

Large scale spatial and temporal variation in recruitment to fish populations on coral reefs

P.F. Sale, P.J. Doherty*, G.J. Eckert, W.A. Douglas, and D.J. Ferrell

School of Biological Sciences, University of Sydney, Sydney, N.S.W., Australia, 2006

Summary. Visual census was used to sample young of the year of fish species recruited to each of two habitats on seven lagoonal platform reefs of the Capricorn-Bunker Group, Great Barrier Reef. The reefs sampled span an area 70 km in extent. In 1983, 62 species from 13 families were detected as recruits on reef slope sites. The total number of recruits, and the number of each of 6 of 16 species tested, differed significantly among reefs, despite the fact that differences among sites within reefs did not exist, and that sampled slopes were chosen to be hydrographically, and physiographically as similar as possible. Lagoonal patch reefs were sampled in two years. In 1982, 76 species of 11 families occurred as recruits. In 1983, 86 species of 12 families were recorded. All of 22 species common enough to test showed some significant variation in abundance among reefs, years, or both. For 9 species, significant year \times reef interactions occurred, demonstrating that relative recruitment success among reefs varied between years. Reasons for the substantial levels of variability are discussed, and implications for the organisation of reef fish communities are considered.

There currently exists substantial interest among ecologists in the ways in which species are assembled as communities (Diamond 1975; Wiens 1977; Connell 1978; Connor and Simberloff 1978; Sousa 1979; Simberloff and Connor 1981; papers in Strong et al. 1984). Recently, a number of studies have examined the structure of communities of fish in coral reef habitats. Two contrasting views have been expressed. Some authors have reported groupings of species of reef fish to show considerable variation in species richness, species composition and species' relative abundances, both from site to site within the same habitat, and through time (Sale and Dybdahl 1975, 1978; Molles 1978; Talbot et al. 1978; Bohnsack and Talbot 1980; Sale and Douglas 1984). We prefer the term "assemblage" to "community" when referring to these groupings of fish at single sites. Other ecologists report groupings of fish showing a more constant, predictable structure in terms of species richness, composition and relative abundance (Smith and Tyler 1972, 1975; Brock et al. 1979; Gladfelter et al. 1980; Ogden and

Ebersole 1981; Anderson et al. 1981; Williams and Hatcher 1983).

For the most part, those who report a more constant structure to assemblages have worked at a larger spatial scale, examining large patch reefs several tens of square meters in surface area (Brock et al. 1979; Gladfelter et al. 1980; Ogden and Ebersole 1981), or continuous reef tracts (Anderson et al. 1981; Williams and Hatcher 1983). Authors reporting more variable results have all used quite small sites seldom in excess of 10m² in area and containing small numbers of fish. The variable results they have obtained have been attributed by others to the small spatial scale at which this work has been pursued (Brock et al. 1979; Gladfelter et al. 1980; Ogden and Ebersole 1981).

Reef fish are rather sedentary organisms. In strongly patchy environments, such as among lagoonal patch reefs, the majority of individuals spend their juvenile and adult lives within a single small patch of habitat no more than 10m² in area, despite the fact that similar patches exist within a few meters. Recruitment to these local assemblages is almost entirely by settlement of juvenile fish from their pelagic larval phase into that patch of habitat. Loss is principally by mortality rather than by emigration to other patches. Evidence is increasing that variability in the recruitment of juvenile fish may play a major role in determining the composition of these assemblages (Williams 1980; Doherty 1983; Victor 1982).

This evidence of profound spatial and temporal variability in the recruitment of new juveniles provides a ready explanation for the variable community structure reported from small-scale studies (Sale 1982; Sale and Douglas 1984). However, the pattern of settlement which exists at a larger spatial scale is not known. It might be expected that the small scale variation will be averaged out as the scale of sampling is increased. If so, larger areas of reef will receive a relatively more constant rate of recruitment overall than would small areas, and this would contribute to the more predictable structure of assemblages that has been reported. Alternatively, variation in settlement might also be pronounced at larger spatial scales.

Although most species of reef fish breed repeatedly over a relatively extended season, there exists a pronounced summer peak to breeding and to settlement of most species on the Great Barrier Reef. This paper reports on autumn surveys of recruitment into two types of habitat on each of seven reefs spanning 70 km in the Capricorn-Bunker Group, Great Barrier Reef.

* *Present address:* Australian Environmental Studies, Griffith University, Nathan, Queensland, Australia 4111

Offprint requests to: P.F. Sale

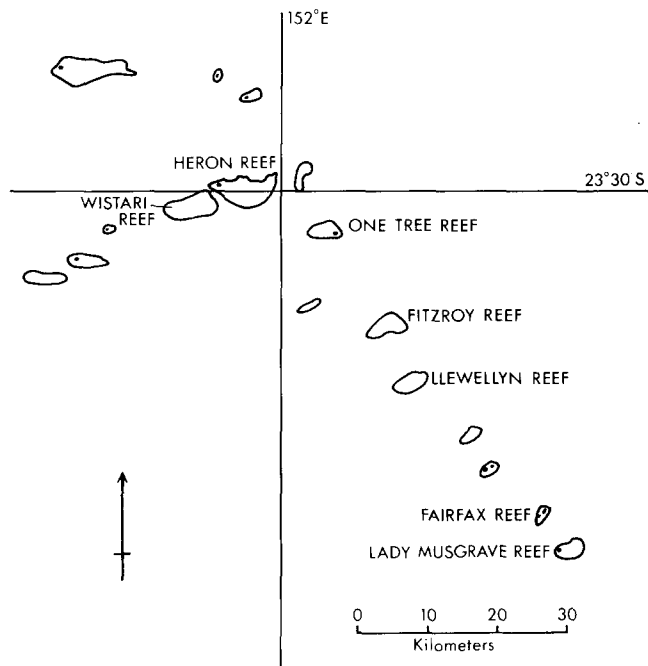


Fig. 1. Map showing the Capricorn-Bunker Group of reefs. The named reefs are the ones sampled for recruitment. They include all reefs in the group which have areas of lagoonal patch reef habitat

Materials and methods

Seven lagoonal platform reefs of the Capricorn-Bunker Group, Great Barrier Reef were sampled. They are arrayed in an approximately straight line from Heron Reef (23° 27' S. Lat., 151°55' E. Long.) at the north-west end, to Lady Musgrave Reef (23°54' S. Lat., 152°54' E. Long.) to the south east. Included also are Wistari Reef, One Tree Reef, Fitzroy Reef, Llewellyn Reef, and Fairfax Reef (Fig. 1).

Two habitats were sampled, lagoonal patch reefs in 1982 and 1983, and windward reef slopes in 1983. Species sampled in each habitat were all those amenable to visual census procedures except for some which tend to occur in dense schools. All divers were well versed in field identification of the species encountered, and could recognise the size-range of individuals of each species recruited from the plankton during the immediately past summer season. Each year, all seven reefs were visited over 10 days, with one day spent sampling at each. Dates of the surveys were April 24th to May 4th, 1982, and April 12th to 21st, 1983. Data at hand permit the evaluation of temporal and reef effects on recruitment to lagoonal sites, and reef effects on recruitment to reef slope sites.

Ten patch reefs were haphazardly selected in the lagoon of each reef. They were chosen to be similar in size, structure, and surroundings. Each patch reef, in 2–4 m water (low tide), reached the surface and had an unbroken, flat upper surface. The greatest length, maximum diameter at 90° to this, and mean height above the lagoon floor were measured using a PVC tape. Surface area was calculated by treating the reef as a rectangular solid with length, width and height as measured. Mean surface area of the 1982 sample of patch reefs (all lagoons) was 91 m² (±3.74 m² S.E.). Surface area of patch reefs sampled in 1983 was 104 m² (±3.75 m² S.E.).

Two divers sampled young of the year on patch reefs. Each was responsible for a different set of target species, and carefully searched the entire patch reef attempting a total count for each species. For logistic reasons, sampling of a lagoon had to be completed within a single high tide period. Therefore, on five patch reefs we censused only labrid and chaetodontid species and one pomacentrid, (about 50% of species present). On the other five patch reefs, complete censuses were done.

In 1983 a second pair of divers censused reef slope sites. On each reef, two sites, each of about 300 m horizontal extent, were chosen on continuous coral slopes at 8–10 m depth. On all except Heron and Wistari Reefs these sites were chosen on the north-eastern face to ensure similar hydrographic environments. On Heron and Wistari Reefs, equivalent habitats were not available on the north-east face (which is a protected lee in each, Fig. 1). Sites comparable in appearance and at the same depth were located on south-eastern faces instead.

Each diver was responsible for censusing all target species on the reef slope. At each site, each diver set out and censused 3 roughly parallel, but otherwise haphazardly positioned line transects 80 m long and 1 m wide. A PVC measuring tape was used to mark the centre of the transect. The edges were marked by means of a T-shaped aluminium rod carried by the diver. The stem of the T, 80 cm long, was held out ahead of the diver and centred over the tape. The crosspiece, 1 m long, marked the width of the transect and also helped to focus the driver's attention onto a particular segment of the transect immediately ahead of him. This procedure required setting of only a single tape, while avoiding the substantial errors inherent in strip transects that are not of explicitly defined width (Sale and Sharp 1983). Each transect sampled an area (80 m²) approximately equal to that of a single lagoonal patch reef. Twelve transects were run on each reef slope. The sampling design for reef slope censuses permits an evaluation of differences between divers and between the two sites surveyed on each reef. Species names follow Russell (1983).

Results

Reef slope habitat

A total of 3439 recruits were detected on the 84 transects run. These belonged to 62 species from 13 families of fish. They included all species present and visible as recruits on the transects, other than species of apogonid. The latter tend to settle in very large numbers and show high post-settlement mortality (Williams and Sale 1981; Sale unpub. data). A number of more cryptic species undoubtedly also settled at these sites, but were not censused.

Data on the total number of individuals recruited, number of species, and the 16 most common individual species (comprising over 90% of individuals recorded), were subjected to analyses of variance. Effects of divers and reefs were orthogonal, and sites were nested within reefs. Reefs were fixed and divers and sites were random factors. Data were tested for heterogeneity of variance using Cochran's test, and transformed appropriately where necessary. Where the effect of sites was found to be non-significant at $P > 0.25$, the sum of squares attributable to this factor was pooled with the residual sum of squares, and a pooled mean square calculated. This allowed a more powerful test of

Table 1. Summary of significant differences detected in reef slope surveys of 7 Capricorn Bunker reefs. Data represent mean number of recruits per transect. Letters in parentheses group together reefs for which densities of recruits do not differ according to results of Student Neuman Keuls tests. No significant differences were detected among reefs by one diver (WAD) for *Chrysiptera rex*

Species/group	Wistari	Heron	One Tree	Fitzroy	Llewellyn	Fairfax	Musgrave
Total recruits	35.0 (b)	49.4 (c)	22.2 (a)	71.1 (c)	47.4 (b)	37.0 (b)	24.5 (a)
<i>Chrysiptera</i>							
<i>rex</i> (WAD)	0.17	0.0	0.5	0.5	0.17	0.17	0.33
(DJF)	0.0 (a)	0.0 (a)	0.17 (a)	1.17 (b)	0.83 (b)	0.17 (a)	0.0 (a)
<i>Pomacentrus</i>							
<i>australis</i> (WAD)	8.17 (d)	0.67 (c)	0.17 (a)	0.0 (a)	1.67 (b)	0.0 (a)	0.0 (a)
(DJF)	11.67 (c)	1.67 (b)	0.0 (a)	0.0 (a)	0.0 (a)	0.0 (a)	0.0 (a)
<i>coelestis</i>	3.17 (b)	2.00 (a)	7.58 (c)	12.58 (d)	20.25 (e)	19.33 (e)	4.25 (b)
<i>lepidogenys</i>	3.00 (a)	24.33 (c)	5.00 (b)	25.25 (c)	9.83 (b)	2.00 (a)	4.83 (b)
<i>wardi</i>	9.50 (b)	8.50 (b)	0.75 (a)	0.08 (a)	0.42 (a)	0.33 (a)	0.92 (a)
<i>Halichoeres</i>							
<i>margaritaceus</i>	0.75 (a)	1.25 (a)	2.75 (b)	2.33 (b)	2.67 (b)	0.75 (a)	0.08 (a)

the reef effect, although in no case in the present instance did this change conclusions drawn. No significant variations were found in the number of species per transect, or in the densities of 10 species: *Neopomacentrus azysron*, *Pomacentrus bankanensis*, *P. molluccensis* (= *popei*), *Pomacentrus* sp., *Chaetodon rainfordi*, *Cirrhilabrus* sp. (= *temmincki*), *Labroides dimidiatus*, *Macropharyngodon meleagris*, *Thalassoma lunare*, and *T. lutescens*. In six species, significant differences were found among reefs in the numbers of recruits per transect. In four of these there were significant diver effects or diver \times reef interactions. In no case were sites within reefs found to differ significantly.

Table 1 summarises differences among reefs. While equivalent numbers of species recruited to each reef, the total number of recruits per transect varied 3-fold among reefs. Among the 6 species individually showing significant differences among reefs, the extent of variation was at least 10-fold, and different species were commonest on different reefs. Significant diver \times reef interactions were detected in *Chrysiptera rex* and *Pomacentrus australis*. These probably arose through chance placement of the different transects, as both species occurred as recruits in occasional clusters of small numbers of fish. Significant diver effects existed for *Pomacentrus coelestis* and *Halichoeres margaritaceus*. One diver consistently recorded larger numbers of *Pomacentrus coelestis* and the other diver did this for *Halichoeres margaritaceus*. In both cases, the likely explanation is that the divers concerned used slightly different size criteria for excluding small fish as not young of the year.

Lagoonal habitat

In 1982 a total of 5366 recruits belonging to 76 species in 11 families were detected on the patch reefs. As on the reef slope sites, these included all young of the year present and visible on the patch reefs, with the exception of apogonids. Some very cryptic species were certainly also present, but unsampled. In 1983, 3258 recruits of 86 species from 12 families were detected.

Because the patch reefs varied in surface area, all lagoonal data were converted to numbers of recruits per 100 m² of patch reef. These data were analysed as an or-

thogonal two-factor analysis of variance with reefs as a fixed and years as a random factor. Depending on the species, there were either 5 or 10 replicate patch reef samples within each reef and year. Again, pooling of sums of squares was used to increase sensitivity of tests where possible. Here, pooling involved the interaction sum of squares when that was found to be non-significant at $P > 0.25$. This permitted a stronger test of differences among reefs.

Twenty-four species recruiting to the lagoon were common enough to warrant separate analyses. Of these, two species (*Dischistodus pseudo-chrysopeilus* and *Acanthurus mata*) occurred in numbers such that very high heterogeneity of variances was present, and not remediable by transformations attempted (log $x + 1$ and square root). Results of analysis of the other 22 species are summarised in Tables 2, 3, and 4. Eckert (1984) has provided a more detailed analysis of the labroid data.

All 22 species show some significant variability. Table 2 summarises results of Student Neuman Keuls tests on 9 species which showed significant year \times reef interactions. For every species, the relative abundance of recruits on reefs changed sufficiently between years to change the rank order of reefs. Table 3 summarises differences among reefs for total recruits and for 9 further species showing significant reef effects. Again, variation among reefs is substantial and the rank order of reefs varies among species. Three of these species also showed significant differences among years, as did the four remaining species, and the total density of recruits. Average densities of these for each year are shown in Table 4.

Table 5 summarises the results of a test of whether the 22 lagoonal species analysed ranked the seven reefs similarly as settlement sites. Kendall's coefficient of concordance was calculated for 27 rankings of the 7 reefs by the 22 species (those species showing significant year \times reef interaction provided two sets of rankings, one for each year). We used the density of recruits of a species as the index for ranking each reef, so that lower rankings were associated with greater densities of recruits. The concordance obtained among the rankings compared is significant ($W = 0.107$, $P < 0.05$), but weak. The value of W obtained is equivalent to an average Spearman's correlation coefficient among all

Table 2. Summary of significant differences among reefs detected by S-N-K tests on 9 lagoonal species for which significant year \times reef interactions were found. Numbers shown are densities of recruits per 100 m² of patch reef. Underlining indicates densities which are not significantly different ($P < 0.05$)

<i>Pomacentrus wardi</i> interaction, $P < 0.01$	1982	12.7 Musgrave	12.8 Llewellyn	11.5 Wistari	8.1 Heron	6.5 Fitzroy	5.5 Fairfax	2.9 One Tree
	1983	25.8 Wistari	12.6 Heron	8.8 Musgrave	9.0 Llewellyn	3.6 Fitzroy	2.0 One Tree	1.1 Fairfax
<i>Coris variegata</i> interaction, $P < 0.01$	1982	2.4 Wistari	2.2 Llewellyn	1.4 Fairfax	1.0 Musgrave	1.0 Heron	0.9 Fitzroy	0.3 One Tree
	1983	3.4 Llewellyn	1.8 Fitzroy	1.4 Fairfax	1.1 Musgrave	0.4 Wistari	0.2 Heron	0.0 One Tree
<i>Labrichthys unilineata</i> interaction, $P < 0.05$	1982	3.0 Fitzroy	2.2 Fairfax	1.1 Musgrave	0.5 One Tree	0.2 Heron	0.0 Wistari	0.0 Llewellyn
	1983	3.4 Fairfax	0.6 One Tree	0.6 Fitzroy	0.4 Musgrave	0.2 Llewellyn	0.1 Heron	0.0 Wistari
<i>Pseudolabrus guentheri</i> interaction, $P < 0.01$	1982	8.0 Wistari	1.2 Heron	0.1 One Tree	0.1 Fairfax	0.0 Fitzroy	0.0 Musgrave	0.0 Llewellyn
	1983	3.0 Wistari	1.0 Fairfax	0.8 Heron	0.4 Fitzroy	0.4 Llewellyn	0.4 One Tree	0.0 Musgrave
<i>Stethojulis strigiventer</i> interaction, $P < 0.01$	1982	14.5 Wistari	9.8 Heron	7.5 Fairfax	4.7 One Tree	4.0 Llewellyn	3.4 Fitzroy	2.3 Musgrave
	1983	7.5 Heron	6.8 Wistari	4.4 Fitzroy	3.4 Musgrave	2.6 Fairfax	2.4 Llewellyn	1.5 One Tree
<i>Scarus sordidus</i> interaction, $P < 0.01$	1982	17.3 One Tree	10.0 Musgrave	6.9 Llewellyn	5.8 Fairfax	4.5 Wistari	2.6 Heron	2.9 Fitzroy
	1983	15.9 Llewellyn	12.7 Musgrave	9.6 Fairfax	7.0 Heron	4.4 One Tree	3.4 Fitzroy	1.5 Wistari
<i>Chelmon rostratus</i> interaction, $P < 0.01$	1982	2.7 Wistari	2.2 Heron	1.2 Llewellyn	0.9 Musgrave	0.6 One Tree	0.5 Fitzroy	0.2 Fairfax
	1983	0.9 Heron	0.8 Llewellyn	0.7 Musgrave	0.6 One Tree	0.4 Wistari	0.2 Fitzroy	0.1 Fairfax
<i>Canthigaster valentini</i> interaction, $P < 0.01$	1982	0.7 Wistari	0.5 Fairfax	0.0 Llewellyn	0.0 Heron	0.0 One Tree	0.0 Fitzroy	0.0 Musgrave
	1983	3.2 Fitzroy	3.0 Musgrave	2.6 Fairfax	2.0 Llewellyn	0.8 Heron	0.2 One Tree	0.2 Wistari
<i>Paraluteres prionurus</i> ^a interaction, $P < 0.005$	1982	0.5 Llewellyn	0.3 Fairfax	0.1 Fitzroy	0.0 Wistari	0.0 Heron	0.0 One Tree	0.0 Musgrave
	1983	1.6 One Tree	0.8 Fairfax	0.6 Llewellyn	0.8 Musgrave	0.7 Wistari	0.4 Fitzroy	0.1 Heron

^a Transformation left variances heterogeneous ($P < 0.05$, Cochran's test) so criterion for significance in S-N-K tests was $P < 0.01$

Table 3. Summary of significant differences among reefs (reef effect, $P < 0.01$ in all cases) detected by S-N-K tests of lagoonal data on total recruits and 9 individual species for which significant year \times reef interactions did not occur. Other details as in Table 2

Total recruits	116.2 Musgrave	83.7 Fairfax	73.7 Fitzroy	60.2 Llewellyn	50.3 Wistari	44.1 Heron	27.7 One Tree
<i>Amphiprion akindynos</i>	1.4 Musgrave	0.6 Fitzroy	0.5 Fairfax	0.3 Heron	0.1 Wistari	0.1 Llewellyn	0.0 One Tree
<i>Dischistodus melanotus</i> ^a	3.5 Fairfax	3.4 Musgrave	2.7 Llewellyn	2.5 Fitzroy	0.3 Wistari	0.1 Heron	0.0 One Tree
<i>Chrysiptera rollandi</i>	6.6 Musgrave	4.6 Heron	2.0 Llewellyn	1.4 Fairfax	1.5 One Tree	1.3 Wistari	1.1 Fitzroy
<i>Pomacentrus amboinensis</i>	2.9 Heron	2.2 Llewellyn	1.6 Fairfax	1.5 Wistari	0.7 Fitzroy	0.1 One Tree	0.0 Musgrave
<i>Pomacentrus molluccensis</i>	51.2 Musgrave	41.7 Llewellyn	37.9 Fairfax	29.8 Fitzroy	8.7 Wistari	8.1 Heron	2.8 One Tree
<i>Halichoeres melanurus</i>	3.1 Heron	1.7 Fairfax	1.3 Wistari	1.1 Musgrave	1.0 Llewellyn	0.6 Fitzroy	0.2 One Tree
<i>Labroides dimidiatus</i>	3.6 Musgrave	2.9 Fairfax	2.4 Llewellyn	1.7 One Tree	1.4 Fitzroy	0.3 Wistari	0.1 Heron
<i>Thalassoma lunare</i>	11.4 Fairfax	5.2 Llewellyn	4.5 Musgrave	1.6 One Tree	1.1 Wistari	1.0 Fitzroy	0.6 Heron
<i>Ostracion cubicus</i>	2.0 Musgrave	1.9 Fairfax	2.2 Llewellyn	1.0 Fitzroy	1.0 One Tree	1.0 Heron	0.3 Wistari

^a Transformation left variances heterogeneous ($P < 0.01$, Cochran's test) so criterion for significance in S-N-K tests was $P < 0.005$

Table 4. Summary of significant differences between years in density of recruits to lagoonal patch reefs, for total recruits and 7 individual species for which year \times reef interactions were not significant. Data shown are mean densities over all 7 reefs in each year

Species/group	Density: 1982	1983
Total recruits**	84.23	46.06
<i>Amphiprion akindynos</i> **	0.3	0.7
<i>Hemigymnus melapterus</i> *	21.8	15.2
<i>Stethojulis bandanensis</i> *	9.4	5.1
<i>Thalassoma lunare</i> **	9.0	5.2
<i>Lutjanus carponotatus</i> ** ^a	0.3	0.03
<i>Ostracion cubicus</i> **	0.7	1.8
<i>Siganus punctatus</i> *	0.2	0.7

*, ** year effect significant at $P < 0.05$, $P < 0.01$, respectively

^a data for three reefs with no recruitment either year were excluded from analysis to stabilise variances

pairs of rankings of $r_s = 0.07$. Weakness of the concordance is also shown by the rather similar mean rankings attributed to the reefs (Table 5) and by the fact that every reef was ranked both first and last at least once.

Table 5. Mean ranks assigned to 7 reefs as determined from 27 rankings by 22 lagoonal species which showed significant differences in density among reefs. Lower rank = greater density of recruits. Kendall's $w = 0.107$ ($P < 0.05$). More details in text

Reef	Mean rank
Wistari	4.11
Heron	4.09
One Tree	5.09
Fitzroy	4.63
Llewellyn	3.61
Fairfax	3.09
Musgrave	3.37

Species present in both habitats

Four species were common enough as recruits to be analysed in both slope and lagoonal habitats. Table 6 summarises the density of recruits of each of these species in each habitat. Only one of the four species (*Pomacentrus wardi*) showed significant among reef variability in both habitats. It showed a range of variability among reefs at slope sites

Table 6. The density of recruits (number per 100 m²) of each of four species common in both lagoonal and slope habitats. The variation in density among reefs is significant for all four species at lagoonal sites, but only for *Pomacentrus wardi* at reef slope sites

Reef	Habitat	<i>Pomacentrus wardi</i>	<i>Pomacentrus molluccensis</i>	<i>Thalassoma lunare</i>	<i>Labroides dimidiatus</i>
Wistari	slope	9.50	1.75	0.0	0.50
	lagoon	25.8	8.71	1.10	0.30
Heron	slope	8.50	2.58	0.50	0.67
	lagoon	12.6	8.10	0.60	0.10
One Tree	slope	0.75	1.83	0.42	0.83
	lagoon	1.99	2.84	1.60	1.70
Fitzroy	slope	0.08	0.92	0.25	1.50
	lagoon	3.63	29.8	1.00	1.40
Llewellyn	slope	0.42	1.00	0.50	1.08
	lagoon	9.04	41.7	5.20	2.40
Fairfax	slope	0.33	0.83	0.25	1.00
	lagoon	1.11	37.9	11.4	2.90
Musgrave	slope	0.92	2.08	0.08	1.92
	lagoon	8.81	51.2	4.50	3.60
Range	slope	0.08–9.50	0.83–2.58	0.0–0.50	0.50–1.92
	lagoon	1.11–25.8	2.84–51.2	0.60–5.20	0.10–3.60

that was four times the range at lagoonal sites (100x vs 25x). Two other species (*Pomacentrus molluccensis* and *Labroides dimidiatus*) showed substantially more variability among reefs at lagoonal sites than they did on the slope sites where variation was not significant. The fourth (*Thalassoma lunare*) showed approximately comparable levels of variation among reefs in both sites although this variation was significant under the more sensitive test possible with the lagoonal data. All except *L. dimidiatus* appear more common as recruits at lagoonal than at slope sites.

Also with the exception of *L. dimidiatus*, the densities of recruits of these species in the two habitats do not vary similarly across the 7 reefs. For example, *P. wardi* is ten times more abundant on the slopes of Wistari and Heron reefs than elsewhere. Yet, while most common at lagoonal sites on these reefs, it is also very common at lagoonal sites of two other reefs. *P. molluccensis* and *T. lunare* both show apparent clines in abundance within lagoons from east to west along the transect, and are both most abundant in the more easterly lagoons. Their abundances on the slopes do not suggest comparable clines.

Discussion

Patterns detected

Our results demonstrate substantial variability in the numbers of recruits of particular species detected at different reefs. At reef slope sites, 6 of 16 species, and the total of all recruits show significant differences in density among reefs. In lagoonal sites, 18 of 22 species show significant variations in density among reefs. Importantly, 9 of these lagoonal species exhibited significantly different patterns of relative abundance among reefs in the two years for

which we have data. The total number of recruits at lagoonal sites also showed a significant difference among reefs with the more eastern reefs obtaining more recruits.

Our autumn survey has detected those juvenile fish which settled onto sampled sites during the summer and which then survived to the end of summer. The differences observed could be caused by differing levels of early mortality on the various reefs, by differing rates of settlement at different reefs, or by a combination of these effects. Experimental data from One Tree Reef (Doherty and Sale MS; Sale, unpub.) suggest that while mortality can be quite high during the first five days after settlement, rates of mortality level off rapidly after that to levels not much higher than that among adults. For site-attached species such as many pomacentrids and some labrids, 25–30% of settled juveniles at reef slope sites are lost during the first five days, but by 10 days after settlement the rate has dropped to unmeasurable levels. For fish of this type, total mortality during the first year after settlement is 40–55%. For more mobile planktivorous species such as *Cirrhitilabrus* sp. or *Pomacentrus lepidogenys*, about 50% are lost during the first few days after settling. This rate also drops to very low levels thereafter so that mortality for the first year is about 60–75% (Doherty and Sale, MS). Limited data from lagoonal sites (Sale et al., unpub.) indicate rates of mortality are substantially lower in this habitat.

The pattern of very high mortality immediately after settling, followed by much lower rates of mortality thereafter, suggests that, depending on the species, we have detected from 45 to 75% of all fish which settled at the sampled sites during the season. The fidelity of any patterns we detected in abundance of recruits, to patterns in abundance of settling fish will depend upon the extent to which mortality rates have been uniform across sites and, for the lagoon, years.

Several lines of indirect evidence suggest that our results are substantially due to a variable settlement of fish among reefs. Firstly, the lack of significant site effects in any of the reef slope data indicates the variation in density of recruits detected in this habitat is not an artifact due to chance variation among sites on different reefs. It is a real phenomenon at the scale of the whole reef. Lagoonal patch reefs were also chosen to be similar sites. Secondly, if the observed patterns were to arise solely through effects of variable mortality after settlement, it would be necessary that rates of mortality, presumably through predation, vary about 10-fold between years and among reefs, and that the relative rates of mortality among reefs vary differently for different species. Thirdly, the significant year × reef interactions detected in recruits of 9 lagoonal species also make it unlikely that a variation among reefs in the rates of mortality of settled fish has caused the variations in numbers of recruits. For this to be so, mortality rates of a species would have to vary substantially from year to year, and in different ways on different reefs. The pattern of this variation would also have to differ among the 9 species.

If we accept that the patterns detected are predominantly a consequence of variation in settlement of fish, to what can these patterns in settlement be attributed? Differences in rates of settlement among reefs could arise because the reefs provided different types of habitat, of greater or lesser attractiveness to any given species. They could also arise if larval fish competent to settle were patchily distributed

in the waters bathing the reefs. We favour the second alternative.

The strongest evidence that the variations detected are due to variation among reefs in the abundance of larvae competent to settle, again comes from the 9 lagoonal species for which significant reef \times year interactions were detected. To explain a change from one year to the next in relative preference of a species for the 7 reefs as due to some intrinsic difference among the reefs, requires that whatever makes one reef more attractive than another must be capable of changing from one year to the next. We know of no such factor, and at present, we interpret our data as indicating a substantial variation in the rate of settlement of larval fish from one reef to another within the Capricorn-Bunker Group. The significant concordance shown among lagoonal species in their relative abundances on the seven reefs suggests that despite this considerable variability in rate of settlement from one reef to another, there are, nevertheless, some reefs which are consistently favoured, and others consistently less favoured by settling fish.

Consequences for reef fish assemblages

Regardless of the cause or causes, we have shown recruitment of fish to be spatially and temporally patchy at the scale of whole reefs. This result is not easily reconciled with claims that reef fish assemblages are stable in structure when examined at a large spatial scale. Since all the species examined here have potential life-spans of several years, this patchiness of recruitment may have important consequences for the structuring of reef fish assemblages. Unless subsequent compensatory mortality occurs, a reef which chances to receive a relatively dense settlement of a particular species one year, is likely to have that species present and reasonably abundant in assemblages for the next several years. This might be a trivial feature except for the fact that the variations we have detected among reefs in density of recruits are often quite large. Of the 6 reef slope species exhibiting significant variation in recruitment, the range of variation of all but one species exceeded 1 order of magnitude, and in one species exceeded two. Among lagoonal species the degree of variability is comparable: excluding zero values, the mean range in density of recruits among reefs and within years is 17 fold, and *Pseudolabrus guentheri* varied 80 fold among reefs in 1982.

The variability shown in size of successive year classes, will not surprise fisheries biologists who have always recognised and routinely coped with the effects of often substantial variation from year to year in recruitment success (Gulland 1977; Cushing 1977, 1981). Rarely have they been concerned with spatial variability since they tend to deal with single stocks. However, our data show that, at the scale of the Capricorn-Bunker Group of reefs, spatial variability in recruitment is fully as important as is variability in year class strength.

We have demonstrated that even on the relatively large scale of the Capricorn-Bunker Group, the recruitment, and almost certainly the prior settlement of coral reef fishes is spatially and temporally variable. This variability occurs because of factors at present unknown, but factors unrelated to the sites at which recruitment takes place. Thus, at this scale, as at smaller scales (Talbot et al. 1978; Sale 1980; Doherty 1980; Williams 1983; Sale and Douglas 1984) the structure of reef fish assemblages appears to be

continually modified by a varying rate of recruitment of component species. The view of the reef fish community as having a structure which is predictable, and maintained at or close to an equilibrium state by intrinsic, chiefly biotic factors (eg. Anderson et al. 1981), even if special concepts such as lottery competition (Sale 1977) are invoked, appears to us increasingly untenable.

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