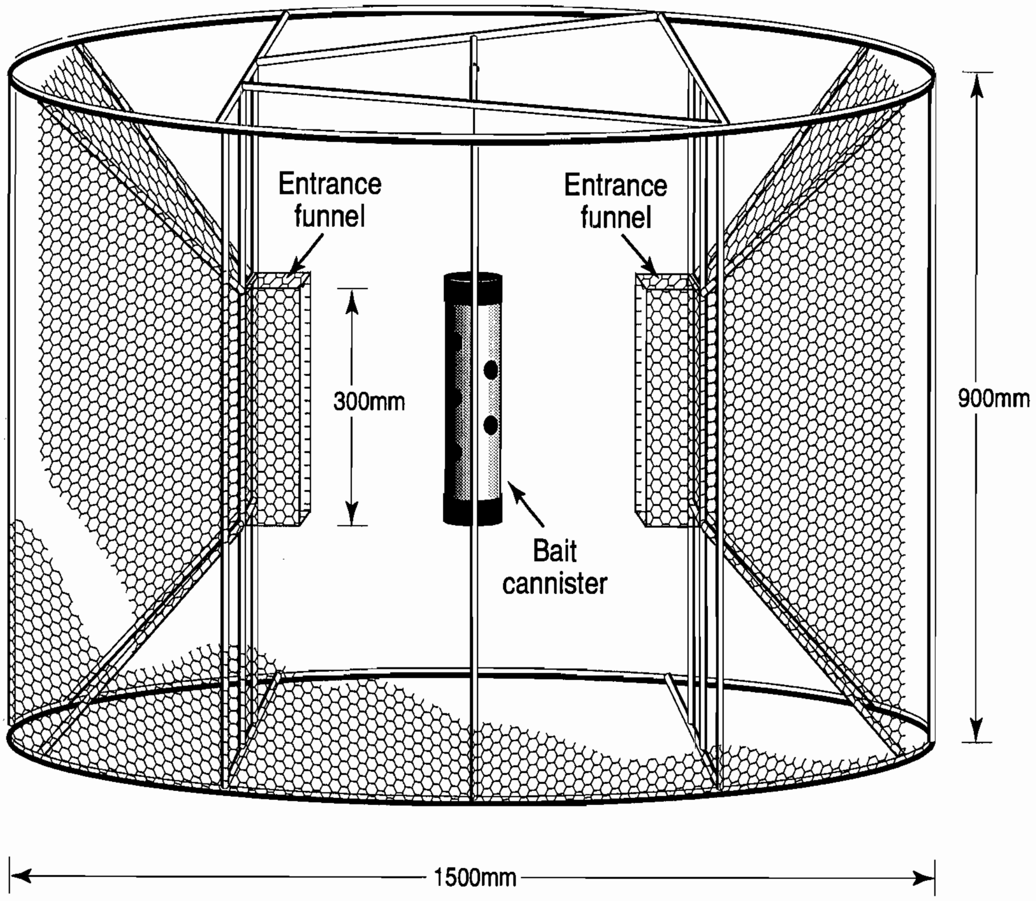

Figure 2.2 : Side profile of the modified 'O' trap showing the two incurved funnel entrances and the relative position of the bait canister between the funnel entrances.

Chapter 3

Distribution and abundance of the reef associated assemblages of the Lutjanidae and Lethrinidae across the entire continental shelf in the central Great Barrier Reef.

3.1 INTRODUCTION

Over the last decade a number of studies investigating the broadscale distribution and abundance of coral reef biota have concentrated on cross shelf variation in the structure and function of coral reef communities along a transect in the central Great Barrier Reef at a latitude of approximately 18°30'. These studies have described the distribution and abundance of hard corals (Done, 1982), soft corals (Dinesen, 1983), zooplankton and fish larvae (Sammarco and Crenshaw, 1984; Williams *et. al.*, 1988), holothuroids (Hammond *et. al.*, 1985), sponges (Wilkinson and Trott, 1985), coral dwelling crustacea (Preston and Doherty, 1990; 1994), calcified green algae (Drew, 1983), the epilithic algal community (Scott and Russ, 1987) and various reef fish communities (Williams 1982, 1983; Williams and Hatcher, 1983; Russ, 1984a) as well as patterns of nitrogen fixation (Wilkinson *et. al.*, 1984) along a cross shelf transect from inshore reefs to the Coral Sea. A recent review of these studies is provided by Wilkinson and Cheshire (1988). The studies all found significant differences in community structure among inshore, midshelf and outershelf reefs. There is a gradation in the environmental parameters along this continental shelf transect in the central Great Barrier Reef ranging from strong terrigenous influences near the coast to near oceanic conditions at the shelf break (Wilkinson and Cheshire, 1988).

Williams (1982) first compared the structure of the coral reef fish communities across the continental shelf by examining the outer reef slopes of reefs and found major cross shelf changes in the abundance of species and structure of the coral reef fish communities. These cross shelf patterns have remained constant for at least 15 years (Williams, 1986; 1991; unpublished data). Additionally, Williams and Hatcher (1983) used explosives to make relatively complete, quantitative collections of all fishes within a standardised area and found that virtually all the taxa collected exhibited cross shelf variability in abundance. Williams and Hatcher (1983) also demonstrated major cross shelf changes in species diversity and trophic structure. Furthermore, the studies of Russ (1984a, 1984b) corroborated the marked cross shelf changes in the distribution of the herbivorous reef fishes and demonstrated that the cross shelf variation in abundance of these fishes occurred for all reef zones, not just the outer reef slopes.

These early studies, based on visual counts, did not describe the distribution and abundance of the large mobile species of demersal reef fishes which tend to inhabit the deeper areas of reefs or are nocturnally active on reefs. While these species are not amenable to traditional visual counts, it was believed that they might be readily caught in fish traps. Fish traps have been used successfully to sample demersal fishes in a variety of structurally heterogeneous environments such as estuaries, rocky and coral reefs over a range of depths (Munro, 1974; Stevenson and Stuart-Sharkey, 1980; Dalzell and Aini, 1987; Newman, 1990; Whitelaw *et. al.*, 1991; Dalzell and Aini, 1992; Sheaves, 1992; Williams *et. al.*, 1992; Newman and Williams, in press). Fish traps have also proved effective at sampling a wide range of species of the large mobile demersal fishes including lutjanids and lethrinids (Williams *et. al.*, 1992; Newman and Williams, in press).

The aim of this study was to describe the broadscale patterns of distribution and abundance of species of the Lutjanidae (snappers) and Lethrinidae (emperors) along a cross shelf transect across the entire continental shelf in the central Great Barrier Reef using fish traps.

3.2 MATERIALS and METHODS

Study Sites

This study was conducted on 3 reefs on the continental shelf in the central region of the Great Barrier Reef (all 3 were studied by Williams (1982), Williams and Hatcher (1983) and Russ (1984a; 1984b)). The reefs were each located at different locations across the continental shelf. One reef was nearshore (Pandora), approximately 10km from the coast, one on the midshelf (Rib), approximately 50km offshore and one on the outer shelf (Myrmidon), approximately 100km offshore (Figure 3.1). The gross morphology and environment of these reefs was described by Done (1982).

The protected leeward slopes of all reefs were sampled and a summary of the dominant benthos in these habitats is given below. The areas sampled within each reef are shown in Figure 3.2. The benthos of the outer shelf reefs is dominated by both corals and coralline algae with the leeward slopes below 10m dominated by a *Montipora/Pachyseris* community (Done, 1982). The midshelf reefs have the greatest diversity of coral communities and species along the cross shelf gradient (Done, 1982). The benthos of the midshelf reefs is dominated by hard corals and the leeward slopes are morphologically complex, consisting of terraces, sand chutes, vertical walls, sloped walls, bommies and rubble accumulations which contain a correspondingly diverse array of communities such as the *Porites* "massive/branching", *Acropora* "staghorn", *Acropora* "*splendida/divaricata*" communities as well as non-conformist assemblages (see Done, 1982). The inner shelf, inshore reefs differ markedly from the midshelf and outer barrier reefs. The leeward slopes are characterised by a *Goniopora* community interspersed with a *Porites* "massive/branching" community along with extensive monotypic stands of a variety of species (see Done, 1982). The inshore reefs have little distinct pattern of zonation in their reefal structure and are characterised by their relatively small size and a lack of the dominant *Acropora* communities of the midshelf and outer barrier reefs.

Additionally, the physical environment is extremely variable across the shelf in the central Great Barrier Reef region. Nearshore reefs receive strong terrigenous influences with variable inputs of fresh water containing relatively high concentrations of inorganic and organic nutrients and sediments, while the outershelf reefs receive oceanic influences characterised by strong wave action, relatively constant salinity and extremely low concentrations of dissolved and particulate organic material (Done, 1982; Wilkinson and Cheshire, 1988). Further, the nearshore reef environment is highly turbid, characterised by high concentrations of resuspended fine sediments (10-100ppm) with the sediments dominated by fine siliceous muds, whereas in the outershelf reef environment suspended sediment levels are low (< 0.2ppm) and the sediments are exclusively carbonate (Scoffin and Tudhope, 1985; Johnson *et. al.*, 1986).

Sampling Methods

The leeward slopes of the midshelf and outershelf reefs in depths of 15-40m, and the leeward slopes of the nearshore reef in depths of 10-15m (maximum depth of these reefs) were sampled. Traps were set across the back reef both day and night at each shelf location during March, 1993. A total 48 trap sets (2 days, 2 nights of sampling with 12 traps) were completed on the outershelf, 24 trap sets (1 day, 1 night of sampling) were completed on the midshelf and 36 trap sets (1 day, 2 nights of sampling) were completed inshore (the unbalanced design caused by logistic constraints). Traps were deployed in a haphazard manner on the deep leeward slopes to ensure independence of the data and to avoid systematic error.

Detailed analysis of the diel variability and the effect of depth on the community structure of the Lutjanidae and Lethrinidae will be examined in subsequent chapters. Spatial effects were considered to be representative through time and not strongly influenced or confounded by the time period of sampling. The trap design used was a modified O or cylindrical shaped trap (see Chapter 2). The traps are cylindrical in shape with a diameter of 1500mm, a height of 900mm, a plan area of approx. 1.8m^2 and a volume of approx. 1.6m^3. Frames were constructed from 10mm diameter steel rod and were covered with 40mm galvanised hexagonal wire mesh. Each trap was individually buoyed.

The traps were released from the research vessel, pulled upright when submerged and then allowed to sink to the substratum. Hauling or setting a trap took less than 3 minutes. The catch of each trap was identified to species, measured to the nearest millimetre, then tagged (see Chapter 2) and released. Each trap was baited with approx. 1kg of mulched pilchards (*Sardinops neopilchardus*). All trap setting was undertaken between 0530 and 1830 hours. "Night" set traps were hauled from 0530 hrs onwards, with sorting and processing of trap catches usually completed by 0830 hrs and soak times varying from 12 to 14 hrs. "Day" set traps were hauled from 1630 hrs onwards, with sorting and processing usually completed by 1830 hrs. Soak times during the day varied from 9 to 11 hrs. Soak times were calculated from the time a trap entered the water to the time it was hauled from the bottom. Traps were set a minimum distance of 50 metres apart and ranged up to a few hundred metres apart in order that the capture field of each trap would not overlap (Eggers *et. al.*, 1982; Davies, 1989). This resulted in less competition (overlap) between the capture fields of adjacent traps.

Analysis of Data

The data from all 108 trap hauls (for the 12 most abundant species) from all continental shelf locations were subjected to an agglomerative hierarchical classification (Williams, 1971). A dendrogram and similarity matrix were generated using Ward's method based on euclidean distances to determine patterns of abundance. Ward's method uses an analysis of variance approach to evaluate the distances between clusters by attempting to minimise the sum of squares of any two clusters that can be formed at each step (Ward, 1963). Euclidean distance is strongly influenced by the absolute magnitude of species abundance and the correlation between species (Jackson, 1993). In the analysis, catches per trap were first standardised (transformed to a double square root ($\sqrt{\sqrt{x}}$)) for the improvement of normality and homogeneity (see Field *et. al.*, 1982). Each major division of the dendrogram derived from the classification analysis resulted in the creation of two groups which were significantly different from one another, as determined by the test of Sandland and Young (1979a; 1979b). Indicator species were ranked by their mean catch per unit effort and according to their abilities to distinguish between all the cross shelf groups derived from the classification analysis.

One way analysis of variance (ANOVA) was carried out on the catch per unit effort data for "total individuals" caught in traps, each family (Lutjanidae, Lethrinidae) trapped and the 12 most abundant species trapped. Continental shelf location was treated as a fixed factor in the analysis (Underwood, 1981). Homogeneity of variance for all analyses ($\alpha = 0.05$) was determined using Cochran's test (Winer, 1971). Gross heterogeneity of variances were evident in the variances of the raw data with the means and variances of some species being correlated significantly. Examination of the raw data revealed that the catch rates of many species in traps were characterised by a number of extremely high catches and numerous zero catches (the zero catches were largely due to an absence of some species in a particular continental shelf location). Thus, the cell variances tended to be functions of the cell means (the larger the mean the larger the variance). This heterogeneity was a consistent feature of abundance patterns and not an error of observation. Since the *a priori* question was to determine the cross shelf variability in the distribution and abundance of the Lutjanidae and Lethrinidae communities, the 12 replicate traps were pooled randomly across day and night sets into two artificial trap strings, each containing six traps. Each artificial string of 6 traps therefore contained 3 night and 3 day set traps which had been selected at random from each location (note that detailed diel (day versus night) comparisons and depth comparisons are examined in subsequent Chapters). This limited the "total replicates" in the ANOVA analysis to 18 (ie. $n = 8$ outershelf, 4 midshelf, 6 inshore) and hence decreased the associated degrees of freedom. Some cell variances were still heterogeneous and the within-cell distribution Poisson-like. The pooled data of the heterogeneous variables were then transformed to a $\sqrt{x} + \sqrt{(x+1)}$ function (see Table 3.2) to remove the variance heterogeneity (as well as the significant mean - variance correlation) and to make treatment effects additive (Winer, 1971; Underwood, 1981). Cochran's test for these variables was set at $\alpha = 0.01$, instead of $\alpha = 0.05$. Since the known effect of this level of heterogeneity is to slightly increase the chance of a Type I error (Snedecor and Cochran, 1989), the analyses of variance of the heterogeneous variables were conducted with the more conservative significance level of $\alpha = 0.01$. Multiple comparison of means ($\alpha = 0.01$) were carried out using Tukey's HSD method (Winer, 1971; Day and Quinn, 1989).

The relative abundance of all the species of the Lutjanidae and Lethrinidae recorded from the central region of the Great Barrier Reef were categorised by a subjective graded estimate of their relative abundance in a number of locations across the entire continental shelf. The relative abundance categories were based on the studies of Jones and Derbyshire (1988), Kramer *et. al.* (1993; 1994), Williams and Russ (1994), Sheaves (personal communication) and the experimental trapping and fishing observations of Newman (unpublished data).

3.3 RESULTS

The first split in the dendrogram generated from the classification analysis of all 108 trap hauls (Figure 3.3), placed all the trap hauls from the inshore (Pandora Reef) shelf location in a group distinct from all the trap hauls of the midshelf and outershelf locations. This latter group split into a group containing all the trap hauls from the midshelf reef (Rib) location, and another group containing all trap hauls from the outershelf reef (Myrmidon) location (Figure 3.3). Species characteristic of the inshore shelf location were the lutjanids, *Lutjanus carponotatus*, *L. russelli* and *L. sebae* (Table 3.1). The midshelf reef location was characterised by *Lutjanus adetii*, *L. quinquelineatus*, *L. russelli*, *L. sebae*, *Lethrinus miniatus*, *L. species 2* and *Gymnocranius audleyi*. The outershelf reef location was characterised by *Lutjanus kasmira*, *L. quinquelineatus*, *Lethrinus erythracanthus*, *L. miniatus*, *L. semicinctus*, *L. species 2* and *Gymnocranius euanus* (Table 3.1). Of the 12 species examined in detail, 3 were recorded inshore, 8 on the midshelf and 7 on the outershelf (Table 3.1). All the species recorded inshore also occurred on the midshelf but not the outershelf. Only 3 species were shared between the midshelf and outershelf.

The one way analysis of variance of the pooled trap catch per unit effort (CPUE) data on cross shelf location found that cross shelf location had a significant effect on the total number of fish trapped, the total lutjanids, the total lethrinids and on all of the 12 species examined (Table 3.2, see also Figures 3.4 and 3.5). The corresponding *a posteriori* Tukey HSD multiple mean comparisons of the analysis of variance results are summarised in Table 3.3. Cross shelf differences account for a very high proportion of the variability in abundance of the lutjanids and lethrinids and hence the total number of fish trapped. The CPUE of the Lutjanidae and Lethrinidae were significantly less inshore, with no significant differences between the midshelf and the outershelf (Table 3.3, Figures 3.4 and 3.5). The CPUE of the total number of fish trapped was similar to the patterns of abundance of the Lutjanidae and Lethrinidae.

The significant effect of cross shelf location on all the species examined (Table 3.2) was attributable to the absence or low abundance of species in one or more cross shelf locations (Table 3.1, Figures 3.4 and 3.5). This cross shelf change accounted for a large proportion of the variability in the catch per trap of all the species examined. *Lutjanus carponotatus* was the only species that was significantly more abundant inshore (Figure 3.4). *Lutjanus russelli* and *L. sebae* were significantly less abundant on the outershelf, with no significant difference between the midshelf and inshore (Figure 3.4). *Lutjanus adetii* and *Gymnocranius audleyi* were both significantly more abundant on the midshelf (Figures 3.4 and 3.5). *G. audleyi* has not been recorded from any other shelf locations (Table 3.1, Figure 3.5; see also Table 3.6). *Lutjanus quinquelineatus*, *Lethrinus miniatus* and *L. species* 2 were significantly less abundant inshore (absent in this location), with no significant difference between the midshelf and the outershelf (Figures 3.4 and 3.5). *Lutjanus kasmira*, *Lethrinus erythracanthus*, *L. semicinctus* and *G. euanus* were all significantly more abundant on the outershelf and were not recorded from the other cross shelf locations (Table 3.1, Figures 3.4 and 3.5).

In addition to these significant cross shelf differences, the distribution and relative abundance of other species of the Lutjanidae and Lethrinidae showed similar, consistent cross shelf trends (Tables 3.4, 3.5 and 3.6). The nearshore coastal habitats are divided into 3 broad areas (Table 3.4). In estuaries the representative species include the juveniles of *L. johnii* and *L. russelli*, as well as the juvenile and subadult *L. argentimaculatus*. Around headlands and rocky promontories the characteristic species is *L. johnii*, which appears to be restricted to the nearshore turbid waters and is rarely found on any of the nearshore reefs in this region. *Lutjanus carponotatus* and *Lethrinus laticaudis* are representative of the inshore reefs and fringing reefs of coastal islands. The shallow nearshore rocky foreshore area of coastal islands and inshore reefs was the only habitats in which *Lethrinus harak* has been observed (Table 3.4). This species appears to be restricted to coastal areas and continental islands. Representative species of the midshelf reefs include *Lutjanus adetii*, *L. fulviflamma*, *L. quinquelineatus*, *Lethrinus species* 2 and *Gymnocranius audleyi* (Tables 3.5 and 3.6). Species representative of the interreefal areas and the shoal grounds between reefs are *Lutjanus erythropterus*, *L. malabaricus*, *L. vitta* and *Lethrinus genivittatus* (Tables 3.5 and 3.6). On the outershelf, representative species include *Lutjanus bohar*, *L. gibbus*, *L. kasmira*, *L. quinquelineatus*, *Macolor niger*, *Gymnocranius euanus*, *G. sp.*, *Gnathodentex aurolineatus*, *Monotaxis grandoculis*, *Lethrinus semicinctus*, *L. erythracanthus* and *L. xanthochilus* (Tables 3.5 and 3.6).

In general, the genera *Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus*, *Gnathodentex*, *Gymnocranius*, *Lethrinus* and *Monotaxis* are all characteristic of the shallow shelf waters less than 100m (Tables 3.5 and 3.6). In contrast, species of the genera *Paracaesio*, *Pristipomoides* and *Wattsia* are characteristic of the intermediate depths (100-200m). The exception is *Pristipomoides argyrogrammicus*, which usually occurs in depths in excess of 200m (Kramer *et. al.*, 1994). The deeper outer reef slope waters in excess of 200m are characterised by species of the genus *Etelis* (Table 3.5).

3.4 DISCUSSION

Logistic constraints prevented spatial replication among reefs within a given shelf location. Consequently the quantitative data of this study is based on only one reef per cross shelf location. The best potential hypothesis to explain this variation are cross-shelf changes in abundance patterns. Williams (1983) has shown in a study on the latitudinal and longitudinal variation in the structure of reef fish communities that although there were differences in the composition of fish assemblages both among sites within reefs, and among reefs at the same cross shelf location, these differences were small relative to those differences among cross shelf locations. Williams (1983) further concluded that while significant latitudinal variation was evident in the composition of fish assemblages among the five latitudes studied (11°S to 22°S), this source of variation was substantially less than the cross shelf variation within a given latitude. Additionally, Russ (1984a; 1984b) found that cross shelf change accounted for as much as 80-90% of the variability in abundance of the large herbivorous fishes (Siganidae, Scaridae and Acanthuridae). Preliminary observations and qualitative data have similarly suggested that while the Lutjanidae and Lethrinidae communities may vary among reefs at similar cross shelf locations, these differences will be small relative to those differences exhibited among cross shelf locations.

The abundance and species richness of the Lutjanidae and Lethrinidae increases across the continental shelf with fewer species located in nearshore coastal habitats (Tables 3.4, 3.5 and 3.6). The diversity of available habitat types also increases across the continental shelf. Significant cross shelf variation occurred in the abundance of all the species of the Lutjanidae and Lethrinidae that were trapped (Table 3.2). The significant variability in the abundance of species was associated with their absence or low abundance in one or more of the cross shelf locations examined. Similarly, Russ (1984a, 1984b) showed that the majority of species of large herbivorous reef fishes also displayed significant cross shelf variation irrespective of the reef zone examined, and this cross shelf change accounted for as much as 80-90% of the variability in abundance. Additionally, this study confirms the findings of Williams (1982) and Williams and Hatcher (1983) that there are generally lower numbers of species on inshore reefs than on reefs of the midshelf and outershelf. Large scale cross shelf differences in community structure have been maintained through time, with Williams (1986, 1991; unpublished data) having observed that cross shelf changes in the community structure of a number of species of reef fish were consistent over a 15 year period.

The proximal factors that are likely to cause or maintain differences in the community structure of coral reef fishes across the continental shelf in the central region of the Great Barrier Reef have been summarised by Williams and Hatcher (1983) and Williams *et. al.* (1986). They have suggested that patterns of distribution and abundance could arise from : (1) differential availability of larvae across the continental shelf; (2) patterns of settlement and habitat selection by post-larvae (eg. in response to food availability, physical factors, etc.); and (3) differential survivorship after settlement.

The cross shelf patterns of distribution and abundance of some species of the Lutjanidae and Lethrinidae also result from movements associated with postsettlement ontogeny (Williams, 1991)..For example, juvenile *L. russelli* are found inshore in estuarine areas and the adults migrate out onto the midshelf reefs. Similarly, juvenile *L. erythropterus* and *L. malabaricus* are found in nearshore coastal habitats and migrate offshore with age and growth as far as the outershelf reefs (Williams and Russ, 1994). The distance moved by some of the larger species such as *L. argentimaculatus*, *L. erythropterus* and *L. malabaricus* is presumably determined by the depth and width of the continental shelf (Williams, 1991).

The cross shelf distribution patterns of adults of the families Lutjanidae and Lethrinidae were comparable to the cross shelf distribution patterns of the larvae of these families (Williams *et. al.*, 1988). The larvae of both the Lutjanidae and the Lethrinidae tended to be more abundant on the midshelf, with significantly lower abundances inshore. The cross shelf distribution of these larvae may be determined by the availability of suitable pelagic habitats which vary greatly from turbid, productive nearshore coastal waters to the clear, low productivity oceanic waters (Williams *et. al.*, 1988). The development of taxonomic techniques to identify the larvae of these families to the species level may allow further correlation of the distribution of the adult fishes with the distribution of the larvae.

The large scale cross shelf patterns may arise as a result of consistent habitat preferences of the settling larvae. Individual *L. quinquelineatus* recruits have been observed to settle directly into the adult habitat of the midshelf reefs (Newman, personal observations). Such preferences may be the consequence of earlier evolutionary periods of interspecific competition, but they may also have arisen for other reasons to do with the evolving adaptation of a genotype to its environment independent of other species (Sale, 1991). The visual pigments of species of the Lutjanidae in the central Great Barrier Reef are correlated with the colour of the water in which they live (Lythgoe *et. al.*, 1994). This may be a key determinant in the habitat selection of the settling larvae and hence the pelagic habitats of these species. For example, *L. bohar* and *L. kasmira* are considered blue water species, whereas *L. quinquelineatus*, which occurs on the outershelf, is not and it's dominance on the midshelf reefs is reflected in its differing pigment structure (see Lythgoe *et. al.*, 1994). Juvenile *L. kasmira* have been observed in mixed species schools of *L. quinquelineatus* among midshelf reefs, but no adult specimens of *L. kasmira* have been observed or trapped (Newman, unpublished data).

The distribution and abundance of species of the Lutjanidae and Lethrinidae at localised reef scales (from reef to reef) are more likely to be determined by a combination of competition (review of Ebeling and Hixon, 1991), recruitment limitation (reviewed by Doherty and Williams, 1988; Doherty, 1991; Doherty and Fowler, 1994), predatory interactions (review by Hixon, 1991) and perhaps physical, abiotic interactions. The degree of exchange of adult fishes of these families among reefs in similar locations and between reefs at different locations and their connectivity with nearshore habitats remains to be quantified.

The cosmopolitan range of species of both the Lutjanidae and Lethrinidae that inhabit specific locations across the continental shelf in the central Great Barrier Reef (Tables 3.5 and 3.6) suggest that management of the exploitation of these species of commercial and recreational importance in terms of reef fisheries and tourism needs to be planned on much broader spatial scales than is currently the case with the usage of only single reef closures, and closures of clusters of reefs. Although the degree of connectivity and exchange of species among cross shelf locations has not been adequately quantified, the present qualitative data that are available suggest a number of species of the Lutjanidae and Lethrinidae undergo movement of several tens of kilometres across the continental shelf in their normal post settlement ontogeny. This is further supported by studies in the nearby waters of New Caledonia by Kulbicki *et. al.* (1987) examining longline catch data and Kulbicki (1988) from visual estimates which both demonstrate that species of the Lutjanidae, Lethrinidae and Serranidae are larger as distance from the coast, and depth, increases. Additionally, Brouard and Grandperrin (1985) and Wright *et. al.* (1986) have suggested a positive relationship between fish size and capture depth for a number of lutjanid species. In the Gulf of Mexico inshore-offshore movements are reported for *Lutjanus* *campechanus*, with juveniles found in shallow inshore waters over sandy and mud bottoms and adults found offshore in deeper waters associated with hard irregular bottom formations (Moseley, 1966; Bradley and Bryan, 1975; Moran, 1988).

The Lutjanidae and Lethrinidae of all the reef associated families possess the closest nearshore habitat links, with a number of species utilising nearshore coastal habitats as their preferred juvenile settlement areas and nursery grounds (Williams and Russ, 1994). Furthermore, as many species of these families undergo major cross shelf movements as part of their complex life histories, they are less likely to complete their entire life cycle on any single reef. Therefore, if these species become threatened or endangered from either natural or anthropogenic sources the current management system is not likely to protect these species adequately. Consequently, it is proposed that the closure of entire cross shelf regions which exhibit marked connectivity, from inshore estuarine areas to the outer slopes of the continental shelf may be more practical in ensuring the long term ecological sustainability of these populations of reef fishes on the Great Barrier Reef.

Table 3.1 : Mean catch rate (fish/trap/set) of 12 species of lutjanid and lethrinid in the three groups derived from classification analysis (*n* = total number of samples per group; -- = absent).

Species	Classification Group		
	Inshore (*n* = 36)	Midshelf (*n* = 24)	Outershelf (*n* = 48)
Lutjanus carponotatus	**0.72**	0.08	--
Lutjanus sebae	**0.31**	**0.21**	--
Lutjanus russelli	**0.25**	**0.58**	--
Lutjanus adetii	--	**1.75**	--
Lutjanus quinquelineatus	--	**4.96**	**2.61**
Lutjanus kasmira	--	--	**3.48**
Gymnocranius audleyi	--	**0.42**	--
Lethrinus species 2	--	**0.38**	0.21
Lethrinus miniatus	--	**0.54**	**0.46**
Lethrinus erythracanthus	--	--	**0.19**
Lethrinus semicinctus	--	--	**0.38**
Gymnocranius euanus	--	--	**0.58**

Table 3.2 : Summaries of the one factor analyses of variance of pooled trap catch per unit effort data for the total catch and selected species of the Lutjanidae and Lethrinidae examining the effect of location on the continental shelf (significance levels : * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$; [1] data transformed to $\sqrt{x} + \sqrt{(x + 1)}$ before analysis).

		Total fish.			Total lutjanids.			*L. adetii*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Location	2	128	55.5	***	101	30.1	***	48.7	354	***
Residual	15	2.30	--	--	3.36	--	--	0.14	--	--

		L. carponotatus[1]			*L. kasmira*[1]			*L. quinquelineatus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Location	2	19.6	47.9	***	146	116	***	128	24.0	***
Residual	15	0.41	--	--	1.26	--	--	5.35	--	--

		L. russelli[1]			*L. sebae*[1]		
Source of Variation	df	MS	F	p	MS	F	p
Location	2	12.2	25.4	***	7.15	18.3	***
Residual	15	0.48	--	--	0.39	--	--

		Total lethrinids.			*L. erythracanthus*[1]			*L. miniatus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Location	2	48.4	90.7	***	3.85	9.33	**	13.9	38.6	***
Residual	15	0.53	--	--	0.41	--	--	0.36	--	--

		L. semicinctus[1]			*L. species 2*			*G. audleyi*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Location	2	9.83	16.0	***	6.32	5.04	*	9.25	405	***
Residual	15	0.62	--	--	1.25	--	--	0.02	--	--

		G. euanus[1]		
Source of Variation	df	MS	F	p
Location	2	18.6	45.6	***
Residual	15	0.41	--	--

Table 3.3 : *A posteriori* multiple comparison of means (Tukey's HSD method) from the one factor analyses of variance of CPUE shown in Table 3.2. The significance level for all comparisons was $p < 0.01$ (Location : I = inshore, M = midshelf; O = outershelf).

Taxon	Location
Total no. individuals	O = M > I
Total lutjanids	O = M > I
Lutjanus carponotatus	I > M = O
Lutjanus sebae	I = M > O
Lutjanus russelli	I = M > O
Lutjanus adetii	M > I = O
Lutjanus quinquelineatus	O = M > I
Lutjanus kasmira	O > M = I
Total lethrinids	O = M > I
Gymnocranius audleyi	M > I = O
Lethrinus species 2	O = M > I
Lethrinus miniatus	O = M > I
Lethrinus erythracanthus	O > M = I
Lethrinus semicinctus	O > M = I
Gymnocranius euanus	O > M = I

Table 3.4 : Summary of the distribution and relative abundance of all the lutjanid and lethrinid species that have been recorded from nearshore coastal habitats in the central Great Barrier Reef (relative abundance category in order of decreasing abundance : very abundant, common, frequent, occasional, uncommon, rare; --- indicates that the species has not been recorded from that zone).

Species	Nearshore Coastal Habitats		
	Mangrove Estuaries*	Headlands/Rocky Shores	Coastal Island Fringing Reefs
Lutjanus erythropterus (juv.)	rare	frequent	rare
Lutjanus malabaricus (juv.)	rare	frequent	rare
Lutjanus sebae (juv. and subadults)	rare	frequent	frequent
Lutjanus fulviflamma	occasional	frequent	frequent
Lutjanus johnii (ad.)	occasional	abundant	---
Lutjanus argentimaculatus (subad.)	frequent	occasional	occasional
Lutjanus johnii (juv.)	frequent	occasional	---
Lutjanus argentimaculatus (Juv.)	abundant	rare	---
Lutjanus russelli (juv.)	abundant	frequent	---
Lutjanus rivulatus (juv.)	---	rare	---
Lutjanus carponotatus (juv.)	---	occasional	occasional
Lutjanus lemniscatus (juv.)	---	frequent	occasional
Lutjanus carponotatus (ad.)	---	frequent	abundant
Lutjanus quinquelineatus	---	---	occasional
Lutjanus russelli (ad.)	---	---	frequent
Lutjanus vitta	---	---	frequent
Lethrinus laticaudis	occasional	frequent	frequent
Lethrinus miniatus	---	---	rare
Lethrinus lentjan	---	---	occasional
Lethrinus atkinsoni	---	---	frequent
Lethrinus harak	---	---	frequent
Lethrinus nebulosus	---	---	frequent

* - Sheaves (personal communication).

Table 5: Summary of the distribution and relative abundance of all the lutjanid species that have been recorded from across the continental shelf in the central Great Barrier Reef region and their greatest recorded depth of capture (relative abundance category in order of decreasing abundance : abundant, frequent, occasional, rare; --- indicates that the species has not been recorded from that zone).

	Cross Shelf Reef Position							
Species	Inshore Reefs	Midshelf Reefs		Shoals, Interreef Areas	Outershelf Reefs		Deep Reef Areas (>100m)	Maximum Depth (m)
		(0-15m)	(>15m)		(0-15m)	(15-100m)		
Lutjanus johnii	occasional	---	---	---	---	---	---	15
Lutjanus rivulatus	occasional	occasional	---	---	occasional	---	---	15
Lutjanus vitta	occasional	---	occasional	frequent	---	---	---	45
Lutjanus argentimaculatus	frequent	occasional	occasional	occasional	---	occasional	---	80
Lutjanus lemniscatus	frequent	occasional	occasional	occasional	---	---	---	40
Lutjanus erythropterus	frequent	---	occasional	abundant	---	---	---	55
Lutjanus malabaricus	frequent	---	occasional	abundant	---	---	---	75
Lutjanus sebae	frequent	occasional	frequent	frequent	---	occasional	---	85
Lutjanus carponotatus	abundant	frequent	occasional	rare	---	---	---	40
Lutjanus russelli	abundant	frequent	frequent	occasional	---	---	---	40
Lutjanus fulviflamma	abundant	abundant	frequent	---	frequent	occasional	---	45
Lutjanus biguttatus	---	rare	---	---	---	---	---	12
Lutjanus lutjanus	---	rare	frequent	frequent	---	---	---	45
Lutjanus kasmira	---	rare	---	---	frequent	frequent	---	65
Symphorus nematophorus	---	rare	frequent	frequent	rare	occasional	---	75
Symphorichthys spilurus	---	occasional	---	---	occasional	---	---	20
Macolor macularis	---	occasional	---	---	occasional	occasional	---	75
Lutjanus monostigma	---	occasional	---	---	frequent	---	---	15
Lutjanus gibbus	---	occasional	---	---	frequent	frequent	---	68
Macolor niger	---	occasional	---	---	frequent	occasional	---	40
Lutjanus fulvus	---	occasional	occasional	---	occasional	---	---	35
Aprion virescens	---	occasional	occasional	frequent	occasional	frequent	occasional	100
Lutjanus bohar	---	occasional	occasional	occasional	frequent	frequent	occasional	93
Lutjanus quinquelineatus	---	abundant	abundant	occasional	occasional	frequent	occasional	128
Lutjanus boutton	---	---	rare	---	---	---	---	40
Lutjanus adetii	---	---	abundant	frequent	---	occasional	occasional	125

Table 5: continued.

Species	Cross Shelf Reef Position							
	Inshore Reefs	Midshelf Reefs		Shoals, Interreef Areas	Outershelf Reefs		Deep Reef Areas (>100m)	Maximum Depth (m)
		(0-15m)	(>15m)		(0-15m)	(15-100m)		
Lutjanus semicinctus	---	---	---	---	rare	---	---	15
Aphareus rutilans	---	---	---	---	rare	occasional	occasional	100
Aphareus furca	---	---	---	---	frequent	occasional	---	70
Pristipomoides multidens	---	---	---	---	---	occasional	frequent	245
Pristipomoides filamentosus	---	---	---	---	---	frequent	frequent	210
Pristipomoides auricilla	---	---	---	---	---	---	rare	150
Etelis radiosus	---	---	---	---	---	---	occasional	185
Pristipomoides argyrogrammicus	---	---	---	---	---	---	occasional	250
Etelis carbunculus	---	---	---	---	---	---	occasional	150
Etelis coruscans	---	---	---	---	---	---	occasional	260
Paracaesio kusakarii	---	---	---	---	---	---	frequent	180
Pristipomoides zonatus	---	---	---	---	---	---	frequent	198
Pristipomoides flavipinnis	---	---	---	---	---	---	frequent	190

Table 6: Summary of the distribution and relative abundance of all the lethrinid species that have been recorded from across the continental shelf in the central Great Barrier Reef region and their greatest recorded depth of capture (relative abundance category in order of decreasing abundance : abundant, frequent, occasional, rare; --- indicates that the species has not been recorded from that zone

	Cross Shelf Reef Position							
Species	Inshore Reefs	Midshelf Reefs		Shoals, Interreef Areas	Outershelf Reefs		Deep Reef Areas (>100m)	Maximum Depth (m)
		(0-15m)	(>15m)		(0-15m)	(15-100m)		
Lethrinus harak	occasional	---	---	---	---	---	---	5
Lethrinus atkinsoni	occasional	frequent	occasional	---	frequent	---	---	40
Lethrinus laticaudis	frequent	---	---	---	---	---	---	25
Lethrinus nebulosus	frequent	frequent	occasional	occasional	frequent	occasional	---	99
Lethrinus erythracanthus	---	rare	---	---	occasional	frequent	---	70
Lethrinus olivaceus	---	rare	rare	rare	occasional	occasional	---	70
Lethrinus species 2	---	rare	abundant	frequent	rare	occasional	occasional	128
Lethrinus xanthochilus	---	rare	---	---	occasional	---	---	15
Lethrinus ornatus	---	occasional	occasional	---	---	---	---	40
Gymnocranius audleyi	---	occasional	frequent	---	---	---	---	40
Lethrinus obsoletus	---	occasional	rare	---	occasional	---	---	40
Lethrinus lentjan	---	frequent	occasional	---	---	---	---	40
Lethrinus miniatus	---	frequent	frequent	frequent	occasional	frequent	frequent	128
Monotaxis grandoculis	---	frequent	---	---	abundant	---	---	20
Lethrinus genivittatus	---	---	rare	frequent	---	---	---	45
Lethrinus rubrioperculatus	rare	---	rare	---	occasional	frequent	---	95
Lethrinus semicinctus	---	---	occasional	occasional	frequent	frequent	---	40
Gymnocranius grandoculis	---	---	occasional	---	---	occasional	---	80
Gymnocranius sp.	---	---	---	---	occasional	occasional	---	40
Gymnocranius euanus	---	---	---	---	occasional	frequent	occasional	128
Gnathodentex aurolineatus	---	---	---	---	frequent	---	---	15
Wattsia mossambica	---	---	---	---	---	---	frequent	198

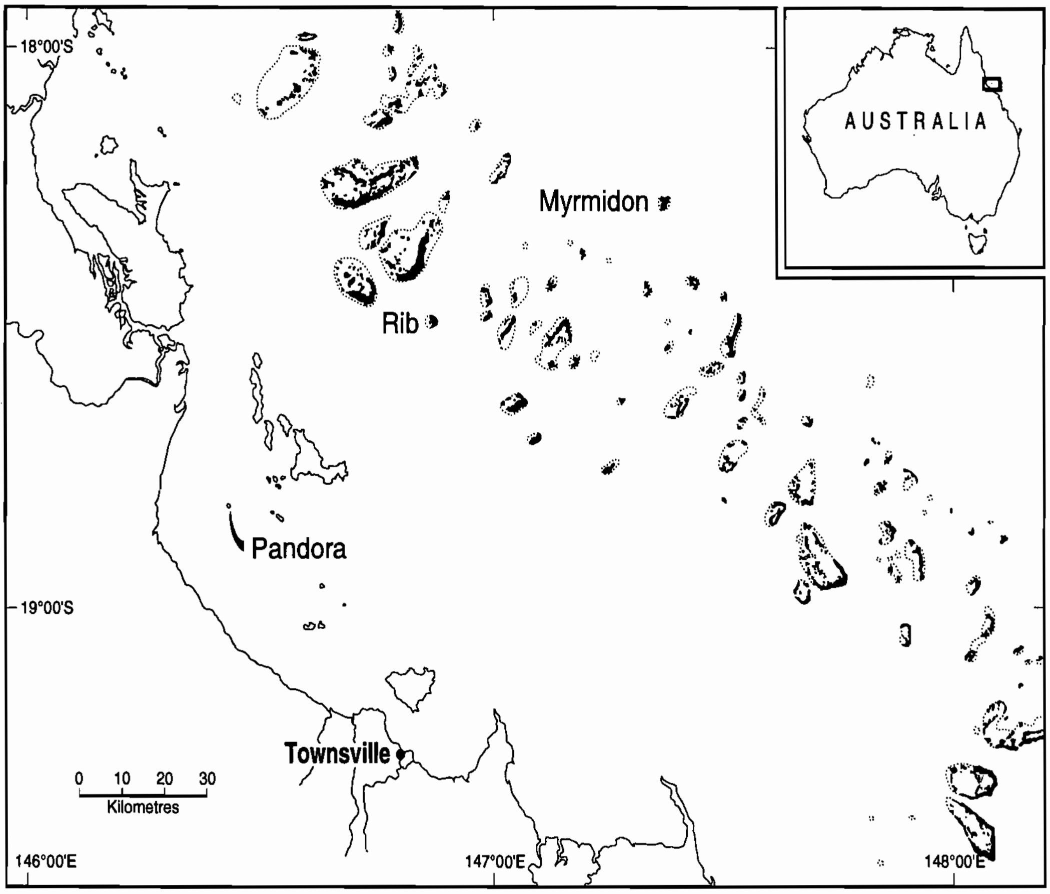

Figure 3.1 : The locations of study reefs in the central region of the Great Barrier Reef of Australia.

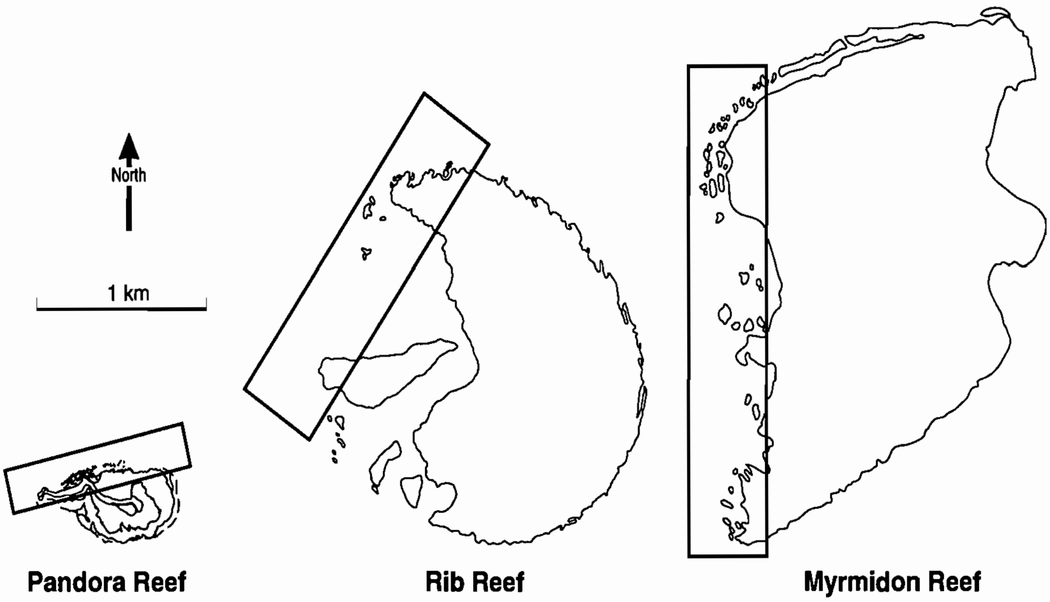

Figure 3.2 : Areas studied within each reef across the continental shelf. Each box represents the general area in which the traps were set on the respective reefs.

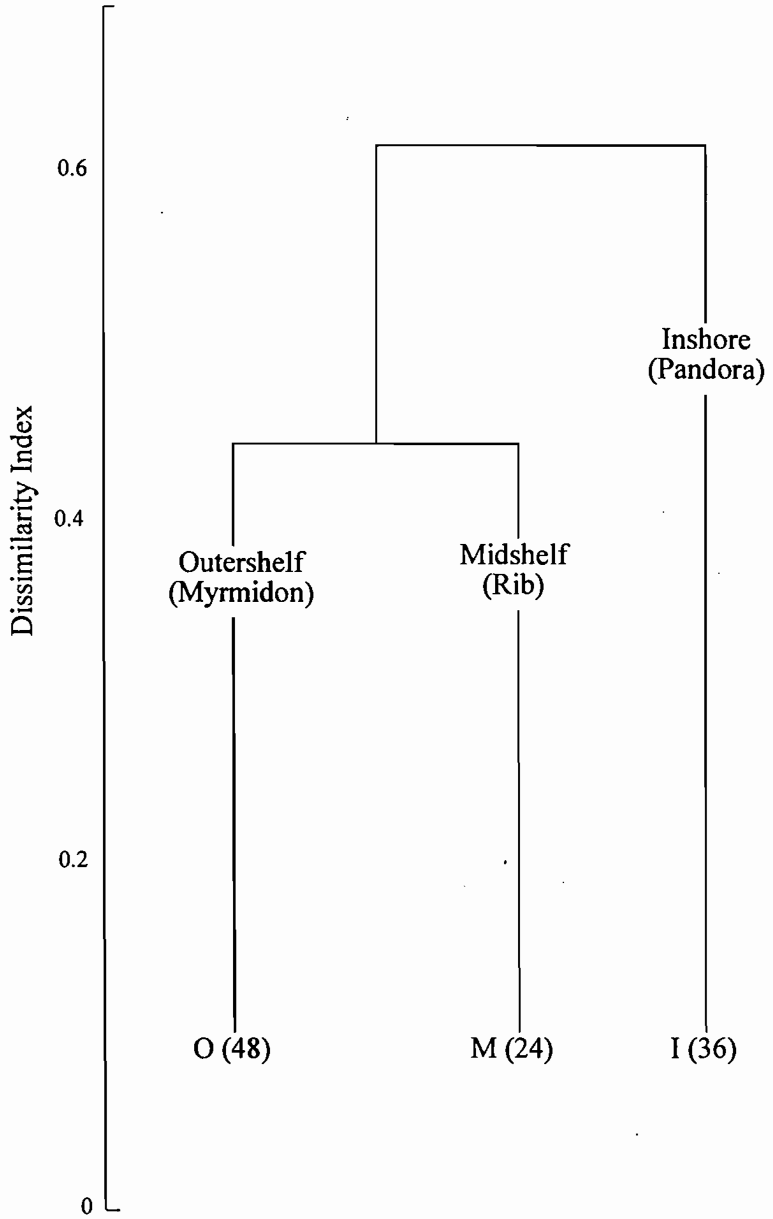

Figure 3.3 : Dendrogram from the classification analysis of the catch per unit effort data of the 12 most abundant species from 108 trap hauls. Numbers in brackets represent the number of replicate traps that fall in each cluster (O = outershelf, M = midshelf, I = inshore).

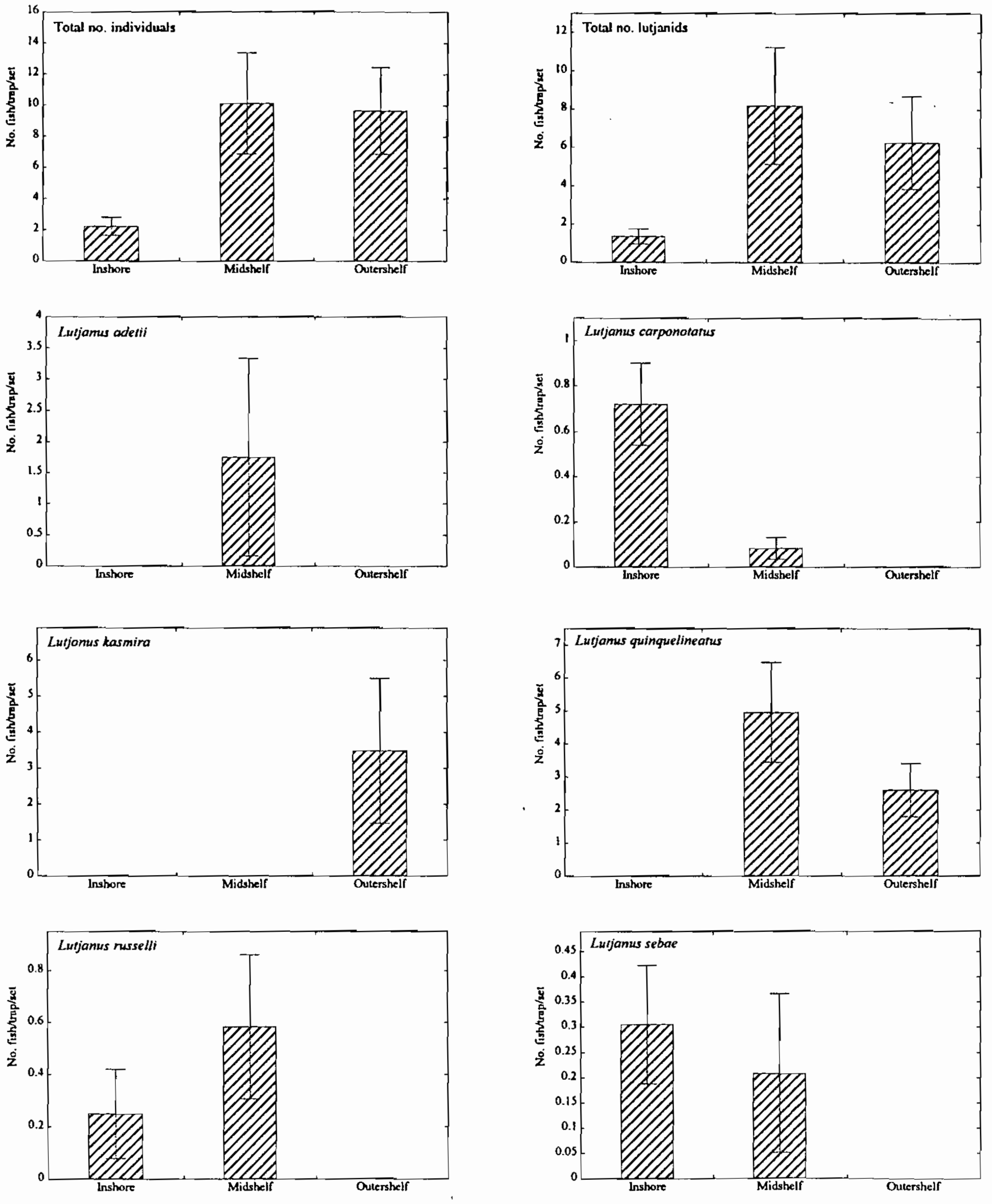

Figure 3.4 : Mean catch per unit effort (no. fish/trap/set +/- standard errors) of total individuals, total lutjanids, and 6 species of lutjanid among cross shelf locations.

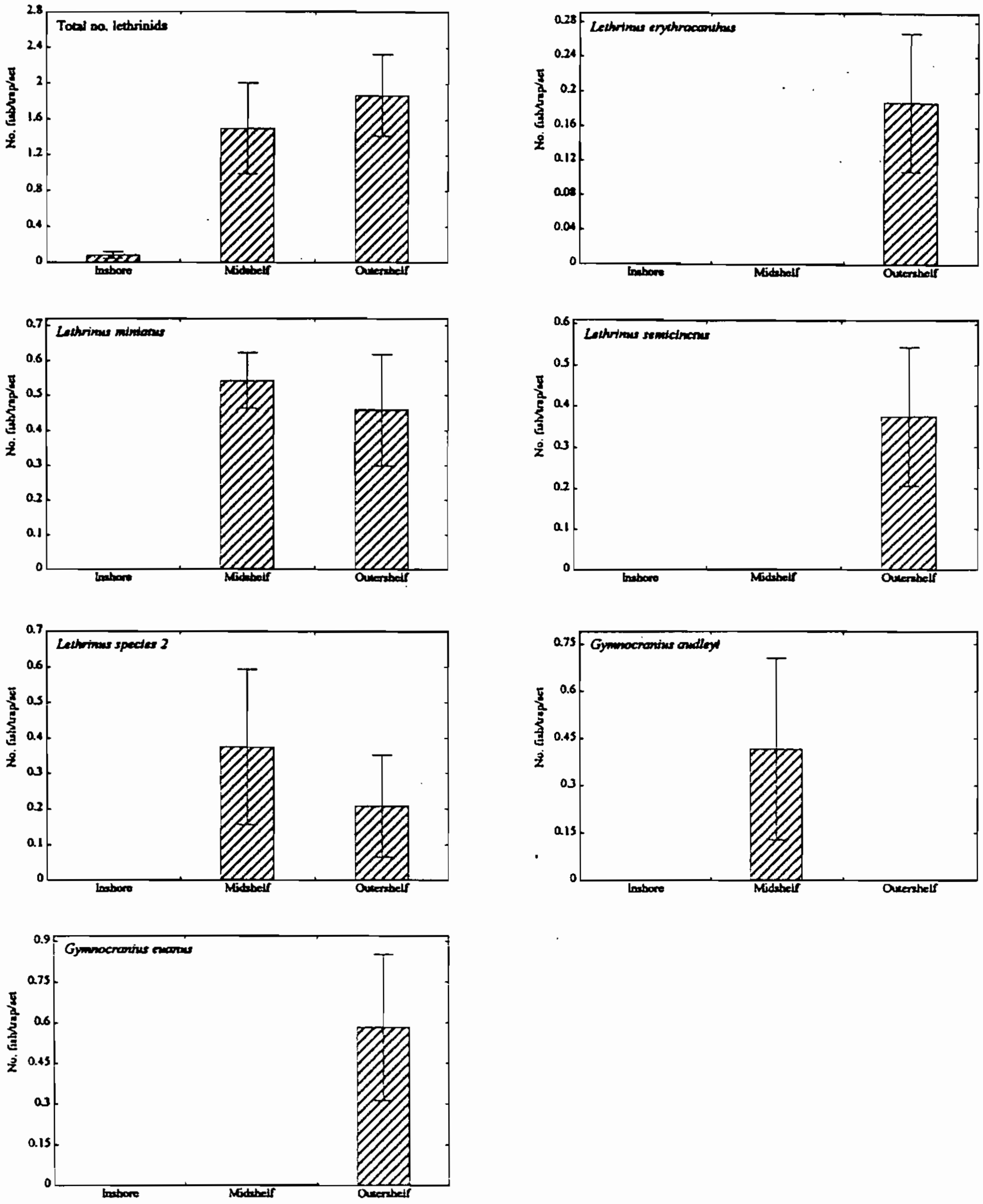

Figure 3.5 : Mean catch per unit effort (no. fish/trap/set +/- standard errors) of total lethrinids and 6 species of lethrinid among cross shelf locations.

Chapter 4

Distribution and abundance of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) in the central Great Barrier Reef : patterns of zonation within and among midshelf and outershelf reefs.

4.1 INTRODUCTION

Distinct assemblages of fishes are characteristically associated with particular zones and habitats within coral reef systems. This association has been documented in many areas of the Pacific (Hiatt and Strasburg, 1960; Jones, 1968; Talbot and Goldman, 1972; Chave and Eckert, 1974; Hobson, 1974; Jones and Chave, 1975; Sale and Dybdahl, 1975; Goldman and Talbot, 1976; Hatcher, 1982; Galzin, 1987a; 1987b), Indian Ocean (Talbot, 1965; Harmelin-Vivien and Bouchon, 1976; Harmelin-Vivien, 1977; Robertson and Polunin, 1981), Red Sea (Bouchon-Navaro and Harmelin-Vivien, 1981; Edwards and Rosewell, 1981), and Caribbean (Clarke, 1977; Gladfelter and Gladfelter, 1978; Alevizon *et. al.*, 1985), as well as between regions (Gladfelter *et. al.*, 1980).

Studies undertaken in the central Great Barrier Reef region (approx. latitude 18°30'S) have characterised the broad scale patterns of distribution and abundance of many coral reef fishes (Williams, 1982; 1983; Williams and Hatcher, 1983; Russ, 1984a) and other biota (eg. hard corals : Done, 1982; soft corals : Dinesen, 1983; calcified green algae : Drew, 1983; sponges : Wilkinson and Trott, 1985; see also the review of Wilkinson and Cheshire, 1988). These studies have concentrated on determining patterns of distribution and abundance among reefs along a transect extending across the continental shelf from the nearshore coastal zone out into the Coral Sea. Williams (1982) and Williams and Hatcher (1983) concluded that there were significant changes in the structure of communities of coral reef fishes among locations along this cross shelf transect. Their studies were restricted to only one reef zone, the windward reef slopes. Russ (1984b) demonstrated that there is distinct within-reef (between-zone) variation in the composition of assemblages of herbivorous grazing fishes (Acanthuridae, Scaridae, Siganidae) at both midshelf and outershelf locations on the central Great Barrier Reef. Zonation patterns of fishes on coral reefs has been reviewed recently by Williams (1991).

There is little information available describing the spatial patterns of distribution and abundance of species of demersal reef fish of commercial and recreational fishing significance (Lutjanidae, Lethrinidae, Serranidae) within or among reefs on the Great Barrier Reef, although Kingsford (1992) recorded significant differences in the distribution of the serranid *Plectropomus leopardus* among zones within One Tree Island, southern Great Barrier Reef.

The present study examines variation in the assemblages of species of the Lutjanidae, Lethrinidae and Serranidae at a range of spatial scales. In particular, the study addresses variability of assemblages of the Lutjanidae, Lethrinidae and

Serranidae within and among reefs at similar locations on the continental shelf and within and among reefs at different locations on the continental shelf.

4.2 MATERIALS and METHODS

Study Sites

The study was conducted on 6 reefs on the continental shelf in the central region of the Great Barrier Reef and includes those studied by Williams (1982) and Russ (1984b). Three reefs were located on the midshelf (Rib, John Brewer, Lodestone), approximately 50km offshore and on the outershelf (Myrmidon, Dip, Bowl), approximately 100km offshore (see Figure 4.1). The gross morphology and environment of these reefs are described in Done (1982).

The areas studied within each zone in each reef are shown in Figure 4.2. The reefs on the midshelf and outershelf display distinctive patterns of zonation (Done, 1982). Three zones were studied within each of these 6 reefs : the windward reef slopes; the lagoon and the leeward back reef (Figure 4.2). A brief description of each zone is given below. The physical characteristics of all the areas censused for each zone were as comparable as possible for all the midshelf and outershelf reefs.

Windward reef slopes : The exposed windward (east to south-east) reef slopes censused were relatively steeply sloping areas of live coral or coral rock. This zone was censused to a depth of 12m. The upper slopes and reef crest zone of the midshelf reefs correspond to the *Acropora palifera/humilis/digitifera* variant coral community and the *Acropora* tabulate/branched community, while the lower slopes corresponds to the *Acropora splendida/divaricata* and *Montipora/Pachyseris* coral communities described by Done (1982). The upper slopes and crests of the outershelf reefs correspond to the *palmerae* and *hyacinthus* variants of the *Acropora palifera/humilis* coral community, while the lower slopes correspond to the *Acropora palifera/Porites* coral community described by Done (1982). The percentage cover of soft corals was comparable to that of hard corals in the area of the lower slopes (Dinesen, 1983). These areas are similar to those studied by Russ (1984b).

Lagoons : A combination of habitats were encountered within the census areas in this zone. This zone included patch reefs from 2 to 20m in diameter, small to large diameter bommies and large expanses of sandy areas and rubble accumulations with a water depth of 3 to 8m. The bases of bommies and the sandy lagoon floor areas often had large stands of *Acropora* thickets. The *Acropora* thickets in both the midshelf and outershelf lagoons corresponded to the *Acropora* staghorn coral community described by Done (1982).

Back reefs : The array of back reef bommies, coral terraces, sand chutes and rubble accumulations comprised this zone. Back reefs were censused to a depth of 12m. On the midshelf reefs the coral communities of the back reef corresponded to the *Acropora splendida/divaricata* and *Porites* massive/branched communities described by Done (1982). The back reef coral communities of the outershelf reefs corresponded to the *Porites/Diploastrea* community described by Done (1982). The abundance of soft corals was comparable to that of hard corals in this zone, as on the lower windward reef slopes (Dinesen, 1983; see also Russ, 1984a).

Sampling Methods

Three families, comprising the majority of demersal reef fishes of commercial and recreational fishing significance on the Great Barrier Reef (Lutjanidae, Lethrinidae and Serranidae) were studied. Assemblages of fishes of these families were identified to species according to Allen and Talbot (1985) and Allen (1985) for the Lutjanidae; Carpenter and Allen (1989) for the Lethrinidae; and Randall and Heemstra (1991) and Heemstra and Randall (1993) for the Serranidae.

The assemblage of fishes in each zone was surveyed using a visual census technique similar to that used by Williams (1982) and Russ (1984a, 1984b). A census dive consisted of a 45 minute swim (using SCUBA) through a zone recording the total number of each target species seen. All individuals within approximately 5 metres either side of the diver were recorded and all target species were censused simultaneously. All data were recorded onto prepared census sheets of waterproof paper and all censuses were made by one observer (SJN) to ensure consistency. Census dives for the reef slope were unidirectional, consisting of a meandering zig-zag swim from the reef crest to a depth of 12m. Census dives in the lagoon and back reef were roughly unidirectional following a meandering path between bommies and coral outcrops, zig-zaging from the surface to a depth of 8m and 12m respectively. The distance covered by each census was approximately 400m, with the area censused approximately 4,000 m^2 (400m × 10m). Censuses were carried out in December, 1993. Three replicate non-overlapping censuses were made once in each of the three zones on each of the three midshelf and three outershelf reefs, making a total of 54 censuses.

Analysis of Data

The data from all 54 censuses, including all 61 species recorded, were subjected to an agglomerative, hierarchical classification (Williams, 1971). A dendrogram and similarity matrix were generated using euclidean distance as a similarity index and Ward's incremental sum of squares sorting strategy. Before the analysis the raw data were standardised (transformed to $\sqrt{x} + \sqrt{[x + 1]}$) for improvement of normality and heterogeneity (see Field *et. al.*, 1982). Each division of the dendrogram derived from the classification analysis resulted in the creation of two groups which were significantly different from one another, as determined by the test of Sandland and Young (1979a; 1979b). The pseudo-Cramer value C, was used to rank species according to their abilities to distinguish between the two locations derived from the classification analysis (Lance and Williams, 1977; Abel *et. al.*, 1985).

Data from visual censuses were also analysed by parametric analysis of variance (ANOVA). Three factor ANOVA's were carried out on the abundance data for all individuals recorded, for each family and for 25 species which were consistently present and represented different relative abundances (see Table 4.2). The three factors in the analysis were location on the continental shelf (midshelf, outershelf), reefs nested within locations (midshelf : Rib, John Brewer, Lodestone; outershelf : Myrmidon, Dip, Bowl) and zones (front slope, lagoon, back reef). Locations and zones were treated as fixed factors and reefs as a random factor in the analysis (Underwood, 1981). Zones were orthogonal to both the location and to the reefs nested in location factors in the analysis. There were three replicate censuses within each combination of the three factors. Homogeneity of variance for all analyses ($\alpha = 0.05$) was determined using Cochran's test (Winer, 1971). The variances of the raw data of most variables were heterogeneous. Variables were transformed to a $\sqrt{x} + \sqrt{(x + 1)}$ function to remove the variance heterogeneity (as well as any significant mean - variance correlation) and to make treatment effects additive (Winer, 1971; Underwood, 1981). Multiple comparison of means ($\alpha = 0.05$) were conducted using Tukey's honestly significant difference (HSD) method (Winer, 1971; Day and Quinn, 1989).

4.3 RESULTS

Species Assemblage Pattern

A total of 61 species were recorded from the 54 censuses (Table 4.1). The classification analysis of all species from all censuses generated the dendrogram in Figure 4.3. The classification analysis places all censuses from the midshelf reefs in a group distinct from all censuses from the outershelf reefs. Censuses from the midshelf reefs split into a group containing all censuses from the lagoons and back reefs, and another containing all censuses from the reef slopes (Figure 4.3). The analysis did not differentiate between the lagoon and back reef censuses of the midshelf reefs. There was however, a single prominent outlier from this cluster, a lagoon census from Lodestone Reef (Figure 4.3).

The analysis did not differentiate among zones on the outershelf reefs as conclusively as it did on the midshelf reefs (Figure 4.3). Censuses from the outershelf reefs formed no significant reef or zone clusters in the analysis.

Of the 61 species recorded, 18 were observed only on the midshelf reefs, and 13 were observed only from outershelf reefs. A total of 30 species were recorded at both shelf locations (see Table 4.1). A number of rare species with low relative abundance were encountered and distinctive species assemblages were associated with the midshelf and outershelf locations.

Results of the 3-factor analyses of variance of abundance of selected taxa are summarised in Table 4.2 and the results of the *a posteriori* Tukey (HSD) multiple comparison of means from the 3-factor analyses of variance are summarised in Table 4.3.

Differences among Locations on the Continental Shelf (Midshelf vs. Outershelf)

Location on the continental shelf had a significant effect on the abundance of 6 species of lutjanids examined, the abundance of the Lethrinidae, 2 lethrinid species and 6 serranid species (Table 4.2). Location was also significant in interaction with zones in 2 lutjanid species, 1 lethrinid species, the Serranidae and 3 serranid species (Table 4.2). Species which were more abundant on the midshelf reefs include *Lutjanus carponotatus*, *L. fulviflamma*, *L. quinquelineatus*, *L. obsoletus*, *Cephalopholis cyanostigma*, *Epinephelus fasciatus*, and *Plectropomus leopardus* (Table 4.3 and Figures 4.4a-4.4d). Additionally, *Lutjanus russelli*, *Cephalopholis boenak* and *C. microprion* were all more abundant in the lagoon and back reef zones of the midshelf reefs (Table 4.3 and Figures 4.4b, 4.4c). Species which were more abundant on the outershelf reefs include *Lutjanus bohar*, *Macolor macularis*, *M. niger*, *Monotaxis grandoculis*, *Cephalopholis argus*, *Epinephelus merra* and *Plectropomus laevis* (Table 4.3 and Figures 4.4a-4.4d). Additionally, *Lutjanus gibbus* and *Cephalopholis urodeta* were more abundant on the windward reef slopes of outershelf reefs (Table 4.3 and Figures 4.4a, 4.4c) and *Gnathodentex aurolineatus* was more abundant on the windward reef slopes and lagoons of the outershelf reefs (Table 4.3, Figure 4.4b). Location on the continental shelf accounts for a high proportion of the variability in abundance of species of the Lutjanidae, Lethrinidae and Serranidae. A large proportion of this variability was due to an absence or low abundance of species in a given zone, reef or continental shelf location and this was the causative factor in a number of the significant interaction effects among the spatial factors (see Tables 4.2, 4.3 and Figures 4.4a-d, 4.5a, 4.5b). Species recorded from the midshelf reefs only were *Lutjanus carponotatus*, *L. fulvus*, *L. lemniscatus*, *L. lutjanus*, *L. russelli*, *L. sebae*, *Lethrinus lentjan*, *L. ornatus*, *Cephalopholis boenak*, *C. microprion*, *Epinephelus caeruleopunctatus*, *E. cyanopodus*, *E. fasciatus*, *E. howlandi*, *E. lanceolatus*, *E. malabaricus*, *E. macrospilos*, and *E. ongus* (Table 4.1). Species recorded from the outershelf reefs only were *Aphareus furca*, *Aprion virescens*, *Lutjanus semicinctus*, *Gnathodentex aurolineatus*, *Lethrinus erythracanthus*, *L. xanthochilus*, *Gymnocranius grandoculis*, *Gymnocranius sp.*, *Cephalopholis leopardus*, *C. urodeta*, *Epinephelus tauvina*, *E. tukula* and *Variola louti* (Table 4.1).

Differences among Reefs

Three species (*Lethrinus atkinsoni*, *Plectropomus laevis* and *P. leopardus*) differed significantly in abundance among reefs. *Lethrinus atkinsoni* was less abundant at Myrmidon than elsewhere and was more abundant at Bowl and Rib than Lodestone, with no significant differences among the other reefs (Table 4.3 and Figure 4.6). *Plectropomus laevis* was more abundant at Bowl than elsewhere and additionally was more abundant among outershelf reefs (Myrmidon, Dip, Bowl) than midshelf reefs (Rib, John Brewer, Lodestone), while *P. leopardus* was more abundant at Lodestone and John Brewer than elsewhere and additionally was more abundant among midshelf reefs (Lodestone, John Brewer, Rib) than outershelf reefs (see Table 4.3 and Figure 4.6).

The Lutjanidae, Serranidae, *Lutjanus carponotatus*, *L. fulviflamma*, *L. russelli*, *Lethrinus miniatus*, *L. nebulosus*, *Monotaxis grandoculis*, *Anyperodon leucogrammicus*, *Cephalopholis argus*, *C. boenak*, *C. cyanostigma*, *C. microprion*, *C. urodeta*, *Epinephelus fasciatus* and *E. merra* all demonstrated significant reef (nested in location) × zone interactions, indicating that patterns of zonation varied significantly among reefs at the same location (see Table 4.3 and Figures 4.5a, 4.5b). The complexity of these patterns are illustrated in Figures 4.5a and 4.5b. Species were often less abundant (or absent) in the visual surveys at Rib and Myrmidon reefs than on the other reefs at the same cross shelf location. These differences account for a large proportion of the among reef variation and significant reef (location) × zone interactions in the ANOVA's (Table 4.2 and Figures 4.5a, 4.5b).

Differences among Zones within Reefs

Three species *Lutjanus quinquelineatus*, *Lethrinus atkinsoni* and *Cromileptes altivelis* differed significantly in abundance among zones (within reef variation) at both shelf locations (Table 4.2 and Figures 4.4b, 4.4d). *Lutjanus quinquelineatus* and *Cromileptes altivelis* were more abundant in lagoons and back reef zones (Table 4.3 and Figures 4.4b, 4.4d). In contrast, *Lethrinus atkinsoni* was more abundant on the windward reef slopes (Table 4.3 and Figure 4.4b).

The Serranidae, *Lutjanus gibbus*, *L. russelli*, *Gnathodentex aurolineatus*, *Cephalopholis boenak*, *C. microprion* and *C. urodeta* all demonstrated significant location × zone interactions, indicating that patterns of zonation varied significantly among continental shelf locations (see above). Many species also demonstrated significant reef (location) × zone interactions (see above). The significant reef (location) × zone interactions resulted from the low abundance (or absence) of species within zones within individual reefs (Figures 4.5a and 4.5b).

A number of generalisations can be made about the patterns of abundance of species both within reefs (among zones) and at different locations on the continental shelf based on the comparison of mean census counts (Tables 4.1, 4.3 and Figures 4.4a-4.4d). For example, *G. aurolineatus* is abundant only in the reef slope and lagoon zones of outershelf reefs, while *C. boenak* and *C. microprion* are only encountered in the lagoon and back reef zones of the midshelf reefs. Thus on the basis of their relative abundance, species of the families Lutjanidae, Lethrinidae and Serranidae can be defined as being characteristic of specific zones among midshelf and outershelf reefs in the central Great Barrier Reef (Table 4.4).

There is a distinct similarity of assemblages across zones within locations (Table 4.4).

4.4 DISCUSSION

The assemblages of species of the Lutjanidae, Lethrinidae and Serranidae displayed distinct patterns of distribution and abundance within the shallow waters of the central GBR at three spatial scales - a between location scale (outershelf and midshelf communities), a between reef scale (high abundance vs. low abundance reefs) and a within reef scale (characteristic communities within zones on individual reefs). Significant spatial variability was identified in the abundances of many different species. Additionally, a large proportion of the species recorded were relatively rare within a given zone, reef or location (Table 4.1). Williams (1982), Williams and Hatcher (1983) and Russ (1984a; 1984b) have also shown marked spatial variation in the abundance of reef fishes on these scales within the central Great Barrier Reef.

Location on the continental shelf accounts for a high proportion of the variation in community structure (Figure 4.3). The Lutjanidae and Serranidae are more abundant on the midshelf while the Lethrinidae (in particular *G. aurolineatus* and *M. grandoculis*) are more abundant on the outershelf reefs (see Figures 4.4a, 4.4b, 4.4c). Williams *et. al.* (1988) have similarly shown that the abundance of lutjanid larvae and lethrinid larvae (genus *Lethrinus*) is higher in waters around the midshelf reefs. Species specific patterns more clearly reflected distributions among locations. Confirmed piscivores such as *L. bohar* (see Hiatt and Strasburg, 1960;

Randall, 1980; Allen, 1985), *L. gibbus* (see Randall and Brock, 1960; Miles, 1963; Randall, 1980) *C. argus* (see Randall and Brock, 1960; Hobson, 1974; Harmelin-Vivien and Bouchon, 1976; Randall, 1980; Heemstra and Randall, 1993), *C. urodeta* (see Hiatt and Strasburg, 1960; Randall and Brock, 1960), *E. merra* (see Hiatt and Strasburg, 1960; Harmelin-Vivien and Bouchon, 1976) and *P. laevis* (see Randall and Brock, 1960; Randall, 1980; Morgans, 1982) were significantly more abundant on the outershelf reefs, while *P. leopardus* (Goedon, 1978; Kingsford, 1992; St. John, unpublished data) and *E. fasciatus* (see Randall and Ben-Tuvia, 1983) were the only dominant piscivores on the midshelf reefs. Additionally, *G. aurolineatus* and *M. grandoculis* were significantly more abundant on the outershelf reefs. However, species of the genus *Lethrinus* appeared more commonly on the midshelf reefs (Table 4.1). Furthermore, the other *Lutjanus* and *Cephalopholis* species (Table 4.3) were significantly more abundant on the midshelf reefs also. Both the *Macolor* species were significantly more abundant on the outershelf reefs where they occur in large schools.

The outershelf reef communities are situated on the edge of the continental shelf and are exposed to oceanic influences, whereas midshelf reef communities are surrounded by the shallow waters of the barrier reef lagoon generally less than 60m deep. Differences in cross-shelf distributions may be related to differences in the surrounding pelagic environments. Significant differences were also found among reefs within locations. On the outershelf, Myrmidon reef is situated on a thin peninsula which extends approximately 8km from the main edge of the continental shelf into the Coral Sea and is located on the continental slope (200m depth contour), whereas Bowl and Dip reefs are situated 6-12km inshore from the edge of the continental shelf.

Consequently, Myrmidon is surrounded by waters of lower productivity than the other two reefs (Williams *et. al.*, 1988). Differences in the fish faunas between Myrmidon and the other two reefs may therefore be a result of differences in the surrounding pelagic environments, either through its effects on food availability to the reefs or the availability of suitable pelagic environments for larval fishes (Williams, 1991). A distinctive example is *C. cyanostigma* which is abundant on the midshelf and occurs in low relative abundances on Dip and Bowl Reefs but is absent from Myrmidon Reef (see Figure 4.5b).

On the midshelf, Rib Reef in contrast to both John Brewer and Lodestone reefs is a relatively small reef and is less well developed structurally and morphologically. The abundance of a number of species at Rib Reef is significantly lower than at John Brewer and Lodestone reefs (see Figure 4.5a) and may be due to reduced reef habitat diversity or availability and hence reduced feeding areas.

Differences among reefs can be determined at a pre settlement phase. Proximal factors which may determine the observed patterns of distribution and abundance of adult fishes both among reefs and locations, include the limitations of larval dispersal (eg. differential availability of larvae across the shelf), patterns of settlement and habitat selection of postlarvae and differential survival of recruits after settlement (Williams and Hatcher, 1983; Russ, 1984a). Alternative explanations include the size of the reef which may enable entrainment of greater larval supply than smaller reefs given that currents are predominantly longshore (see Williams *et. al.*, 1984). Other factors which are also likely to influence the distribution of these fishes across the reef include the percentage of live coral cover (Bell and Galzin, 1984) (and hence shelter as the Serranidae are primarily ambush predators) and hydrodynamic activity. Some coral reef fish assemblages at a particular spatial scale appear to be correlated with the physical and biological complexity of the reef (Luckhurst and Luckhurst, 1978), although this was not examined here.

The species of the Lutjanidae, Lethrinidae and Serranidae occur in assemblages which are characteristic of major zones (windward reef slopes, lagoons and leeward back reefs) and this pattern is consistent within and among locations (Table 4.4). Similar variations in the assemblages of communities of reef fishes among different zones within reef systems have been described (Sale and Dybdahl, 1975; Goldman and Talbot, 1976; Gladfelter and Gladfelter, 1978; Gladfelter *et. al.*, 1980; Williams, 1983; Galzin, 1987a). Chave and Eckert (1974) also reported similar patterns of zonation of species at Fanning Island, with *L. bohar* and *L. argus* common and abundant respectively, on the outer reef slopes and *E. merra* found commonly among lagoon patch reefs and tide pools. Similarly, results presented here support the observations of Heemstra and Randall (1993) who reported *A. leucogrammicus* from protected reef waters, *C. boenak* and *C. microprion* from silty protected reef waters, *C. argus* and *C. urodeta* commonly on outer reef slopes and *E. merra* as a shallow water species found around lagoonal areas. Additionally, the results presented here support the observations of

Carpenter and Allen (1989) that *L. atkinsoni* is characteristic of outer reef slopes and *M. grandoculis* is commonly found in sand and rubble lagoon areas. In contrast to my results, Kingsford (1992) described higher abundances of *P. leopardus* on the outer reef slopes of One Tree Island than elsewhere. Despite this anomaly, the distinctive spatial patterns of zonation of species observed in this study may be applicable to a wide range of reef systems throughout the Indo-Pacific region.

A high degree of variation in the recruitment of juveniles within the same zones on different reefs may account to a large degree for the significant zone × reef interactions recorded for some species (Table 4.2, see also Figures 4.5a and 4.5b). Spatial patterns of species may originate, or at least be maintained by habitat selection at the time of, or soon after, settlement. Habitat selection by species of reef fish has been demonstrated by Williams (1980), Williams and Sale (1981) and Eckert (1985), and discussed as possible determinants of zonation of fishes of coral reefs by Russ (1984a; 1984b), Galzin (1987a) and Williams (1991).

Zone associated differences are possibly attributable not only to recruitment patterns but also the food resource requirements of adults. Consequently there appears to be a partitioning of resources between species among zones. The consistent patterns of relative abundance of species among zones within reefs and among reefs suggest that these spatial patterns are likely to be maintained through time (Russ, 1984b). The assemblages of fishes of the Lutjanidae, Lethrinidae and Serranidae may however, vary through time as a direct consequence of variable juvenile recruitment and hence year class strength (Doherty and Fowler, 1994) in combination with fishing pressure. Parrish (1987) has suggested that active fisheries targeting specific species of lutjanids and serranids may directly enhance the populations of other non-target species of these families through diminished predation pressures.

In summary, factors likely to determine cross-shelf differences in abundance include the suitability of pelagic environments for larval fishes, food availability and exposure of reefs, as well as differential survivorship after settlement (Williams and Hatcher, 1983; Williams *et. al.*, 1986). Differences at localised reef scales (among reefs within locations) are more likely to be determined by a combination of competition (review of Ebeling and Hixon, 1991), recruitment limitation (reviewed by Doherty and Williams, 1988; Doherty, 1991; Doherty and Fowler, 1994), predatory interactions (review by Hixon, 1991) and perhaps physical, abiotic interactions. Further, within reef (zonation) differences are likely to be determined by habitat selection at the time of or soon after settlement, food requirements and also shelter requirements (eg. *Acropora* "staghorn" thickets) and coral cover (Russ, 1984a; 1984b; Galzin, 1987a; Williams, 1991).

The descriptions of the patterns of spatial variation of species of the Lutjanidae, Lethrinidae and Serranidae within reefs and among reefs and locations is an important consideration for any future experimental manipulations of fishing pressure. Care will need to be taken in determining the appropriate spatial scales of sampling to ensure that the effects of smaller scale spatial differences are not confounded when larger scale comparisons are made.

Table 4.1 : Mean numbers (per census) of 61 species of the Lutjanidae, Lethrinidae and Serranidae within zones of the midshelf and outershelf reefs, ranked in order of their ability to distinguish among locations according to the pseudo-Cramer value, *C* (*n* = 9 censuses per zone; --- = absent).

Species	*C*	Midshelf			Outershelf		
		Reef Slope	Lagoon	Back Reef	Reef Slope	Lagoon	Back Reef
Lutjanus quinquelineatus	0.9653	2.67	54.6	17.7	---	2.0	0.89
Cephalopholis boenak	0.9417	0.11	14.9	12.3	---	---	---
Lutjanus russelli	0.9003	0.78	7.22	6.33	---	---	---
Lutjanus carponotatus	0.8695	3.22	2.11	2.89	---	---	---
Cephalopholis cyanostigma	0.8670	20.8	18.7	19.3	0.111	4.89	4.33
Cephalopholis microprion	0.8627	---	2.44	2.22	---	---	---
Lutjanus fulviflamma	0.8084	18.2	23.0	18.9	2.78	4.44	---
Lethrinus obsoletus	0.7555	---	2.89	3.44	---	1.22	---
Lutjanus fulvus	0.7151	---	0.22	---	---	---	---
Plectropomus leopardus	0.7028	12.1	8.89	16.1	2.33	4.33	5.67
Lutjanus lemniscatus	0.6798	---	0.67	0.56	---	---	---
Epinephelus fasciatus	0.6347	0.22	0.78	0.89	---	---	---
Epinephelus ongus	0.5228	---	0.11	0.44	---	---	---
Lethrinus lentjan	0.4630	---	0.11	0.89	---	---	---
Lethrinus nebulosus	0.4541	5.33	4.78	1.44	---	2.44	1.0
Aethaloperca rogaa	0.3759	0.44	---	0.33	---	0.11	---
Lutjanus sebae	0.3578	---	0.33	---	---	---	---
Lutjanus argentimaculatus	0.3353	---	0.11	0.11	---	---	0.11
Epinephelus fuscoguttatus	0.3174	0.33	---	0.22	---	---	0.22
Epinephelus caeruleopunctatus	0.3071	0.11	---	---	---	---	---
Lutjanus lutjanus	0.3071	0.22	---	---	---	---	---
Epinephelus lanceolatus	0.2893	---	---	0.22	---	---	---
Epinephelus macrospilos	0.2519	0.11	0.11	0.11	---	---	---
Epinephelus cyanopodus	0.2026	---	---	0.22	---	---	---
Epinephelus howlandi	0.2026	---	---	0.11	---	---	---
Epinephelus malabaricus	0.2026	---	---	0.11	---	---	---
Lethrinus ornatus	0.2026	---	---	0.11	---	---	---
Epinephelus maculatus	0.1782	---	---	0.78	---	---	0.11
Gnathodentex aurolineatus	0.9496	---	---	---	45.2	63.0	---
Macolor niger	0.8883	0.33	0.22	---	22.3	7.56	21.7
Monotaxis grandoculis	0.8663	1.67	5.56	4.44	20.4	53.0	12.3
Plectropomus laevis	0.8446	0.78	0.44	0.67	5.56	4.78	5.44
Cephalopholis argus	0.8237	2.67	---	0.33	12.2	0.22	1.11
Cephalopholis urodeta	0.8082	---	---	---	8.78	---	0.89
Lutjanus bohar	0.7273	1.89	0.78	4.56	10.3	15.2	9.67
Lutjanus kasmira	0.7188	---	0.11	---	0.22	---	---
Epinephelus merra	0.7061	---	1.33	0.56	0.11	5.56	2.11
Lethrinus xanthochilus	0.6177	---	---	---	0.89	0.22	0.33
Macolor macularis	0.5934	0.11	---	---	0.78	0.89	1.78
Lutjanus gibbus	0.5884	---	---	1.78	4.56	2.89	0.22
Lethrinus erythracanthus	0.5211	---	---	---	0.33	0.11	0.56
Gymnocranius sp.	0.4703	---	---	---	---	0.22	---
Aprion virescens	0.4609	---	---	---	0.55	---	0.11
Variola louti	0.4583	---	---	---	0.33	---	0.22
Lutjanus monostigma	0.4229	---	---	0.44	0.11	0.11	0.22
Gymnocranius grandoculis	0.4221	---	---	---	---	0.44	0.33
Aphareus furca	0.3409	---	---	---	1.33	---	0.11
Symphorus nematophorus	0.3068	---	0.11	0.11	0.33	---	---
Lutjanus semicinctus	0.2918	---	---	---	0.11	0.11	---
Lutjanus rivulatus	0.2866	0.11	---	---	0.11	---	0.22
Lethrinus olivaceus	0.2502	0.11	---	---	---	1.67	---
Cephalopholis leopardus	0.2322	---	---	---	---	---	0.33
Epinephelus tauvina	0.2322	---	---	---	---	0.33	---
Epinephelus tukula	0.2322	---	---	---	---	---	0.11
Lethrinus atkinsoni	0.5666	3.67	2.22	0.56	3.67	2.22	0.56
Anyperodon leucogrammicus	0.5443	0.11	1.22	0.44	---	1.33	0.33
Cromileptes altivelis	0.4998	---	0.67	0.67	---	0.67	0.22
Epinephelus hexagonatus	0.4064	---	---	0.11	0.11	---	---
Epinephelus polyphekadion	0.3742	---	0.22	---	---	0.22	---
Lethrinus miniatus	0.2753	1.11	1.22	0.78	0.56	2.44	2.11
Symphorichthys spilurus	0.1677	---	0.22	---	---	---	0.11

Table 4.2 : Summaries of three factor analyses of variance for selected taxa (significance levels : ns = p > 0.05; * = 0.05 > p > 0.01; ** = 0.01 > p > 0.001; *** = p < 0.001; $^{@}$ = data transformed to $\{\sqrt{x} + \sqrt{(x+1)}\}$ before analysis).

	d.f.	Total individuals[1].			Lutjanidae$^{@}$			Lethrinidae$^{@}$		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	439.2	0.06	ns	119.5	3.41	ns	560.5	28.4	**
Reefs (Location)	4,36	7243	1.03	ns	35.1	1.46	ns	19.7	0.71	ns
Zone	2,8	20770	3.32	ns	37.3	0.67	ns	155.8	3.98	ns
Location × Zone	2,8	11995	1.92	ns	103.1	1.86	ns	119.4	3.05	ns
Reefs (Location) × Zone	8,36	6261	0.89	ns	55.5	2.30	*	39.2	1.41	ns
Residual		7025	---	---	24.1	---	---	27.6	---	---

	d.f.	Serranidae			*Lutjanus bohar*$^{@}$			*L. carponotatus*$^{@}$		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	7969	4.72	ns	174.3	36.3	**	80.15	22.0	**
Reefs (Location)	4,36	1688	35.7	***	4.80	0.66	ns	3.64	17.5	***
Zone	2,8	169.6	1.15	ns	0.86	0.06	ns	0.44	0.92	ns
Location × Zone	2,8	715.6	4.84	*	13.8	1.02	ns	0.44	0.92	ns
Reefs (Location) × Zone	8,36	148.0	3.13	**	13.5	1.85	ns	0.47	2.27	*
Residual		47.3	---	---	7.32	---	---	0.21	---	---

	d.f.	*L. fulviflamma*$^{@}$			*L. gibbus*			*L. quinquelineatus*$^{@}$		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	442.6	14.1	*	52.02	12.1	*	472.7	57.2	**
Reefs (Location)	4,36	31.5	30.5	***	4.30	0.81	ns	8.26	0.53	ns
Zone	2,8	17.1	2.37	ns	7.57	1.80	ns	132.2	7.25	*
Location × Zone	2,8	10.7	1.49	ns	44.9	10.7	**	55.3	3.03	ns
Reefs (Location) × Zone	4,36	7.2	6.98	***	4.21	0.79	ns	18.2	1.17	ns
Residual		1.03	---	---	5.31	---	---	15.5	---	---

	d.f.	*L. russelli*$^{@}$			*Macolor macularis*			*M. niger*$^{@}$		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	124.5	45.9	**	16.7	9.78	*	436.7	26.1	**
Reefs (Location)	4,36	2.71	8.02	***	1.70	1.39	ns	16.7	1.64	ns
Zone	2,8	17.6	4.75	*	1.19	0.79	ns	17.9	1.17	ns
Location × Zone	2,8	17.6	4.75	*	1.56	1.03	ns	14.9	0.98	ns
Reefs (Location) × Zone	8,36	3.70	11.0	***	1.51	1.23	ns	15.3	1.49	ns
Residual		0.34	---	---	1.22	---	---	10.2	---	---

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[1] - Total individuals is all 3 families (Lutjanidae, Lethrinidae, Serranidae) combined.

Table 4.2 : continued.

	d.f.	*Gnathodentex*[2]			*Lethrinus atkinsoni*@			*L. miniatus*		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	647.4	22.6	**	4.25	0.66	ns	6.00	0.34	ns
Reefs (Location)	4,36	28.7	0.74	ns	6.47	3.49	*	17.4	13.3	***
Zone	2,8	164.3	17.3	**	19.4	8.43	*	4.57	1.51	ns
Location × Zone	2,8	164.3	17.3	**	4.22	1.84	ns	5.06	1.66	ns
Reefs (Location) × Zone	8,36	9.48	0.24	ns	2.30	1.24	ns	3.04	2.31	*
Residual		38.8	---	---	1.85	---	---	1.31	---	---

	d.f.	*L. nebulosus*			*L. obsoletus*			*Monotaxis*[3]@		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	98.7	3.55	ns	39.2	27.8	**	512.9	54.6	**
Reefs (Location)	4,36	27.8	2.92	*	1.41	0.25	ns	9.39	1.92	ns
Zone	2,8	26.1	0.79	ns	21.9	2.81	ns	70.1	4.34	ns
Location × Zone	2,8	27.4	0.82	ns	13.4	1.71	ns	52.4	3.25	ns
Location × Reef × Zone	8,36	33.2	3.48	**	7.80	1.37	ns	16.1	3.29	**
Residual		9.54	---	---	5.69	---	---	4.90	---	---

	d.f.	*Anyperodon*[4]@			*Cephalopholis argus*@			*C. boenak*@		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	0.31	0.11	ns	34.1	8.83	*	243.2	33.6	**
Reefs (Location)	4,36	2.98	8.00	***	3.87	10.7	***	7.25	19.1	***
Zone	2,8	7.67	7.47	*	64.7	14.3	**	57.1	28.6	***
Location × Zone	2,8	0.01	0.01	ns	7.07	1.56	ns	57.1	28.6	***
Reefs (Location) × Zone	8,36	1.03	2.75	*	4.53	12.6	***	1.99	5.24	***
Residual		0.37	---	---	0.36	---	---	0.38	---	---

	d.f.	*C. cyanostigma*			*C. microprion*@			*C. urodeta*@		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	3667	24.4	**	28.1	22.0	**	49.4	20.2	*
Reefs (Location)	4,36	150	8.85	***	1.28	6.83	***	2.44	17.6	***
Zone	2,8	11.1	0.19	ns	7.13	7.30	*	29.1	8.71	**
Location × Zone	2,8	60.8	1.06	ns	7.13	7.30	*	29.1	8.71	**
Reefs (Location) × Zone	8,36	57.6	3.39	**	0.98	5.21	***	3.34	24.0	***
Residual		17.0	---	---	0.19	---	---	0.14	---	---

[2] - *Gnathodentex aurolineatus*

[3] - *Monotaxis grandoculis*

[4] - *Anyperodon leucogrammicus*

Table 4.2 : continued.

	d.f.	*Cromileptes*[5@]			*Epinephelus fasciatus*[@]			*E. merra*[@]		
Source of Variation	F-ratio	MS	F	p	MS	F	p	MS	F	p
Location	1,4	0.67	0.48	ns	8.30	16.2	*	18.1	13.9	*
Reefs (Location)	4,36	1.40	2.58	ns	0.51	3.52	*	1.30	4.40	**
Zone	2,8	2.55	4.58	*	0.86	0.74	ns	31.8	8.69	**
Location × Zone	2,8	0.38	0.69	ns	0.86	0.74	ns	5.07	1.39	ns
Reefs (Location) × Zone	8,36	0.56	1.02	ns	1.17	8.05	***	3.65	12.4	***
Residual		0.54	---	---	0.15	---	---	0.30	---	---

	d.f.	*Plectropomus laevis*[@]			*P. leopardus*[@]		
Source of Variation	F-ratio	M	F	p	M	F	p
Location	1,4	111.9	26.0	**	110.6	13.2	*
Reefs (Location)	4,36	4.30	5.01	**	8.38	6.16	***
Zone	2,8	0.43	0.75	ns	6.01	3.45	ns
Location × Zone	2,8	0.05	0.10	ns	5.32	3.05	ns
Reefs (Location) × Zone	8,36	0.57	0.66	ns	1.74	1.28	ns
Residual		0.86	---	---	1.36	---	---

[5] - *Cromileptes altivelis*

Table 4.3 : *A posteriori* multiple comparison of means (using Tukey's HSD method) from the three factor analyses of variance shown in Table 4.2 (significance level for all comparisons was $p < 0.05$; Location : O = Outershelf, M = Midshelf; Reefs : Myr = Myrmidon, Dp = Dip, Bwl = Bowl, Rib = Rib, JB = John Brewer. Lod = Lodestone; Zone : S = front (windward) reef slopes, L = lagoon, B = back reef). The complex reef (location) × zone interactions are presented graphically in Figures 4.5a and 4.5b.

Taxa	Significant Effects		
Lutjanidae			reef (location) × zone interaction - see Figure 4.5a
Lethrinidae	O > M		
Serranidae		M : (L = B) > S; O : L = B = S S : M = O; L : M > O; B : M > O	reef (location) × zone interaction - see Figure 4.5a
Lutjanus bohar	O > M		
L. carponotatus	M > O		reef (location) × zone interaction - see Figure 4.5a
L. fulviflamma	M > O		reef (location) × zone interaction - see Figure 4.5a
L. gibbus		M : B > (L = S); O : (S = L) > B S : O > M; L : O > M; B : O = M	
L. quinquelineatus	M > O	(L = B) > S	
L. russelli		M : (L = B) > S; O : nil. S : M > O; L : M > O; B : M > O	reef (location) × zone interaction - see Figure 4.5a
Macolor macularis	O > M		
M. niger	O > M		
Gnathodentex aurolineatus		M : nil.; O : (S = L) > B S : O > M; L : O > M; B : nil.	
Lethrinus atkinsoni		Myr < Dp, Bwl, Rib, JB, Lod (Bwl = Rib) > Lod; Bwl = Dp = JB = Rib S > (L = B)	
L. miniatus			reef (location) × zone interaction - see Figure 4.5a
L. nebulosus			reef (location) × zone interaction - see Figure 4.5a
L. obsoletus	M > O		
Monotaxis grandoculis	O > M		reef (location) × zone interaction - see Figure 4.5a

Table 4.3 : continued.

Taxa	Significant Effects		
Anyperodon leucogrammicus			reef (location) × zone interaction - see Figure 4.5b
Cephalopholis argus	O > M		
			reef (location) × zone interaction - see Figure 4.5b
C. boenak		M : (L = B) > S; O : nil.	
		S : M = O; L : M > O; B : M > O	
			reef (location) × zone interaction - see Figure 4.5b
C. cyanostigma	M > O		
			reef (location) × zone interaction - see Figure 4.5b
C. microprion		M : (L = B) > S; O : nil.	
		S : nil.; L : M > O; B : M > O	
			reef (location) × zone interaction - see Figure 4.5b
C. urodeta		M : nil.; O : S > (L = B)	
		S : O > M; L : nil.; B : O = M	
			reef (location) × zone interaction - see Figure 4.5b
Cromileptes altivelis		(L = B) > S	
Epinephelus fasciatus	M > O		
			reef (location) × zone interaction - see Figure 4.5b
E. merra	O > M		
			reef (location) × zone interaction - see Figure 4.5b
Plectropomus laevis	O > M		
		Bwl > Dp > Myr > (Rib = JB = Lod)	
P. leopardus	M > O		
		(Lod = JB) > Rib > (Myr = Dp = Bwl)	

Table 4.4 : Species of the Lutjanidae, Lethrinidae and Serranidae that are characteristic of zones and locations in the central Great Barrier Reef.

Zone	Midshelf	Outershelf
Reef Slope	*Lutjanus carponotatus* *L. fulviflamma* *Lethrinus atkinsoni* *L. nebulosus* *Cephalopholis cyanostigma* *Plectropomus leopardus*	*Lutjanus bohar* *L. gibbus* *Macolor macularis* *M. niger* *Gnathodentex aurolineatus* *Lethrinus atkinsoni* *Lethrinus xanthochilus* *Cephalopholis argus* *C. urodeta* *Plectropomus laevis*
Lagoon	*Lutjanus carponotatus* *L. fulviflamma* *L. quinquelineatus* *L. russelli* *Lethrinus nebulosus* *L. obsoletus* *Anyperodon leucogrammicus* *Cephalopholis boenak* *C. cyanostigma* *C. microprion* *Cromileptes altivelis* *Epinephelus fasciatus* *Plectropomus leopardus*	*Lutjanus bohar* *Macolor macularis* *M. niger* *Gnathodentex aurolineatus* *Lethrinus miniatus* *Monotaxis grandoculis* *Anyperodon leucogrammicus* *Cromileptes altivelis* *Epinephelus merra* *Plectropomus laevis*
Back Reef	*Lutjanus carponotatus* *L. fulviflamma* *L. quinquelineatus* *L. russelli* *Lethrinus obsoletus* *Cephalopholis boenak* *C. cyanostigma* *C. microprion* *Cromileptes altivelis* *Epinephelus fasciatus* *Plectropomus leopardus*	*Lutjanus bohar* *Macolor macularis* *M. niger* *Lethrinus miniatus* *Cromileptes altivelis* *Epinephelus merra* *Plectropomus laevis*

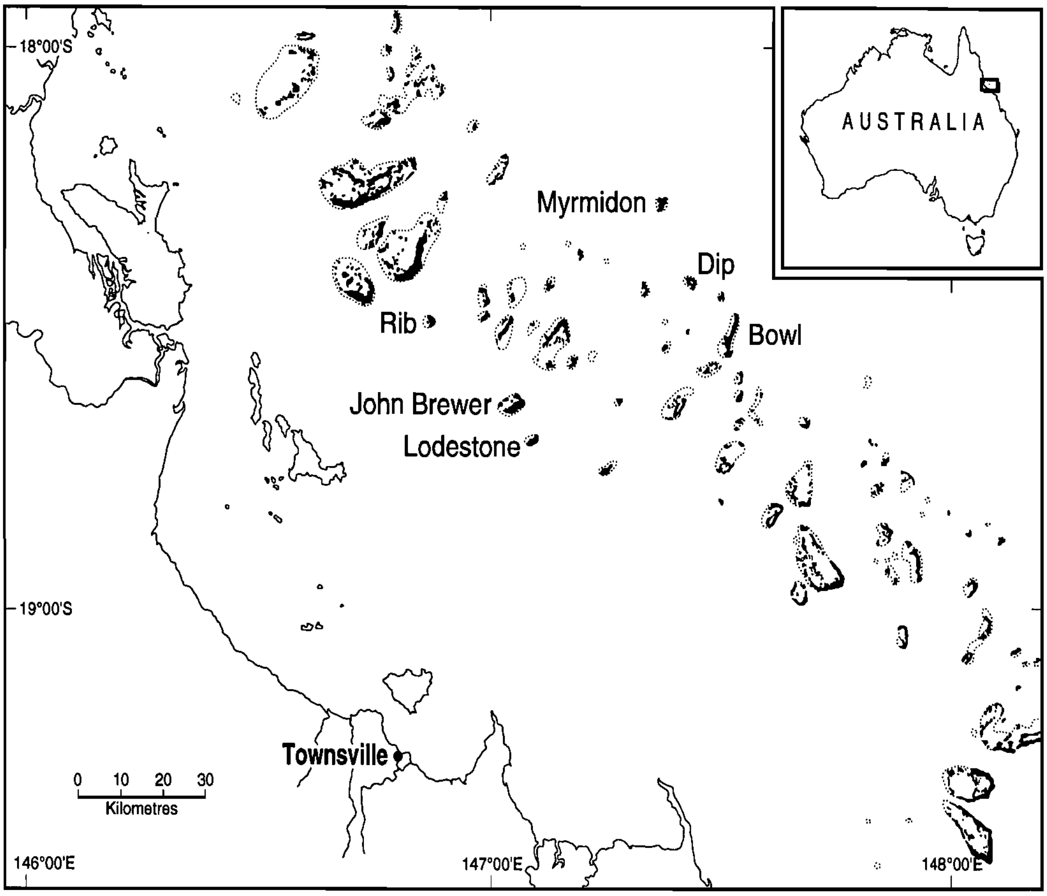


Figure 4.1 : The locations of study reefs in the central region of the Great Barrier Reef of Australia.

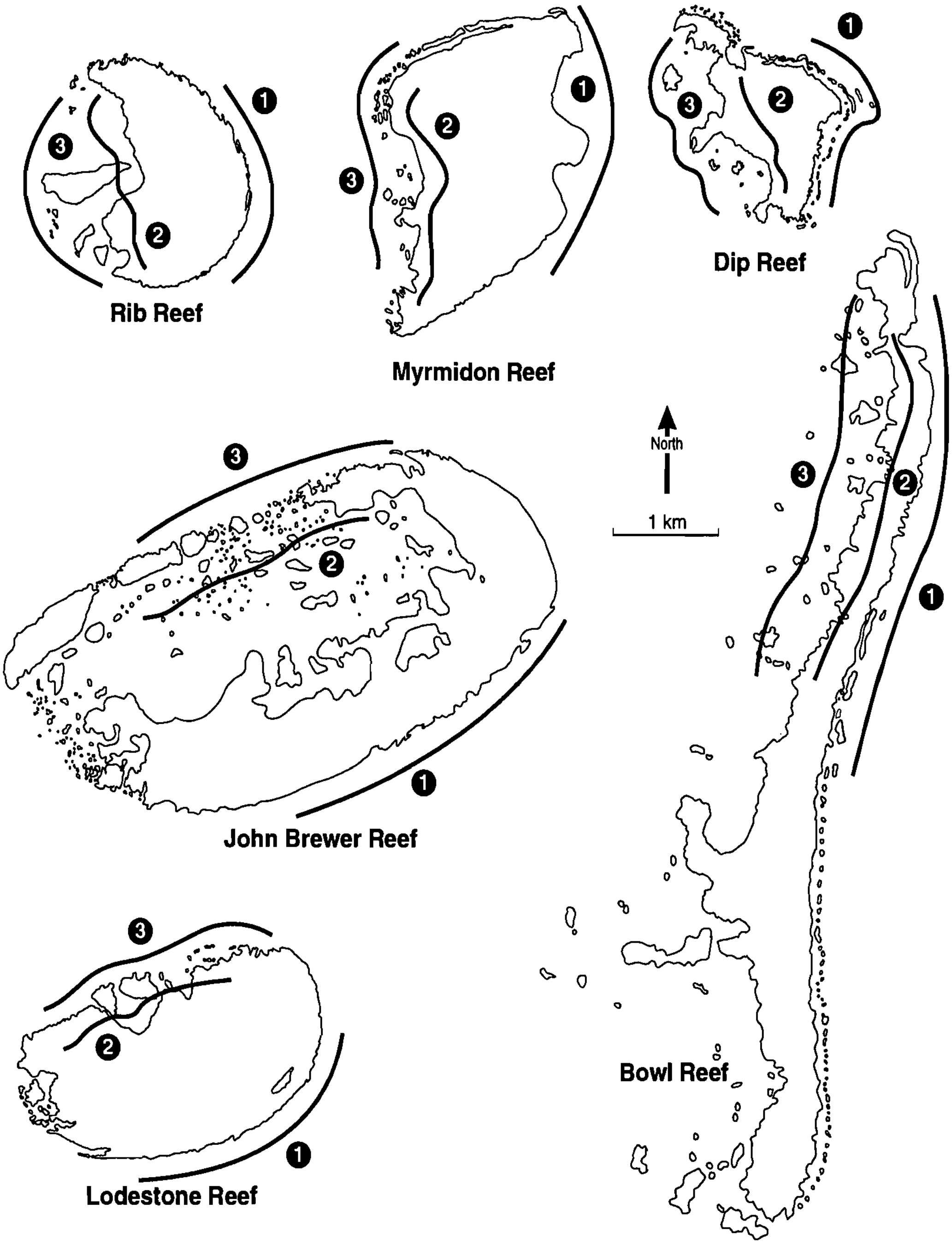


Figure 4.2 : Areas studied within the midshelf and outershelf reefs. Each line shows the general area in which 3 non-overlapping replicate censuses were made on each respective reef (1 = windward reef slope; 2 = lagoon; 3 = back reef).

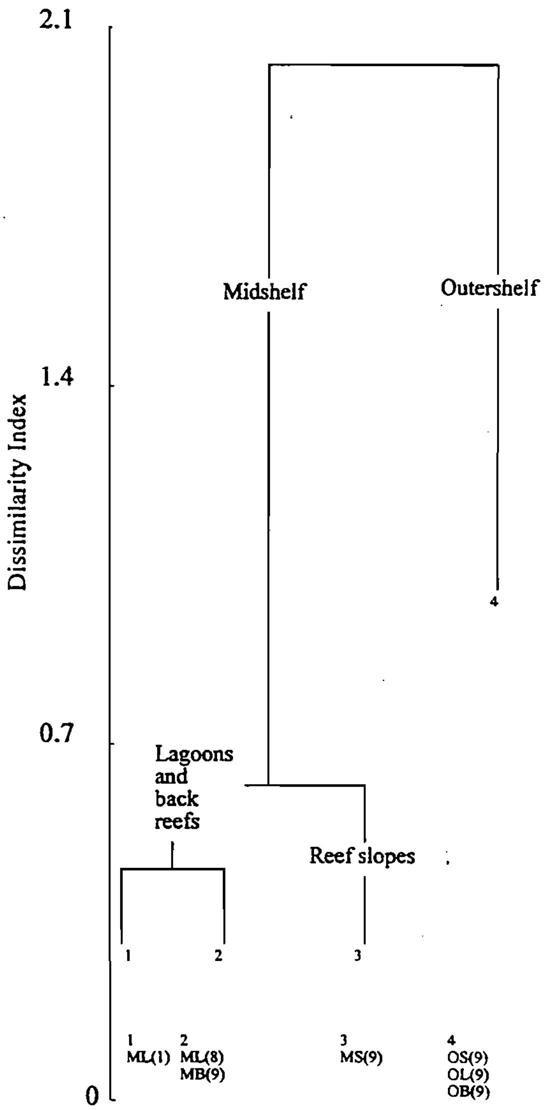


Figure 4.3 : Dendrogram from the classification analysis of 54 visual censuses (M = midshelf; O = outershelf; S = front slopes; L = lagoons; B = back reef).

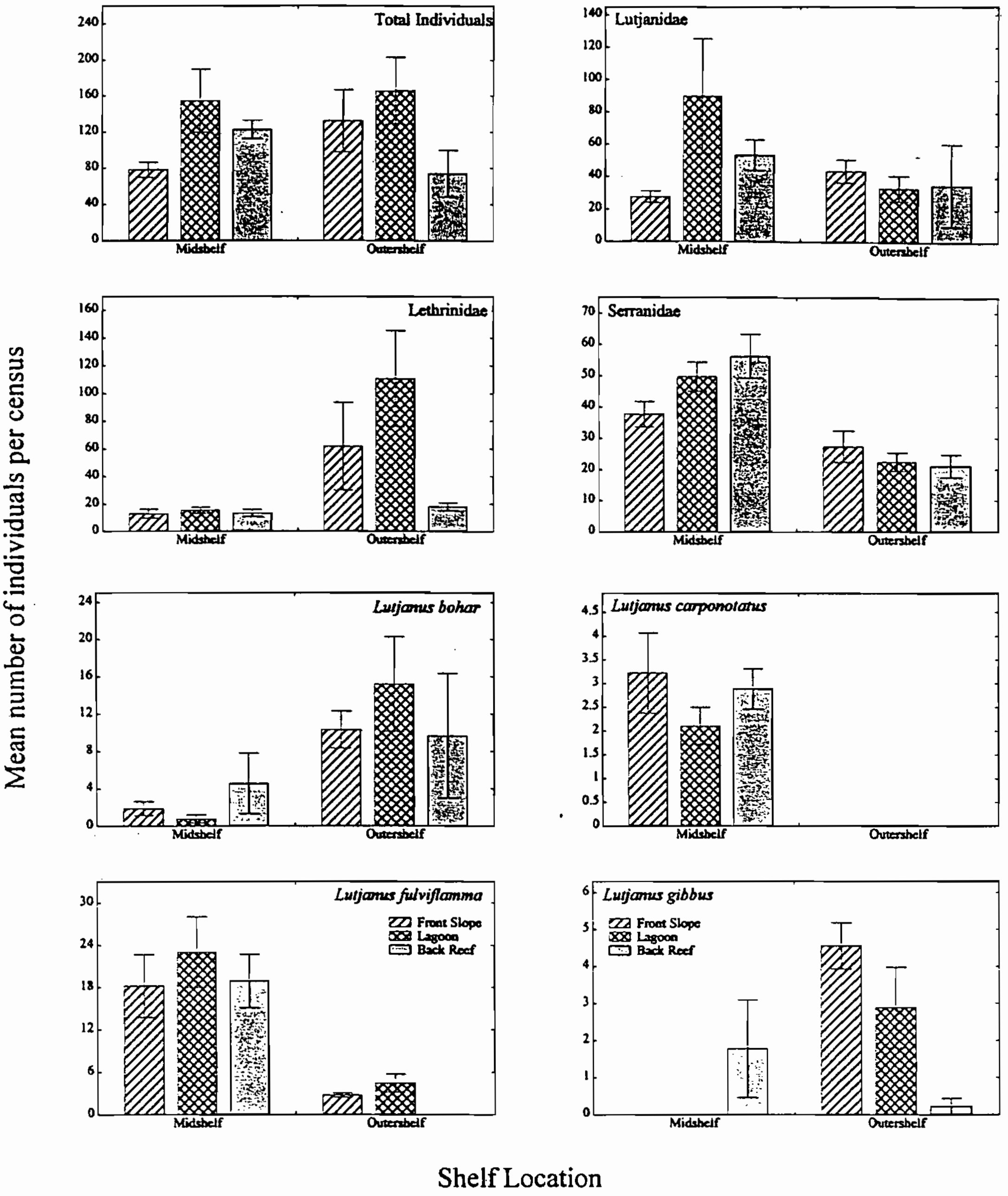


Figure 4.4a : Mean number of individuals per census (+/- standard error) of selected taxa in three zones between continental shelf locations.

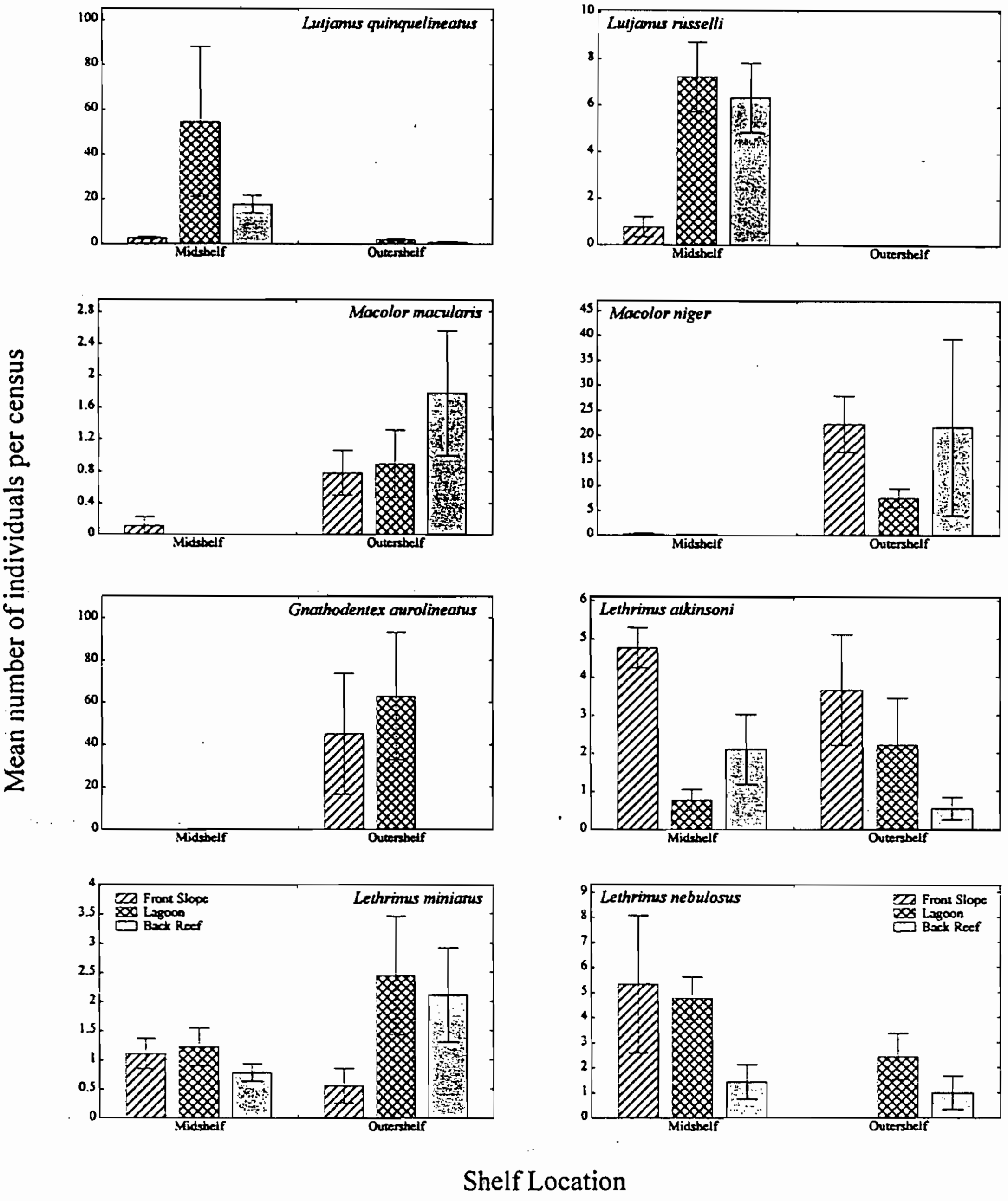


Figure 4.4b : Mean number of individuals per census (+/- standard errors) of selected taxa in three zones between continental shelf locations.

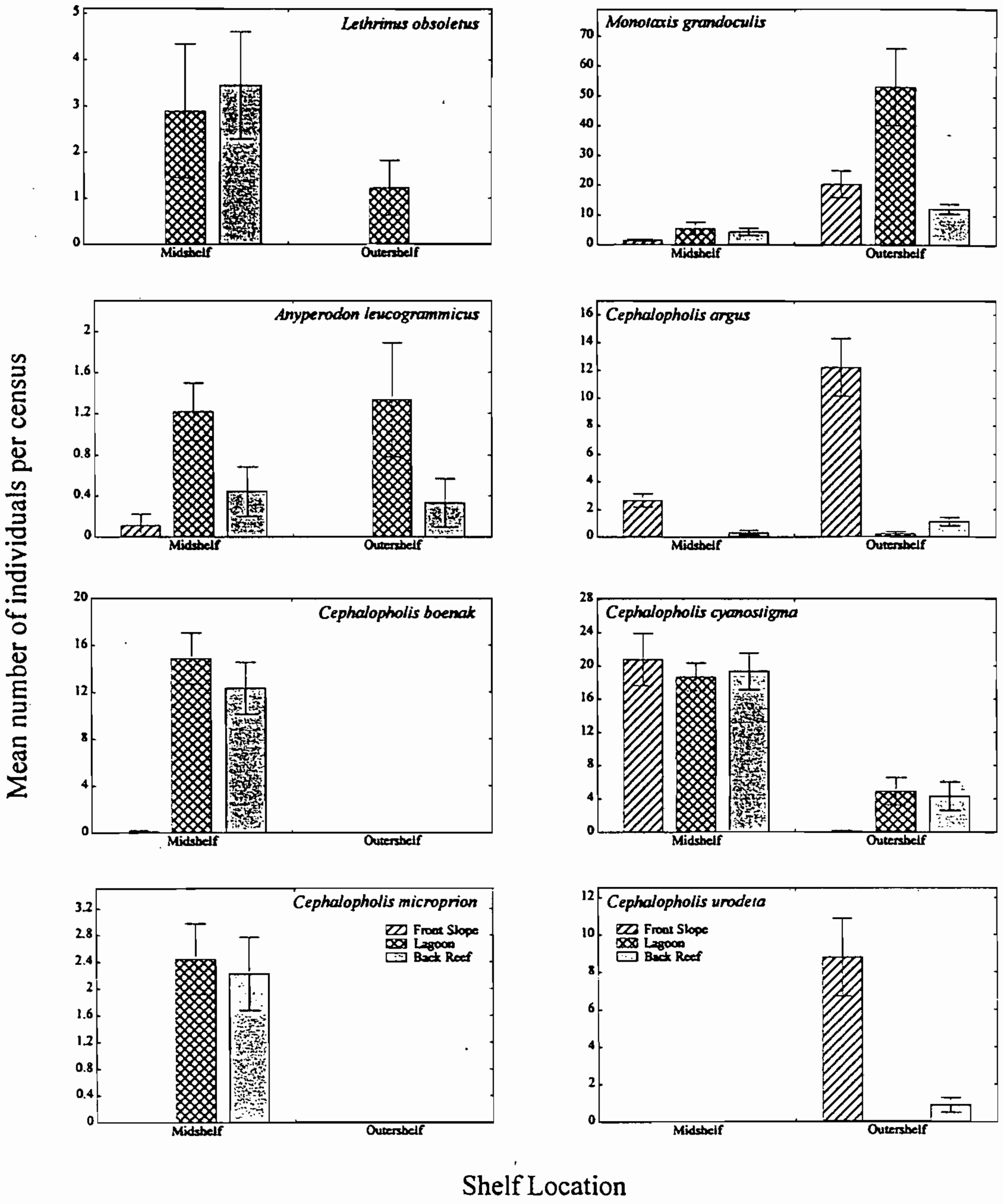


Figure 4.4c : Mean number of individuals per census (+/- standard errors) of selected taxa in three zones between continental shelf locations.

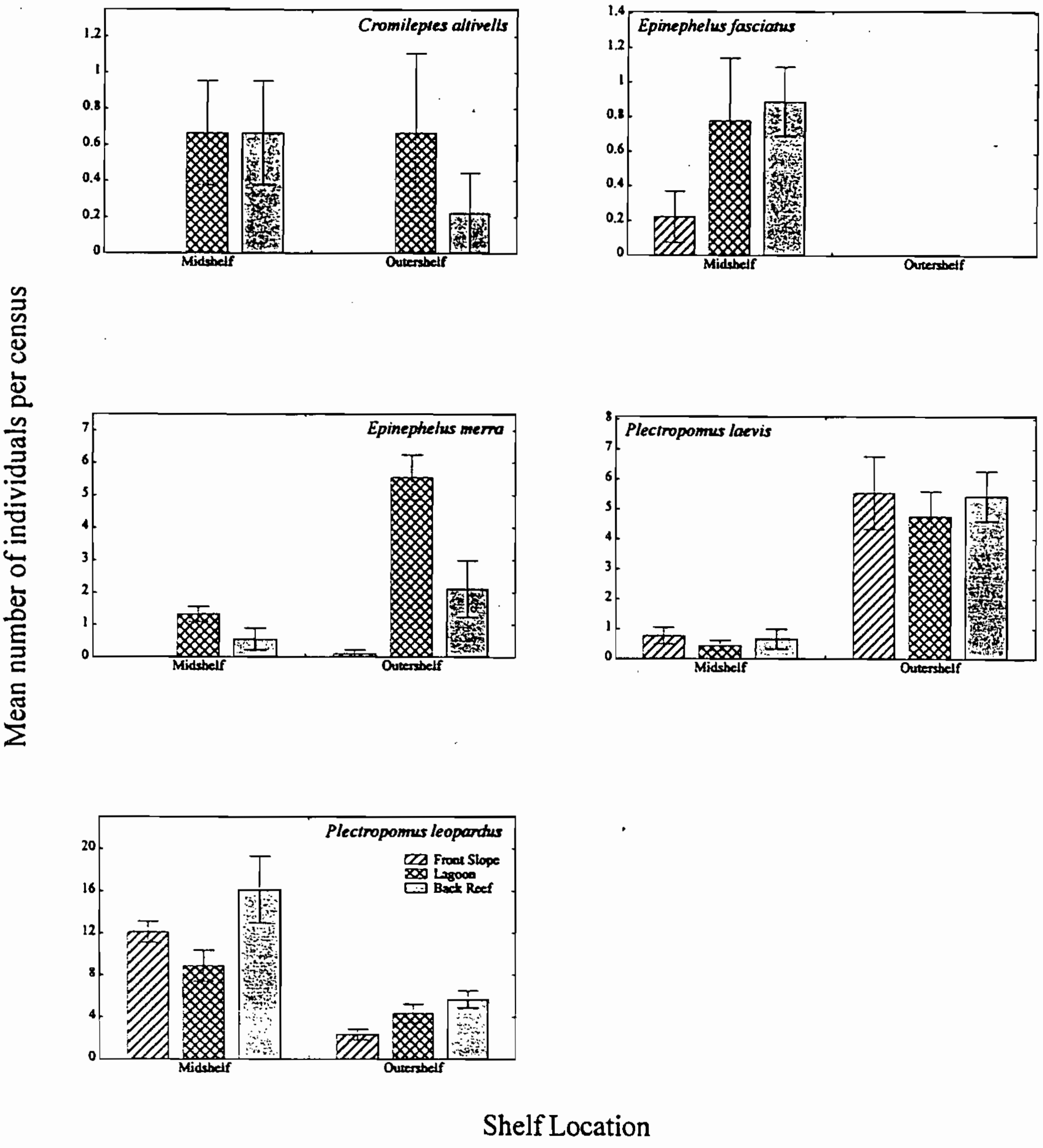


Figure 4.4d : Mean number of individuals per census (+/- standard error) of selected taxa in three zones between continental shelf locations.

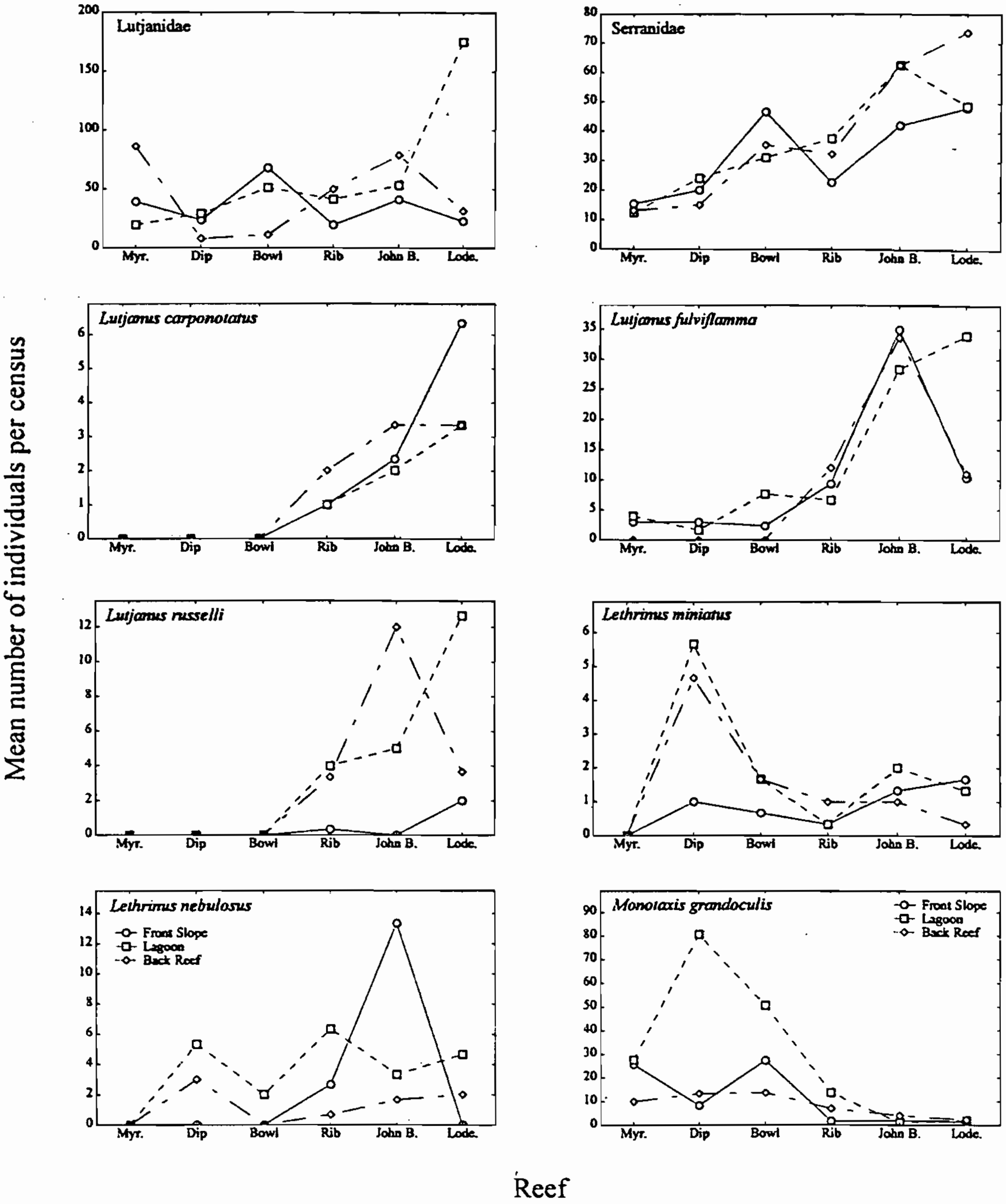


Figure 4.5a : Mean number of individuals per census within each zone at each reef.

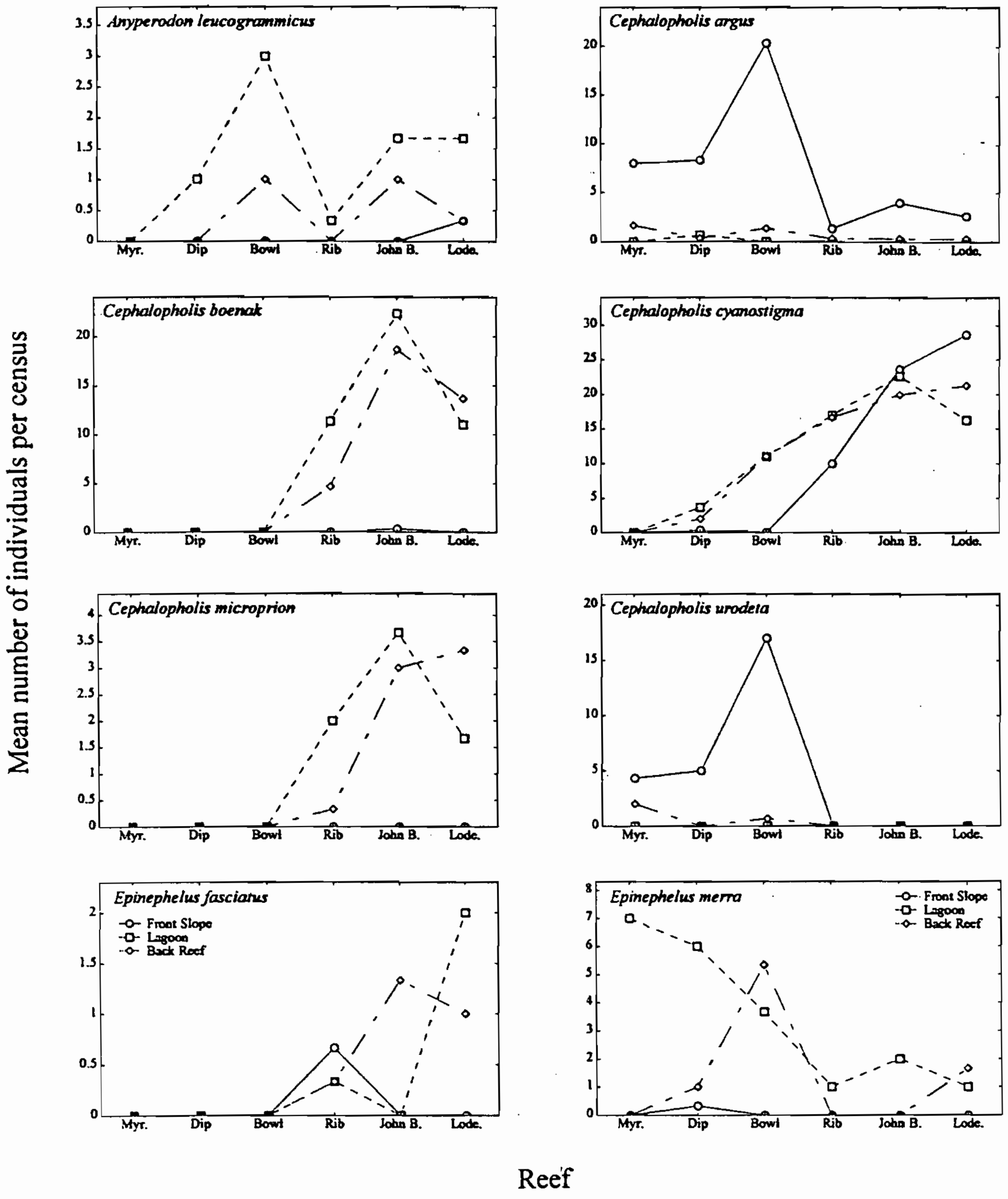


Figure 4.5b : Mean number of individuals per census within each zone at each reef.

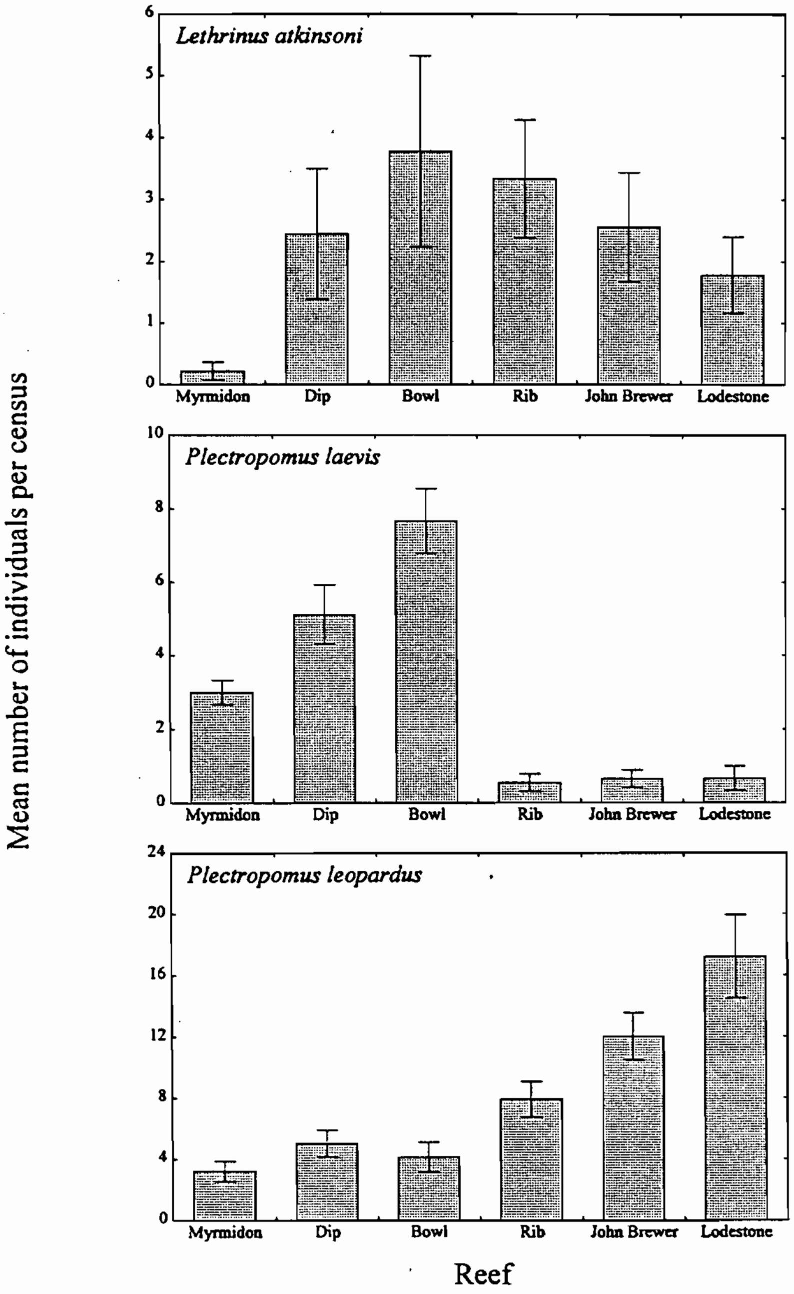


Figure 4.6 : Mean number of individuals per census (+/- standard error) of selected taxa among reefs.

Chapter 5

Spatial and temporal patterns in the distribution and abundance of the Lutjanidae (snappers) and Lethrinidae (emperors) among midshelf reefs of the central Great Barrier Reef.

5.1 INTRODUCTION

The Lutjanidae and Lethrinidae are widely distributed in the Indo-Pacific region (Allen and Talbot, 1985; Allen, 1985; Carpenter and Allen, 1989) and are conspicuous inhabitants of the approximately 2,900 individual coral reefs of the Great Barrier Reef off northeastern Australia. Species of these families contribute significantly to the commercial and recreational fishing catch on the Great Barrier Reef (Hundloe, 1985; McPherson *et. al.*, 1988; Williams and Russ; 1994). Despite the commercial and recreational value of the species of Lutjanidae and Lethrinidae, their patterns of distribution and abundance have received little attention.

Previous studies of patterns of distribution and abundance of coral reef fish within the central Great Barrier Reef have been conducted along a cross shelf environmental gradient and have concentrated on the more site attached and less mobile taxa of coral reef fishes (Williams, 1982; Williams and Hatcher, 1983; Russ, 1984a; 1984b). These studies have primarily used visual census techniques to assess the fish communities of coral reefs (Williams, 1982; Russ, 1984a; 1984b). Significant differences were found in the abundance of species on reefs kilometres and tens of kilometres apart at similar locations (eg. differences between replicate inshore reefs or between replicate midshelf reefs). For some of the species censused in these studies, the differences between reefs at similar locations have been maintained over a period of 15 years (Williams, 1986; unpublished observations). Russ (1984a, 1984b) compared the distributions of herbivorous fishes (Scaridae, Acanthuridae and Siganidae) across the central Great Barrier Reef and found significant differences in abundance and species richness at the family level among reefs at the same cross shelf location. Temporal and spatial variability in the distribution and abundance of the Lutjanidae and Lethrinidae among reefs at similar locations are unknown. Similarly, the fish communities of the deepwater areas (below diveable depths) of reefs and hence the vertical zonation of fishes within reefs in the Great Barrier Reef have been previously either poorly studied or not studied at all. Edwards and Rosewell (1981) described differing degrees of vertical zonation (0-20m) of coral reef fishes in the Sudanese Red Sea and Newman (1990) found that vertical zonation had a significant effect on the structure of coral reef fish communities over depths of 2 - 20 metres.

Fish traps have recently been employed successfully to sample fishes in a variety of depths over a number of structurally heterogeneous environments from estuaries to rocky and coral reefs within Australia (Davies, 1989; Newman, 1990; Sheaves, 1990; Whitelaw *et. al.*, 1991; Sheaves, 1992; Williams *et. al.*, 1992; Newman and Williams, in press) and overseas (Munro, 1974; Stevenson and Stuart-Sharkey, 1980; Dalzell and Aini, 1987; Dalzell and Aini, 1992), and have proved effective at sampling a wide range of lutjanid and lethrinid species (Newman, 1990; Williams *et. al.*, 1992; Newman and Williams, in press).

This study aims to combine the use of two techniques, visual census and fish trapping, to describe the spatial and temporal patterns of distribution and abundance of the Lutjanidae and Lethrinidae among midshelf reefs in the central Great Barrier Reef from both the shallow and deep waters of the back reef zone. Specifically, this study will examine the distribution and abundance of the Lutjanidae and Lethrinidae. Temporal scales to be examined are intra-annual (seasonal) variability and diel variability and the spatial scales to be examined are among reef and between depth (vertical zonation) variability within the back reef zone of reefs.

5.2 MATERIALS and METHODS

Study Sites

This study was conducted on three midshelf reefs on the continental shelf in the central region of the Great Barrier Reef (Figure 5.1) from September, 1992 to July, 1993, with sampling occurring at approximately two month intervals. Different aspects of the coral reef fish communities of these reefs have been examined previously by Williams (1982) and Russ (1984a, 1984b). The midshelf reefs are located approximately 50 to 60 km offshore (see Figure 5.1) and are reported to have the greatest diversity of coral communities in the central Great Barrier Reef (Done, 1982). Descriptions of the gross morphology and environment of these study reefs are provided in Done (1982).

The prevailing winds and waves in the region are from east to south east. The lagoonal back reef habitat (NW aspect) was surveyed to ensure that sampling could be carried out at all times of the year. The areas studied within each reef are shown in Figure 5.2.

The lagoonal back reef habitat surveyed is morphologically complex, consisting of terraces, sand chutes, vertical walls, sloped walls, bommies and rubble accumulations. There is a correspondingly diverse array of communities present, including massive and branching *Porites*, staghorn *Acropora* and *Acropora splendida/divericata* communities, sand and rubble terraces, as well as an array of "non conformist" assemblages (Done, 1982). The bases of bommies and the sandy back reef areas often had large stands of *Acropora* thickets. These *Acropora* thickets correspond to the *Acropora* staghorn coral community described by Done (1982). In a number of areas on the back reef, soft corals are almost as abundant as hard corals, a condition seen also on the deep windward reef slopes (Dinesen, 1983). The areas censused on each of the reefs were as comparable as possible in terms of their physical characteristics.

Sampling Design

The sampling design involved using two techniques (visual census and fish trapping) to examine the back reef habitat of the midshelf reefs from the surface to the base of the back reef slope. The design incorporated temporal and spatial aspects of the distribution and abundance of the Lutjanidae and Lethrinidae.

The visual census sampling design involved determining the variability in composition of the lutjanid and lethrinid communities of the shallow back reef zone

(0 - 10m) among three midshelf reefs through time. The reefs were a minimum distance of 5.6 kilometres (3.1 nautical miles) apart (see Figure 5.1). Six replicate non-overlapping censuses were made in the back reef zone of each reef during each sampling period. The census dives were conducted in a haphazard manner along the back reef zone. Transects were not fixed and no two censuses over any sampling period covered exactly the same census area. This resulted in a total of 108 censuses being carried out approximately bimonthly from September, 1992 to July, 1993 (3 reefs × 6 replicates/reef × 6 sampling times - see Figure 5.3a).

The sampling design for the trap surveys involved determining the variability in composition of the lutjanid and lethrinid communities by incorporating two temporal and two spatial scales in a multi-stage sampling design. The sampling design incorporated replication at all levels of treatment effects. Temporal scales examined were the medium scale, intra-annual (seasonal) patterns and the fine scale, diel patterns. The spatial scales examined were the large scale differences among reefs and the fine scale differences in vertical zonation (depth) within reefs. During each of the 6 sampling periods (time of year), 12 traps were set both day and night in each of two depth zones (shallow : 12-18m, and deep : 30-40m) at each reef (see Figure 5.3b). Traps were deployed haphazardly in each depth zone to ensure independence of the data and to avoid systematic error.

Sampling Methods

The lutjanid and lethrinid fish assemblages were identified to species according to Allen and Talbot (1985), Allen (1985) and Carpenter and Allen (1989) and were surveyed using two techniques. The shallow back reef zone (0-10m) was surveyed using a 45 minute rapid visual census technique (see Chapter 2). The distance covered by a census dive was approximately 400m in any reef zone, so that the total area censused was approximately 4,000m^2 (400m × 10m). The deep back reef zone (12-40m) was surveyed using fish traps (see Chapter 2). Twelve traps were set in each of two depths (the edge of the back reef in approx. 12-18m, and at the base of the back reef slope in approx. 30-40m) both day and night at each reef during each of the six sampling periods.

Analysis of Data

The data from all 108 visual censuses of the 16 most abundant species from all reefs and times were subjected to an agglomerative, hierarchical classification (Williams, 1971). The rationale for analysing only the most abundant species is that variation in the abundance of the most common taxa should more clearly reflect differences among temporal and spatial variables than that of rare or occasionally encountered species. A dendrogram and similarity matrix were generated using euclidean distance as a similarity index and Ward's incremental sum of squares sorting strategy. Minimum variance clustering of this type has a great advantage in providing descriptive classifications (Pielou, 1984). In the analysis, all counts of abundance were standardised first (transformed to a double square root - $\sqrt{\sqrt{x}}$) so that observations were scale independent and for improvement of normality and homogeneity (see Field *et. al.*, 1982). Each division of the dendrogram was determined by the test of Sandland and Young (1979a; 1979b). The Cramer value *C*, was used to rank species according to their abilities to distinguish between all groups derived from the classification analysis (Lance and Williams, 1977; Abel *et. al.*, 1985).

Data from both visual censuses and traps were analysed by parametric analysis of variance (ANOVA). Two factor ANOVA's were carried out on the abundance data collected by visual censuses for each family and the 16 most abundant species censused. The two factors in the analysis were sampling time (time of year) and reefs on the midshelf (Rib, John Brewer, Lodestone). Time of year and reefs were treated as fixed and orthogonal factors in the analysis (Underwood, 1981). There are six replicate censuses within each combination of the two factors. Homogeneity of variance for all analyses (at a significance level $\alpha = 0.05$) was determined using Cochran's test (Winer, 1971). The variances of the raw data of some variables were heterogeneous and the frequency distributions of the data positively skewed. Transformations to $\log_e (x + 0.5)$ removed this heterogeneity and satisfied Cochran's test (Winer, 1971; Underwood, 1981). Multiple comparison of means (with $\alpha = 0.05$) were conducted using Tukey's honestly significant difference method (HSD) in preference to the much used Student Newman-Keuls procedure because HSD is a more conservative test (Winer, 1971; Day and Quinn, 1985). Patterns of abundance of families and the 16 most abundant species at each sampling time and reef are presented graphically. The abundance is expressed as the mean number of individuals (of six replicate censuses) per time and reef.

The data from all 864 trap hauls for the 12 most abundant species from all reefs and times were subjected to an agglomerative hierarchical classification also (see above). Four factor ANOVA's were carried out on the abundance data for all individuals caught in traps, for each family (Lutjanidae, Lethrinidae) trapped and for the 12 most abundant species trapped. The four factors in the analysis were sampling time (time of year = 6), reef (Rib, John Brewer, Lodestone), diel sampling time (day, night) and depth (shallow and deep). All factors were fixed and orthogonal in the analysis (Underwood, 1981).

Homogeneity of variance for all analyses ($\alpha = 0.05$) was determined using Cochran's test (Winer, 1971). Gross heterogeneity of variances were evident in the variances of the raw data with the means and variances being correlated significantly. Examination of the raw data revealed that the catch rates of many species in traps were characterised by a number of extremely high catches and numerous zero catches, thus the cell variances tended to be functions of the cell means (the larger the mean the larger the variance). This heterogeneity was a consistent feature of the trapping data and not an error of observation. To alleviate this problem the 12 replicate traps were pooled randomly into two "strings" of six traps each. This limited the replicates per cell in the ANOVA to 2 (see Figure 5.3b). Some cell variances were still heterogeneous and the within cell distribution Poisson-like in form. Pooled data were then transformed to a $\sqrt{x} + \sqrt{(x + 1)}$ function to remove the variance heterogeneity (as well as the significant mean - variance correlation) and to make treatment effects additive (Winer, 1971; Underwood, 1981). Cochran's tests were satisfied at $\alpha = 0.01$. Since the known effect of this level of heterogeneity is to slightly increase the chance of a Type I error (Snedecor and Cochran, 1989), the analyses of variance were conducted with the more conservative significance level of $\alpha = 0.01$. Multiple comparison of means ($\alpha = 0.01$) were carried out using Tukey's HSD method (Winer, 1971; Day and Quinn, 1989). Patterns of abundance in the trap catch of all individuals, families and the 12 most abundant species at each sampling time and reef are presented graphically. The abundance is expressed as the mean number of individuals (catch per trap) per sampling time and reef.

The relative abundance of all the species of the Lutjanidae and Lethrinidae recorded in each of two zones (shallow back reef vs deep back reef) were categorised by a subjective graded estimate of their relative abundance. The total number of individuals, families and species for each reef was also categorised by the number per $1000m^2$ (from visual censuses) and the catch rate of traps per diel sampling period.

5.3 RESULTS

Visual Censuses (shallow water assemblages)

The classification analysis of the visual censuses defined three distinct clusters corresponding to each of the three reefs. The first split separated Rib from John Brewer and Lodestone, the second split censuses at the latter two reefs (Figure 5.4). Rib was distinguished from the other two reefs by the relatively high abundance of 2 lethrinids, *Lethrinus lentjan* and *L. obsoletus*, and the relatively low abundance of 6 lutjanids, *Lutjanus carponotatus*, *L. fulviflamma*, *L. fulvus*, *L. monostigma*, *L. russelli* and *L. quinquelineatus*. Lodestone was distinguished from John Brewer by the relatively high abundance of *L. quinquelineatus* and the relatively low abundance of 3 lethrinids, *Lethrinus atkinsoni*, *L. lentjan* and *L. nebulosus*, and 3 lutjanids, *Lutjanus bohar*, *L. fulviflamma* and *L. gibbus* (see Tables 5.1a and 5.1b).

Results of the two factor analyses of variance of the visual census counts of selected taxa are summarised in Table 5.2, and the results of the *a posteriori* Tukey (HSD) multiple comparison of means from these analyses of variance are summarised in Table 5.3.

While mean numbers of most species exhibited fluctuations in visual counts over the duration of this study (Figures 5.5a-c), this variation was statistically significant for only 1 of 18 taxa, *Lethrinus obsoletus* (Table 5.2b and see Figure 5.5c). The visual counts of *L. obsoletus* were significantly higher in July than in September, February and May, but were not significantly different between June, May, February, September and November (Table 5.3). There were no significant time × reef interactions in the analyses.

Significant differences in visual counts among reefs were found for 14 of the 18 taxa examined (Table 5.2), but there were no significant differences among reefs in the visual counts of *Lutjanus monostigma*, *Lethrinus nebulosus*, *Plectropomus leopardus* and the total count of lethrinids (Table 5.2). As anticipated in the interpretation of the classification analyses above, lutjanid taxa tended to be relatively more abundant at John Brewer and less abundant at Rib (Table 5.3). In contrast, lethrinid species tended to be relatively abundant at Rib Reef (Tables 5.2 and 5.3).

Among reef differences accounted for a high proportion of the variability in abundance of species of the Lutjanidae and Lethrinidae from visual census counts, and a large proportion of this variability was attributable to a low abundance of a given species at a given reef (Table 5.1a).

Fish Traps (deeper water assemblages)

The classification of the trap hauls resulted in five distinct clusters (Figure 5.6). The major split separates ninety seven percent of the night catches from the day catches. The cluster containing the night catches split into a group containing predominantly deep (30-40m) set traps, and another containing predominantly shallow (12-18m) set traps (Figure 5.6).

The cluster containing day catches split into one group containing predominantly shallow traps, and another group containing a combination of deep and shallow traps (Figure 5.6). This latter cluster split further into one group containing predominantly deep set traps, and another group containing similar proportions of deep and shallow traps (see Figure 5.6).

The Cramer values suggest that these groupings were distinguished by relatively high mean catch rates and frequency of occurrence data (Table 5.4) of the following taxa :

Night sets : all *Lutjanus* species.

Day sets : *Gymnocranius audleyi*, *Lethrinus species* 2, *Plectropomus leopardus* and *Abalistes stellaris*.

Night/Deep sets : *Lutjanus adetii*, *L. russelli*, *L. sebae* and *L. vitta*.

Night/Shallow sets : *Lutjanus fulviflamma* and *Lethrinus miniatus*.

Day/Deep sets : *Lethrinus species 2* and *Abalistes stellaris*.

Day/Shallow/Deep sets : *Plectropomus leopardus*.

Day/Shallow sets : *Lutjanus carponotatus* and *Lethrinus miniatus*.

Results of the 4-factor analyses of variance of trap catch per unit effort data of selected taxa are summarised in Table 5.5 and the results of the *a posteriori* Tukey (HSD) multiple comparison of means tests from these analyses of variance are summarised in Table 5.6.

Amongst the analyses of the total number of individuals and the 14 separate taxa analysed, differences in abundance were observed mainly between diel sampling periods and the depth zones examined (Table 5.5). There were more significant differences at the small spatial scale of vertical (depth) zonation (13 of the 15 analyses) than at the larger spatial scale of reefs (4 out of 15). Similarly, there were more significant differences at the finer temporal scale of diel period (13 out of 15) than at the larger temporal scale of time of year (1 out of 15). Diel differences and depth differences accounted for a high proportion of the variability in abundance of the selected taxa examined. A large proportion of this variability was attributable to the absence or low abundance of a given species in a particular depth zone or diel sampling period (see Table 5.4a and Figures 5.7 and 5.8), and this was the causative factor in the significant interaction effects among the temporal and spatial factors examined (Table 5.5 and see Figure 5.9).

Fine scale temporal variation among diel periods was significant for 13 of 15 taxa examined (Table 5.5 and see Figure 5.7). The catch rate of the total number of individuals trapped, *Lutjanus quinquelineatus* and *L. sebae* were significantly higher in night set traps at both depths (Table 5.6 and Figure 5.7). Fine scale spatial variation among vertical (depth) zones was significant for 13 of 15 taxa examined (Table 5.5 and see Figure 5.8). The catch rate of the total number of individuals trapped, *Lutjanus sebae* and *Gymnocranius audleyi* were significantly higher in the deep set traps, while the catch rate of *L. miniatus* was significantly higher in shallow set traps (Table 5.6 and Figure 5.8). Significant diel × depth interactions occurred for 8 of the 15 taxa examined (Table 5.6). The catch rate of the total number of lutjanids, *Lutjanus adetii*, *L. russelli* and *L. vitta* were significantly higher in the deep night set traps, while the catch rate of *L. fulviflamma* was significantly higher in shallow night set traps (Table 5.6 and Figure 5.9). Conversely, the catch rate of total lethrinids, *Lethrinus species* 2 and *Abalistes stellaris* were significantly higher in the deep day set traps (Table 5.6 and Figure 5.9). These interaction terms resulted from the low abundance or absence of species in some combinations of diel sampling period and depth (see Figure 5.9).

Large scale spatial variation among reefs was significant in 4 of 15 analyses (Table 5.5). The catch rate of *Gymnocranius audleyi* was significantly lower at Rib Reef than John Brewer and Lodestone reefs (Table 5.6). Significant diel × reef interactions occurred in the catch rates of *L. fulviflamma*, *L. miniatus* and *P. leopardus* (Table 5.6). The catch rate of *L. fulviflamma* in night set traps at Rib Reef was significantly higher than elsewhere, while the catch rate of *L. miniatus* in night set traps at Rib and Lodestone reefs was significantly higher than the day set traps at these reefs (Table 5.6). Additionally, the catch rate of *P. leopardus* was significantly higher in the day set traps at Rib and John Brewer reefs than elsewhere (Table 5.6). Furthermore, a significant reef × depth interaction occurred in the catch rate of *L. carponotatus* (Table 5.5), with the catch rate of shallow set traps significantly higher at Rib Reef than elsewhere (Table 5.6 and see Table 5.7). Differences in the catch rates of traps per diel period among reefs and visual census counts of species per 1000m^2 among reefs are shown in Table 5.7.

Medium scale temporal variation in the time of year sampled (intra-annual (seasonal) variation) was significant in only 1 of 15 analyses (Table 5.5). Most species exhibited fluctuations in catch rates per trap over the duration of this study but these were not statistically significant (see Figures 5.10a-c). The abundance of only *Gymnocranius audleyi* was significantly different among seasonal sampling periods (Table 5.5 and see Figure 5.10c). The abundance of this species was significantly higher in July than in September and February (Table 5.6).

While there were no significant differences in the abundance of *P. leopardus* between depths, the mean fork length of *P. leopardus* was significantly larger in the deeper waters (ANOVA : 1,85 d.f.; $F = 10.41$; $p < 0.01$; see Figure 5.11). Mean fork length of *P. leopardus* in the shallower waters was 416.73mm, while the mean fork length of *P. leopardus* in the deeper waters was 476.82mm.

The relative abundance of species of the Lutjanidae and Lethrinidae recorded over the duration of this study in each of two depth zones are described in Table 5.8. Within the shallow back reef zone *Lutjanus biguttatus*, *Symphorus nematophorus*, *Lethrinus erythracanthus*, *L. olivaceus*, *L. species* 2 and *L. xanthochilus* were seen rarely, while a further 7 species that were trapped in deeper waters were not observed in visual censuses (see Table 5.8). Additionally, *Lutjanus lemniscatus*, *L. lutjanus*, *L. malabaricus*, *Lethrinus genivittatus*, *L. obsoletus*, *L. olivaceus* and *L. rubrioperculatus* were rare in trap catches from the deep (30-40m) back reef zone, and 10 species recorded from visual censuses were not recorded in the fish trap catches (Table 5.8).

5.4 DISCUSSION

Significant intra-annual (seasonal) variability was detected for only two lethrinid species, *Lethrinus obsoletus* and *Gymnocranius audleyi* (Tables 5.2b and 5.5). Peaks in abundance of these two species occurred during the July sampling period (Figures 5.5c and 5.10c). During this period a number of lethrinid species were captured in the running ripe phase of reproductive development (personal observations). This suggested that these localised peaks in abundance may have resulted from aggregations related to spawning activity. The majority of the species examined exhibited temporal fluctuations in local abundances from both visual census counts and catches per trap over the duration of this study (see Figures 5.5a-c and 5.10a-c). The abundance of smaller species of fishes of coral reefs has similarly been shown to vary unpredictably in time (Sale and Douglas, 1984; Sale and Steel, 1989). The factors determining seasonal variations in the abundances of large mobile reef fishes such as the Lutjanidae and Lethrinidae are little known and may be linked with movements associated with spawning aggregations and ontogenetic movements (eg. among depth zones). However, as species of the Lutjanidae and Lethrinidae are sufficiently mobile to exploit local abundances of food, this appears to be a major proximal factor in explaining the intra-annual fluctuations in abundance of local populations (see also Talbot, 1960). Additionally, predation can potentially affect the local diversity of the smaller species of the Lutjanidae and Lethrinidae by altering their abundances (Hixon, 1986; 1991). The lack of significant seasonal variation in the majority of species in both the shallow and deeper water assemblages suggests that the high sampling variability in both the visual census counts and trap catch per unit effort is natural in species of highly mobile reef fishes. This is supported by the covariation in visual census counts and trap catch per unit effort which exhibit similar peaks in abundance. Additionally their is covariation among reefs (in particular John Brewer and Lodestone) in seasonal patterns.

The structure of the shallow water assemblages of the Lutjanidae and Lethrinidae observed by visual censuses varied significantly among reefs (Table 5.2a, 5.2b, 5.3) with significant among reef differences detected in 14 of the 18 taxa examined. Rib Reef was found to have significantly lower abundances of lutjanids in general and certain species of lutjanid, and significantly higher abundances of some lethrinid species than the other midshelf reefs. Rib Reef is a relatively small reef compared to both John Brewer and Lodestone reefs and is less well developed morphologically. The shallow back reef at Rib Reef is not as structurally complex as that of the other midshelf reefs and therefore the diversity of available habitats is much reduced with more large expanses of sand and rubble. Further, John Brewer Reef was different to Lodestone Reef. John Brewer is the most structurally complex reef of the midshelf reefs surveyed with numerous caves, ledges and sloped terraces. John Brewer has the greatest diversity of habitats in the shallow back reef zone and also a greater number of lutjanids.

In contrast to the visual census counts, trap catch per unit effort was significantly higher for *Lutjanus carponotatus* at Rib Reef in the 12-18m zone and for *L. fulviflamma* at Rib Reef at night, and significantly lower at Rib Reef for the lethrinid, *G. audleyi.* This shallow zone is punctuated by isolated bommies and patch reefs. Significant differences in trap catch per unit effort of the serranid *P. leopardus* were found among reefs, but no significant differences were found among reefs from the visual census counts. It is hypothesised that reef structure and habitat complexity are strongly correlated with lutjanid abundance. This hypothesis is supported by the experimental manipulation of artificial reefs by Hixon and Beets (1989), who found a significant correlation between the number of large fishes inhabiting reefs and the number of large holes present in the reef.

The greatest opportunity for movement and dispersal among reefs is during the larval phase (Williams *et. al.*, 1984). The distribution and availability of reef fish larvae may be critical in determining the distribution and abundance of species among reefs (Williams, 1991), as it has been shown that local assemblages of coral reef fishes are likely to be recruitment limited (reviews by Doherty and Williams, 1988; Doherty, 1991; also see Doherty and Fowler, 1994). Additionally, temporal variability in recruitment patterns has also been shown to vary among reefs at similar locations (Fowler *et. al.*, 1992). This variability may explain how differences in the abundance of species among reefs at similar locations are maintained. Further, Eckert (1984) found that large differences in the recruitment of species among reefs was reflected in the distribution and abundance of adults.

Factors such as hydrology (Leis, 1982; 1986), shelf location and reef geomorphology (Williams, 1982; Williams and Hatcher, 1983; Russ, 1984a & 1984b) and percentage cover of live coral (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984) have also been postulated as possible determinants to explain among reef differences. Additionally, spatial variation in the rates of settlement and recruitment of coral reef fishes are important also in determining the patterns of spatial variability of adults among reefs (Williams and Sale, 1981; Williams, 1983; Doherty and Williams, 1988; Fowler *et. al.*, 1992).

The deeper water assemblages of the Lutjanidae and Lethrinidae varied significantly in catch rates between diel periods (nocturnal/diurnal) and depth zones (Tables 5.5 and 5.6). Diel variability in trap catches is consistent with what is known of the feeding behaviour of the taxa examined. Distinct nocturnal and diurnal assemblages of the Lutjanidae and Lethrinidae were found in the present study (Table 5.6). The nocturnal catches of the total lutjanids and all lutjanid species (except *L. carponotatus*) were significantly higher than the diurnal catches (Figure 5.7). A common behaviour pattern in the Lutjanidae is the formation of large aggregations and schools in the vicinity of some form of bottom structure during the day with active foraging over surrounding areas at night (eg. Randall and Brock, 1960; Hobson, 1965; Starck and Davis, 1966; Hobson, 1968; 1974; Randall, 1967; Starck, 1971; Parrish, 1987). Opportunistic foraging has also been reported close to shelter during the day (eg. Ormond, 1980). Starck and Davis (1966) and Hobson (1968) have suggested that lutjanid species that prey on fish may be more active diurnally, while those species that prey more heavily on benthic invertebrates may be more active at night. The almost equally abundant catches of *L. carponotatus* both diurnally and nocturnally (Table 5.4a and Figure 5.7) suggest that fish may be an important prey item for this species.

In contrast, the catch of total lethrinids, *Lethrinus species* 2, *Abalistes stellaris* and *Plectropomus leopardus* were significantly higher by day. There have been no specific studies on the timing of feeding in the Lethrinidae, although species specific patterns are present (Table 5.4a and Figure 5.7; see also Carpenter and Allen, 1989). In general, from this study the Lethrinidae appear to forage actively on a diurnal basis and are also opportunistic predators nocturnally (see Figure 5.7). Studies of fish trap catches off the North West Shelf of Australia have shown that lethrinids dominate diurnal catches (Anon., 1990; Whitelaw *et. al.*, 1991). The presence of strong diurnal foraging patterns in the Lethrinidae may explain the relative dominance of lethrinids in both the catch of traps set off the North West Shelf of Australia and in the day set traps in this study.

Similarly, the significantly higher diurnal catch of the serranid *P. leopardus* in this study reflects the observations of Goeden (1978), Choat (1968) and Samoilys (1986), who found that *P. leopardus* feeds throughout the day and is inactive at night. Additionally, Ormond (1980) found similar daytime activity patterns in the congeneric species, *P. maculatus*. Groupers (Serranidae) are, in general, diurnal predators and exhibit peaks in activity associated with the crepuscular periods of dawn and dusk (Starck and Davis, 1966; Ormond, 1980; Parrish, 1987). The significantly higher diurnal catch of the balistid, *Abalistes stellaris* presumably reflects a similar diurnally active foraging habit, although little is known of the biology of this species.

The high correlation of means and variances of the raw data in the trap catches was indicative of a highly clumped pattern of distribution and can best be explained by the presence of schooling and aggregating behaviour in the target species (eg. Randall and Brock, 1960; Hobson, 1968; Starck and Davis, 1966; Randall, 1967; Potts, 1970). The traps catches were generally very high or very low. The location of traps relative to bottom irregularities such as ledges and bommies has also been shown to be critical in determining the nature and magnitude of trap catches (Sylvester and Dammann, 1972). The location of a trap in relation to bottom structure is an important factor in determining the number of species and individuals caught within traps. Further, fish traps are point sampling units and sample a much reduced area compared to the visual censuses. The different results between the two techniques may be related to both the area sampled by each technique and the habitat complexity of the census area of each technique.

The depth of set of traps on the back reef caused significant variation in the abundance of a number of species. The deep water assemblages at the base of the back reef slope at 30-40m depth was dominated by greater abundances of both lutjanids and lethrinids and by the following species : *Lutjanus adetii*, *L. russelli*, *L. sebae*, *L. vitta*, *Lethrinus species 2*, *Gymnocranius audleyi* and *Abalistes stellaris*. These species were usually not seen or were encountered rarely in the visual censuses. *Lutjanus carponotatus*, *L. fulviflamma* and *Lethrinus miniatus* were dominant in the shallower 12-18m depths of the back reef slope that were trapped and were regularly seen in visual censuses. Both lutjanids and lethrinids are primarily demersal species that are associated strongly with hard substrata or substrata having some type of vertical relief and both groups feed primarily in deep waters (Parrish, 1987). The distribution of these species may therefore be correlated strongly with structure and shelter (aggregation sites) and not prey species, since most lutjanids and lethrinids can utilise a broad array of prey items (Parrish, 1987; Birdsey, 1988). Depth preferences may coincide with the selection of large shelter sites and structure and this may be a major determining factor in the depth distribution of lutjanids and lethrinids (see Hixon and Beets, 1989).

Habitat selection, at the time of settlement or soon after, has been demonstrated by Williams (1980), Williams and Sale (1981), and Eckert (1985), and it has been discussed as a possible determinant of zonation of coral reef fishes by Russ (1984b) and Galzin (1987a). Habitat selection, independent of interactions with resident fish assemblages, appears to be a major process determining the depth distribution of many of the small fishes of coral reefs (Williams, 1980; Eckert, 1985). Additionally, evidence of enhanced development of sensory systems in reef fishes prior to settlement (eg. McCormick, 1993) suggests that habitat selection may play an important role in structuring reef fish assemblages. Habitat selection may also cause differences among zones within reefs.

The depth preference of species such as *L. adetii* suggest that they also recruit in the deeper waters, possibly into the same habitat as adults. Juveniles of *L. quinquelineatus* have been observed to recruit into the same habitat as adult conspecifics, with a preferred depth of recruitment in excess of 10m (personal observation). Additionally, juveniles of *L. fulviflamma* (approx. 25mm FL) have been captured from a depth of 40m on featureless bottom (Newman, unpublished data). The movements of species among zones has not been described and none have been observed in tagging studies (Newman, unpublished data). Hobson (1968; 1974) observed ontogenetic movements of fish related to depth, with the larger fish found in deeper water. This also occurs in some lutjanid and lethrinid species (see Williams and Russ, 1994), although it has not been observed in the species examined over the duration of this study. Some observations and empirical data for some species (eg.

Lutjanus fulviflamma) suggest the opposite view of the Hobson hypothesis, that is, that recruitment is occurring in deep water and the adults are moving onto the reef into shallow water as adults.

Predation is considered to contribute substantially to community regulation (Hixon and Beets, 1993). The extent to which the assemblages of larger, mobile reef fishes of the families Lutjanidae and Lethrinidae are affected by predation remains to be investigated. It seems plausible that species of these families with individuals of small average size may be regulated through predation by larger congeneric species and predators such as elasmobranches and serranids. The role of predation as a major factor contributing to the regulation of species who themselves exhibit major predation pressures on benthic fishes and invertebrates is paradoxical. The validity of these predation hypotheses remains to be examined and will require multifactorial field experimentation. Additionally, it has been suggested by Parrish (1987) that major reductions in populations of lutjanids (due to fishing pressure) will reduce predation pressure and feeding competition and possibly enhance the populations of other demersal carnivores, including lutjanids and serranids. Russ (1991) found no evidence of this in the literature. Furthermore, localised depletions of populations of lutjanids and lethrinids may initially lead to recruitment enhancement in these areas due to less predation. Conversely, if recruitment overfishing occurs there will be a flow on effect in terms of decreased recruitment to local reefs as there will be a reduction in the availability of larvae to the total available pool of larvae.

The activity patterns, preferred depth strata and behaviour of species contribute to the spatial and temporal organisation of the lutjanid and lethrinid assemblages on coral reefs. The detection of long term temporal changes in assemblages such as those induced by catastrophic events like cyclones, by anthropogenic influences such as fishing or simply by natural variations in species composition and abundance will require long term monitoring. The usage of a combination of techniques to assess both the shallow water and the deeper water communities may be an objective way of repeatedly censusing reefs for monitoring purposes.

The visual census method herein described is easily adaptable across a wide range of structurally complex coral reef systems and is proficient in providing replicate censuses of species of the Lutjanidae and Lethrinidae and in documenting the relative abundance of the more cryptic and rare species (Table 5.8). Because such a large area is covered by a number of replicate censuses and a broad range of habitats can be surveyed this visual census methodology has provided a means of comparing the relative abundances of species among reefs that is consistent through time. This methodology will be a useful monitoring tool, especially where differences among reefs are important.

Table 5.1a : Mean number (per census) of selected taxa in the three groups derived from the classification analysis, ranked by their ability to distinguish among the initial groups (Rib versus John Brewer and Lodestone; *C* = Cramer values; *n* = total number of samples per group; -- = absent).

Species	*C*	Classification Group		
		Rib (*n* = 36)	John Brewer (*n* = 36)	Lodestone (*n* = 36)
Lutjanus gibbus	0.978	--	4.28	0.50
Lethrinus lentjan	0.975	3.67	0.69	0.17
Lethrinus nebulosus	0.975	3.25	27.39	4.6
Lutjanus quinquelineatus	0.971	3.47	16.92	29.64
Lutjanus monostigma	0.947	0.22	2.08	0.89
Lutjanus bohar	0.942	2.53	5.19	0.67
Lutjanus russelli	0.933	2.00	8.39	5.56
Lethrinus miniatus	0.918	0.5	1.42	1.97
Lutjanus fulvus	0.911	0.08	0.69	0.44
Lethrinus atkinsoni	0.907	1.50	3.58	0.56
Lutjanus fulviflamma	0.876	3.47	31.17	16.53
Lutjanus carponotatus	0.873	3.25	8.91	6.39
Plectropomus leopardus	0.814	10.33	9.39	8.50
Lethrinus obsoletus	0.677	1.72	0.83	0.17
Plectropomus laevis	0.667	0.39	1.08	0.75
Lutjanus lemniscatus	0.544	0.33	0.92	1.00

Table 5.1b : Frequency of occurrence of species in visual censuses in the three groups derived from classification analysis, ranked as above.

Species	*C*	Classification Group		
		Rib (*n* = 36)	John Brewer (*n* = 36)	Lodestone (*n* = 36)
Lutjanus gibbus	0.978	0	12	4
Lethrinus lentjan	0.975	20	10	5
Lethrinus nebulosus	0.975	19	21	27
Lutjanus quinquelineatus	0.971	32	35	33
Lutjanus monostigma	0.947	4	11	8
Lutjanus bohar	0.942	12	27	14
Lutjanus russelli	0.933	22	31	30
Lethrinus miniatus	0.918	14	19	29
Lutjanus fulvus	0.911	3	19	9
Lethrinus atkinsoni	0.907	26	28	13
Lutjanus fulviflamma	0.876	30	36	26
Lutjanus carponotatus	0.873	34	36	36
Plectropomus leopardus	0.814	35	36	35
Lethrinus obsoletus	0.677	24	9	6
Plectropomus laevis	0.667	10	22	21
Lutjanus lemniscatus	0.544	9	25	22

Table 5.2a : Summaries of two factor analyses of variance of visual census data for selected Lutjanidae (significance levels : ns = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$).

		Total lutjanids.[1]			*L. bohar*[1]			*L. carponotatus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	0.77	1.69	ns	0.39	0.34	ns	0.31	0.76	ns
Reef	2	29.9	65.5	***	14.8	13.0	***	8.37	20.5	***
Time × Reef	10	0.30	0.66	ns	0.82	0.72	ns	0.43	1.06	ns
Residual	90	0.46	--	--	1.15	--	--	0.41	--	--

		L. fulviflamma[1]			*L. fulvus*			*L. gibbus*		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	2.29	1.35	ns	0.21	0.40	ns	6.28	0.27	ns
Reef	2	46.3	27.4	***	3.40	6.33	**	197	8.58	***
Time × Reef	10	0.93	0.55	ns	0.79	1.47	ns	8.15	0.36	ns
Residual	90	1.69	--	--	0.54	--	--	23.0	--	--

		L. lemniscatus			*L. monostigma*[1]			*L. quinquelineatus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	0.31	0.39	ns	0.12	0.13	ns	1.11	0.80	ns
Reef	2	4.75	6.01	**	2.57	2.83	ns	18.6	13.3	***
Time × Reef	10	0.41	0.51	ns	0.54	0.60	ns	0.55	0.39	ns
Residual	90	0.79	--	--	0.91	--	--	1.40	--	--

		L. russelli[1]		
Source of Variation	df	MS	F	p
Time of Year	5	0.47	0.33	ns
Reef	2	15.3	11.0	***
Time × Reef	10	1.08	0.77	ns
Residual	90	1.40	--	--

[1] Data transformed to log (x + 0.5) before analysis.

Table 5.2b : Summaries of two factor analyses of variance of visual census data for selected Lethrinidae and for *Plectropomus* species (significance levels : ns = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$).

		Total lethrinids[1]			*L. atkinsoni*[1]			*L. lentjan*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	1.35	0.94	ns	0.79	1.01	ns	0.61	0.73	ns
Reef	2	2.24	1.55	ns	9.85	12.6	***	9.04	10.9	***
Time × Reef	10	1.30	0.91	ns	0.79	1.01	ns	0.58	0.70	ns
Residual	90	1.44	--	--	0.78	--	--	0.83	--	--

		L. miniatus[1]			*L. nebulosus*[1]			*L. obsoletus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	0.23	0.39	ns	2.52	1.01	ns	2.03	4.25	**
Reef	2	6.94	11.9	***	3.96	1.59	ns	8.64	18.1	***
Time × Reef	10	1.13	1.93	ns	2.29	0.92	ns	0.69	1.45	ns
Residual	90	0.58	--	--	2.49	--	--	0.48	--	--

		P. laevis			*P. leopardus*		
Source of Variation	df	MS	F	p	MS	F	p
Time of Year	5	0.82	0.97	ns	18.4	1.28	ns
Reef	2	4.34	5.17	**	30.3	2.10	ns
Time × Reef	10	0.43	0.51	ns	14.8	1.02	ns
Residual	90	0.84	--	--	14.4	--	--

[1] Data transformed to log (x + 0.5) before analysis.

Table 5.3 : *A posteriori* multiple comparison of means (using Tukey's HSD method) from the two factor analyses of variance shown in Tables 5.2a and 5.2b (significance level for all comparisons was $p < 0.05$; Reef : RIB = Rib; JB = John Brewer; L = Lodestone).

Taxon	Factor	
	Time of Year	Reef
Total lutjanids	--	JB > L > RIB
Lutjanus bohar	--	JB > (RIB = L)
L. carponotatus	--	(JB = L) > RIB
L. fulviflamma	--	JB > L > RIB
L. fulvus	--	JB > RIB, JB = L, RIB = L
L. gibbus	--	JB > (L = RIB)
L. lemniscatus	--	(JB = L) > RIB
L. monostigma	--	--
L. quinquelineatus	--	(JB = L) > RIB
L. russelli	--	(JB = L) > RIB
Total lethrinids	--	--
Lethrinus atkinsoni	--	(RIB = JB) > L
L. lentjan	--	RIB > (JB = L)
L. miniatus	--	L > (JB = RIB)
L. nebulosus	--	--
L. obsoletus	##	RIB > (JB = L)
Plectropomus laevis	--	JB > RIB, JB = L, RIB = L
P. leopardus	--	--

: July June November September February May

Table 5.4a : Mean catch (per trap) of taxa of the 12 highest *C* values in the groups derived from classification analysis, ranked by their ability to distinguish among each diel group (*C* = Cramer value; *n* = total number of trap hauls per group; -- = absent).

Species	*C*	Classification Groups			
		Day		Night	
		Shallow (n = 216)	Deep (n = 216)	Shallow (n = 216)	Deep (n = 216)
Gymnocranius audleyi	0.799	0.08	0.36	0.02	0.24
Lethrinus species 2	0.798	0.24	1.42	0.05	0.39
Plectropomus leopardus	0.758	0.19	0.14	0.03	0.03
Abalistes stellaris	0.753	0.13	1.34	0.01	0.40
Lutjanus carponotatus	0.654	0.10	--	0.13	0.03
Lutjanus russelli	0.837	0.01	0.02	0.27	0.53
Lethrinus miniatus	0.820	0.14	0.03	0.32	0.09
Lutjanus vitta	0.785	--	0.04	--	0.44
Lutjanus sebae	0.784	--	0.03	0.04	0.14
Lutjanus quinquelineatus	0.769	0.01	0.01	2.08	2.86
Lutjanus adetii	0.737	--	0.06	0.01	1.86
Lutjanus fulviflamma	0.727	0.01	--	0.27	0.10

Table 5.4b : Frequency of individual species of selected taxa in traps in the groups derived from the classification analysis, ranked as above.

Species	*C*	Classification Groups			
		Day		Night	
		Shallow (n = 216)	Deep (n = 216)	Shallow (n = 216)	Deep (n = 216)
Gymnocranius audleyi	0.799	11	42	4	26
Lethrinus species 2	0.798	32	78	8	34
Plectropomus leopardus	0.758	32	25	5	6
Abalistes stellaris	0.753	23	115	1	52
Lutjanus carponotatus	0.654	19	0	23	6
Lutjanus russelli	0.837	1	4	42	68
Lethrinus miniatus	0.820	24	5	45	18
Lutjanus vitta	0.785	0	5	0	40
Lutjanus sebae	0.784	0	7	8	23
Lutjanus quinquelineatus	0.769	2	2	133	123
Lutjanus adetii	0.737	0	5	2	87
Lutjanus fulviflamma	0.727	1	0	34	17

Table 5.5 : Summary of four factor analyses of variance for trap catch per unit effort data for the total catch, selected Lutjanidae and Lethrinidae, *Abalistes stellaris* and *Plectropomus leopardus* (significance levels : ns = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$; [1] data transformed to $\sqrt{x} + \sqrt{(x + 1)}$ before analysis, therefore $\alpha = 0.01$ and ns = $p > 0.01$).

		Total fish.[1]			Total lutjanids.[1]			*L. adetii*		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	575	1.22	ns	177	0.69	ns	83.4	1.81	ns
Reef	2	519	1.10	ns	550	2.16	ns	76.8	1.66	ns
Diel	1	9735	20.6	**	23281	91.5	***	1067	23.1	***
Depth	1	17205	36.4	***	3354	13.2	***	1179	25.6	***
Time × Reef	10	341	0.72	ns	148	0.58	ns	49.1	1.07	ns
Time × Diel	5	184	0.39	ns	163	0.64	ns	59.6	1.29	ns
Reef × Diel	2	885	1.87	ns	450	1.77	ns	82.0	1.77	ns
Time × Depth	5	126	0.27	ns	109	0.43	ns	81.5	1.77	ns
Reef × Depth	2	527	1.12	ns	146	0.57	ns	81.4	1.77	ns
Diel × Depth	1	469	0.99	ns	3202	12.6	***	1045	22.7	***
Time × Reef × Diel	10	249	0.53	ns	186	0.73	ns	52.2	1.13	ns
Time × Reef × Depth	10	229	0.49	ns	151	0.59	ns	48.5	1.05	ns
Time × Diel × Depth	5	62.3	0.13	ns	90.3	0.36	ns	58.0	1.26	ns
Reef × Diel × Depth	2	1.67	0.01	ns	72.4	0.29	ns	86.0	1.87	ns
T × R × Di × De	10	183	0.39	ns	165	0.65	ns	51.4	1.12	ns
Residual	72	473	--	--	255	--	--	46.1	--	--

		L. carponotatus[1]			*L. fulviflamma*[1]			*L. quinquelineatus*		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	0.62	1.38	ns	0.70	1.07	ns	47.2	0.53	ns
Reef	2	6.70	15.1	***	4.25	6.57	**	131	1.46	ns
Diel	1	1.46	3.28	ns	35.7	55.2	***	7847	87.5	***
Depth	1	13.5	30.4	***	5.62	8.68	**	198	2.21	ns
Time × Reef	10	0.44	0.98	ns	1.04	1.60	ns	54.7	0.61	ns
Time × Diel	5	0.19	0.42	ns	0.82	1.27	ns	44.0	0.49	ns
Reef × Diel	2	0.03	0.06	ns	3.34	5.16	**	132	1.47	ns
Time × Depth	5	0.42	0.93	ns	0.53	0.83	ns	16.3	0.18	ns
Reef × Depth	2	6.41	14.4	***	1.89	2.91	ns	129	1.44	ns
Diel × Depth	1	0.04	0.09	ns	4.56	7.04	**	198	2.21	ns
Time × Reef × Diel	10	0.38	0.86	ns	1.06	1.64	ns	54.4	0.61	ns
Time × Reef × Depth	10	0.79	1.77	ns	0.81	1.25	ns	49.4	0.55	ns
Time × Diel × Depth	5	0.25	0.57	ns	0.50	0.77	ns	17.8	0.20	ns
Reef × Diel × Depth	2	0.07	0.16	ns	1.32	2.03	ns	125	1.39	ns
T × R × Di × De	10	0.34	0.76	ns	0.97	1.50	ns	50.1	0.56	ns
Residual	72	0.45	--	--	0.65	--	--	89.7	--	--

Table 5.5 : continued.

		L. russelli			*L. sebae*[1]			*L. vitta*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	3.96	1.76	ns	0.93	1.49	ns	1.57	1.64	ns
Reef	2	4.69	2.09	ns	0.37	0.59	ns	1.87	1.94	ns
Diel	1	194	86.3	***	6.61	10.6	**	25.6	26.7	***
Depth	1	22.6	10.1	**	6.00	9.63	**	42.9	44.6	***
Time × Reef	10	4.32	1.93	ns	0.27	0.43	ns	0.54	0.56	ns
Time × Diel	5	4.96	2.21	ns	0.98	1.57	ns	0.92	0.95	ns
Reef × Diel	2	5.19	2.32	ns	0.09	0.15	ns	3.17	3.29	ns
Time × Depth	5	2.35	1.05	ns	1.24	1.98	ns	1.57	1.64	ns
Reef × Depth	2	1.33	0.59	ns	0.06	0.09	ns	1.87	1.94	ns
Diel × Depth	1	19.5	8.70	**	0.83	1.34	ns	25.6	26.7	***
Time × Reef × Diel	10	3.90	1.74	ns	0.17	0.28	ns	0.75	0.78	ns
Time × Reef × Depth	10	2.19	0.98	ns	0.18	0.28	ns	0.54	0.56	ns
Time × Diel × Depth	5	1.92	0.86	ns	1.21	1.95	ns	0.92	0.95	ns
Reef × Diel × Depth	2	2.11	0.94	ns	0.47	0.75	ns	3.16	3.29	ns
T × R × Di × De	10	2.65	1.18	ns	0.28	0.45	ns	0.75	0.78	ns
Residual	72	2.24	--	--	0.62	--	--	0.96	--	--

		Total lethrinids.			*L. miniatus*			*L. species 2*		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	47.3	1.09	ns	2.11	1.21	ns	59.4	2.01	ns
Reef	2	8.88	0.21	ns	0.30	0.17	ns	3.26	0.11	ns
Diel	1	248	5.71	*	18.1	10.4	**	484	16.4	***
Depth	1	925	21.3	***	35.0	20.1	***	756	25.6	***
Time × Reef	10	38.3	0.88	ns	2.77	1.59	ns	36.2	1.22	ns
Time × Diel	5	20.6	0.48	ns	1.53	0.88	ns	36.8	1.24	ns
Reef × Diel	2	16.2	0.37	ns	9.78	5.61	**	3.15	0.11	ns
Time × Depth	5	26.9	0.62	ns	2.57	1.48	ns	37.5	1.27	ns
Reef × Depth	2	12.0	0.28	ns	3.26	1.87	ns	16.9	0.57	ns
Diel × Depth	1	403	9.29	**	4.34	2.49	ns	230	7.78	**
Time × Reef × Diel	10	33.0	0.76	ns	2.46	1.41	ns	20.0	0.68	ns
Time × Reef × Depth	10	32.6	0.75	ns	3.40	1.95	ns	25.2	0.85	ns
Time × Diel × Depth	5	59.1	1.36	ns	1.91	1.09	ns	26.8	0.91	ns
Reef × Diel × Depth	2	30.1	0.69	ns	4.26	2.44	ns	10.9	0.37	ns
T × R × Di. × De.	10	20.2	0.47	ns	2.15	1.23	ns	18.9	0.64	ns
Residual	72	43.4	--	--	1.74	--	--	29.6	--	--

Table 5.5 : continued.

		G. audleyi			*A. stellaris*			*P. leopardus*[1]		
Source of Variation	df	MS	F	p	MS	F	p	MS	F	p
Time of Year	5	8.44	2.84	*	27.5	1.54	ns	1.65	3.18	ns
Reef	2	17.0	5.72	**	55.0	3.08	ns	7.36	14.1	***
Diel	1	10.0	3.37	ns	367	20.5	***	22.9	44.0	***
Depth	1	78.0	26.3	***	831	46.5	***	0.35	0.67	ns
Time × Reef	10	5.28	1.78	ns	9.83	0.55	ns	1.13	2.17	ns
Time × Diel	5	4.99	1.68	ns	3.54	0.20	ns	1.14	2.19	ns
Reef × Diel	2	5.38	1.81	ns	3.11	0.17	ns	4.60	8.84	***
Time × Depth	5	2.03	0.68	ns	28.0	1.57	ns	1.36	2.62	ns
Reef × Depth	2	6.38	2.15	ns	55.4	3.09	ns	0.01	0.02	ns
Diel × Depth	1	1.00	0.34	ns	215	12.0	***	0.33	0.64	ns
Time × Reef × Diel	10	2.22	0.75	ns	4.59	0.26	ns	1.16	2.22	ns
Time × Reef × Depth	10	3.76	1.26	ns	13.3	0.74	ns	0.95	1.83	ns
Time × Diel × Depth	5	1.90	0.64	ns	2.93	0.16	ns	0.41	0.79	ns
Reef × Diel × Depth	2	0.40	0.13	ns	8.78	0.49	ns	0.63	1.21	ns
T × R × Di. × De.	10	0.47	0.16	ns	7.09	0.40	ns	0.90	1.72	ns
Residual	72	2.97	--	--	17.9	--	--	0.52	--	--

Table 5.6 : *A posteriori* multiple comparison of means (using Tukey's HSD method) from the four factor analyses of variance shown in Table 5.5 (significance level for all comparisons was $p < 0.01$; Diel : N = Night, D = Day; Reef : RIB = Rib, JB = John Brewer: L = Lodestone; Depth : SH = shallow, DP = deep).

Taxon	Variables with significant main effects only
Total no. individuals	N > D DP > SH
Lutjanus sebae	N > D DP > SH
L. quinquelineatus	N > D
Gymnocranius audleyi	(JB = L) > RIB DP > SH July June November May February September

Taxon	Variables with significant interaction effects
Total lutjanids	N : DP > SH; D : DP = SH DP : N > D; SH : N > D
Lutjanus russelli	N : DP > SH; D : DP = SH DP : N > D; SH : N > D
L. adetii	N : DP > SH; D : DP = SH DP : N > D; SH : N = D
L. vitta	N : DP > SH; D : DP = SH DP : N > D; SH : N = D
Total lethrinids	D : DP > SH; N : DP = SH DP : D > N; SH : D = N
Lethrinus species 2	D : DP > SH; N : DP = SH DP : D > N; SH : D = N
Abalistes stellaris	D : DP > SH; N : DP = SH DP : D > N; SH : D = N
Lutjanus carponotatus	DP : RIB = JB = L; SH : RIB > (JB = L) RIB : SH > DP; JB : DP = SH; L : DP = SH
Plectropomus leopardus	D : (RIB = JB) > L; N : RIB = JB = L RIB : D > N; JB : D > N; L : D = N
Lutjanus fulviflamma	N : SH > DP; D : SH = DP DP : N > D; SH : N > D N : RIB > (JB = L); D : RIB = JB = L RIB : N > D; JB : N = D; L : N = D
Lethrinus miniatus	SH > DP N : (RIB = L) > JB; D : JB > (RIB = L) RIB : N > D; JB : D > N; L : N > D

Table 5.7 : Numbers of lutjanids, lethrinids and associated taxa on each of three midshelf reefs, mean number of fish per $1000m^2$ of census area (mean count), and catch rate of fish traps per diel (day/night) sampling period pooled over two depths are shown.

	Reef								
Taxon	Rib			John Brewer			Lodestone		
	Mean count	Day catch rate (SE)	Night catch rate (SE)	Mean count	Day catch rate (SE)	Night catch rate (SE)	Mean count	Day catch rate (SE)	Night catch rate (SE)
Total individuals	--	2.72 (0.33)	6.68 (0.60)	--	3.28 (0.35)	4.44 (0.48)	--	3.35 (0.36)	6.44 (0.71)
Total lutjanids	15.5	0.22 (0.05)	5.11 (0.53)	19.7	0.09 (0.04)	3.15 (0.37)	3.95	0.14 (0.06)	4.90 (0.66)
Lutjanus adetii	--	0.01 (0.01)	1.41 (0.25)	--	0.00	0.58 (0.17)	--	0.08 (0.05)	0.81 (0.28)
L. bohar	0.17	--	--	1.30	--	--	0.63	--	--
L. carponotatus	1.60	0.13 (0.03)	0.15 (0.03)	2.23	0.01 (0.00)	0.03 (0.02)	0.81	0.02 (0.01)	0.05 (0.02)
L. fulviflamma	4.13	0.01 (0.00)	0.34 (0.08)	7.79	0.00	0.10 (0.03)	0.87	0.00	0.12 (0.03)
L. fulvus	0.11	--	--	0.17	--	--	0.02	--	--
L. gibbus	0.13	--	--	1.07	--	--	0.00	--	--
L. lemniscatus	0.25	--	--	0.23	--	--	0.08	--	--
L. monostigma	0.22	--	--	0.52	--	--	0.06	--	--
L. quinquelineatus	7.41	0.02 (0.01)	2.64 (0.30)	4.23	0.01 (0.00)	1.85 (0.24)	0.87	0.00	2.92 (0.48)
L. russelli	1.39	0.01 (0.00)	0.34 (0.05)	2.10	0.03 (0.02)	0.33 (0.07)	0.50	0.00	0.54 (0.09)
L. sebae	--	0.01 (0.00)	0.83 (0.05)	--	0.14 (0.02)	0.09 (0.07)	--	0.03 (0.00)	0.10 (0.09)
L. vitta	--	0.01 (0.00)	0.15 (0.03)	--	0.04 (0.00)	0.14 (0.03)	--	0.01 (0.01)	0.36 (0.04)
Total lethrinids	1.90	0.99 (0.22)	0.77 (0.13)	8.52	1.31 (0.23)	0.72 (0.13)	2.71	1.24 (0.21)	0.75 (0.12)
Lethrinus atkinsoni	0.14	--	--	0.90	--	--	0.38	--	--
L. lentjan	0.04	--	--	0.17	--	--	0.92	--	--
L. miniatus	0.49	0.04 (0.02)	0.24 (0.05)	0.35	0.17 (0.04)	0.11 (0.03)	0.13	0.06 (0.03)	0.26 (0.06)
L. nebulosus	1.15	--	--	6.85	--	--	0.13	--	--
L. obsoletus	0.04	--	--	0.21	--	--	0.43	--	--
L. species 2	--	0.83 (0.21)	0.18 (0.06)	--	0.91 (0.22)	0.24 (0.10)	--	0.75 (0.18)	0.24 (0.08)
G. audleyi	--	0.08 (0.03)	0.04 (0.02)	--	0.22 (0.06)	0.22 (0.07)	--	0.35 (0.09)	0.14 (0.04)
Plectropomus laevis	0.19	--	--	0.27	--	--	0.10	--	--
P. leopardus	2.13	0.25 (0.05)	0.05 (0.02)	2.35	0.23 (0.04)	0.03 (0.02)	2.58	0.03 (0.02)	0.01 (0.00)
Abalistes stellaris	--	0.60 (0.09)	0.14 (0.04)	--	0.62 (0.11)	0.10 (0.03)	--	0.99 (0.20)	0.36 (0.11)

Table 5.8 : List of all the lutjanid and lethrinid species recorded and their relative abundance in each of two depth zones on the midshelf reefs of the central Great Barrier Reef (relative abundance index in order of decreasing abundance : abundant; frequent; occasional; rare; -- indicates species not recorded in that zone).

Species	Zone	
	Shallow Back Reef Habitat (0-10m, from visual censuses)	Deep Back Reef Habitat (30-40m, from trapping data)
Lutjanus adetii	--	abundant
L. argentimaculatus	occasional	--
L. biguttatus	rare	--
L. bohar	frequent	--
L. carponotatus	frequent	occasional
L. fulviflamma	abundant	frequent
L. fulvus	occasional	--
L. gibbus	frequent	--
L. lemniscatus	frequent	rare
L. lutjanus	--	rare
L. malabaricus	--	rare
L. monostigma	frequent	--
L. quinquelineatus	abundant	abundant
L. rivulatus	occasional	--
L. russelli	frequent	frequent
L. sebae	occasional	frequent
L. vitta	--	frequent
Symphorichthys spilurus	occasional	--
Symphorus nematophorus	rare	occasional
Lethrinus atkinsoni	frequent	occasional
L. erythracanthus	rare	--
L. genivittatus	--	rare
L. lentjan	frequent	occasional
L. miniatus	frequent	frequent
L. nebulosus	abundant	occasional
L. obsoletus	frequent	rare
L. olivaceus	rare	rare
L. ornatus	occasional	occasional
L. rubrioperculatus	--	rare
L. species 2	rare	abundant
L. xanthochilus	rare	--
Gymnocranius audleyi	--	frequent

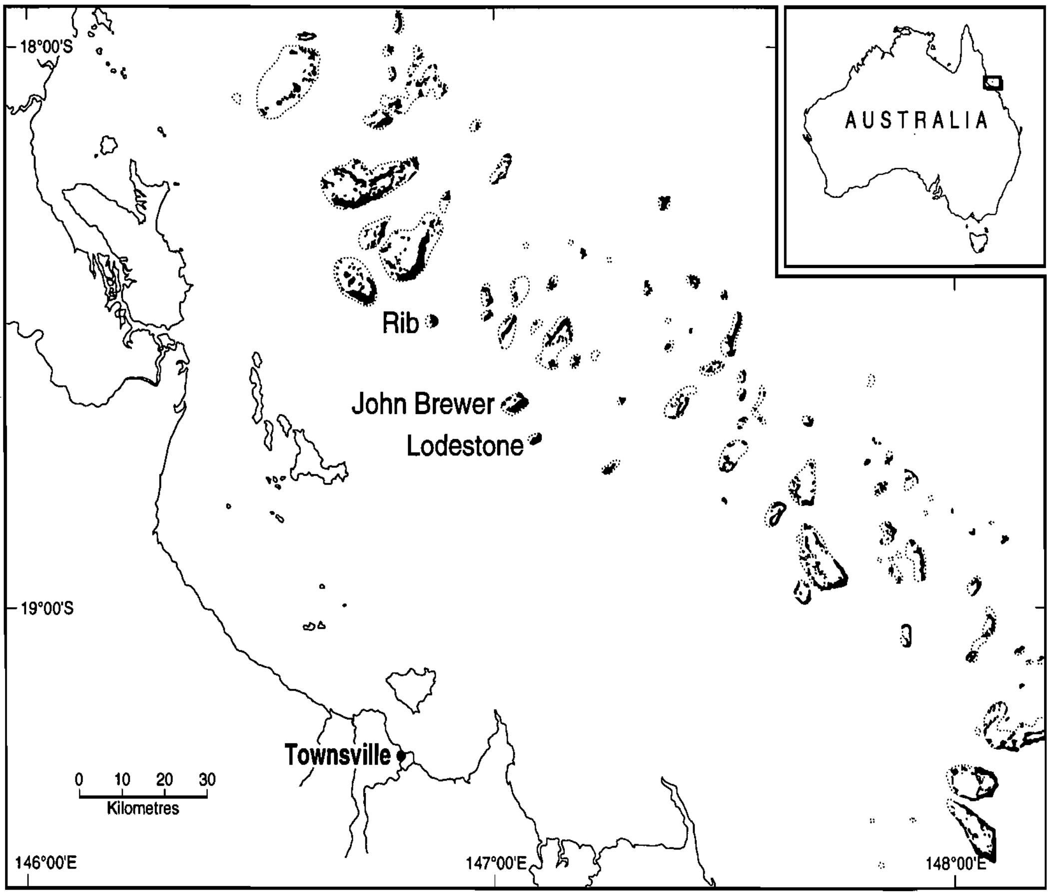


Figure 5.1 : The locations of study reefs in the central region of the Great Barrier Reef of Australia.

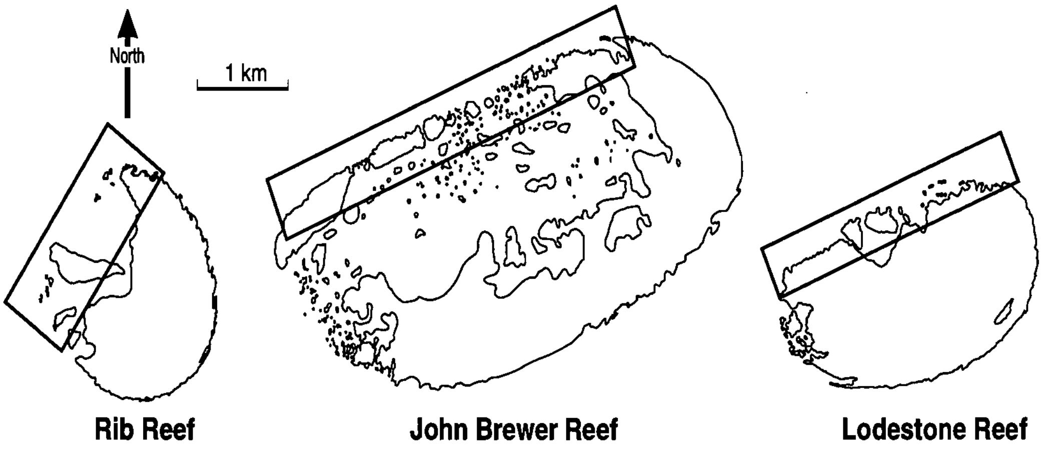


Figure 5.2 : The back reef areas studied within the midshelf reefs. Each box represents the general area in which the traps were set and where replicate visual censuses were made on the respective reefs.

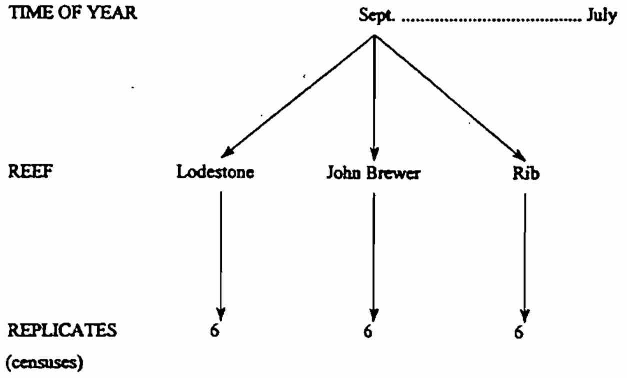


Figure 5.3a : Visual census sampling design. Six replicate censuses were carried out at each reef during each of 6 sampling periods (bimonthly from Sept. '92 to July '93).

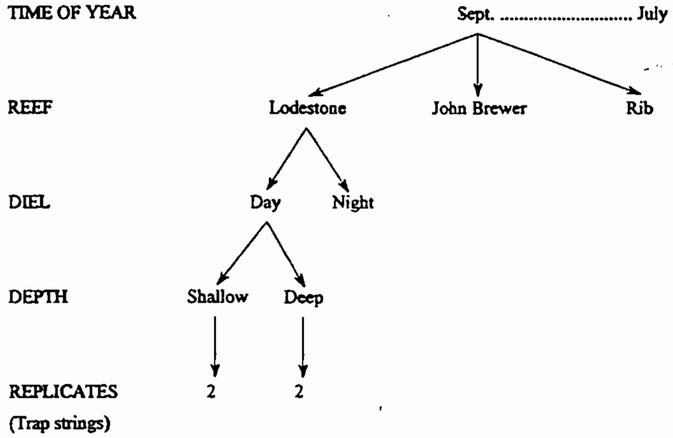


Figure 5.3b : Hierarchical trapping sampling design. Two replicate strings (of 6 traps each) were fished in each depth zone during each diel period at each reef during each of 6 sampling periods (bimonthly from Sept. '92 to July '93).

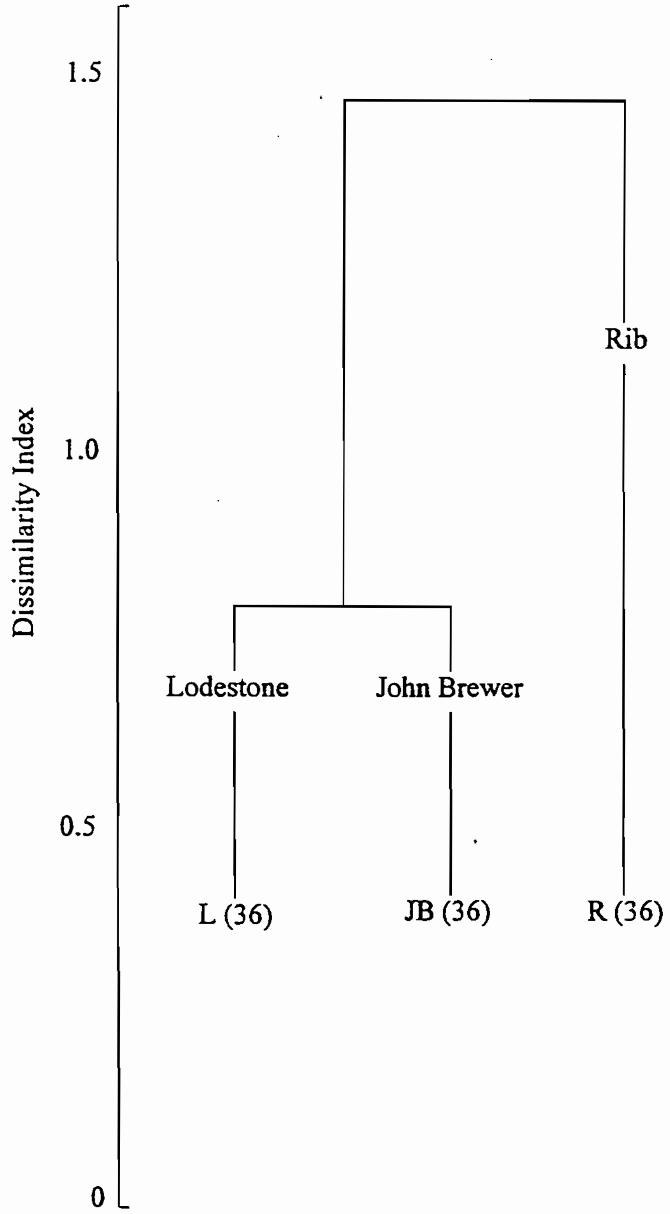


Figure 5.4 : Dendrogram from the classification analysis of 108 visual censuses. Numbers in brackets indicate the number of replicate censuses from individual reefs that fall into each cluster (L = Lodestone; JB = John Brewer; R = Rib).

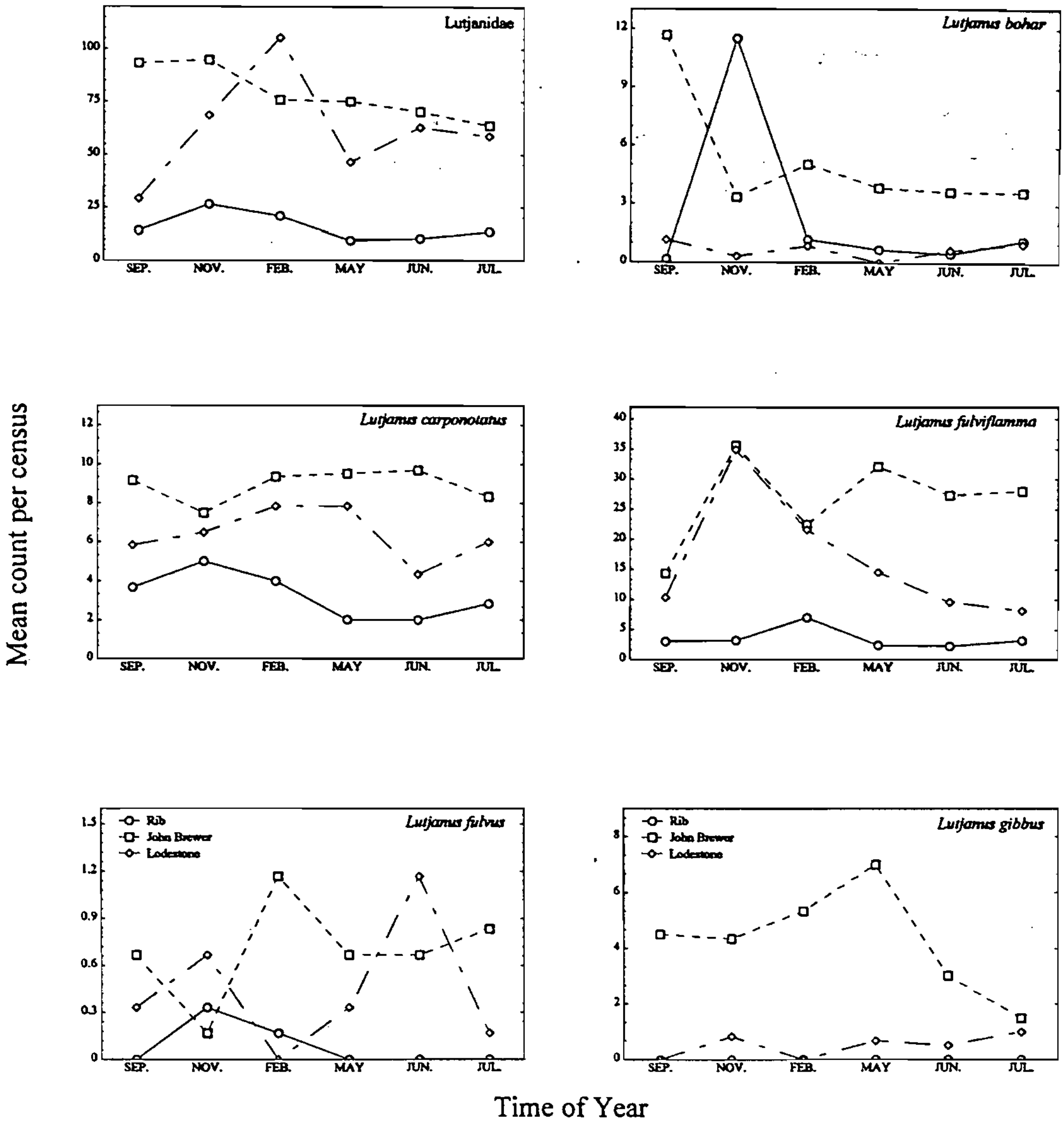


Figure 5.5a : Seasonal variability in the mean counts (per census) of selected taxa among reefs.

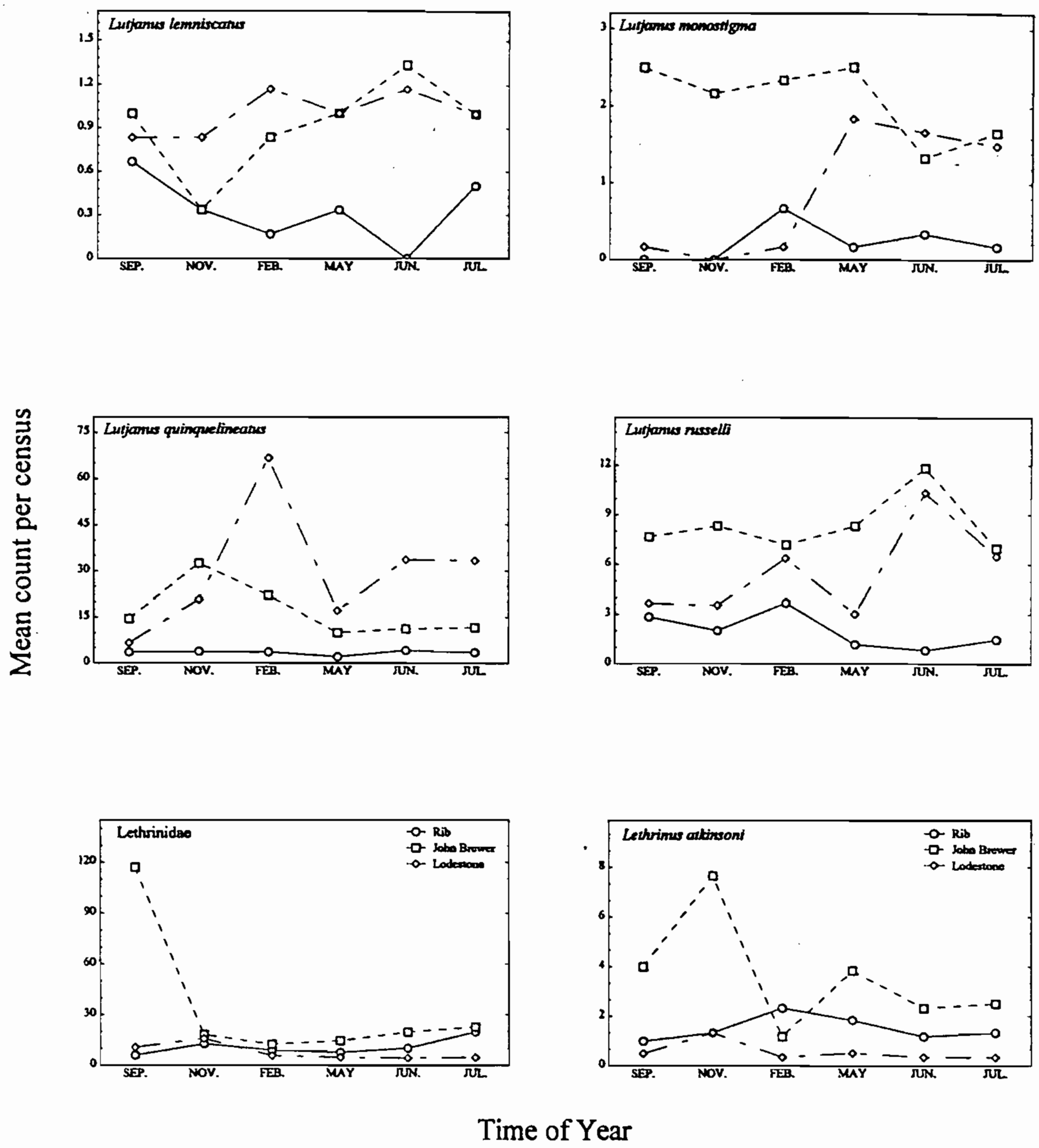
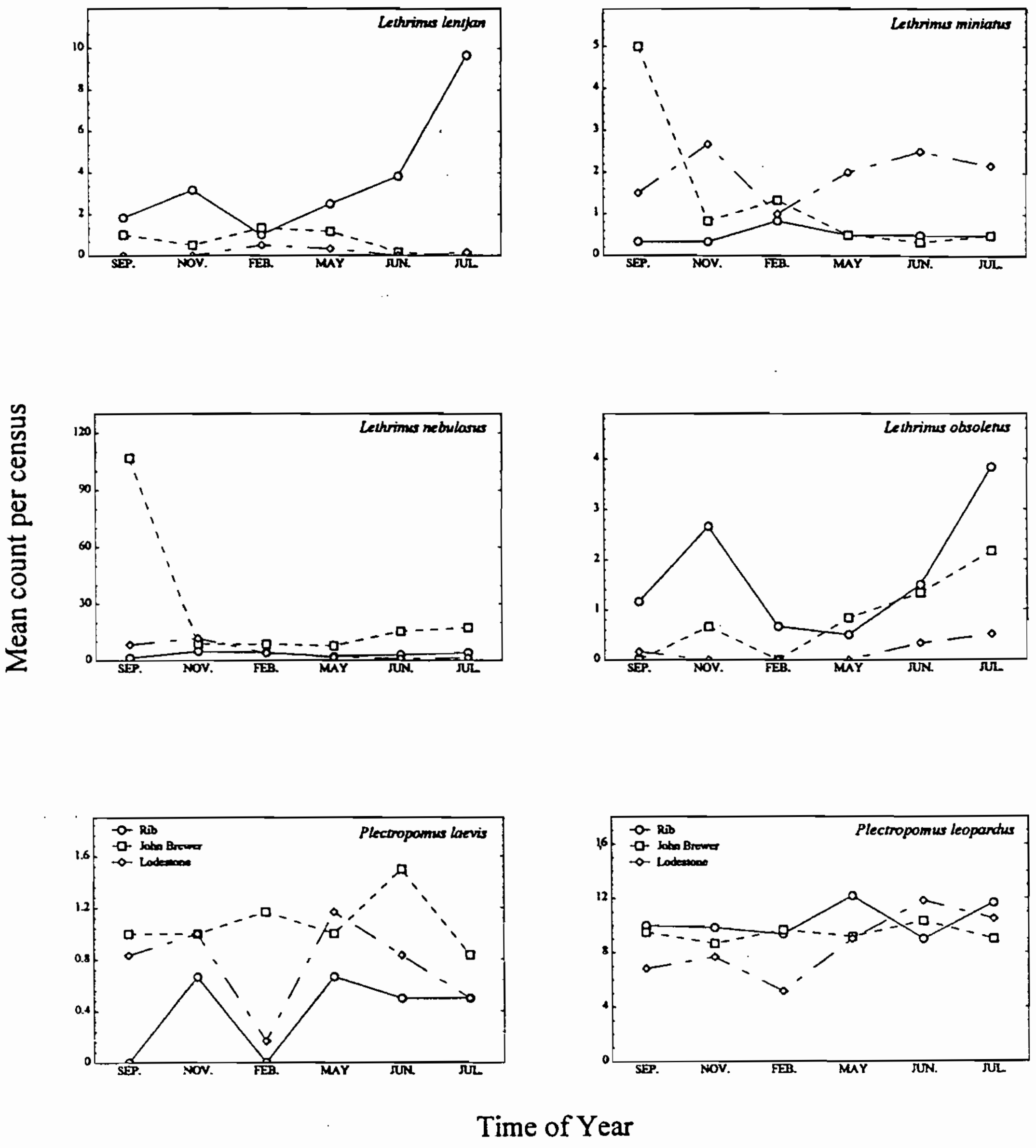


Figure 5.5b : Seasonal variability in the mean counts (per census) of selected taxa among reefs.



Figue 5.5c : Seasonal variability in the mean counts (per census) of selected taxa among reefs.

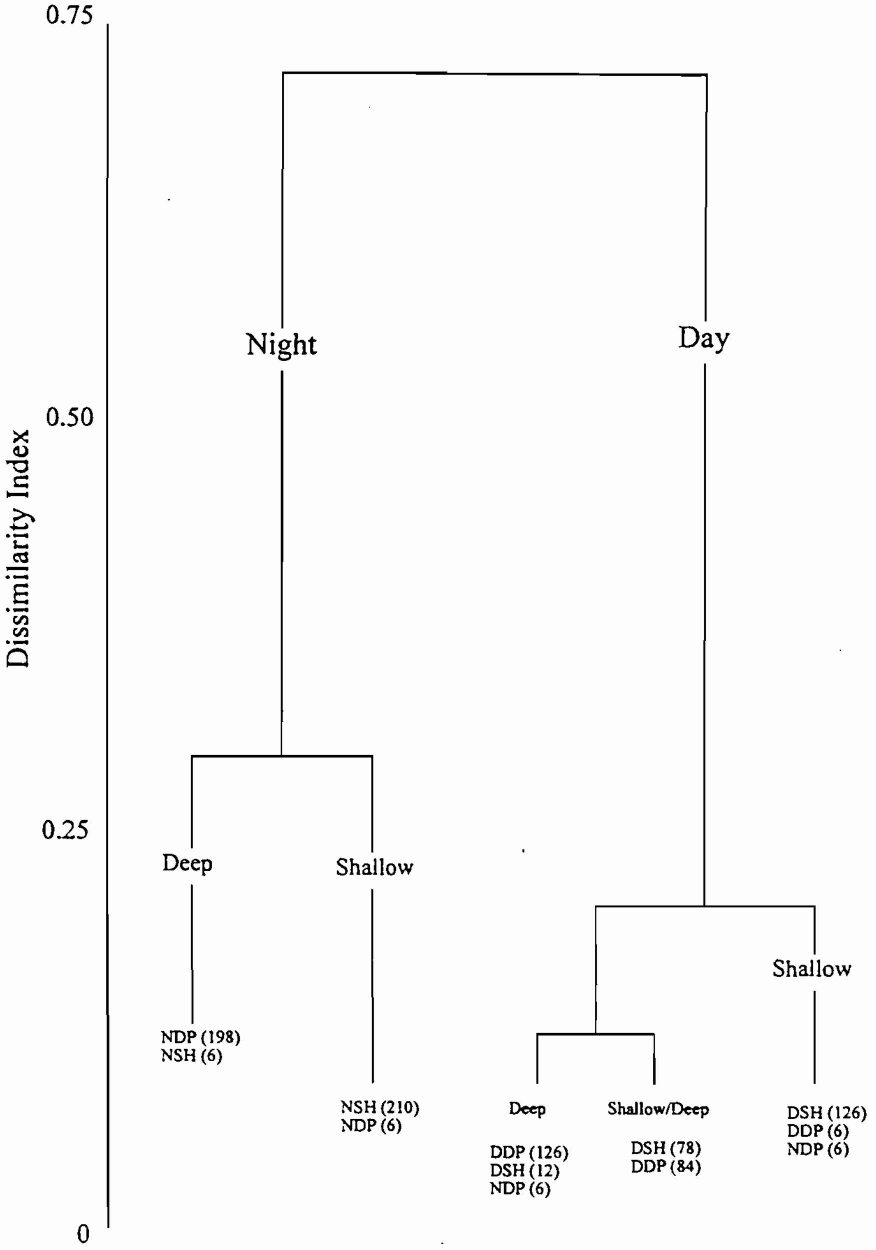


Figure 5.6 : Dendrogram from the classification analysis of the catch per unit effort data of 864 trap hauls. Numbers in brackets indicate the number of replicate trap hauls from each combination of diel sampling period and depth that fall into each cluster (N = night, D = day, SH = shallow, DP = deep).

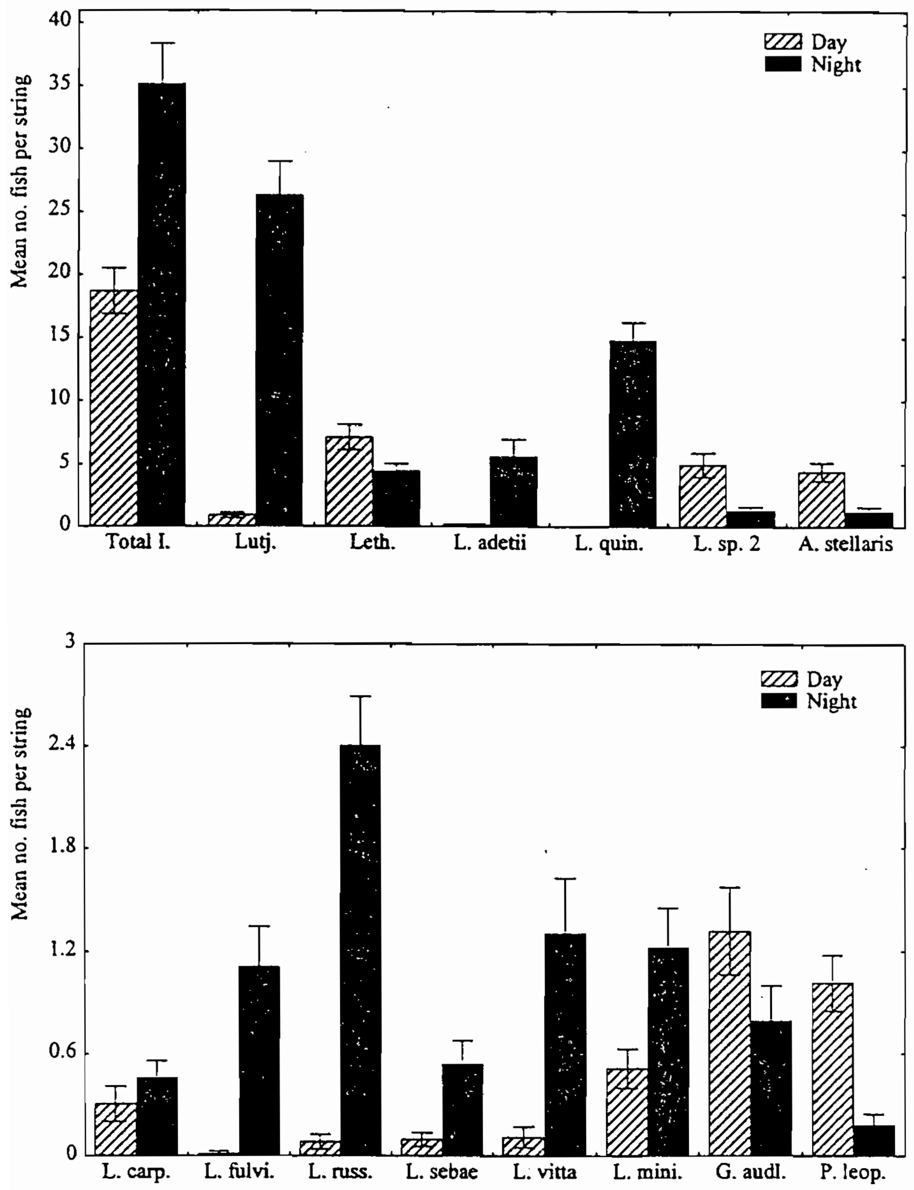
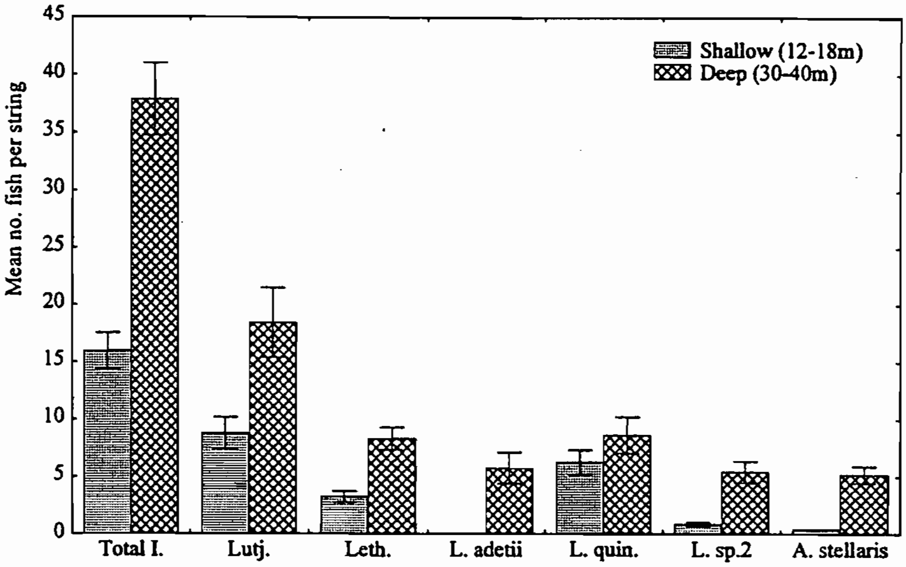


Figure 5.7 : Mean catch per trap string (6 traps) per set (+/- standard error) of selected taxa for each diel sampling period.



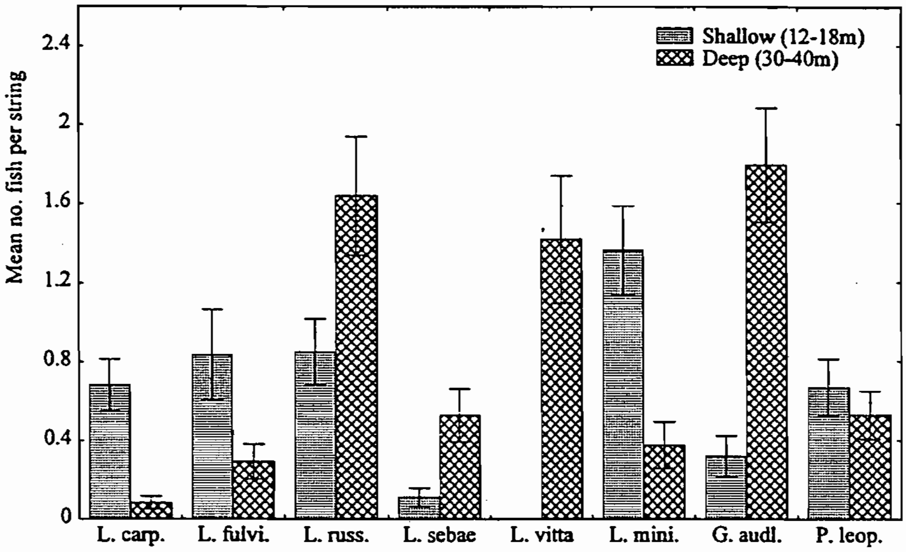


Figure 5.8 : Mean catch per trap string (6 traps) per set (+/- standard error) of selected taxa for each depth zone.

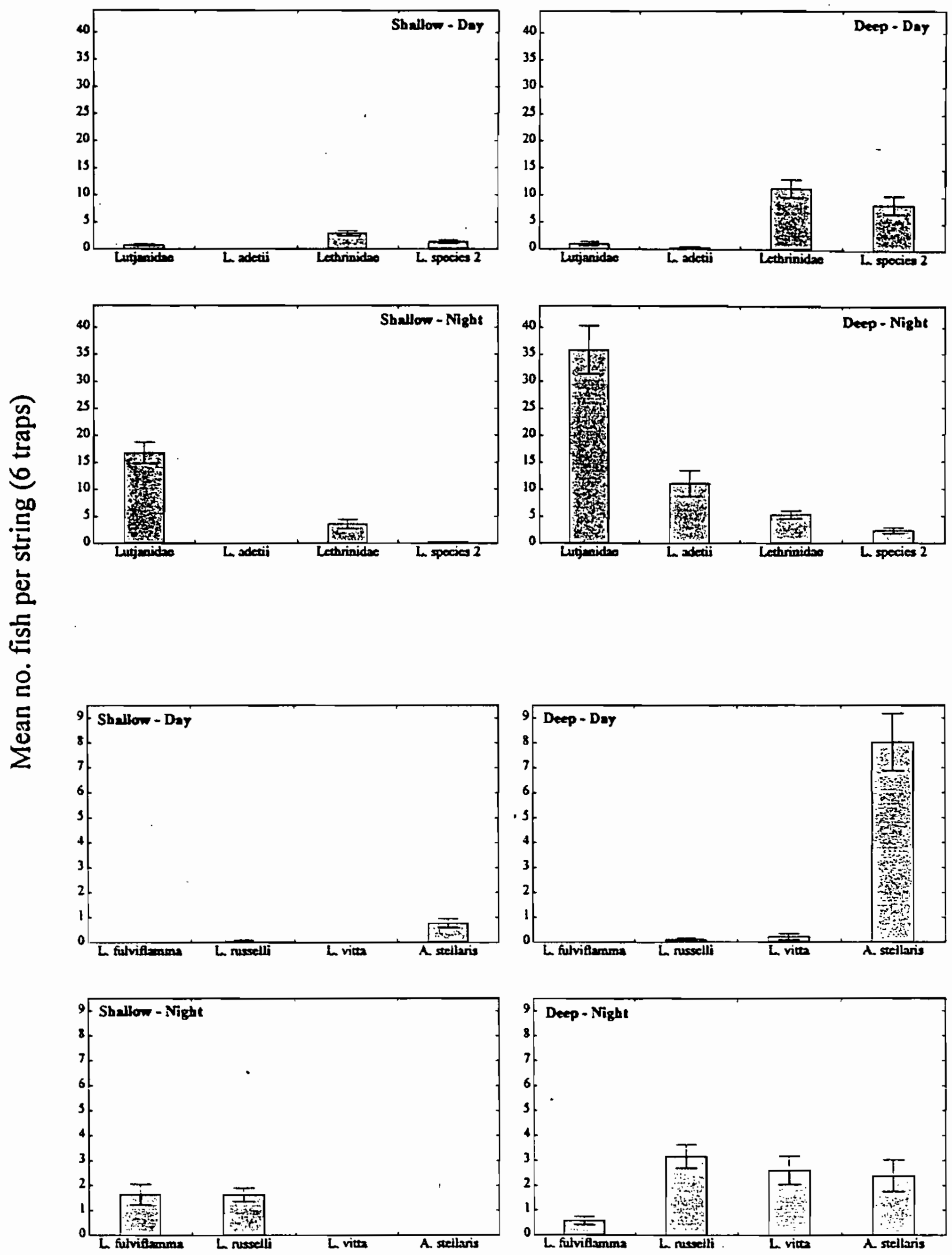


Figure 5.9 : Mean catch per trap string (6 traps) per set (+/- standard error) of selected taxa in each depth zone within each diel sampling period.

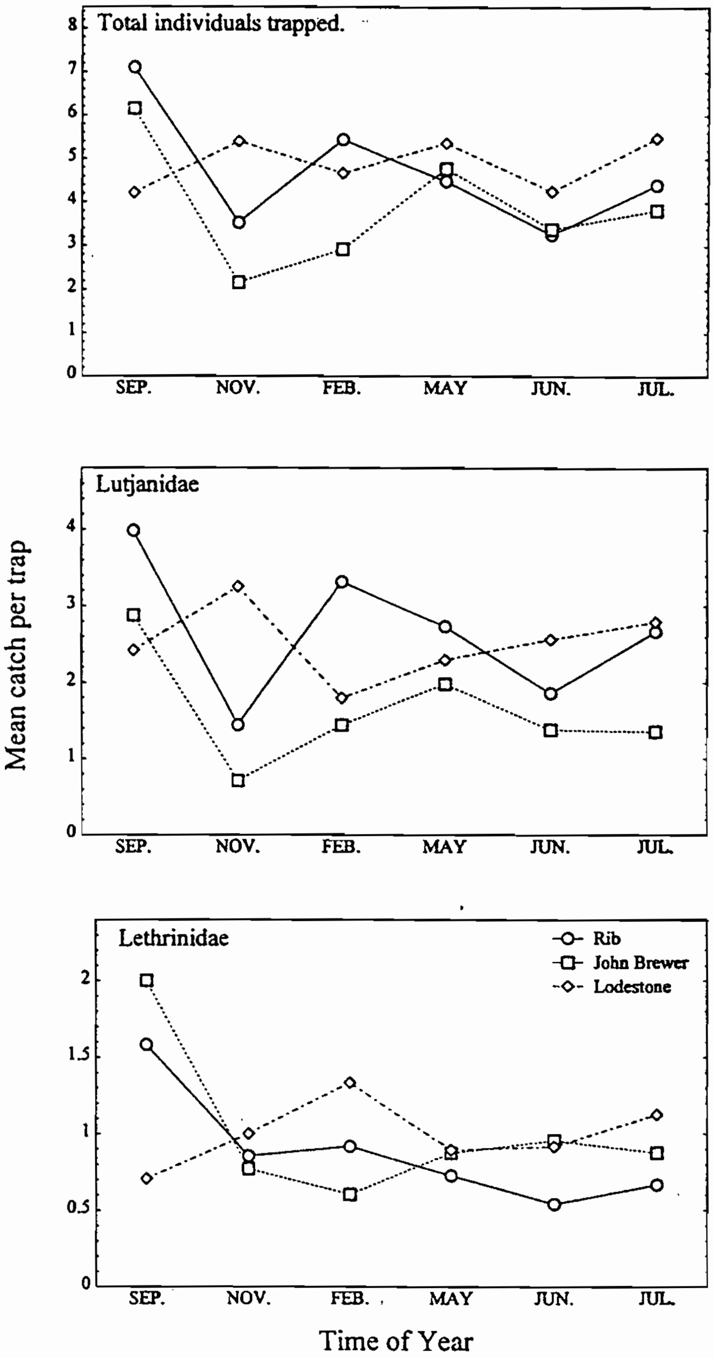


Figure 5.10a : Seasonal variability in the mean catch (per trap) of selected taxa among reefs.

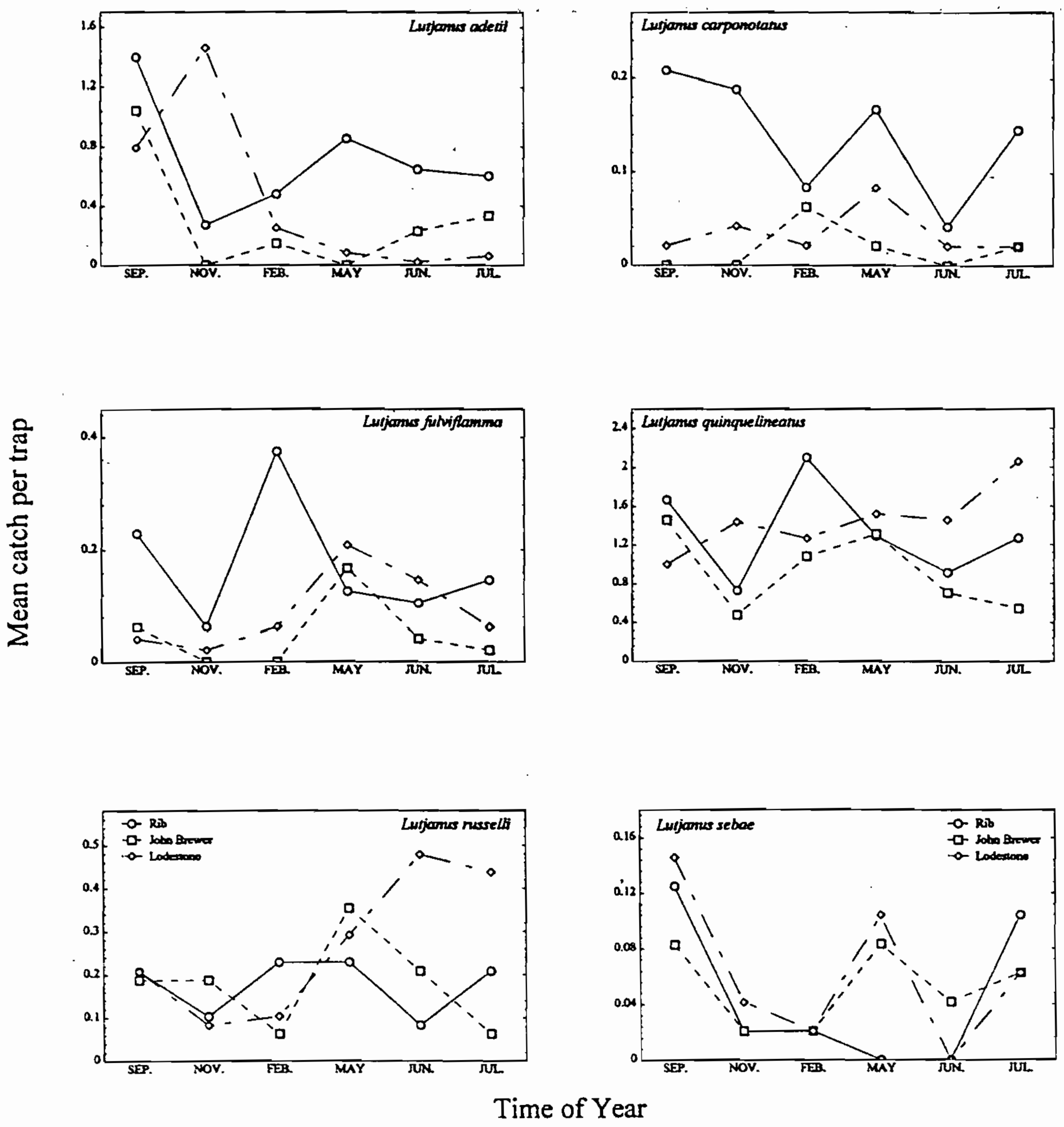


Figure 5.10b : Seasonal variability in the mean catch (per trap) of selected taxa among reefs.

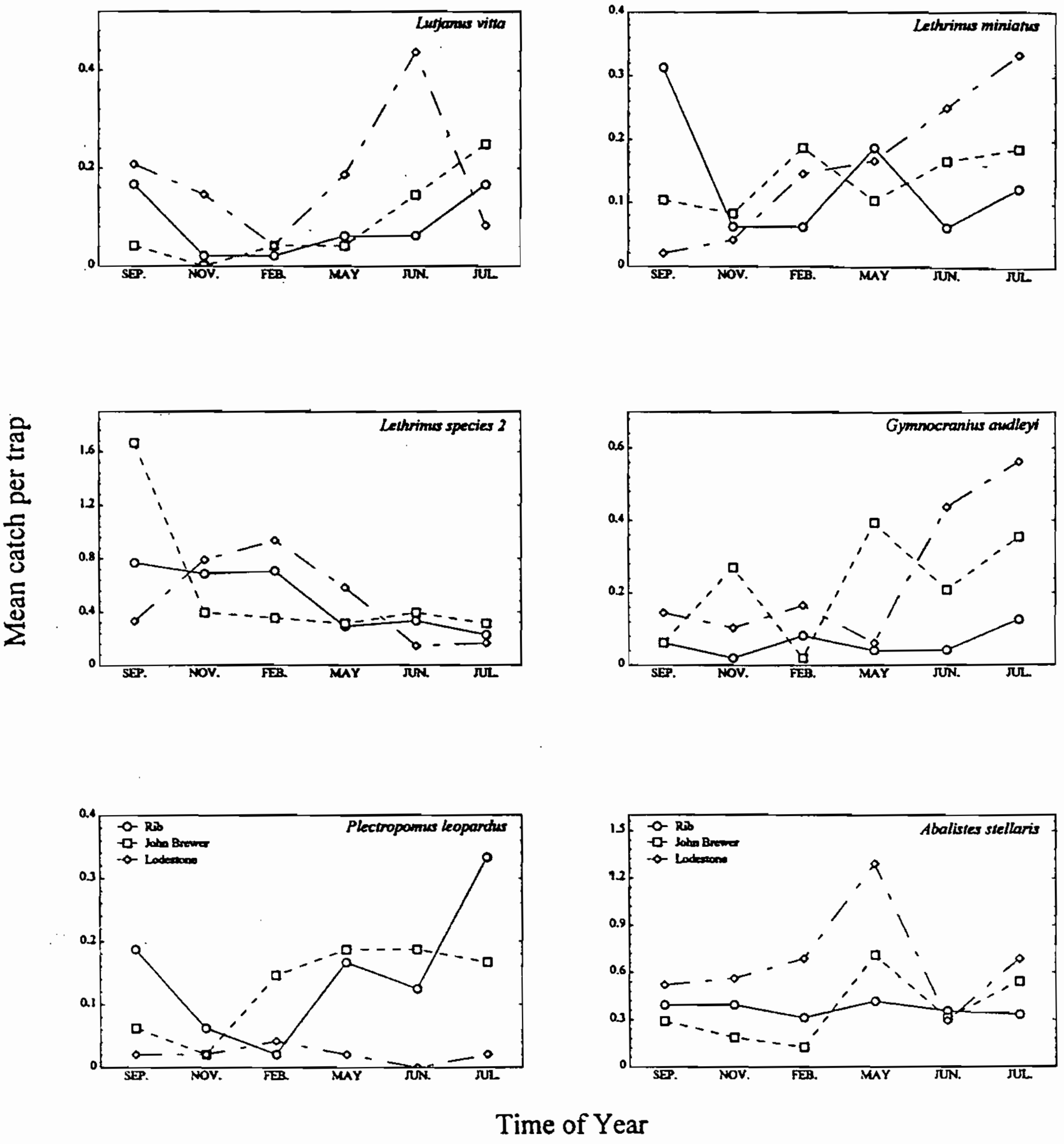
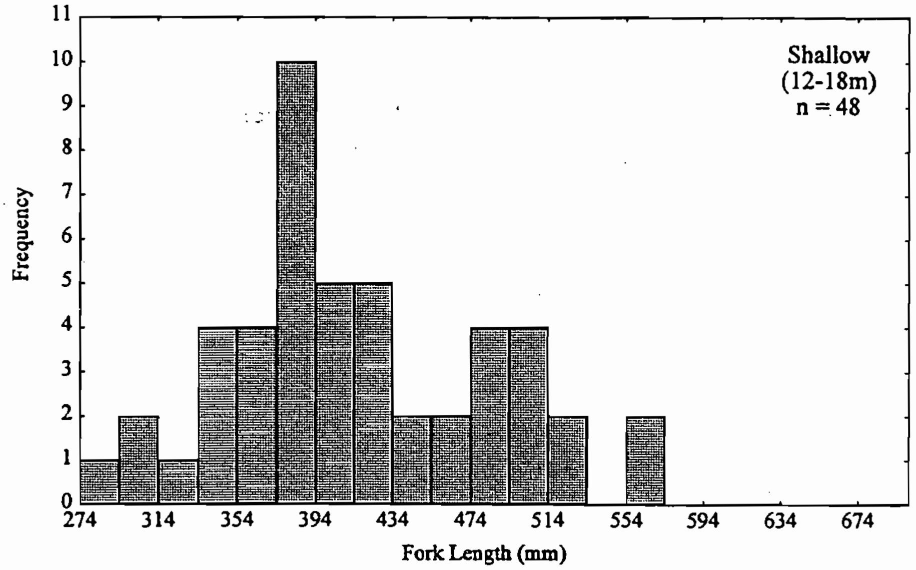


Figure 5.10c : Seasonal variability in the mean catch (per trap) of selected taxa among reefs.



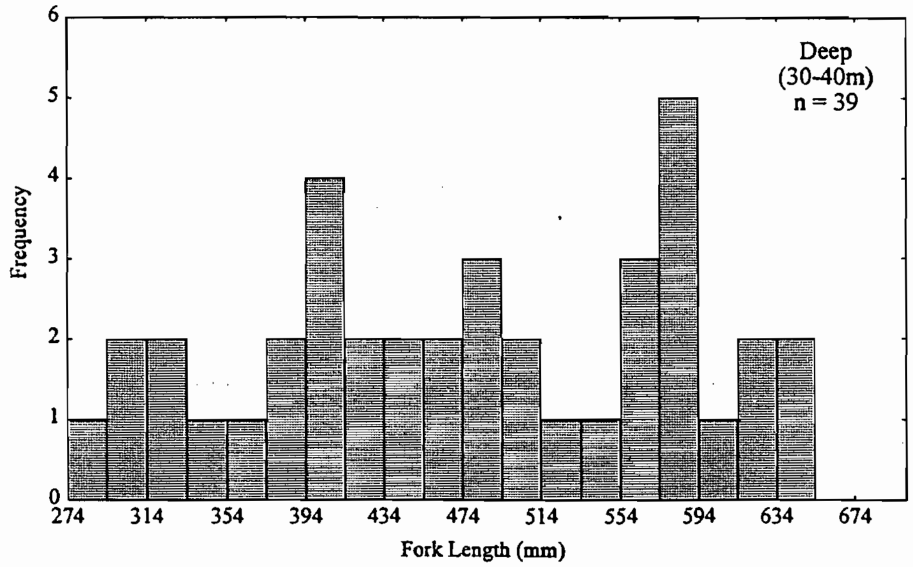


Figure 5.11 : Size frequency distribution of *Plectropomus leopardus* trapped by depth zone (size classes represent a 20mm size range).

Chapter 6

Age validation, growth and mortality rates of the tropical snappers (Pisces : Lutjanidae), *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia.

6.1 INTRODUCTION

The hussar, *Lutjanus adetii* (Castelnau, 1873) is a coral reef associated species that occurs usually in small groups or large schools at depths ranging from 10-20m to at least 100m, and is common in the central Great Barrier Reef from 30-40m (Chapter 5). It's distribution is restricted to the east coast of Australia and New Caledonia in the Coral Sea (Allen, 1985). Although it is common in the central Great Barrier Reef, to date it is only of commercial importance in the southern section of the Great Barrier Reef (20.5°S-22.5°S) where it forms a small but significant component of the line fishing catch, contributing a mean annual commercial catch from 1989-1993 of approximately 1093 kg yr^{-1} (mixed with *L. vitta*) in this region (Georgina Eliason, personal communication; see Appendix 3). In the central Great Barrier Reef, *L. adetii* is occasionally caught by recreational fishermen, but is used mainly as bait (Higgs, 1993).

The five line snapper, *Lutjanus quinquelineatus* (Bloch, 1790) is the most abundant lutjanid occurring in the central Great Barrier Reef and is frequently encountered in large aggregations of 100 or more individuals at depths ranging from 5 to at least 128m (Chapter 3, 4 and 5, see also Appendix 1). Although this species is widespread throughout the central Indo-Pacific region (Allen, 1985), it is of no commercial value on the Great Barrier Reef. However, due to increased fishing pressure by recreational fishermen, the smaller lutjanid species are becoming more important in catches and there is little known about the biology of these species (Williams and Russ, 1994). Worldwide studies of the Lutjanidae indicate that in general they are long lived and slow growing fishes and have relatively low rates of natural mortality (Manooch, 1987; Ralston, 1987) and are therefore considered vulnerable to overfishing.

Previous studies on the age, growth and longevity of these species are restricted to the extensive studies of Loubens (1980b) in the waters of New Caledonia. Loubens (1980b) estimated the age and growth of both species based on counts of annuli in sectioned otoliths. Observations of annuli in otoliths of the Lutjanidae have been observed by Loubens (1978), Mathews and Samuel (1985), McPherson *et. al.* (1988) and McPherson and Squire (1992), suggesting that annuli may occur more generally among congeneric species of this family. Otoliths may therefore potentially provide a valuable tool for age and growth studies of these species. Basic requirements for otolith increments to be useful for aging purposes are that the otoliths continue to grow throughout the life of the fish; that they exhibit interpretable growth increments that are laid down as the fish ages, and that such increments are formed on a deterministic time scale (Fowler, 1990). The direct validation of annuli in *Lutjanus* species has not yet been attempted.

Additionally a number of studies suggest that there is a functional relationship between the increase of otolith size and age of the fish, independent of fish size (Boehlert, 1985; Casselman, 1990; Beckman *et.al.*, 1991; Worthington *et.al.*, in press). Both Boehlert (1985) and Worthington *et.al.* (1994) have similarly suggested the use of otolith weight as a non-subjective methodology for age determination. The relationship between otolith size, fish size and age was investigated to assess the applicability of otolith dimensions in predicting age of the study species.

The aims of this study were to determine the validated age, growth and mortality of *L. adetii* and *L. quinquelineatus* from the central Great Barrier Reef, Australia.

6.2 MATERIALS and METHODS

Samples of *L. adetii* (n = 370) and *L. quinquelineatus* (n = 578) were obtained from a fish trap (O-trap design with 40mm galvanised hexagonal wire mesh) research program investigating the distribution and abundance of lutjanids among reefs in the central Great Barrier Reef region (latitudes 18°S-19°S) (Newman and Williams, in press; Chapters 3, 4 and 5). Fish were collected at regular intervals from October, 1991 to December, 1993. Individual *L. adetii* less than 16cm total length were not vulnerable to trap fishing and specimens in this size range were unable to be obtained for analysis. Similarly, individual *L. quinquelineatus* less than 10cm total length were not vulnerable to trap fishing.

Individuals less than 10cm total length were captured at Lodestone Reef (18°41'S, 147°06'E) by scuba divers using the fish anaesthetic Quinaldine ($n = 4$).

All fish, once identified to species, were measured to the nearest millimetre fork length (FL) and standard length (SL) on a measuring board, and weighed to the nearest gram total weight (TW) and cleaned weight (CW) on a balance scale. Snout length (SNL, mm), eye diameter (ED, mm), upper jaw length (UJL, mm) and head length (HL, mm) were also measured from a subsample of fish covering a wide size range of the fish sampled. Morphometric measurements were undertaken in an attempt to establish robust relationships between fish length and head dimensions, such that future research programs might be further simplified by the collection of heads of specimens only. All individuals were measured on the left side of the body, with the body flattened and the jaw closed. Where possible the sex of each fish was determined by macroscopic examination of the gonads. The sagittal otoliths were removed by opening the otic bulla from under the operculum, a process made easier once the gills and viscera are removed.

The relationship between length and weight was described by the power relationship :

$$W = aL^b$$

where W is the weight of an individual fish (g) and L is the fork length (mm). Cleaned weight was used in preference to total weight since the relationship is not influenced by the size and spawning condition of the gonads or by contents in the stomach and intestines. Cleaned weight is defined as the total weight after removal of the gills and viscera. The relationship between length and weight was determined using a non-linear least squares regression on log transformed data. The systematic bias introduced by the logarithmic transformation was corrected using the correction factor of Sprugel (1983).

One-way analysis of variance ($\alpha = 0.05$) was used to compare mean age, size and weight between sexes of each species (Underwood, 1981). Analysis of covariance ($\alpha = 0.05$) was used to determine if there were differences in length-at-age, weight-at-age and weight-at-length between sexes for each species (Underwood, 1981). Additionally, the slopes of the regression lines were also compared using the comparison of slopes technique described in Zar (1984), to test for differences in the length-weight relationships between the sexes of each species.

The sagittae are the largest pair of otoliths in *Lutjanus*. Preliminary work indicated that these calcareous structures were more suitable for ageing purposes than other calcareous structures such as scales. Scale markings were irregular and thus considered unreliable for ageing. Additionally, McPherson *et. al.* (1988) found that a large proportion of the scales in *L. malabaricus* and *L. sebae* appeared as either replacements or had undergone considerable resorption. Further, McPherson *et. al.* (1988) reported discontinuities in the urohyals and could not detect regular annuli, rendering them unsuitable for ageing purposes. After dissection, sagittae were washed in freshwater and stored dry in envelopes prior to processing. When dry, the intact left and right sagittae, were individually weighed (to 10^{-2} mg) and measured along two axes (total length and breadth) to the nearest 0.1 millimetre. Measurements were made as close as possible through the central core of the otolith. The dimensions of the otoliths were related to the size, weight and ages of the fish using Model II type linear and multiple regression techniques (Ricker, 1973; 1975; Laws and Archie, 1981).

The interpretation of whole otolith structure in recent studies has resulted in the under-estimation of the age of fishes compared to sectioned otoliths (Campana, 1984; Fujiwara and Hankin, 1988; Ferreira and Russ, 1994). To avoid this bias and potential under-estimation of true ages, all aging work in this study was based on the analysis of transverse sections of otoliths. The terminology used to describe otoliths and for otolith readings follows the definitions described by Wilson *et. al.* (1987).

Initially section counts of both the left and right sagittae of 10 individuals of each species were examined to determine if there were any differences between pairs of sagittae. No differences between the numbers of annuli counted in left and right sagittae were detected. Additionally, the relationship between otolith pairs were not significantly different in length, breadth or weight. Consequently, one sagitta was examined from each fish. This was done by haphazardly selecting one sagitta per fish and embedding this in an epoxy resin (FERRO 166) to form a small rectangular block which was allowed to harden completely. Embedded otoliths were sectioned on a Buehler Isomet low-speed jewellery saw. Thin transverse sections (250-400 μm) were made through the core of each otolith from the dorsal apex to the ventral apex. Sections were mounted on glass slides with EPIREZ mounting media and cover slips and allowed to clear and harden prior to reading (<24 hours). Mounted otolith sections were examined under a dissecting microscope at 50× magnification with reflected light from fibre optics on a black background.

Four juvenile *L. quinquelineatus* were examined for daily bands using a different technique. This was done by haphazardly selecting one sagitta per fish and embedding this in Spurr's histological resin (Spurr, 1969) to form a small rectangular block. A large transverse section (>500 µm) of this block was made that included the otolith core. The section was then ground and polished from each side to a level near the core, perpendicular to the long axis of the otolith. This was done by hand using ebony paper (1000) and several grades of lapping film (3, 1 µm). A polished, thin transverse section approximately 100 µm was produced. The section was placed on a microscope slide and all sections were examined under oil immersion using a Leitz compound microscope incorporating an Ikegami high resolution, black and white video camera, connected to a Commodore Amiga personal computer with a high resolution colour monitor. The image was displayed on the monitor and the daily increments were counted. Additional counts were also made without the aid of the monitor image.

Ages were assigned based on counts of annuli from sectioned otoliths. The periodicity of annulus formation was determined with the use of tetracycline labelling. From October 1991 to July 1993, 1,439 *L. adetii* and 1,611 *L. quinquelineatus* were caught in a trapping program on midshelf reefs off Townsville in the central Great Barrier Reef, tagged with T-bar anchor tags and injected with terramycin (oxytetracycline hydrochloride, 100mg/ml) before being released. Injection of both species was done with a 1.0ml syringe and 26 gauge

(0.45 × 13mm) needle which was inserted under the scales and through the skin into the coelomic cavity in close proximity to the pelvic fin region with a minimum dosage of 0.5ml of oxytetracycline hydrochloride per kg of fish (see McFarlane and Beamish, 1987; Fowler, 1990; Ferreira and Russ, 1992).

Eight *L. adetii* were recaptured after periods at liberty in excess of one year. A further 16 were recaptured that had been at liberty for periods exceeding 300 days, but marginally less than one year. Three *L. quinquelineatus* were recaptured after a period in excess of 300 days at liberty. The otoliths of all fishes treated with tetracycline were removed, stored dry and concealed in foil until examination (the OTC mark is photolabile), sectioned and viewed under ultra-violet light.

Prior to the interpretation of increment counts in otoliths as an evaluation of age it is necessary to determine the confidence that can be placed in the interpretation of the otolith structure. Therefore the precision of the counts of more than 300 sectioned otoliths of each species were assessed. Individual otoliths were examined independently on 2 occasions (a minimum of two months apart) with the counts compared between each reading. The percentage agreement was then calculated for each age class. Additionally, the precision of age estimates was calculated using the Index Average Percent Error (IAPE) of Beamish and Fournier (1981).

Initially a number of growth models were fitted to the observed length-at-age data (see Kaufman, 1981). Observed lengths-at-age for both species displayed aysmptotic growth and while the younger age classes of both species were not sampled well, growth of younger individuals was relatively linear. The von Bertalanffy growth function (VBGF) was chosen as the best empirical assessment of growth (the VBGF has also been shown to describe growth better than other polynomial functions, eg. Chen *et. al.*, 1992) for both species and was fitted to estimates of size-at-age using nonlinear least squares estimation procedures (Prager *et. al.*, 1989). The VBGF is defined as :

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)} \right)$$

where L_t = length at age t; L_∞ = asymptotic length; K = Brody growth coefficient and defines the growth rate towards L_∞; t = age of the fish; and t_0 = the theoretical origin of the growth curve, that is, the hypothetical age at which fish would have zero length if it had always grown in a manner described by the equation. In reality, however, t_0 is a time at which the fish already has attained a finite size. Minimum, maximum and mean lengths and ages were also recorded for each species from the central Great Barrier Reef population. Parameters of the VBGF were also derived independently from mark-release-recapture data for *L. adetii* using nonlinear estimation procedures following the method of Fabens (1965).

Preliminary total mortality rate (Z) estimates of both species were obtained using the general regression equation of Hoenig (1983) for fish, where : $\log_e Z = 1.46 - 1.01 \log_e t_{max}$ (t_{max} is the maximum age in years). More reliable estimates of the instantaneous rate of total mortality (Z) were then obtained using the age based catch curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class (Nt) was plotted against their corresponding age (t) and Z estimated from the descending slope, b.

Estimates of the survival rate of each species (S) was then calculated from the Z derived from catch curves, since $Z = -\log_e S$, $S = e^{-Z}$ (Ricker, 1975). Independent estimates of the rate of natural mortality were derived using the general regression equation of Pauly (1980) based on parameters of the VBGF and mean water temperature (in °C), where : $\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$, and the mean annual water temperature for the central Great Barrier Reef (18°S-20°S) is 25.7°C (Lough, 1994); and additionally from the equation of Ralston (1987) for snappers and groupers, where : $M = -0.0666 + 2.52 K$ (K is the Brody growth coefficient of the VBGF).

6.3 RESULTS

Length-Weight Relationships

Length-weight relationships were calculated separately for males, females and for sexes combined (FL and SL) for both species (Table 6.1 and Figures 6.1, 6.2, 6.3, 6.4). The comparison of slopes of the length-weight regression were significantly different between sexes ($p < 0.01$) for *L.adetii* (Figure 6.1), but were not significantly different between sexes ($p > 0.05$) for *L. quinquelineatus* (Figure 6.2). Additionally, ANCOVA of weight-at-length was significantly different between sexes for both species (Table 6.2), with males larger than females. Further, female *L. adetii* displayed significant allometric growth (Table 6.1), indicating that the relationship of length to weight is not constant.

The mean weight (CW, g) of both *L. adetii* and *L quinquelineatus* sampled was significantly different between sexes (ANOVA - Table 6.3), with males larger than females. Conversely, the mean age of both *L. adetii* and *L. quinquelineatus* sampled did not differ significantly between sexes (ANOVA - Table 6.3). The mean length (FL, mm) of *L. quinquelineatus* was significantly different between sexes, with males larger than females, while for *L. adetii*, mean length was not significantly different between sexes (Table 6.3).

Otolith Morphology and Interpretation

The sagittae are the largest of the three pairs of otoliths in the *Lutjanus* genus (personal observation). The left and right sagitta pairs were not significantly different in length, breadth or weight for either *L. adetii* or *L. quinquelineatus* (ANOVA of all cases, $p > 0.05$). Similarly, coefficients of determination of the linear relationship of otolith dimensions between pairs of sagittae demonstrated distinct affinity between otolith pairs (Table 6.4). The sagittae are laterally compressed, elliptical structures, with a concave distal surface and a slightly pointed rostrum. A curved sulcus crosses the proximal surface longitudinally. The depth of the sulcal groove increases with the increasing age of each species. The core of the otolith surrounding the primordium is usually opaque and is succeeded by alternating translucent and opaque zones (annuli). Annuli appear darker than the adjacent translucent zones under transmitted light, but are more clearly differentiated under reflected light on a black background. Under reflected light the opaque zones are milky in appearance and are preceded by relatively clear translucent zones (Figure 6.5). The first two annuli in both species were substantially wider and less well defined than the succeeding annuli. The sagittae from the juvenile *L. quinquelineatus* contained numerous fine bands (assumed to be daily bands) and these sections were useful in confirming the relative position of the first annulus. The counts of annuli in the sectioned otoliths were usually undertaken in the region from the primordium to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus to ensure consistency. The annuli in this region were usually well defined and easily interpretable.

The precision of otolith readings of both species was high, with the Index Average Percent Error (IAPE) of Beamish and Fournier (1981) marginally lower for *L. adetii* (0.72%) than for *L. quinquelineatus* (1.73%). There was also high percentage agreement among counts in successive age classes of both species (Tables 6.5 and 6.6). For 89.2% of otoliths of *L. adetii* and 76.1% of otoliths of *L. quinquelineatus* counts were identical (Tables 6.5 and 6.6). These results indicate a high level of precision between replicate readings and suggest that the otoliths were interpreted in a similar manner on both occasions. For those fish whose two counts of the same otolith were different, the second independent estimate of age was used for analysis of age and growth, since by this time more experience had been gained in the interpretation of the structure of these otoliths.

Validation of Annulus Formation

The presence of regular rings, presumably representing daily growth increments were observed in the otoliths of juvenile *L. quinquelineatus* (Figure 6.6). The mean total increment counts of the sagittae of the four juvenile *L. quinquelineatus* ranged from 90 to 118 daily growth increments for individuals 60 to 92mm fork length. While these counts may underestimate actual age by 4-5 days because they are the mean of several counts (Fowler, personal communication), they indicate that the formation of the first annulus occurs a conspicuous distance from the primordium and that initial growth is quite rapid.

All fishes of both species treated with tetracycline displayed clear fluorescent marks in their otoliths (Figures 6.7 and 6.8). Individual *L. adetii* ranging in age from 7 to 20 years old, recaptured after at least one year at liberty (n = 8) all indicated that annuli are formed once per year. Three *L. adetii* recaptured after 23 months at large, had each laid down two annual rings (see Figure 6.7). Individual *L. quinquelineatus* ranging in age from 5 to 14 years old, were all recaptured after at least 300 days at liberty and all (n = 3) indicated that annuli are formed once per year (Figure 6.8). The relative positions of the fluorescent tetracycline bands in relation to the otolith margin and the translucent and opaque zones (annuli) indicated that annulus formation occurred in both species during the winter months (May/June-August).

Otolith Growth

Otolith length and breadth were not good predictors of fish length, weight or age in *L. adetii* (see Figures 6.9, 6.10 and 6.11). Additionally, otolith weight was not a good predictor of fish length or weight in both *L. adetii* and *L. quinquelineatus*, accounting for less than 60% of the variability. However, in *L. quinquelineatus* both otolith length and breadth were good predictors of both fish length and weight, accounting for greater than 65% of the variability (see Figures

6.12 and 6.13). Otolith length and breadth were poor predictors of age in both species.

Otolith weight was a good predictor of age in both species, and alone accounted for 81% of the variability in age of *L. adetii*, and 91% of the variability in age of *L. quinquelineatus* (Table 6.7 and see Figures 6.11 and 6.14). The addition of independent variables to these equations to produce predictive multiple regression models only marginally increased the total amount of variability in age that was accounted for (Table 6.7).

Age and Growth Models

All samples of *L. adetii* were obtained from trap catches. Traps appeared to select against individuals younger than 6+ years of age and less than 220mm fork length (Figures 6.15 and 6.16). Additionally, fish over 300mm fork length were not sampled by fish traps (Figure 6.16). Consequently, individuals were not represented in the 0+ and 1+ age classes. Further, only 29 individuals were represented in the 2+, 3+, 4+ and 5+ year classes. Juvenile *L. adetii* were not sampled in this study and their distribution on the Great Barrier Reef is not presently known.

The rate of growth of *L. adetii* appeared to decline exponentially with age. The von Bertalanffy growth curve was fitted to observed length-at-age data for all individuals (Figure 6.17) and separately for each sex (Figure 6.18 and Table 6.8). Due to the absence of small *L. adetii* of a young age and because the majority of the broad range of ages sampled were restricted to a narrow length range (see

Figure 6.17) difficulties were encountered in fitting a VBGF which accounted for a high degree of the variability in length-at-age. The length-at-age and weight-at-age of *L. adetii* was significantly different between sexes (ANCOVA - Table 6.2), with males larger than females at a given age (Tukey HSD analysis; see also Figure 6.18).

As specimens of *L. adetii* under 6 years of age were poorly sampled, Louben's (1980b) length at birth data for this species was incorporated into the von Bertalanffy growth model as a first approximation of the nature of growth in the early life history of *L. adetii*. The parameters of the VBGF with the addition of Loubens length-at-birth data are : $L_t = 254.1\ (1 - e^{-0.3216\,(t + 1.491)})$. This resulted in a better fit of the von Bertalanffy growth model ($r^2 = 0.559$) than that derived from the original data ($r^2 = 0.39$; see Figure 6.17). Further, a VBGF was derived using Faben's (1965) method on 53 tag-recapture data pairs of individual *L. adetii* which had been at liberty for between 5 days and 23 months (see Figure 6.17). The parameters of the VBGF derived from the tag-recapture data are : $L_t = 268.8\ (1 - e^{-0.3909\,(t + 0.6718)})$. The addition of Loubens length-at-birth data and the VBGF derived from tag-recapture data both indicate that growth declines rapidly with age in *L. adetii* (Figure 6.17). Consequently, the growth rate is much slower for age classes beyond 4 years, which is indicated in the lower value of the Brody growth coefficient (K) derived from the observed length-at-age data. The higher values of the Brody growth coefficient (K) obtained from the addition of Loubens length-at-birth data and from tag-recapture data indicate that initial growth towards L_∞ is quite rapid (see Figure 6.17).

Samples of *L. quinquelineatus* obtained from trap catches were selective against individuals less than approximately 180mm fork length and 4+ years of age (Figures 6.19 and 6.20). These samples were supplemented by collecting smaller individuals using Quinaldine (see Figure 6.20) to determine the nature of growth over the first few years of their life history. The sample collected using Quinaldine was composed entirely of individuals of the 0+ age class (n = 4). Individuals in the 1+ age class were also poorly represented (n = 4) in the trap sample.

The rate of growth of *L. quinquelineatus* declines exponentially with age and the von Bertalanffy growth curve was fitted to observed length-at-age data for all individuals (Figure 6.21) and separately for each sex (Figure 6.22 and Table 6.8). Length-at-age and weight-at-age of *L. quinquelineatus* was significantly different between sexes (ANCOVA - Table 6.2), with males larger than females at a given age (see also Figure 6.22). The initial growth of *L. quinquelineatus* within the first two years of life is very rapid (see Figure 6.21). Despite undersampling of the 0+ and 1+ age classes, their appears to be no difference in the early growth of either sex until the 4+ age class. After age 4 males always appear larger than females (Figure 6.22).

Significant relationships were found to exist between head length, upper jaw length and snout length to fork length. In *L. adetii*, head length, upper jaw length and snout length each accounted for 82%, 77%, and 74% of the variability in fork length respectively (Table 6.7). While in *L. quinquelineatus*, head length, upper jaw length and snout length each accounted for 96%, 94%, and 86% of the variability in fork length respectively (Table 6.7).

Among-Year Variation in Age Structure

The age structure of *L. adetii* was examined over three successive years from 1991 to 1993 (Figure 6.23). Classes of fish aged six or older showed good persistence through time, especially the 6+ and 7+ age classes of 1991. Fish under six years of age were poorly sampled in all years. In 1993 individuals in the 6+ age class were poorly represented in the catch following the two strong 6+ year classes of the preceding two years. The strong 6+ and 7+ year classes of 1991, persisted as strong 7+ and 8+ year classes in 1992 and were still distinct and present as 8+ and 9+ year classes in 1993 (Figure 6.23). The increase in fish aged over 20 years in 1993 resulted from sampling at Kelso reef, which had not been trapped previously.

The age structure of *L. quinquelineatus* was examined over two successive years from 1992 to 1993 (Figure 6.24). The modal progression of age classes between successive years is not distinct and this is partly due to confounding of reef effects (see Chapter 7). However, the dominant 4+ and 5+ year classes of 1992 are still persistent as 5+ and 6+ year classes in 1993 (Figure 6.24). Conversely, the strong 12+ and 14+ year classes of 1992 are not distinctive in 1993.

Mortality

Individual *L. adetii* less than 7 years of age were not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. The total rate of mortality Z of the central GBR population of *L. adetii*, estimated using fish of ages 7 to 24 years, was 0.235 (r^2 = 0.870), representing an annual survivorship of approximately 79%. With the exclusion of the 20-24 year age classes, represented by only 16 individuals, the calculated rate of total mortality estimated using ages 7 to 19 was 0.300 (r^2 = 0.926), representing an annual survivorship of approximately 74% (see Figure 6.25).

Additionally, mortality rates were calculated separately for each sex, as there was significant differences in the growth rates between sexes of *L. adetii*. Both male and female *L. adetii* less than 7 years of age were not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. The total rate of mortality Z of male *L. adetii*, estimated using fish of ages 7 to 24 years, was 0.180 (r^2 = 0.724), representing an annual survivorship of approximately 83% (Figure 6.26). The total rate of mortality Z of female *L. adetii*, estimated using fish of ages 7 to 23 years, was 0.193 (r^2 = 0.849), representing an annual survivorship of approximately 82% (Figure 6.26). Mortality rates between sexes were not significantly different ($p > 0.05$).

Individual *L. quinquelineatus* less than 5 years of age were not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. The total rate of mortality Z of *L. quinquelineatus*, estimated using fish of ages 5 to 31 years, was 0.154 (r^2 = 0.887), representing an annual survivorship of approximately 86%. With the exclusion of the 26-31 year age classes, represented by only 6 individuals, the calculated rate of total mortality estimated using ages 5 to 25 years was 0.118 ($r^2 = 0.848$), representing an annual survivorship of approximately 89% (see Figure 6.27).

Additionally, mortality rates were calculated separately for each sex, as there were significant differences in the growth rates between sexes of *L. quinquelineatus*. Both male and female *L. quinquelineatus* less than 5 years of age were not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. The total rate of mortality Z of male *L. quinquelineatus*, estimated using fish of ages 5 to 30 years, was 0.126 ($r^2 = 0.744$), representing an annual survivorship of approximately 88.2% (Figure 6.28). The total rate of mortality Z of female *L. quinquelineatus*, estimated using fish of ages 5 to 31 years, was 0.132 ($r^2 = 0.826$), representing an annual survivorship of approximately 87.6% (Figure 6.28). Mortality rates between sexes were not significantly different ($p > 0.05$).

Initial total mortality rate estimates from the equation of Hoenig (1983) for populations of *L.adetii* and *L. quinquelineatus* were 0.174 and 0.134, respectively. These estimates of total mortality rate were lower than those derived from catch curves and therefore predict a higher survivorship rate. The estimates of natural mortality from the equation of Pauly (1980) for populations of *L.adetii* and *L. quinquelineatus* were 0.265 and 0.462, respectively. Additionally, estimates of natural mortality from the equation of Ralston (1987) for *L.adetii* and *L. quinquelineatus* were 0.300 and 0.706, respectively. These estimates of natural mortality are considered inappropriate, since by definition M cannot be greater than Z (Ricker, 1975). However, for both populations of *L. adetii* and *L. quinquelineatus*, Z = M by definition, due to the absence of fishing mortality (Ricker, 1975).

6.4 DISCUSSION

There was significant differential growth between the sexes in observed length-at-age and weight-at-age for both *L. adetii* and *L. quinquelineatus* (Table 6.2). Males were significantly larger than females in both species, and this was clearly evident from age class 6 onwards for *L. adetii* and from age class 4 onwards for *L. quinquelineatus* (Figures 6.18 and 6.22). Similarly, Loubens (1980b) found that male *L. adetii* were larger than females at a given age, and Manickehand-Dass (1987) also reported males at a larger size than females for *L. synagris*. Faster growth of males over females in older age classes has been reported for many lutjanid species (eg. *L. buccanella* - Thompson and Munro, 1983; *L. carponotatus* - McPherson *et. al.*, 1988; *L. malabaricus* - McPherson *et. al.*, 1988; McPherson and Squire, 1992; *L. sebae* - Druzhinin and Filatova, 1980; Tarbit, 1980; McPherson *et. al.*, 1988; McPherson and Squire, 1992; *L. vitta* - Davis and West, 1992; *L. vivanus* - Thompson and Munro, 1983), while other studies of lutjanids have found no significant difference in the growth rates between males and females (*L. campechanus* - Moseley, 1966; *L. griseus* - Baez-Hidalgo *et. al.*, 1980; *L. campechanus* - Nelson and Manooch, 1982; *L. erythropterus* - McPherson and Squire, 1992).

Conversely, female lutjanids are reported to obtain larger lengths-at-age than males in a number of species (*L. synagris* - Rodriguez-Pino, 1962; (in contrast to the study of Manickehand-Dass (1987)); *Rhomboplites aurorubens* - Grimes and Huntsman, 1980; *Etelis carbunculus* - Everson, 1984; *Aprion virescens* and *E. coruscans* - Everson *et. al.*, 1989; see also review of Grimes, 1987) and have been shown to outlive males in a few studies (Rodriguez-Pino, 1962; Grimes and Huntsman, 1980; Loubens, 1980b). With the exception of *L. synagris* the majority of these species are from deepwater habitats. Further, Grimes (1987) determined from a number of studies of lutjanid fishes in which a wide range of sizes were sampled, that females tended to dominate the larger size classes.

Grimes (1987) concluded that the differences in size were the result of differential mortality and longevity between sexes. In the present study the mortality rates and longevity between sexes were not significantly different for both species. The most plausible explanation of why females grow more slowly than males after the initial phase of their life history is because they presumably expend proportionally more energy on the production of gametes than do males. As the investment of females in reproductive propagules is higher than that of males, the channelling of energy in females into gonadal growth may occur at the expense of somatic growth and result in smaller size-at-age. While the pattern of size differentiation between sexes is not consistent within the *Lutjanus* genus in general, all studies to date on the Great Barrier Reef indicate that males reach a larger size-at-age and grow faster than females (McPherson *et. al.*, 1988; McPherson and Squire, 1992; this study).

The otoliths displayed a clear internal structure of increments, and when viewed under reflected white light showed opaque increments alternating with translucent increments, similar to the pattern described in other tropical fish species (Loubens, 1978; Fowler, 1990; Ferreira and Russ, 1992; 1994). However, the intelligibility of the annuli was dependent upon the orientation of the sections, and the amount of individual variation. The proximity of the transverse section to the core of the otolith and its alignment perpendicular to the sagittal plane of the otolith was a key determinant in their degree of interpretability.

The validation of rings as annuli was achieved directly by marking otoliths with tetracycline over a large range of ages. Tetracycline has been successfully used as a time marker in the structure of otoliths so that otolith growth can be interpreted relative to the interval between the time of treatment with tetracycline and the final capture of the fish (eg. Fowler, 1990; Ferreira and Russ, 1992; 1994). The direct validation of ages of fishes by marking hard parts, particularly otoliths, with tetracycline antibiotics is increasing in frequency (eg. Leaman and Nagtegaal, 1987; Murphy and Taylor, 1991; Hendricks *et. al.*, 1991; Ferreira and Russ, 1992; 1994).

The annual ring in both these lutjanids is laid down during the winter months (May/June-August). Loubens (1978) concluded that the appearance of the annulus was correlated with changes in the water temperature and not with the condition of the fish or with reproductive activity as suggested by McPherson *et.al.* (1988). Additionally, Ralston and Williams (1989) observed apparent annual marks in the otoliths of the deepwater lutjanid *Pristipomoides zonatus* and attributed their formation to the seasonal temperature minimum. The presence of annuli in immature individuals is further empirical evidence indicating that the formation of the annual ring is not dependent on the spawning period. However, the stimulus for annulus formation may be correlated with exoteric factors that also initiate spawning cycles in mature individuals. Reshetnikov and Claro (1976) have observed that ring formation in *L. synagris* coincides with the start of spawning and have concluded that the major factor in the formation of the annual ring is an internal physiological rhythm that is stimulated by changes in the external conditions.

Pozo (1979) found two opaque rings were formed annually on the otoliths and urohyals of *L. analis* from Cuban waters, and Pozo and Espinosa (1982) have similarly observed that two opaque rings were formed annually in the otoliths and urohyals of *L. vivanus*. The observation of two opaque rings per year in the hard parts of some lutjanid species further emphasises the need for validation to authenticate ages and to provide longevity estimates in adult fishes. Additionally, it has been shown that validation of annual rings in young fish cannot necessarily be extrapolated across all age classes (Beamish and McFarlane, 1983; Gauldie, 1990) and Beamish and Harvey (1969) and Prince *et. al.* (1986) have shown that rings in hardparts may not be reliable for aging fish throughout all age classes. However, this has not been shown for the Lutjanidae and it appears from this study and others that otoliths are a reliable aging tool across all age classes. Further, the tagging studies also support the idea that rings formed in the otoliths are annuli.

The high precision of repeated age readings and the validation of annuli across a range of ages indicate that otolith sections represent a highly reliable method for the ageing of *Lutjanus* species. The location of the first annulus is sometimes difficult to establish and often requires experience in the interpretation of the structure of these otoliths. However, all subsequent annuli are distinct and easily interpretable. Additionally, otolith sections do not have the problems associated with reading whole otoliths, such as the potential underestimation of true age in older fishes (eg. Ferreira and Russ, 1994).

Growth in otolith length with increasing age in both species appears to be linear only up to a certain size of fish (Figures 6.11 and 6.14), after which otolith growth increases are measurable only in otolith weight with the additional depositions occurring mainly on the proximal surface of the sagittae along the sulcul region (eg. Boehlert, 1985; Brothers, 1987; Beamish and McFarlane, 1987). Otolith lengths showed a poor correlation with fish age, while otolith weight exhibited a strong linear relationship with age and indicates otolith growth increments are continuous with age, independent of fish growth. This supports the suggestion of Mosegaard *et. al.* (1988) that a process other than somatic growth, such as metabolic rate governs the rate of otolith accretion. Otolith growth occurs at a faster rate than the torso during slow somatic growth especially as individuals approach asymptotic length, and therefore they are superior structures for recording age in slow growing and old fish (Casselman, 1990) and are highly reliable (low IAPE, high precision). The high correlation between otolith weight and age in both species indicate that otolith weight measurements may provide a quick method of assessing age and growth of these fishes in preference to the lengthy process of sectioning and reading numerous otoliths. However, although appropriate models based on otolith weight-fish size relationships can predict ages in populations where growth rates are known, they have a limited application in ageing fish from wild populations with highly variable growth rates (Pawson, 1990).

Both *L adetii* and *L. quinquelineatus* are relatively long lived, slow growing and have low rates of natural mortality. The initial growth rates of both species appear to be relatively fast, but growth declines rapidly as asymptotic length is approached. The variability in the observed lengths-at-age of both *L. adetii* and *L. quinquelineatus* indicate that length is a poor predictor of age, especially in fish older than age 5. The majority of growth occurs within the first 5 years of life of both species, with length becoming essentially asymptotic after this age. Similarly, Mathews and Samuel (1985) reported virtual cessation of growth in length of *L. malabaricus* at about 7-8 years of age, with length becoming essentially asymptotic after this age. Therefore, the distinction of age classes of older fish would not be possible because of the complete overlap of size-specific age frequency distributions (see Figures 6.16 and 6.20).

The growth parameter estimates reported here are similar to those reported by Loubens (1980b) for the same species in New Caledonia (Table 6.9). However, the length-weight relationships of both species in this study were relatively different from the New Caledonia populations (Figures 6.3 and 6.4). The distribution of *L. adetii* in this study is truncated with few specimens collected under 5 years of age and this may have biased comparisons between the two populations.

Comparisons of growth parameters and longevities among other *Lutjanus* species are difficult because other estimates are often based on different ageing methods (see Table 6.9a and 6.9b). The most frequently used method of determining age and growth in *Lutjanus* species has been the analysis of rings formed on calcareous structures (73% of studies - Table 6.9a; see also review of Manooch, 1987). However, a variety of methodologies have been utilised to examine the rings formed on calcareous structures. The mean age of *Lutjanus* species derived from studies based on annuli in sectioned otoliths (21.5 years, n = 22) is nearly double the mean age based on the analysis of scales (11.5 years, n = 17) and is substantially higher than studies based on annuli in vertebrae (8.7 years, n = 15) and whole otoliths (6.8 years, n = 12) or on mean ages based on length frequency analysis (5.8 years, n = 12) (see Tables 6.9a and 6.9b).

Length frequency analysis underestimates actual age in *Lutjanus* species because there is a lack of clear modal classes in the length distributions of the older age fishes (eg. Figures 6.16 and 6.20). Age estimates based on daily bands in otoliths that match length frequency analysis (eg. Morales-Nin and Ralston, 1990) must therefore be interpreted with caution. Additionally, Casey and Natanson (1992) provide evidence that ages can be underestimated by vertebral counts in elasmobranches and this may similarly apply to the use of vertebral counts in reef fishes, further supporting the need for the validation of age across a large range of age classes. Previous studies have also occasionally utilised back-calculated rather than observed lengths-at-age and recent evidence indicates that back-calculated lengths-at-age may generate biased results (Campana, 1990; Ricker, 1992). Despite this, most previous studies of *Lutjanus* species conclude that they are long lived and slow growing, with longevity estimates generally in excess of 10 years (Tables 6.9a and 6.9b). However, growth parameter estimates based on sectioned otoliths appear the most accurate. Furthermore, the validation of increment formation (age) in hard parts on a deterministic time scale (eg. days, years) is essential to ensure accuracy is sufficient to make management decisions with a high level of precision.

The longevity of both species differs from those described by Loubens (1980b) in New Caledonia. Loubens (1980b) estimated a maximum longevity for male and female *L. adetii* of 33 and 37 years respectively (Table 6.9a), while in the present study observed maximum ages were 24 and 23 years, respectively. Additionally, Loubens (1980b) estimated a maximum longevity for both male and female *L. quinquelineatus* of 18 years (Table 6.9a), while in the present study observed maximum ages of males was 30 years and 31 years for females.

The shape of the growth curve of both of these lutjanid species was initially quite steep over the first few years and then became essentially asymptotic. This form of asymptotic growth curve suggests that catch curves describing natural mortality as a function of age will also be initially steep (representing high initial mortality) and then flatten substantially over the asymptotic growth period (low mortality) before increasing again with senility. This is in contrast to most classical fisheries models which assume that natural mortality (M) is constant and low over a wide range of ages. Sampling programs that can obtain a representative sample of individuals over the entire size range (especially small young fish and large old fish) of a species with this type of asymptotic growth curve will test the generality of this hypothesis and may facilitate the evolution of new polynomial functions in order to better describe schedules of natural mortality for these long lived species. In this study however, mortality rates were derived using the classical linear age based catch curve method of Beverton and Holt (1957) and Ricker (1975).

The estimates of annual instantaneous rates of total mortality in this study were low for lutjanids (Tables 6.9a and 6.9b), with the mortality estimates of *L. adetii* similar to those described by Mason and Manooch (1985) for *L. analis*, a larger Atlantic species. The mortality estimates of *L. quinquelineatus* were similar to those described by Mathews and Samuel (1985) for the larger *L. malabaricus*, a similarly long lived species which has a longevity of 46 years. Because exploitation of these species is negligible in the study area, the total mortality rate estimates (Z) can be considered as an independent estimate of natural mortality (M). Natural mortality in lutjanids is mainly due to predation, parasitism, disease and senility (review of Ralston, 1987). Predation by the serranid *Plectropomus leopardus* on *L. quinquelineatus* was observed directly and predation is probably the main agent of natural mortality for these smaller lutjanid species. However, it is clear form this study that the natural mortality rate of unexploited populations of lutjanids is exceptionally low.

The regression equation of Hoenig (1983) was more conservative in the estimation of total mortality than catch curves and is a good first approximation for long lived lutjanid fishes. Conversely, the estimates of natural mortality obtained from the equations of Pauly (1980) provide overestimates of natural mortality rates for long lived fishes such as *L. adetii* and *L. quinquelineatus* and hence underestimate survivorship. Ralston (1987) has argued that in the absence of other information, a reasonable estimate of M for a lutjanid is 2K. The data presented in this study for *L. adetii* generally conform to that suggestion. However, the Ralston (1987) equation provided an overestimate of natural mortality in the longer lived *L. quinquelineatus*. Similarly, Mathews and Samuel (1985) assumed natural mortality to be 25% of the total mortality derived from catch curves because the Pauly estimate was substantially higher than Z. Mason and Manooch (1985) also judged the natural mortality estimate of Pauly to be false as it was higher than the Z derived from catch curves. Additionally, in a survey of studies from the literature (Tables 6.9a and 6.9b) where natural mortality rates have been derived for *Lutjanus* species, 89.1% of these studies based estimates on the equations of Pauly and Ralston (82.6% and 6.5%, respectively). It is therefore highly likely that most of these studies have provided overestimates of the natural mortality rates of *Lutjanus* species. It has also been shown that if natural mortality is overestimated, fishing mortality (F) is generally underestimated (Agger *et. al.*, 1973). This has important implications for fisheries management as yield per recruit analyses, estimates of stock size (eg. Virtual Population Analysis) and models of potential yields of fish stocks require estimates of the rate of natural mortality. Consequently, overestimates of natural mortality rates will provide overestimates of the potential yield of fish stocks and this may lead to the overexploitation of these resources and ultimately recruitment overfishing. Clearly, regression methods used to produce estimates of total and natural mortality rates such as those described by Pauly (1980), Hoenig (1983) and Ralston (1987) should be applied with caution. Furthermore, it can be assumed that the equation of Pauly (1980) will provide overestimates of natural mortality in long lived fishes.

The life history characteristics of *L. adetii* and *L. quinquelineatus* that have been described herein have important fisheries management implications. Their slow growth, protracted longevity and low natural mortality rates imply that both these tropical snappers are vulnerable to overfishing despite their small size. Further, if a commercial fishery develops for these species in the central Great Barrier Reef or recreational fishing pressure increases, conservative catch regulations should be promulgated until the effects of fishing on stock dynamics can be resolved.

Table 6.1 : Length weight relationships of *Lutjanus adetii* and *L. quinquelineatus* from the central Great Barrier Reef. For each species estimates were obtained of the parameters a and b of the relationship $W = aL^b$, the sample size (n), the regression r^2 value and the length type used (lengths are in mm and weight in g). Sexes demonstrating significant allometric growth ($p < 0.05$) are marked with an asterisk.

Species	a	b	n	r^2	Length Type
L. adetii	2.395×10^{-5}	2.9356	303	0.930	Fork
L. adetii	6.613×10^{-5}	2.8349	303	0.928	Standard
L. adetii (male)	1.780×10^{-5}	2.9925	132	0.951	Fork
L. adetii (female)*	4.415×10^{-5}	2.8217	171	0.912	Fork
L. quinquelineatus	1.232×10^{-5}	3.0663	577	0.964	Fork
L. quinquelineatus	3.955×10^{-5}	2.9476	577	0.960	Standard
L. quinquelineatus (male)	1.581×10^{-5}	3.0201	304	0.929	Fork
L. quinquelineatus (female)	1.815×10^{-5}	2.9912	264	0.944	Fork

Table 6.2 : Analyses of covariance comparing length-at-age, weight-at-age and weight-at-length among sexes of both *Lutjanus adetii* and *L. quinquelineatus* (significant p values are in bold type).

Lutjanus adetii

Source of Variation	df	MS	F	p
Dependent variable : Length-at-age				
Sex	1	2101.17	11.369	**< 0.001**
Residual	340	184.82		
Dependent variable : Weight-at-age				
Sex	1	38988.72	21.196	**< 0.001**
Residual	300	1839.42		
Dependent variable : Weight-at-length				
Sex	1	5360.31	25.95	**< 0.001**
Residual	300	206.59		

Lutjanus quinquelineatus

Source of Variation	df	MS	F	p
Dependent variable : Length-at-age				
Sex	1	20922.09	154.931	**< 0.001**
Residual	564	135.04		
Dependent variable : Weight-at-age				
Sex	1	95830.09	165.26	**< 0.001**
Residual	564	579.89		
Dependent variable : Weight-at-length				
Sex	1	1694.54	14.98	**< 0.001**
Residual	565	113.14		

Table 6.3 : One-way analyses of variance comparing mean length, age and weight among sexes of both *Lutjanus adetii* and *L. quinquelineatus* (significant p values are in bold type).

Lutjanus adetii

Source of Variation	df	MS	F	p
Dependent variable : Fork Length (mm)				
Sex	1	916.43	3.2213	> 0.05
Residual	342	284.49		
Dependent variable : Age (years)				
Sex	1	31.312	1.9527	> 0.15
Residual	341	16.035		
Dependent variable : Clean Weight (g)				
Sex	1	29343.1	11.375	< **0.001**
Residual	301	2579.51		

Lutjanus quinquelineatus

Source of Variation	df	MS	F	p
Dependent variable : Fork Length (mm)				
Sex	1	24641.5	87.74	< **0.001**
Residual	566	280.833		
Dependent variable : Age (years)				
Sex	1	43.2048	1.1686	> 0.25
Residual	565	36.9719		
Dependent variable : Clean Weight (g)				
Sex	1	110891.9	104.295	< **0.001**
Residual	566	1063.248		

Table 6.4 : Comparison of coefficients of determination (r^2) for the linear relationship between otolith weight, otolith length and otolith breadth among otolith pairs of *Lutjanus adetii* and *L. quinquelineatus* (all regressions were significant at $p < 0.001$).

Variables	*L.adetii*	*L. quinquelineatus*
Otolith Weight Left vs Right	0.9897	0.9960
Otolith Length Left vs Right	0.9259	0.9585
Otolith Breadth Left vs Right	0.8502	0.9277

Table 6.5 : Comparison of 2 counts of annuli in otolith sections of *Lutjanus adetii*. Difference refers to the deviation of the first count from the second count (-ve indicates that the second count was lower than the first; +ve indicates that the first count was lower than the second). Variation refers to the percentage of otoliths per age class whose counts varied.

Second	Difference					Variation among readings		
Count	-1	0	1	2	Total	0	±1	±2
0								
1								
2		1			1	100.0		
3		5			5	100.0		
4	1	8			9	88.9	11.1	
5		14			14	100.0		
6	1	38	4		43	88.4	11.6	
7		70	6	1	77	90.9	7.8	1.3
8	2	51	5		58	87.9	12.1	
9		34	8		42	81.0	19.0	
10		20	1		21	95.2	4.8	
11	1	18	3	1	23	78.3	17.4	4.3
12		11	2		13	84.6	15.4	
13		10			10	100.0		
14		8	1		9	88.9	11.1	
15	1	11	1		13	84.6	15.4	
16		6			6	100.0		
17		5			5	100.0		
18		3			3	100.0		
19		1			1	100.0		
20		7			7	100.0		
21		5			5	100.0		
22		1	1		2	100.0		
23		1			1	100.0		
24		1			1	100.0		
Total	6	329	32	2	369			
% of total	1.6	89.2	8.7	0.5				

Table 6.6 : Comparison of 2 counts of annuli in otolith sections of *Lutjanus quinquelineatus*. Difference refers to the deviation of the first count from the second count (-ve indicates that the second count was lower than the first; +ve indicates that the first count was lower than the second). Variation refers to the percentage of otoliths per age class whose counts varied.

Second	Difference						Variation among readings		
Count	-2	-1	0	1	2	Total	0	±1	±2
0									
1			3			3	100.0		
2		3	11			14	78.6	21.4	
3		2	17			19	89.5	10.5	
4	1	4	29			34	85.3	11.8	2.9
5	2	7	28	3		40	70.0	25.0	5.0
6	1	5	14	1		21	66.7	28.6	4.8
7	1	4	19			24	79.2	16.7	4.2
8		2	13			15	86.7	13.3	
9		2	11			13	84.6	15.4	
10	1	2	8	1		12	66.7	25.0	8.3
11		1	8			9	88.9	11.1	
12	1	3	16	2		22	72.7	22.7	4.6
13		1	5			6	83.3	16.7	
14		3	12	1		16	75.0	25.0	
15		1	3	2		6	50.0	50.0	
16		1	5	3		9	55.6	44.4	
17		2	6			8	75.0	25.0	
18			3	2	1	6	50.0	33.3	16.7
19			2	2		4	50.0	50.0	
20			8			8	100.0		
21		2	3	1		6	50.0	50.0	
22			5			5	100.0		
23			2	1		3	66.7	33.3	
24			3			3	100.0		
25			2			2	100.0		
26									
27									
28									
29									
30									
31			1			1	100.0		
Total	7	45	237	19	1	309			
% of total	2.3	14.6	76.7	6.1	0.3				

Table 6.7 : Comparison between otolith dimensions and sizes and ages of *L. adetii* and *L. quinquelineatus*. The predictive equations are of the simple linear regression form $y = a + bx$, and the multiple regression form $y = a + b_1x_1 + b_2x_2$. Codes for the independent variables are described in the text (all lengths are in mm and weights in g). For regression analyses fish length, clean weight and age were used as the dependent variables (all regressions were significant at $p < 0.001$; in the multiple regression models using more than one independent variable, adjusted r^2 values are displayed for comparative purposes).

L. adetii

Dep. Var.	Ind. Var.	Sample Size	Equation	r^2	SE of Estimate
FL	HL	96	FL = 59.057 + 2.622 (HL)	0.816	6.2631
FL	UJL	96	FL = 61.062 + 6.177 (UJL)	0.772	6.9754
FL	SNL	96	FL = 117.653 + 5.1564 (SNL)	0.740	7.4467
FL	Ol	363	FL = 41.684 + 19.0856 (Ol)	0.609	10.525
FL	Ow	369	FL = 188.395 + 307.45 (Ow)	0.576	10.988
FL	Ob	369	FL = 62.849 + 26.612 (Ob)	0.568	11.090
CW	Ol	303	CW = 65.116 (Ol) - 440.86	0.611	32.265
CW	Ob	303	CW = 83.616 (Ob) - 322.33	0.542	35.010
CW	Ow	303	CW = 85.66 + 903.213 (Ow)	0.498	36.647
Age	Ow + CW	303	Age = 106.30 (Ow) - 0.0184 (CW) - 4.47	0.836	1.6331
Age	Ow + SL	324	Age = 4.297 + 105.85 (Ow) - 0.0639 (SL)	0.829	1.6548
Age	Ow + ED	96	Age = 69.845 (Ow) + 0.3986 (ED) - 10.58	0.810	1.5037
Age	Ow	368	Age = 87.901 (Ow) - 5.75	0.807	1.7448
Age	ED	96	Age = 2.0081 - 30.749 (ED)	0.684	1.9503
Age	Ob	368	Age = 5.827 (Ob) - 29.714	0.459	2.9176
Age	Ol	362	Age = 3.738 (Ol) - 29.7472	0.354	3.1950

L. quinquelineatus

Dep. Var.	Ind. Var.	Sample Size	Equation	r^2	SE of Estimate
FL	HL	130	FL = 10.063 + 3.3333 (HL)	0.956	5.2315
FL	UJL	130	FL = 18.845 + 7.395 (UJL)	0.942	6.0438
FL	SNL	130	FL = 48.466 + 8.296 (SNL)	0.856	9.4780
FL	Ol	573	FL = 6.2558 + 21.2725 (Ol)	0.845	7.9755
FL	Ob	573	FL = 35.228 + 25.633 (Ob)	0.793	9.2089
FL	Ow	573	FL = 152.151 + 364.882 (Ow)	0.599	12.819
CW	Ol	572	CW = 35.935 (Ol) - 185.896	0.736	18.803
CW	Ob	572	CW = 43.045 (Ob) - 135.359	0.684	20.583
CW	Ow	572	CW = 57.724 + 642.66 (Ow)	0.568	24.077
Age	Ow + SL	573	Age = 3.75 + 159.29 (Ow) - 0.075 (SL)	0.930	1.6093
Age	Ow + CW	572	Age = 155.74 (Ow) - 0.031 (CW) - 3.80	0.927	1.6478
Age	Ow	573	Age = 135.81 (Ow) - 5.5891	0.912	1.8061
Age	Ow + ED	129	Age = 1.012 + 146.415 (Ow) - 0.4891 (ED)	0.898	1.7435
Age	ED	129	Age = 1.9419 (ED) - 23.348	0.596	3.4884
Age	Ob	573	Age = 6.513 (Ob) - 30.62	0.563	4.0317
Age	Ol	573	Age = 5.0583 (Ol) - 34.96	0.525	4.2019

Table 6.8 : Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth function ($L_t = L_\infty\ (1 - e^{-K\ (t\ -\ t0)}\ )\ )$ and means, minima and maxima of fork length (mm), age (years) and clean weight (g) for *Lutjanus adetii* and *L. quinquelineatus* from the central Great Barrier Reef (n = sample size).

Parameters	*Lutjanus adetii*			*Lutjanus quinquelineatus*		
	Male	Female	All Fish	Male	Female	All Fish
n	147	196	369	304	264	577
L_∞ (FL)	269.1	315.1	265.2	214.5	204.3	206.9
ASE	6.651	93.15	4.229	1.183	2.153	0.9794
K	0.1652	0.0289^{+}	0.1454	0.2599	0.1664	0.3064
ASE	0.0447	0.0387	0.0285	0.0198	0.0231	0.0174
t_0	-6.117	-40.29^{+}	-8.077	-3.427	-7.552	-2.587
ASE	2.459	33.06	2.132	0.4622	1.271	0.2708
r^2	0.385	0.317	0.390	0.705	0.617	0.638
n	147	197	370	304	264	578
FL_{mean}	243.32	240.02	241.07	198.57	185.36	191.64
FL_{min}	185	202	185	139	134	60*
FL_{max}	301	285	301	233	225	233
n	147	196	369	304	263	577
t_{mean}	8.946	9.508	9.274	9.474	8.886	9.118
t_{min}	2	3	2	1	1	0.25
t_{max}	24	23	24	30	31	31
n	132	171	303	304	264	577
CW_{mean}	250.84	230.99	239.64	141.12	113.11	127.26
CW_{min}	111	137	111	47	41	3
CW_{max}	451	348	451	228	215	228

* the sex of juvenile *L. quinquelineatus* was indeterminable.

\+ the poor fit to the female *L. adetii* data is an artefact of the range of ages fitted. This has a profound effect on the parameter estimates from a von Bertalanffy fit (see Hirschhorn, 1974).

Table 6.9a : Growth parameters of the von Bertalanffy growth function (L_∞, K, t_0), mortality parameters (Z, M, F), longevity and method of growth determination of *Lutjanus* species known to occur on the Great Barrier Reef (modified from Williams and Russ, 1994; Otoliths : W = whole; TS = transverse sections).

Species	Growth Parameters			Mortality Parameters			Maximum Longevity (yrs)	Method of Growth Determination	Locality	Reference
	L_∞ (cm)	K	t_0(yr.)	Z	M	F				
L.adetii $_{(m)}$	33.4(SL)	0.26	--	--	0.67 ^{P}	--	33	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. adetii $_{(f)}$	29.3(SL)	0.343	--	--	0.83 ^{P}	--	37	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. argentimaculatus	82.7(FL)	0.26	--	--	0.65 ^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. argentimaculatus	75.5(FL)	0.20	--	--	0.51 ^{P}	--	--	Elefan	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. argentimaculatus	105(TL)	0.187	-0.0437	--	--	--	7	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1986)
L. argentimaculatus	L_{max} = 60.7(SL)		--	0.25 ^{H}	--	--	18	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. bohar	81.0(FL)	0.30	--	--	0.64 ^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. bohar	81.7(FL)	0.27	0.013	0.640 ^{LC} $_{Deep}$ 1.181 ^{LC} $_{Shallow}$	0.59 ^{P}	--	10	Petersen	Kavieng, PNG	Wright *et. al.* (1986)
L. bohar	52.0(SL)	0.11	--	--	0.34 ^{P}	--	38	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. bohar	66.0(SL)	0.27	--	--	--	--	13	Scales	Kenya East Africa	Talbot (1960)
L. bohar	89.0(TL)	0.33	--	--	--	--	4	Petersen	Seychelles	Wheeler & Ommaney (1953)
L. carponotatus	56.0(FL)	0.31	--	--	0.72 ^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. decussatus	(paper not sighted, reference cited in Loubens, 1980b)				--	--	16	Aquarium	----	de Graaf (1977)
L. erythropterus $_{(m)}$	60.0(FL)	0.41	0.21	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. erythropterus $_{(f)}$	60.0(FL)	0.44	0.21	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. erythropterus	72.1(FL)	0.2136	-0.8288	--	--	--	7	Vertebrae	Arafura Sea	Ju *et. al.* (1989)
L. erythropterus	72.6(FL)	0.2096	-0.7140	--	--	--	7	Vertebrae	N.W. Australia	Ju *et. al.* (1988)
L. fulviflamma	24.8(SL)	0.30	--	--	0.80 ^{P}	--	23	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. fulvus	28.0(TL)	0.89	-0.05	--	--	--	5	Otoliths (daily bands)	French Polynesia	Caillart *et. al.* (1986)
L. gibbus	36.0	0.81	--	--	0.80 ^{P}	--	--	Otoliths (daily bands)	French Polynesia	Morize & Caillart (1988)

Table 6.9a : continued.

Species	Growth Parameters			Mortality Parameters			Maximum Longevity (yrs)	Method of Growth Determination	Locality	Reference
	L_∞ (cm)	K	t_0(yr.)	Z	M	F				
L. gibbus	44.2(FL)	0.31	--	--	--	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. gibbus	L_{max} = 37.0(SL)		--	0.25 ^{H}	--	--	18	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. johnii	91.6(FL)	0.116	--	--	--	--	9	Scales	Andaman Sea	Druzhinin (1970)
L. kasmira	34.0(TL)	0.29	-1.37	--	--	--	6	Otoliths (daily bands)	Hawaii	Morales-Nin & Ralston (1990)
L. kasmira	33.71	0.27	--	--	--	--	6	Otoliths (daily bands)	Hawaii	Morales-Nin (1989)
L. kasmira	39.6(FL)	0.212	-0.75	--	--	--	5	Otoliths (daily bands)	Marianas (Deepwater)	Ralston & Williams (1988a)
L. kasmira	29.6(FL)	0.384	-1.349	--	--	--	4	Otoliths (daily bands)	American Samoa	Ralston & Williams (1988b)
L. kasmira	21.1(SL)	0.38	--	--	0.98 ^{P}	--	8	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. lutjanus	20.0(SL)	0.265 (0.26-0.27)	-0.089	2.12	--	--	2	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1987)
L. lutjanus	25.1(TL)	0.497	0.0888	--	--	--	3	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1986)
L. lutjanus $^{\text{Total Length-at-age}}$	22.0(TL)	0.144	-3.397	1.53	0.49 ^{P}	1.04	12	Scales	Gulf of Suez	Sanders *et. al.* (1984)
L. lutjanus $^{\text{Age-at-Total Length}}$	24.4(TL)	0.101	-4.681	1.53	0.49 ^{P}	1.04	12	Scales	Gulf of Suez	Sanders *et. al.* (1984)
L. malabaricus $_{(m)}$	98.7(FL)	0.18	-0.13	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. malabaricus $_{(f)}$	83.8(FL)	0.23	-0.13	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. malabaricus $_{(m)}$	95.0(FL)	--	--	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson *et. al.* (1988)
L. malabaricus $_{(f)}$	81.6(FL)	--	--	--	--	--	7	Otoliths (W)	Great Barrier Reef	McPherson *et. al.* (1988)
L. malabaricus	86.1(FL)	0.2524	-0.0849	--	0.3403 +	--	--	Length Frequency	N.W. Australia	Yeh (1988)
L. malabaricus	52.0(FL)	0.37	--	--	0.82 ^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. malabaricus	59.5(SL)	0.195 (0.19-0.20)	-0.054	0.71	--	--	6	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1987)
L. malabaricus	--	--	--	0.499 ^{HE} (0.37-0.69)	--	--	10	Length Frequency	N.W. Australia	Yeh & Chen (1986)

+ = natural mortality estimate derived from the plot of Z vs. F (see Ricker, 1975).

Table 6.9a : continued.

Species	Growth Parameters			Mortality Parameters			Maximum Longevity	Method of Growth Determination	Locality	Reference
	L_∞ (cm)	K	t_0(yr.)	Z	M	F	(yrs)			
L. malabaricus	60.0(SL)	0.31	--	0.447^{CC} (0.441)	0.545^{P}	--	--	Otoliths (daily bands)	Vanuatu	Brouard & Grandperrin (1985)
L. malabaricus	70.7(SL)	0.168	0.418	--	--	--	10	Vertebrae/Scales	N.W. Australia	Edwards (1985)
L. malabaricus	68.9 (L_{max} = 89.0)	0.358	-0.76	0.176^{CC}	0.040 ++ (0.664^{P})	0.136	46	Otoliths (TS)	Kuwait	Mathews & Samuel (1985)
L. malabaricus	86.1(FL)	0.252	-0.085	--	--	--	10	Otoliths (TS)	N.W. Australia	Chen *et. al.* (1984)
L. malabaricus	68.0(TL)	0.344	0.544	--	--	--	31	Otoliths (TS)	Kuwait	Mansour (1982)
L. malabaricus	96.4(FL)	0.1195	-1.2913	--	--	--	8	Vertebrae	Arafura Sea	Lai & Liu (1979)
L. malabaricus	93.7(FL)	0.1257	-1.3391	--	--	--	8	Vertebrae	N.W. Australia	Lai & Liu (1979)
L. malabaricus	92.7(FL)	0.1417	-0.8185	--	--	--	11	Vertebrae	Gulf of Tonkin	Lai & Liu (1974)
L. malabaricus	96.5(FL)	0.1484	-0.6698	--	--	--	10	Vertebrae	Northern Sunda	Lai & Liu (1974)
L. malabaricus	>90(FL)	0.132	--	--	--	--	--	Scales	Andaman Sea	Druzhinin (1970)
L. monostigma	55.0(FL)	0.22	--	--	0.60^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. monostigma	47.9(FL)	0.23	--	--	0.64^{P}	--	--	Elefan	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. quinquelineatus	17.3(SL)	0.366	--	--	1.02^{P}	--	22	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. rivulatus	70.0(FL)	0.22	--	--	0.73^{P}	--	--	Petersen	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. rivulatus	67.4(FL)	0.33	--	--	0.55^{P}	--	--	Elefan	Kavieng, PNG	Wright *et. al.* (unpubl.)
L. sebae	95.1(FL)	0.307	--	--	--	--	--	Elefan	Seychelles	Mees (1992)
L. sebae	92.9(FL)	0.157	--	--	--	--	--	MPA	Seychelles	Mees (1992)
L. sebae $_{(m)}$	90.0(FL)	0.38	--	1.141^{LC}	0.65^{P}	0.491	--	Elefan	Seychelles	Mees (1992)
L. sebae $_{(f)}$	84.0(FL)	0.27	--	1.500^{LC}	0.53^{P}	0.97	--	Elefan	Seychelles	Mees (1992)
L. sebae $_{(m)}$	103(FL)	0.15	-0.32	--	--	--	8	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. sebae $_{(f)}$	88.7(FL)	0.18	-0.32	--	--	--	8	Otoliths (W)	Great Barrier Reef	McPherson & Squire (1992)
L. sebae	--	--	--	--	--	--	27	Otolith (TS)	N.W. Australia	Seyama *et. al.* (1991)
L. sebae	84.1(FL)	0.1662	-0.378	(Walford Plot)		--	11	Vertebrae	Arafura Sea	Liu & Yeh (1991)

++ = natural mortality was assumed to be 25% of Z, since the Pauly estimate (0.664) was substantially higher than Z.

Table 6.9a : continued.

Species	Growth Parameters			Mortality Parameters			Maximum Longevity (yrs)	Method of Growth Determination	Locality	Reference
	L_{∞} (cm)	K	t_0(yr.)	Z	M	F				
L. sebae	79.8(FL)	0.1797	-0.403	(Non linear regression)		--	11	Vertebrae	Arafura Sea	Liu & Yeh (1991)
L. sebae	96.0(FL)	0.23		0.73 ^{LC} 0.78 ^{J}	0.48 ^{P}	0.25 0.3	--	Length Frequency	Seychelles	Lablache & Carrara (1988)
L. sebae $_{(m)}$	102(FL)	--	--	--	--	--	8	Otoliths (W)	Great Barrier Reef	McPherson *et. al.* (1988)
L. sebae $_{(f)}$	87.5(FL)	--	--	--	--	--	8	Otoliths (W)	Great Barrier Reef	McPherson *et. al.* (1988)
L. sebae	81.7(FL)	0.13	-1.09	--	--	--	10	Vertebrae	N.W. Australia	Yeh *et. al.* (1986)
L. sebae	85.1(FL)	0.157	-1.015	--	--	--	11	Scales	Gulf of Aden	Druzhinin & Filatova (1980)
L. sebae	L_{max} = 69.5(SL)		--	0.13 ^{H}	--	--	35	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. vitta $_{(m)}$ Back calculated length-at-age	40.3(FL)	0.26	0.02	--	--	--	8	Urohyals	N.W. Australia	Davis & West (1992)
L. vitta $_{(f)}$ Back calculated length-at-age	32.3(FL)	0.39	0.17	--	--	--	7	Urohyals	N.W. Australia	Davis & West (1992)
L. vitta $_{(m)}$ Length at absolute age	42.2(FL)	0.22	-0.56	0.98 ^{CC}	0.59 ^{R}	--	8	Urohyals	N.W. Australia	Davis & West (1992)
L. vitta $_{(f)}$ Length at absolute age	32.5(FL)	0.37	-0.23	0.98 ^{CC}	0.92 ^{R}	--	7	Urohyals	N.W. Australia	Davis & West (1992)
L. vitta	24.2(SL)	0.255 (0.25-0.26)	-0.280	2.74 ^{LC}	--	--	2	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1987)
L. vitta	42.5(TL)	0.2563	-0.0001	--	--	--	5	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1986)
L. vitta $_{(m)}$	28.2(SL)	0.324	--	--	0.81 ^{P}	--	12	Otoliths (TS)	New Caledonia	Loubens (1980b)
L. vitta $_{(f)}$	23.8(SL)	0.302	--	--	0.81 ^{P}	--	12	Otoliths (TS)	New Caledonia	Loubens (1980b)

Note : Loubens (1980b) found similar longevities in related lutjanid species such as *Symphorus nematophorus* (L_{max} = 745mm, t_{max} = 43 years) and *Aprion virescens* (L_{max} = 705mm, t_{max} = 26 years) using transverse sections of otoliths.

Legend for derivation of Mortality Parameters

^{H} = estimates of total mortality Z, derived from the equation of Hoenig (1983).
^{CC} = estimates of total mortality Z, derived from catch curves.
^{LC} = estimates of total mortality Z, derived from length converted catch curves.
^{J} = estimates of total mortality Z, derived from Jones' length cohort analyses.
^{HE} = estimates of total mortality Z, derived from Heincke's formula (see Ricker, 1975).
^{P} = estimates of natural mortality M, derived from the equation of Pauly (1980).
^{R} = estimates of natural mortality M, derived from the equation of Ralston (1987).

Table 6.9b : Growth parameters of the von Bertalanffy growth function (L_∞, K, t_0), mortality parameters (Z, M, F), longevity and method of growth determination of *Lutjanus* species that do not occur on the Great Barrier Reef. Localities reviewed include the Atlantic Ocean region and the Indo-Pacific including the eastern Pacific region (Otoliths : W = whole; TS = transverse sections).

Species	Growth Parameters			Mortality Parameters			Maximum Longevity (yrs)	Method of Growth Determination	Locality	Reference
	L_∞ (cm)	K	t_0(yr.)	Z	M	F				
L. analis	102.8	0.17	-0.62	--	--	--	8	Urohyals	Venezuela	Palazon & Gonzalez (1986)
L. analis	86.2(TL)	0.1534	-0.5788	0.33 ^{CC}	0.20 +++ (0.38 ^{P})	0.13	14 (Prob. 15-20)	Otoliths (TS)	Florida East Coast	Mason & Manooch (1985)
L. analis	88.0(FL)	0.152	--	--	--	--	9	Otoliths (?) /Urohyals	Cuba	Claro (1981)
L. analis	81.4(FL)	0.143	--	--	--	--	9	Otoliths (?) /Urohyals	Cuba	Pozo (1979)
L. analis	118(FL)	0.160	--	--	--	--	9	Otoliths (?) /Urohyals	Cuba	Claro (1976)
L. analis	78.1(FL)	0.246	--	--	--	--	9	Otoliths (?) /Urohyals	Cuba	Montes (unpubl.)
L. buccanella (m)	54.0(FL)	0.70	--	--	2.2 ^{P}	--	--	Length Frequency	Jamaica	Thompson and Munro (1983)
L. buccanella (f)	46.0(FL)	0.35	--	--	1.8 ^{P}	--	--	Length Frequency	Jamaica	Thompson and Munro (1983)
L. campechanus	92.5(TL)	0.140	-0.10	--	--	--	10	Otoliths (TS)	Gulf of Mexico	Nelson *et. al.* (1985)
L. campechanus	95.0(TL)	0.175	0.10	0.94 ^{RC} 0.78 ^{CC}	0.20 ^{P}	0.74 0.58	13	Scales	Louisiana	Nelson & Manooch (1982)
L. campechanus	94.1(TL)	0.170	-0.10	0.44 ^{RC} 0.42 ^{CC}	0.19 ^{P}	0.25 0.23	11	Scales	West Florida	Nelson & Manooch (1982)
L. campechanus	97.0(TL)	0.155	-0.01	0.50 ^{RC} 0.50 ^{CC}	0.19 ^{P}	0.31 0.31	12	Scales	East Florida	Nelson & Manooch (1982)
L. campechanus	97.0(TL)	0.165	-0.01	0.42 ^{RC} 0.39 ^{CC}	0.18 ^{P}	0.24 0.21	16	Scales/Otoliths (TS)	Carolinas	Nelson & Manooch (1982)
L. campechanus	94.1(TL)	0.170	-0.10	--	0.195 ^{P}	--	13	Scales	Gulf of Mexico	Nelson & Manooch (1982)
L. campechanus	97.5(TL)	0.160	0.00	--	0.185 ^{P}	--	16	Scales/Otoliths (TS)	Atlantic Ocean	Nelson & Manooch (1982)
L. campechanus	97.0(TL)	0.162	0.010	--	0.19 ^{P}	--	16	Scales/Otoliths (TS)	All areas pooled	Nelson & Manooch (1982)
L. campechanus	95.4(TL)	0.225	--	--	--	--	--	Elefan	Florida	Saloman & Fable (1981)
L. campechanus	--	--	--	--	--	--	4	Scales	Gulf of Mexico	Wakeman *et. al.* (1979)
L. campechanus	60.0(TL)	0.35	--	--	--	--	20	Tag Returns	Florida	Futch & Bruger (1976)
L. campechanus	--	--	--	--	--	--	9	Length Frequency	Gulf of Mexico	Bradley & Bryan (1974)

+++ = natural mortality estimate of Pauly (0.38) was judged to be false as it was higher than Z.

Table 6.9b : continued.

Species	Growth Parameters			Mortality Parameters			Maximum Longevity (yrs)	Method of Growth Determination	Locality	Reference
	L_∞ (cm)	K	t_0(yr.)	Z	M	F				
L. campechanus	--	--	--	--	--	--	6	Scales	Gulf of Mexico	Moseley (1966)
L. griseus	89.0	0.1009	-0.3161	0.39_{North}^{CC} 0.60_{South}^{CC}	0.22^{P}	0.17_{North} 0.38_{South}	21	Otoliths (TS)	East Coast Florida	Manooch & Matheson (1983)
L. griseus	54.8(FL)	0.228	-1.065	--	--	--	9	Otoliths (?)	Cuba	Claro (1983)
L. griseus	51.3(FL)	0.24	-0.616	--	--	--	7	Otoliths (?)	Cuba	Baez-Hidalgo *et. al.* (1980)
L. griseus	--	--	--	--	--	--	9	Scales	Florida	Starck (1971)
L. madras	23.1(SL)	0.27	-0.189	3.07	--	--	2	Length Frequency	Malaysia Peninsula	Ambak *et. al.* (1987)
L. purpureus	98.9(TL)	0.09	0.000	--	--	--	12	Scales	Brazil	Menezes & Gesteira (1974)
L. purpureus	97.7(TL)	0.117	0.000	--	--	--	18	Otoliths	Brazil	Lima (1965)
L. synagris	45.0(FL)	0.23	--	1.65^{LC}	0.527^{R}	1.13	10	Elefan	Puerto Rico	Acosta & Appledoorn (1992)
L. synagris (m)	70.8(TL)	0.22	-0.55	--	--	--	4	Otoliths (W)	Trinidad	Manickehand-Dass (1987)
L. synagris (f)	60.3(TL)	0.20	-0.68	--	--	--	4	Otoliths (W)	Trinidad	Manickehand-Dass (1987)
L. synagris	50.1(TL)	0.1337	-1.49	0.678^{CC}	0.40^{P}	0.28	10	Otoliths (TS)	East Coast Florida	Manooch & Mason (1984)
L. synagris	47.5(FL)	0.20	-0.50	--	0.439	--	6	Otoliths (?)	Cuba	Claro & Reshetnikov (1981)
L. synagris	35.0(FL)	0.35	-0.90	--	0.739	--	6	Otoliths (?)	Cuba	Rodriguez-Pino (1962)
L. vivanus	75.67	0.10	-2.80	--	--	--	--	Urohyals/Otoliths	S.E. Cuban Shelf	Pozo & Espinosa (1982)

Legend for derivation of Mortality Parameters

As for Table 6.9a, with the addition of : ^{RC} = estimates of total mortality Z, derived from the method of Robson and Chapman (1961).

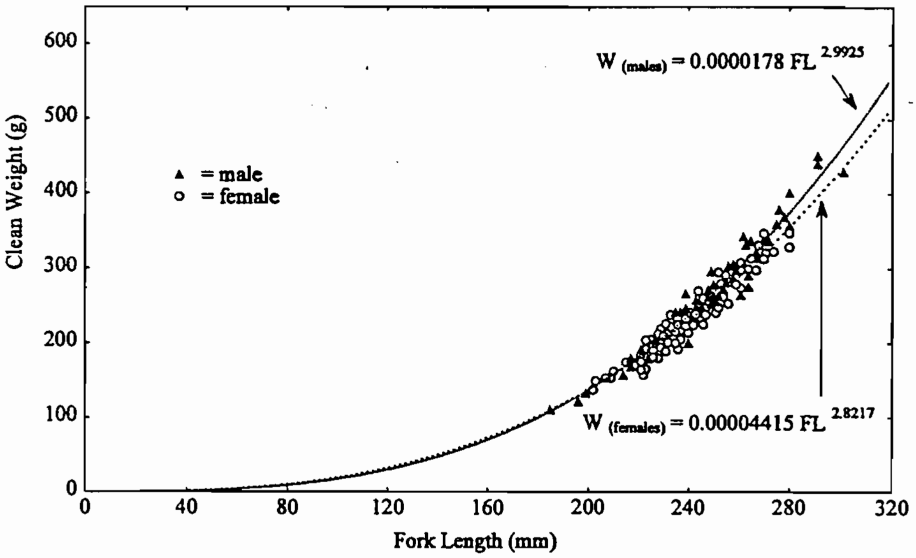


Figure 6.1 : Length-weight relationships for male and female *L. adetii* from the central Great Barrier Reef.

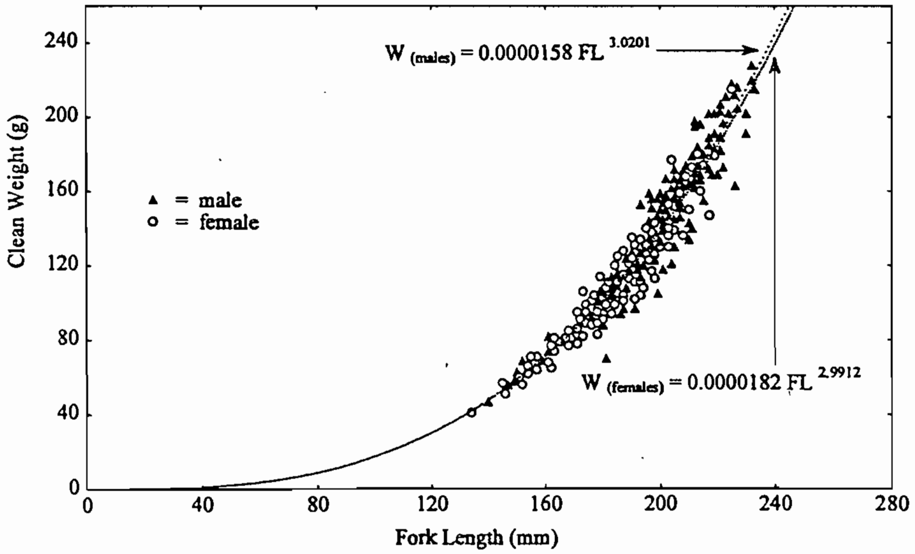


Figure 6.2 : Length-weight relationships for male and female *L. quinquelineatus* from the central Great Barrier Reef.

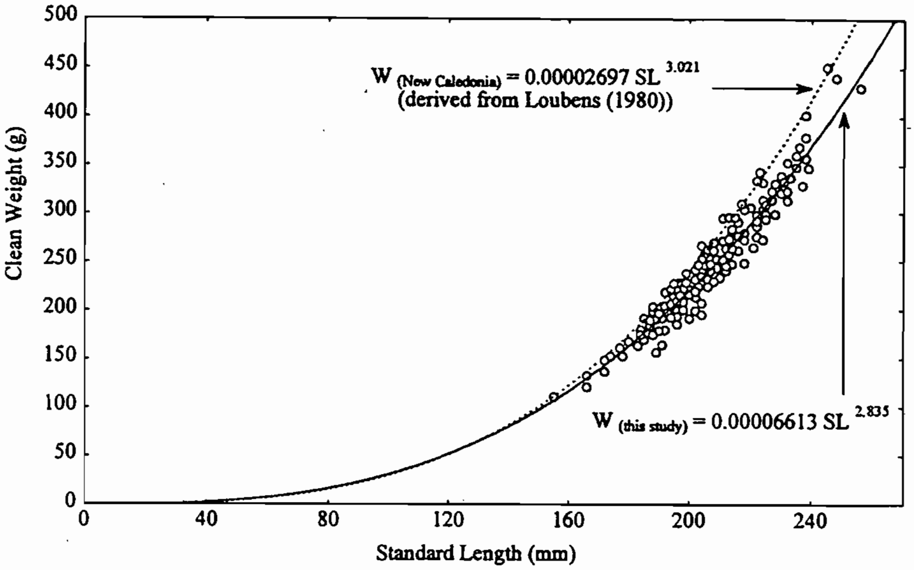


Figure 6.3 : A comparison of the length-weight relationships for populations of *L. adetii* from the central Great Barrier Reef and New Caledonia (raw data is from the GBR population only).

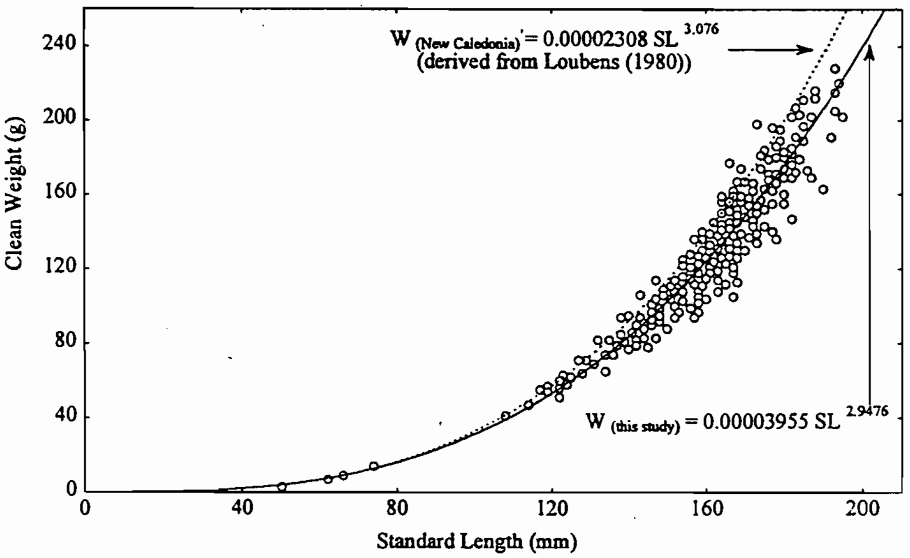


Figure 6.4 : A comparison of the length-weight relationships for populations of *L. quinquelineatus* from the central Great Barrier Reef and New Caledonia (raw data is from the GBR population only).

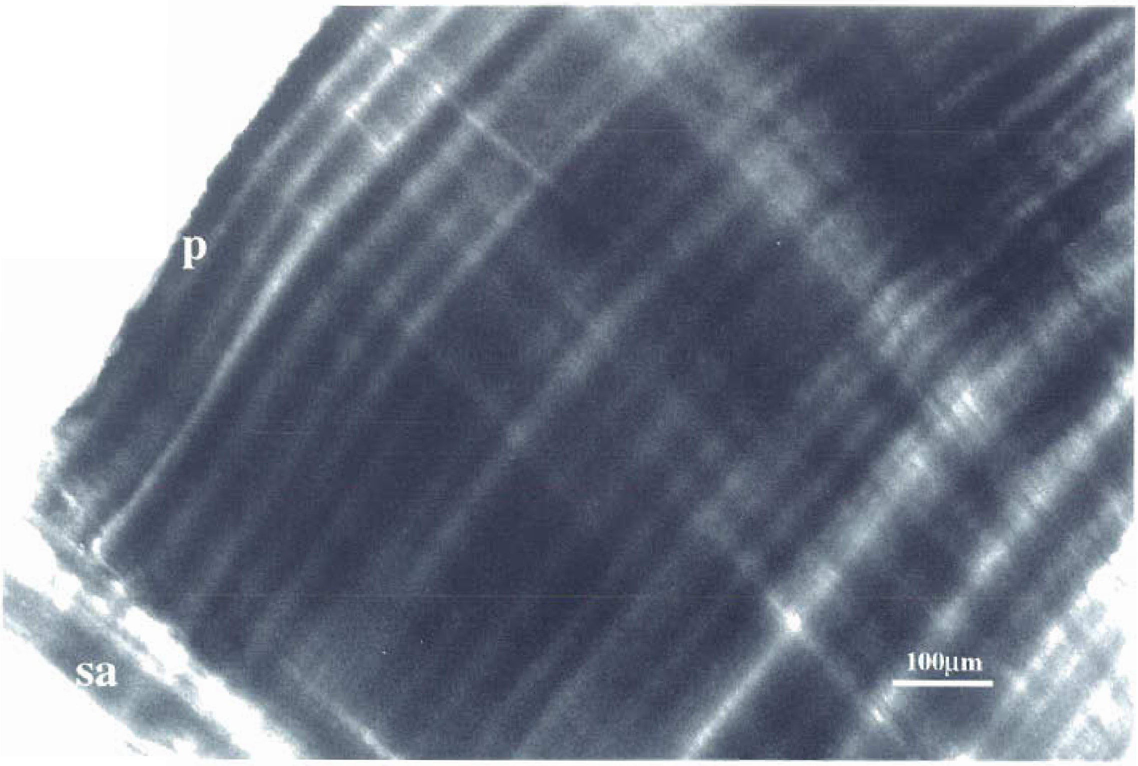


Figure 6.5: Annual bands in a sectioned otolith of *L. quinquelineatus* (observed age 27 years) viewed under reflected light, showing the pattern of opaque (light) and translucent (dark) zones. p = proximal surface, sa = sulcus acousticus.

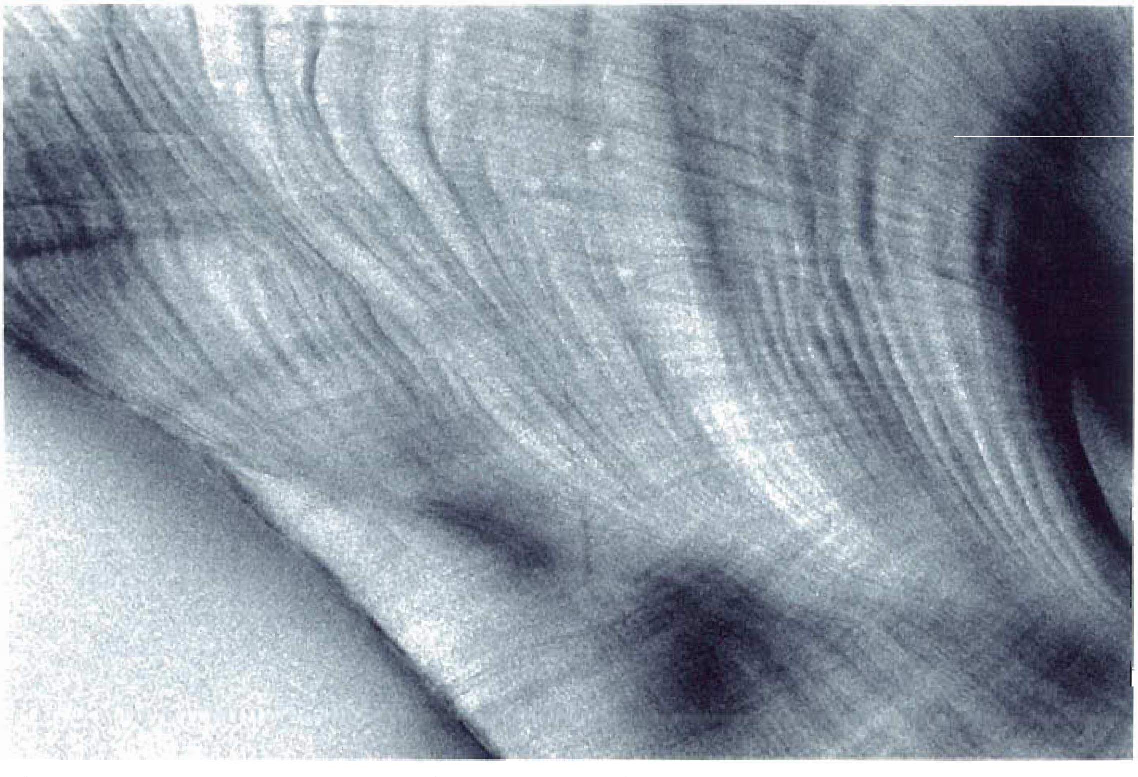


Figure 6.6: Daily bands in a sectioned otolith of a juvenile *L. quinquelineatus*. Magnification x1000.

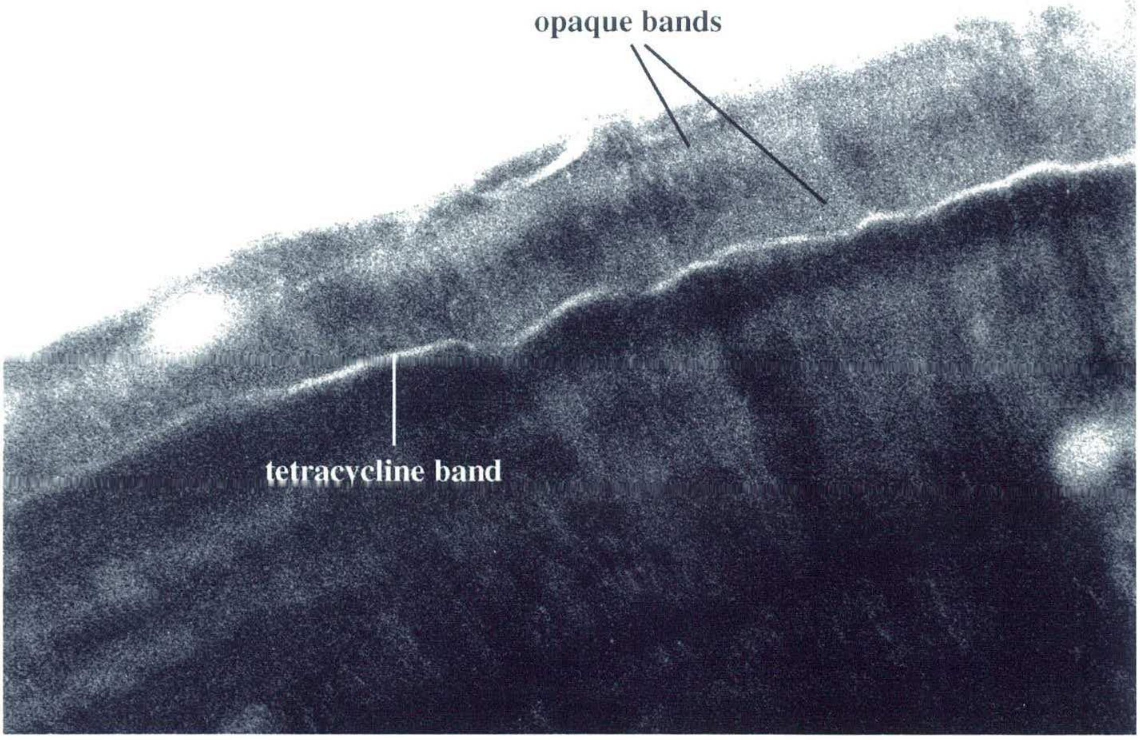


Figure 6.7: Sectioned otolith of a *L. adetii* specimen injected with tetracycline in April 1992 and recaptured in March 1994, viewed under fluorescent and reflected light. Note the tetracycline band positioned at the opaque zone and the two opaque bands following the tetracycline band.

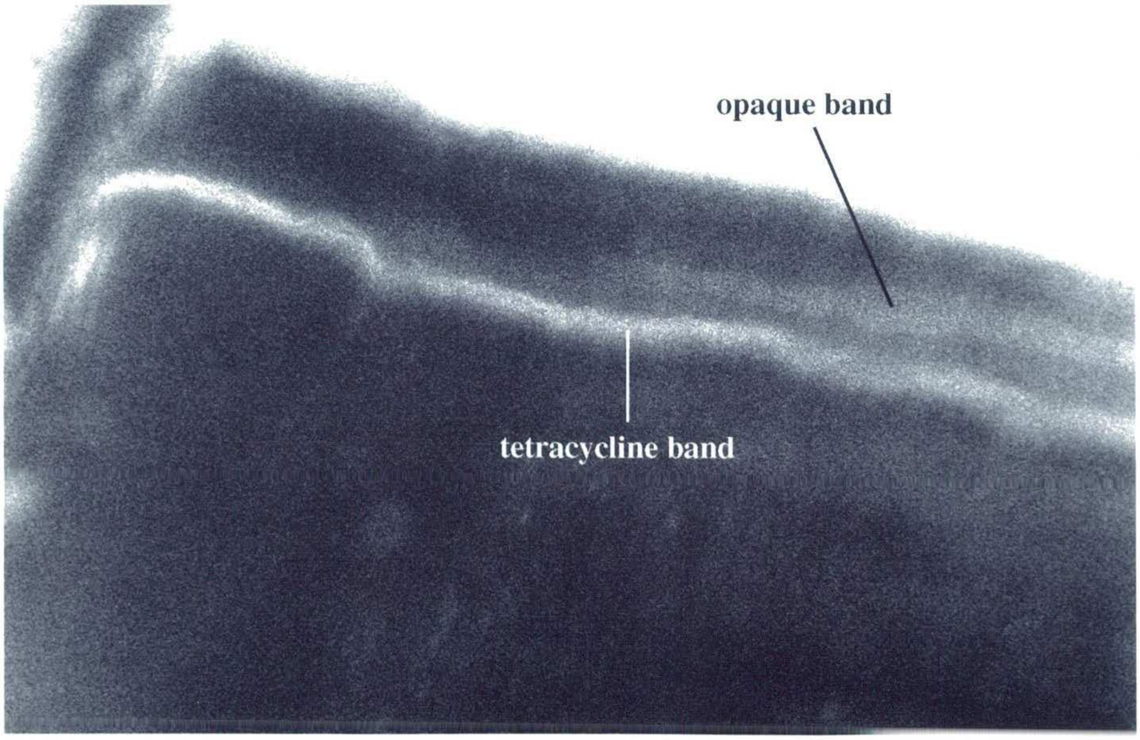


Figure 6.8: Sectioned otolith of a *L. quinquelineatus* specimen injected with tetracycline in January 1992 and recaptured in November 1992, viewed under fluorescent and reflected light. Note the single opaque band following the tetracycline band.

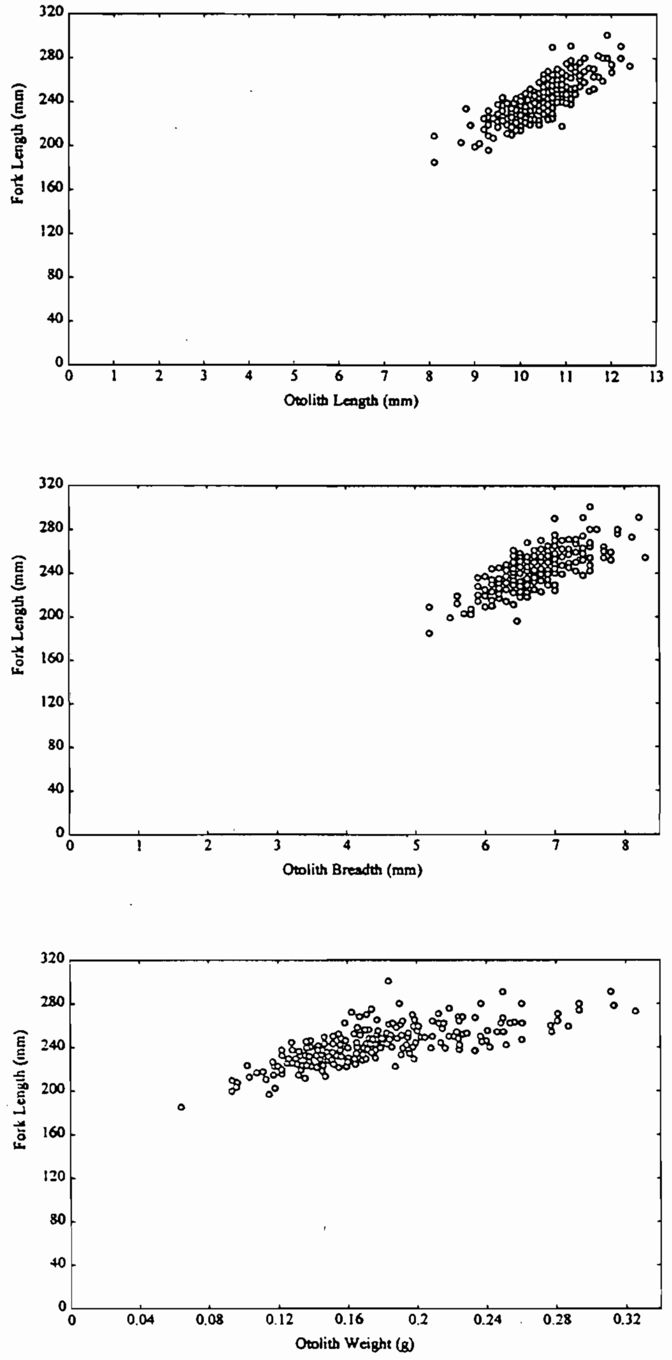


Figure 6.9 : Relationships of fish length to otolith dimensions for *L. adetii* from the central Great Barrier Reef.

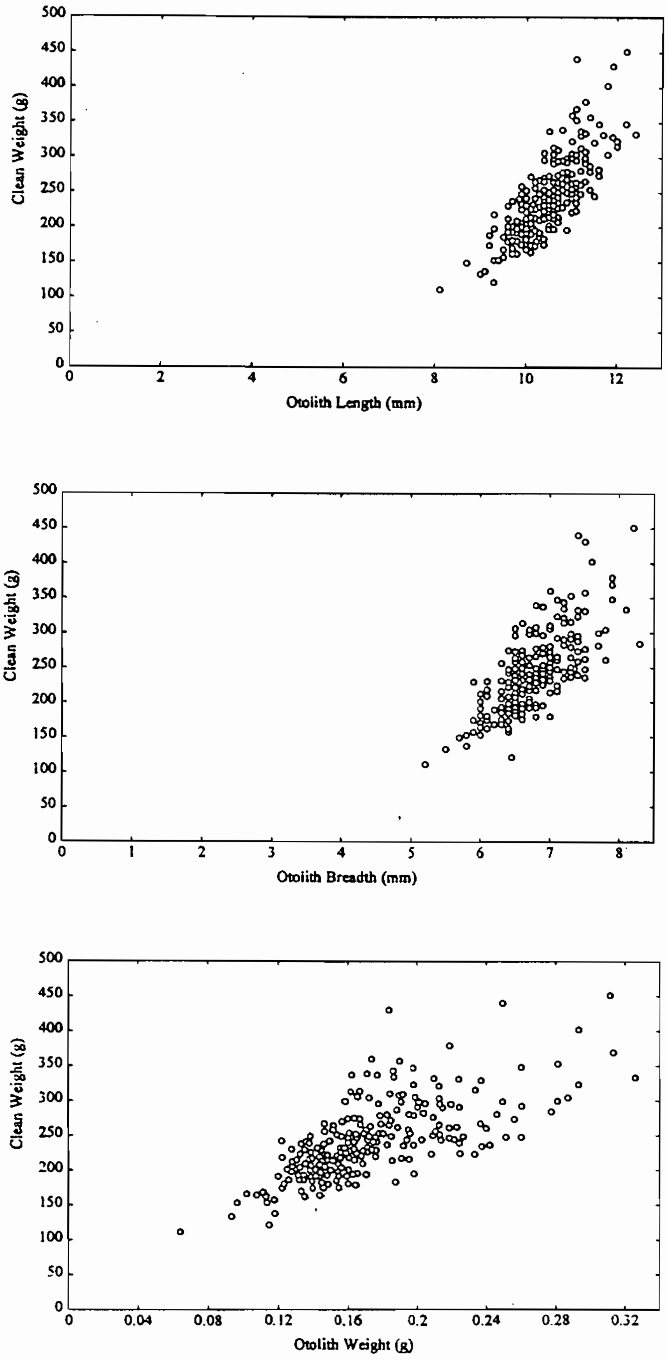


Figure 6.10 : Relationships of fish weight to otolith dimensions for *L. adetii* from the central Great Barrier Reef.

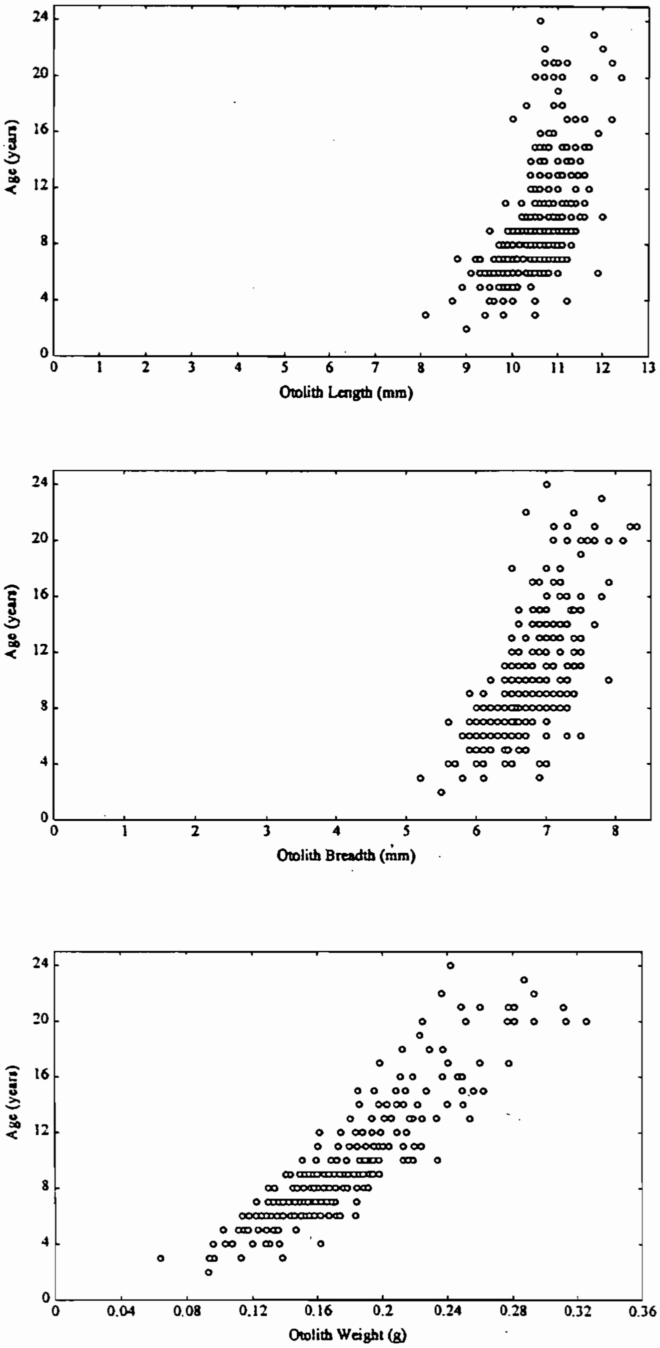


Figure 6.11 : Relationships of fish age to otolith dimensions for *L. adetii* from the central Great Barrier Reef.

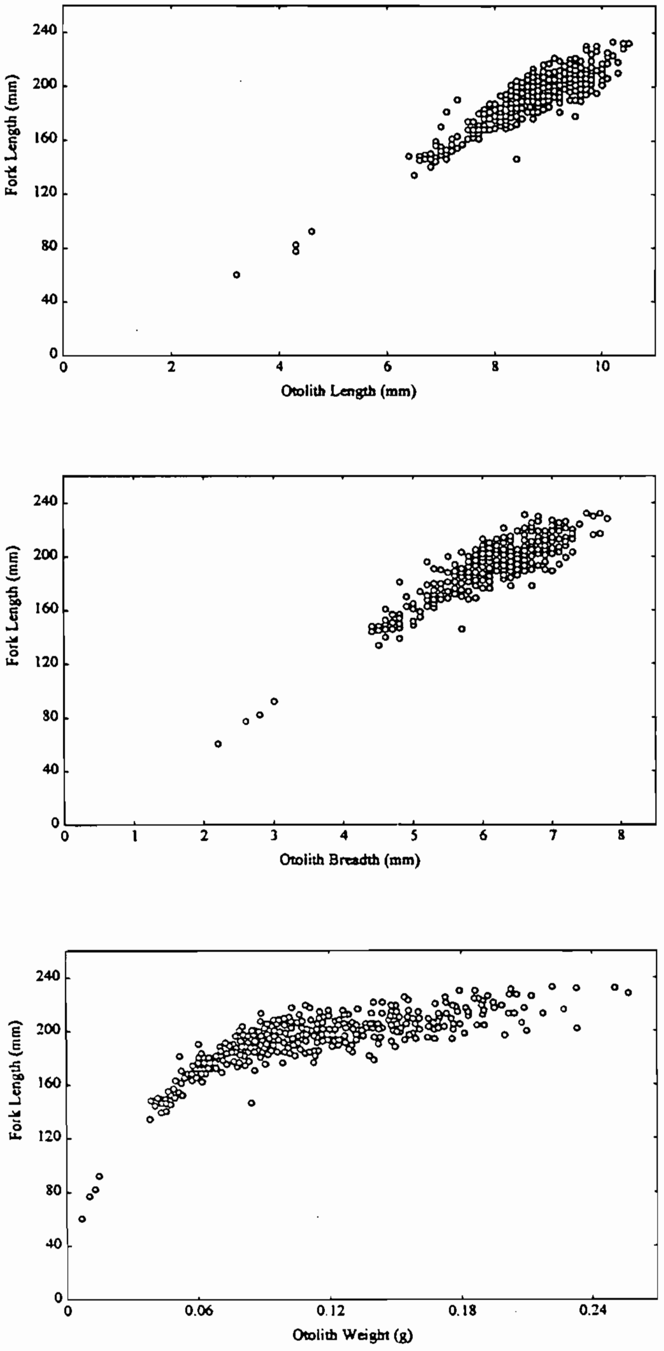


Figure 6.12 : Relationships of fish length to otolith dimensions for *L. quinquelineatus* from the central Great Barrier Reef.

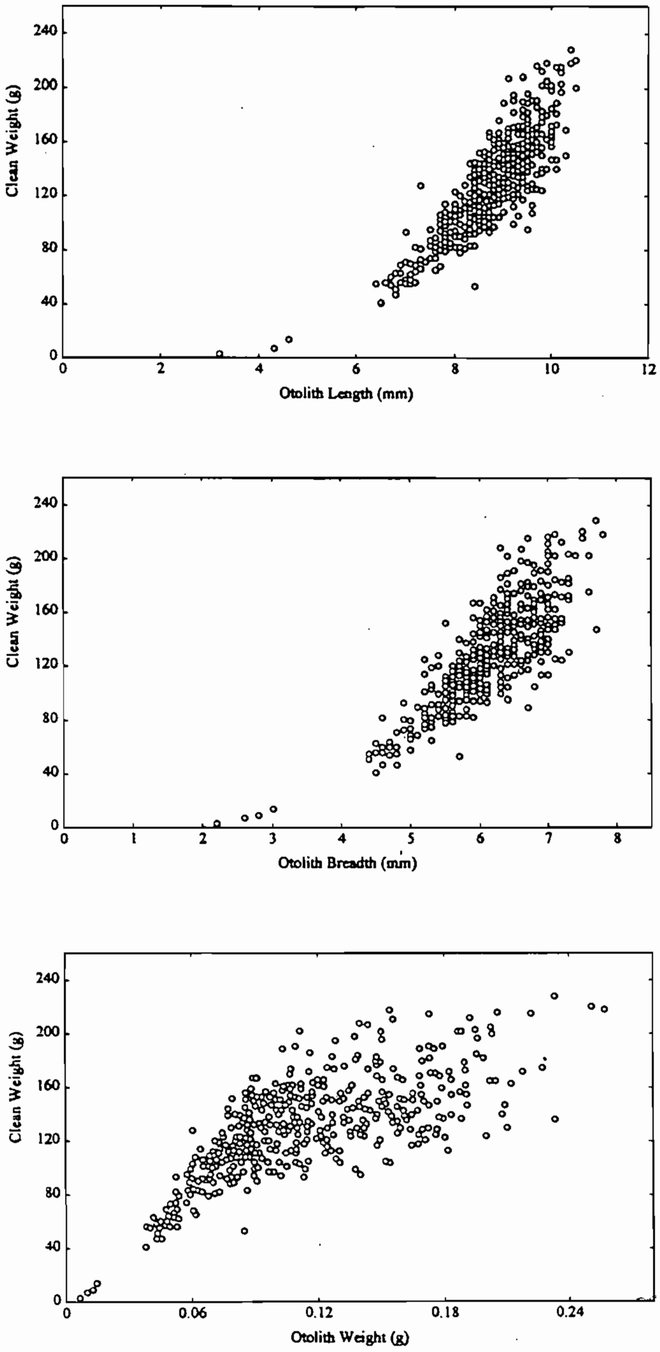


Figure 6.13 : Relationships of fish weight to otolith dimensions for *L. quinquelineatus* from the central Great Barrier Reef.

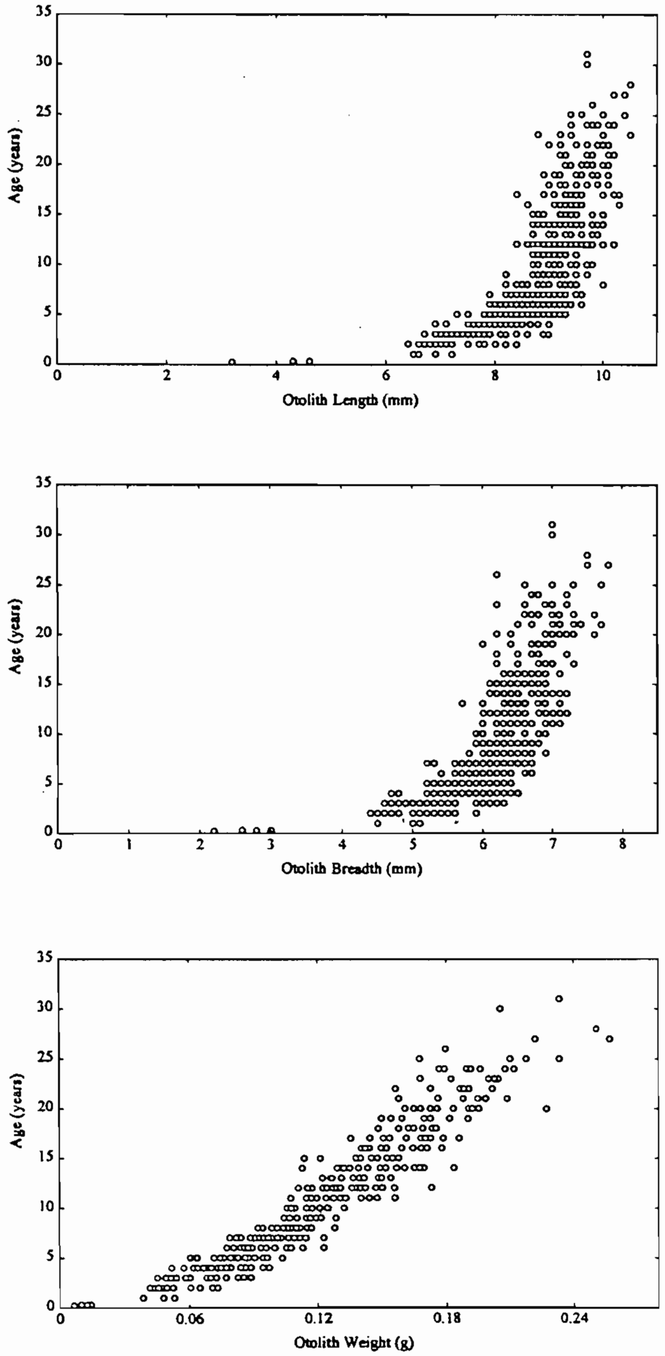


Figure 6.14 : Relationships of fish age to otolith dimensions for *L. quinquelineatus* from the central Great Barrier Reef.

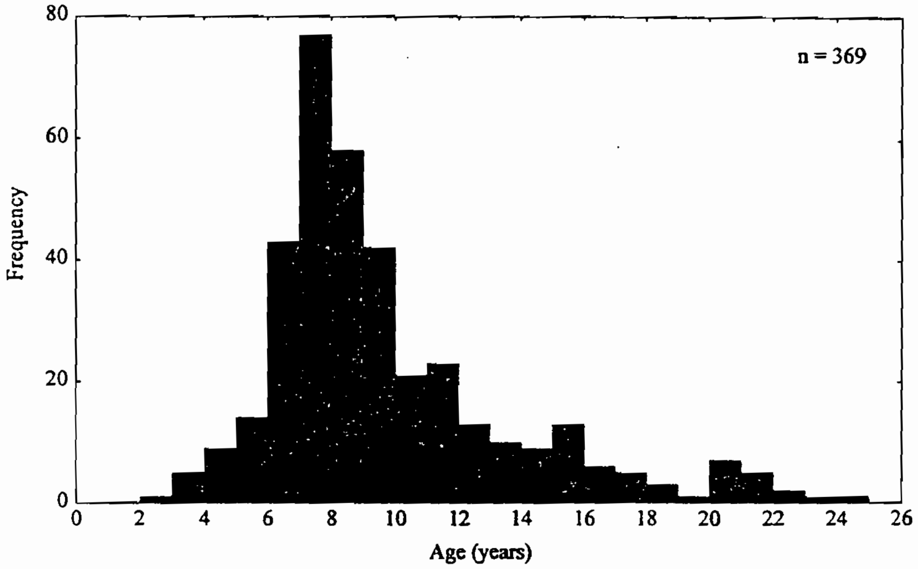


Figure 6.15 : Age frequency distribution of *L. adetii* from 8 reefs in the central Great Barrier Reef.

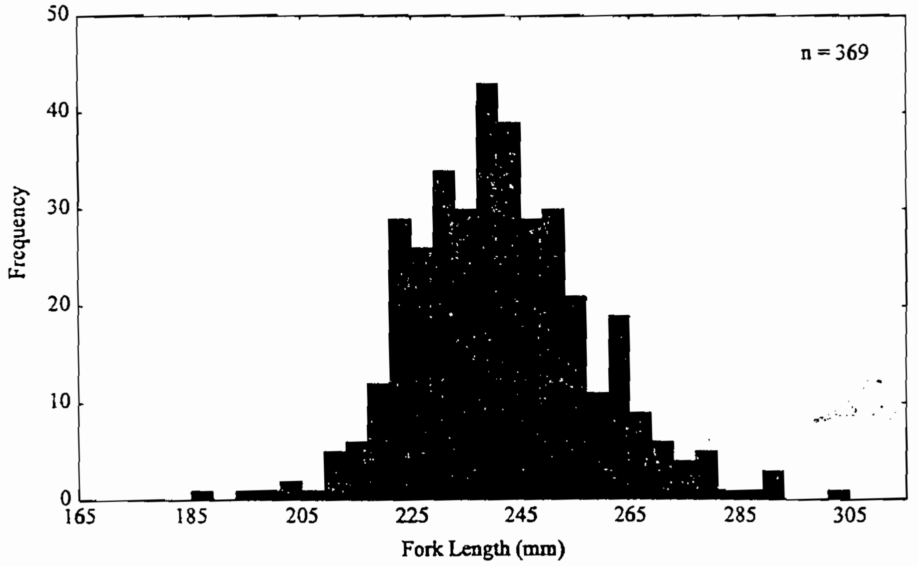


Figure 6.16 : Length frequency distribution of *L. adetii* sampled for age determination (lengths indicate initial points of 5mm size classes).

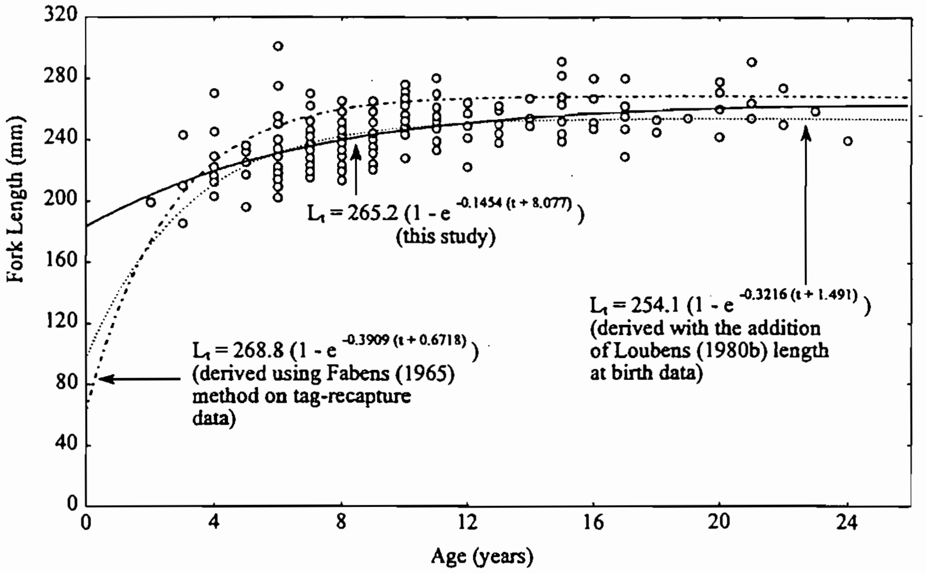


Figure 6.17 : The von Bertalanffy growth curve for *L. adetii* and observed length-at-age from the central Great Barrier Reef.

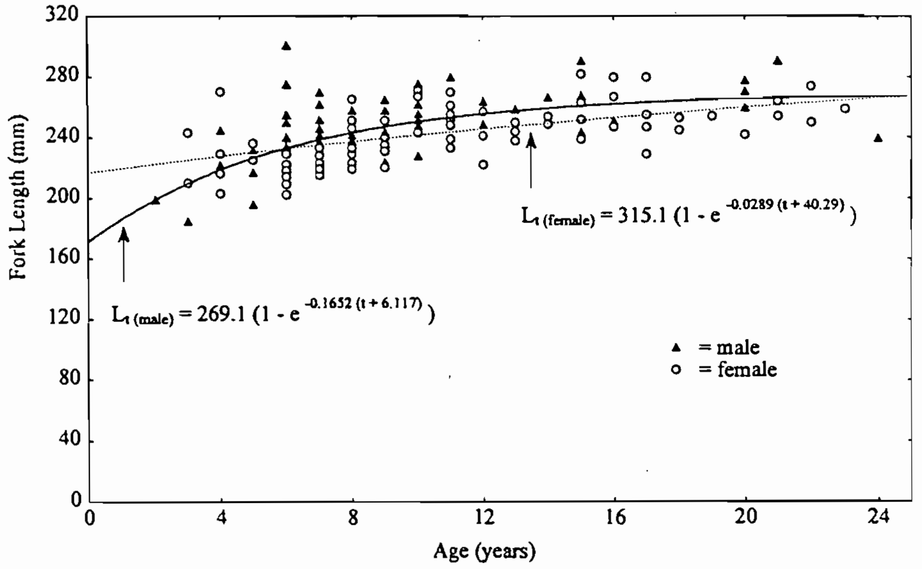


Figure 6.18 : von Bertalanffy growth curves for male and female *L. adetii* and observed length-at-age from the central Great Barrier Reef.

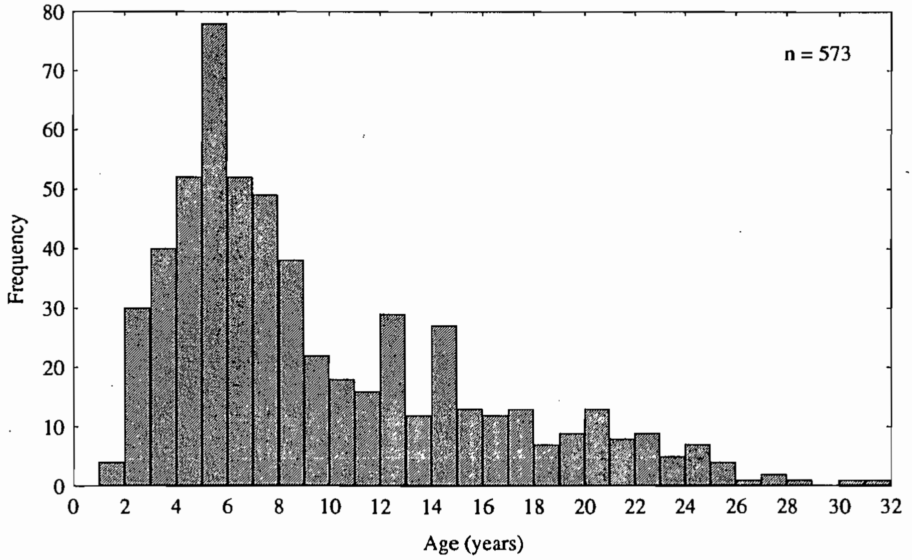


Figure 6.19 : Age frequency distribution of *L. quinquelineatus* from the central Great Barrier Reef.

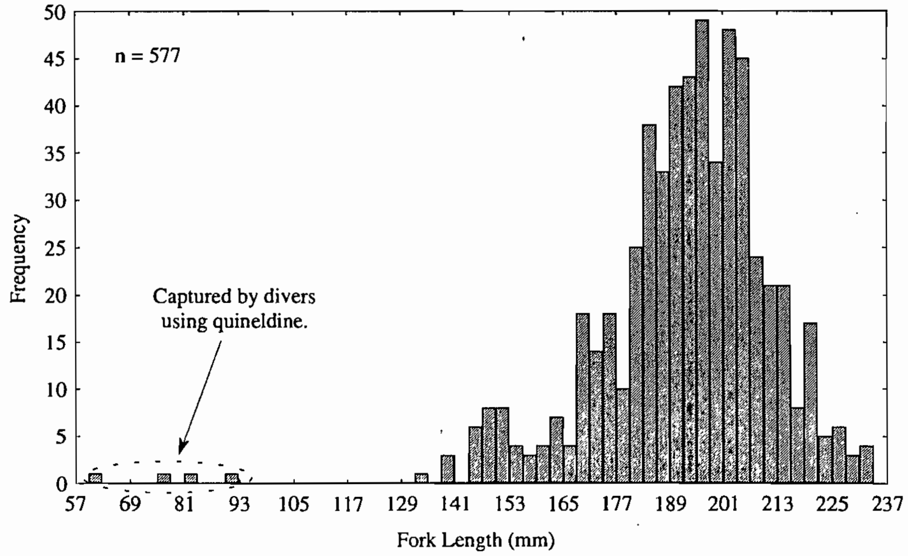


Figure 6.20 : Length frequency distribution of *L. quinquelineatus* sampled for age determination (lengths indicate initial points of 3mm size classes).

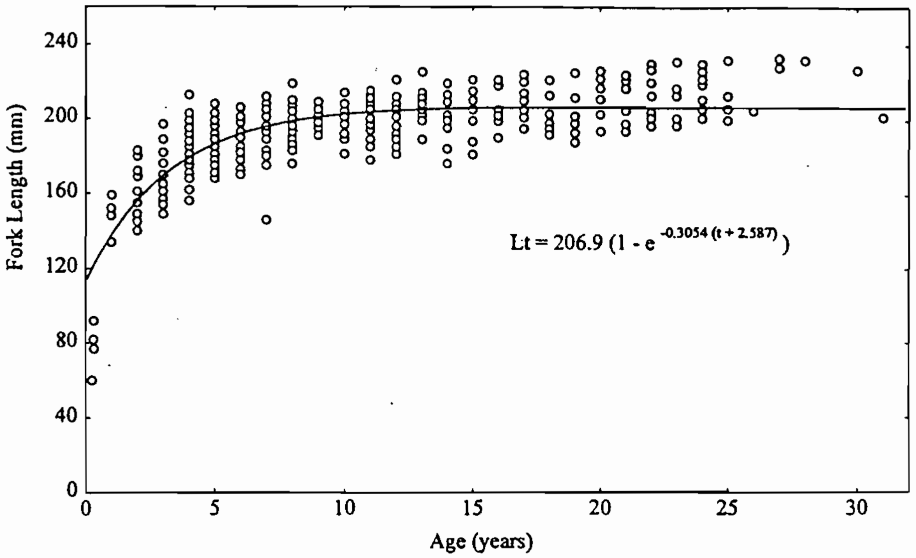


Figure 6.21 : The von Bertalanffy growth curve for *L. quinquelineatus* and observed length-at-age from the central Great Barrier Reef.

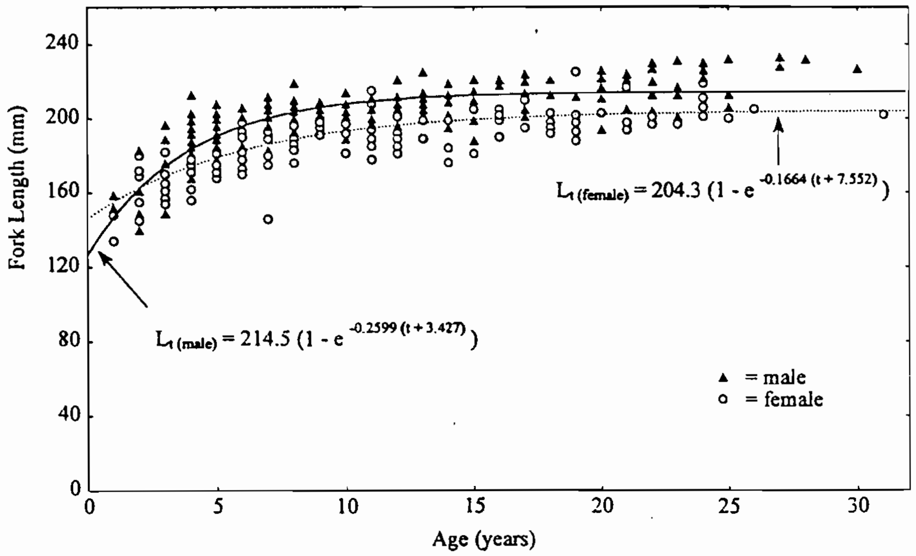


Figure 6.22 : von Bertalanffy growth curves for male and female *L. quinquelineatus* and observed length-at-age from the central Great Barrier Reef.

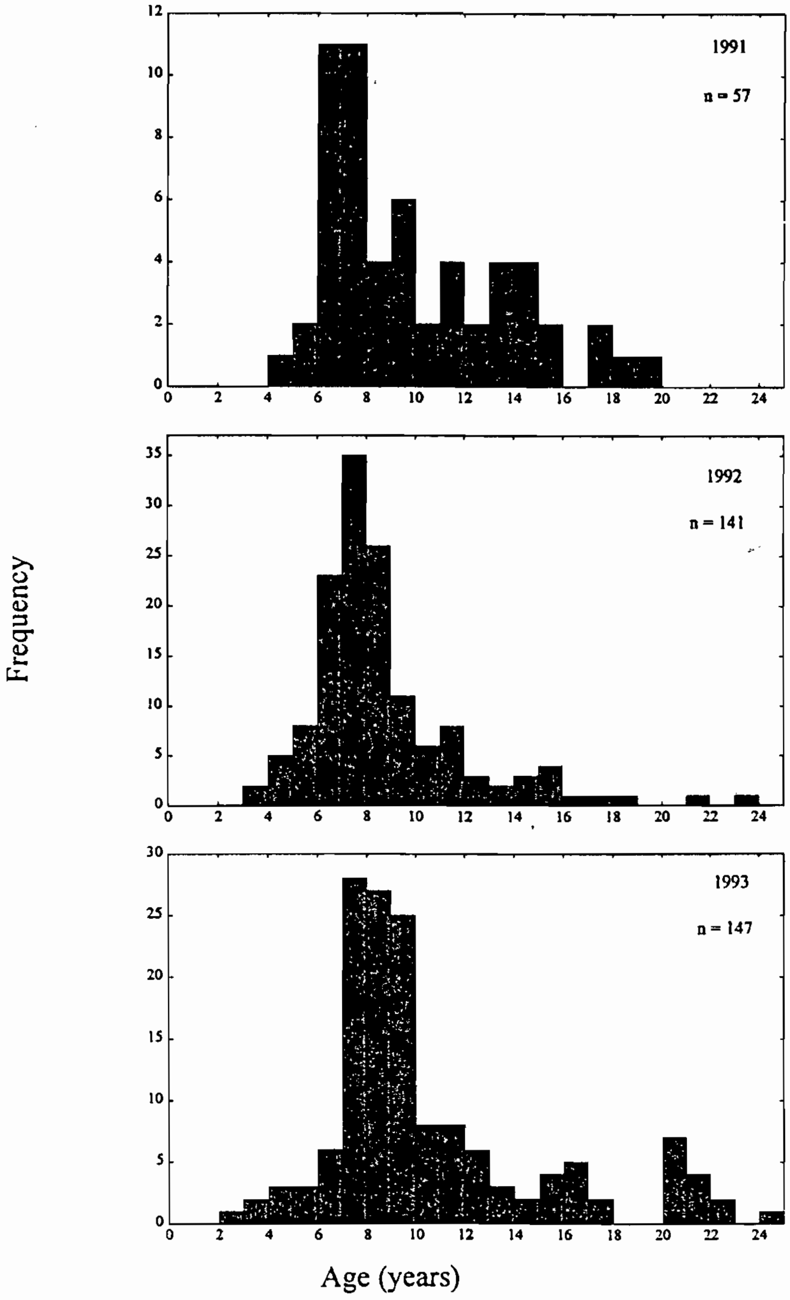
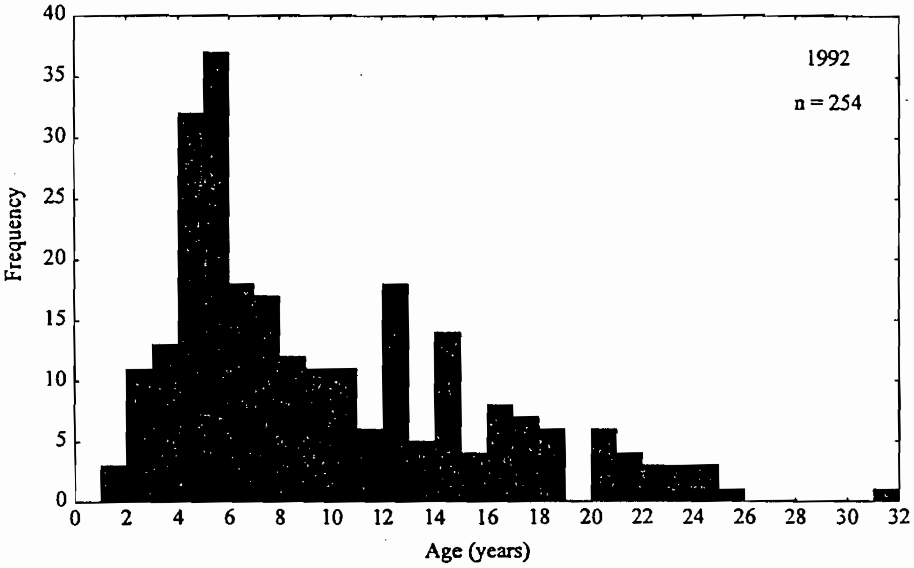


Figure 6.23 : Age frequency distributions of *L. adetii* caught between 1991 and 1993 in the central Great Barrier Reef.



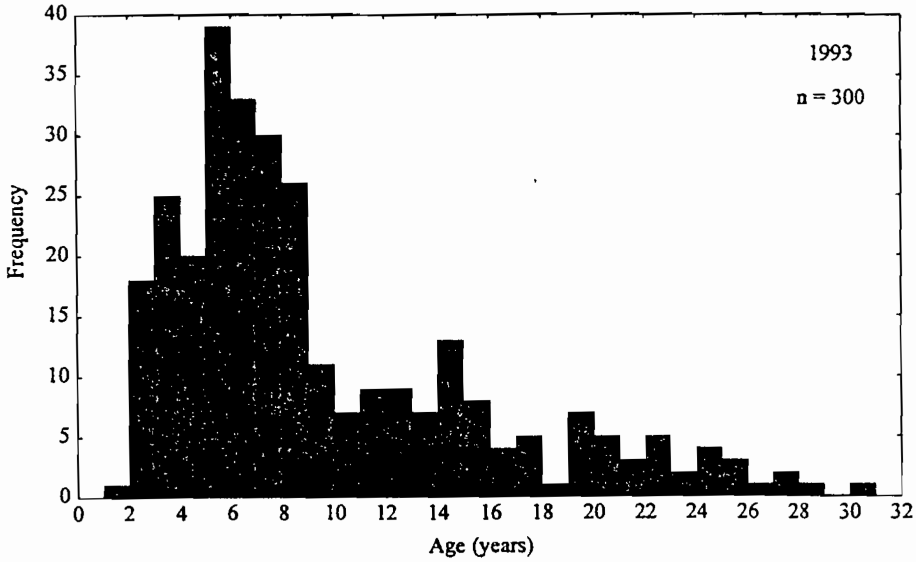
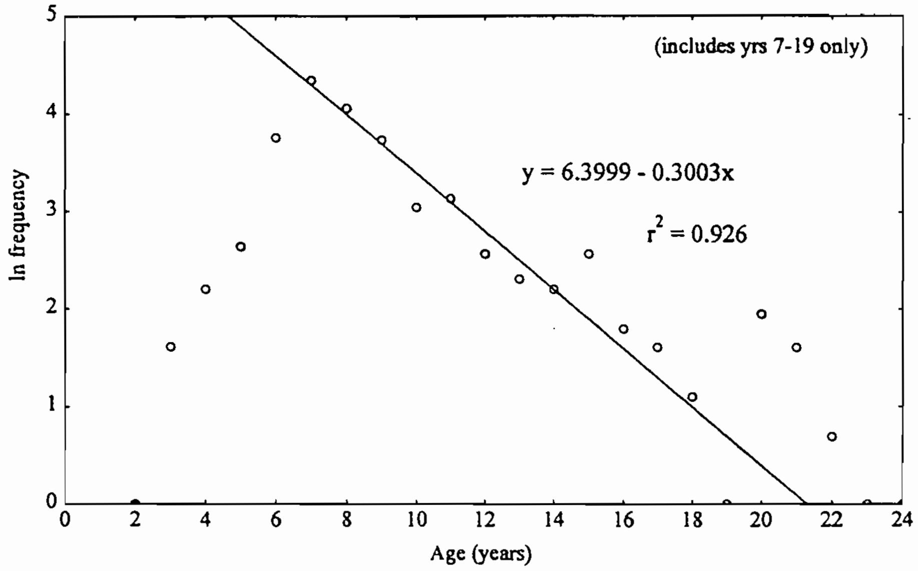


Figure 6.24 : Age frequency distributions of *L. quinquelineatus* caught in 1992 and 1993 in the central Great Barrier Reef.



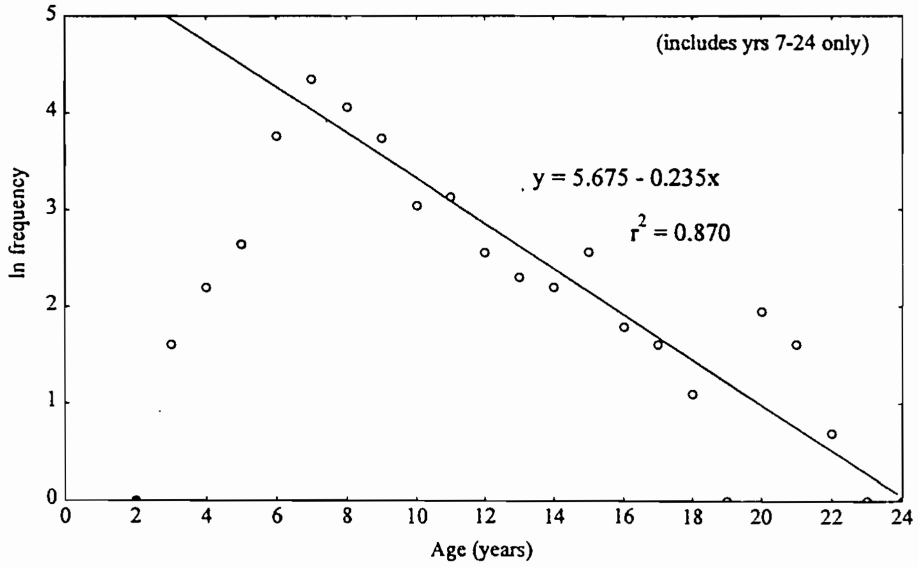
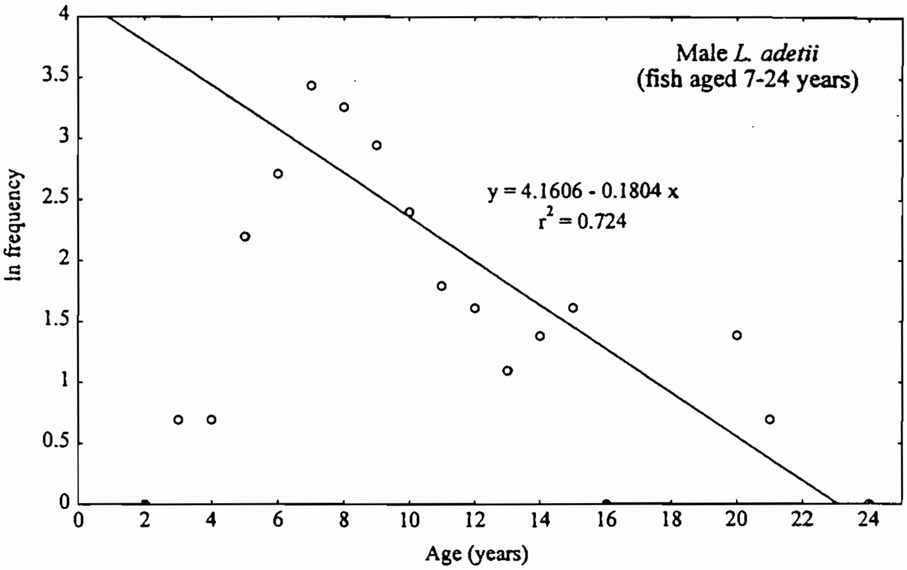


Figure 6.25 : Catch-curve for *L. adetii*, based on observed ages.



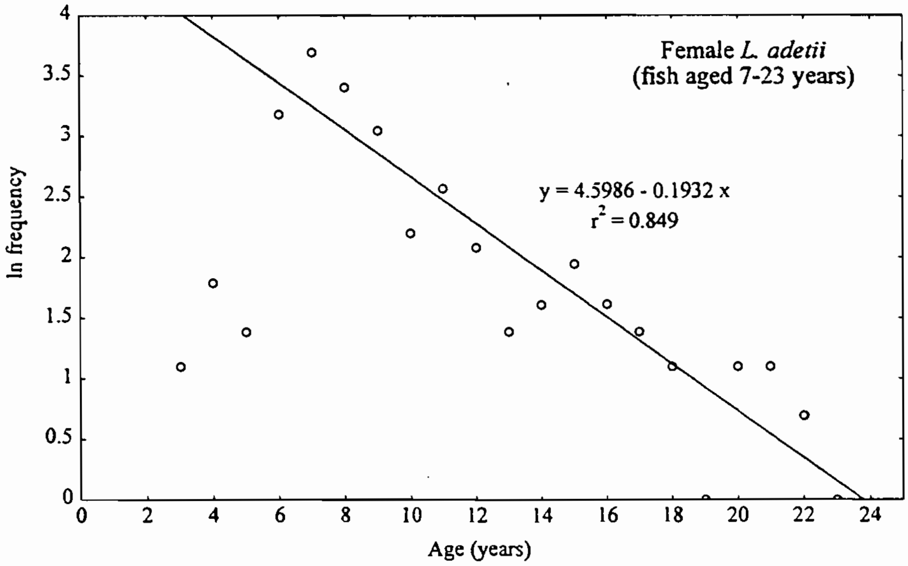
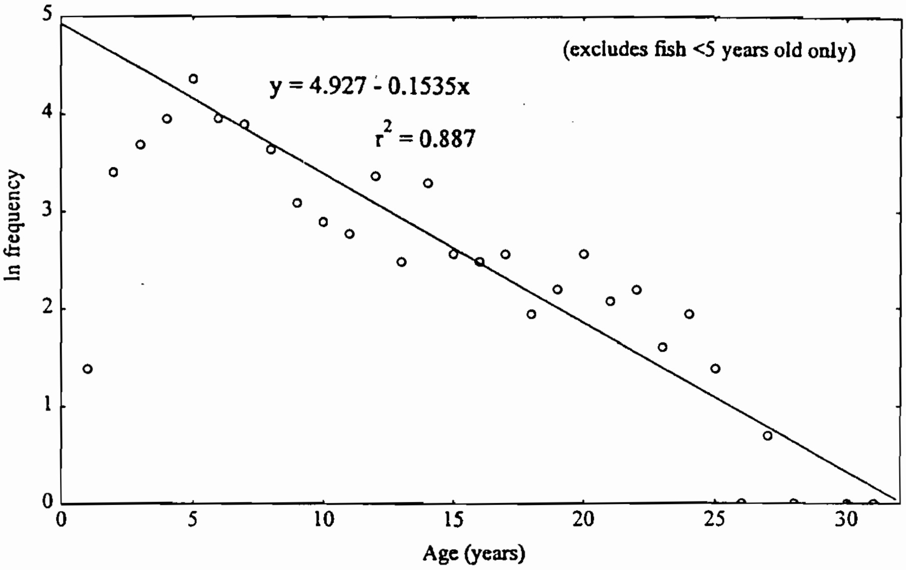


Figure 6.26 : Catch curves for male and female *L. adetii*, based on observed ages.



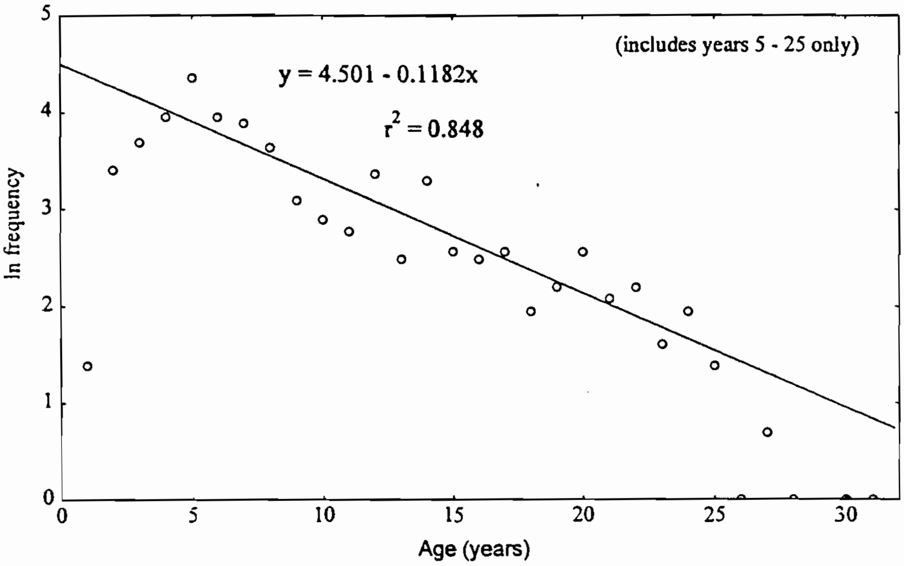
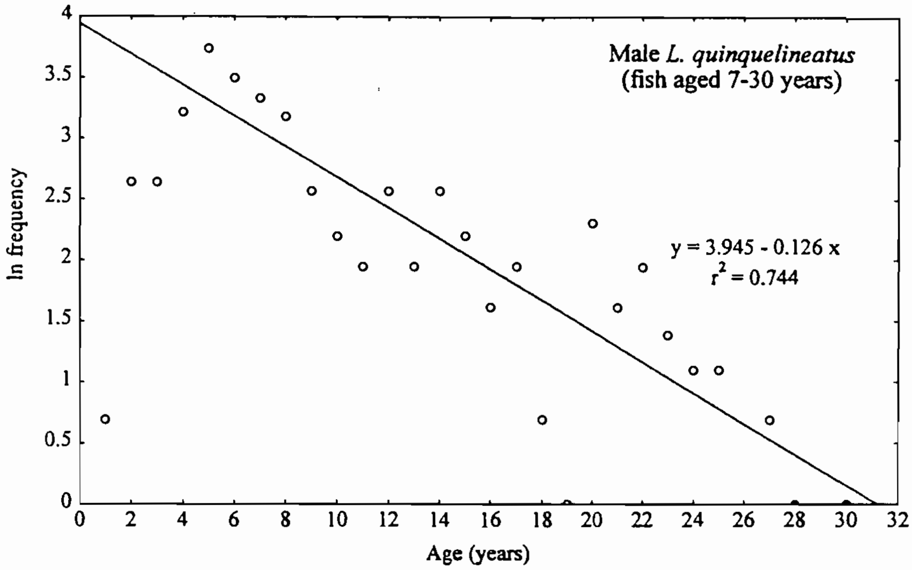


Figure 6.27 : Catch-curve for *L. quinquelineatus*, based on observed ages.



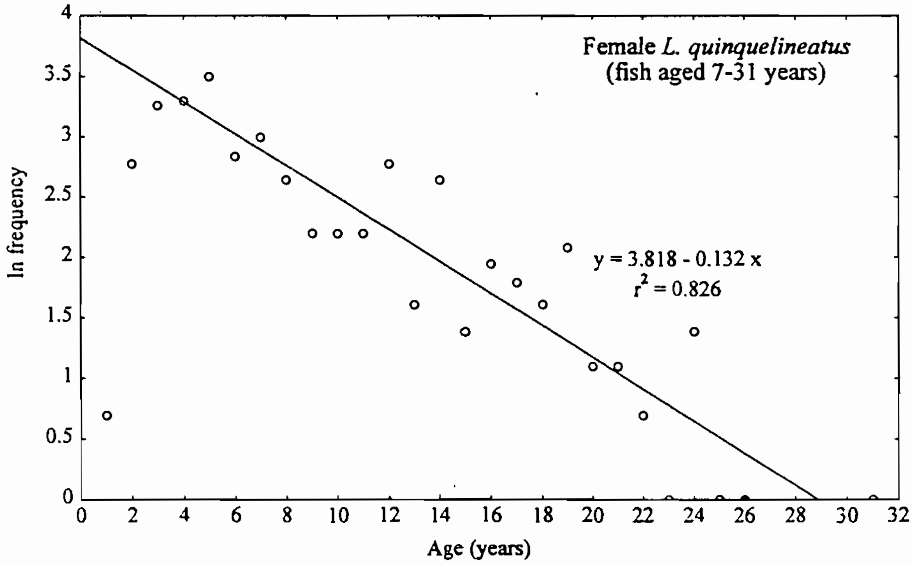


Figure 6.28 : Catch curves for male and female *L. quinquelineatus*, based on observed ages.

Chapter 7

Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia.

7.1 INTRODUCTION

The hussar *Lutjanus adetii*, and the five-line snapper *L. quinquelineatus*, are both widely distributed along the entire length of the Great Barrier Reef and occur as far south as Sydney (latitude 34°S) (Kuiter, 1993). The habitats of both species vary throughout their range, although they commonly occur in association with hard bottom areas. In the central Great Barrier Reef region, *L. adetii* is common in depths greater than 30m among the midshelf group of reefs (Chapter 5) and is known to occur on the outershelf to depths of at least 99m (Chapter 3), whereas *L. quinquelineatus* is common in both shallow and deep waters on both midshelf and outershelf reefs to a depth of at least 128m (Chapter 3, 5).

Neither of these lutjanid species forms a significant component of the commercial catch in the central Great Barrier Reef, and they form only a nominal contribution to the recreational catch in this region (Appendix 3; Higgs, 1993). However, in the southern Great Barrier Reef *L. adetii* contributes a significant proportion to the commercial lutjanid catch (Georgina Eliason, personal communication) and may become of increasing significance to the recreational line fishery in future years (Williams and Russ, 1994). Relatively little information is available concerning the ecology of these species in Australian waters. Loubens (1980b) has demonstrated that both species are relatively long lived and slow growing in New Caledonia and similar conclusions have been obtained in this study from the central Great Barrier Reef (Chapter 6).

The spatial comparison of life history parameters of species of the Lutjanidae have only been undertaken among broad geographic areas (eg. Nelson and Manooch, 1982). The majority of life history studies of lutjanids have been based on widespread collections of individuals within broad geographic areas (eg. Druzhinin and Filatova, 1980; Loubens, 1980b; Sanders *et. al.*, 1984; Liu and Yeh, 1991; Davis and West, 1992; Mees, 1992) and not at the localised reef scale. No published studies appear to have directly compared age and growth parameters of lutjanids among individual reefs within a single geographic area. On the Great Barrier Reef, however, individual coral reefs are the primary management unit. The fishing industry and other resource users (eg. tourism, recreation, etc.) are managed under a system of marine protected areas (which includes six types of zones) within the Great Barrier Reef Marine Park (GBRMPA, 1985).

On the Great Barrier Reef, comparison of age structure from a number of reefs within a single geographic area have been published for only one species, the pomacentrid *Pomacentrus moluccensis* (Doherty and Fowler, 1994). A number of studies have compared the abundance and size structure of the serranid, *Plectropomus leopardus* between reefs open to fishing and closed to fishing (Ayling and Ayling, 1984; 1986; Ayling and Mapstone, 1991). More recently, Ferreira and Russ (submitted) have examined the size, age, and sex structure of populations of *P. leopardus* on closed and open reefs in the central Great Barrier Reef region. The recent validation (Chapter 6) of age and growth of both *L. adetii* and *L. quinquelineatus* has facilitated the comparison of demographic parameters of both these species at the spatial scale of individual reefs. More specifically, the aims of this study are to examine spatial variability in the growth, mortality and age structures of populations of *L. adetii* and *L. quinquelineatus* among reefs within the central Great Barrier Reef region (latitudes 18°S to 19°S).

7.2 MATERIALS and METHODS

Specimens of *L. adetii* (n = 355) and *L. quinquelineatus* (n = 573) were all obtained from a fish trap (O-trap design with 40mm galvanised hexagonal wire mesh : see Chapter 2) research program investigating the distribution and abundance of lutjanids among reefs in the central Great Barrier Reef region (latitudes 18°S-19°S) (Newman and Williams, in press). Samples of *L. adetii* were obtained from 4 reefs (Rib, John Brewer, Lodestone and Kelso), while samples of *L. quinquelineatus* were obtained from 6 reefs (Rib, John Brewer, Lodestone, Davies, Myrmidon and Kelso) in the central region of the Great Barrier Reef (Figure 7.1). Fish were collected from October, 1991 to December, 1993. Individual *L. adetii* less than 17cm fork length (FL) were usually not vulnerable to trap fishing and specimens in this size range were unable to be obtained for analysis. Similarly, individual *L. quinquelineatus* less than 10cm fork length were also usually not vulnerable to trap fishing.

Individuals of each species were measured (FL, SL) and weighed (clean weight after removal of the gills and viscera) and sexes were determined by macroscopic examination of the gonads. The sagittal otoliths of individuals of each species were removed by opening the otic bulla from under the operculum. After dissection, sagittae were washed in freshwater and stored dry in envelopes prior to processing. All otoliths were sectioned laterally through the focus with a Beuhler Isomet low-speed jewellery saw and ages were determined following the methodology described in Chapter 6.

Analysis of Data

Significant differential growth between the sexes was observed in both species (Chapter 6). In order to prevent confounding differences among reefs with differences between sexes, two-way factorial analyses of variance were used to compare the mean length (fork length, mm), age (years) and clean weight (g) of each species both among reefs and between sexes. Reefs and sexes were both treated as fixed and orthogonal factors in the analysis. Multiple comparisons were performed using Tukey's honestly significant difference (HSD) test. Levels of significance for all analyses were set at $\alpha = 0.05$.

The Kruskal-Wallis one-way analysis of variance by ranks was used to test for differences in the age structures of each species among reefs (Siegel and Castellan, 1988). The nonparametric Kruskal-Wallis test is more power efficient than the median test because it utilises more of the information in the observations by converting values into ranks (Siegel and Castellan, 1988). Multiple pair wise comparisons were performed using Kolmogorov-Smirnov (K-S) tests to determine differences in the age structure of each species between individual reefs (Zar, 1984).

Growth rates for each species at each reef were also examined. Observed lengths-at-age for both species at all reefs displayed asymptotic growth and while the younger age classes of both species were not sampled well, growth of younger individuals was approximately linear. The von Bertalanffy growth function (VBGF) was fitted to lengths-at-age for each species from each reef using nonlinear least squares estimation procedures (Prager *et. al.*, 1989). The VBGF is defined as :

$$L_t = L_\infty (1 - e^{-K(t-t0)})$$

where L_t = length at time t; L_∞ = asymptotic length; K = Brody growth coefficient; t = age of the fish; t_0 = theoretical origin of the growth curve.

The von Bertalanffy growth curves were compared using the likelihood ratio test (Kimura, 1980). Cerrato (1990) concluded from simulation studies among likelihood ratio, *t*-, univariate χ^2, and Hotelling's T^2 tests, that the likelihood ratio test was the most accurate of the procedures considered to compare parameters of the von Bertalanffy equation. Additionally, an analysis of the residual sum of squares (ARSS) was also employed to compare VBGF's among reefs. The procedures of the ARSS are described in Chen *et. al.* (1992). This method is modified from the model developed by Zar (1984). Further, one way analysis of variance was used to determine if their were significant differences in the mean length (FL) of the early age classes of each species among reefs ($\alpha = 0.05$).

Analysis of covariance was used to determine if there were significant differences in the weight (clean)-at-length (FL) relationships among reefs and between sexes for each species. Length and weight data were transformed to a natural logarithm function ($\log_e x$) to satisfy assumptions of normality and homogeneity. Homogeneity of variance ($\alpha = 0.05$) for both species analysed was satisfied using Cochran's test (Winer, 1971). Reefs and sexes were both treated as fixed and orthogonal factors in the analysis. Multiple comparisons were performed using Tukey's honestly significant difference (HSD) test. Levels of significance for all analyses were set at $\alpha = 0.05$.

Estimates of the annual instantaneous rate of total mortality (Z) of each species among individual reefs were obtained using the age based catch curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish in each age class (Nt) was plotted against their corresponding age (t) and Z estimated from the descending slope, b. Estimates of the survival rate of each species among reefs was then calculated from the Z derived from catch curves, since $Z = -\log_e S$ (Ricker, 1975).

7.3 RESULTS

There were significant differences in the mean length, age and weight of both species among reefs and these differences were independent of the sex of the fish (Tables 7.1 and 7.2, and see also Figures 7.2, 7.3, 7.4 and 7.5). Tukey (HSD) comparisons showed that in general, mean length and weight were larger and mean age greater for both species at Kelso Reef, although the multiple comparisons among reefs were not all clear cut (Tables 7.1 and 7.2). The significant differences in mean length, age and clean weight of both species between sexes were the same as those described in Chapter 6, with Tukey (HSD) tests concluding that males were larger than females in each species (Tables 7.1 and 7.2).

Age Structures

The age structure of *L. adetii* was significantly different among reefs (Kruskal-Wallis statistic : H = 13.85, $p < 0.01$). K-S tests (Table 7.3) showed that the age structure of Rib was not significantly different from Lodestone or Kelso, but was significantly different to that of John Brewer. Rib had equal strength in age classes 7, 8 and 9 and the relative abundance of age classes 10 through 22 at Rib, Lodestone and Kelso was greater than at John Brewer (Figure 7.6). The age structure of Kelso was significantly different from both John Brewer and Lodestone, and the age structure of John Brewer was significantly different to that of Lodestone. John Brewer and Lodestone had "strong modes in age class 7", while Kelso suggested a mode in year class 9 (Figure 7.6). The abundance of age classes 10 through 22 at Lodestone Reef were greater compared to John Brewer (Figure 7.6). The pattern of peaks in abundance of age classes were not consistent across all reefs. The small sample size taken from Kelso Reef may have biased the results, however the sample covered a range of 10 age classes and was similar to the age structure of Rib Reef. The multiple pairwise comparisons used here increase the chance of a Type I error. In Table 7.3, six tests were conducted each with a 0.05 chance of a Type I error, therefore the probability of a Type I error in Table 7.3 equals 0.30 (0.05 × 6).

The age structure of *L. quinquelineatus* was also significantly different among reefs (Kruskal-Wallis statistic : H = 21.41, $p < 0.001$). K-S tests (Table 7.4) showed that Myrmidon and Lodestone were significantly different to all the other reefs. Kelso was not significantly different from Rib, but was significantly different from all the other reefs. John Brewer was not significantly different from either Davies or Rib, while Davies was significantly different from Rib. Myrmidon reef had a peak in age class 5 and relatively strong age classes 6, 7 and 8 (Figure 7.7). However, few fish older than 8 years were represented in the catch. Lodestone had relatively strong 2, 3, 4 and 5 year age classes and abundance per age class declined approximately exponentially to year 26, except for a strong mode in age class 14 (Figure 7.7). Davies was somewhat similar, with strong modes in age classes 5 and 6 with the abundance of subsequent age classes declining approximately exponentially to year 22 (Figure 7.7). Data were more limited for Kelso Reef, with a relatively even distribution from age classes 2 through 30, with peaks in age classes 5 and 14. Compared to the other reefs, older age classes were relatively dominant at Kelso. John Brewer and Rib Reefs had relatively flat age distributions from age class 2 through 24 compared to Lodestone, Davies and Myrmidon. The only pattern that was consistent across all reefs was the strong mode of 5 year old individuals (Figure 7.7) and this may reflect the age at full recruitment to the sampling gear (fish traps). The probability of a Type I error in Table 7.4 is greater than in Table 7.3 because a total of 15 comparisons were made, therefore the probability of a Type I error in Table 7.4 is 0.75.

Growth Models

The von Bertalanffy models of the length-age relationship among reefs for *L. adetii* are shown in Figure 7.8, with the coefficient of determination among reefs ranging from 0.177 to 0.462. The low coefficients of determination were attributable to the absence of younger and smaller fish in the samples. Therefore no point of inflexion was evident in the growth models among reefs. As a result the parameters of the von Bertalanffy models of *L. adetii* among individual reefs were characterised by large asymptotic standard errors (Table 7.5), with Lodestone Reef having the best fitting model. The von Bertalanffy model from Lodestone Reef is similar to that derived from all reefs pooled within the central Great Barrier Reef (Table 7.5). Despite the absence of small and younger fish caused by bias in sampling, the von Bertalanffy growth function was however, considered the best empirically based assessment of growth in *L. adetii* due to the asymptotic nature of growth (Figure 7.8). The von Bertalanffy growth curves of *L. adetii* were not significantly different among reefs (likelihood ratio test, $p >> 0.05$; ARSS : $F = 1.13$, $p >> 0.05$), and the resulting growth curves (Figure 7.8) appear similar. Additionally, there were no significant differences in the mean length (FL) of the early age classes (6+, 7+, 8+ and 9+) of *L. adetii* among reefs (see Table 7.6).

The von Bertalanffy model provided a better description of the length-age relationship among reefs for *L. quinquelineatus* (Figure 7.9), with the coefficient of determination among reefs ranging from 0.267 to 0.752. The younger and smaller fish were underrepresented in the catch samples from some reefs and this was reflected in the coefficients of determination (Table 7.5 and Figure 7.9). The parameters of the von Bertalanffy models of *L. quinquelineatus* among individual reefs were characterised by relatively small asymptotic standard errors (Table 7.5). The growth curves of *L. quinquelineatus* were significantly different among reefs (likelihood ratio test, $p < 0.01$; ARSS : $F = 8.401$, $p < 0.001$). Differences among reefs were observed also in values of L_∞, K and t_0 (see Table 7.5). However, there were no significant differences in the mean length (FL) of the early age classes (2+, 3+, 4+, 5+ and 6+) of *L. quinquelineatus* among reefs (see Table 7.7).

Analysis of covariance (ANCOVA) demonstrated that the relationship between weight and length in *L. adetii* was significantly different both among reefs and between sexes and that the among reef differences were independent of the sex of the fish (Table 7.8). The relationships between weight and length among reefs for *L. adetii* are shown in Table 7.9.

Similarly, ANCOVA demonstrated that the relationship between weight and length in *L. quinquelineatus* was also significantly different both among reefs and between sexes (Table 7.8). However, the significant among reef differences were not independent of the sex of the fish (a significant interaction effect occurred between reefs and sex). The differences among reefs were different for each sex (see Table 7.8). The relationships between weight and length among reefs for *L. quinquelineatus* are shown in Table 7.9. There was significant differential growth in the observed length and weight of both species among reefs and between sexes. These results all indicate that rates of growth in terms of weight-at-length of both species were variable at the spatial scale of individual reefs.

Mortality

In general, individual *L. adetii* less than 7 years of age did not appear to be fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. The reef-specific total annual rate of mortality, Z, of *L. adetii*, was 0.179 (fish aged 8-24 years, r^2 = 0.729, SE = 0.0292), 0.304 (fish aged 7-15 years, r^2 = 0.512, SE = 0.1123), 0.225 (fish aged 7-21 years, r^2 = 0.781, SE = 0.0344) and 0.286 (fish aged 9-15 years, r^2 = 0.795, SE = 0.0726) representing an annual survivorship of approximately 83%, 74%, 80% and 75% respectively for Rib, John Brewer, Lodestone and Kelso (Figure 7.10). The mortality rates of *L. adetii* among reefs were significantly different (homogeneity of slopes test, $p < 0.01$), with multiple comparison of slopes indicating that the mortality rate at Rib Reef was significantly lower than all other reefs (Rib < John Brewer = Lodestone = Kelso).

Individual *L. quinquelineatus* less than 5 years of age were usually not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. Estimates of mortality with high coefficients of determination were only obtainable from two reefs, Lodestone and Myrmidon. The other reefs had a poor fit to the catch curve regressions (Figure 7.11), or did not enable the derivation of mortality rates. This was attributable either to the persistence of numerous strong year classes or age-varying mortality rates (Figure 7.11). The estimates of total mortality rate Z of *L. quinquelineatus* at Lodestone and Myrmidon were 0.153 (fish aged 4-22 years, $r^2 = 0.711$, SE = 0.0245) and 0.335 (fish aged 5-16 years, $r^2 = 0.661$, SE = 0.0703), representing an annual survivorship of approximately 86% and 72%, respectively. The mortality rates of *L. quinquelineatus* between Lodestone and Myrmidon reefs were significantly different (homogeneity of slopes test, $p < 0.01$). Figure 7.11 shows that mortality rates and hence survivorship of *L. quinquelineatus* among reefs is highly variable. The natural mortality rate M of both species among reefs is considered to be equal to total mortality due to the negligible amount of fishing mortality.

The comparison of mortality rates among successive years (with a relatively large sample size) could only be determined for *L. quinquelineatus* at Lodestone Reef. The total rate of mortality Z of *L. quinquelineatus* at Lodestone Reef in 1992 was 0.176 (fish aged 4-17 years, $r^2 = 0.615$, SE = 0.0402, n = 109), representing an annual survivorship of approximately 84% (Figure 7.12), while the total rate of mortality Z of *L. quinquelineatus* at Lodestone Reef in 1993 was 0.155 (fish aged 3-14 years, $r^2 = 0.409$, SE = 0.0621, n = 64), representing an annual survivorship of approximately 86% (Figure 7.12). The mortality rates of *L. quinquelineatus* at Lodestone Reef were not significantly different between successive years (homogeneity of slopes test, $p > 0.05$; see also Figure 7.12).

7.4 DISCUSSION

There was significant differential weight-at-length among reefs in both *L.*

adetii and *L. quinquelineatus*. However, statistical and visual comparisons of the VBGF of *L. adetii* indicate that the pattern of growth in individuals among reefs was relatively similar (see also Table 7.6). The growth patterns in *L. adetii* may have been biased due to the sampling methodology (fish traps did not sample small, young fish effectively). Since only one gear type was used and the distribution of juvenile *L. adetii* was not determined and is presently not known, it was not possible to obtain a sufficient range of sizes to describe the initial growth pattern over the first few years of their life history. The growth patterns of *L. adetii* among reefs were not significantly different in individuals older than 6 years (see Figure 7.8) and the mean lengths of individuals in age classes 6 through 9 were also not significantly different (Table 7.6).

The growth patterns of *L. quinquelineatus* described by the VBGF were significantly different among reefs. However, no significant differences were detected in the mean lengths of individuals in age classes 2 through 6 among reefs (Table 7.6). These results indicated that initial growth rates among reefs were not significantly different and that the significant differences among reefs in the overall growth rates may reflect the variable size range sampled among reefs (in particular the number of young fish collected at each reef).

The necessary pooling of size-at-age data over a number of different years may have biased the resulting growth patterns, if growth was variable among years. There was no evidence to suggest that growth of either species was variable among years. The pooling of data over a number of years was necessary in order to sample a wide cross section of age classes. The inclusion of size-at-age data over a number of years has the advantage of providing a general description of the growth patterns of each species at each reef. However, large sample sizes covering a range of age classes from a number of consecutive years would be needed to determine if growth rates were variable between years.

The age structures of populations of *L. adetii* and *L. quinquelineatus* among reefs were usually dominated by the presence of several strong year classes, with the strong year classes variable among reefs (Figures 7.6 and 7.7). The occurrence of strong year classes is well documented in the commercial catches of many temperate species (Hjort, 1914; Sissenwine, 1984; Rothschild, 1986) and has recently been observed in a number of tropical species (Doherty and Fowler, 1994; Ferreira and Russ, submitted). Year class strength in both temperate and tropical species has been linked to early life history processes (eg. Hjort, 1914; Sissenwine, 1984; Doherty and Fowler, 1994). Further, the suggestion that recruitment variability is a major factor influencing both the distribution and local densities of coral reef fishes has been recognised for a number of years (Williams, 1980; Doherty, 1981; 1983; Victor, 1983; reviews of Doherty and Williams, 1988; Doherty, 1991). Subsequently, Doherty and Fowler (1994) have shown that for the common tropical damselfish *Pomacentrus moluccensis*, age structures from individual reefs have preserved major temporal variations in the recruitment patterns over at least 10 years, providing empirical evidence of a strong effect of recruitment history on subsequent year class strength. It is therefore conceivable that the varying age structures of both lutjanid species among reefs is a consequence of variability in recruitment at the localised scale of individual reefs, and good recruitment years persisting in the age structure of populations over time.

Estimates of the rate of natural mortality in fish populations are essential to fishery management (see Ricker, 1975; Gulland, 1983 and Russ, 1991). The mortality rate of *L. adetii* was significantly different among reefs, although these differences were small. The mortality rates in general were low and correspondingly the rates of survivorship were high. Mortality rates of *L. quinquelineatus* were not obtainable from all reefs due to either the persistence of strong year class modes, or possibly non-constant mortality rates at a number of reefs (although this was not detected among years at Lodestone Reef), or by differential mortality of cohorts (as opposed to interannual variability in mean (cross-cohort) mortality rates). The results observed here suggest that interannual variation in recruitment may be retained in the age structure at each reef as found for *P. moluccensis* (Doherty and Fowler, 1994). Ricker (1975) also suggests that differences in mortality rate estimated from a catch curve analysis could be due to differences in the pattern of recruitment of year-classes among reefs. Mortality rates derived using the catch curve method of Beverton and Holt (1957) and Ricker (1975) are subject to the assumption that recruitment is constant in the population under consideration. Mortality estimates derived by the catch curve regression method are least sensitive to minor violations of this assumption (Ricker, 1975) and this is particularly evident in *L. quinquelineatus*. Despite this, it is evident from Figure 7.11 that mortality rates of *L. quinquelineatus* are variable among reefs, and they are similar to populations of *L. adetii* in that they are characterised by low rates of total mortality and high rates of survivorship. However, mortality estimates cannot be derived with great confidence from populations where significant recruitment variability is retained in the age structure (eg. Ferreira and Russ, submitted), and although Ricker (1975) has suggested that irregularities in catch curves caused by variable recruitment can be reduced by combining samples over successive years this was not expected to reduce variability among age classes in the present study. Additionally, the mortality rates of *L. quinquelineatus* at Lodestone Reef were not significantly different between successive years (see Figure 7.12). This result suggests that the variable mortality rates and hence survivorship of *L. quinquelineatus* among reefs may persist through time.

In conclusion, this study demonstrated that significant variability exists in the growth, mortality and age structures of *L. adetii* and *L. quinquelineatus* at the spatial scale of individual reefs. The demography of both these lutjanid species at the spatial scale of individual coral reefs is most likely to be a consequence of the nonequilibrial balance of variable recruitment interacting with density independent mortality (Doherty and Fowler, 1994). This spatial variability in demographic parameters among reefs should be considered when developing management models. Further, the significant differences in mortality rates and age structures of the populations of *L. adetii* and *L. quinquelineatus* among reefs would have more impact on management models than the differences in growth. Extended longevity is characterised by low rates of natural mortality, however when longevity is reduced, relatively higher rates of natural mortality are evident (compare

Lodestone and Myrmidon Reefs in *L. quinquelineatus*, see Figures 7.7 and 7.11). Further, greater longevity conveys a selective advantage by increasing the cumulative life time fecundity (egg production) of the female parent (see Beverton, 1987). Therefore in terms of the current management models of the Great Barrier Reef Marine Park it would be advantageous to protect reefs that are characterised by species with extended longevity and low rates of natural mortality (when compared to reefs of similar population size which are characterised by reduced longevity and high rates of natural mortality). The primary advantage of adopting this strategy would be in protecting the spawning biomass of the longer lived fishes. This has the capacity to act as a recruitment source for the surrounding fished areas.

Table 7.1 : Analyses of variance comparing mean length, age and weight among reefs and between sexes for *L. adetii* (significant p values are in bold type) and *a posteriori* multiple comparison of means using Tukey (HSD) analysis ($\alpha = 0.05$; reefs are presented in order of decreasing magnitude).

Source of Variation	df	MS	F	p
Dependent variable : Fork Length (mm)				
Reefs	3	3106.15	12.912	**< 0.001**
Sex	1	462.23	1.92	> 0.15
Reefs × Sex	3	54.45	0.23	> 0.85
Residual	321	240.56		
Dependent variable : Age (years)				
Reefs	3	128.85	8.57	**< 0.001**
Sex	1	43.67	2.90	> 0.05
Reefs × Sex	3	7.24	0.48	> 0.65
Residual	320	15.04		
Dependent variable : Clean Weight (g)				
Reefs	3	31684.62	14.70	**< 0.001**
Sex	1	23013.95	10.68	**< 0.01**
Reefs × Sex	3	799.39	0.37	> 0.75
Residual	288	2154.85		

Tukey HSD analysis ($\alpha = 0.05$), Reefs :

Fork Length : Kelso Lodestone Rib John Brewer

Age : Kelso Rib Lodestone John Brewer

Clean Weight : Kelso > Lodestone > (Rib = John Brewer)

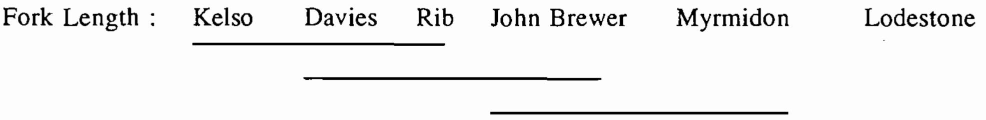
Tukey HSD analysis ($\alpha = 0.05$), Sex :

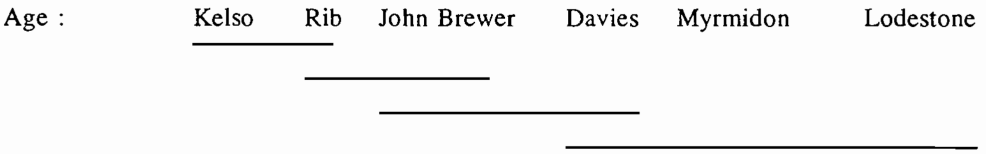
Clean Weight : Males > Females

Table 7.2 : Analyses of variance comparing mean length, age and weight among reefs and between sexes for *L. quinquelineatus* (significant p values are in bold type) and *a posteriori* multiple comparison of means using Tukey (HSD) analysis (α = 0.05; reefs are presented in descending order).

Source of Variation	df	MS	F	p
Dependent variable : Fork Length (mm)				
Reefs	5	5944.89	25.70	< **0.001**
Sex	1	19962.29	86.31	< **0.001**
Reefs × Sex	5	166.94	0.72	> 0.60
Residual	551	231.29		
Dependent variable : Age (years)				
Reefs	5	547.00	17.03	< **0.001**
Sex	1	40.95	1.27	> 0.25
Reefs × Sex	5	41.13	1.28	> 0.25
Residual	550	32.11		
Dependent variable : Clean Weight (g)				
Reefs	5	28723.22	35.83	< **0.001**
Sex	1	98157.42	122.45	< **0.001**
Reefs × Sex	5	1524.81	1.90	> 0.05
Residual	551	801.60		

Tukey HSD analysis (α = 0.05), Reefs :


Fork Length : Kelso Davies Rib John Brewer Myrmidon Lodestone


Age : Kelso Rib John Brewer Davies Myrmidon Lodestone

Clean Weight : Kelso > (Rib = Davies = John Brewer) > (Myrmidon = Lodestone)

Tukey HSD analysis (α = 0.05), Sex :

Fork Length : Males > Females
Clean Weight : Males > Females

Table 7.3 : Differences in the distribution of age structures of *Lutjanus adetii* between reefs were determined using the Kolmogorov-Smirnov test (values of $D_{max.}$ are shown, significance level $\alpha = 0.05$, significant results are marked with an asterisk (*); *NB* : the probability of at least one Type I error in this table is 0.30).

Reef	Reef		
	John Brewer	Lodestone	Kelso
Rib	0.38*	0.17	0.19
John Brewer		0.21*	0.56*
Lodestone			0.35*

ie. John Brewer Lodestone Rib Kelso

Table 7.4 : Differences in the distribution of age structures of *Lutjanus quinquelineatus* between reefs were determined using the Kolmogorov-Smirnov test (values of $D_{max.}$ are shown, significance level $\alpha = 0.05$, significant results are marked with an asterisk (*); *NB* : the probability of at least one Type I error in this table is 0.75).

Reef	Reef				
	John Brewer	Lodestone	Davies	Myrmidon	Kelso
Rib	0.14	0.31*	0.23*	0.43*	0.14
John Brewer		0.27*	0.20	0.43*	0.27*
Lodestone			0.35*	0.30*	0.41*
Davies				0.28*	0.36*
Myrmidon					0.54*

ie. Myrmidon Lodestone Davies John Brewer Rib Kelso

Table 7.5 : Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth function ($L_t = L_\infty (1 - e^{-K(t-t_0)})$), mean fork length (FL : mm) and age (years) of *L. adetii* and *L. quinquelineatus* among reefs in the central Great Barrier Reef.

Lutjanus adetii

Parameters	Reefs				All Reefs Pooled
	Rib (n = 122)	John Brewer (n = 84)	Lodestone (n = 126)	Kelso (n = 23)	Central GBR (n = 369)
L_∞ (FL)	290.8	266.7	270.4	296.8	265.2
ASE	59.95	34.27	8.93	119.4	4.229
K	0.0399	0.0769	0.1336	0.0466	0.1454
ASE	0.0511	0.0959	0.0484	0.1638	0.0285
t_0	-34.09	-20.06	-8.613	-32.22	-8.077
ASE	31.26	22.10	3.961	94.31	2.132
r^2	0.257	0.177	0.462	0.333	0.390
FL_{mean} (SE)	240.3 (1.48)	234.6 (1.67)	242.0 (1.39)	256.7 (2.59)	241.1 (0.88)
FL_{min}	185	196	209	233	185
FL_{max}	285	301	291	291	301
t_{mean} (SE)	10.24 (0.397)	7.79 (0.350)	8.93 (0.314)	11.17 (0.934)	9.27 (0.206)
t_{min}	2	3	3	7	2
t_{max}	24	23	21	22	24

Lutjanus quinquelineatus

Parameters	Reefs						All Reefs Pooled
	Rib (n = 110)	John Brewer (n = 108)	Lodestone (n = 175)	Davies (n = 63)	Myrmidon (n = 75)	Kelso (n = 42)	Central GBR (n = 577)
L_∞ (FL)	214.1	204.1	198.1	211.5	208.0	220.4	206.9
ASE	5.221	1.665	1.697	2.417	11.26	2.72	0.979
K	0.1125	0.3138	0.4665	0.3048	0.1711	0.2182	0.3064
ASE	0.0433	0.0506	0.0367	0.0694	0.1290	0.0474	0.0174
t_0	-14.12	-2.789	-1.108	-2.313	-8.238	-3.978	-2.587
ASE	5.774	0.8787	0.1942	1.456	7.443	1.588	0.2708
r^2	0.421	0.652	0.745	0.603	0.267	0.752	0.638
FL_{mean} (SE)	198.5 (1.5)	193.2 (1.5)	180.3 (1.9)	199.3 (1.6)	190.5 (1.3)	207.0 (2.8)	191.6 (0.8)
FL_{min}	148	146	60	163	170	155	60
FL_{max}	231	230	230	224	219	233	233
t_{mean} (SE)	11.6 (0.66)	10.2 (0.59)	6.9 (0.39)	9.06 (0.60)	6.65 (0.28)	13.43 (1.21)	9.12 (0.25)
t_{min}	2	2	< 1	3	3	2	< 1
t_{max}	31	25	25	22	16	30	31

Table 7.6 : Mean length of early age classes of *L. adetii* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs (*n* = number of samples per age class).

Age Class	Reefs						d.f.	F	p
	Rib		John Brewer		Lodestone				
	Mean FL	(*n*)	Mean FL	(*n*)	Mean FL	(*n*)			
2+	199.0	(1)	----	(0)	----	(0)	----	----	----
3+	196.0	(2)	226.5	(2)	209.0	(1)	----	----	----
4+	203.0	(1)	238.3	(4)	226.0	(3)	----	----	----
5+	227.0	(1)	212.2	(5)	226.3	(7)	----	----	----
6+	237.1	(7)	228.5	(17)	234.1	(17)	2, 38	0.744	ns
7+	231.3	(20)	233.2	(26)	234.4	(27)	2, 70	0.507	ns
8+	235.3	(22)	239.6	(11)	238.9	(21)	2, 51	0.920	ns
9+	238.3	(21)	245.5	(6)	243.9	(9)	2, 33	1.825	ns

Table 7.7 : Mean length of early age classes of *L. quinquelineatus* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs (*n* = number of samples per age class).

Age Class	Reefs						d.f.	F	p
	Rib	John Brewer	Lodestone	Davies	Myrmidon	Kelso			
	Mean (*n*) FL	Mean (*n*) FL	Mean (*n*) FL	Mean (*n*) FL	Mean (*n*) FL	Mean (*n*) FL			
1+	------	------	113.0 (8)	------	------	------	----	----	----
2+	163.0 (3)	160.5 (6)	154.3 (20)	------	------	155.0 (1)	3,26	0.523	ns
3+	179.9 (7)	167.6 (7)	166.8 (22)	163.0 (1)	174.0 (1)	172.0 (2)	5,34	1.171	ns
4+	185.0 (8)	179.1 (8)	179.1 (23)	180.0 (3)	181.1 (8)	173.0 (1)	5,45	0.360	ns
5+	188.7 (9)	187.2 (13)	186.8 (20)	191.7 (10)	187.8 (20)	193.6 (5)	5,71	0.984	ns
6+	193.4 (7)	195.7 (3)	188.6 (14)	193.4 (12)	189.4 (13)	193.0 (2)	5,45	0.754	ns

Table 7.8 : Analyses of covariance comparing weight-at-length (transformed to $\log_e$, covariate : length) among reefs and between sexes for *L. adetii* and *L. quinquelineatus* (significant p values are in bold type; note Kelso Reef was not included in analyses because of the small sample size) and *a posteriori* multiple comparison of means using Tukey (HSD) analysis ($\alpha = 0.05$).

Source of Variation	df	MS	F	p
L. adetii				
Reefs	2	0.0328	11.917	< **0.001**
Sex	1	0.0484	17.577	< **0.001**
Reefs × Sex	2	0.0004	0.127	> 0.85
Residual	266	0.0028	----	----

Tukey HSD analysis ($\alpha = 0.05$), Reefs :
Lodestone > Rib > John Brewer

Tukey HSD analysis ($\alpha = 0.05$), Sex :
Males > Females

Source of Variation	df	MS	F	p
L. quinquelineatus				
Reefs	4	0.0683	15.647	< **0.001**
Sex	1	0.0258	5.907	< **0.05**
Reefs × Sex	4	0.0129	2.948	< **0.05**
Residual	510	0.0044	----	----

Tukey HSD analysis ($\alpha = 0.05$), Reefs :
Male : Rib Davies John Brewer Myrmidon Lodestone

Female : Rib Davies John Brewer Myrmidon Lodestone

Tukey HSD analysis ($\alpha = 0.05$), Sex :
Rib : Males > Females
John Brewer : Males > Females
Lodestone : Males > Females
Davies : Males > Females
Myrmidon : Males > Females

Table 7.9 : Length-weight relationships of *L. adetii* and *L. quinquelineatus* among reefs in the central Great Barrier Reef. For each species at each reef estimates were obtained of the parameters *a* and *b* of the relationship $W = aL^b$, the sample size (*n*) and the coefficient of determination (r^2) (lengths are fork lengths in mm and weight is clean weight in g).

L. adetii

Reef	*a* ($\times10^{-5}$)	*b*	*n*	r^2
Rib	3.944	2.8411	106	0.927
John Brewer	2.264	2.9467	78	0.920
Lodestone	1.751	2.9958	89	0.927
Kelso	0.820	3.1318	23	0.901

L. quinquelineatus

Reef	*a* ($\times10^{-5}$)	*b*	*n*	r^2
Rib	1.625	3.0144	109	0.915
John Brewer	2.292	2.9502	108	0.942
Lodestone	1.152	3.0803	175	0.985
Davies	1.520	3.0269	63	0.884
Myrmidon	1.245	3.0528	75	0.864
Kelso	4.030	2.8554	42	0.954

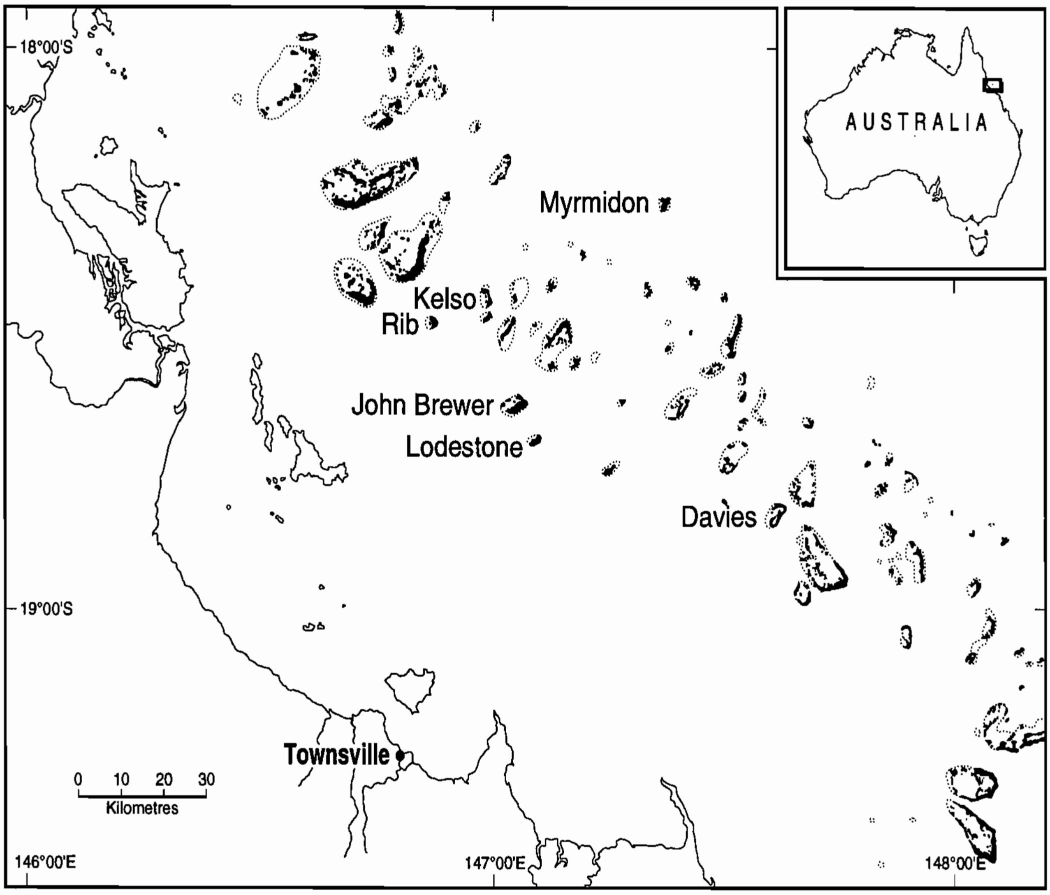


Figure 7.1 : The locations of study reefs in the central region of the Great Barrier Reef of Australia.

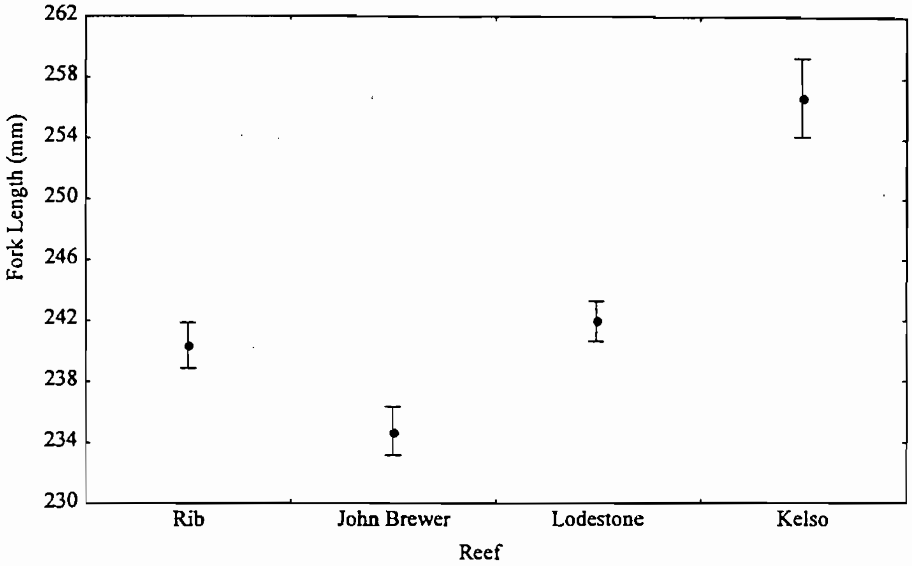


Figure 7.2 : Mean size (fork length) of *L. adetii* among reefs and standard error bars.

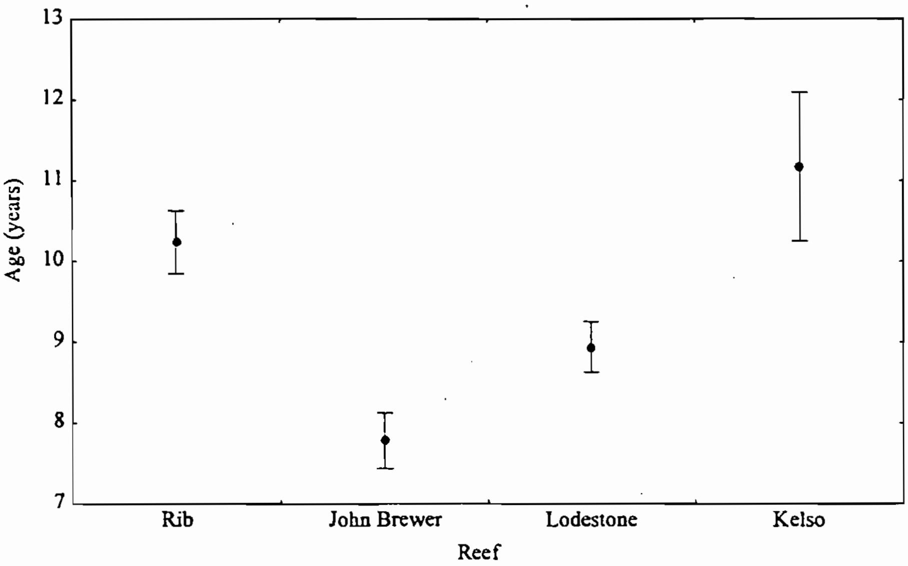


Figure 7.3 : Mean age of *L. adetii* among reefs and standard error bars.

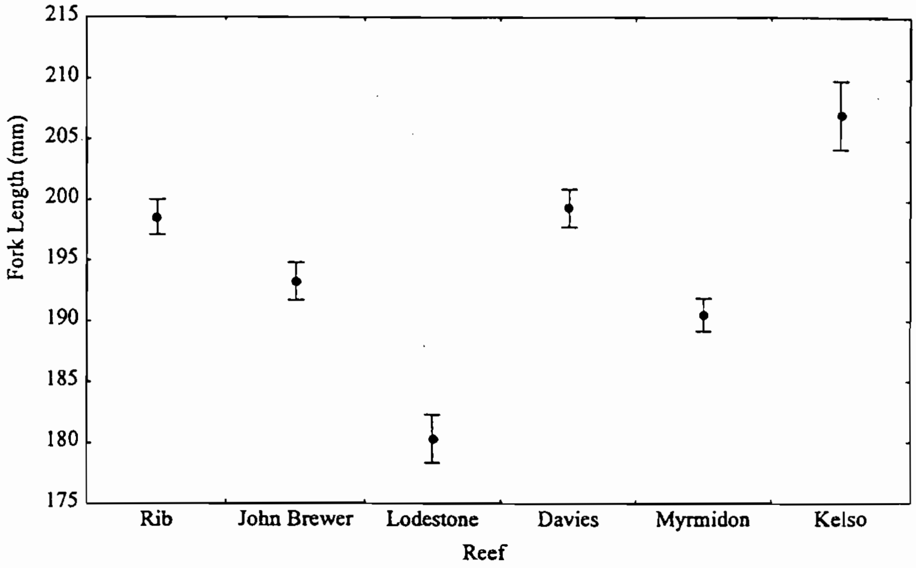


Figure 7.4 : Mean size (fork length) of *L. quinquelineatus* among reefs and standard error bars.

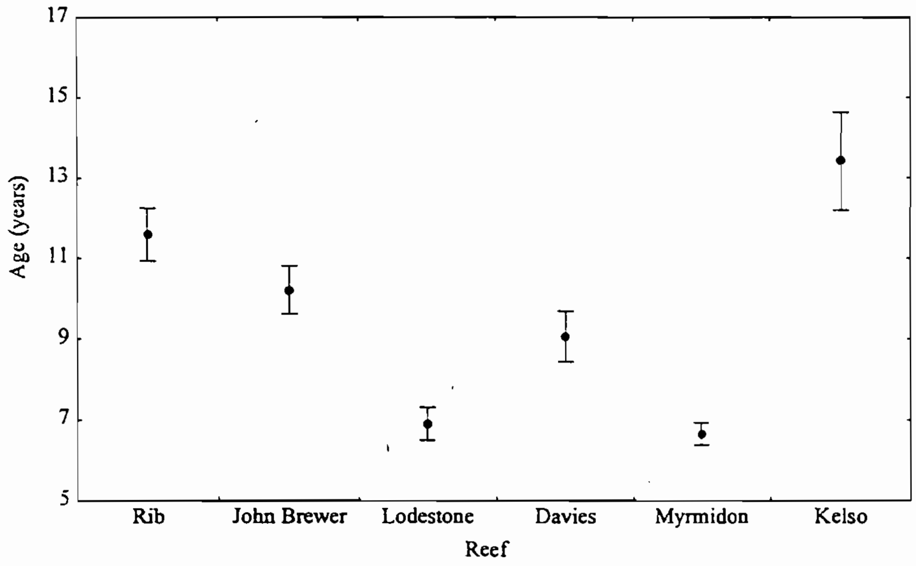


Figure 7.5 : Mean age of *L. quinquelineatus* among reefs and standard error bars.

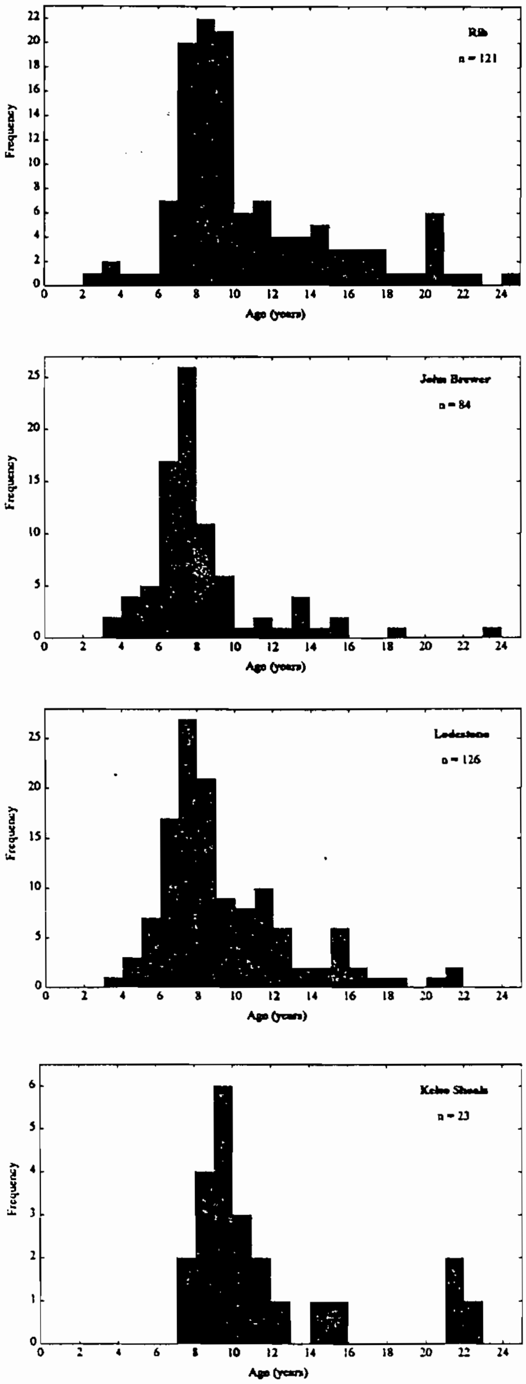


Figure 7.6 : Age frequency distributions of *L. adetii* among reefs from the central Great Barrier Reef.

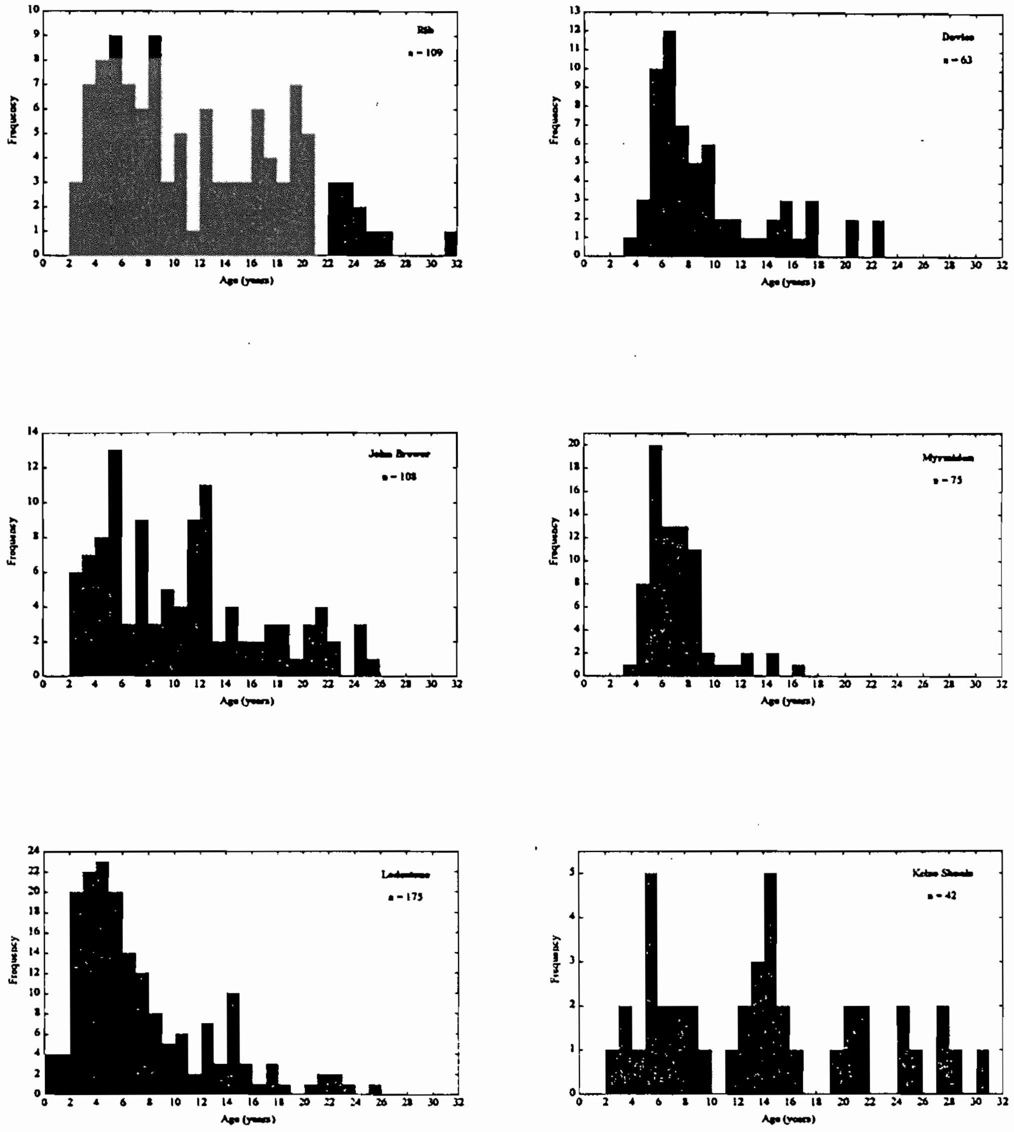


Figure 7.7 : Age frequency distributions of *L. quinquelineatus* among reefs from the central Great Barrier Reef.

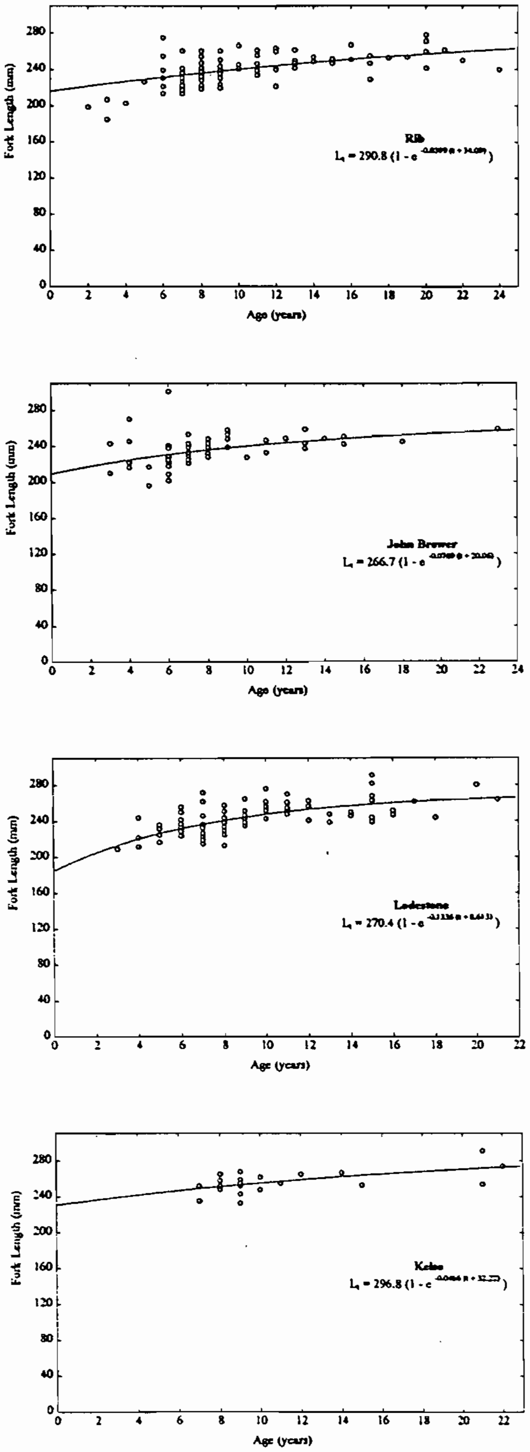


Figure 7.8 : von Bertalanffy growth curves and observed length-at-age for *L. adetii* among reefs from the central Great Barrier Reef.

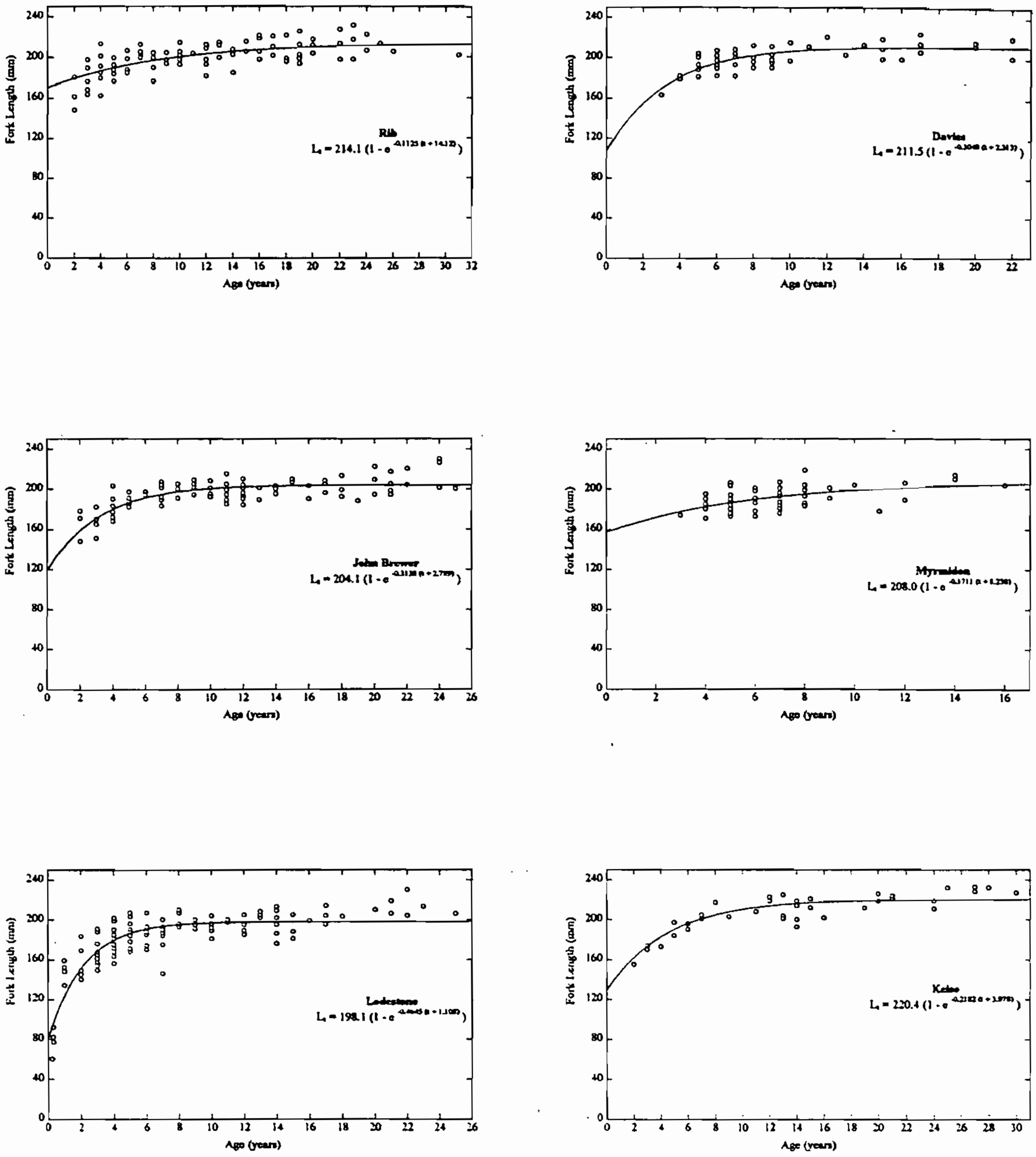


Figure 7.9 : von Bertalanffy growth curves and observed length-at-age for *L. quinquelineatus* among reefs from the central Great Barrier Reef.

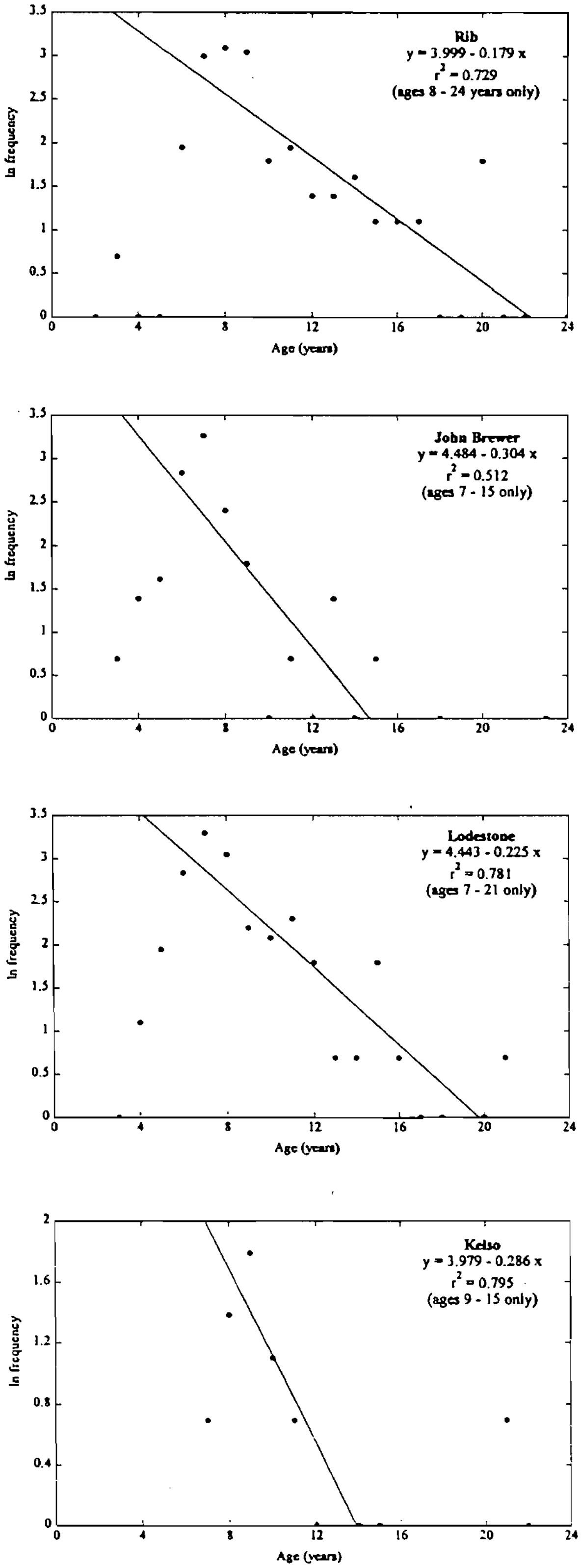


Figure 7.10 : Catch curves of *L. adetii* among reefs, based on observed ages.

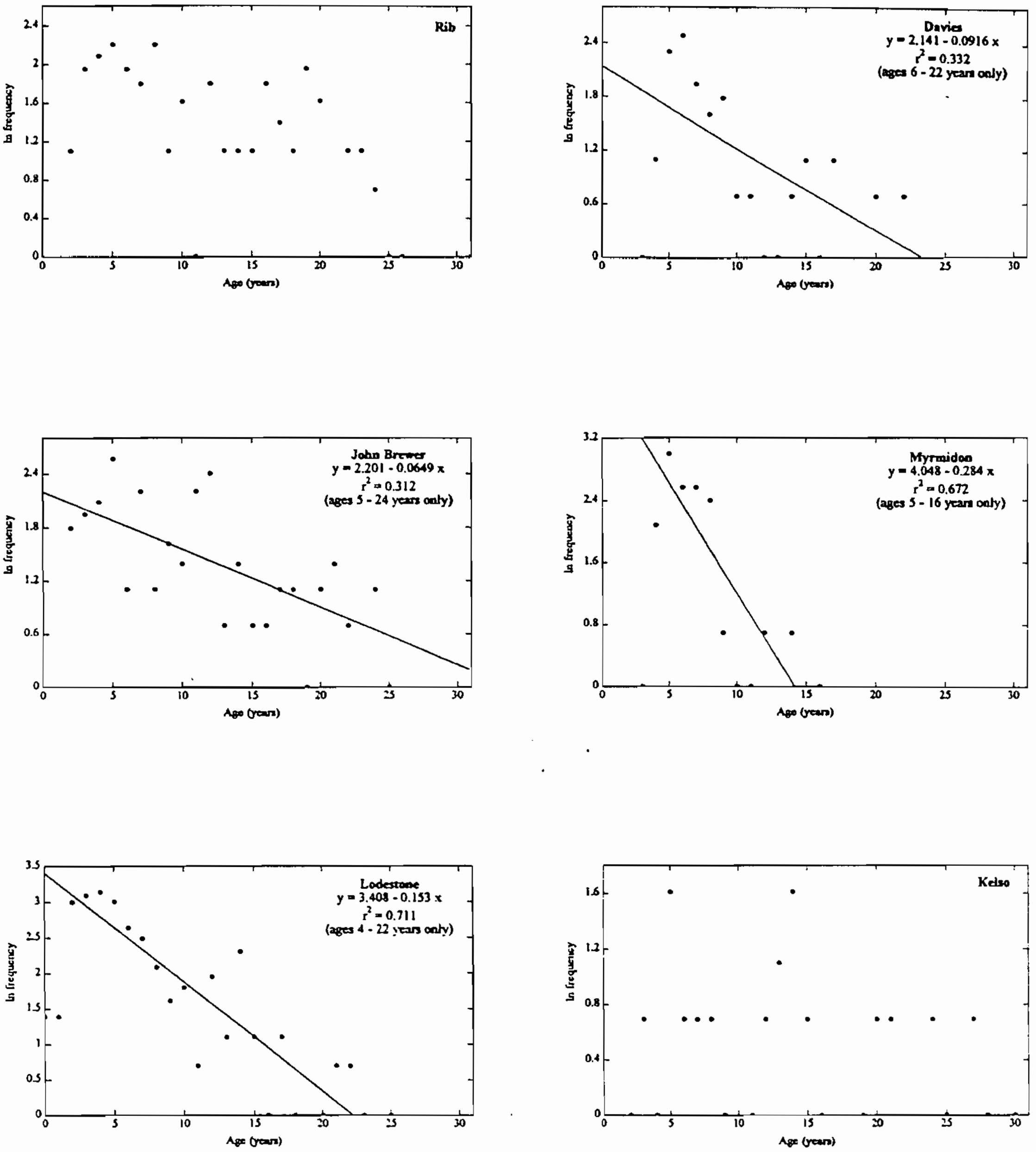
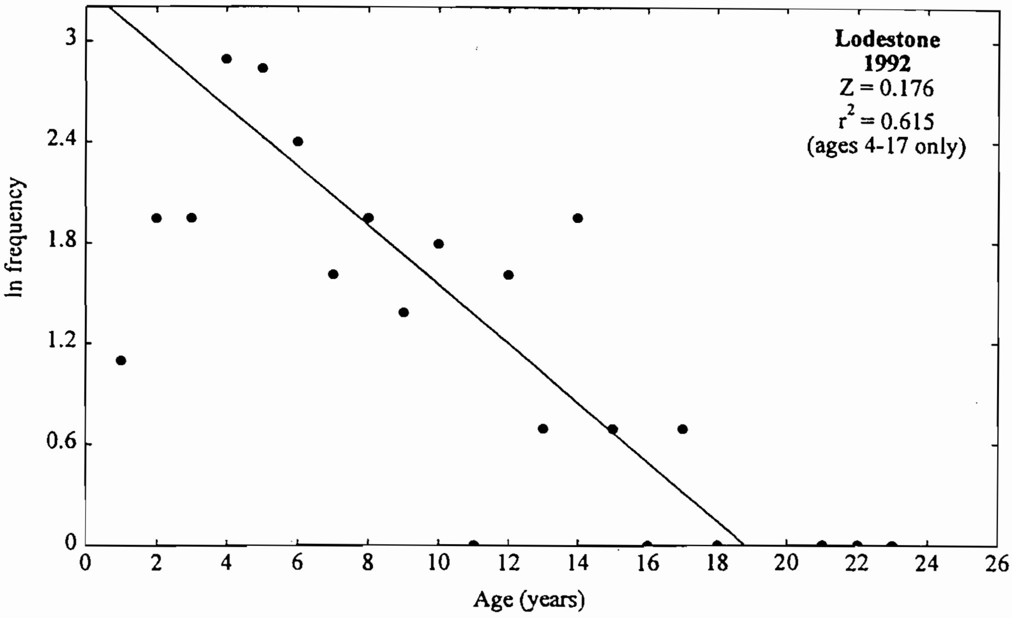


Figure 7.11 : Catch curves of *L. quinquelineatus* among reefs, based on observed ages.



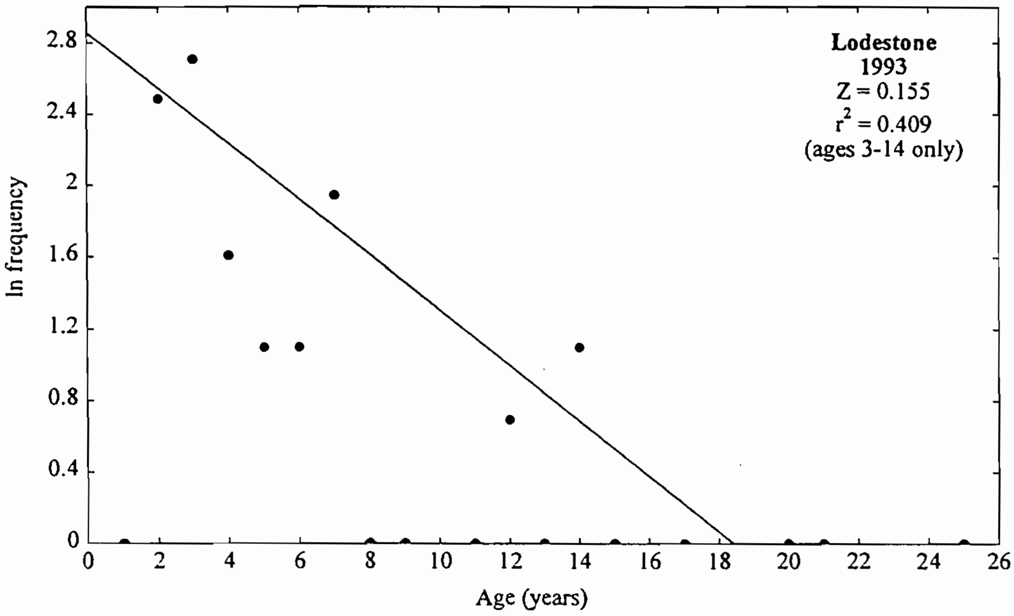


Figure 7.12 : Catch curves of *L. quinquelineatus* from Lodestone Reef between years, based on observed ages.

Chapter 8

General Discussion and Conclusions

Until recently most ecological studies of fishes on the Great Barrier Reef have concentrated on species consisting of small individuals of no direct interest to fisheries (see Sale, 1991). Published studies of the distribution and abundance of reef species of commercial and recreational importance have largely been restricted to coral trout, *Plectropomus* species (eg. Ayling and Ayling, 1983a; 1983b; 1984), as have demographic studies (eg. Ferreira and Russ, 1992; Ferreira, 1993; Ferreira and Russ, 1994; Rimmer *et. al.*, 1994). A review of the available ecological data to 1992 is given in Williams and Russ (1994). The aim of this thesis was to determine the distribution and abundance of the three major families of commercial and recreational importance in the central Great Barrier Reef (Lutjanidae, Lethrinidae and Serranidae), with particular emphasis on the snappers (Lutjanidae), and to examine the age structures, growth rates and mortality rates of two snappers, *Lutjanus adetii* and *L. quinquelineatus*. The thesis has provided data on distribution and abundance at four spatial scales : cross-shelf, among reefs, among reef zones within reefs and with depth and two temporal scales : night versus day and two-monthly intervals over a 12 month period.

Fish traps were used to quantify the distribution and abundance of the

Lutjanidae and Lethrinidae on reefs across the central Great Barrier Reef. The assemblages of fishes on inshore reefs were distinctive from those assemblages on midshelf and outershelf reefs. There were significantly fewer individuals of the Lutjanidae and Lethrinidae on inshore reefs. All species examined displayed significant cross shelf changes in abundance. This variation in abundance was due to an absence or low abundance of individuals at one or more cross shelf locations. Williams (1983) has shown that while significant latitudinal variation was evident in the composition of fish assemblages among five latitudes studied from 11°S to 22°S, this source of variation was substantially less than the cross shelf variation within a given latitude. Additionally, Russ (1984a; 1984b) found that cross shelf change accounted for as much as 80-90% of the variability in abundance of the large herbivorous fishes (Siganidae, Scaridae and Acanthuridae).

The genera *Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus*, *Gnathodentex*, *Gymnocranius*, *Lethrinus* and *Monotaxis* were all characteristic of the shallow shelf waters less than 100m. In contrast, species of the genera *Paracaesio*, *Pristipomoides* and *Wattsia* were characteristic of the intermediate depths (100-200m) and the deeper outer reef slope waters in excess of 200m were characterised by species of the genus *Etelis*. The Lutjanidae and Lethrinidae of all the reef associated families possess the closest nearshore habitat links, with a number of species utilising nearshore coastal habitats as their preferred juvenile settlement areas and nursery grounds and many species of these families undergo major cross shelf movements as part of their complex life histories (Williams and Russ, 1994). It is hypothesised that the closure of entire cross shelf regions which exhibit marked connectivity, from inshore estuarine areas to the outer slopes of the continental shelf may be more practical in ensuring the long term ecological sustainability of these populations of reef fishes on the Great Barrier Reef.

Visual censuses were used to quantify the distribution and abundance of the Lutjanidae, Lethrinidae and Serranidae in three zones (reef slope, lagoon, back reef) of three reefs on the mid-shelf and three reefs on the outer continental shelf in the central region of the central Great Barrier Reef. The assemblages of species of the Lutjanidae, Lethrinidae and Serranidae displayed distinct patterns of distribution and abundance within the shallow waters of the central GBR at three spatial scales, between locations (outershelf and midshelf communities), between reefs (high abundance vs. low abundance reefs) and within reefs (characteristic communities within zones on individual reefs). Williams (1982), Williams and Hatcher (1983) and Russ (1984a; 1984b) have also shown marked spatial variation in the abundance of reef fishes on these scales within the central Great Barrier Reef.

Significant spatial variability was identified in the abundances of many species and species of the Lutjanidae, Lethrinidae and Serranidae were found to occur in assemblages which were characteristic of major zones (windward reef slopes, lagoons and leeward back reefs) and this pattern was consistent within and among shelf locations. Location on the continental shelf accounted for a high proportion of the variation in community structure. The Lutjanidae and Serranidae were more abundant on the midshelf while the Lethrinidae (in particular *Gnathodentex aurolineatus* and *Monotaxis grandoculis*) were more abundant on the outershelf reefs. Additionally, a large proportion of the species recorded were relatively rare within a given zone, reef or location. The descriptions of the patterns of spatial variation of species of the Lutjanidae, Lethrinidae and Serranidae within reefs and among reefs and locations is an important consideration for any future experimental manipulations of fishing pressure. Care will need to be taken in determining the appropriate spatial scales of sampling to ensure that the effects of smaller scale spatial differences are not confounded when larger scale comparisons are made.

Spatial and temporal patterns in the distribution and abundance of the Lutjanidae and Lethrinidae were examined among midshelf reefs using a combination of two techniques, visual censuses and fish traps. Visual censuses were used to survey the shallow water assemblages, while fish traps were used to survey deeper water assemblages below diveable depths. The assemblages of the Lutjanidae and Lethrinidae were found to vary significantly among reefs and between depths and also between diel sampling periods. Significant among reef differences were observed in the shallow water assemblages of both the Lutjanidae and Lethrinidae. This was generally attributable to the low abundance of a species at a given reef. It is hypothesised that reef structure and habitat complexity are strongly correlated with lutjanid abundance. This hypothesis is supported by the experimental manipulation of artificial reefs by Hixon and Beets (1989), who found a significant correlation between the number of large fishes inhabiting reefs and the number of large holes present in the reef.

The deeper water assemblages of the Lutjanidae and Lethrinidae varied more between depths and between diel sampling periods than among reefs or over the 12 month sampling period. *Lutjanus carponotatus*, *L. fulviflamma* and *Lethrinus miniatus* were significantly more abundant in the shallow set traps (12-18m), whereas *Lutjanus adetii*, *L. russelli*, *L. sebae*, *L. vitta*, *Gymnocranius audleyi*, *Lethrinus sp.2* and *Abalistes stellaris* were all significantly more abundant in the deep set traps (30-40m). Depth preferences may coincide with the selection of large shelter sites and structure and this may be a major determining factor in the depth distribution of lutjanids and lethrinids (see Hixon and Beets, 1989). Additionally, *Lutjanus adetii*, *L. fulviflamma*, *L. quinquelineatus*, *L. russelli*, *L. sebae*, *L. vitta* and *Lethrinus miniatus* were all significantly more abundant in night set traps. In contrast, *Lethrinus sp. 2*, *Abalistes stellaris* and *Plectropomus leopardus* were all significantly more abundant in day set traps. The diel variability in trap catches is consistent with what is known of the feeding behaviour of the species examined (eg. Randall and Brock, 1960; Hobson, 1965; Starck and Davis, 1966; Choat, 1968; Hobson, 1968; 1974; Randall, 1967; Starck, 1971; Goeden, 1978; Parrish, 1987).

The age and growth of *Lutjanus adetii* and *L. quinquelineatus* from the central Great Barrier Reef were determined from studies of annuli in sectioned otoliths (sagittae). The periodicity of formation of the annuli (ages) was validated through a field study involving oxytetracycline labelling of tagged fishes. Validation was obtained from tagged fishes which were recaptured after 12 months or more at liberty. This is the first time that the direct validation of ages has been achieved in *Lutjanus* species. A single opaque and translucent zone (viewed under transmitted light) was found to be formed once per year with the opaque band (annulus) formed during the winter months, May - August. Otolith (sagittae) lengths showed a poor correlation with fish age, while otolith weight exhibited a strong linear relationship with the age of individuals of both species and indicates otolith growth increments are continuous with age, independent of fish growth. This supports the suggestion of Mosegaard *et. al.* (1988) that a process other than somatic growth, such as metabolic rate governs the rate of otolith accretion.

There was significant differential growth between the sexes in observed length-at-age and weight-at-age for both *L. adetii* and *L. quinquelineatus*. Males were larger than females in both species. Faster growth of males over females in older age classes has been reported for many lutjanid species (Thompson and Munro, 1983; McPherson *et. al.*, 1988; McPherson and Squire, 1992; Druzhinin and Filatova, 1980; Tarbit, 1980; Davis and West, 1992).

The ageing of coral reef fish is a relatively new field. Historically coral reefs were considered to be highly productive, high-turnover ecosystems. The estimates of longevity of these species provided by this study are clearly contrary to this historic model.

The oldest individuals examined were a male *L. adetii* 24 years of age and a female *L. quinquelineatus* 31 years of age. The shape of the growth curve of both of these lutjanid species was initially quite steep over the first few years and then became essentially asymptotic. This form of asymptotic growth curve implies that natural mortality curves will also be initially steep and then flatten substantially over the asymptotic growth period before descending again with senility and suggests that natural mortality curves may not decline at a continuous rate as is assumed in most classical fisheries models. The annual instantaneous rate of total mortality (Z) was estimated to be 0.300 for *L. adetii*, representing an annual survivorship of approximately 74%. The annual instantaneous rate of total mortality for *L. quinquelineatus* was estimated to be 0.154, representing an annual survivorship of approximately 86%. Regression methods used to produce estimates of total and natural mortality rates such as those of Pauly (1980) and Ralston (1987) were found to produce overestimates of mortality for these long lived species and hence underestimate survivorship. Regression methods used to produce estimates of total and natural mortality rates such as those described by Pauly (1980), Hoenig (1983) and Ralston (1987) should be applied with caution. The slow growth (low K), protracted longevity and low natural mortality rates imply that both *L. adetii* and *L. quinquelineatus* are vulnerable to overfishing despite their small size.

Further, there was significant variability in the growth, mortality and age structures of *L. adetii* and *L. quinquelineatus* at the spatial scale of individual reefs. Significant differences in the mean length, age and weight of both species was observed among reefs independent of the sex of the fish. There were also significant differences in observed weight-at-length among reefs for both species. The age structures of both *L.adetii* and *L. quinquelineatus* were also significantly different among reefs. Peaks in abundance of year classes were variable from reef to reef. Comparisons of the von Bertalanffy growth curves indicated that the pattern of growth in individuals of *L. quinquelineatus* was significantly different among reefs, while the pattern of growth in individuals of *L. adetii* was not significantly different. However, there were no significant differences in the mean length of the early age classes of either species among reefs. The mortality rates and hence survivorship of both *L. adetii* and *L. quinquelineatus* among reefs were highly variable. It is hypothesised that the varying age structures and mortality rates of both these species at the spatial scale of individual coral reefs is determined by the non-equilibrial balance of variable recruitment interacting with density independent mortality (but see also Jones (1991)). Hence the effect of good recruitment years may persist in the age structure of populations over time, as observed in *Pomacentrus moluccensis* in the southern Great Barrier Reef (Doherty and Fowler, 1994) and for the coral trout *Plectropomus leopardus* in the central Great Barrier Reef (Ferreira and Russ, submitted).

Stock assessment of species of the Lutjanidae on the Great Barrier Reef has not been undertaken to date. Significant variation in the demography of lutjanid species (Chapter 7) among reefs will need to be taken into account in such assessments. Because of their utility and widespread use by scientists on the Great Barrier Reef, much attention to date on the management of fishes of the Great Barrier Reef has centred on visual survey techniques. Management plans have been based on emergent reefs because these are readily observable on charts and in satellite imagery. Much, if not most, of the fisheries resources in the Great Barrier Reef region are, however, below diveable depths and their distribution has not yet been described. Until these resources are mapped and the interactions between "deep" and "shallow" populations are determined, these resources will not be accurately assessed.

This thesis has begun to clarify the distribution of lutjanids and growth, mortality and age structure of two species in the central Great Barrier Reef but there remains a scarcity of data on the reproduction and recruitment of lutjanids in general on the Great Barrier Reef. McPherson *et. al.* (1992) have reported that the spawning activity of *L. sebae*, *L. malabaricus* and *L. erythropterus* occurs during the spring and summer months in the GBR waters, with a single summer spawning peak. Similarly, the data of Loubens (1980a) indicate that lutjanids in New Caledonia (latitude 23°S) also have a single midsummer spawning peak. Detailed reproductive studies are required to determine the distribution of the effective egg spawning biomass of lutjanids (and other species of fisheries importance) on the Great Barrier Reef in order to determine the impacts of fishing. Additionally, the source of most of the recruitment of these species to the fisheries (whether it is inshore or offshore, shallow or deep) is unknown. Such data is also necessary to allow understanding of the processes that influence temporal fluctuations in recruitment and subsequent year class strength.

The juveniles of many of the larger species of lutjanids are difficult to find and the settlement sites for the larvae of the majority of species across the continental shelf are unknown. It will require a relatively sophisticated and expensive program of sampling methodologies (eg. beam trawls, baited video cameras, traps, submersibles, etc.) to determine settlement sites and to select settlement areas for monitoring purposes. Although it has not yet been demonstrated empirically for the Lutjanidae *per se*, variation in recruitment is expected to be preserved in subsequent year classes (eg. Doherty and Fowler, 1994; Ferreira and Russ, submitted). One of the initial hopes in this study was that it might identify the habitat of newly settled *Lethrinus miniatus*. This species is the second most important in the commercial fishery but the distribution of juvenile fish remains unknown.

The resolution of individual stocks of lutjanids through genetic studies has been inconclusive. Camper *et. al.* (1993) examined the mitochondrial DNA of *Lutjanus campechanus* from three localities in the northern Gulf of Mexico and reported that *L. campechanus* comprises a single, panmictic (randomly mating) population there. The observed genetic homogeneity also indicates considerable gene flow among individual *L. campechanus*. Further, Johnson *et. al.* (1993) analysed the genetic structure of *Lutjanus sebae* from 5 locations over a distance greater than 1400km in north-western Australia and found that there were extensive genetic connections of populations over large distances. Reef fish in general show population genetic patterns consistent with significant gene flow over large (> 1000km) distances (eg. Shaklee, 1984; and see also Doherty and Williams, 1988). While the utility of electrophoretic studies in stock assessment of lutjanids presently appears to be limited, it is an invaluable taxonomic tool which allows closely related species to be separated on the basis of reproductive isolation (see also Johnson *et. al.*, 1993). Developing genetic techniques which utilise mitochondrial DNA and microsatellites (eg. Rico *et. al.*, 1993; Slettan *et. al.*, 1993) have become increasingly important in studies of relatedness among species and the technique may become a useful tool for stock discrimination purposes.

Otolith morphology has been used in stock discrimination (Messieh, 1972; Postuma, 1974; Castonguay *et. al.*, 1991) and may provide a useful alternative to genetic studies for purposes of stock discrimination. Smith (1992) has shown that the deepwater snapper *Etelis carbunculus* exhibits regional differences in otolith morphology and allows separation of the population of Fiji and Vanuatu from the population of Hawaii, Northern Marianas Islands and French Polynesia. Campana and Casselman (1993) used otolith shape analysis on otoliths of the Atlantic cod, *Gadus morhua*, collected from spawning grounds throughout the northwest Atlantic. Highly significant differences in otolith shape were found among most of the cod samples and shape also differed among ages, sexes and year classes. The first discriminant function was highly correlated with both fish and otolith growth rates which indicated that stock discrimination improved as the difference in stock-specific growth rate increased. The analysis of otolith morphology as an indicator to the identity of unit stocks may be more cost effective and indicative of demographic variation than genetic analyses when examining regions as large as the Great Barrier Reef. The elucidation of separate unit stocks of species of commercial and recreational fishing significance would have important implications for the management of these species, as they are currently managed as a single unit stock.

8.1 Future Considerations and Directions

There is the potential for development of fisheries for the deepslope lutjanid resources off the Great Barrier Reef. Stocks of deepwater lutjanids, lethrinids and serranids are sensitive to over-exploitation and their productive capacity is restricted because of their slow growth, protracted longevity, low rate of natural mortality, late maturity and large size (Polovina and Ralston, 1987). For example, it has been estimated in the northern Marianas that one handline hour of fishing effort can remove approximately 2.2 percent of the bottomfish population inhabiting one hectare of habitat (Ralston *et. al.*, 1986). However, the annual MSY (maximum sustainable yield) for the deep slope fishes (primarily lutjanids and serranids) of the Mariana Archipelago is estimated to be 109 tonne, which for comparative purposes is equivalent to 222kg/nmi of 200m isobath (Polovina and Ralston, 1986) and the estimated MSY from fisheries stocks in the South Pacific ranged from 0.25-1464 tonne, which for comparative purposes is equivalent to 23.6-200kg/nmi of 200m isobath, with Nauru having the lowest and Papua New Guinea the highest (Dalzell and Preston, 1992). The initial experimental CPUE of these demersal deepwater stocks on the Great Barrier Reef compares favourably to the average CPUE of many South Pacific Islands (Dalzell and Preston, 1992 and see Kramer *et. al.*, 1993) which suggests that over the length of the Great Barrier Reef a substantial and sustainable fishery could develop for these deepslope species provided that management of the resources is tightly controlled.

However, care needs to be taken that overcapitalisation of a fishery on accumulated virgin stocks does not take place, because although the initial catch rates will be very high, they would be expected to decline rapidly if fishing effort is not regulated. Hilborn and Walters (1992) maintain that using initial CPUE to estimate MSY is one of the most common mistakes in stock assessment and leads to an over-estimate of both the MSY and the corresponding level of fishing effort. Therefore, effort will need to be constrained at the lower levels to maximise optimal fisheries potential. The management options in the commercial sector include : limited entry to the fishery (fleet regulation), regional area closures (protection of the spawning biomass, which has the capacity to act as a recruitment source for the surrounding fished areas), seasonal closures (to conserve and protect spawning stocks and aggregations), catch quotas (total allowable catch - TAC; either for the total fishery or by species), size limits (probably of little use in the depths fished, see below), and gear limitations. Recreational fishing interest in these species may also be managed with a combination of gear limitations, size limits, bag limits and closures.

While size limits are commonly used in shallow water fisheries they are generally viewed as useless in deepwater fisheries due to the limited survivorship of fishes from depths greater than 40m because of embolism of the swim bladder. Gear limitations may be a useful alternative, in particular the regulation of hook sizes and types. Ralston (1990) examined the selectivity of two sizes of circle hooks and found that the small hooks caught substantially more small fish, and the large hooks were somewhat more effective at capturing the larger size classes. Small hooks were also found to catch substantially more individuals of the smaller species (ie. *Pristipomoides auricilla*). Additionally, Otway and Craig (1993) have examined the selectivity of three different sizes of circle hooks on the capture of undersized *Pagrus auratus*. Increasing the absolute size of the hook resulted in significantly fewer individuals under legal size being caught, while larger hooks resulted in the capture of significantly larger sized individuals. The length of the bill of the hook was found to be inversely correlated with the number of fish under legal size being retained (Otway and Craig, 1993). Further, Correa-Ivo and Sobreira-Rocha (1988) have shown that larger hook sizes protect the juveniles of *Lutjanus purpureus* from being caught. The evidence to date suggests that small hooks will catch large fish but large hooks will not catch many small fish. Further studies will need to be undertaken on the Great Barrier Reef to ensure that gear limitations exclude smaller sized fishes from the catch.

The deep reef slope fishery resources of the GBR have potential as both a domestic and an export product. Deepwater lutjanids have a high export potential, they are popular food fish in Hawaii and the U.S. West Coast and are in high demand (and are of high value) in Japanese markets (Wessel-Daae, 1988). Markets generally require fresh fish which is highly valued and of a high quality.

Further, the development of the deep slope resources of the Great Barrier Reef also offers a unique opportunity to examine the biology of these species from one of the last remaining virgin stocks in the world. In virgin stocks, or lightly exploited stocks, the length at first capture is larger than those in exploited stocks and fish are generally older. The longevity of these species and estimates of their natural rates of mortality, which are of great importance in stock assessment, can potentially be established before the effects of fishing are impacted on these populations.

As an overall conclusion to this thesis the use of a combination of both visual censuses and fish traps to determine spatial variability in the distribution and abundance of the Lutjanidae and in particular the use of age structure to derive both rates of growth and mortality have led to greater insights into the population dynamics and fishery potential of these species on coral reefs.

The use of a combination of techniques such as visual census and fish traps to assess both the shallow water and the deeper water communities of fishes of coral reefs may be an objective way of repeatedly censusing reefs for monitoring purposes. The spatial structure of populations of large mobile reef fishes such as the Lutjanidae and Lethrinidae will directly affect how the stock responds to varying levels of exploitation. Spatial replication will be important in any experiment to predict how stocks will respond to exploitation and will ensure that small scale differences are not confounded when larger scale comparisons are made.

Further, the analysis of fisheries data on coral reef species should where possible, be based on age structured models. Fisheries management advice should also be based on validated ages and age structured models where possible, particularly where there is a storage effect of many older fishes in the larger size classes. The protracted longevity and low rates of natural mortality of both lutjanid species in this study suggests that they are vulnerable to overfishing despite their small size. Therefore the use of age structure in preference to length frequency analysis for such species must be emphasised. Despite its widespread use in the tropics length frequency analysis is limited to species which have very seasonal reproduction, and a very short life span (either naturally or caused by overexploitation) (see Hilborn and Walters, 1992).

Management strategies for these lutjanid stocks must also be robust to biological uncertainty such as variability in recruitment which can persist in the age structure of populations over time. Dominant year classes may also form a substantial proportion of the catch of the fishery and dominate the population (see Ferreira and Russ, submitted).

The settlement sites and nursery grounds for many lutjanid species are unknown. However, major recruitment episodes may be back-calculated from the age structure of populations and the annual monitoring of age structure of these populations may be a reliable and also cost effective method of monitoring recruitment to the fishery for management purposes.

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Appendix 1

Synopsis of the distribution and habitats of the Lutjanidae of the Great Barrier Reef.

The following summary of the distribution and habitats of lutjanids of the GBR is based on Randall *et. al.* (1990), Kramer *et. al.* (1993; 1994), Williams and Russ (1994) and personal observations, with additional information on distributions and general ecology in the wider Indo-Pacific from various sources. Common names and synonyms are also described.

***Aphareus furca* (Lacepede, 1802)**

Frequently seen on fore-reef slopes and occasionally in lagoons of the outer barrier reefs of the GBR, usually solitary or in small groups. Known to a depth of at least 70m (Randall *et. al.*, 1990). Found as far south as Seal Rocks, New South Wales (Kuiter, 1993). In waters south of the GBR, off south eastern Australia, adults occur in small aggregations on reef slopes near deep drop offs and juveniles school loosely in shallow coastal bays (Kuiter, 1993). In Micronesia, it occurs in open waters above clear lagoons and seaward reefs from 1-122m (Myers, 1989). In Vanuatu, it is characteristic of the species of the shallow depth (<120m) assemblage (Brouard and

Grandperrin, 1985). Feeds mainly on fishes and crustaceans (Myers, 1989) and reported as a roving piscivore (Randall *et. al.*, 1990). Max. length 40cm, common to 30cm.

Common synonyms : Commonly referred to as *A. furcatus*, an incorrect spelling (Anderson, 1987), also sometimes referred to as *A. flavivultus*.

Common names : Smalltoothed jobfish.

Aphareus rutilans Cuvier, 1830

Inhabits the outer barrier reefs of the GBR over rocky bottoms and sandy areas to depths of at least 100m. Seen rarely in the shallow waters of the outer barrier reefs. This species is also commonly associated with ledges and the edges of steep coral drop offs (Grant, 1987). This species is sometimes caught in association with *Aprion virescens* and is reportedly rare on the southern GBR (Grant, 1987). In the Philippines, it is found over sandy bottoms associated with reefs at depths of 20-80m (Schroeder, 1980). In Vanuatu, it is characteristic of species of the intermediate depth (120-240m) assemblage, occurring from 80-320m and common in 120-200m (Brouard and Grandperrin, 1985). Feeds on small crustaceans and other benthic invertebrates (Schroeder, 1980). In Vanuatu spawning occurs during the spring and summer, with peak activity in November and December (Brouard and Grandperrin, 1985). Max. length 80cm, common to 50cm.

Common synonyms : Sometimes referred to as *A. thompsoni*.

Common names : Rusty jobfish.

Aprion virescens **Valenciennes, 1830**

Inhabits the outer slopes, channels, back reef slopes and adjacent lagoons of the midshelf reefs, interreef shoals and outer barrier reefs of the GBR to at least 150m depth. More commonly found on the outer barrier reefs. Usually solitary or in small groups. This species is reportedly more abundant on the northern GBR reefs (Grant , 1987). In South Africa, occurs from shallow waters to 100m (van der Elst, 1981) and in Micronesia, occurs in open waters above outer reef slopes, channels and adjacent lagoon waters at depths of 3-180m (Myers, 1989). In Vanuatu, it is characteristic of species of the shallow depth (<120m) assemblage, occurring from 40-220m, but common in 40-120m (Brouard and Grandperrin, 1985). Primarily a piscivore of reef species and occasionally eats crustaceans and octopuses (Randall *et. al.*, 1990). In South Africa, 50% of the diet is of small reef fish and the rest is plankton such as fish eggs, larval mantis shrimps, megalopa crab larvae and swimming crabs (van der Elst, 1981). In Micronesia it is a voracious piscivore occasionally feeding on benthic and planktonic crustaceans and cephalopods (Myers, 1989). In East Africa spawning occurs from January to May and sexual maturity is reached at 70-75cm (age 3-4 years), with juveniles recorded in ocean currents far from land (van der Elst, 1980). In Micronesia, this species aggregates to spawn on outer reef slopes on the full moon or a few days thereafter from January to May (Myers, 1989). Max. length 100cm, common to 60cm.

Common names : Green jobfish, uku.

Etelis carbunculus Cuvier, 1828

Inhabits the deep reef areas of the outer barrier reefs of the GBR between depths of 190-318m (Kramer *et. al.*, 1994). Prefers steep slopes (eg. Ribbon reefs) or pinnacles/shoals at depth and usually occurs in small groups or large schools. In Vanuatu, it is characteristic of the deep species assemblage (>240m), occurring from 140-440m and commonly in 240-360m (Brouard and Grandperrin, 1985). In Hawaii, feeds primarily on fishes (98% of diet) and occasionally on small pelagic crustaceans, shrimp and cephalopods (Haight, *et. al.*, 1993). In Vanuatu, spawning occurs throughout most of the year with peak activity during November and this population exhibits relatively slow rates of growth and relatively low exponential rates of mortality (K=0.07, M=0.08; Brouard and Grandperrin, 1985). Although relatively unfished on the GBR this species is commercially valuable in Guam, Hawaii, New Caledonia, Vanuatu and other areas in the wider Indo-Pacific region (Masuda *et. al.*, 1984; Allen, 1985; Brouard and Grandperrin, 1985; Polovina, 1987; Anonyme, 1989; Dalzell and Preston, 1992). Max. length 100cm, common to 80cm.

Common synonyms : *E. coruscans* (Fischer and Bianchi, 1984) and *E. marshi* (Masuda *et. al.*, 1980; Carcasson, 1977).

Common names : Ruby snapper, short-tailed red snapper, red dog snapper, vivaneau chien rouge, ehu.

Etelis coruscans Valenciennes, 1862

Inhabits the deep reef areas of the outer barrier reefs of the GBR between depths of 215-335m (Kramer *et. al.*, 1994). Prefers steep slopes (eg. Ribbon reefs) or pinnacles/shoals at depth and occurs solitary or in small groups and may also occur in large schools. Occurs as far south as Sydney, New South Wales (Grant, 1987). All species of *Etelis* appear to form loose mixed species aggregations. In Vanuatu, it is characteristic of the deep species assemblage (>240m) occurring from 140-440m and commonly in 240-360m (Brouard and Grandperrin, 1985). In Hawaii, feeds primarily on fishes (80%), pelagic urochordates (11%) and shrimps (4%), as well as cephalopods and small pelagic crustaceans (Haight *et. al.*, 1993). Low relative rates of growth and exponential rates of mortality have been documented from both the Vanuatu (K=0.13, M=0.12; Brouard and Grandperrin, 1985) and the Marianas (K=0.16, M=0.36; Ralston, 1987) populations. This species is an important component of the commercial fisheries of several Indo-Pacific localities (Masuda *et. al.*, 1984; Allen, 1985; Brouard and Grandperrin, 1985; Polovina, 1987; Anonyme, 1989; Dalzell and Preston, 1992). It has been reported as far south as northern NSW (Grant, 1987) and Lord Howe Island (31.5°S)(Kramer *et. al.*, 1994).. Max. length 120cm, common to 70cm.

Common synonyms : *E. carbunculus* (Masuda *et. al.*, 1980; Carcasson, 1977; Fischer and Bianchi, 1984), *E. oculatus* (Fourmanoir and Laboute, 1976), and sometimes referred to as *E. evurus*. Closely related to *E. oculatus* of the western Atlantic Ocean.

Common names : Ruby snapper, long-tailed red snapper, flame snapper, large eyed jobfish, vivaneau la flamme, onaga.

Etelis radiosus Anderson, 1981

Inhabits the deep reef areas of the outer barrier reefs of the GBR between depths of 185-275m (Kramer *et. al.*, 1994). Prefers steep slopes (eg. Ribbon reefs) or pinnacles/shoals at depth and occurs either solitary or in small groups. Probably feeds primarily on fishes as it seems closely related to *E. carbunculus* in form and habit. In Vanuatu, it is characteristic of the deep species assemblage (>240m) occurring from 140-330m and commonly in 200-320m (Brouard and Grandperrin, 1985). Max. length 100cm, common to 60cm.

This species was only identified in 1981 and little is known about its biology. This species has probably been often confused with the other *Etelis* species. It has been recorded in commercial catches of these species in many areas of the Indo-West Pacific region (Masuda *et.al.*, 1984; Allen, 1985; Dalzell and Preston, 1992).

Common names : Long-jawed red snapper, pale snapper.

Lutjanus adetii (Castelnau, 1873)

The distribution of *L. adetii* is restricted to the east coast of Australia and New Caledonia. In Australia it occurs primarily between Cape Moreton and the Capricorn-Bunker Group and it is rarely seen north of this region in depths frequented by divers. It is however, common in depths exceeding 30m on the central GBR. Usually forms large aggregations both in the shallows in the southern GBR (Grant, 1987) and in depths of >30m at the base of the reef slope north of this region. In waters south of the GBR, off south eastern Australia, this species inhabits coastal reefs and astuaries in lagoons with rocky outcrops, often in large schools and is found as far south as Sydney harbour (Kuiter, 1993). Presently the distribution of juveniles of this species is unknown and the only known records of small specimens are from trawl catches (3 specimens weighing 10-15g.) over hard substrata with very little sediment in 80m of water in the Chesterfield Islands, New Caledonia (ORSTOM-Noumea fish data base : Michel Kulbicki, pers. comm.). Additionally, *L. adetii* is a common species in New Caledonian waters and is typically found associated with isolated patch reefs in waters of at least 15m and preferably deeper. It is found down to 200m on the outer reef, with the larger fish (approx. 2kg) found in the deepest part of the lagoon (ORSTOM-Noumea fish data base : Michel Kulbicki, pers. comm.). In New Caledonia, spawning occurs from August to February with the peak activity from November to January, and individuals mature at approx. 20-30cm (Loubens, 1980). Max. length 50cm, common to 30cm throughout its range.

Small juveniles are plain whitish with a distinct black spot on the caudal peduncle and a yellowish spinous dorsal fin (Kuiter, 1993). The longitudinal yellow stripe develops with age and adults become reddish with a whitish belly.

Common synonyms : *L. amabilis* (Fourmanoir and Laboute, 1976; Grant, 1982 - plate 173 and 174; Russell, 1983; Coleman, 1986; Grant, 1987).

Common names : Hussar, yellow banded hussar/seaperch/snapper.

Lutjanus argentimaculatus **(Forsskal, 1775)**

Widespread on the GBR, with the juveniles and subadults common in coastal estuarine systems and the lower reaches of freshwater streams. The adults undergo a migration to offshore reefs where they occur in depths of at least 100m and usually occur as solitary individuals. Individuals occurring inshore in estuarine systems of the central GBR region are immature, with mature fish found only on offshore reefs (M.J. Sheaves, pers. comm.). The juveniles and subadults occurring inshore prefer the shelter of submerged snags (eg. trees, etc.) and mangroves (Grant, 1987). As adults are encountered only occasionally on the offshore reefs of the GBR, the proportion of individuals that undergo the migration and are part of the spawning stock is unknown. In waters south of the GBR, off south eastern Australia, the adults are located deep offshore in depths of 100m, and the juveniles occur in mangroves, estuaries and in the lower reaches of freshwater streams with the juveniles known from as far south as the Sydney area (Kuiter, 1993). In northwest Australia, it is dominant in the hard bottom assemblage, occurring in 20-60m, commonly in 45-60m (Okera, 1982). In the Philippines, juveniles are found in estuaries and adults on the deep reefs (Schroeder, 1980) and in South Africa, juveniles occur commonly in estuaries and larger fish on offshore reefs to 80m (van der Elst, 1981). In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 80-260m, commonly in 80-200m usually close to mangroves and rivers (Brouard and Grandperrin, 1985). In Micronesia, prefers turbid inshore reefs and continental coastlines to 120m depth and the juveniles are common in the brackish freshwaters of rivers (Myers, 1989). Feeds on mullet and stumpnose in estuaries (van der Elst, 1981) and adults on offshore reefs feed on a variety of benthic fishes and invertebrates (Schroeder, 1980; Myers, 1989). Spawning activity peaks from late spring to summer among fish larger than 45-60m on offshore reefs, with the fry migrating into estuarine nursery areas (van der Elst, 1981). Adults in the Philippines undergo a migration to deep lagoons and deep outer reefs where they spawn around the time of the full moon in late spring and summer (Schroeder, 1980; Myers, 1989). Max. length 120cm, common to 50cm.

Common names : Mangrove jack, mangrove red snapper, red chopper, creek/reef red bream, dog bream.

***Lutjanus biguttatus* (Valenciennes, 1830)**

Observed occasionally on midshelf and outer shelfs reefs of the GBR in depths of 5-25m as far south as Rib reef (central GBR), but nowhere common, occurring solitary or in small groups usually associated with staghorn *Acropora*. Observed in large aggregations of more than 100 individuals on Scott reef in Western Australia. In the Philippines, occurs on coral reefs between 5-10m (Schroeder, 1980). In Micronesia, it occurs on the outer reef slopes in 3-36m (Myers, 1989). Feeds on small fishes, crabs, shrimps and shelled molluscs (Schroeder, 1980). Max. length 30cm, common to 25cm.

Common names : Two spot banded snapper.

***Lutjanus bitaeniatus* (Valenciennes, 1830)**

This species has only recently been recorded from the GBR. It appears to be quite common in inshore interreef areas characterised by trenches or holes at depths of 50-60m between the mainland and the Whitsunday Group, central GBR, and may be widely distributed on the GBR. Local fishermen report that this species rarely exceeds a total length of 30cm, as does Allen (1985). This species forms part of the "red snapper complex" and can be readily confused with subadult *L. erythropterus* and *L. malabaricus*. Previously this species was known only from the Eastern Indian Ocean and the Indonesian Archipelago with specimens recorded from Western Australia and Indonesia where it inhabits deeper reef areas in depths of 40-65m (Allen, 1985). Max. length 30cm, possibly grows larger.

Reference material has been deposited in the Western Australian Museum (WAM) under the registration number : WAM p. 30740 - 001.

Common names : Indonesian snapper.

Lutjanus bohar **(Forsskal, 1775)**

Inhabits coral reefs and rocky areas from midshelf reefs to bluewater outershelf coral reefs at 5-100m on the GBR. Commonly encountered on steep outer reef slopes of the outerbarrier reefs and occasionally on the midshelf reefs. Occurs solitary or in groups of up to 50 individuals, but may form large aggregations. An aggregation of over 500 individuals was observed at a depth of 23m off Myrmidon reef (an outerbarrier reef) in the central GBR in November, 1989 (D.McB. Williams, pers. comm.). In northwest Australia occurs predominately on the shelf break to 120m depth (Okera, 1982). In the Philippines and South Africa this species occurs from shallow reefs to a depth of 70m (Schroeder, 1980; van der Elst, 1981). In Vanuatu, characteristic of the shallow depth (<120m) species assemblage, occurring in 20-220m, commonly in 20-120m (Brouard and Grandperrin, 1985). In Micronesia, occurs on exposed seaward reefs and adjacent lagoon and channel waters from 4-180m and more abundant around atolls and low islands than high islands (Myers, 1989). Also dominant on the exposed rocky sides of Tutia reef, east Africa (Talbot, 1965). Frequently seen cruising in midwater above the outer reef slopes preying on fishes. Feeds primarily on fishes and to a lesser extent on crustaceans such as crabs, prawns, mantis shrimps, pteropods and mysids, as well as cephalopods and molluscs (Schroeder, 1980; van der Elst, 1981; Myers , 1989). Spawning in South Africa occurs throughout the year with peaks during March and October-November and occurs mainly over the continental slope. Sexual maturity is attained after approx. 5 years of age at approx. 45-50cm and the males grow larger than the females (van der Elst, 1981). In Micronesia *L. bohar* aggregates to spawn along the outer reef slope around the full moon throughout the year with a peak in spawning activity from April-July and sexual maturity is attained at approx. 45cm (Myers, 1989). Max. length 85cm, commonly 40-60cm.

Juvenile *L. bohar* are common in shallow waters of the outer barrier reefs of the GBR where they mimic *Chromis ternatensis* (Russell *et. al.*, 1976; personal observations). In its juvenile phase *L. bohar* is also known to mimic *C. flavomaculata*, *C. weberi*, *C. miyakeensis*, and *C. lepidolepis* (Moyer, 1977). This is a form of aggressive mimicry which enables *L. bohar* to approach unwary prey more easily (Russell *et. al.*, 1976).

Adult *L. bohar* are sometimes confused with *L. argentimaculatus*. These species are easily distinguished with *L. bohar* having a deep nostril groove anterior to each eye and this is absent in *L. argentimaculatus*.

Common synonyms : *L. coatesi* (Whitley, 1934; Munro, 1967 - in part; Carcasson, 1977 - in part).

Common names : Two-spot red snapper, red bass, red seabass.

Lutjanus boutton **(Lacepede, 1803)**

A single specimen of this species was recorded from Rib reef central Great Barrier Reef, from the base of the reef slope in 40m depth (the upper limit of its known depth range). This species probably occurs in large schools like the a similar species, *L. adetii.* Possibly widespread on the GBR and common in the deeper waters. It is a common component of trap catches in Vanuatu in depths of 100-200m (Guerin and Cillaurren, 1989). Occurs on reefs and adjacent sandy areas to depths of 80m in the Philippines (Schroeder, 1980). In Samoa, it is found in depths of 50-160m, but is more common in the deeper slope waters (Mizenko, 1984). In Vanuatu it is found from 100-280m and it is characteristic of the intermediate depth (120-240m) species assemblage (Brouard and Grandperrin, 1985). The diet consists of fishes, shrimps, crabs, other crustaceans, cephalopods and some planktonic items and spawning occurs during autumn and winter over the full moon (Mizenko, 1984). Max. length 30cm, common to 20cm.

Reference material has been deposited in the Western Australian Museum (WAM) under the registraion number : WAM p. 30597-001

Common synonyms : *L. caeruleovittatus* (Schroeder, 1980; Masuda *et. al.*, 1984 - plate 158G; Shen, 1984) and *L. rufolineatus* (Shinohara, 1966; Fourmanoir and Laboute, 1976; Masuda *et. al.*, 1980; Masuda *et. al.*, 1984 - plate 158F; Burgess *et. al.*, 1990 - plate 197).

Common names : Moluccan snapper.

Lutjanus carponotatus (Richardson, 1842)

Inhabits sheltered lagoons to outer slopes of coral reefs and is most abundant on the inshore coral reefs and to a lesser extent the midshelf reefs of the GBR. It rarely occurs on the outerbarrier reefs of the GBR. Additionally, this species is found in the vicinity of rocky coastal outcrops and headlands and is common in all shallow coastal reef waters (Grant, 1987). Occurs solitary or in small groups usually at depths between 2 and 40m, but may form large aggregations. Widespread on the GBR but particularly abundant in the lagoons of the southern Capricorn-Bunkers section. In northwest Australia, *L. carponotatus* forms part of the hard bottom assemblage in low numbers and occurs from 20-60m (Okera, 1982). In the Philippines, occurs on coral reefs from 10-60m (Schroeder, 1980) and is also known from trawls to 80m depth (Allen, 1985; location not given). Feeds nocturnally on fishes and benthic invertebrates in the Philippines (Schroeder, 1980), while on the GBR *L. carponotatus* is known to actively forage diurnally as well as nocturnally. Grant (1987) observed that *L. carponotatus* feeds regularly on schools of *Spratelloides delicatulus*. Max. length 40cm, common to 30cm.

Common synonyms : *L. chrysotaenia* (Munro, 1967; Carcasson, 1977 - in part; Grant, 1982).

Common names : Stripey, spanish flag.

Lutjanus decussatus (Cuvier, 1828)

Inhabits coral reefs usually at depths between 5 and 30m and occurs both solitary and in schools (Allen, 1985). Relatively rare on the GBR and is encountered only in the far northern section. In the Philippines occurs in 2-40m (Schroeder, 1980) and in Micronesia *L. decussatus* inhabits both inshore and offshore reefs from 2-30m (Myers, 1989). Feeds on small fishes and invertebrates and is nocturnally active (Schroeder, 1980). Max. length 30cm, common to 20cm.

Common names : Checkered snapper/seaperch.

Lutjanus ehrenbergii (Peters, 1869)

This species is known only from the observation of a school of these fish on Hicks reef in the northern GBR near Lizard Island (A.M. Ayling, pers. comm.). It is possibly more widespread on the GBR but can be readily confused with *L. fulviflamma*. This species is known to inhabit coral reefs at 5-20m and the juveniles frequent inshore areas over sand, silt or rubble bottoms, occasionally occurring in mangrove lined streams and estuaries (Allen, 1985). In Micronesia *L. ehrenbergii* inhabits lagoon and seaward reefs around high islands and the juveniles frequent turbid inshore areas over sand, coral rubble and occasionally are known to enter mangroves (Myers, 1989). Max. length 35cm, common to 20cm.

Common synonyms : *L. fulviflamma* (plate of *L. fulviflamma* in van der Elst (1981) is *L. ehrenbergii*).

Common names : Black spot snapper.

Lutjanus erythropterus Bloch, 1790

Commonly inhabits inshore reefs, interreef shoals and trawl grounds and is occasionally encountered around the base of the reef slope of midshelf and outerbarrier reefs of the GBR to a depth of at least 80m. Primarily a schooling species that often forms mixed species schools with *L. malabaricus*, both as juveniles and adults. This species has a nearshore juvenile phase and undergoes a migration to inshore reef and shoal areas as a subadult and then to offshore interreef shoal areas to depths of at least 80m as an adult. Juveniles as small as 2.5cm are trawled regularly in the shallow waters (<5m) in Cleveland Bay and Bowling Green Bay near Townsville, central GBR (Williams and Russ, 1994). In an extensive trawl survey of the central GBR, juvenile *L. erythropterus* formed part of a coastal species assemblage found only in the shallowest stations sampled (15-24m)(Jones and Derbyshire, 1988). These sites were the only sites sampled that had high silt and clay fractions, presumably of terrigenous origins (Dredge, 1988). Juveniles ranging in size from 6-22cm also form part of the by-catch of prawn trawlers on the northern GBR (Jones and Goeden, 1985). In northwest Australia, *L. erythropterus* is dominant and characteristic of the hard bottom species assemblage and occurs in 20-90m, and is common in depths of 80-90m (Okera, 1982). Max. length 70cm, common to 50cm.

Common synonyms : *L. altifrontalis* (Chan, 1970), *L. malabaricus* (Fischer and Whitehead, 1974), *L. sanguineus* (Grant, 1982 - plate 166 and 167) and *Pinjalo pinjalo* (Shen, 1984; in part).

Common names : Small mouth nannygai\seaperch, saddle tailed seaperch, crimson snapper.

***Lutjanus fulviflamma* (Forsskal, 1775)**

Commonly found from the inshore reefs to the outerbarrier reefs on the GBR in depths of 2 to at least 40m. This species is abundant in a wide range of habitats from coastal estuaries to the outer slopes of outerbarrier reefs and is probably the most widely distributed of all GBR lutjanids. Juveniles are sometimes found in the brackish waters of mangrove estuaries or in the lower reaches of freshwater streams as well as rocky headlands and breakwaters. Juveniles (2.5cm) have also been recorded from depths of 40m on featureless bottom at the base of the reef slope of the midshelf reefs of the central GBR (Newman, unpublished data). In waters south of the GBR, off south eastern Australia, adults inhabit coastal reefs and estuaries in 3-30m, and the juveniles enter brackish water and are distributed as far south as Sydney harbour (Kuiter, 1993). In the Philippines, occurs in the shallow waters of estuaries, rocky and coral reefs to 10m and the juveniles are common in mangroves and brackish waters (Schroeder, 1980). In South Africa, occurs commonly off rocky shores, estuaries, mud and eelgrass, with the juveniles (2-12cm) common in the estuarine areas (van der Elst, 1981). Talbot (1960) considered this species to be the most widely distributed lutjanid in east Africa. Feeds on a wide variety of fishes (eg. anchovies, gobies) and benthic invertebrates (eg. crabs, prawns, mantis shrimps, mysids and marine worms) (Schroeder, 1980; van der Elst, 1981). Spawning in South Africa occurs over deep reefs from August to March (spring to summer) and sexual maturity is attained at a length 16-17cm (van der Elst, 1981). Max. length 35cm, common to 25cm.

On the GBR this species is often confused with *L. russelli* and misidentified as the juvenile of *L. johnii.*

Common synonyms : *L. russelli* (plate of *L. russelli* in van der Elst (1981) is *L. fulviflamma*), also sometimes referred to as *L. unimaculatus*.

Common names : Black spot snapper/seaperch.

Lutjanus fulvus **(Schneider, 1801)**

Inhabits inshore to outerbarrier reefs of the GBR in habitats from lagoons to outer reef slopes in depths of 2-40m. It also occurs inshore around rocky headlands and juveniles are sometimes found in mangroves and the lower reaches of freshwater streams. Widespread on the GBR, but is only encountered occasionally and is nowhere common. In the Philippines, occurs on coral reefs to depths of 50m (Schroeder, 1980). In Vanuatu, it is characteristic of species of the shallow (<120m) depth assemblage and occurs in 0-20m (Brouard and Grandperrin, 1985). In Micronesia, this species inhabits lagoon and semiprotected seaward reefs from 1-75m and prefers sheltered areas with deep holes or large bommies and sometimes enters mangroves or the lower reaches of rivers (Myers, 1989). Primarily a nocturnal feeder on fishes (eg. goatfishes and damselfishes) and benthic invertebrates such as calapid crabs (Schroeder, 1980; Myers, 1989). Max. length 40cm, common to 25cm.

This species is often confused with *L. lemniscatus* and both have been called *L. marginatus* in the past.

Common synonyms : *L. vaigiensis* (Randall and Brock, 1960; Shinohara, 1966; Munro, 1967; Grant, 1982; Burgess *et. al.*, 1990 - plate 199), misspelt as *L. pulvus* in Bagnis *et. al.* (1984) and sometimes referred to as *L. marginatus*.

Common names : Black tailed snapper, yellow margined seaperch.

Lutjanus gibbus **(Forsskal, 1775)**

Inhabits the midshelf and outerbarrier reefs of the GBR in depths of 2-70m. This species is most abundant on the steep outer slopes of outer barrier reefs. Sometimes occurs solitary or in small groups but often seen in large dense aggregations of up to 300 individuals. Juveniles are known to occur in the mangrove areas of islands, but on the GBR they occur on shallow sandy coral rock/rubble areas and coral rock outcrops of the protected leeward reef flat of outershelf reefs. Similar juvenile habitats were observed on Scott reef, Western Australia (personal observations) where small individuals were observed associated with seagrass beds in similar areas. In waters south of the GBR, off south eastern Australia, this species is distributed as far south as Sydney and the adults occur on coastal reef slopes, with the juveniles occurring in mangroves and seagrass beds (Kuiter, 1993). In the Philippines, occurs around rocky and coral reefs from 2-60m and the juveniles inhabit mangrove areas (Schroeder, 1980). In South Africa, occurs on rocky and coral reefs from shallow waters to 60m and the juveniles are found in estuaries (van der Elst, 1981). In Vanuatu, characteristic of species of the shallow (<120m) depth assemblage and occurs from 0-160m (Brouard and Grandperrin, 1985). In Micronesia, juveniles inhabit seagrass beds and mixed sand and coral habitats of sheltered reefs while adults prefer deeper lagoon and seaward reefs to 150m usually forming tight aggregations on the upper region of steep outer reef slopes and occasionally occurring on outer reef flats (Myers, 1989). This species disperses at night to feed primarily on invertebrates (mainly crustaceans) and to a lesser extent on echinoids, gastropods, cephalopods and small fishes (Schroeder, 1980; van der Elst, 1981; Myers, 1989).

Grant (1987) observed large schools of *L. gibbus* in shallow waters of the northern GBR feeding over the reef flat on making tides. In Micronesia spawning aggregations form along the outer reef slopes near the time of the full moon throughout the year (Myers, 1989). Sexual maturity is reached at 25-30cm (van der Elst, 1981). Max. length 50cm, common to 35cm.

Common synonyms : sometimes referred to as *L. comoriensis.*

Common names : Humpback red snapper, paddletail snapper/seaperch.

Lutjanus johnii (Bloch, 1792)

This species is encountered only occasionally on the inshore reefs of the GBR and is primarily a coastal species commonly found as adults in turbid waters around rocky shores, rock outcrops, shallow rocky reefs, islands and headland areas along the coast, generally associated with rivers, with the smaller fish and juveniles reported from the lower reaches of rivers and estuaries and from mangrove areas (see Grant, 1987). This species has not been reported from the midshelf and outerbarrier reefs of the GBR. However, further north in Princess Charlotte Bay and Weipa anglers report catches of this species from inshore coral reefs and rocky shoals often mixed with catches of *L. malabaricus* and Grant (1987) reports that this species is common on the eastern reefs of the Gulf of Carpentaria. Occurs in schools of similar size individuals or can also occur solitary as adults. Large adults have been trawled to depths of 80m (Allen, 1985). The trawl areas in the South China and North Andaman Seas where *L. johnii* is most abundant are characterised by shallow waters (30-40m) that are under the influence of nearby rivers (Anon. 1975). This species is cultured extensively in Singapore and Malaysia. Wild fingerlings of *L. johnii* for the Penang fishery are caught in the turbid, high current areas of the Middle Bank of the South Channel of Penang Island (Seng and Yong, 1987). Max. length 100cm.

Along the GBR coastline juveniles and adults of *L. johnii*, *L. fulviflamma* and *L. russelli* are often misidentified because of their similar appearance.

Common synonyms : *L. argentimaculatus* (Shen, 1984 - in part).

Common names : Fingermark, spotted scale seaperch, red bream, big scale red, John's snapper, golden snapper.

Lutjanus kasmira (Forsskal, 1775)

Common on the outer shelf reefs of the GBR to depths of at least 60m and can occur singly or in small groups, but often forms large aggregations. Rarely occurs on the midshelf reefs of the GBR. Forms mixed species schools with *L. quinquelineatus*, both as juveniles and adults. This species spends its entire life cycle from juvenile to adult in the coral reef environment. Juveniles have been observed in the lagoonal waters of outer shelf reefs in depths exceeding 10m and in low numbers in similar depths among schools in excess of 500 juvenile *L. quinquelineatus* on the midshelf reefs of the central GBR. In waters south of the GBR, off south eastern Australia, occurs on coastal reef slopes in small aggregations and sometimes in large schools, and the juveniles are found in harbours (Kuiter, 1993). In South Africa, occurs on coral reefs to 60m (van der Elst, 1981). In Vanuatu, characteristic of the shallow (<120m) depth species assemblage and occurs from 0-140m (Brouard and Grandperrin, 1985). In Micronesia, occurs from shallow inshore lagoons to outer reef slopes at depths of 265m, often forming large aggregations around prominant benthic structure and the juveniles may occur in seagrass beds as well as on the seaward reefs (Myers, 1989). A nocturnally active species which disperses at night to feed on benthic crustaceans and fishes (van der Elst, 1981; Myers, 1989). Spawning occurs once a year in South Africa, in late winter to early spring and sexual maturity is attained at approx. 17-20cm (van der Elst, 1981). Max. length 35cm, common to 25cm.

Australian populations of *L. kasmira* differ slightly in their colour patterns (Kuiter, 1993).

Common synonyms : Often confused with *L. quinquelineatus*, which has five blue stripes on the side instead of four and is yellow ventrally instead of white.

Common names : Blue-lined hussar/seaperch, moonlighter, blue stripe snapper, four-lined snapper.

Lutjanus lemniscatus (Valenciennes, 1828)

Inhabits primarily inshore reefs of the GBR and occurs infrequently on the midshelf and outerbarrier reefs, and interreef shoal areas to depths of at least 40m. Also occurs around headlands and rocky nearshore reefs. Individuals from deeper waters are frequently reddish pink and are often confused with the "red" species (*L. erythropterus* and *L. malabaricus*). Larger individuals tend to occur in deeper waters. Juveniles occur inshore in estuaries and are sometimes encountered in the vicinity of reefs close to shore where silting is moderate and visibility reduced (Allen, 1985). Feeds on fishes and a variety of benthic invertebrates (Allen, 1985). Max. length

65cm, common to 35cm.

This species is often confused with *L. fulvus* and both have been called *L. marginatus* in the past.

Common synonyms : *L. janthinuropterus* (Munro, 1967; Fischer and Whitehead, 1974; Grant, 1982), also sometimes referred to as *L. rangus* (Druzhinin, 1970), *L. furvicaudatus* and *L. marginatus.*

Common names : Dark tailed seaperch, yellow streaked snapper.

Lutjanus lutjanus **Bloch, 1790**

Occurs from rocky inshore interreef areas to offshore reefs and interreef shoals on the GBR to depths of least 40m and occurs either solitary or in small schools. Generally associated with depths in excess of 30m on interreef shoals and at the base of reef slopes of the midshelf reefs. This species is seen rarely while diving on the midshelf reefs of the GBR in depths shallower than 20m, however schools of 20 fish or more commonly are seen in depths in excess of 30m. In northwest Australia, it is characteristic of the hard bottom species assemblage, but it is present in low numbers and occurs in 40-80m, commonly in 50-60m (Okera, 1982). In the Philippines, occurs from shallow coral reefs to depths of 80m (Schroeder, 1980). Feeds on fishes and crustaceans (Allen, 1985). Max. length 30cm, common to 20cm.

Common synonyms : *L. lineolatus* (Shinohara, 1966; Munro, 1967; Fischer and Whitehead, 1974; Fourmanoir and Laboute, 1976; Masuda *et. al.*, 1980; Schroeder, 1980; Masuda *et. al.*, 1984; Shen, 1984), also sometimes referred to as *L. blochii.*

Common names : Big eye snapper.

***Lutjanus malabaricus* (Schneider, 1801)**

Generally considered an interreef species on the GBR, inhabiting the shoals and rubble grounds of the interreef plains within the reef matrix usually in depths greater than 30m. The deeper the water the larger the fish (McPherson *et. al.*, 1988). Juveniles are trawled regularly in the shallow waters of Cleveland Bay off Townsville. In an extensive trawl survey of the central GBR, juveniles of this species and *L. erythropterus* formed part of a coastal species assemblage found only in the shallowest (15-24m) stations sampled (Jones and Derbyshire, 1988). Juveniles ranging in size from 4-20cm form part of the by-catch of prawn trawlers on the northern GBR (Jones and Goeden, 1985). In northwest Australia, it is dominant in the midshelf (60-120m) species assemblage and occurs from 10-120m, commonly in 60-100 (Okera, 1982). In Vanuatu, it is characteristic of the intermediate depth (120-240m) species assemblage and occurs in 40-280m, commonly in 40-240m (Brouard and Grandperrin, 1985). In Micronesia, inhabits coastal and offshore reefs from 12-90m (Myers, 1989). Max. length 100cm, common to 50cm.

Common synonyms : *L. erythropterus* (Masuda *et. al.*, 1984; Shen, 1984 - in part), *L. sanguineus* (Fischer and Whitehead, 1974; Masuda *et. al.*, 1980) and is usually referred to as *L. coccineus* in the Kuwaiti literature. It is also sometimes referred to as *L. longmani*.

Common names : Large mouth nannygai, scarlet seaperch, Malabar blood snapper, red jew.

Lutjanus monostigma **(Cuvier, 1828)**

Frequently inhabits the lagoons and seaward slopes of outershelf reefs and is occasionally encountered on the midshelf reefs of the GBR. Usually solitary or in small groups. In Micronesia, prefers reef margins where there are deep cuts, caves, holes or large coral formations (Myers, 1989). Feeds on fishes such as squirrelfish, goatfishes, surgeonfishes and filefishes and on benthic crustaceans such as crabs and prawns (Myers, 1989). Max. length 60cm, common to 25-50cm.

Common names : One-spot snapper/seaperch.

Lutjanus quinquelineatus **(Bloch, 1790)**

On the GBR this species is common and widespread on the midshelf and outershelf reefs, occurring on the front reef slopes, but is more commonly found in the lagoon and back reef habitats. It is also occasionally encountered around the fringing reefs of coastal islands. Occurs either solitary or in small groups and may form aggregations in excess of 500 individuals. Known to occur to at least 128m depth on the GBR. Sometimes forms mixed species schools with *L. kasmira* on the outershelf reefs of the GBR. Juveniles have been observed in the lagoonal waters of midshelf reefs in depths of approx. 8-10m in aggregations in excess of 500 individuals on bommies surrounded by sand and rising to a height of 4m and located at a depth of approx. 10m. Small numbers of juvenile *L. kasmira* are often associated with these schools. In waters south of the GBR, off south eastern Australia, this species is found commonly south to Sydney and occurs in coastal reefs and lagoons, with the juveniles found in rocky estuaries in small aggregations (Kuiter, 1993). In the Philippines, occurs on rocky and coral reefs at depths of 10-50m (Schroeder, 1980). Max. length 35cm, common to 25cm.

Common synonyms : *L. kasmira* (Munro, 1967; Grant, 1982 - plate 170; Grant, 1987 - plate 433) and *L. spilurus* (Shinohara, 1966; Masuda *et. al.*, 1980; Schroeder, 1980; Masuda *et. al.*, 1984; Shen, 1984).

Common names : Blue banded seaperch, five lined snapper, moonlighter.

Lutjanus rivulatus (Cuvier, 1828)

On the GBR, encoutered only occasionally in a wide range of habitats from coastal rocky headlands to the outer barrier reefs. Usually seen as either solitary individuals or occasionally in pairs. Reported to depths of at least 100m (Allen, 1985). Additionally, Grant (1987) observed that this species is more common on the northern GBR reefs. In the Philippines inhabits patch reefs on sandy bottoms to 80m (Schroeder, 1980). In Micronesia, occurs inshore as well as on offshore reefs from shallow reef flats to 100m (Myers, 1989). Diet consists mainly of slow swimming reef fishes, crabs and molluscs, as well as polychaetes, squid, octopuses, sea urchins and ascidians (Schroeder, 1980; van der Elst, 1981). In South Africa sexual maturity is attained at 45cm (van der Elst, 1981). Max. length 100cm.

Common names : Maori snapper/seaperch/bream, blubberlip snapper.

Lutjanus russelli (Bleeker, 1849)

On the GBR this species is widespred and is common mainly on inshore and midshelf reefs to depths of 50m. This species occurs commonly along the entire

Queensland coastline (Grant, 1987). However, it is rarely encountered on outerbarrier reefs. Juveniles are frequently encountered in mangrove estuaries as well as the lower reaches of freshwater rivers and streams. Large adults are reported from trawl catches well offshore in depths of 70-80m (Allen, 1985). In waters south of the GBR, off south eastern Australia, inhabits coastal reefs and estuaries and large adults are found deep offshore in depths of 70-80m (Kuiter, 1993). In Northwest Australia, dominant in the hard bottom assemblage but in small numbers and found from 20-130m and commonly in 90-100m (Okera, 1982). In the Philippines, found in nearshore rocky and coral reefs to depths of 60m, with the juveniles commonly occurring in mangroves (Schroeder, 1980). In South Africa encountered commonly on shallow coral and rocky reefs, prefering caves and rocky overhangs and known as an aggressive territorial species whose juveniles use mangroves as nursery areas (van der Elst, 1981). Feeds primarily on crustaceans, especially small crabs and other benthic invertebrates as well as fishes (Schroeder, 1980; van der Elst, 1981). In South Africa, spawning occurs from October to February (van der Elst, 1981). In the central GBR this species is immature in inshore estuarine areas. Mature individuals are found only on offshore reefs (Sheaves, personal communication). A different form of this species occurs in the Indian Ocean (Allen, 1985). Max. length 45cm, commonly to 35cm.

On the GBR, this species is readily confused with *L. fulviflamma* and along the coastal zone it is freqently misidentified as *L. johnii.*

Common names : Russell's snapper, moses perch.

Lutjanus sebae **(Cuvier, 1828)**

On the GBR, *L.sebae* is generally regarded as an inter-reef species with the larger individuals found in deeper waters to at least 100m. Adults are always found in the deeper waters and swift running channels about reefs (Grant, 1987). Usually forms schools of similarly sized individuals (Grant, 1987; personal observations). Juveniles of 10-40cm are commonly encountered on turbid shallow inshore reefs and headland areas from 5-15m. Juveniles in the same size range are also encountered frequently in depths in excess of 25-40m at the base of reef slopes across the shelf. *L. sebae* is only occasionally seen in the lagoon waters of the outershelf and midshelf reefs, preferring the deeper slope waters. Small juveniles are frequently commensal with sea urchins, occurring among the sea urchin spines (Allen, 1985; Kuiter, 1993). Extensive trawl surveys in the central GBR caught juvenile *L. sebae* throughout the 15-62m depth range sampled (Jones and Derbyshier, 1988; Watson and Goeden, 1989). Juveniles ranging in size from 4-18cm form part of the by-catch of prawn trawlers on the northern GBR (Jones and Goeden, 1985). In waters south of the GBR, off south eastern Australia, occurs occasionally as far south as Sydney and inhabits coastal sand flats and deep lagoons usually in small aggregations near rocky outcrops in 10-100m (Kuiter, 1993). In Northwest Australia, forms part of the hard bottom assemblage and is found in depths of 10-120m (Okera, 1982). In the Philippines, occurs on reefs to 100m and juveniles commonly inhabit shallow mangrove and seagrass beds (Schroeder, 1980). In South Africa, occurs on reefs to depths of 100m (van der Elst, 1981). In Vanuatu, it is characteristic of the intermediate depth (120-240m) species assemblage and found from 100-200m (Brouard and Grandperrin, 1985). Feeds primarily on crustaceans, benthic fishes and other benthic invertebrates, as well squid. In South Africa, sexual maturity is reached after 4 years and from 60-70cm, and the males grow larger than the females (van der Elst, 1981). Max. length 120m.

Common synonyms : Usually referred to as *L. civis* in the early Indian Ocean literature.

Common names : Red emperor, emperor red snapper, government bream.

Lutjanus semicinctus Quoy and Gaimard, 1824

On the GBR, this species is relatively rare and is seen infrequently. It appears restricted to the outershelf reefs of the northern GBR and occurs south to at least Dip reef off Townsville and is usually solitary or in pairs. It is known to occur in depths of 10-30m. In Micronesia, this species inhabits reef flats and lagoons and seaward reefs to depths of 36m and is relatively common in the eastern Caroline Islands (Myers, 1989). Max. length 35cm.

Common names : Black banded snapper.

Lutjanus vitta (Quoy and Gaimard, 1824)

On the GBR, this species occurs usually from the base of the reef slopes of fringing reefs and midshelf reefs out onto the interreef rubble zones and shoal grounds as well as areas of flat bottom with occasional low coral outcrops, sponges and seawhips in depths of 10 to at least 50m. In Northwest Australia, it is dominant and recurrent in the midshelf assemblage from 60-120m, and found from 10-120m, commonly in 70-100m; it is also part of the hard bottom assemblage and the offshore sandy bottom assemblage in 80-90m in relatively small numbers (Okera,1982). In the Philippines, occurs on shallow coastal reefs (Schroeder, 1980). In Micronesia, occurs on relatively flat bottoms with scattered coral outcrops from 10 to 72m (Myers, 1989). Feeds on a range of prey items from fishes to benthic crustacea and polychaetes (Schroeder, 1980). Max. length 35cm.

Common synonyms : *L. lutjanus* (Munro, 1967; Masuda *et. al.*, 1980; Schroeder, 1980; Masuda *et. al.*, 1984; Shen, 1984), commonly referred to as *L. vittus* an incorrect spelling adopted by most previous authors.

Common names : Brown stipe snapper, striped seaperch.

Macolor macularis Fowler, 1931

Commonly inhabits the steep slopes of outer barrier reefs of the GBR and occasionally encountered on the midshelf reefs between at least 5 and 50m. Forms mixed species schools with *M. niger*. Juveniles are usually solitary in lagoons and closely resemble juvenile *Plectorhinchus picus*. In Micronesia, occur on the steep slopes of lagoons, channels and seaward reefs at 3-50m and are often seen in large aggregations with *M. niger*. In Vanuatu, characteristic of the intermediate depth species (120-240m) and is found from 100-200m (Brouard and Grandperrin, 1985). Primarily plankton feeders especially on large zooplankton at night, hence their large eyes and numerous long gill rakers (Myers, 1989). Max. length 60cm.

Common synonyms : Commonly misidentified and confused in the literature as *M. niger* (Fourmanoir and Laboute, 1976 - adult and subadult plates; Schroeder, 1980 - plate 219B and page 171; Coleman, 1986; Burgess *et. al.*, 1990 - plate 206 : 1st juvenile is *M. niger*, following two specimens are *M. macularis*).

Common names : Midnight snapper.

Macolor niger (Forsskal, 1775)

Forms large midwater schools on the edge of outerbarrier reefs of the GBR, particularly on the upper section of steep outer slopes between 5 and 50m and are occasionally encountered on the midshelf reefs. Juveniles usually occur solitary in lagoons and closely resemble juvenile *Plectorhinchus picus*. In the Philippines, common from 3-30m around large coral reefs and vertical drop offs. Local fishermen claim juveniles hide between the long spines of sea urchins (Schroeder, 1980). In Micronesia, occur in large aggregations along steep slopes of lagoons, channels and seaward reefs from 3-90m (Myers, 1989). In Vanuatu, characteristic of species of the shallow depth assemblage (<120m) and occur from 20-40m (Brouard and Grandperrin, 1985). Primarily plankton feeders which diperse at night to feed (Myers, 1989). Also feed on fishes and crustaceans (Schroeder, 1980). Max. length 60cm, common to 35cm.

Common names : Black and white snapper/seaperch.

Paracaesio kusakarii Abe, 1960

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 110-310m (Kramer *et. al.*, 1994) and usually occurs in small schools. In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 100-280m, commonly in 200-240m (Brouard and Grandperrin, 1985). Max. length 60cm.

This species is distributed widely in the western Pacific (Masuda *et. al.*, 1984; Allen, 1985) and has been reported from the northwest shelf of Australia (Gloerfelt-Tarp and Kailola, 1984).

Common names : Saddle back snapper.

Paracaesio stonei Raj and Seeto, 1983

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 200-318m and usually occurs in small groups (Kramer *et. al.*, 1994). In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 200-300m (Brouard and Grandperrin, 1985). Max. length 50cm.

This species is now known from the Ryukyu Islands, Fiji, Vanuatu and the GBR (Raj and Seeto, 1983; Masuda *et. al.*, 1984; Allen, 1985; Brouard and Grandperrin, 1985; Kramer *et. al.*, 1993; 1994). Probably widespread within the western Pacific region.

Common names : Cocoa snapper.

Paracaesio xanthura (Bleeker, 1869)

Occurs over rocky bottoms of the outer reef slopes of the outerbarrier reefs of the southern GBR at depths of 20-150m, as well as on southern Queensland coastal reefs, sometimes forming very large schools (Grant, 1987). Probably more widespread on the GBR. Found as far south as Montague Island, southern New South Wales (Kuiter, 1993). There is little variation in colour from the juvenile to the adult form. Feeds mostly on zooplankton (Allen, 1985). Max. length 40cm.

Common synonyms : Commonly referred to as *P. xanthurus*, an incorrect spelling used by most previous authors (Anderson, 1987) and *P. pedleyi* (Grant, 1982 - plate 361; Coleman, 1986; Grant, 1987 - plate 440).

Common names : Yellowtail blue snapper, southern fusilier.

Pristipomoides argyrogrammicus (Valenciennes, 1831)

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 280-335m (Kramer *et. al.*, 1994). Usually occurs in small schools. It is the smallest species of the *Pristipomoides* and it is usually found at greater depths than the other species. In Vanuatu, characteristic of the deep species assemblage (>240m) and occurs in 120-380m, commonly in 200-320m (Brouard and Grandperrin, 1985). Feeds on small fishes, crustaceans and squids (Allen, 1985). Max. length 40cm, common to 25cm.

Common synonyms : *P. amoenus* (Carcasson, 1977: Amesbury and Myers, 1982), *Tropidinius amoenus* (Shinohara, 1966; Masuda *et. al.*, 1980; Masuda *et. al.*, 1984 - plate 153H) and *Tropidinius argyrogrammicus* (Fourmanoir and Laboute, 1976; Brouard and Grandperrin, 1985).

Common names : Large-eyed flower snapper, ornate jobfish.

Pristipomoides auricilla (Jordan, Evermann & Tanaka, 1927)

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of at least 150m, but presently not common (Kramer *et. al.*, 1994). In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 200-220m (Brouard and Grandperrin, 1985). Feeds on fishes, pelagic tunicates and salps (Allen, 1985). Low relative rates of growth and relatively high exponential rates of mortailty have been documented from the Marianas (K=0.27, M=0.66; Ralston, 1987) population. Max. length 45cm, common to 25cm.

Common names : Goldflag jobfish, gold-tailed jobfish.

Pristipomoides filamentosus (Valenciennes, 1830)

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 70-210m and occurs as far south as Lord Howe Island (31.5°S), sometimes forming large aggregations (Kramer *et. al.*, 1994). Common in northern New South Wales and southern Queensland waters where they are commonly fished together with *Pagrus auratus* (Grant, 1987). In Vanuatu, characteristic of the shallow species assemblage (<120m) and occurs in 100-320m (Brouard and Grandperrin, 1985). In South Africa, diet comprises squid, fish and a variety of crustaceans such as mantis shrimps and mysids (van der Elst, 1981). In Hawaii, feed primarily on pelagic urochordates (47%), small pelagic crustaceans (31%), pteropod molluscs (13%) and fish (7%) and to a lesser extent siphonophores and cephalopods (Haight *et. al.*, 1993). Low relative rates of growth and exponential rates of mortailty have been documented from the Marianas (K=0.15, M=0.25; Ralston, 1987) population, wheras the Vanuatu population has a relatively high exponential rate of mortailty (K=0.29, M=0.53; Brouard and Grandperrin, 1985). It is a commercially important handline species in Hawaii (Polovina, 1987) and other areas of the Indo-West Pacific region (Dalzell and Preston, 1992). Estimated max. age 18 years. Max. length 80cm, common to 50cm.

Common synonyms : *Aprion microlepis* (Grant, 1982 - plate 181), and *P. argyrogrammicus* (van der Elst, 1981). Sometimes referred to as *P. microlepis.*

Common names : Rosy jobfish, crimson jobfish, king snapper, opakapaka.

Pristipomoides flavipinnis Shinohara, 1963

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 125-240m and sometimes forms large aggregations (Kramer *et. al.*, 1994). In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 60-340m, commonly in 80-200m (Brouard and Grandperrin, 1985). Feeds primarily on benthic fishes and to a lesser extent on crustaceans, larval squids and pelagic tunicates (Allen, 1985). Slow relative rates of growth and relatively high exponential rates of mortailty have been documented from the Vanuatu (K=0.36, M=0.83; Brouard and Grandperrin, 1985) population. It is a commercially important species in some West-Pacific Ocean areas (Allen, 1985; Polovina, 1987; Anonyme, 1989; Dalzell and Preston, 1992). Max. length 60cm, common to 40cm.

Common names : Golden eye jobfish, yellow finned jobfish, yellow jobfish.

Pristipomoides multidens **(Day, 1870)**

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 75-245m and sometimes forms large aggregations (Kramer *et. al.*, 1994). In northwest Australia, it is characteristic of the hard bottom assemblage, and is dominant and recurrent in the midshelf assemblage (60-120m) and occurs in 50-120m (Okera, 1982). In Vanuatu, characteristic of species of the intermediate depth assemblage (120-240m) and occurs in 60-360m, commonly in 80-240m (Brouard and Grandperrin, 1985). Feeds on fishes, shrimps, crabs, lobsters, stomatopods, squids and pelagic gastropods and urochordates (Allen, 1985). Low relative rates of growth and relatively high exponential rates of mortailty have been documented from both the Vanuatu (K=0.24, M=0.42; Brouard and Grandperrin, 1985) and the Marianas (K=0.19, M=0.63; Ralston, 1987) population. Max. length 90cm, common to 50cm.

Common names : Goldbanded jobfish, large-scaled jobfish.

Pristipomoides zonatus **(Valenciennes, 1830)**

Occurs over rocky bottoms of the deep outer reef slopes of the outerbarrier reefs of the GBR at depths of 120-295m and is solitary or occurs in small groups (Kramer *et. al.*, 1994). In Vanuatu, characteristic of species of the deep assemblage (>240m) and occurs in 80-340m (Brouard and Grandperrin, 1985). In Hawaii, feeds primarily on fishes (55%), pelagic urochordates (38%), crabs (6%) and to a lesser extent shrimps (Haight *et. al.*, 1993). Low relative rates of growth and relatively high exponential rates of mortailty have been documented from the Marianas (K=0.20, M=0.53; Ralston, 1987) population. This species is commercially important species in many areas of the Indo-Pacific region (Allen, 1985; Polovina, 1987; Anonyme, 1989; Dalzell and Preston, 1992). Max. length 50cm, common to 35cm.

Common synonyms : *Tropidinius zonatus* (Shinohara, 1966; Fourmanoir and Laboute, 1976; Masuda *et. al.*, 1980; Masuda *et. al.*, 1984 - plate 153G; Bagnis *et. al.*, 1984; Brouard and Grandperrin, 1985; Burgess *et. al.*, 1990 - plate 205).

Common names : Oblique banded snapper, banded flower snapper.

Symphorichthys spilurus **(Gunther, 1874)**

Occurs in the vicinity of sand and rubble areas within and around reefs of the GBR in depths of 2 to at least 30m, generally in shallow lagoons. Widespread from inshore to outerbarrier reefs, but more commonly seen on the outerbarrier reefs. Usually solitary or in small groups of up to 15 individuals. The long filamentous rays on the dorsal and anal fins diminish with age. In Micronesia, a seasonal migration occurs mostly on inshore lagoon and channel reefs, with large aggregations forming at specific sites along the reef edge several days before each new moon from March to July. They remain to spawn at the full moon then return to their usual lagoonal habitats. These aggregations occur in shallow water and move to deeper water each day before noon (Myers, 1989). A similar observation was made at Seringapatam reef in Western Australia, where an aggregation of approximately 70 individuals was seen in a channel on the drop off of the outer reef slope, generally indulging in nuzzling behaviour characteristic of prespawning (personal observations). In the Philippines, occasionally encountered near coral reefs and sandy areas to 60m (Schroeder, 1980).

Feeds on fishes, crustaceans living in sand and other benthic invertebrates (Schroeder, 1980). Myers (1989) suggests that they feed primarily on molluscs hence the strong pharyngeal teeth. Max. length 60cm, common to 35cm.

Juvenile *Symphorus nematophorus* are sometimes confused with *S. spilurus*.

Common synonyms : Sometimes referred to as *Symphorus spilurus*.

Common names : Sailfin snapper, blue lined seabream\seaperch.

***Symphorus nematophorus* (Bleeker, 1860)**

Inhabits inshore and midshelf reefs, interreef shoals and outerbarrier reefs of the GBR from 2 to at least 70m and is usually solitary or in small groups. Common in the deeper waters of the GBR to 60m and the older individuals appear bright pink in colour (Grant, 1987). Juveniles are occasionally encountered in shallow lagoonal waters. Juveniles are dissimilar from the adults. They exhibit elongate white trailing filaments from the posterior soft dorsal and display a series of longitudinal blue stripes on the reddish yellow body. In northwest Australia, found associated with hard bottom structure at the shelf break at approx. 120m (Okera, 1982). In the Philippines, is usually solitary on rocky or coral reefs to 50m (Schroeder, 1980). Feeds primarily on fishes and benthic invertebrates (Schroeder, 1980). Max. length 100cm, common to 60cm.

Common synonyms : *Glabrilutjanus nematophorus* (Shinohara, 1966; Fischer and Whitehead, 1974; Masuda *et. al.*, 1980), also sometimes referred to as *Symphorus taeniolatus*.

Common names : Chinaman, galloper, threadfin seaperch.

Appendix 2

Summary of the nominal commercial catch and effort data for species of Lutjanidae from the entire Great Barrier Reef from January 1988 to December 1993.

The catch figures are from the commercial fisheries database (CFISH) of the Queensland Department of Primary Industries (Georgina Eliason, personal communication).

Note : where there are less than 5 boats for the species specified, no data is provided.

Table A2.1 : Total catch of species of Lutjanidae on the Great Barrier Reef from 1988 to 1993.

Species	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Lutjanidae (all species)	29931	34426	46343	66596	55710	33941
Lutjanus sebae	18991	23888	26096	38526	21669	15283
L. malabaricus	----	----	----	----	4257	6691
L. carponotatus	----	----	----	----	----	286
L. argentimaculatus	2560	764	883	969	1013	1360
Pristipomoides species	1695	3520	14079	19406	22657	6400
L. adetii & *L. vitta* (mixed)	311	1259	416	1311	1777	1307
L. erythropterus & *L. malabaricus* (mixed)	6014	4212	2988	5192	3364	2433

Table A2.2 : Number of boats targeting species of Lutjanidae on the Great Barrier Reef from 1988 to 1993.

Species	Number of Boats					
	1988	1989	1990	1991	1992	1993
Lutjanus sebae	90	99	99	100	67	56
L. malabaricus	----	----	----	----	8	19
L. carponotatus	----	----	----	----	----	6
L. argentimaculatus	38	27	34	37	32	38
Pristipomoides species	18	24	31	35	35	26
L. adetii & *L. vitta* (mixed)	6	9	7	5	8	15
L. erythropterus & *L. malabaricus* (mixed)	19	26	21	21	23	15

Table A2.3 : Number of days fished for species of Lutjanidae on the Great Barrier Reef from 1988 to 1993.

Species	Number of Days Fished					
	1988	1989	1990	1991	1992	1993
Lutjanus sebae	1360	1947	1867	1778	1199	1049
L. malabaricus	----	----	----	----	71	216
L. carponotatus	----	----	----	----	----	67
L. argentimaculatus	467	245	415	374	299	407
Pristipomoides species	186	221	390	383	404	278
L. adetii & *L. vitta* (mixed)	92	166	41	33	76	158
L. erythropterus & *L. malabaricus* (mixed)	142	151	182	153	182	122

Table A2.4 : Average catch per day for species of Lutjanidae on the Great Barrier Reef from 1988 to 1993.

Species	Average Catch (kg) per Day					
	1988	1989	1990	1991	1992	1993
Lutjanus sebae	13.96	12.27	13.98	21.67	18.07	14.57
L. malabaricus	----	----	----	----	59.96	30.98
L. carponotatus	----	----	----	----	----	4.27
L. argentimaculatus	5.48	3.12	2.13	2.59	3.39	3.34
Pristipomoides species	9.11	15.93	36.10	50.67	56.08	23.02
L. adetii & *L. vitta* (mixed)	3.38	7.58	10.15	39.73	23.38	8.27
L. erythropterus & *L. malabaricus* (mixed)	42.35	27.89	16.42	33.93	18.48	19.94

Table A2.5 : Average number of days fished per boat for species of Lutjanidae on the Great Barrier Reef from 1988 to 1993.

Species	Average Number of Days per Boat					
	1988	1989	1990	1991	1992	1993
Lutjanus sebae	15.11	19.67	18.86	17.78	17.90	18.73
L. malabaricus	----	----	----	----	8.88	11.37
L. carponotatus	----	----	----	----	----	11.17
L. argentimaculatus	12.29	9.07	12.21	10.11	9.34	10.71
Pristipomoides species	10.33	9.21	12.58	10.94	11.54	10.69
L. adetii & *L. vitta* (mixed)	15.33	18.44	5.86	6.60	9.50	10.53
L. erythropterus & *L. malabaricus* (mixed)	7.47	5.81	8.67	7.29	7.91	8.13

Appendix 3

Summary of the nominal commercial catches of species of Lutjanidae by region within the Great Barrier Reef from January 1988 to December 1993.

The catch figures are from the commercial fisheries database (CFISH) of the Queensland Department of Primary Industries (Georgina Eliason, personal communication).

Note : where there are less than 5 boats for the species specified, no data is provided.

Table A3.1 : Total catch of the Lutjanidae (all species) by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	12534	12519	25254	32938	26256	11255
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	5133	5869	6039	4340	3431	3661
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	9334	8365	8747	19105	16896	8286
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	2930	7673	6303	10213	9127	10739

Table A3.2 : Total catch of *Lutjanus sebae* by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	9285	8817	11848	13984	8199	2543
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	2921	2536	4418	3013	2393	2431
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	5301	6094	5495	13225	3639	1758
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	1484	6441	4335	8304	7438	8551

Table A3.3 : Total catch of *Pristipomoides* species by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	825	1334	11261	15588	11397	2862
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	----	896	----	----	38	----
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	----	582	1401	2872	10383	3331
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	542	708	1381	936	839	----

Table A3.4 : total catch of *Lutjanus argentimaculatus* by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	423	313	156	158	212	312
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	948	199	283	177	459	163
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	543	201	360	427	234	374
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	646	----	----	----	----	511

Table A3.5 : Total catch of *Lutjanus adetii* and *Lutjanus vitta* (mixed) by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	----	1191	406	1311	1777	780
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	----	----	----	----	----	----
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	----	----	----	----	----	----
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	----	----	----	----	----	----

Table A3.6 : Total catch of *Lutjanus erythropterus* and *Lutjanus malabaricus* (mixed) by region within the Great Barrier Reef.

Region	Total Catch (kg)					
	1988	1989	1990	1991	1992	1993
Southern Section (Mackay) - (latitudes 20.5 to 22.5°S)	----	----	----	----	----	3387
Central Section (Townsville) - (latitudes 18.5 to 20.5°S)	1058	2080	----	1038	457	----
Northern Section (Cairns) - (latitudes 16.0 to 18.5°S)	3219	1488	1199	2534	2049	2685
Far Northern Section (Cooktown) - (latitudes 10.6 to 16.0°S)	----	----	479	----	594	371