

Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef

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Synopsis

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 and all species examined displayed significant cross-shelf changes in abundance. These significant cross shelf changes in abundance were due to an absence or low abundance of individuals of a species at one or more cross shelf locations, with many species present in only one location on the continental shelf. The genera *Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus*, *Gnathodentex*, *Gymnocranius*, *Lethrinus* and *Monotaxis* were all characteristic of the shallow shelf waters less than 100 m. In contrast, species of the genera *Paracaesio*, *Pristipomoides* and *Wattsia* were characteristic of the intermediate depths (100–200 m) and the deeper outer reef slope waters in excess of 200 m were characterised by species of the genus *Etelis*.

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 in the central Great Barrier Reef. The common study area comprises a cross shelf transect extending from inshore reefs to the Coral Sea at a latitude of approximately 18°30' S. These studies have described the distribution and abundance of hard corals (Done 1982), soft corals (Dinesen 1983), zooplankton and fish larvae (Sammarco & Crenshaw 1984, Williams et al. 1988), holothuroids (Hammond et al. 1985), sponges (Wilkinson & Trott

1985), coral dwelling crustacea (Preston & Doherty 1990, 1994), calcified green algae (Drew 1983), the epilithic algal community (Scott & Russ 1987), various reef fish communities (Williams 1982, 1983, Williams & Hatcher 1983, Rus 1984a), and patterns of nitrogen fixation (Wilkinson et al. 1984). A recent review of these studies is provided by Wilkinson & 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 ranging from strong terrigenous influences near the coast, to near oceanic conditions at the shelf break (Wilkinson & Cheshire 1988).

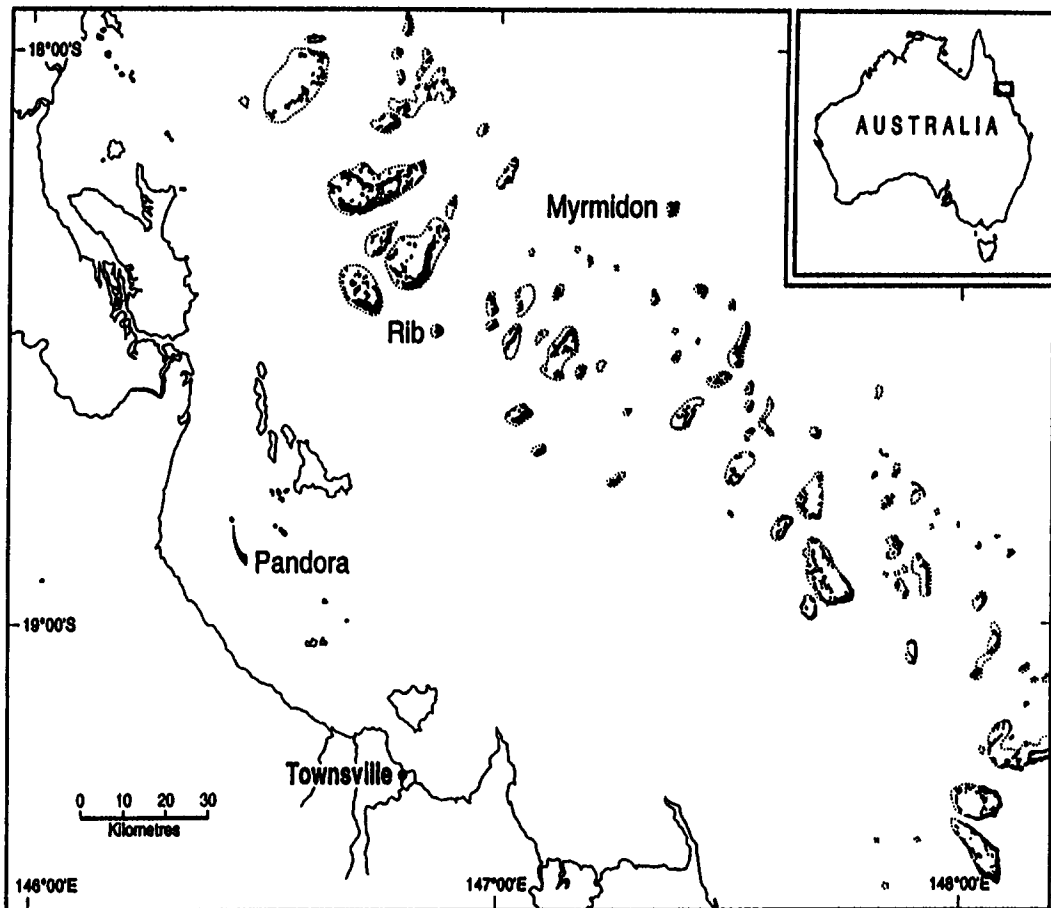


Fig. 1. The locations of study reefs in the central region of the Great Barrier Reef of Australia.

Williams (1982) first compared the structure of the coral reef fish communities across the continental shelf by examining the exposed windward 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 consistent for at least 15 years (Williams 1986, 1991, unpublished data). Additionally, Williams & 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 & Hatcher (1983) also demonstrated major cross-shelf changes in species diversity and trophic structure. Furthermore, the studies of Russ (1984a, 1984b) corroborat-

ed 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 such as lutjanids and lethrinids 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, they are readily caught in fish traps (Newman & Williams 1995). Fish traps have been used successfully to sample demersal fishes in a variety of structurally heterogeneous environments, such as rocky and coral reefs and estuaries,

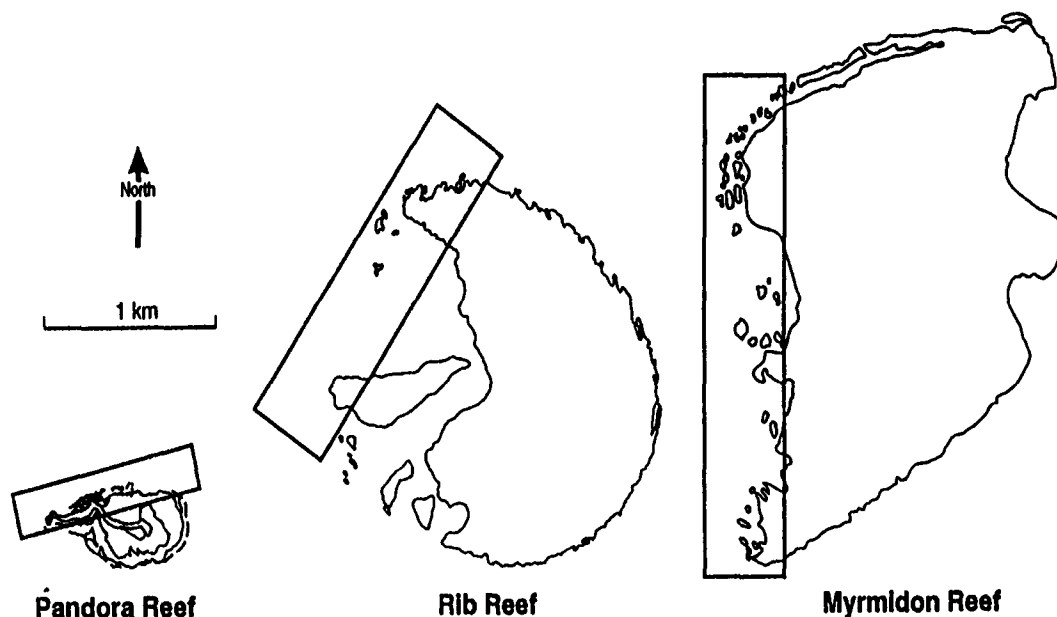


Fig. 2. Areas studied within each reef across the continental shelf. Each box represents the general area in which the traps were set on the respective reefs.

over a range of depths (Munro 1974, Stevenson & Stuart-Sharkey 1980, Dalzell & Aini¹, 1992, Newman 1990, Whitelaw et al. 1991, Sheaves 1992, Newman & Williams 1995).

The aim of this study was to describe the broad-scale patterns of distribution and abundance of species of the Lutjanidae (snappers) and Lethrinidae (emperors) along the well-studied cross shelf transect spanning the continental shelf in the central Great Barrier Reef using fish traps.

Material 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 & Hatcher (1983) and Russ (1984a, 1984b)].

The reefs were each located at different locations across the continental shelf: one reef was nearshore (Pandora), approximately 10 km from the coast; one on the midshelf (Rib), approximately 50 km offshore; and one on the outershelf (Myrmidon), approximately 100 km offshore (Fig. 1). The gross morphology and environment of these reefs was described by Done (1982).

The physical environment is extremely variable across the continental 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 & Cheshire 1988). Further, the nearshore reef environment is highly turbid, characterised by high concentrations of resuspended fine sediments (10–100 ppm) with the sediments dominated by fine siliceous muds, whereas in the outershelf reef environment suspended sediment

¹ Dalzell, P. & J.W. Aini. 1987. Preliminary results of fishing trials with arrowhead fish traps in Papua New Guinea. South Pacific Commission Fisheries Newsletter No. 41. 7 pp.

levels are low (< 0.2 ppm) and the sediments are exclusively carbonate (Scoffin & Tudhope 1985, Johnson et al.²).

The protected leeward slopes of all reefs were sampled and the areas sampled within each reef are shown in Fig. 2. The benthos of Myrmidon Reef, typical of the outershelf reefs, is dominated by both hard corals and coralline algae with the leeward slopes below 10 m dominated by a *Montipora/Pachyseris* community (Done 1982). Rib Reef and other 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 (massive coral colonies that are similar in all dimensions) and rubble accumulations which contain a correspondingly diverse array of communities such as the *Porites* 'massive/branching', *Acropora* 'staghorn' and *Acropora* '*splendida/divaricata*' communities as well as non-conformist assemblages (see Done 1982). Pandora Reef and other inner shelf reefs differ markedly from the midshelf and outershelf reefs. The leeward slopes of inshore reefs 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). Inshore reefs are characterised by their relative small size and their lack of the dominant *Acropora* communities of the midshelf and outershelf reefs. In addition, their structure is not characterised by the distinct zone types (e.g. lagoon, back reef) that are representative of the midshelf and outershelf reefs.

Sampling methods

The leeward slopes of the midshelf and outershelf

reefs in depths of 15–40 m, and the leeward slopes of the nearshore reef in depths of 10–15 m (maximum depth of these reefs) were sampled (Fig. 2). Traps were set in a random manner on the leeward slopes to ensure independence of the data and to avoid systematic error. Each trap was set a minimum distance of 50 metres apart and ranged up to a few hundred metres apart in order to reduce possible overlap in the capture fields of adjacent traps (see Eggers et al. 1982, Davies 1989).

Traps were set across the leeward slopes both day and night at each shelf location during March, 1993. A total of 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).

The trap design used was a modified 'O' or cylindrical shaped trap (see Newman & Williams 1995). The traps are cylindrical in shape with a diameter of 1500 mm, a height of 900 mm, a plan area of approx. 1.8 m² and a volume of approx. 1.6 m³. Frames were constructed from 10 mm diameter steel rod and were covered with 40 mm galvanised hexagonal wire mesh. Each trap was individually buoyed, and was baited with approx. 1 kg of mulched pilchards, *Sardinops neopilchardus*.

The traps were released from the research vessel, pulled upright when submerged and then allowed to sink to the substratum. Setting or hauling a trap took less than 3 minutes. The catch of each trap was identified to species, measured to the nearest millimetre, then tagged and released.

Soak times were calculated from the time a trap entered the water to the time it was hauled from the bottom. 'Day' set traps were set between 5:30–8:30 h and were hauled from 16:30 h onwards, with sorting and processing usually completed by 18:30 h. Soak times during the day varied from 9 to 11 h. 'Night' set traps were set between 16:30–18:30 h, left overnight and were hauled from 5:30 h onwards, with sorting and processing of trap catches usually completed by 8:30 h. 'Night' soak times varied from 12 to 14 h.

² Johnson, D.P., A.P. Belperio & D. Hopley. 1986. A field guide to mixed-terrigenous-carbonate sedimentation in the central Great Barrier Reef province, Australia. Australasian Sedimentologists Group Field Guide Series No. 3, Geological Society of Australia, Sydney. 173 pp.

Analysis of data

The catch per unit effort (CPUE) data from all 108 trap hauls (for the 12 most abundant species) from all three 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 & Young (1979).³ In-

³ Sandland, R.L. & P.C. Young. 1979. Tables of probabilities associated with the fission of replicate samples in classification. CSIRO Aust. Div. Fish. Oceanogr. Rep. 108. 21 pp.

Table 1. Mean catch rate (no. fish trap⁻¹ set⁻¹) of 12 species of lutjanids and lethrinids in the three groups derived from the classification analysis (v = total number of samples per group; - = absent).

Species	Classification group		
	Inshore (v = 36)	Midshelf (v = 24)	Outershelf (v = 48)
Lutjanidae:			
<i>Lutjanus carponotatus</i>	0.72	0.08	-
<i>Lutjanus sebae</i>	0.31	0.21	-
<i>Lutjanus russelli</i>	0.25	0.58	-
<i>Lutjanus adetii</i>	-	1.75	-
<i>Lutjanus quinquelineatus</i>	-	4.96	2.61
<i>Lutjanus kasmira</i>	-	-	3.48
Lethrinidae:			
<i>Gymnocranius audleyi</i>	-	0.42	-
<i>Lethrinus species 2</i>	-	0.38	0.21
<i>Lethrinus miniatus</i>	-	0.54	0.46
<i>Lethrinus erythracanthus</i>	-	-	0.19
<i>Lethrinus semicinctus</i>	-	-	0.38
<i>Gymnocranius euanus</i>	-	-	0.58

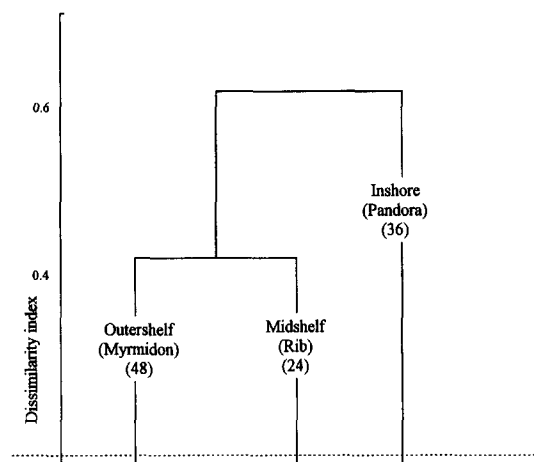


Fig. 3. Dendrogram from the classification analysis of the catch per unit effort data of the 12 most abundant species from 108 trap hauls. Numbers in parentheses represent the number of replicate traps that fall in each cluster.

dicator species were ranked by their mean CPUE 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 CPUE data for 'total individuals' caught in traps, for each family (Lutjanidae, Lethrinidae) trapped and for the 12 most abundant species trapped. Continental shelf location was treated as a

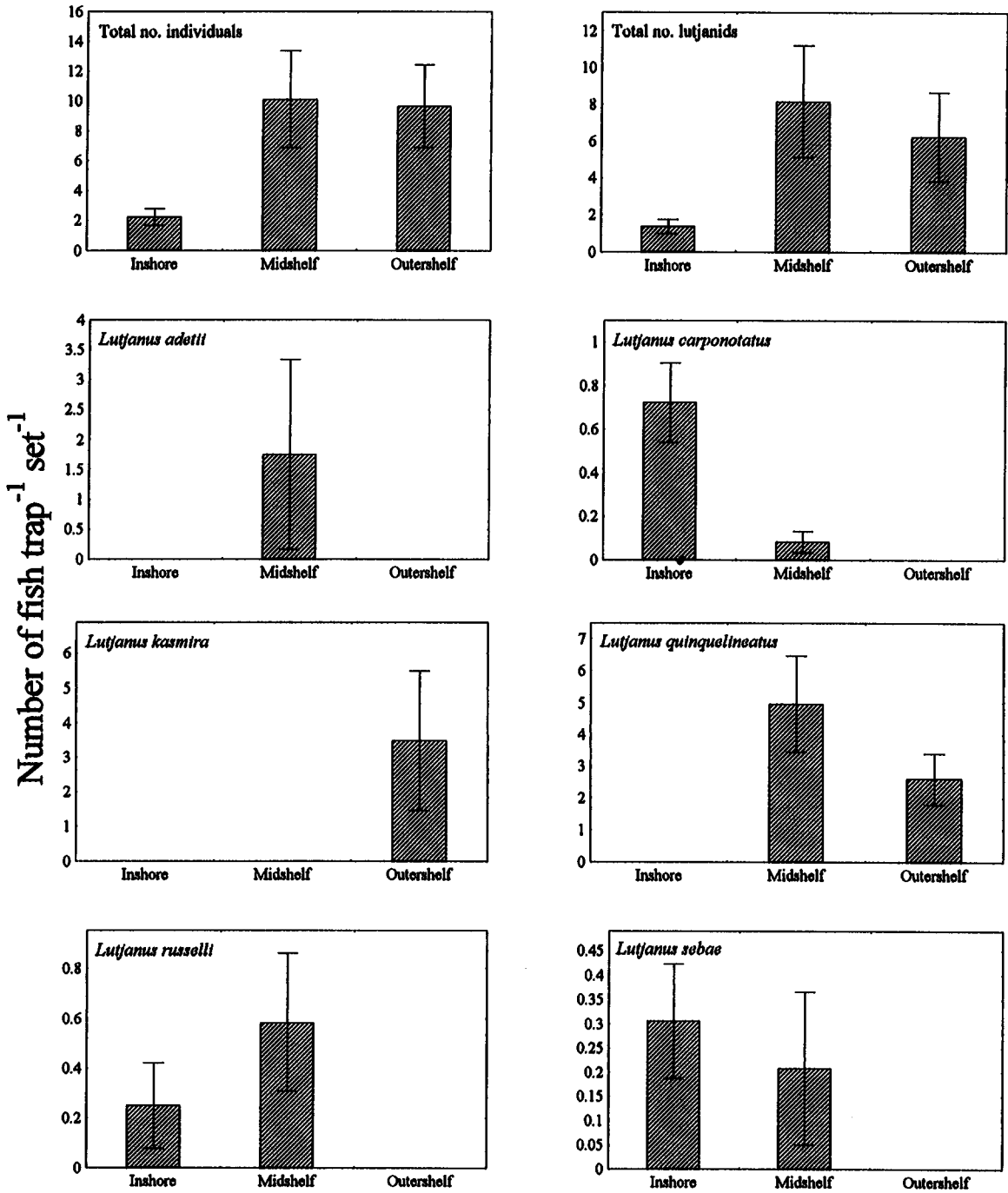


Fig. 4. Mean catch per unit effort (no. fish trap⁻¹ set⁻¹ ± standard errors) of total individuals, total lutjanids, and 6 species of lutjanid among cross-shelf locations.

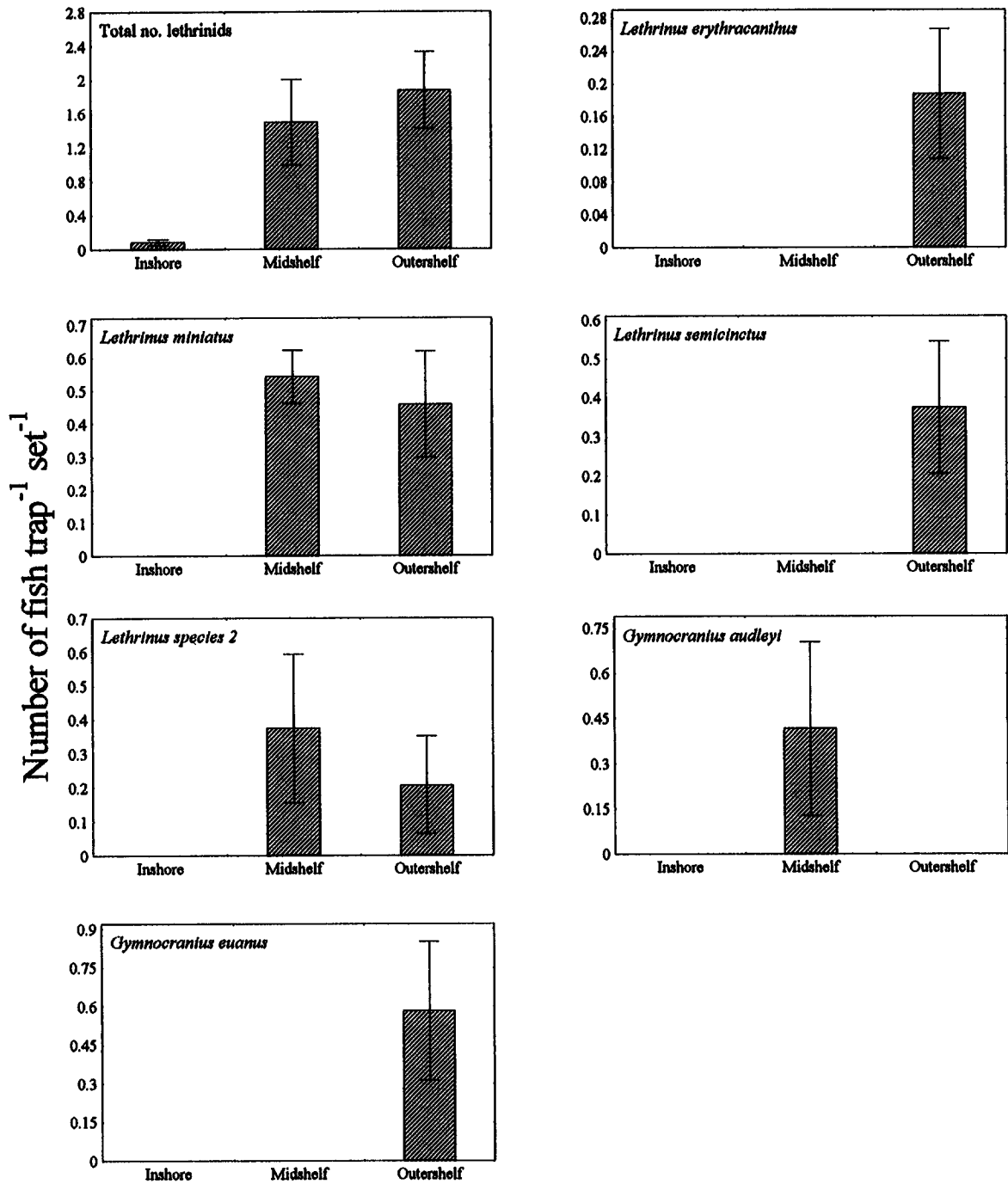


Fig. 5. Mean catch per unit effort (no. fish trap⁻¹ set⁻¹ ± standard errors) of total lethriniids and 6 species of lethriniid among cross-shelf locations.

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 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 – detailed diel (day

Table 2. Summaries of 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 $\sqrt{x + \sqrt{(x + 1)}}$ function before analysis).

Source of variation	df	Total fish			Total lutjanids			<i>L. adetii</i> ¹		
		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	–	–

Source of variation	df	<i>L. carponotatus</i> ¹			<i>L. kasmira</i> ¹			<i>L. quinquelineatus</i> ¹		
		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	–	–

Source of variation	df	<i>L. russelli</i> ¹			<i>L. sebae</i> ¹		
		MS	F	p	MS	F	p
Location	2	12.2	25.4	***	7.15	18.3	***
Residual	15	0.48	–	–	0.39	–	–

Source of variation	df	Total lethrinids			<i>L. erythracanthus</i> ¹			<i>L. miniatus</i> ¹		
		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	–	–

Source of variation	df	<i>L. semicinctus</i> ¹			<i>L. species 2</i>			<i>G. audleyi</i> ¹		
		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	–	–

Source of variation	df	<i>G. euanus</i> ¹		
		MS	F	p
Location	2	18.6	45.6	***
Residual	15	0.41	–	–

versus night) comparisons and depth comparisons will be examined in related papers. This procedure limited the 'total replicates' in the ANOVA analysis to 18 (i.e. $n = 8$ 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 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 & 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 & 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

Table 3. A posteriori multiple comparison of means (Tukey's HSD method) from the one factor analyses of variance of CPUE shown in Table 2. The significance level for all comparisons was $p < 0.01$ (Location: I = Inshore, M = Midshelf; O = Outershelf).

Taxon	Location
Total number individuals	O = M > I
Total lutjanids	O = M > I
<i>Lutjanus carponotatus</i>	I > M = O
<i>Lutjanus sebae</i>	I = M > O
<i>Lutjanus russelli</i>	I = M > O
<i>Lutjanus adetii</i>	M > I = O
<i>Lutjanus quinquelineatus</i>	O = M > I
<i>Lutjanus kasmira</i>	O > M = I
Total lethrinids	O = M > I
<i>Gymnocranius audleyi</i>	M > I = O
<i>Lethrinus species 2</i>	O = M > I
<i>Lethrinus miniatus</i>	O = M > I
<i>Lethrinus erythracanthus</i>	O > M = I
<i>Lethrinus semicinctus</i>	O > M = I
<i>Gymnocranius euanus</i>	O > M = I

abundance in a number of locations across the continental shelf. The relative abundance categories were based on the studies of Jones & Derbyshire (1988), Kramer et al. (1993, 1994), Williams & Russ,⁴ Sheaves (personal communication) and the experimental trapping and fishing observations of Newman (unpublished data).

Results

The first split in the dendrogram generated from the classification analysis of the CPUE of all 108 trap hauls (Fig. 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. Species characteristic of the inshore shelf location were the lutjanids, *Lutjanus carponotatus*, *L. russelli* and *L. sebae* (Table 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*. Of the 12 species examined in detail, 3 were recorded inshore, 8 on the midshelf and 7 on the outershelf. All the species recorded inshore in the trap catches also occurred on the midshelf but not the outershelf. Only 3 species recorded in the trap catches were shared between the midshelf and outershelf.

The one way analysis of variance of the pooled trap CPUE data 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 2, Figs 4, 5). The corresponding a posteriori Tukey HSD multi-

⁴ Williams, D.McB & G.R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Volume I. Great Barrier Reef Marine Park Authority Research Publication No. 33. 106 pp.

ple mean comparisons of the analysis of variance results are summarised in Table 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. 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 the CPUE of all the species examined (Table 2) was attributable to the absence or low abundance of species in one or more cross-shelf locations (Table 1, Figs 4, 5). This cross-shelf change accounted for a large proportion of the variability in the CPUE of all the species examined. *Lutjanus carponotatus* was the only species that was significantly more

abundant in trap catches inshore (Fig. 4). *Lutjanus russelli* and *L. sebae* were significantly less abundant in trap catches on the outershelf with no significant difference in the trap CPUE between the midshelf and inshore. *Lutjanus adetii* and *Gymnocranius audleyi* were both significantly more abundant in trap catches on the midshelf (Figs 4, 5). *G. audleyi* has not been recorded from any other shelf locations (Tables 1, 6). *Lutjanus quinquelineatus*, *Lethrinus miniatus* and *L. species 2* were absent from trap catches inshore, with no significant difference between the midshelf and the outershelf trap CPUE. *Lutjanus kasmira*, *Lethrinus erythracanthus*, *L. semicinctus* and *G. euanus* were only recorded in trap catches on the outershelf.

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 (Ta-

Table 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: abundant, frequent, occasional, 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
<i>Lutjanus erythropterus</i> (juv.)	rare	frequent	rare
<i>Lutjanus malabaricus</i> (juv.)	rare	frequent	rare
<i>Lutjanus sebae</i> (juv. and subadults)	rare	frequent	frequent
<i>Lutjanus fulviflamma</i>	occasional	frequent	frequent
<i>Lutjanus johnii</i> (ad.)	occasional	abundant	–
<i>Lutjanus argentimaculatus</i> (subad.)	frequent	occasional	occasional
<i>Lutjanus johnii</i> (juv.)	frequent	occasional	–
<i>Lutjanus argentimaculatus</i> (juv.)	abundant	rare	–
<i>Lutjanus russelli</i> (juv.)	abundant	frequent	–
<i>Lutjanus rivulatus</i> (juv.)	–	rare	–
<i>Lutjanus carponotatus</i> (juv.)	–	occasional	occasional
<i>Lutjanus lemniscatus</i> (juv.)	–	frequent	occasional
<i>Lutjanus carponotatus</i> (ad.)	–	frequent	abundant
<i>Lutjanus quinquelineatus</i>	–	–	occasional
<i>Lutjanus russelli</i> (ad.)	–	–	frequent
<i>Lutjanus vitta</i>	–	–	frequent
<i>Lethrinus laticaudis</i>	occasional	frequent	frequent
<i>Lethrinus miniatus</i>	–	–	rare
<i>Lethrinus lentjan</i>	–	–	occasional
<i>Lethrinus atkinsoni</i>	–	–	frequent
<i>Lethrinus harak</i>	–	–	frequent
<i>Lethrinus nebulosus</i>	–	–	frequent

* M.J. 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).

Species	Cross shelf reef position							Maximum depth (m)
	Inshore reefs	Midshelf reefs		Shoals interreef areas	Outershelf reefs		Deep reef areas (> 100 m)	
		(0–15 m)	(> 15 m)		(0–15 m)	(15–100 m)		
<i>Lutjanus johnii</i>	occasional	–	–	–	–	–	–	15
<i>Lutjanus rivulatus</i>	occasional	occasional	–	–	occasional	–	–	15
<i>Lutjanus vitta</i>	occasional	–	occasional	frequent	–	–	–	45
<i>Lutjanus argentimaculatus</i>	frequent	occasional	occasional	occasional	–	occasional	–	80
<i>Lutjanus lemniscatus</i>	frequent	occasional	occasional	occasional	–	–	–	40
<i>Lutjanus erythropterus</i>	frequent	–	occasional	abundant	–	–	–	55
<i>Lutjanus malabaricus</i>	frequent	–	occasional	abundant	–	–	–	75
<i>Lutjanus sebae</i>	frequent	occasional	frequent	frequent	–	occasional	–	85
<i>Lutjanus carponotatus</i>	abundant	frequent	occasional	rare	–	–	–	40
<i>Lutjanus russelli</i>	abundant	frequent	frequent	occasional	–	–	–	40
<i>Lutjanus fulviflamma</i>	abundant	abundant	frequent	–	frequent	occasional	–	45
<i>Lutjanus biguttatus</i>	–	rare	–	–	–	–	–	12
<i>Lutjanus lutjanus</i>	–	rare	frequent	frequent	–	–	–	45
<i>Lutjanus kasmira</i>	–	rare	–	–	frequent	frequent	–	65
<i>Symphorus nematophorus</i>	–	rare	frequent	frequent	rare	occasional	–	75
<i>Symphoricthys spilurus</i>	–	occasional	–	–	occasional	–	–	20
<i>Macolor macularis</i>	–	occasional	–	–	occasional	occasional	–	75
<i>Lutjanus monostigma</i>	–	occasional	–	–	frequent	–	–	15
<i>Lutjanus gibbus</i>	–	occasional	–	–	frequent	frequent	–	68
<i>Macolor niger</i>	–	occasional	–	–	frequent	occasional	–	40
<i>Lutjanus fulvus</i>	–	occasional	occasional	–	occasional	–	–	35
<i>Aprion virescens</i>	–	occasional	occasional	frequent	occasional	frequent	occasional	100
<i>Lutjanus bohar</i>	–	occasional	occasional	occasional	frequent	frequent	occasional	93
<i>Lutjanus quinquelineatus</i>	–	abundant	abundant	occasional	occasional	frequent	occasional	128
<i>Lutjanus bouton</i>	–	–	rare	–	–	–	–	40
<i>Lutjanus adetii</i>	–	–	abundant	frequent	–	occasional	occasional	125
<i>Lutjanus semicinctus</i>	–	–	–	–	rare	–	–	15
<i>Aphareus rutilans</i>	–	–	–	–	rare	occasional	occasional	100
<i>Aphareus furca</i>	–	–	–	–	frequent	occasional	–	70
<i>Pristipomoides multidentis</i>	–	–	–	–	–	occasional	frequent	245
<i>Pristipomoides filamentosus</i>	–	–	–	–	–	frequent	frequent	210
<i>Pristipomoides auricilla</i>	–	–	–	–	–	–	rare	150
<i>Etelis radiosus</i>	–	–	–	–	–	–	occasional	185
<i>Pristipomoides argyrogrammicus</i>	–	–	–	–	–	–	occasional	250
<i>Etelis carbunculus</i>	–	–	–	–	–	–	occasional	150
<i>Etelis coruscans</i>	–	–	–	–	–	–	occasional	260
<i>Paracaesio kusakarii</i>	–	–	–	–	–	–	frequent	180
<i>Pristipomoides zonatus</i>	–	–	–	–	–	–	frequent	198
<i>Pristipomoides flavipinnis</i>	–	–	–	–	–	–	frequent	190

bles 4, 5, 6). The nearshore coastal habitats are divided into 3 broad areas. 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 water and is rarely found on any of the inshore reefs in this region. *Lutjanus carponotatus* and *Lethrinus laticaudis* are representative of the inshore reefs and fringing reefs of coastal islands in this region. The shallow rocky foreshore area of coastal islands and inshore reefs were the only habitats in which *Lethrinus harak* has been observed (Table 4). This species appears to be restricted to coastal areas and continental islands. Representative species of the midshelf reefs include *Lutjanus adetii*, *L. quinquelineatus*, *Lethrinus species 2* and *Gymnocranius audleyi* (Tables 5, 6). Species repre-

sentative of the interreefal areas and the shoal grounds between reefs are *Lutjanus erythropterus*, *L. malabaricus*, *L. vitta* and *Lethrinus genivittatus*. On the outershelf, representative species include *Lutjanus bohar*, *L. gibbus*, *L. kasmira*, *Macolor niger*, *Gymnocranius euanus*, *G. sp.*, *Gnathodentex aurolineatus*, *Monotaxis grandoculis*, *Lethrinus semicinctus*, *L. erythracanthus* and *L. xanthochilus*.

In general, the genera *Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus*, *Gnathodentex*, *Gymnocranius*, *Lethrinus* and *Monotaxis* are all characteristic of the shallow shelf waters less than 100 m (Tables 5, 6). In contrast, species of the genera *Paracaesio*, *Pristipomoides* and *Wattsia* are characteristic of the intermediate depths (100–200 m). The exception is *Pristipomoides argyrogrammicus*, which usually occurs in depths in excess of 200 m (Kramer et al. 1994). The deeper outer reef

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).

Species	Cross shelf reef position						Maximum depth (m)	
	Inshore reefs	Midshelf reefs		Shoals interreef areas	Outershelf reefs			Deep reef areas (AM 100 m)
		(0–15 m)	(> 15 m)		0–15 m)	(15–100 m)		
<i>Lethrinus harak</i>	occasional	–	–	–	–	–	5	
<i>Lethrinus atkinsoni</i>	occasional	frequent	occasional	–	frequent	–	40	
<i>Lethrinus laticaudis</i>	frequent	–	–	–	–	–	25	
<i>Lethrinus nebulosus</i>	frequent	frequent	occasional	occasional	frequent	occasional	99	
<i>Lethrinus erythracanthus</i>	–	rare	–	–	occasional	frequent	70	
<i>Lethrinus olivaceus</i>	–	rare	rare	rare	occasional	occasional	70	
<i>Lethrinus species 2</i>	–	rare	abundant	frequent	rare	occasional	occasional	128
<i>Lethrinus xanthochilus</i>	–	rare	–	–	occasional	–	15	
<i>Lethrinus ornatus</i>	–	occasional	occasional	–	–	–	40	
<i>Gymnocranius audleyi</i>	–	occasional	frequent	–	–	–	40	
<i>Lethrinus obsoletus</i>	–	occasional	rare	–	occasional	–	40	
<i>Lethrinus lentjan</i>	–	frequent	occasional	–	–	–	40	
<i>Lethrinus miniatus</i>	–	frequent	frequent	frequent	occasional	frequent	frequent	128
<i>Monotaxis grandoculis</i>	–	frequent	–	–	abundant	–	20	
<i>Lethrinus genivittatus</i>	–	–	rare	frequent	–	–	45	
<i>Lethrinus rubrioperculatus</i>	rare	–	rare	–	occasional	frequent	95	
<i>Lethrinus semicinctus</i>	–	–	occasional	occasional	frequent	frequent	40	
<i>Gymnocranius grandoculis</i>	–	–	occasional	–	–	occasional	80	
<i>Gymnocranius sp.</i>	–	–	–	–	occasional	occasional	40	
<i>Gymnocranius euanus</i>	–	–	–	–	occasional	frequent	occasional	128
<i>Gnathodentex aurolineatus</i>	–	–	–	–	frequent	–	15	
<i>Wattsia mossambica</i>	–	–	–	–	–	frequent	198	

slope waters in excess of 200 m are characterised by species of the genus *Etelis*.

Discussion

Logistic constraints prevented spatial replication among reefs within a given shelf location. Consequently the quantitative data of this study are based on only one reef at each cross-shelf location. However, 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. In addition, 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 are 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 4, 5, 6). The diversity of available habitat types also increases across the continental shelf (Done 1982). Significant cross-shelf variation occurred in the abundance of all the species of the Lutjanidae and Lethrinidae that were trapped (Table 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 (e.g. reef flat, lagoon) examined, and this cross-shelf change accounted for as much as 80–90% of the variability in abundance. This study confirms the findings of Williams (1982) and Williams & 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 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 & 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 juveniles (e.g. 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 increasing age and growth as far as the outershelf reefs (Williams & Russ).⁴ 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 and their survivorship may be limited 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). 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). It is likely that ocean currents can retain larvae in 'similar' water types to adult conspecifics (e.g. midshelf species are retained in midshelf waters as larvae) and that the adaptation of different pigment structures reflects the water clarity in which they live. For example, *L. bohar* and *L. kasmira* are considered blue water species, whereas *L. quinquelineatus*, which occurs on the outershelf, is not and the dominance of this species 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 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 5, 6) have important management implications. 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 presently undertaken using only single reef closures, and closures of clusters of reefs. Although the degree of exchange of adult fishes of these families among reefs in similar locations and between reefs at different cross shelf locations and

their connectivity with nearshore habitats remains to be quantified, the presently available qualitative data suggest that a number of species of the Lutjanidae and Lethrinidae undergo movement of several tens of kilometres across the continental shelf in their normal postsettlement ontogeny (Williams 1991, Williams & Russ).⁴ This pattern is further supported by two studies in the nearby waters of New Caledonia by Kulbicki et al.,⁵ who examined longline catch data, and Kulbicki (1988) from visual surveys. Both these studies found that species of the Lutjanidae, Lethrinidae and Serranidae are larger as distance from the coast, and depth, increases. Additionally, Brouard & Grandperrin⁶ and Wright et al. (1986) have suggested a positive relationship between fish size and capture depth for a number of lutjanid species, similar to the temperate Scorpaenidae (Love et al. 1991). 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 & Bryan 1975, Moran).⁷

Of all the reef-associated families of commercial and recreational fishing significance on the Great Barrier Reef, the Lutjanidae and Lethrinidae 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 & Russ).⁴ Since many species of these families undertake major cross-shelf movements as part of their complex life histories (Williams 1991, Williams & Russ),⁴ they are less likely to complete their entire life cycle on any single reef.

⁵ Kulbicki, M., G. Mou-Tham, G. Bargibant, J.L. Menou & P. Tizard. 1987. Resultats preliminaires des peches experimentales a la palangre dans le lagon SW de Nouvelle Caledonie. ORSTROM Noumea, Rapport Scientifique et Technique Oceanographie 49, 104 pp.

⁶ Brouard, F. & R. Grandperrin. 1985. Deep-bottom fishes of the outer reef slope in Vanuatu. South Pacific Commission 17th Regional Technical Meeting on Fisheries (Noumea, New Caledonia, 5-19 August, 1985). SPC/Fisheries 17/WP. 12. 127 pp.

⁷ Moran, D. 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) - red snapper. U.S. Fish. Wildl. Serv. Biol. Rep. 82 (11.83). U.S. Army Corps of Engineers, TR-EL-82-4. 19 pp.

Therefore, if these species become threatened or endangered from either natural or anthropogenic sources the current localised 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.

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