Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs

Andrew R. Lewis[*]

Department of Marine Biology, James Cook University of North Queensland, Douglas QLD 4811, Australia

Abstract

The effects of disturbance to coral on the abundances of fishes were investigated experimentally on the Great Barrier Reef. Fishes on ten large (108–267 m^2) isolated patch reefs or 'bommies' were monitored at 1–2 month intervals for a year. The hard corals on five of these were disturbed by breaking the colonies into small pieces with a mallet. Fishes were counted for the next year. Cover of coral on the damaged bommies decreased from $\approx 66\%$ to $\approx 29\%$ by the end of the study, but increased by 5% at the control bommies. Linear mixed-effects models were used to examine the numbers of 53 species of fishes (from a total pool of 150 species). Significant declines in abundance were detected in five species, all of which associate closely with live coral: an apogonid (*Cheilodipterus artus*), a chaetodontid (*Chaetodon rainfordi*) and three pomacentrids (the species complex *Chromis atripectoralis-viridis*, *Dascyllus reticulatus*, and *Pomacentrus moluccensis*). One herbivorous pomacentrid (*Pomacentrus grammorhynchus*) significantly increased in abundance. Each of the affected species showed a different temporal response to the disturbance, ranging from emigration and local extinction within one month, to changes in recruitment six months later. This study shows that many species of fishes are robust to physical disturbances which substantially reduce cover of coral and modify the fine-scale (1 m) heterogeneity provided by the veneer of live corals on the surface of a reef. The few negatively affected species frequently sheltered in live coral; the one positively affected species was herbivorous. Many coral-associated species and many herbivores were not affected, so it is not yet possible to make precise predictions about which species will be affected by disturbance to coral. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Coral reef fish; Habitat disturbance; Linear mixed-effects model; Migration; Population dynamics; Recruitment

[*]Corresponding author. Tel.: + 61 7 4781 5338; Fax: + 61 7 4725 1570; E-mail: andrew.lewis@jcu.edu.au

1. Introduction

Coral reef fishes live close to the reef surface, and the spatial structure of the substratum or the composition of the coral community can affect the associated fish community (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984; Sale and Douglas, 1984; Hixon and Beets, 1993). This is evident at several spatial scales, from zones hundreds of meters wide within whole reefs (Meekan et al., 1995; Green, 1996; Ormond et al., 1996), to individual coral heads less than a metre in diameter (Williams and Sale, 1981; Jones, 1988). Furthermore, the way that fishes associate with the reef habitat often changes with ontogeny. Many species settle into distinct habitats as larvae (Booth and Beretta, 1994; Tolimieri, 1995; McCormick and Makey, 1997), while post-settlement movements allow habitat choices to be refined throughout the juvenile and adult phases of the life-cycle (McCormick, 1995; Lewis, 1997a).

Coral reefs are subject to frequent disturbances that can affect the physical appearance of the reef surface and modify coral community structure. Crown of thorns starfish (*Acanthaster planci*) outbreaks have affected coral communities over many hundreds of kilometres of the Great Barrier Reef (Moran et al., 1990), while tropical cyclones create high seas that affect reefs over tens to hundreds of kilometres (Done, 1992a,b). Anthropogenic disturbances such as anchor damage, tourism and dredging affect smaller areas within individual reefs at scales of tens to hundreds of meters (Allison, 1996; Clarke et al., 1993).

This raises two important questions with respect to populations and communities of reef fishes. First, how do reef fishes respond to the modification of the reef surface by disturbance? Second, do populations within large disturbed areas respond differently to populations in small disturbed areas? Information about the responses of fishes to disturbance at different spatial scales and in different habitats is needed to answer these questions. Studies of large-scale events are necessary to quantify responses to massive changes in resource availability that cannot be simulated through controlled experiments. However, the sampling designs used in such studies frequently suffer from low statistical power because control locations and pre-disturbance data are unavailable (Robertson, 1991), and changes in populations of corals and fishes become increasingly difficult to measure accurately as the size of the study area increases. Thus, these studies are useful for detecting broad trends, but they cannot provide accurate data on the degree of substratum modification or the responses of fishes.

In contrast, small-scale studies can employ manipulative experiments to separate disturbance responses from natural patterns of temporal and spatial variability, enabling researchers to link changes in population dynamics with known levels of disturbance (Lewis, 1997b). Furthermore, large-scale disturbances often result in a mosaic of small disturbed patches (Done, 1992b; Moran, 1986), so data from small-scale manipulative experiments may have direct relevance to the modelling of the effects of large-scale disturbances.

Most studies of the responses of reef fishes to disturbance of coral have examined relatively large-scale phenomena, such as El Niño warming events (Wellington and Victor, 1985; Guzmán and Robertson, 1989), cyclones (Kaufman, 1983; Lassig, 1983; Walsh, 1983), crown of thorns starfish (Williams, 1986; Hart and Russ, 1996), terrestrial

run-off (Chabanet et al., 1995), and coral mining (Dawson Shepard et al., 1992). These studies suggest that a wide variety of responses are likely, with some species appearing sensitive to coral disturbance (eg. Williams, 1986) and others remaining unaffected (eg. Guzmán and Robertson, 1989). However, the lack of small scale manipulative experiments means there is little quantitative information on interspecific differences in susceptibility to coral disturbance, the time scale of responses, or whether certain species respond more through variations in recruitment, post-settlement relocation, or post-settlement mortality. Manipulative experiments in a range of different reef habitats will be necessary to provide this information, and until such experiments have been conducted, it will be difficult to predict how coral disturbance will affect populations of reef fishes.

In a recent paper, I described results of a small-scale disturbance experiment conducted on lagoonal patch reefs or 'bommies' within a mid-shelf reef of the Great Barrier Reef system (Lewis, 1997b). I found that the composition of the fish communities on these bommies was unaffected by disturbance to the living corals; however, there were significant reductions in total numbers and total species richness, and the abundance and species richness of certain families and ecological categories of fishes. In this paper, I quantify the responses in a pool of 53 species. Those which showed significant changes in abundance are identified, and I illustrate the temporal and spatial variability in their numbers.

2. Methods

2.1. Study locations

The study location is 52 km off the north east coast of Australia at Little Trunk Reef (18° 19′S, 146° 45′E), which forms part of the Great Barrier Reef. Little Trunk Reef is elliptical (≈ 8 km $\times 3$ km) with the major axis orientated north-east to south-west. Ten bommies located in an open sandy zone at the western margin of the reef flat were used in the experiment. These bommies were selected from the hundreds in the lagoon because they were similar in size, physical structure, and degree of isolation. They were all surrounded by at least 20 m of open sand (typically 40–50 m), were at least 100 m from each other (typically 200–500 m), and were in 3 m of water at low tide. It is unlikely that fishes ever moved directly between any two of the experimental bommies, so in this sense, they were independent replicates. Each bommie consisted of a mound of consolidated substratum approximately 3 m high and 5–10 m wide, and before the disturbance live coral colonies covered 29–91% 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 to 267 m^2.

The ten bommies were subdivided into two classes on the basis of fish sampling frequency. Six bommies (labelled A–F) were censused most frequently and are referred to as core bommies, while four bommies (labelled G–J) were censused less frequently and are referred to as non-core bommies. On a given sample occasion, all bommies

scheduled for sampling were censused within a four day period between the hours of 0830 and 1600. The sampling program extended over 25 months (June 1993–July 1995) and encompassed two larval recruitment periods (October–February). During the sampling program, fishes on the core bommies were censused approximately every 30 days between October and February, and every 60 days between March and September. Fishes on the non-core bommies were censused four times in the 12 month pre-disturbance phase of the study, and then at the same frequency as the core bommies in the 13 month post-disturbance phase.

2.2. Fish sampling

All fish censuses were conducted by the author while using SCUBA. Underwater visibility always exceeded 15 m, and the census of an individual bommie took from 55 to 70 min to complete. Species from the following families were counted at each bommie at each census time: Centriscidae, Serranidae, Apogonidae, Lutjanidae, Caesionidae, Nemipteridae, Mullidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Sphyraenidae, Labridae, Scaridae, Blennidae (genus *Plagiotremus* only), Acanthuridae, Siganidae, Balistidae, Monocanthidae, Ostracidae, Tetraodontidae, and Diodontidae. This selection was made to include fishes with favourable attributes for visual sampling (ie. moderate to large size, non-cryptic appearance or behaviour). Species were identified on the basis of visual appearance after comparison of video footage taken during the study with photographic references (Randall et al., 1990). Taxonomic authorities follow Randall et al. (1990) and Allen (1997).

A list of 150 frequently sighted species was printed onto waterproof paper and used to record community composition. A single estimate of abundance was made for each species on the list, and abundance was also estimated for any rare species that were not on the list. For the majority of species that formed aggregations or inhabited distinct zones, I counted the number of fishes in the aggregation or habitat zone respectively. For dispersed species, I censused fish while swimming a zigzag course up the longest axis of the bommie.

Within each census, species were partitioned into recruits and older post-recruit fishes. 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 (see Brothers et al., 1983); 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 Labridae *Cheilinus chlorurus*, *Coris schroderi*, *Halichoeres melanurus*, *H. trimaculatus*, and *Thalassoma lunare* could not be accurately counted, as they were shy and cryptically colored. These species are not analysed here. Two con-generic species of pomacentrids, *Chromis atripectoralis* and *C. viridis*, were similar in appearance and usually schooled together, making it difficult to obtain accurate counts of each species during the visual censuses. Hence, I counted these two species as a single group, and in this paper, this species complex is referred to as *Chromis atripectoralis-viridis*. Similarly, the apogonids *Apogon cyanosoma* and *A. properupta* were counted as a single group, and are referred to as *Apogon cyanosoma-properupta*.

2.3. Coral sampling

The coral communities on each bommie were sampled with visual censuses and video mapping at regular intervals throughout the study (see Lewis, 1997b for further details). Corals were disturbed in July 1994, after 12 months of monitoring. Bommies were selected for disturbance so that control and damaged bommies were evenly distributed down the length of the lagoon to avoid confounding the disturbance treatment with spatial position. At the bommies designated for disturbance (three core and two non-core bommies), a mallet was used to break corals with bushy, arborescent, and tabular morphologies into small pieces, which were left where they fell. Massive, encrusting, and soft corals were not disturbed. This disturbance treatment is comparable to the effects of small scale anthropogenic disturbances such as anchor damage and destructive fishing, and the localised effects of large-scale disturbances such as cyclones and crown of thorns starfish outbreaks.

2.4. Data analyses

More than 150 species of fishes were observed over the 24 month study period (see Lewis, 1997a); however, many of these were seen on only one or two bommies, which prevented valid statistical tests for disturbance effects. Data on the abundance of a given species (ie. number of fish per bommie) were analysed only if that species was found on at least two of the core control bommies and two of the core impact bommies; altogether 53 species were included under this criterion.

Linear Mixed Effects (LME) models were used to test for statistically significant disturbance effects in these 53 species. In the context of repeated measures data arising from disturbance experiments with a BACI sampling design (see Underwood, 1991, 1992), LME models offer a useful alternative to traditional univariate or multivariate repeated-measures ANOVA models (eg. Green, 1993), because they accommodate unbalanced data, data collected at different times, and offer the possibility of modelling covariance structures (see Laird and Ware, 1982; Jennrich and Schluchter, 1986; Lindstrom and Bates, 1990). LME models use restricted maximum likelihood iteration to estimate the parameters of a linear expectation function containing both fixed effects (ie. the disturbance treatment) and random effects (ie. the effect of time on the individual responses from each bommie). Output is in the form of approximate z-ratios or normal deviates, which allows a statistical test of the hypothesis that a given fixed parameter is significantly different from zero. In this case, the basic LME model contained fixed parameters for treatment (control vs impact) effects, temporal effects (before vs after disturbance), and 'treatment*before/after' interaction effects. The z-ratio for the interaction effect is of primary interest, because it can be used to test the hypothesis that the mean temporal profile of the damaged bommies diverged from that of the control bommies after the coral disturbance.

Preliminary analyses revealed that the population dynamics of many species had a component of seasonal variability due to the summer influx of larval recruits, and significant serial correlations between censuses. Consequently, for each species, a stepwise procedure was used to evaluate whether terms for these factors should be

included in the LME model. In the first step, the basic model was compared to a model containing the same terms plus a term for seasonal adjustment (incorporated as a sine/cosine function with a period of one year). The log-likelihood ratio statistic was used to test whether there was a significant difference (at $\alpha = 0.05$) in the fit of the two models; if there was, the seasonally adjusted model was retained. In the second step, the seasonally adjusted model without correction for serial correlation (ie. the model was specified with a uniform within-bommie covariance structure) was compared to a seasonally adjusted model with serial correlation incorporated as a first-order auto-regressive (AR1) covariance structure. The log-likelihood ratio statistic was again used to test whether there was a significant difference in the fit of the two models; if there was, the model with the AR1 covariance structure was retained. This provides a more conservative estimate of the 'treatment*before/after' fixed effect, as the z-ratios are automatically corrected for the serial correlations in the data. The results section indicates whether the LME models for particular species were adjusted for seasonality, serial correlations, or both. Data analyses were performed using S-Plus for Windows software. The LME functions were written by J.C. Pinheiro at Bell Laboratories, Murray Hill, NJ, USA, and D.M. Bates at the University of Wisconsin-Madison, USA, and can be obtained from these authors.

3. Results

3.1. Coral disturbance

All bommies had moderate to high coral cover (29–91%) before the disturbance, and corals with compact arborescent, open arborescent, and tabular morphologies were the most common. The disturbance substantially altered the fine-scale (1 m) spatial heterogeneity of the damaged bommies, and initially produced large amounts of living coral rubble. Percentage coral cover at the damaged bommies had fallen on average by 34% at the end of the study, while coral cover increased by about 5% in the same period at the control bommies (see Lewis, 1997b for further details). Coral fragment mortality was offset by regrowth of the surviving colonies and fragments, so total cover of living coral remained stable on the damaged bommies in the post-disturbance period. Fragment recovery was rapid, with pieces from the same colony fusing after 1 month and establishing new margins of active growth after 2 months. Surviving colonies had re-established their specific morphologies after 6 months, so the coral communities at the damaged bommies consisted of numerous small colonies and very little live rubble in the last 6 months of the sampling program. Regrowth of up to 200 mm had occurred in some tabular and open arborescent *Acropora* sp. by the end of the study.

3.2. Affected species of fishes

The 53 species of fishes which were analysed in this study are listed in Table 1. This group contains representatives from 30 genera, 11 families, and each of the eight major ecological categories previously identified for this habitat (Lewis, 1997b). The coral

Table 1
Species of fishes tested for responses to the coral disturbance treatment

Species	Species
Cephalopholis cyanostigma	*Neopomacentrus cyanomos*
Apogon cyanosoma-properupta	*Neoglyphidodon melas*
Apogon doederleini	*Pomacentrus adelus*
Cheilodipterus artus*	*Pomacentrus amboinensis*
Cheilodipterus quinquilineatus	*Pomacentrus bankanensis*
Caesio caerulaurea	*Pomacentrus brachialis*
Caesio cuning	*Pomacentrus chrysurus*
Pterocaesio marri	*Pomacentrus coelestis*
Scolopsis bilineatus	*Pomacentrus grammorhynchus**
Chaetodon aureofasciatus	*Pomacentrus lepidogenys*
Chaetodon auriga	*Pomacentrus moluccensis**
Chaetodon plebius	*Pomacentrus nagasakiensis*
Chaetodon rainfordi*	*Pomacentrus pavo*
Chaetodon trifascialis	*Pomacentrus wardi*
Pomacanthus sexstriatus	*Stegastes apicalis*
Acanthochromis polyacanthus	*Cirrhilabrus punctatus*
Amblyglyphidodon curacao	*Halichoeres chloropterus*
Amphiprion akindynos	*Hemigymnus melapterus*
Chromis atripectoralis-viridis*	*Labrichthys unilineatus*
Chrysiptera rollandi	*Labroides dimidiatus*
Chrysiptera rex	*Stethojulis strigiventer*
Dascyllus aruanus	*Thalassoma hardwicke*
Dascyllus reticulatus*	*Chlorurus sordidus*
Dischistodus melanotus	*Scarus rivulatus*
Dischistodus perspicillatus	*Siganus doliatus*
Dischistodus pseudochrysopoecilus	*Ostracion cubicus*
Neopomacentrus azysron	

Linear mixed-effects models were fitted separately to the data for each species. Those species which showed significant 'treatment*before/after' interactions (at $\alpha = 0.05$) are marked (*).

disturbance was associated with significant changes in numbers of six of the 53 species (Table 2); one apogonid (*Cheilodipterus artus*), one chaetodontid (*Chaetodon rainfordi*) and four pomacentrids (*Chromis atripectoralis-viridis*, *Dascyllus reticulatus*, *Pomacentrus grammorhynchus*, and *P. moluccensis*). One of these species (*P. grammorhynchus*) showed an increase in abundance on the damaged bommies, whereas the other five species all declined. The remainder of the results section describes the specific responses of the six affected species.

The numbers of *Cheilodipterus artus* consistently increased on control bommies during the study (Fig. 1a). These increases were due to immigration; there was virtually no larval recruitment to the bommies (Table 3). In both years, most immigration occurred at the end of the summer (October–February), with annual population maxima between April and June.

On four of the five damaged bommies, numbers of *C. artus* were zero by the August 1994 census, one month after disturbance (Fig. 1B). Small groups of fishes (< 10 individuals) were seen intermittently on the damaged bommies during the following five months. On three of the five damaged bommies, immigration in the February–April

Table 2
Model parameters for the six species of fishes which showed significant changes in abundance after the coral disturbance treatment

Species	z-ratio	P-value
Cheilodipterus artus	$-3.47^{\dagger,\#}$	<0.001
Chaetodon rainfordi	$-1.78^{\dagger,\#}$	0.038
Chromis atripectoralis-viridis	-3.40	<0.001
Dascyllus reticulatus	$-4.00^{\#}$	<0.001
Pomacentrus grammorhynchus	$+2.24^{\dagger,\#}$	0.012
Pomacentrus moluccensis	$-3.03^{\dagger,\#}$	0.001

Disturbance effects were estimated by z-ratios for the 'treatment*before/after' interaction term in a Linear Mixed Effects model.
Models that included terms for seasonal variability and serial correlation are marked (†) and ($^{\#}$) respectively.

1995 period (after summer) caused a substantial recovery in numbers, whereas populations on the other two damaged bommies remained small or zero to the end of the study.

Populations of *Chaetodon rainfordi* were relatively small (<5 individuals) and invariant on the control bommies E and H through the whole study. On the other three control bommies, populations were slightly larger and there were consistent temporal changes which were repeated in both years. Populations were at their minima during December. Recruitment occurred during January and February of both years, but recruitment was less in the second summer, with only two of the five control bommies receiving recruits (Table 3). Immigration was also important to this species, with immigrants arriving in the period of February to July in both years, resulting in maximal numbers during winter (Fig. 2A).

There was little difference in numbers between the control and damaged bommies for several months after the coral was disturbed, but divergence did occur over the following summer (Fig. 2A). This was due to a combination of failure of recruitment during January and February (Table 3) and minimal immigration during the following autumn and winter (Fig. 2B). Populations on two of the damaged bommies (B and G) became locally extinct after the disturbance; there were three or fewer fish on the others. Two fish immigrated to bommie (D) in the last four months of the study.

There were large differences in the abundance of *Chromis atripectoralis-viridis* among the control bommies, however numbers on each bommie were consistent through the study, with populations at their maxima during the January to April period of both years (Fig. 3A). Immigration was important in these fishes, as recruitment in the first summer was insufficient to explain population increases on most bommies (Table 3).

Numbers of this species complex varied on the damaged bommies after the coral was disturbed. On three bommies (B, D, and F) numbers slowly declined through the end of the study (Fig. 3B), while on bommie I, numbers fell from approximately 40 to 4 within one month. On bommie G, numbers fell from 30 to 12 within one month, and remained at around this level until July 1995, when only a single fish remained. Two of the five control bommies received considerable recruitment in the second summer, however none
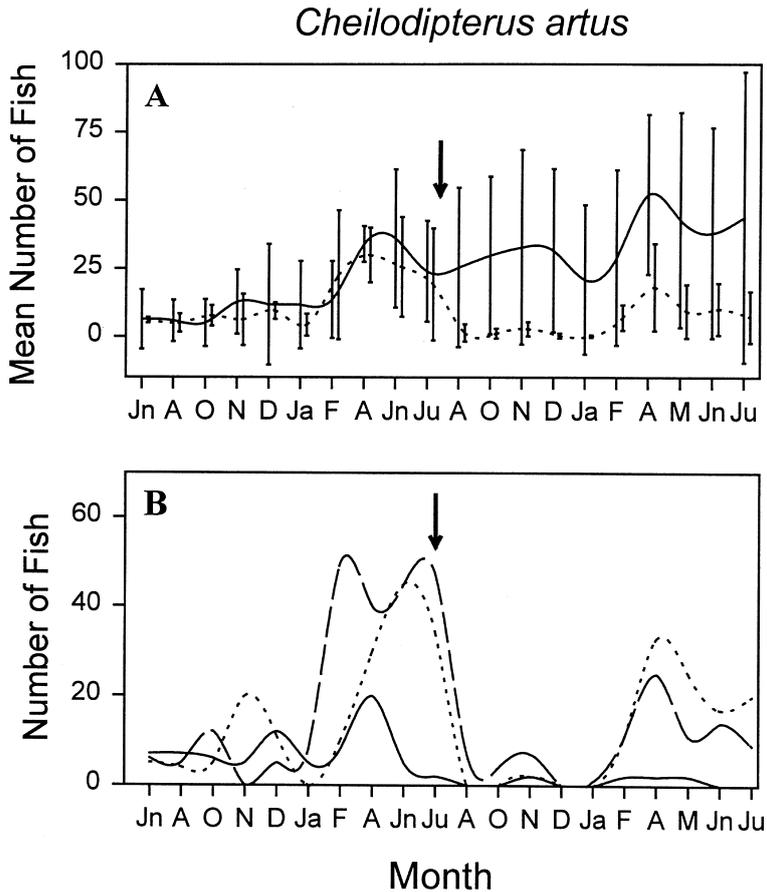
Cheilodipterus artus

Fig. 1. (A) Mean number (± S.D.) of *Cheilodipterus artus* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *C. artus* on the three core damaged bommies, referred to in the text as bommies B (solid line), D (long dashed line), and F (short dashed line).

of the damaged bommies received recruits in the second summer except bommie D, where two recruits were recorded (Table 3).

There was no recruitment of *Dascyllus reticulatus* on the control bommies in the first summer, however they all received some recruitment in the second summer which increased the size of these populations (Table 3, Fig. 4A). *Dascyllus reticulatus* had not been present on two control bommies prior to the second summer, however the recruitment event resulted in one to two fishes persisting on these bommies through the end of the study.

Populations of *D. reticulatus* were found on three damaged bommies. On bommies B and F, numbers fluctuated in the pre-disturbance period, and there were several instances

Table 3
Total larval recruitment of each of the six affected species of fishes to each core bommie in the pre-disturbance (June 1993–June 1994) and post-disturbance (July 1994–July 1995) phases of the study

Species	Recruitment season	Control Bommies			Damaged Bommies		
		A	C	E	B	D	F
Cheilodipterus artus	'93–'94	0	0	10	0	0	0
Cheilodipterus artus	'94–'95	0	0	4	0	0	0
Chaetodon rainfordi	'93–'94	2	8	2	3	2	0
Chaetodon rainfordi	'94–'95	2	1	0	0	0	0
Chromis atripectoralis-viridis	'93–'94	0	16	5	5	38	0
Chromis atripectoralis-viridis	'94–'95	2	82	128	0	2	0
Dascyllus reticulatus	'93–'94	0	0	0	0	0	0
Dascyllus reticulatus	'94–'95	5	3	9	3	0	0
Pomacentrus grammorhynchus	'93–'94	2	0	5	0	8	5
Pomacentrus grammorhynchus	'94–'95	4	5	10	2	12	10
Pomacentrus moluccensis	'93–'94	45	47	60	30	50	42
Pomacentrus moluccensis	'94–'95	51	66	128	15	31	35

of immigration (Fig. 4B). Numbers fell sharply on these two bommies in the month following the disturbance. *D. reticulatus* was extinct on bommies F and I three and five months respectively after the disturbance. In contrast, the population on bommie B slowly declined and there were still seven fish present at the end of the study.

Populations of *Pomacentrus grammorhynchus* on the control bommies generally showed minima in November, recruitment between November and February, and maxima from February to April (Fig. 5A). Despite the fact that recruitment was greater on all bommies in the second summer (Table 3), three control bommies (A, C, and H) had smaller populations at the end of the study than in the first year. Bommies E and J received the greatest recruitment in the second summer, and populations on these two bommies slightly increased in size.

Numbers of *P. grammorhynchus* on the damaged bommies were similar to the controls in the first year of the study (Fig. 5A). There was some immigration onto several bommies during the winter of 1994, however this was not related to coral disturbance because fish arrived on bommies F and G before the disturbance (Fig. 5B), and two fishes also arrived on bommie J during this time. Numbers on the damaged bommies showed greatest divergence from the controls after the second recruitment season, with populations on four of the five damaged bommies at their maxima during this time. Similar numbers of recruits arrived at the control and damaged bommies in the second summer (Table 3), therefore the divergence was due to lower recruit mortality on the damaged bommies in the post-summer period.

Numbers of *Pomacentrus moluccensis* on the control bommies had similar patterns of temporal change that were repeated in both years of the study. Populations were at their minima in November, recruitment occurred in December and January, and immigration of post-recruits occurred in the autumn and early winter, so populations were at their maxima around July or August. Numbers then decreased from September through to November (Fig. 6A). The November minima in 1994 were not as small as those in 1993, and recruitment was greater in the second summer (Table 3); as a result, numbers were highest in the last winter of the study.
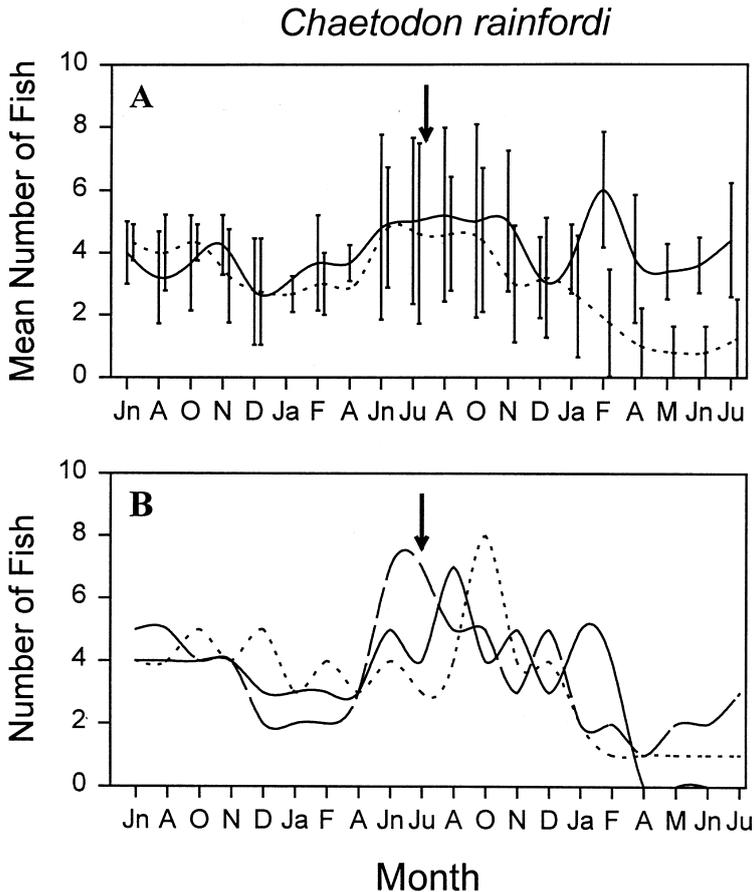
Fig. 2. (A) Mean number (± S.D.) of *Chaetodon rainfordi* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *C. rainfordi* on the three core damaged bommies, referred to in the text as bommies B (solid line), D (long dashed line), and F (short dashed line).

Numbers on the damaged bommies showed little divergence from the controls until the summer following the disturbance. Recruitment to the three core damaged bommies was lower in the second summer than the first, whereas the control bommies showed higher recruitment in the second summer (Table 3). There also appeared to be greater recruit mortality, as four of the five damaged bommies had smaller populations in April–May 1995 than they had in November 1994, prior to the second recruitment season (Fig. 6B).

4. Discussion

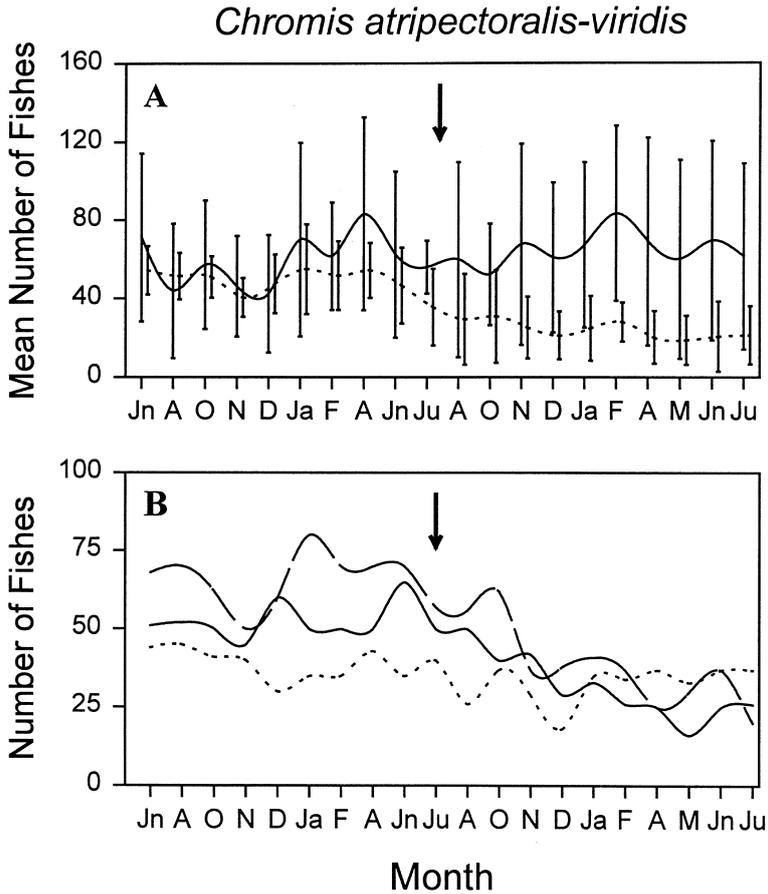Disturbance to live corals affected certain aspects of fish community structure on

Fig. 3. (A) Mean number (± S.D.) of *Chromis atripectoralis-viridis* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *C. atripectoralis-viridis* on the three core damaged bommies, referred to in the text as bommies B (solid line), D (long dashed line), and F (short dashed line).

these bommies, including the total abundance of fishes, total species richness, and the abundance of some families and ecological groups. However, these effects were relatively small in comparison to the between-bommie differences in community structure, which were maintained throughout the study and were unaffected by disturbance to the coral (Lewis, 1997b). The data presented in this paper expand these results. The temporally consistent patterns of community structure indicate that the populations of very few species were affected by disturbance to the coral, and I have shown here that only 6 from 53 species showed changes in abundance that could be attributed to the disturbance. Three of these six species (*Cheilodipterus artus*, *Chromis atripectoralis-viridis* and *Pomacentrus moluccensis*) were amongst the most abundant
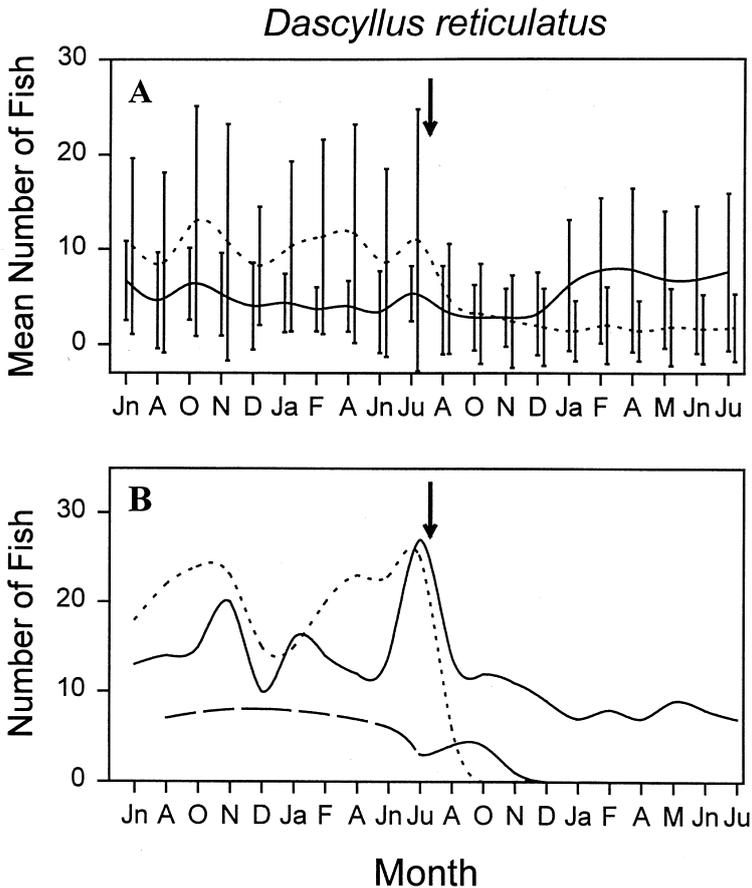
Fig. 4. (A) Mean number (± S.D.) of *Dascyllus reticulatus* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *D. reticulatus* on two core damaged bommies, referred to in the text as bommies B (solid line) and F (short dashed line), and on the non-core damaged bommie I (long dashed line).

fishes in the study (Lewis, 1997a). Hence, the declines shown by these species caused a significant reduction in the total number of fishes on the disturbed bommies, without greatly affecting community structure.

Two important caveats must be attached to these conclusions. First, the number of affected species is a function of the statistical power of the experiment. If I had sampled more bommies, I would have found significant responses in more than six species. This is because more rare species would have met the criteria for analysis (ie. populations on two control and two damaged bommies), and because the increased power would enable the detection of smaller responses. Second, some species may have shown significant declines in abundance after the termination of sampling, due to the cumulative effects of depressed recruitment, low immigration, or higher mortality over several years. These
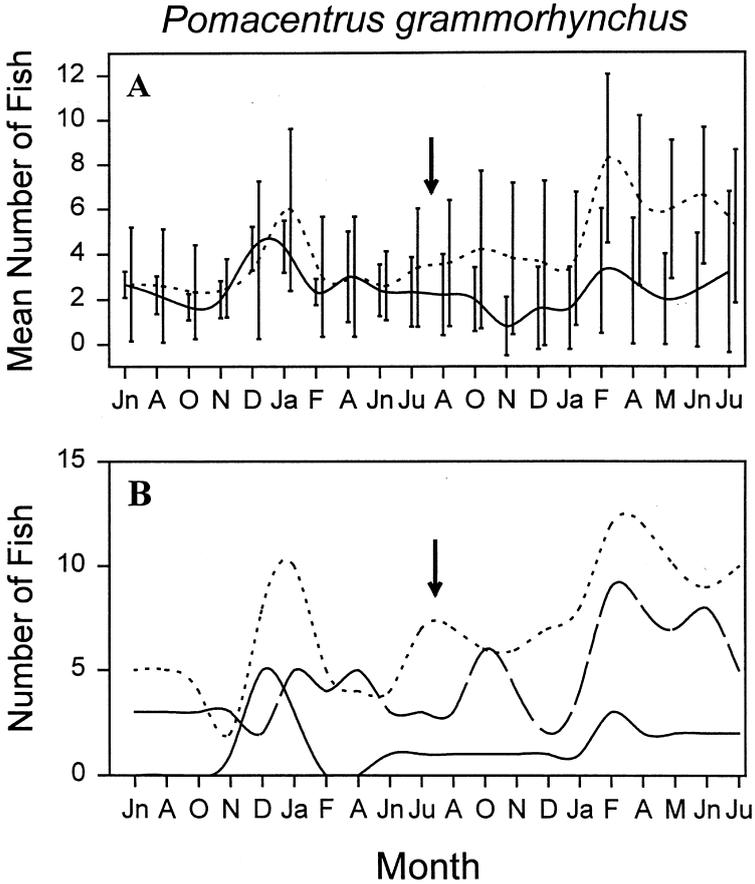
Fig. 5. (A) Mean number (± S.D.) of *Pomacentrus grammorhynchus* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *P. grammorhynchus* on the three core damaged bommies, referred to in the text as bommies B (solid line), D (long dashed line), and F (short dashed line).

factors are unlikely to alter the basic finding that the majority of species are robust to disturbance to corals, however they do indicate that the six affected taxa should be considered a minimum subset of a larger pool of potentially sensitive species.

Reef fishes are influenced by live corals in three important ways. First, the larvae of some species settle specifically in the vicinity of live coral colonies (eg. Sweatman, 1985). Second, the adults of many species use corals as refuges (eg. Munday et al., 1997), and third, some species feed on live coral polyps or other prey species associated with live corals (eg. Guzmán and Robertson, 1989). Accordingly, coral disturbance may affect the abundance of reef fishes by modifying larval settlement, lowering the number or quality of refuge sites, or reducing the food resources of certain species. Previous studies have shown that corallivorous species are highly susceptible to changes in coral
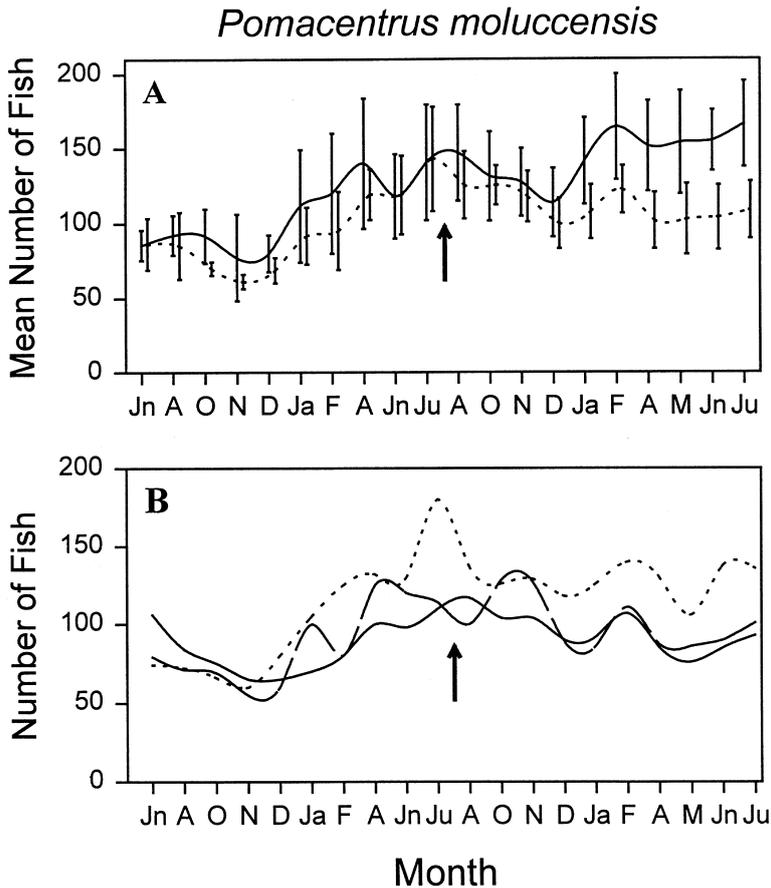
Pomacentrus moluccensis

Fig. 6. (A) Mean number (± S.D.) of *Pomacentrus moluccensis* at the five control (solid line) and five damaged (dashed line) bommies. The x-axis refers to the month in which a given census was taken; the sampling program began in June 1993 and extended to July 1995, and the arrow marks the time of the coral disturbance. (B) Number of *P. moluccensis* on the three core damaged bommies, referred to in the text as bommies B (solid line), D (long dashed line), and F (short dashed line).

cover (Sano et al., 1984; Williams, 1986), however in this experiment, the loss of habitat structure provided by the live coral appeared more important than the reduction in the coral food resource. All five negatively affected species settled directly into live corals as larvae and were found in close association with living coral throughout the adult life. However, there was only one corallivore (*Chaetodon rainfordi*; see Anderson et al., 1981) amongst these five species; the other four are primarily water column feeders (Lewis, 1997b). Furthermore, several other corallivores showed no change in abundance (eg. *Chaetodon plebius*, *C. trifascialis*, and *Labrichthys unilineatus*; Table 1). This result reflects the particular nature of the disturbance treatment applied in this study, which caused a substantial change to the physical structure provided by the coral, but did not eliminate the coral food resource because of high fragment survival. Considered together

with the findings of Sano et al. (1984) and Williams (1986), these results show that the loss of habitat structure and the reduction in food resources associated with coral disturbance may both affect the abundance of reef fishes.

The only species to show a significant increase in population size after the disturbance was the herbivorous damselfish *Pomacentrus grammorhynchus*. It has been suggested that herbivorous fishes may respond positively to disturbance on reefs, because reductions in coral cover often lead to an increase in algal biomass (Hart and Klumpp, 1996). However, studies of large scale natural disturbances have produced a range of results; some workers found increases in herbivore abundance (Carpenter, 1990; Robertson, 1991), others found increases in growth rates but no increases in numeric abundance (Hart and Russ, 1996), while others found no numeric response at all (Wellington and Victor, 1985; Williams, 1986). In this study, the proximate reason for the positive response in *P. grammorhynchus* was increased recruit survivorship, however the ultimate reasons are harder to determine. Field observations and analyses of benthic video data showed that there was little change in the algal communities on the disturbed bommies, so it is unlikely that the higher recruit survivorship is related to increased algal biomass. *P. grammorhynchus* shares its microhabitat with two herbivorous congeners (*Pomacentrus adelus* and *Pomacentrus wardi*), and these species showed no significant change in abundance (Table 1). In previous studies of herbivorous damselfishes, small differences in microhabitat quality have been found to have a large effect on species distributions and competitive abilities (Ebersole, 1985; Lirman, 1994), so the coral disturbance may have altered the microhabitat characteristics in favour of the *P. grammorhynchus* recruits, allowing them to successfully compete for and defend territories against the established adult congeners.

On the basis of this and other studies of the effects of coral disturbance on reef fishes, three important points can be made. First, many species of fishes are robust to disturbances which affect the veneer of live corals on the reef surface (eg. Walsh, 1983; Williams, 1986; Lewis, 1997b). Second, the few species which are negatively affected are likely to be corallivores, or species that frequently associate with live coral, and the positively affected species are likely to be herbivorous (eg. Sano et al., 1984; Williams, 1986; Robertson, 1991; Hart and Russ, 1996). Third, it is difficult to forecast which species will respond, because some coral associates and some herbivores are likely to remain unaffected by disturbance (eg. Wellington and Victor, 1985; Guzmán and Robertson, 1989). Obviously, there must be subtle differences in the way that reef fishes perceive the quality of their habitat in terms of the distribution and abundance of coral colonies, and dietary categories such as 'corallivore' and 'herbivore' appear too broad to be of any value in predicting the identity of affected species. Further research on the habitat preferences and mechanisms of niche differentiation in reef fishes will be necessary before it is possible to make precise predictions about which species will be affected by disturbance to corals.

While it is useful to know which species change in abundance after disturbance, it is also important to obtain information on the time-scales of these responses. These data can indicate which demographic processes are causing the changes, and they can be used to design effective sampling programs for impact assessment or monitoring. For example, the delayed responses in *Chaetodon rainfordi*, *Pomacentrus grammorhynchus*,

and *Pomacentrus moluccensis* (Figs. 2, 5 and 6) indicate that sampling should continue for at least 12 months after a disturbance event which affects live coral. This study has shown that there is considerable variation in the time scale and magnitude of responses to disturbance, and the relative effects of recruitment and movement on population size. Furthermore, this variability was evident both between species, and between replicate bommies within each species.

Recruitment modification probably arose through lower larval settlement and increased post-settlement mortality due to fewer refugia from predation. Reef fish larvae are known to settle preferentially into certain habitats (Williams, 1991), and some may 'test' the quality of the substratum during the transition phase between the pelagic and benthic environments, and return to the water column if conditions are unsuitable (Kaufman et al., 1992). *Chaetodon rainfordi*, *Chromis atripectoralis-viridis* and *Pomacentrus moluccensis* settle directly into live branching corals (pers. obs.), so some of the larvae of these species may have perceived the altered conditions on the disturbed bommies during the transition phase. Refuge availability also affects the mortality of newly settled reef fishes (Caley and St. John, 1996), and the disturbed bommies had fewer suitable refugia for these species because much of the coral was lying flat on the substratum rather than extending into the water column.

The disturbed bommies also attracted fewer immigrants relative to the controls, especially for *Cheilodipterus artus*, *Chaetodon rainfordi* and *Pomacentrus moluccensis*. This is an important finding for several reasons. Before the disturbance, immigration increased the numbers of all five negatively affected species. Furthermore, most immigration occurred in autumn and winter, so movement was facilitating the redistribution of fishes that had arrived as larvae in the preceding summer recruitment season. In this way, patterns of movement may determine how the annual larval influx affects local abundance over large areas of the reef. Therefore, any modification of immigration could affect the overall impact of habitat disturbance on the population size of fishes, and this may not become apparent for many months after the disturbance event. Clearly, the timing of the habitat disturbance relative to the peaks in immigration is relevant. In this experiment, the coral community had achieved 8 months of regrowth before the autumn immigration period, so the affects on immigration may have been less than if disturbance had occurred immediately prior to autumn.

Can the results of this small scale study be used as a model for the effects of larger disturbances that result in a mosaic of simultaneously disturbed small patches? Some of the results from this study and Lewis (1997b) are in common with other studies of large-scale disturbance, so it appears that some general responses may be scale independent, for example, a tendency for little change in the majority of species, declines in abundance of some coral associated species, and increases in the abundance of some herbivores. However, movement was integral to the responses of the six affected species, so populations of fishes on individual bommies were part of a larger 'patchy-population' (sensu Harrison and Taylor, 1997). In such a system, local population size could be influenced by factors which affect movement rates or population densities on neighbouring bommies. If disturbance was widespread, then patterns of movement could also be affected over large areas, resulting in very different disturbance effects at the scale of an individual bommie to those observed here. Until

additional manipulative experiments have been conducted, the results from this study should be considered relevant to coral disturbances of a similar nature and spatial scale, but should be applied with caution to other reef habitats and large scale disturbance events.

Acknowledgements

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