

Recruitment and post-recruit immigration affect the local population size of coral reef fishes

A. R. Lewis

Department of Marine Biology, James Cook University of North Queensland, Douglas, QLD. 4811. Australia
e-mail: Andrew.Lewis@jcu.edu.au

Accepted: 30 January 1997

Abstract. This study quantifies the contributions of larval recruitment and post-recruit (juvenile and adult) immigration to net increases in population size for 150 species of fishes found on ten isolated coral patches or 'bommies' (108–267 m²) within a typical reef of the Great Barrier Reef system. At least one third of the total number of recruits and immigrants to all bommies were post-recruit fishes, and movement between bommies in 136 species was detected at some time during the 22 month sampling period. The relative numbers of recruits and post-recruit immigrants per species varied widely within the assemblage, and between the replicate bommies. Populations of 95 species received both types of immigrants, 41 species had only post-recruit immigrants, and 14 species received only larval recruitment. In most species, recruitment occurred over the austral summer between October and February, while post-recruit movements occurred in both summer and winter. Rates of post-recruit immigration varied temporally within bommies, and pulses of post-recruits were less temporally concordant between bommies than pulses of recruits. This study is further evidence that post-settlement processes can have a significant effect on the local population size of reef fishes.

Introduction

On the Great Barrier Reef, the topographies of individual reefs are characterised by numerous patches of coral substratum (tens to hundreds of metres in diameter) distributed within the reef boundary. The regions between patches are filled with carbonate sediments, resulting in a two component habitat mosaic. At the larger spatial scale, whole reefs (dimensions in kilometres) are scattered along the continental shelf, separated by substantial expanses of open water. The reproductive outputs of reef fishes (eggs and larvae) are transported away from the natal coral patch by currents, and settlement is likely to occur on a different reef (Williams et al. 1984). Post-recruits may move among coral patches within a reef after

settlement, but they do not usually cross the expanses of open water among reefs (Robertson and Foster 1982, Williams 1991). Thus, for populations of fishes inhabiting the coral-sand habitat mosaic, all increases in population size are the result of either recruitment of larvae from other reefs (Williams et al. 1984), or the movement of post-recruits (juveniles and adults) from other patches within the same reef.

Most research on reef fish population dynamics has focused on the delivery of larval fishes to whole reefs and habitat patches within reefs (Sweatman 1985, Doherty and Fowler 1994), and the role of post-recruitment processes such as predation and competition (Shulman 1985, Caley 1993). Many species of reef fishes show strong site fidelity (Sale 1971; Hixon and Beets 1993), and it is often assumed that reef fishes in general rarely move after settlement. However, there are many literature reports of movement in post-recruit fishes (e.g. Robertson 1988; Warner 1995), and the rapid recolonisation of defaunated coral patches by adult and sub-adult fishes in experiments at several separate geographic locations (Hawaii, Brock et al. 1979; the Caribbean, Ogden and Ebersole 1981; the Great Barrier Reef, Walsh 1985) suggests that within reef movement may be an important determinant of local population size for many species. Consequently, quantitative estimates of recruitment and post-recruit movement will be a prerequisite for the development of realistic models of the spatio-temporal dynamics of reef fish populations, and will be essential to understand many general aspects of reef fish ecology (Jones 1991).

The ideal field study to quantify rates of recruitment and post-recruit movement in reef fishes would combine an extensive tagging program (Jones 1991) with a schedule of frequent (preferably daily) population monitoring. Tagging allows estimation of the range of dispersal, and could facilitate the detection of movement events which resulted in only small net changes in population size (i.e. when simultaneous immigration and emigration take place). Frequent monitoring decreases the probability that consecutive changes in population size will occur in the interval between censuses, which could lead to an underestimate of population turnover (Bohnsack 1983).

Unfortunately, the logistic difficulties involved with tagging large numbers of small fishes usually prevent the adoption of this approach at the community level. A more practical option is precise and repeated monitoring of population size in several size classes, which indicates the timing and magnitude of net changes in population size.

In this study, fish assemblages on ten isolated bommies (108–267 m²) within a large individual reef of the Great Barrier Reef complex were sampled at 30–60 day intervals over 22 months, and the size of fishes (new recruits versus post-recruits) was recorded. The aim of this research was to quantify how recruitment and post-recruit immigration affects the size of populations of reef fishes. In this study, I focus on the whole assemblage to provide a general overview of these processes; later studies will examine the population dynamics of individual species in more detail. The data analyses presented here were undertaken with the following specific objectives:

1. To estimate the minimum number of recruits and post-recruits arriving at a series of replicate bommies for a large assemblage of coral reef fish species (150 sp.)
2. To assess interspecific variation in the number of recruit and post-recruit arrivals
3. To examine how the number of recruit and post-recruit arrivals varied spatially among replicate bommies
4. To examine how the number of recruit and post-recruit arrivals varied temporally over a 2 y period

Materials and methods

Study sites

The study location was 52 km off the north east coast of Australia at Little Trunk Reef (18° 19'S, 146° 45'E). Little Trunk Reef is elliptical (8 km × 3 km) with the major axis orientated northeast to southwest. Ten bommies located in an open sandy zone at the western margin of the reef flat were sampled. These sites were selected from the hundreds of bommies on the reef flat because they were similar in size, benthic structure, and degree of isolation. They were all surrounded by at least 20 m of open sand (typically 40–50m), were at least 100 m from each other (typically 200–500 m), and were in 3 m of water at low tide. I consider these bommies to be independent replicates, because it is unlikely that fishes ever moved directly between any two of them. Each bommie consisted of a mound of consolidated substratum approximately 3 m high and 5–10 m wide. Live coral colonies covered 50–80% of the surface area of the mounds. A zone of dead coral rubble and isolated live coral colonies surrounded the mounds to a distance of 2–5 m. Total planar area of the bommies including the rubble zones varied from 108–267 m², and in this work they are labelled consecutively A to J.

Fish sampling program

Species from the following families were counted at each bommie at each census time: Centriscidae, Serranidae, Apogonidae, Lutjanidae, Caesionidae, Nemipteridae, Mullidae, Chaetodontidae, Pomacentridae, Pomacentridae, Sphyraenidae, Labridae, Scaridae, Blenniidae (genus *Plagiotremis* only), Acanthuridae, Siganidae, Balistidae, Monacanthidae, Ostracidae, Tetraodontidae, and Diodontidae. A list of 150 frequently sighted species was printed onto waterproof paper and used to record assemblage composition. A single estimate of abundance was made for each species, and for any rare species that were not on the list. The majority of species were not evenly

dispersed over the bommie, but either formed aggregations in the water column or inhabited distinct spatial zones near the substratum. Abundance estimates were made for these species by counting the number of fishes in the aggregation or habitat zone respectively. A zigzag course was swum up the longest axis of the bommie to obtain the abundance estimate for dispersed species.

Recruits and older post-recruit fishes were counted separately. Recruits were generally considered to be those fishes smaller than 20 mm standard length, but different maximum size limits were set for the following families; Serranidae 25–30 mm, Apogonidae 10–15 mm, Chaetodontidae 15–20 mm, Labridae 15 mm, Scaridae 15 mm, Acanthuridae 25–30 mm. The recruits of the abundant Labridae *Chelinus chlorurus*, *Coris schroderi*, *Halichoeres melanurus*, *H. trimaculatus*, and *Thalassoma lunare* were not counted, as they were shy and cryptically colored; these species are not analysed in this study. Several groups of congeneric species were combined in the censuses, because the species in each group were similar in appearance. I aggregated the Apogonids *Apogon cyanosoma* and *A. properupta*, the Pomacentrids *Chromis atripectoralis* and *C. viridis*, and the Acanthurids *Acanthurus blochii*, *A. dussumieri*, *A. grammoptilus*, and *A. xanthopterus*, and hereafter, these groups are referred to as *Apogon cyanosoma-properupta*, *Chromis atripectoralis-viridis*, and *Acanthurus spp. complex* respectively.

The ten bommies are subdivided into two classes on the basis of sampling intensity. Bommies A to F were censused most frequently and are referred to as core bommies, while bommies G to J were censused less frequently and are referred to as non-core bommies. Censuses at the core bommies were taken on 18 occasions from late October 1993 to mid July 1995. At each occasion, all bommies were censused within a four day period, between the hours of 0830 and 1600. The sampling program encompassed two annual larval recruitment periods (October-February), and generally maintained ≈ 30 days between summer samples and ≈ 60 days between winter samples. The non-core bommies were censused from June 1994 to June 1995.

Data analyses

The aim of the analyses was to make an estimate for each species of the minimum number of recruits and post recruit immigrants to the bommies over the 2 y sampling period. This was accomplished by first calculating, for each bommie, any increases in the abundance of each species between two consecutive censuses. The estimated minimum number of recruits during the interval was taken to be the number of recruits present at the second census. The estimated minimum number of post-recruit immigrants involved more detailed calculations that adjusted net population increases for sample error and the growth of recruits during the census interval (see later).

To quantify the error associated with the visual census technique, repeat censuses of particular bommies were made 2–3 h apart. On these occasions, the usual sampling technique was employed, with at least 2 h between the censuses. All core and non-core bommies had at least one set of within-day censuses taken, and several bommies had multiple within-day censuses, resulting in 15 within-day census pairs being available for the estimation of sample error.

The difference in estimated population size for a given species at a given bommie on a given day was expressed as a proportion of the mean abundance over the two within-day censuses;

$$\text{i.e. } D_{xnf} = \frac{|N_{xn1} - N_{xn2}|}{(N_{xn1} + N_{xn2})/2} \quad (1)$$

where:

N_{xn1} = the estimate of the number of fishes of species x at bommie n at the first census

N_{xn2} = the estimate of the number of fishes of species x at bommie n at the second census

D_{xnf} = the proportional sample error for species x at bommie n on day f

Proportional sample error values (D_{xnf}) were calculated for all f pairs of within-day censuses for each species. From this set of values, the mean proportional error ($D_{x,mean}$) was calculated over all f censuses for each species, and the upper bound of the 99.9% confidence interval around the mean ($D_{x99.9}$) was also calculated for each species. Some rare species were not seen during the whole series of within-day censuses, or seen on so few occasions as to prevent the calculation of realistic mean proportional errors. These species were allocated the mean proportional error values and associated confidence intervals of an ecologically similar congeneric or confamilial species.

The estimate of the minimum number of post-recruit immigrants for a given species at a given bommie over a given time interval between two censuses was calculated as follows. First, the raw population increase was calculated by subtracting the post-recruit population estimate at time 1 from that at time 2 (negative values, implying a population reduction, were constrained to zero). Second, the raw population increase was corrected for sample error by subtracting the product of the mean population size and the proportional sample error estimate from the raw value of population increase. Third, an adjustment for the growth of recruits was made by subtracting the number of recruits present at time 1 from the corrected value of the population increase. This procedure is summarised in Eq. 2.

$$A_{xnc} = (N_{xn(t+1)} - N_{xn(t)}) - \left[\left(D_{x,mean} \cdot \left(\frac{N_{xn(t)} + N_{xn(t+1)}}{2} \right) \right) + R_{xn(t)} \right] \quad (2)$$

where:

$N_{xn(t)}$ = the estimate of the number of post-recruit fishes of species x at bommie n at time t ($t = 1..j$ where j is the total number of censuses taken at bommie n)

$N_{xn(t+1)}$ = the estimate of the number of post-recruit fishes of species x at bommie n at time $t + 1$

$D_{x,mean}$ = the mean proportional error value for species x , derived from the distributions of D_{xnf} (Eq. 1).

$R_{xn(t)}$ = the estimate of the number of recruits of species x at bommie n at time t

A_{xnc} = the estimate of the minimum number of post-recruit fishes of species x that immigrated to bommie n during comparison period c [where $c = 1..(j - 1)$]

Values of A_{xnc} were calculated according to Eq. (2) for all species (x) over all sequential census intervals (c) for each bommie (n). In the first series of calculations, the mean proportional sample error value ($D_{x,mean}$) was used for each species. The calculations were then repeated using the more conservative sample error value ($D_{x99.9}$). For analyses of the spatial, temporal, and species specific patterns in post-recruit immigration, the latter data compiled from Eq. (2) using ($D_{x99.9}$) as the estimate of sample error were used. This ensured that the estimates are conservative and relatively free from sample error contamination.

Results

Overall recruitment and post-recruit immigration

11 581 fishes were estimated to have recruited as larvae to the bommies. The number of post-recruit immigrants was estimated to be 10 994 when the least conservative sample error value ($D_{x,mean}$) was used to estimate post-recruit immigration, and 7320 when the more conservative value ($D_{x99.9}$) was used (Eq. 2). Therefore, post-recruit immigrants accounted for at least one third of the total influx of new fishes to the bommies.

There were significant differences between bommies in the total number of recruits and post-recruit immigrants (paired sample t -test after standardisation of abundance

Table 1. Estimated minimum number of recruits and post-recruit immigrants of all species (except *A. polyacanthus*) to each of the ten study bommies over 22 months. The upper 99.9% confidence interval of the proportional sample error distribution was used to calculate the number of post-recruit immigrants

Bommie	Minimum recruits	Minimum post-recruit immigrants	Proportion due to post-recruits
A	1144	1192	51%
B	1227	1416	54%
C	1569	744	32%
D	935	1054	53%
E	979	780	44%
F	933	901	49%
G	2886	709	20%
H	1040	175	14%
I	379	111	23%
J	489	237	33%

across bommies, $P = 0.024$; Table 1). Bommie H had the lowest proportion of post-recruit immigrants (14.4%), while bommie B had the highest (53.6%). Bommie C had the lowest proportion (32.2%) of the six core bommies, while at bommies A, B, D, and F, post-recruits accounted for at least half of the total number of immigrants. The mean magnitude of the percentage of post-recruit immigrants over all ten bommies was $37 \pm 11\%$ (95% confidence interval). The proportional contribution of post-recruits varied between the bommies because of variance in both larval recruitment and post-recruit immigration (Table 1).

Variability between species

Post-recruit immigrants contributed to changes in population size for 136 of the 150 species examined (Appendix 1). The mean percentage of the total number of immigrants (recruits and post-recruits) that were post-recruits, over all species, was $58\% \pm 6\%$. Forty one species had post-recruit immigration percentages of 100%, indicating that all observed immigrants were post-recruits, and 14 species had post-recruit immigration percentages of 0%, indicating that all observed immigrants were in the recruit class (Fig. 1A). The distribution of percent post-recruit immigration values across the remaining 95 species was remarkably even, with immigrants from both sources affecting population size in most species to some degree.

In order to compare the relative numbers of recruits and post-recruit immigrants among species with different population sizes, the numbers of recruits and post-recruits for a given species were standardised by that species' abundance. The number of post-recruit immigrants was expressed as a percentage of the total abundance of post-recruit fishes of that species over all bommies and sampling times, while the number of recruits was expressed as a percentage of the total abundance of recruits and post-recruit fishes for that species. These parameters are called adjusted post-recruit immigrants and adjusted recruits respectively (Appendix 1). The values of adjusted

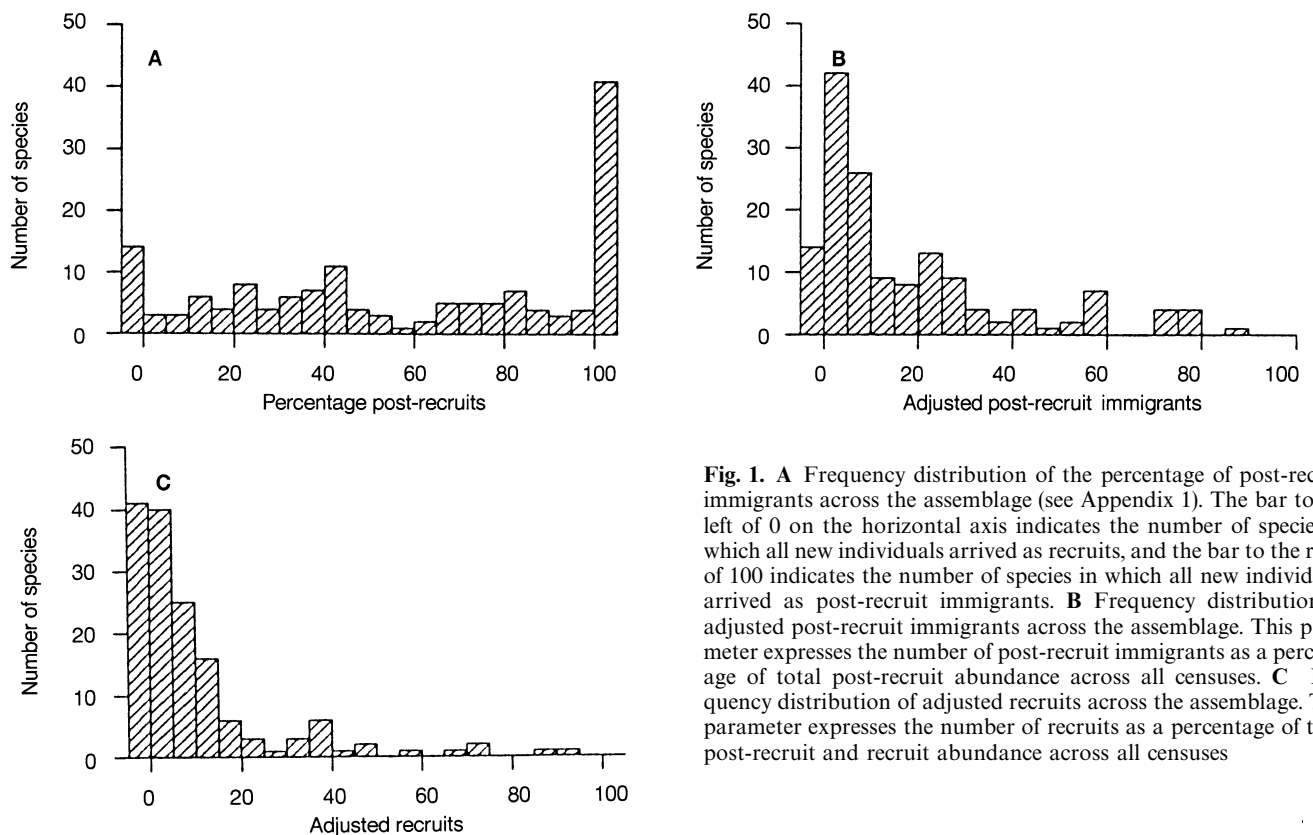


Fig. 1. **A** Frequency distribution of the percentage of post-recruit immigrants across the assemblage (see Appendix 1). The bar to the left of 0 on the horizontal axis indicates the number of species in which all new individuals arrived as recruits, and the bar to the right of 100 indicates the number of species in which all new individuals arrived as post-recruit immigrants. **B** Frequency distribution of adjusted post-recruit immigrants across the assemblage. This parameter expresses the number of post-recruit immigrants as a percentage of total post-recruit abundance across all censuses. **C** Frequency distribution of adjusted recruits across the assemblage. This parameter expresses the number of recruits as a percentage of total post-recruit and recruit abundance across all censuses

post-recruit immigrants ranged from 0 to 88% across the species pool, with a mean of $18\% \pm 4\%$ and a median of 8.3%. The distribution of values was positively skewed (Fig. 1B), with 60% of all species having values lower than 15%. The values of adjusted recruits had a similar distribution (Fig. 1C), with a range from 0 to 92%, a mean of $11\% \pm 3\%$, and a median value of 4.2%. These distributions indicate that, for recruits or post-recruits, most species receive a relatively small input, while a few species receive large inputs relative to their population size.

Temporal patterns in recruit and post-recruit immigration

All bommies showed peaks in larval recruitment during the periods October to February of both years covered by the sampling program, and few recruits in the winter periods from March to August (Fig 2). Three bommies (A, B, and C) had greater recruitment in the second summer than the first, while the other three bommies received relatively even numbers in both summers.

The temporal patterns in post-recruit immigration were more complex. At all bommies, post-recruit immigration continued through the winter periods when recruitment was very low. However, the numbers of post-recruit immigrants varied considerably between censuses. Maximum post-recruit immigration occurred during the summer months for five of the six core bommies, although three bommies (A, E, and F) all recorded minor peaks in immigration outside this time. Summer post-recruit immi-

gration maxima generally occurred 2–3 months after recruitment peaks and often consisted of sub-adult fishes (personal observation), particularly Apogonidae (eg. *Apogon doederleini*, *A. cyanosoma-properupta*, and *Rhabdamia gracilis*) and some planktivorous Pomacentridae (eg. *Neopomacentrus azysron*), suggesting that post-settlement redispersal of fishes occurs within Little Trunk Reef lagoon. The number of post-recruit immigrants at bommie E (Fig. 2E) showed a regular oscillation which was maintained over the whole 22 month sampling period. This pattern was largely due to regular migrations of the plankton-feeding pomacentrids *Chromis atripectoralis-viridis*, which contributed to four of the six maxima. Groups of individuals (principally of *C. viridis*) in breeding coloration (Randall et al. 1990) regularly engaged in mass spawning activities at this bommie, and this behaviour may have driven the regular migrations. Repeated, regular migrations of this species did not occur on the other nine bommies.

Spatial variability in immigration

The relative number of recruits and post-recruit immigrants in 38 common species varied considerably between bommies. The maximum and minimum values of percent post-recruit immigrants had a mean range of $55 \pm 9\%$ (Table 2). Three species primarily received post-recruit immigrants on all bommies (the Caesionidae *Caesio caerulea* and *Ptercaesio marri*, and the Apogonid

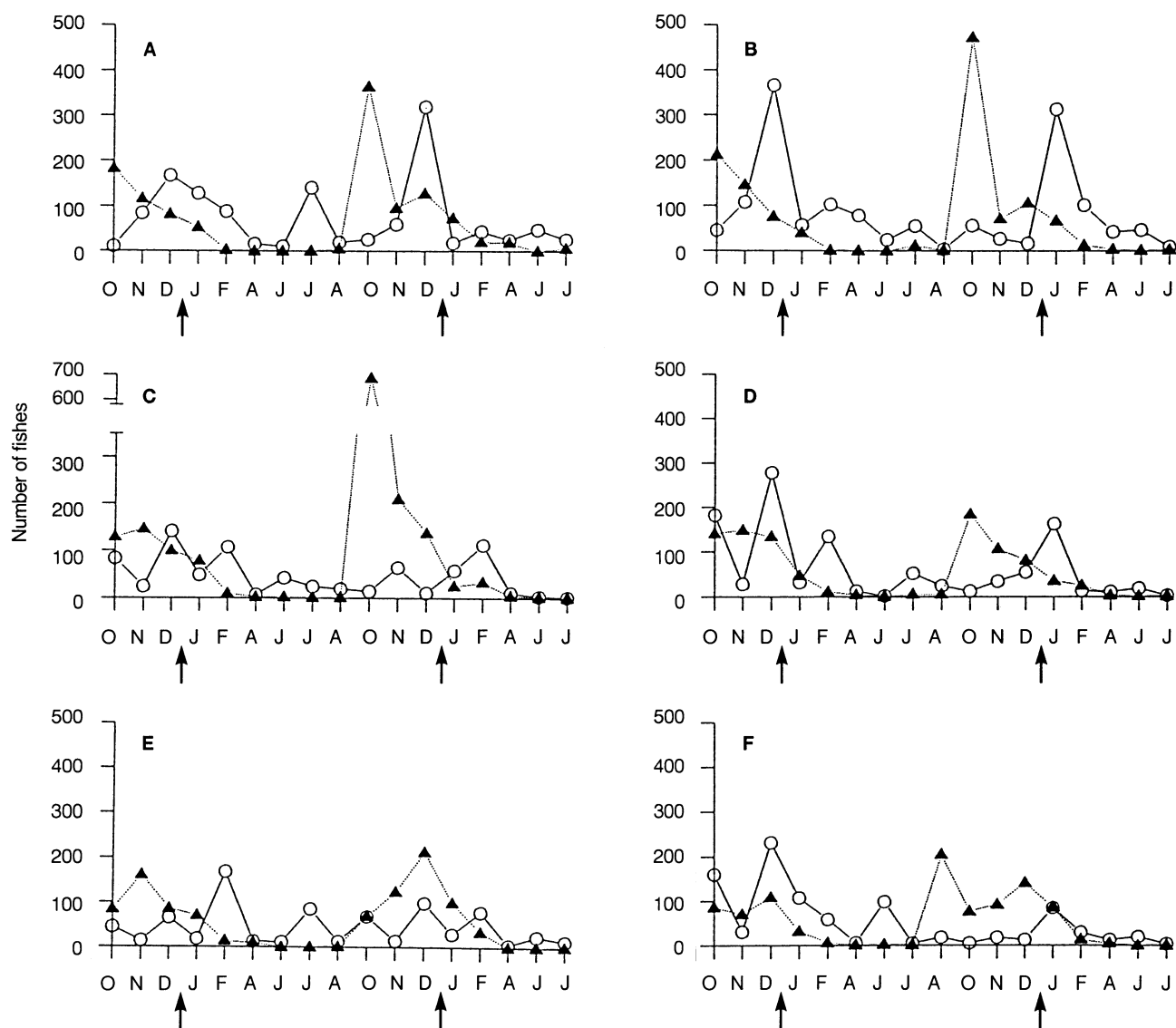


Fig. 2. Temporal variation in the estimated minimum total number of recruits (solid triangles) and post-recruit immigrants (open circles) to the six core bommies (A–F) over 22 months. Recruitment and immigration was estimated for the intervals between all pairs of

consecutive censuses; the horizontal axis refers to the month of the first census of each pair. Arrows mark the end of each year. Data are presented from October–November 1993 to June–July 1995

Chelodipterus artus). Twelve species primarily received larval recruits on all bommies (the Pomacentridae *Dischistodus melanotus*, *D. perspicillatus*, *D. pseudo-chrysopecilus*, *Pomacentrus adelus*, *P. amboinensis*, *P. coelestis*, *P. moluccensis*, *P. nagasakiensis*, and *P. wardi*; the Labridae *Cirrhilabrus punctatus* and *Hemigymnus melapterus*, and the Scarid *Chlorurus sordidus*). Thirty-four of the 38 species showed no significant difference in the spatial variability of the number of recruit and post-recruit immigrants (Table 2). Four species (*Apogon doederleini*, *Halichoeres chloropterus*, *Ptercaesio marri*, and *Stegastes apicalis*) had higher spatial variation in recruitment than the number of post-recruit immigrants across the core bommies, while one species (*Chlorurus sordidus*) had higher spatial variation in the total number of post-recruit immigrants.

Discussion

Highly episodic larval replenishment is common in many marine organisms (see Bertness et al. 1992; Raimondi 1990, and references therein), and is of obvious importance to the maintenance of population size (e.g. Roughgarden et al. 1988; Hughes 1990). Often, recruitment results in sharp increases in numbers over short time intervals, followed by much longer periods of decline. Local adult density can be expressed as a relatively simple function of the number of prior residents, the size of the last settlement pulse, and the post-settlement mortality rate (e.g. Doherty 1991). In this study, population size in species that were relatively unaffected by post-recruitment immigration increased due to the summer recruitment pulse, and then declined for the next year until the

Table 2. Variation in recruitment and post-recruit immigration across the six core bommies for 38 common species. Percent post-recruit immigrants expresses the number of post-recruit immigrants as a percentage of the sum of post-recruit immigrants and recruits; maxima and minima for this parameter over the six core bommies are presented. Coefficients of variation (CV) for recruits and post-recruit immigrants were calculated across bommies for each species. The number of recruits and post-recruit immigrants at each bommie were summed over the complete series of comparisons. The F-ratio column presents F-statistics for the comparison of coefficients of variation between the recruits and post-recruits, based on the log variance F-ratio (Zar 1984)

Species	Max.% post-recruit immigrants	Min% post-recruit immigrants	CV post-recruits	CV recruits	^a F-ratio
<i>Apogon doederleini</i>	100	10.2	70.38	122.28	10.08*
<i>Apogon cyanosoma-properupta</i>	83.1	39.9	29.56	83.84	3.53
<i>Chelodipterus artus</i>	100	75.7	35.73	244.95	6.93
<i>Rhabdamia gracilis</i>	100	0	88.13	176.82	2.11
<i>Caesio caeruleaurea</i>	100	83.4	83.11	130.98	1.01
<i>Caesio cuning</i>	100	32.4	46.85	172.97	7.15
<i>Ptercaesio marri</i>	100	70.6	40.79	147.48	10.96*
<i>Chaetodon aureofasciatus</i>	100	0	120.06	64.52	1.04
<i>Chaetodon rainfordi</i>	100	22.3	36.86	92.30	5.58
<i>Chromis atripectoralis-viridis</i>	100	0	146.34	117.60	1.25
<i>Chrysiptera rollandi</i>	72	5.5	79.56	101.68	4.22
<i>Chrysiptera rex</i>	100	18.4	100.05	86.72	1.25
<i>Dischistodus melanotus</i>	24.8	0	95.44	47.51	1.21
<i>Dischistodus perspicillatus</i>	43.2	1.1	96.33	75.35	3.06
<i>Dischistodus pseudochrysopoecilus</i>	46.1	0	75.57	44.09	1.54
<i>Neopomacentrus azyrson</i>	100	1.1	99.09	89.19	1.17
<i>Neopomacentrus cyanomos</i>	100	42.3	119.94	159.50	1.36
<i>Neoglyphidodon melas</i>	100	20.7	73.43	147.48	1.01
<i>Pomacentrus adelus</i>	31.8	0	75.54	44.74	1.62
<i>Pomacentrus amboinensis</i>	27.8	11.1	40.17	23.50	2.50
<i>Pomacentrus brachyalis</i>	100	26.6	96.09	163.33	2.95
<i>Pomacentrus chrysurus</i>	69.3	24.5	86.26	60.13	1.26
<i>Pomacentrus coelestis</i>	43.5	0	154.06	81.75	1.73
<i>Pomacentrus lepidogenys</i>	100	27.2	53.51	125.74	7.89
<i>Pomacentrus moluccensis</i>	46	8.5	65.81	44.49	4.95
<i>Pomacentrus nagasakiensis</i>	33.8	7.3	68.06	50.91	1.08
<i>Pomacentrus wardi</i>	46	5.8	68.54	51.71	2.23
<i>Stegastes apicalis</i>	100	43.7	105.68	244.95	10.61*
<i>Cirrhilabrus punctatus</i>	37.7	1	79.01	53.94	1.10
<i>Halichoeres chloropterus</i>	100	36.8	25.88	70.71	7.49*
<i>Hemigymnus melapterus</i>	24.3	0	80.63	26.85	3.58
<i>Labrichthys unilineatus</i>	100	15.7	60.79	123.94	6.86
<i>Labroides dimidiatus</i>	58.9	13.2	42.22	56.54	4.03
<i>Stethojulis strigiventer</i>	83	0	67.45	87.32	1.53
<i>Scarus rivulatus</i>	80.1	0	55.39	49.09	3.64
<i>Chlorurus sordidus</i>	14.2	0	140.67	33.85	13.76*
<i>Acanthurus spp. complex</i>	100	14.8	70.48	106.58	2.10
<i>Ostracion cubicus</i>	100	51.7	34.24	109.54	1.87

^a The critical F-value for $\alpha = 0.05$ and (5,5) df is 7.15; values greater than this are marked *

following recruitment event. In fishes with this type of dynamic, the main determinants of local population size will be the same as for sessile organisms such as barnacles or corals; namely, (1) large-scale factors contributing to the number of larvae that come in contact with the patch, (2) local factors which affect the number of larvae that settle, and (3) subsequent schedules of local post-settlement mortality (e.g. Bertness et al. 1992).

Post-recruitment immigration in the fishes studied affected the patterns of density established by larval recruitment in two important ways. Firstly, immigration occurred throughout the year and was not restricted to the summer reproductive season. Secondly, the small scale of movement of post-recruits (tens to hundreds of metres) meant that immigration occurred independently at differ-

ent bommies within the same coral reef (Fig. 2). These characteristics mean that modelling local populations affected by post-recruit immigration will be more difficult than modelling populations mainly affected by the recruitment of larvae, because inputs of post-recruits are frequent but temporally stochastic, as opposed to infrequent and temporally predictable for larvae.

Reef fishes migrate for reproductive purposes (Shibuno et al. 1993; Warner 1995; Aguilar-Perera and Aguilar-Dávila 1996), and there was at least one species (*Chromis viridis*) in this study which displayed such behaviour. Ontogenetic habitat shifts also take place (Itzkowitz 1985; Lirman 1994; Eggleston 1995; McGehee 1995), and there were numerous species in this study which did not settle on the study bommies, but which arrived as juveniles 4–6

weeks after settlement (personal observation). Some larger species had home ranges which incorporated several patch reefs, so that individuals were often seen intermittently on the same bommies. In these cases, interpatch migration occurred as part of regular foraging activities (e.g. Ogden and Buckman 1973; Noda et al. 1994). While there have been no previous studies of post-recruit immigration in diverse reef fish assemblages, there is abundant evidence of movement capabilities. Within-reef movements of post-recruit fishes have been specifically documented in *Epinephelus striatus* (Aguilar-Perera and Aguilar-Dávila 1996) *Amphiprion clarkii* (Hattori 1995), *Chromis chrysurus* (Noda et al. 1994), *Mulloides flavolineatus* (Holland et al. 1993), *Halichoeres marginatus* (Shibuno et al. 1993), *Acanthurus bahainus*, *A. chirugus*, and *A. coeruleus* (Robertson 1988; Sweatman and Robertson 1994), *Stegastes leucostictus* (Itzkowitz 1985), and *Scarus croicensis* (Ogden and Buckman 1973). There were ancillary reports of migration in *Dascyllus marginatus* (Lieberman et al. 1995), *Pomacentrus australis* (Brothers et al. 1983), *Pomacentrus wardi* (Sale 1979), and *Chromis atripectoralis* (Williams et al. 1994), while numerous authors have reported migration in a range of species during the course of assemblage level studies (see Molles 1978; Brock et al. 1979; Ogden and Ebersole 1981, Lassig 1983; Sweatman 1985; Walsh 1985; Doherty and Sale 1985; Baelde 1990; Caley 1993).

The relative number of recruits and post-recruit immigrants varied across the whole spectrum of possible values, from species which only received larval recruits, to those which only received post-recruit immigrants. The distribution of these values was quite even across the species pool, with a mean contribution of post-recruit immigrants of $58\% \pm 6\%$ (Fig. 1A). However, the relative number of immigrants from each source varied considerably from bommie to bommie for a given species. These results highlight the great variety of population dynamics present in reef fishes. Based on the findings of this study, a general model of the population dynamics of reef fishes should incorporate the following features: (1) two scales of spatial separation between habitat patches (i.e. patches within reefs, and patches on separate reefs), with different life history stages (post-recruits and larvae) linking the patches at each scale; (2) populations on patches within reefs influenced by infrequent pulses of larvae from patches on distant reefs, and more frequent inputs of post-recruit immigrants from patches on the same reef; and (3) relative contributions of recruitment and post-recruit immigration that may vary between 0 and 100% for populations on within reef patches, depending on the species.

The ability of fishes to move within reefs after settlement has implications for the spatial scales over which recruitment limitation may operate. A recruitment limited

population is defined as one in which abundance varies as some function of the larval recruitment rate (e.g. Doherty and Fowler 1994). Some populations of reef fishes are recruitment limited at the scale of small coral patches (Doherty 1983), and others at the scale of whole coral reefs (Victor 1986; Doherty and Fowler 1994). In species which rarely move after settlement, it is possible that populations at both spatial scales could be recruitment limited if mortality and competition are not density dependent. However, in mobile species, movement has the potential to decouple the relationship between recruitment and adult population size on patches within reefs (Robertson 1988), so that the potential for recruitment limitation at this scale will be inversely related to the propensity for movement. Larval settlement obviously remains an important process for these species. However, in the absence of density dependent mortality, the size of local populations will be a function of reef wide settlement and local rates of movement, rather than local rates of settlement per se. In this context, it is important to note the distribution of the proportion of post-recruit immigrants (Fig. 1A). Most species studied showed some evidence of post-recruit immigration, and the even distribution of values (Fig. 1A) means that there is no clear distinction between potentially recruitment limited species and those with high immigration rates. Furthermore, even in species with very low overall rates of post-recruit immigration, there were specific sites which received a relatively large proportion of post-recruit immigrants (Table 2). These data suggest that few species will ever be completely recruitment limited at the scale of patches within reefs, and therefore the concept of recruitment limitation is most relevant to populations at the scale of whole coral reefs.

This study has shown that the size of local populations of reef fishes can be influenced by movement within reefs after settlement, and that the magnitude of these movements varies enormously through time, among replicate sites, and among different species. More research in this area is needed to establish the mechanisms of movement (i.e. diurnal or nocturnal), the effects of habitat structure (i.e. patch size and isolation), and the causes (i.e. feeding excursions, spawning aggregations, ontogenetic shifts). This study is further evidence that reef fishes exhibit a diverse range of population dynamics, and that factors operating during the whole life-span, including the larval and post-larval phases, all contribute to this diversity.

Acknowledgements. This work was funded by grants from James Cook University and the Great Barrier Reef Marine Park Authority. I thank Robert C. Lewis for logistic support, the staff of Orpheus Island Research Station, the numerous friends who assisted with field work, and Terry Hughes, Howard Choat, Glen De'ath, Hugh Sweatman, and two anonymous referees, for helpful comments on the manuscript.

Appendix 1

Immigration data for 150 species of reef fishes that arrived at ten bommies over 22 months. Data were calculated using the upper 99.9% C.I. of the distribution of within day sample errors (see Methods), and pooled over all sequential comparisons and bommies. *Percent post-recruit immigrants* expresses the number of post-recruit immigrants as a percentage of the sum of post-recruit immigrants and recruits. *Total post-recruit abundance* is the sum of the abundances for a given species over all sites and times used in the sequential comparisons. *Adjusted post-recruit immigrants* expresses the number of post-recruit immigrants as a percentage of total post-recruit abundance, while *Adjusted recruits* expresses the number of recruits as a percentage of total post-recruit and recruit abundance.

Species	Total post-recruit immigrants	Total recruits	Percent post-recruit immigrants	Total post-recruit Abundance	Adjusted post-recruit immigrants	Adjusted recruits
<i>Aeoliscus strigatus</i>	0	7	0	13	0	35.0
<i>Cephalopholis cyanostigma</i>	12.5	3	80.6	479	2.6	0.6
<i>Cromileptes altivelis</i>	3.5	0	100	7	50.1	0
<i>Epinephelus maculatus</i>	2.6	0	100	6	43.8	0
<i>Epinephelus ongus</i>	0.9	0	100	1	88.0	0
<i>Plectropomus leopardus</i>	17.3	2	89.6	41	42.2	4.7
<i>Diploprion bifasciatus</i>	2.6	0	100	10	26.3	0
<i>Apogon aureus</i>	8.6	2	81	12	71.2	14.3
<i>Apogon cyanosoma-properupta</i>	826.0	1377	37.5	10122	8.2	12.0
<i>Apogon doederleini</i>	431.3	2176	16.5	6141	7.0	26.2
<i>Apogon moluccensis</i>	113.6	1	99.1	557	20.4	0.2
<i>Apogon notatus</i>	181.4	30	85.8	2163	8.4	1.4
<i>Cheliodipterus artus</i>	281.2	14	95.3	2991	9.4	0.5
<i>Cheliodipterus quinquilineatus</i>	55.3	29	65.6	948	5.8	3.0
<i>Rhabdamia gracilis</i>	2215.3	623	78	10896	20.3	5.4
<i>Lutjanus carponotatus</i>	5.0	0	100	24	20.9	0
<i>Lutjanus fulvus</i>	5.5	1	84.6	89	6.2	1.1
<i>Lutjanus quinquilineatus</i>	34.7	15	69.8	127	27.3	10.6
<i>Lutjanus russelli</i>	4.9	0	100	67	7.4	0
<i>Caesio caeruleaurea</i>	295.7	11	96.4	1165	25.4	0.9
<i>Caesio cuning</i>	41.6	15	73.5	390	10.6	3.7
<i>Caesio trilineata</i>	5.3	0	100	22	24.2	0
<i>Ptercaesio marri</i>	329.2	48	87.3	2265	14.5	2.1
<i>Scolopsis bilineatus</i>	12.3	35	26.1	659	1.9	5.0
<i>Mulloides flavolineatus</i>	7.7	0	100	24	32.2	0
<i>Parupeneus barberinoides</i>	0.7	1	42.5	1	74	50.0
<i>Parupeneus barberinus</i>	10.3	0	100	45	23.0	0
<i>Parupeneus ciliatus</i>	2.9	0	100	33	8.7	0
<i>Parupeneus cyclostomus</i>	0.7	0	100	3	24.7	0
<i>Parupeneus heptacanthus</i>	2.9	0	100	5	59.0	0
<i>Parupeneus multifasciatus</i>	9.8	1	90.8	33	29.8	2.9
<i>Parupeneus pleurostigma</i>	2.9	1	74.7	5	59.0	16.7
<i>Chaetodon aureofasciatus</i>	3.9	8	32.7	327	1.2	2.4
<i>Chaetodon auriga</i>	9.1	14	39.3	113	8.0	11.0
<i>Chaetodon baronessa</i>	1.8	2	47.9	55	3.4	3.5
<i>Chaetodon citrinellus</i>	0	1	0	9	0	10.0
<i>Chaetodon flavivostrius</i>	0	1	0	11	0	8.3
<i>Chaetodon kleinii</i>	1.4	2	41.3	12	11.8	14.3
<i>Chaetodon plebius</i>	6.3	10	38.6	153	4.1	6.1
<i>Chaetodon rainfordi</i>	32.3	20	61.7	542	6.0	3.6
<i>Chaetodon speculum</i>	0	3	0	1	0	75.0
<i>Chaetodon trifascialis</i>	0.4	0	100	85	0.5	0
<i>Chaetodon trifasciatus</i>	4.2	1	80.8	26	16.2	3.7
<i>Chaetodon vagabundus</i>	2.3	1	70	32	7.3	3.0
<i>Chelmon rostratus</i>	0.7	1	41.2	4	17.5	20.0
<i>Heniochus acuminatus</i>	0.7	1	41.2	14	5.0	6.7
<i>Pomacanthus sexstriatus</i>	29.1	0	100	136	21.4	0
<i>Abudefduf sexfasciatus</i>	16.7	0	100	390	4.3	0
<i>Abudefduf vaigiensis</i>	0.9	0	100	2	45	0
<i>Abudefduf whitleyi</i>	5.5	0	100	112	4.9	0
<i>Acanthochromis polyacanthus</i> ¹	120.5	7498	1.6	5498	2.2	57.7
<i>Amblyglyphidodon curacoa</i>	27.1	2	93.1	320	8.5	0.6
<i>Amphiprion akindynos</i>	2.1	15	12.2	385	0.5	3.8
<i>Amphiprion melanopus</i>	1.6	11	12.8	134	1.2	7.6
<i>Amphiprion perideraion</i>	0.8	1	44.8	145	0.6	0.7
<i>Chelioprion labiatus</i>	0	1	0	4	0	20.0
<i>Chromis atripectoralis-viridis</i>	185.9	244	43.2	7424	2.5	3.2
<i>Chromis nitida</i>	1.7	0	100	3	58.0	0

Appendix 1 (continued)

Species	Total post-recruit immigrants	Total recruits	Percent post-recruit immigrants	Total post-recruit Abundance	Adjusted post-recruit immigrants	Adjusted recruits
<i>Chromis ternatensis</i>	0.6	2	23.4	9	6.8	18.2
<i>Chromis weberi</i>	1.7	0	100	3	58.0	0
<i>Chrysiptera biocellata</i>	0.9	3	22.7	4	22.0	42.9
<i>Chrysiptera flavipinnis</i>	10.7	10	51.7	209	5.1	4.6
<i>Chrysiptera rollandi</i>	38.3	153	20	1173	3.3	11.5
<i>Chrysiptera rex</i>	22.0	27	44.9	501	4.4	5.1
<i>Chrysiptera talboti</i>	0	2	0	6	0	25.0
<i>Dascyllus aruanus</i>	13.9	4	77.6	452	3.1	0.9
<i>Dascyllus reticulatus</i>	46.5	21	68.9	812	5.7	2.5
<i>Dascyllus trimaculatus</i>	9.0	16	36	405	2.2	3.8
<i>Dischistodus melanotus</i>	6.9	83	7.7	642	1.1	11.4
<i>Dischistodus perspicillatus</i>	68.5	224	23.4	718	9.5	23.8
<i>Dischistodus pseudochrysopoecilus</i>	14.1	145	8.9	1087	1.3	11.8
<i>Dischistodus prosopotaenia</i>	0	6	0	1	0	85.7
<i>Neopomacentrus azysron</i>	256.5	359	41.7	8140	3.2	4.2
<i>Neopomacentrus cyanomos</i>	38.2	16	70.5	855	4.5	1.8
<i>Neoglyphidodon melas</i>	22.4	27	45.3	364	6.2	6.9
<i>Neoglyphidodon nigroris</i>	0	7	0	16	0	30.4
<i>Plectroglyphidodon lacrymatus</i>	1.8	3	37.4	159	1.1	1.9
<i>Pomacentrus adelus</i>	29.5	106	21.8	1920	1.5	5.2
<i>Pomacentrus amboinensis</i>	161.7	829	16.3	8970	1.8	8.5
<i>Pomacentrus bankanensis</i>	15.4	29	34.8	523	3.0	5.3
<i>Pomacentrus brachyalis</i>	22.3	40	35.8	918	2.4	4.2
<i>Pomacentrus chrysurus</i>	73.1	101	42	2876	2.5	3.4
<i>Pomacentrus coelestis</i>	27.7	2006	1.4	6646	0.4	23.2
<i>Pomacentrus grammorhynchus</i>	22.8	70	24.6	533	4.3	11.6
<i>Pomacentrus lepidogenys</i>	79.0	96	45.1	1865	4.2	4.9
<i>Pomacentrus moluccensis</i>	325.9	790	29.2	18337	1.8	4.1
<i>Pomacentrus nagasakiensis</i>	47.4	264	15.2	2770	1.7	8.7
<i>Pomacentrus pavo</i>	65.7	8	89.1	652	10.1	1.2
<i>Pomacentrus philippinus</i>	0	1	0	6	0	14.3
<i>Pomacentrus wardi</i>	71.8	230	23.8	3498	2.0	6.2
<i>Premnas biaculeatus</i>	17.2	7	71.1	293	5.9	2.3
<i>Stegastes apicalis</i>	30.1	3	90.9	942	3.2	0.3
<i>Stegastes nigricans</i>	0.9	0	100	49	1.9	0
<i>Sphyaena flavicauda</i>	46.2	0	100	96	48.1	0
<i>Anampses geographicus</i>	6.3	3	67.8	24	26.4	11.1
<i>Chelinus unifasciatus</i>	3.2	1	76	30	10.5	3.2
<i>Cirrhilabrus punctatus</i>	18.4	116	13.7	903	2.0	11.4
<i>Coris dorsomacula</i>	0.8	0	100	5	15.4	0
<i>Coris gaimard</i>	0	2	0	2	0	50.0
<i>Gomphosus varius</i>	0	1	0	15	0	6.3
<i>Halichoeres chloropterus</i>	18.5	18	50.6	153	12.1	10.5
<i>Halichoeres hortulanus</i>	0	4	0	6	0	40.0
<i>Halichoeres marginatus</i>	0.8	6	11.4	9	8.6	40.0
<i>Halichoeres nebulosus</i>	3.4	1	77.2	16	21.2	5.9
<i>Hemigymnus melapterus</i>	7.3	58	11.1	277	2.6	17.3
<i>Hologymnosus doliatus</i>	0.8	0	100	1	77.0	0
<i>Labrichthys unilineatus</i>	5.4	18	22.9	172	3.1	9.5
<i>Labroides dimidiatus</i>	12.5	24	34.3	567	2.2	4.1
<i>Labropsis australis</i>	0	4	0	6	0	40.0
<i>Macropharyngodon negrosensis</i>	2.3	5	31.6	8	28.9	38.5
<i>Stethojulis bandanensis</i>	9.8	15	39.6	65	15.2	18.8
<i>Stethojulis interrupta</i>	10.6	4	72.5	31	34.1	11.4
<i>Stethojulis strigiventer</i>	20.4	49	29.3	779	2.6	5.9
<i>Thalassoma amblycephalum</i>	0.8	7	10.7	3	28.0	70.0
<i>Thalassoma hardwicke</i>	8.3	7	54.3	122	6.8	5.4
<i>Thalassoma janseni</i>	9.3	12	43.7	163	5.7	6.9
<i>Scarus altipinnis</i>	1.5	3	32.9	32	4.6	8.6
<i>Scarus bleekeri</i>	0.7	0	100	1	74.0	0
<i>Scarus flavipectoralis</i>	2.2	0	100	3	73.7	0
<i>Scarus frenatus</i>	2.2	5	30.7	11	20.1	31.3
<i>Scarus ghobban</i>	4.6	0	100	23	20.1	0
<i>Chlorurus gibbus</i>	3.4	0	100	21	16.0	0

Appendix 1 (continued)

Species	Total post-recruit immigrants	Total recruits	Percent post-recruit immigrants	Total post-recruit Abundance	Adjusted post-recruit immigrants	Adjusted recruits
<i>Scarus niger</i>	0	3	0	1	0	75.0
<i>Scarus psittatus</i>	25.1	5	83.4	112	22.4	4.3
<i>Scarus rivulatus</i>	93.9	106	47	979	9.6	9.8
<i>Scarus schlegeli</i>	3.9	0	100	11	35.3	0
<i>Chlorurus sordidus</i>	29.3	567	4.9	1008	2.9	36.0
<i>Plagiotremis rhinorhynchus</i>	9.1	0	100	29	31.2	0
<i>Plagiotremis tapinosoma</i>	12.7	0	100	54	23.6	0
<i>Acanthurus spp. complex</i>	26.4	19	58.1	373	7.1	4.8
<i>Ctenochaetus spp.</i>	4.9	6	44.8	64	7.6	8.6
<i>Zebrasoma scopas</i>	1.6	0	100	12	13.4	0
<i>Zebrasoma veliferum</i>	1.6	1	61.7	6	26.8	14.3
<i>Naso annulatus</i>	9.6	3	76.3	34	28.4	8.1
<i>Naso unicornis</i>	6.4	0	100	11	58.4	0
<i>Siganus argenteus</i>	3.0	45	6.3	4	75.2	91.8
<i>Siganus corallinus</i>	7.0	0	100	42	16.7	0
<i>Siganus doliatus</i>	7.5	20	27.3	124	6.1	13.9
<i>Siganus puellus</i>	3.5	14	20.1	23	15.3	37.8
<i>Siganus punctatus</i>	5.3	1	84	10	52.6	9.1
<i>Balistoides viridescens</i>	2.2	0	100	6	37.5	0
<i>Rhinacanthus aculeatus</i>	6.8	0	100	47	14.4	0
<i>Oxymonocanthus longirostris</i>	21.1	1	95.5	114	18.5	0.9
<i>Ostracion cubicus</i>	22.3	5	81.7	151	14.8	3.2
<i>Arothron hispidus</i>	1.5	0	100	2	77.0	0
<i>Arothron nigropunctatus</i>	4.6	0	100	8	57.6	0
<i>Arothron stellatus</i>	0.8	0	100	1	77.0	0
<i>Canthigaster bennetti</i>	2.6	0	100	8	32.6	0
<i>Canthigaster valentini</i>	3.1	0	100	7	43.9	0
<i>Diodon hystrix</i>	2.3	0	100	4	57.5	0

¹In *Acanthochromis polyacanthus*, broods of larvae are reared at the natal site and do not have a pelagic dispersal phase, so these figures refer to the total number of larvae observed in all broods over 22 months

References

- Aguilar-Perera A, Aguilar-Dávila W (1996) A spawning aggregation of the nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environ Biol Fish* 45: 351–361
- Baeldé P (1990) Differences in the structures of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, French West Indies, and their ecological significance. *Mar Biol* 105: 163–173
- Bertness MD, Gaines SD, Stephens EG, Yund PO (1992) Components of recruitment in the acorn barnacle *Semibalanus balanoides* (Linnaeus). *J Exp Mar Biol Ecol* 156: 199–215
- Bohnsack JA (1983) Species turnover and the order versus chaos controversy concerning reef fish community structure. *Coral Reefs* 1: 223–228
- Brock RE, Lewis C, Wass RC (1979) Stability and structure of a fish community on a coral patch reef in Hawaii. *Mar Biol* 54: 281–292
- Brothers EB, Williams DMcB, Sale PF (1983) Length of larval life in twelve families of fishes at “One Tree Lagoon”, Great Barrier Reef, Australia. *Mar Biol* 76: 319–324
- Caley MJ (1993) Predation, recruitment and the dynamics of communities of coral reef fishes. *Mar Biol* 117: 33–43
- Doherty PJ (1983) Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology* 64: 176–190
- Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Doherty PJ, Fowler AJ (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* 263: 935–939
- Doherty PJ, Sale PF (1985) Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4: 225–234
- Eggleston DB (1995) Recruitment in Nassau grouper *Epinephelus striatus*: post settlement abundance, microhabitat features, and ontogenetic habitat shifts. *Mar Ecol Prog Ser* 124: 9–22
- Hattori A (1995) Coexistence of two anemonefishes, *Amphiprion clarkii* and *A. perideraion*, which utilize the same host sea anemone. *Environ Biol Fish* 42: 345–353
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Mon* 63(1): 77–101
- Holland KN, Peterson JD, Lowe CG, Wetherbee BM (1993) Movements, distribution, and growth rates of the white goatfish *Mulloidae flavolineatus* in a fisheries conservation zone. *Bull Mar Sci* 52(3): 982–992
- Hughes TP (1990) Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71: 12–20
- Iitzkowitz M (1985) Aspects of the population dynamics and reproductive success in the permanently territorial beaugregory damselfish. *Mar Behav Physiol* 12: 57–69
- Jones GP (1991) Post-settlement processes in the ecology of coral reef fish populations: a multi factorial perspective. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Lassig BR (1983) The effects of a cyclonic storm on coral reef fish assemblages. *Environ Biol Fish* 9(1): 55–63
- Liberman T, Genin A, Loya Y (1995) Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Mar Biol* 121: 741–746
- Lirman D (1994) Ontogenetic shifts in habitat preferences in the three spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *J Exp Mar Biol Ecol* 180: 71–81
- McGehee MA (1995) Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfish in the genus *Stegastes*. *Environ Biol Fish* 44: 393–401

- Molles MC Jr (1978) Fish species diversity on model and natural patch reefs: experimental insular biogeography. *Ecol Mon* 48:289–305
- Noda M, Gushima K, Kakuda S (1994) Local prey search based on spatial memory and expectation in the planktivorous reef fish, *Chromis chrysurus* (Pomacentridae). *Anim Behav* 47:1413–1422
- Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54:589–596
- Ogden JC, Ebersole JP (1981) Scale and community structure of coral reef fishes: a long term study of a large artificial reef. *Mar Ecol Prog Ser* 4:97–103
- Raimondi PT (1990) Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol Mon* 60(3):283–309
- Randall JE, Allen GR, Steene RC (1990) *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Press, Bathurst
- Robertson DR (1988) Abundances of surgeonfishes on patch reefs in Caribbean Panama: Due to settlement or post settlement events? *Mar Biol* 97:495–501
- Robertson DR, Foster SA (1982) Off reef emigration of young adults of the labrid fish *Epibulus insidiator*. *Copeia* 1:227–229
- Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460–1466
- Sale PF (1971) Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae). *Copeia* 1971:324–327
- Sale PF (1979) Recruitment, loss and coexistence in a guild of territorial reef fishes. *Oecologia* 42:159–177
- Shibuno T, Gushima K, Kakuda S (1993) Female spawning migrations of the protogynous wrasse, *Halichoeres marginatus*. *Japan J Ichthyol* 39(4):357–361
- Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66(3):1056–1066
- Sweatman HPA (1985) The influence of adults of some coral reef fishes on larval recruitment. *Ecol Mon* 55(4):469–485
- Sweatman HPA, Robertson DR (1994) Grazing halos and predation on juvenile Caribbean surgeonfishes. *Mar Ecol Prog Ser* 111:1–6
- Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol Mon* 56(2):145–160
- Walsh WJ (1985) Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. *Bull Mar Sci* 36:357–376
- Warner RR (1995) Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. *Environ Biol Fish* 44:337–345
- Williams DMcB (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego
- Williams DMcB, Wolanski E, Andrews, JC (1984) Transport mechanisms and the potential movement of planktonic larvae in the central section of the Great Barrier Reef. *Coral Reefs* 3:229–236
- Williams DMcB, English S, Milicich MJ (1994) Annual recruitment surveys of coral reef fishes are good indicators of patterns of settlement. *Bull Mar Sci* 54(1):314–331
- Zar JH (1984) *Biostatistical analysis*. Prentice Hall, New Jersey