

Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef

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ABSTRACT: The potential causes of the variable nature of recruitment of marine organisms can be inferred from the scales over which they vary. Sampling for recruits of *Chaetodon rainfordi* on the Great Barrier Reef, Australia, was done at the end of the recruitment season in 3 yr at 3 spatial scales: at regions separated by hundreds of km; at reefs separated by up to tens of km; and at different sites on 1 coral reef. Despite a background of variability suggesting the influence of stochastic processes, the data showed considerable pattern, implicating the involvement of deterministic processes. At each spatial scale, recruitment was higher in 1985 than 1986 or 1987. Furthermore, despite the general reduction in recruitment with time, the distribution patterns were consistent in each year. Southern regions always had higher rates of recruitment than northern ones, some reefs always received higher rates than neighbouring ones and some sites consistently had higher rates than others only hundreds of metres away. Recruitment rates of *C. rainfordi* were attributed to settlement rates. Consequently, the observed patterns were related, at each spatial scale, to either the availability of pre-settlement fish, or habitat selection acting at the time of settlement. This study was not able to distinguish between such alternative hypotheses at any scale, but indicated the types of studies required to do so.

INTRODUCTION

Many species of marine organisms which occupy shallow habitats are characterised by having a bipartite life-history cycle (Sale 1980, Roughgarden et al. 1988). The post-settlement phase of this life-cycle consists of comparatively sedentary, long-lived individuals, whose populations are characteristically replenished on a seasonal basis, from the initial free-living, pre-settlement phase. The benthic populations are considered to be 'open' because of the general lack of homeostatic relationships between stock size and recruitment, apparently related to the likely long-distance dispersal of the pre-settlement organisms (Scheltema 1986, Doherty & Williams 1988, Mapstone and Fowler 1988). The rates at which the post-settlement populations are replenished by settlement from the plankton are characteristically variable in space and time (e.g. Caffey 1985, Connell 1985, Doherty 1988, Doherty & Williams 1988, Doherty 1991).

Variable recruitment can influence the population dynamics of both intertidal and subtidal populations (Underwood & Denley 1984, Connell 1985, Lewin 1986,

Doherty & Williams 1988, Mapstone & Fowler 1988, Sale 1988, Underwood & Fairweather 1989, Sale 1990, Jones 1991). From an ecological perspective it is important to understand the causes of such variability. Observed recruitment is the consequence of 2 phenomena; the rates at which larvae leave the planktonic habitat and join the community where the adults are found ('settlement'), and the ensuing mortality that takes place before recruitment is documented (Connell 1985). The spatial scale over which processes such as competition and predation operate on newly-settled individuals must be local. Alternatively, the variation in abundance of pre-settlement organisms in the plankton is likely to be the consequence of numerous processes that interact at different scales of space and time (Cowen 1985, Dayton & Tegner 1985, Williams 1986, Dayton et al. 1989). The documentation of recruitment at a range of spatial and temporal scales, particularly in a way designed to minimise variability in habitats amongst places, provides a mechanism from which inferences on the relative influence of such pre- and post-settlement events can be made (Williams 1986).

Information for coral reef fish has contributed to the overall impression of variability in recruitment of marine organisms (Sale 1988). Recruitment analysis for some species from this group of organisms ranges in the spatial scale from tens of metres up to >1000 km, whilst the temporal range is from days to years (see reviews; Doherty & Williams 1988, Doherty 1991). Initially, authors emphasized the variability in recruitment regardless of the spatial scale being addressed (Eckert 1984, Sale et al. 1984), implying that recruitment was largely a stochastic process. However, with the availability of multi-scale and longer term datasets, some coherent patterns have been described (Victor 1986, Williams 1986, Doherty 1987a, 1988, Doherty & Williams 1988), and recruitment is now considered to reflect the interactive influence of deterministic and stochastic variations (Doherty & Williams 1988). Various hypotheses have been presented to account for these observations, and these have generally related recruitment to the availability of settlement-competent larvae, as related to such things as hydrographic processes (Cowen 1985, Victor 1986, Doherty 1987a, Doherty & Williams 1988, Pitcher 1988a, b). For example the 'larval patch' hypothesis was developed from recruitment patterns over scales of metres to tens of km and observations of the distribution and abundance of larvae in inter-reefal waters (Williams 1986, Doherty 1987a, Doherty & Williams 1988, Pitcher 1988a, Williams & English in press).

The number of coral reef fish species for which there exists a comprehensive recruitment analysis over numerous spatial scales and across a number of years is extremely limited (reviewed Doherty & Williams 1988). Furthermore, there has been little coherence demonstrated amongst these taxa, suggesting that the significance of different processes must vary amongst taxa. Consequently, any multi-scale recruitment analysis of a species will make a significant contribution to the database in this field. In this paper the recruitment of one member of the family Chaetodontidae (butterflyfish), 1 of the 10 most significant families in terms of biomass on the Great Barrier Reef (GBR) (Williams & Hatcher 1983), was analysed. This was done by combining the results from several contemporaneous studies allowing a multi-scale assessment of recruitment. The species considered here is *Chaetodon rainfordi*, one of the dominant chaetodontid species, both in the central (Williams 1982) and the southern GBR (Fowler 1990). At the largest scale, recruitment was compared amongst 5 regions of the GBR, over a linear distance of >1000 km. A study at the regional scale compared recruitment to 1 habitat amongst 7 coral reefs over a linear distance of 70 km. At the within-reef scale, estimates of recruitment were compared both within and amongst sites, which presented different habitats.

The specific aim of this paper was to analyse the recruitment patterns of *Chaetodon rainfordi* at a number of spatial scales, to assess the degree of variation in recruitment and to determine the repeatability of spatial patterns over time. From this, inferences could be drawn regarding the mechanisms most likely to account for the observations.

MATERIALS AND METHODS

Spatial and temporal patterns in recruitment. Recruitment of *Chaetodon rainfordi* was documented on 3 spatial scales. A description of each scale and the methodology used to sample each is described below.

Geographic patterns: Recruitment was described at 5 different regions of the GBR which varied in latitude (16 to 24° S) and distance from shore. Within each of the 5 regions (identified as Cairns, Townsville, Whitsundays, Swains and the Capricorn/Bunkers), 5 reefs separated by distances of from several km to tens of km were sampled. These reefs had been originally selected in 1984 as presenting a consistent reef slope habitat, to minimise habitat differences amongst reefs. In April of 1985, 1986 and 1987 the oblique reef slopes of these 25 reefs were sampled. Sampling was done at 3 haphazardly-chosen places using 8 transects (40 × 2 m), within a depth zone of 5 to 8 m. The transect line was laid out parallel to the reef crest. The transect length was then swum and the new recruits of many species counted (Sale et al. 1984). Data for *Chaetodon rainfordi* were extracted and analysed by a 4-factor analysis of variance with both regions and years treated as fixed factors, and reefs nested within regions and places nested within reefs.

Longshore – within region: The long-shore, within-region study was carried out in the Capricorn/Bunker Reefs at the southern end of the GBR. Here, a further 2 reefs were considered as well as the 5 already involved as part of the geographic study. The 7 reefs lie in an approximate straight line from the north-west (23° 27' S, 155° 55' E) to south-east (23° 54' S, 152° 54' E), parallel to the coastline over a distance of 70 km. Between 1985 and 1987 the oblique reef slopes were sampled using the same methodology and regime described for the geographic study. Levels of recruitment were compared for years, reefs and places using a mixed-model 3-factor analysis of variance. Years and reefs were treated as fixed factors and places as random, as in the geographic analysis.

Among sites – within year classes: The within-reef analysis of recruitment was done at One Tree Reef (23° 30' S, 152° 06' E) in the Capricorn Group. Here, 10 sites were sampled for new recruits on numerous occasions over a 21 mo period. These sites varied in

position on the reef, and the habitat they presented to pre-settlement fish. The sites formed 2 parallel transects (East Transect, West Transect) that crossed the main lagoon from south-east to north-west. Of the 5 sites along each transect, 4 were in the lagoon in 2 to 4 m of water, and the fifth was on the leeward reef slope at a depth of approximately 10 m. Adjacent sites along and between each transect were several hundred metres apart, except the 2 sites on the south-west corner of the East Transect. These latter 2 sites were adjoining but presented different habitat types, the one (Shark Alley Wall) being a vertical wall adjacent to the second (Shark Alley Top), a shallow, horizontal, sandy area, supporting many small bommies and coral heads.

Permanent rope transects were established at each site in August 1985 and maintained until April 1987. These transects (75 m long) were sampled by swimming down one side of the transect line and searching for recruits over a transect width of 1 m, and then swimming back searching the other side of the line, resulting in a transect width of 2 m being sampled as 1 m strips (Fowler 1987). Three transects gave a total area of 450 m² site⁻¹.

Sites in the lagoon were sampled on 20 occasions over the 21 mo study, more intensively during the summer/autumn months, the peak period of settlement (Russell et al. 1977, Williams & Sale 1981). The leeward reef slope could not be sampled on all occasions as access was limited by weather and tides and so these sites were sampled as close in time to the lagoon sites as possible. When a new recruit of *Chaetodon rainfordi* was found, the coral head in which it was located was tagged. On subsequent sampling occasions this recruit was not re-counted but its persistence in the coral head or vicinity was monitored. The total number of recruits per summer were compared amongst sites, by single factor analyses of variance (1 for each year). It was not possible to do an analysis comparing rates of recruitment between years as recruitment to the same transects was not statistically independent between years.

Among sites – among year classes: At One Tree Reef recruitment was also described by end-of-summer surveys at 9 sites which differed in their reef geography and habitat (described in Table 1; Fowler 1990), and which were separated by tens to hundreds of metres. These surveys were carried out in April 1985, 1986 and 1987. Three transects (75 × 2 m) were sampled at each of 2 haphazardly-chosen places within each site. Here, recruits were counted as part of a general sampling program for chaetodonts using a technique developed to sample all size classes (Fowler 1987). A transect line was swum out and the recruits were sampled by swimming down one side of the transect line and back along the other, searching over

a transect width of 1 m. Densities of recruitment, expressed as no. 150 m⁻², were compared among years, sites and places using a 3-factor, mixed model analysis of variance with Years and Sites as fixed factors and Places as random.

RESULTS

Spatial and temporal patterns in recruitment

Geographic patterns

There were 1578 recruits counted on 25 reefs in the 5 regions of the geographic study between 1985 and 1987. Of these, 1013 (64.2 % of total) were recorded in 1985, 373 (23.6 %) in 1986 and 192 (12.2 %) in 1987, a highly significant temporal variation (Table 1). In 4 of the 5 regions recruitment was approximately twice as high in 1985 as in the following 2 yr (Fig. 1). The Cairns region, which showed little recruitment of *Chaetodon rainfordi*, was the only exception. This suggests an inter-regional synchrony in the year-to-year variation in recruitment.

In 1985, recruits were distributed unevenly, with the 3 southern regions presenting higher counts than the significantly lower numbers found in the 2 northern regions (Fig. 1). This large-scale pattern of distribution remained consistent in 1986. In 1987, the 2 northern regions again received negligible input whilst recruitment to the Capricorn/Bunkers was relatively greater, receiving the highest levels for this year. This is likely to have caused the significant statistical interaction between years and regions (Table 1).

Longshore – within region

A total of 685 recruits were counted on the oblique reef slopes of the 7 Capricorn/Bunker Reefs between 1985 and 1987. Density of recruits was generally at least twice as high in 1985, than either of the following years (Fig. 2). This indicates a significant region-wide phenomenon of synchronised variation in recruitment experienced by reefs separated by a distance of up to 70 km.

Multiple comparisons amongst means could only identify significant differences amongst reefs for 1985. In this year, recruitment was highest at Llewellyn and Wistari Reefs, intermediate at One Tree, Heron, Fairfax, and Lady Musgrave and lowest at Fitzroy (Fig. 2). The statistical analysis of results from 1985 to 1987 indicated no significant interaction between years and reefs (Table 1), thus suggesting that the distribution of recruits was approximately the same in the following 2 yr as that in 1985.

Table 1 Analyses of variance done on rates of recruitment at 3 different spatial scales. For all analyses, data were transformed using $\log_e(x + 1)$, to make variances homogeneous. df: degrees of freedom; MS: mean square; ns: not significant

Spatial scale	Source	df	MS	F-ratio	Result
Geographic	Year	2	37.8865	54.1313	**
	Region	4	35.7350	8.1611	**
	Reef	20	4.3787	17.8795	**
	Place	150	0.2449	1.5230	**
	Year × Region	8	5.2756	7.5376	**
	Year × Reef	40	0.6999	4.3526	**
	Residual	1575	0.1608		
	Total	1799			
Regional	Year	2	29.582	59.5451	**
	Reef	6	1.6197	3.2603	**
	Place	42	0.4968	2.16	**
	Year × Reef	12	0.5383	1.0835	ns
	Residual	441	0.23		
	Total	503			
Within-reef	Year	2	2.2439	9.3652	**
	Site	8	8.9402	37.3130	**
	Place	27	0.2396	0.8008	ns
	Year × Site	16	0.85	3.5476	**
	Residual	108	0.2992		
	Total	161			

*p < 0.05; **p < 0.01

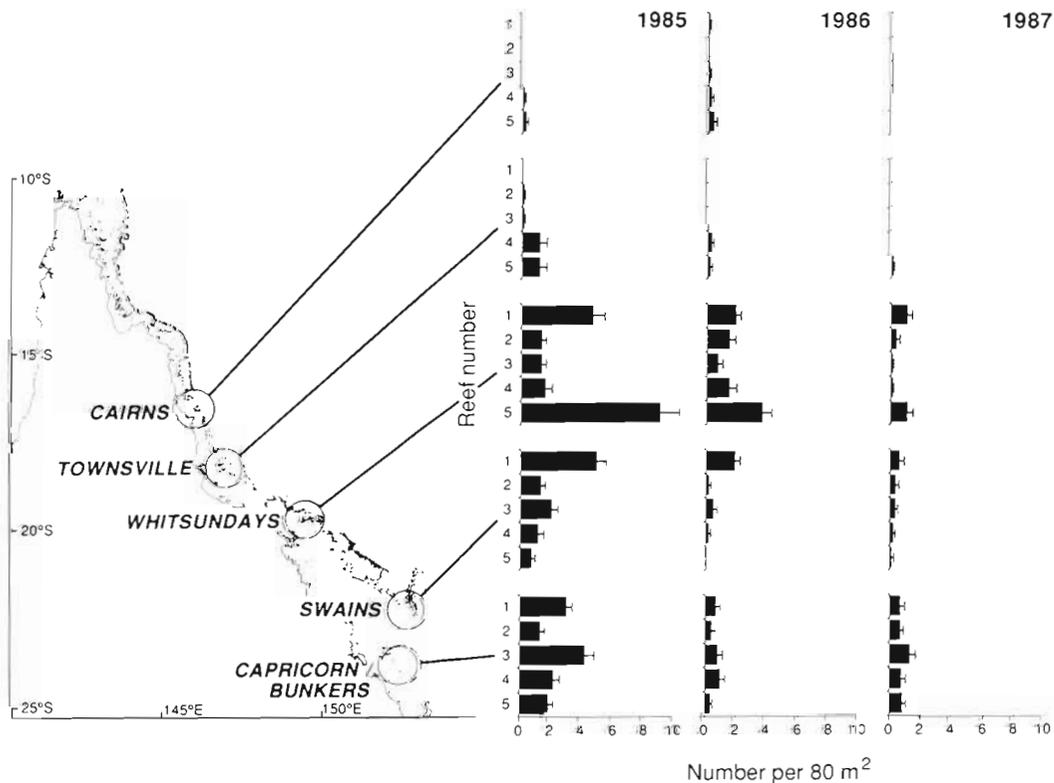


Fig. 1 Mean (\pm SE) rates of recruitment to the reef slopes of 5 reefs at 5 regions of the GBR for the years indicated

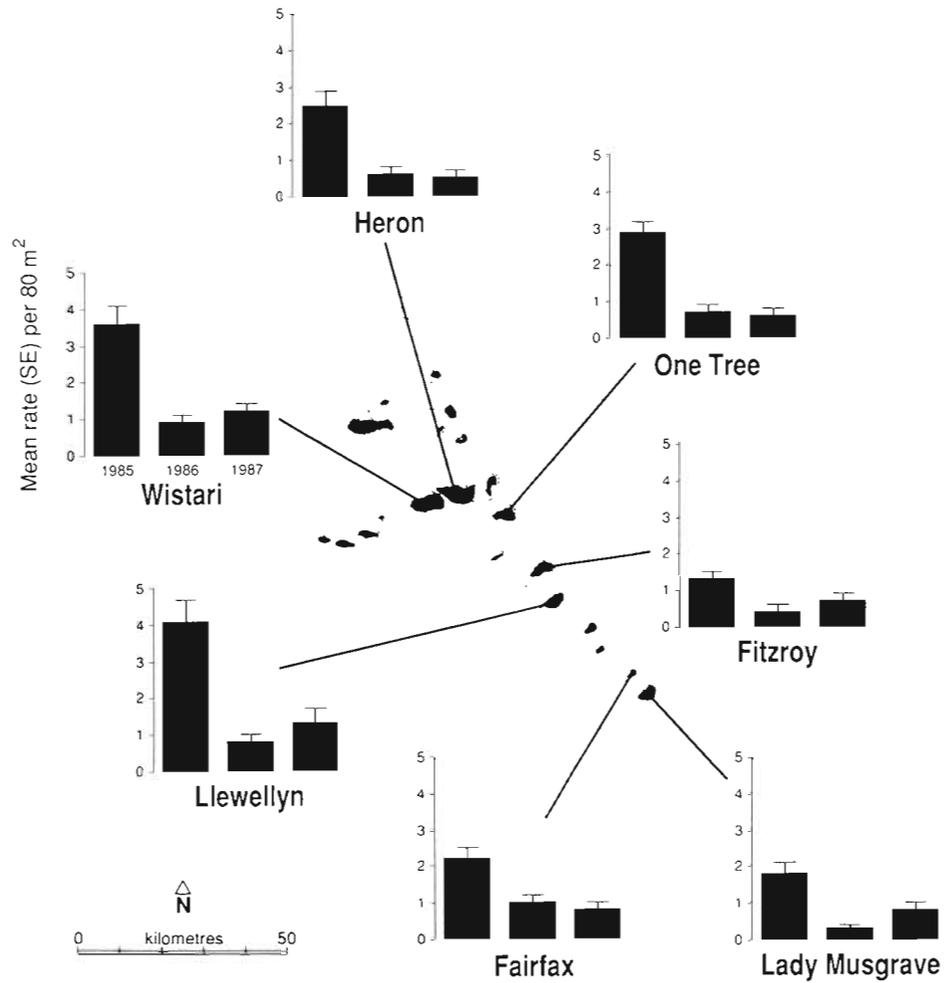


Fig. 2. Mean (\pm SE) rates of recruitment to the reef slopes of each of 7 reefs of the Capricorn/Bunker Group over 3 yr

The results from the other 2 geographic regions which had received reasonable rates of input (Whitsundays and Swains), provide a further opportunity for analysis of recruitment patterns at the regional scale over the same period. These data indicate considerable inter-annual variability in rates of recruitment, yet the distribution of recruits amongst reefs within each region was generally consistent amongst years (Fig. 1). For example, the high mean density of recruits in the Whitsundays in 1985 and 1986 was the consequence of particularly high recruitment at 1 reef (Fig. 1). In summary, for the 3 southern regions the ranks of reefs based on rates of recruitment, when compared amongst the 3 yr, show more consistency than would be expected by chance (Table 2).

Among sites – within year classes

In total, 213 *Chaetodon rainfordi* recruits were counted in the 30 permanent transects at the 10 sites on One Tree Reef between August 1985 and April 1987.

New recruits were found only from late January to April/May in each year, indicating that settlement was a seasonal phenomenon (Table 3). In the first summer the accrued number of new recruits, 116 in total, varied significantly in their distribution amongst the 10 sites ($F_{9,20} = 8.15, p < 0.01$), with a significantly higher number counted in 3 sites, the 2 on the leeward slope (LW1, LW2) and the 1 at Shark Alley Top (SAT) (Table 3). Shark Alley Wall (SAW) was intermediate and the remaining lagoonal localities generally re-

Table 2. Comparisons of the ranks of reefs within each region over the 3 yr of the study. *W*: Kendall's Coefficient of Concordance; χ^2 : chi-squared statistic; *df*: degrees of freedom; *p*: probability

Region	<i>W</i>	χ^2	<i>df</i>	<i>p</i>
Whitsundays	0.8778	10.5333	4	0.025 < <i>p</i> < 0.05
Swains	0.9722	11.6667	4	0.010 < <i>p</i> < 0.025
Capricorn/Bunkers	0.6270	11.286	6	0.05 < <i>p</i> < 0.1

Table 3. Summary of recruits counted on each sampling occasion at each permanent site at One Tree Reef, for the 2 sampling periods of August 1985 – May 1986 and September 1986 – April 1987. Data shown are total number of new recruits at each site, total at end of recruitment season and percentage of total. LW1: Leeward Slope 1; SAT: Shark Alley Top; LW2: Leeward Slope 2; SAW: Shark Alley Wall; TG: The Gutter; CM1: Central Maze 1; HR: H-Reef; CM2: Central Maze 2; LB: Long Bank; 3B: 3rd Bank; (-): no recruits counted; na: sampling was not done due to bad weather

Site	Aug	Nov	Nov	Jan	Feb	Feb	Mar	Mar	Apr	May	Total	%	Sep	Sep	Nov	Dec	Jan	Jan	Feb	Feb	Mar	Apr	Total	%
LW1	-	-	-	na	11	12	12	na	na	1	36	31.0	-	na	na	-	-	1	-	5	na	23	29	29.9
SAT	-	-	-	13	9	-	8	1	-	-	31	26.7	-	-	-	-	-	-	1	1	11	3	16	16.5
LW2	-	-	-	na	7	9	8	na	na	4	28	24.1	-	na	na	-	-	4	-	7	na	24	35	36.1
SAW	-	-	-	8	4	-	1	-	-	-	13	11.2	-	-	-	-	-	-	-	-	4	-	4	4.1
TG	-	-	-	3	-	-	-	1	-	-	4	3.5	-	-	-	-	-	-	1	-	1	-	2	2.1
CM1	-	-	-	1	-	1	-	-	-	-	2	1.7	-	-	-	-	-	-	-	-	4	1	5	5.2
HR	-	-	-	1	-	-	-	-	-	-	1	0.9	-	-	-	-	-	-	1	-	-	-	1	1.0
CM2	-	-	-	-	-	-	-	1	-	-	1	0.9	-	-	-	-	-	-	-	-	1	-	1	1.0
LB	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-	1	-	1	1.0
3B	-	-	-	-	-	-	-	-	-	-	0	0	-	-	-	-	-	-	-	-	3	-	3	3.1
Total											116												97	

ceived low recruitment levels. In the second summer the distribution of recruits was also significantly different amongst sites ($F_{9,20} = 7.95$, $p < 0.01$), again reflecting consistently higher recruitment in some sites than others (Table 3).

In both years the same 3 of the 10 permanent sites (LW1, LW2, SAT) had the highest accumulated recruitment, whilst 3 others (HR, CM2, LB) were consistently ranked amongst the 4 lowest localities (Table 3). When the ranks of these were compared between years, they were more similar than expected by chance (Spearman's rank test, $r_s = 0.8121$, $p < 0.001$), indicating a coherent spatial pattern in recruitment both within and amongst years. This coherent spatial pattern was related to the site-specific differences in recruitment being consistent throughout and between the 2 recruitment seasons (Table 3).

Among sites – among year classes

End-of-summer sampling in 3 yr at the 9 widely-dispersed sites across One Tree Reef produced a total of 500 recruits which varied significantly in their distribution in time and space (Table 1). Total recruitment was significantly greater in 1985 (47.2% of the 3 yr total) than in 1986 (22.0%) and 1987 (30.8%). Six sites received their highest rates of input in 1985, 2 of which (Shark Alley Top & The Gutter) were significantly higher than the following years (Fig. 3). At no locality was recruitment in 1985 significantly less than either 1986 or 1987.

In 1985 the distribution of recruits was uneven amongst the 9 sites. Despite a significant Year \times Site interaction in the ANOVA (Table 1), when sites were ranked according to density of recruits in each year,

and the ranks compared amongst years, there was higher agreement than expected by chance (Kendall's Coefficient of Concordance = 0.74, $\chi^2_8 = 17.69$, $0.01 < p < 0.025$). This indicates a coherent spatial pattern at the end of each recruitment season. Leeward Slope and Shark Alley Top always had the greatest recruitment, whilst several lagoonal localities, including North Reef Walls and N-West Wall, consistently had the lowest (Fig. 3). Therefore, although total recruitment varied unpredictably among years, the distribution of recruits among sites was consistent over the 3 yr.

DISCUSSION

A multi-scale analysis of recruitment can be rewarding because of the inferences that can be made about the processes likely to determine recruitment rates (Cowen 1985, Williams 1986). In this study such a comprehensive analysis was achieved by documenting recruitment at different spatial scales, and interpreting the results by looking for coherent spatial patterns over time.

Spatial and temporal patterns of recruitment

This study has presented a comprehensive multi-scale example of coherent inter-annual covariance in recruitment of a coral reef fish (cf. Doherty & Williams 1988). At 4 regions located along approximately 1000 km of the GBR, at 7 reefs within 1 region stretching over a linear distance of 70 km, and at numerous sites on 1 reef separated by hundreds of metres, recruitment was considerably higher in 1985 than 1986 and 1987.

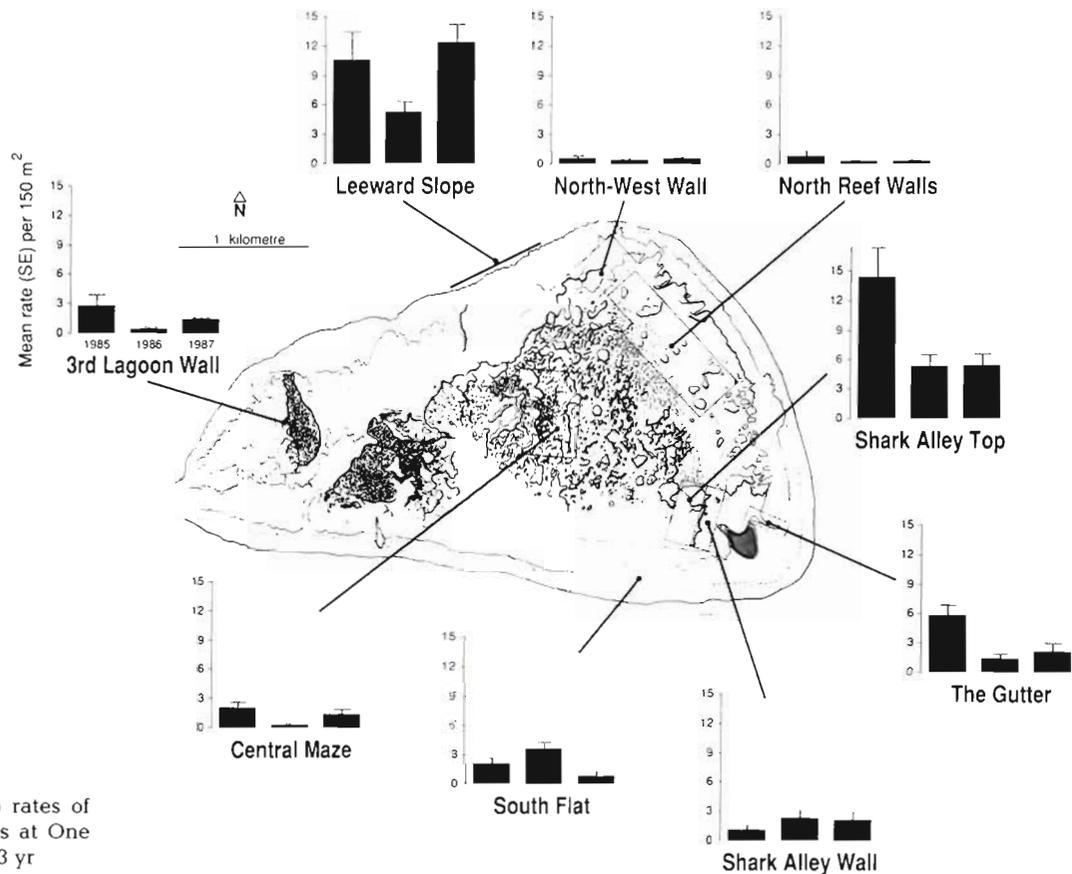


Fig. 3. Mean (\pm SE) rates of recruitment to 9 sites at One Tree Reef over 3 yr

Geographic patterns

Although recruitment was lower after 1985, the distribution of recruits amongst regions was consistent in each year. The 2 most northern regions received negligible input in 1985 to 1987, receiving a total of up to 100 \times less than the Whitsundays in 1985 and 1986 and the Capricorn/Bunkers in 1987. Furthermore, 2 of the southern regions were ranked either first or second in each year. Other species sampled at the same time as *Chaetodon rainfordi* also showed stable patterns in the distribution of recruits amongst regions, but these differed amongst species (cf. *Pomacentrus wardi*, *P. popei* and *Thalassoma hardwicki*; Doherty 1987a, Doherty & Williams 1988). Such patterns suggest the influence of strong deterministic processes operating over distances of hundreds of km, such influence varying amongst species (Doherty 1987a, Doherty & Williams 1988).

Longshore – within region

At the regional scale consistent differences were found in the distribution of recruits amongst reefs, and these were maintained for at least 3 yr. This phe-

nomon was strongest in the Whitsunday and the Swains groups where the ranks of the 5 reefs were maintained almost perfectly from year-to-year. This phenomenon has been described previously for *Pomacentrus wardi* (Williams 1986, Doherty 1988), *P. popei* and *Labrichthys unilineata* (Doherty & Williams 1988). This reflects a deterministic component to variation in recruitment at the spatial scale of km to tens of km, that strongly contrasts with the stochastic view that was initially presented for the GBR (Eckert 1984, Sale et al. 1984). Victor (1986) described a consistent pattern in the distribution of recruits of *Thalassoma bifasciatum* amongst 24 reefs of the San Blas Islands of the Caribbean. For the temperate wrasse *Pseudolabrus celidotus* there was a consistent difference in recruitment rates between rocky reefs approximately 20 km apart (Jones 1984). These examples indicate that coherence in the spatial distribution of recruits at the regional scale is not restricted to the GBR.

Among sites

At One Tree Reef, 2 within-reef scales were considered. The smaller scale of 'places' were tens of

metres apart, and presented similar habitat types. The larger scale of 'sites' were hundreds of metres apart and offered different habitat types. At the scale of places recruits of *Chaetodon rainfordi* were distributed evenly, however, among sites of different habitat there was a strong differential pattern maintained across the 3 recruitment seasons. This uneven distribution recorded at the end of summer, reflected the accumulation of recruits in some sites, and the consistent failure of recruitment in others. This pattern was not confined to this species, as several unrelated taxa have demonstrated the same general pattern (Williams & Sale 1981, Eckert 1985). Recruitment of the barnacle *Balanus glandula* in central California has also demonstrated a similar type of differential spatial pattern at the local scale as that documented here (Gaines et al. 1985).

Processes affecting recruitment

Variation in recruitment rates, be it between 2 places or at the same place over time, results from 1 or a combination of variations in the availability of settlement-competent larvae and their success at finding appropriate habitat within which to settle and/or differential post-settlement mortality regimes. Assessing the relative significance of both processes is difficult because of problems associated with documenting settlement at different places at the same time (Caffey 1985, Connell 1985). Furthermore, any study of settlement for organisms such as butterflyfish would be particularly fruitless because they have low recruitment rates and relatively rare larvae (Leis 1989).

Recruitment variability of coral reef fish has been most often attributed to the availability of pre-settlement fish, as determined from the results of multi-scale analyses of recruitment (Victor 1984, 1986, Doherty 1987a, 1988, Doherty & Williams 1988, Pitcher 1988b). Furthermore, studies of the survivorship patterns of recently settled fish under different recruitment regimes have provided little evidence for differential post-settlement mortality that could be related to density (Victor 1986, Meekan 1988, Sale & Ferrell 1988). In general, this conclusion aligns the recruitment dynamics of coral reef fish with their temperate, commercially-important counterparts where recruitment variability is largely attributed to survivorship during the egg and larval stages (Gulland 1982, Cushing 1988).

It is likely that recruitment of *Chaetodon rainfordi* is strongly related to differential settlement. Survivorship very soon after settlement is high (Fowler 1988), probably related to their use of hard corals as settlement sites, which provide a good refuge from predation (Eckert 1985). Furthermore, the coherence in patterns

of recruitment at several spatial scales is difficult to reconcile in terms of synchronised changes to post-settlement mortality regimes. Such a hypothesis would imply a synchronous change in predator density or a change in resources over a spatial scale much greater than 1 coral reef. The observed pattern is more parsimonious with recruitment being related to the availability of larvae, whose density is controlled by factors operating at scales of tens and hundreds of kilometres (Cowen 1985).

When recruitment is related to settlement, variation in levels of settlement at different scales of space and time are the consequence of one or a combination of differential availability of pre-settlement fish and habitat selection by such fish at the time of settlement. The extent to which each of these hypotheses may account for the observed recruitment patterns for *Chaetodon rainfordi* at each spatial scale are considered below.

Geographic patterns

Differential availability of pre-settlement fish and habitat selection by such fish may both contribute to the differences in recruitment of *Chaetodon rainfordi*, found between the northern and southern regions of the GBR. In the early 1980s, the northern regions were severely impacted by *Acanthaster planci*, the Crown-of-Thorns starfish, which caused massive coral mortality on some of the reefs included in the present study (Reichelt et al. 1990). Since this time, the abundances of adults of *C. rainfordi*, an obligate corallivore (Fowler 1988), have decreased significantly on these reefs (Williams 1986). This has probably resulted in a reduction in reproductive output, relative to southern regions where the impact of *A. planci* has been minimal. Furthermore, the pre-settlement individuals of this species settle preferentially into live corals such as *Pocillopora damicornis* and plate *Acropora* spp. (Fowler 1988). The loss of these specific settlement sites from these reefs may have reduced settlement even further.

At this geographic scale, the coherent inter-annual covariance in levels of recruitment cannot be related to habitat differences as the habitats were relatively consistent from year-to-year. This phenomenon reflects the impact of some large-scale deterministic process over an extensive part of the GBR, influencing the availability of pre-settlement fish. Factors that could operate at such an extensive scale in terms of latitude, longitude and distance off-shore are few. The result implies the physical forcing associated with some meteorological or climatic phenomenon making conditions in 1985 particularly favourable for either

enhanced fecundity, survivorship or rate of delivery of pre-settlement *Chaetodon rainfordi*. In other marine systems variations in recruitment have been related to large-scale oceanographic phenomena such as El Niño events (Cowen 1985), wind-driven currents (Bailey 1981, Fechhelm & Fissel 1988) and enhanced food supplies associated with currents (Kondo 1980). The processes that account for the observed patterns here cannot be clearly defined. However, it is likely that their influence was restricted in time since no other species sampled with *C. rainfordi* showed a comparable pattern of amongst-year variation (cf. Doherty & Williams 1988).

Longshore – within region

At each region of the GBR, some reefs consistently received higher rates of recruitment of *Chaetodon rainfordi* than others. This may be related to the differential availability of pre-settlement fish or their habitat selection. The modelling of the dispersal and advection of planktonic organisms via physical oceanographic phenomena through the GBR complex has predicted that some reefs are predisposed to the delivery of higher rates of planktonic organisms than others (Dight et al. 1990). Independent empirical support for this prediction has been provided by the recruitment patterns of scleractinian corals (Harriott & Fisk 1988) and fish (Williams 1986). In contrast to this Jones (1984) demonstrated that differential patterns of recruitment of *Pseudolabrus celidotus* constituted an obvious case of habitat selection.

For *Chaetodon rainfordi* we have insufficient information at present to distinguish between the 2 alternative hypotheses of differential availability of pre-settlement fish or their habitat selection. Appropriate tests can be done by comparing inter-reefal patterns of the abundances of pre-settlement fish and comparing these to models of regional current patterns, and also comparing these to recruitment rates amongst reefs (cf. Meekan 1988, Milicich 1988).

Amongst sites

At the local scale there was a differential distribution pattern of recruits which is likely to have been related to both active habitat selection and passive transport of larvae. The local circulation at One Tree Reef provides a likely mechanism for a general differential rate of delivery of larvae amongst sites (Ludington 1979, Frith 1981, Frith & Mason 1986). Circulation across and around this reef is strongly related to the South-East trade winds, which results in a general net flow of

water across the lagoon from the south-east to the north-west, such flow generally being deflected around the central region of the lagoon by a maze of patch reefs and reticulated reef. Intuitively, this should lead to more larvae being delivered to the southern and eastern lagoonal sites than the central and northern ones, leading to a related differential pattern of recruitment. The pattern of recruitment of *Chaetodon rainfordi* and other taxa (Williams & Sale 1981, Eckert 1985) is consistent with this model. The sampling of pre-settlement fish with light traps or the comparison of recruitment rates to standard experimental settlement units (Sweatman 1985), located at different places around a reef, would be required to clearly distinguish between these alternative hypotheses.

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