

Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment

Shaun K. Wilson^{1,2*}, Scott C. Burgess^{2,3}, Alistair J. Cheal², Mike Emslie², Rebecca Fisher⁴, Ian Miller², Nicholas V. C. Polunin¹ and Hugh P. A. Sweatman²

¹School of Marine Science & Technology, University of Newcastle, Newcastle-upon-Tyne, NE1 7RU, UK, ²Australian Institute of Marine Science, TMC, Townsville, Queensland 4810, Australia, ³School of Integrative Biology, University of Queensland, Brisbane Queensland 4072, Australia, ⁴School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4810, Australia

Summary

1. The impact of environmental disturbance and habitat loss on associated species is expected to be dependent on a species' level of specialization. We examined habitat use and specialization of coral reef fish from the diverse and ecologically important family Pomacentridae, and determined which species are susceptible to declines in coral cover due to disturbance induced by crown-of-thorns seastar (COTS, *Acanthaster planci* L.).

2. A high proportion of pomacentrid species live in association with live coral as adults (40%) or juveniles (53%). Adults of many species had strong affiliations with branching corals, while juveniles favoured plating growth forms, reflecting the sizes of refuge provided by coral types.

3. Juveniles of species that associated with coral had narrower niche breadths than adult conspecifics, due to associations with specific coral types. The especially high coral association and narrower niche breadth of juveniles suggest that the presence of live coral is crucial for many species during early life history, and that disturbance-induced coral loss may have serious flow-on effects on adult abundance.

4. Microhabitat availability was a poor predictor of fish species abundance. Significant correlations between coverage of coral types and abundance of five adults and two juvenile species were detected; however, these relationships explained <35% and <10% of the variation in abundance of adult and juvenile species, respectively.

5. Niche breadth explained 74% of the variation in species' mean response to coral decline and it is clear that disturbance has a greater impact on resource specialists, suggesting that increasing frequency and intensity of coral loss will cause reef fish communities to become dominated by habitat generalists at the expense of coral-dwelling specialists.

Key-words: coral reefs, damselfish, disturbance, resource dependency

Introduction

Environmental disturbances are an integral component of ecology that influence the dynamics and structure of both terrestrial and aquatic communities (Sousa 1984). In marine systems, disturbances often result in the loss of habitat-forming structures such as kelp (Dayton 1985; Steneck *et al.* 2002), seagrass (Duarte 2002), mangroves (Alongi 2002) and coral (Bruno & Selig 2007), which has an indirect effect on associated faunal communities. Understanding the impacts of disturbance-induced habitat changes on the distribution and abundance of species requires a comprehensive knowledge

of species' dependence on local habitat features. In general, those species that are habitat specialists are more likely to be governed by habitat availability than generalists that utilize a range of habitat types (Brown 1984). Dramatic changes in the availability of habitat should therefore have greater impact on the abundance of habitat specialists (Vazquez & Simberloff 2002), as observed in communities of birds (Julliard, Jiguet & Couvet 2004), mammals and amphibians (Swihart *et al.* 2003), butterflies (Cleary & Genner 2004) and coral reef fishes (Munday 2004). Consequently, habitat specialists are more susceptible to extinction (McKinney 1997), and increasing levels of habitat loss and fragmentation raise concerns about the future of many of these species (Tilman *et al.* 1994; Travis 2003).

*Correspondence author. E-mail: shaun.wilson@ncl.ac.uk

For mobile animals, habitat preferences can also change with ontogeny, and thus the degree of habitat specialization may differ among life stages. While the adults of some species may be habitat generalists, juveniles of the same species may have quite specific habitat requirements, potentially creating a bottleneck for these populations (Halpern, Gaines & Warner 2005). However, the influence of juvenile specialization on adult stocks may vary depending on the relative availability of adult and juvenile habitats and on species longevity (Halpern, Gaines & Warner 2005). For example, specific habitat requirements of adults rather than juveniles regulate populations of stone crabs when adult sites are limited (Beck 1995). Thus specialization at different life-history stages can influence population size, and habitat preferences should be examined at a variety of life stages to assess the influence of specialization on species demographics.

Coral reefs provide a unique opportunity to explore habitat associations of fauna, as they are systems of extremely high biodiversity where species exhibit an array of habitat relationships. Reefs are also subject to high levels of both anthropogenic and natural disturbances, which can result in dramatic shifts in habitat type (Hughes 1994; Pandolfi *et al.* 2005). Of particular concern are predictions that climate change will increase the frequency of disturbances such as coral bleaching and storms (Hoegh-Guldberg 1999; Goldenberg *et al.* 2001; Webster *et al.* 2005) and that eutrophication (Birkeland 1982) and fishing (Dulvy, Freckleton & Polunin 2004) may encourage outbreaks of coral feeding seastar, *Acanthaster planci* L., also known as crown-of-thorns seastar (COTS). Major changes in reef habitats have already been documented, the most pronounced being loss of coral cover (Gardner *et al.* 2003; Bruno & Selig 2007), which affects reef-associated fish and invertebrate communities (Wilson *et al.* 2006; Pratchett *et al.*, in press), and can lead to changes in community structure (Bellwood *et al.* 2006). The species most susceptible to coral loss are those that depend on live coral for food and shelter (Williams 1986; Halford *et al.* 2004). Previous studies have focused on specialization within one life-history stage of coral feeding butterflyfish or obligate coral-dwelling gobies (Munday 2004; Pratchett 2005). However, many fish undertake ontogenetic shifts in habitat use (Lecchini & Galzin 2005) and the extent of specialization may vary among life-history phases.

Here we examined habitat specialization and the effects of disturbance on one of the most abundant and ecologically diverse families of coral reef fishes, the pomacentrids, commonly known as the damselfish. Fish from this family display a wide array of habitat associations and diets (Allen 1991), and territorial behaviour by many species has a major influence on the structure of benthic reef communities (Ceccarelli, Jones & McCook 2001). This influence can extend over large spatial and temporal scales, as territories often cover extensive areas of reef (Ceccarelli, Jones & McCook 2005) and individuals may live for more than 20 years (Meekan, Ackerman & Wellington 2001). Most pomacentrids are also small-bodied and highly abundant, making them major prey for many reef predators (Hiatt & Strasburg 1960). Thus

pomacentrids are an ecologically diverse and important family on coral reefs, and disturbance-induced changes to pomacentrid communities may subsequently affect the composition of benthic communities and reef trophodynamics.

We used a unique, long-term data set to test the hypothesis that habitat specialists are more susceptible to disturbance than generalists. Specialization was quantified based on the strength of pomacentrid associations with live coral and niche breadth of both adult and juveniles. The relationship between fish abundance and habitat availability was then assessed to gauge the dependence of the abundance of specialist species on specific microhabitat types. Finally, breadth of habitat use was used to examine the relationship between habitat specialization and the effects of COTS-instigated habitat degradation on fish populations. Disturbances caused by COTS have resulted in extensive loss of live coral on reefs throughout the Indo-Pacific, and are known to have a detrimental impact on elements of pomacentrid communities (Williams 1986; Sano, Shimizu & Nose 1987; Feary *et al.* 2007a). This study provides a comprehensive evaluation of reliance on coral within an ecologically important family of reef fish, and examines the implications of disturbance for persistence of reef fish.

Methods

Underwater visual surveys were used to assess microhabitat use of pomacentrids at 10 mid-shelf reefs within the northern section of the Great Barrier Reef (GBR) during December 2005 (Fig. 1). Within each reef a standard reef slope habitat was surveyed on the north-eastern flank, and within this habitat three sites were sampled, each containing five permanent 50-m transects lying approximately parallel to the reef crest. Transects were set along the slope at depths ranging between 6 and 9 m. All pomacentrids within transects were identified to species level, and habitat use for each fish was assessed by recording microhabitats directly beneath each fish. Microhabitats were categorized as: branching, plate, submassive, massive, encrusting, soft or dead coral, rubble or consolidated pavement. Microhabitat use by fish >1 m above the substratum was not recorded as it could not be assigned reliably for these individuals. The presence of these fish was noted and used to provide total counts of each species within transects, which were subsequently used to assess the relationship between abundance and microhabitat availability, although they were not included in selectivity calculations. These fish accounted for 30% of all pomacentrids observed.

Fish were identified as juveniles or adults based on body size and coloration. The number of individuals within fish groups sharing the same microhabitat was also recorded, as many pomacentrid species form large schools, and habitat use by juveniles can be influenced by the presence of conspecifics (Sweatman 1985; Booth 1992; Wellington 1992). Differences in adult and juvenile distribution patterns were examined using χ^2 homogeneity tests.

Microhabitat cover on reefs was assessed using a video camera held \approx 50 cm from the substratum to record substrata along each transect. Coverage of each microhabitat category was expressed as a percentage of total substrate area based on the substratum recorded under five points on each of 40 systematically selected frames from each transect.

Selectivity indices were used to determine if species used any of the microhabitats preferentially. For each species, selectivity indices (w) were calculated for each microhabitat using the equation:

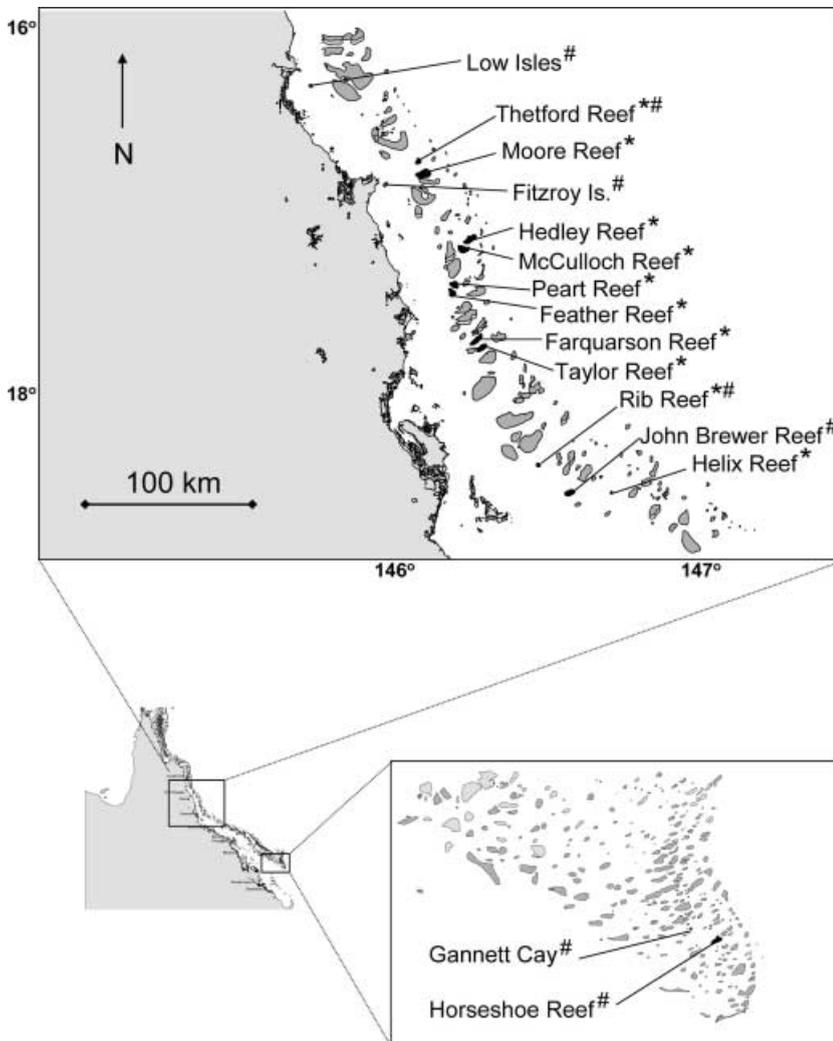


Fig. 1. Location of reefs surveyed. *, Reefs where habitat availability, pomacentrid abundance and habitat use were surveyed in December 2005 and used to assess habitat associations and niche breadth. #, Reefs where coral cover and pomacentrid abundance were collected between 1997 and 2003 and used to assess impact of *Acanthaster planci*-mediated coral decline on specialist species abundance.

$$w_i = o_i / \pi_i \quad (\text{eqn 1})$$

where o_i is the proportion of used microhabitat and π_i is the proportion of microhabitat available for microhabitat type i (Manly, McDonald & Thomas 1993). Values of o_i and π_i were calculated as the mean of the proportion of microhabitat used and available at the 10 reefs surveyed in 2005. Bonferroni-corrected confidence intervals encompassing selectivity indices were used to assess if fish used any microhabitat significantly more often than expected, based on its availability. Confidence intervals (CI) were calculated using the formula:

$$\text{CI} = z_{\alpha/2} [o_i(1 - o_i) / u_+ \pi_i^2]^{-2} \quad (\text{eqn 2})$$

where u_+ was the total number of microhabitats used by a pomacentrid species (Manly, McDonald & Thomas 1993). Fish were considered to be using a microhabitat significantly more often than expected if selectivity indices and associated confidence intervals were >1 . Indices were calculated only for those species seen on >10 transects and more than three reefs, and were based on the number of fish groups rather than individuals occurring in each microhabitat, alleviating the influence of conspecifics on habitat use. Because niche breadth and selectivity indices for both adults and juveniles are based on the

proportion (rather than total numbers) of fish of each type seen in each microhabitat type, comparisons between species, adults and juveniles were possible.

To determine if pomacentrid abundance is influenced by the availability of preferred microhabitats, fish abundance data collected from the 10 reefs during December 2005 were fitted to an exponential increase to maximum model:

$$y = a[1 - \exp(-b \times x)] + c \quad (\text{eqn 3})$$

where x is the proportion of preferred habitat available on each transect and y is the number of fish aggregates present on that transect. In the model, a represents asymptotic population levels; b the rate of population change with increasing habitat availability; and c the abundance when habitat is absent. This model was chosen in preference to a linear relationship, as although habitat availability may directly affect coral-dependent species when coral cover is low, the effect of high coral cover is expected to be negligible (Holbrook, Brooks & Schmitt 2006). Parameters were constrained such that only a positive relationship between abundance and the cover of a preferred microhabitat was allowed.

The response of coral-reliant fish to declines in coral cover was assessed using data collected from seven reefs on the GBR where

Table 1. Severe decline in mean coral cover at seven GBR reefs

Reef	Before		After		Percentage decline
	Year	Percentage coral	Year	Percentage coral	
John Brewer	2001	16.1 (0.9)	2003	0.8 (0.4)	95
Low Isles	1997	14.3 (1.0)	2000	1.5 (0.5)	89
Thetford	1999	22.8 (1.6)	2002	2.4 (0.7)	89
Rib	1999	37.5 (1.7)	2001	5.5 (1.0)	85
Fitzroy Island	1999	14.6 (1.1)	2000	3.0 (0.9)	79
Gannet Cay	1997	28.3 (1.6)	1998	12.4 (1.8)	56
Horseshoe	1997	26.0 (1.4)	1999	11.9 (1.5)	54

Values in parentheses are standard errors based on values from three sites at each reef. Decline primarily attributable to COTS outbreak (>1500 COTS km⁻²), although cyclone Rona contributed to coral decline at Low Isles (Cheal *et al.* 2002) and coral bleaching reduced coral cover at Fitzroy Island (Sweatman *et al.* 2003).

there was >50% decline in coral cover (Table 1; Fig. 1). Coral decline was primarily attributed to COTS outbreak (>1500 COTS km⁻²), although coral bleaching and storms are likely to have contributed to coral loss, particularly at Fitzroy Island and the Low Isles (Sweatman *et al.* 2003). For this analysis, coral cover was taken as the summed percentage coverage of those coral growth forms preferentially used by fish (branching, plate and submassive). Data were collected by the long-term monitoring team (Australian Institute of Marine Science), 2–8 years before habitat and fish abundance data were collected for assessment of microhabitat use and niche breadth of pomacentrids. The sampling protocol and design for collection of both data sets were, however, identical (for detailed description of sampling protocols and species lists see Halford & Thompson 1996; Abdo *et al.* 2003).

The response to coral decline by pomacentrid species was calculated as the percentage change in abundance of fish divided by the percentage change in coral cover at each of the seven reefs. This accounted for differences in the abundance of various fish species and percentage coral cover between sites. Large positive values indicated declining fish abundance, while negative values were indicative of increasing abundance.

The niche breadth was calculated for each pomacentrid species using the proportional similarity index (Feinsinger, Spears & Poole 1981), which considers both proportional use and availability of resources. This metric ranges between 0 and 1; lower values indicate smaller niche breadths and greater habitat specialization.

To determine if there was a relationship between habitat specialization and disturbance, niche breadth of the six coral-dwelling pomacentrid species was plotted against changes in fish abundance both before and after COTS-induced coral decline. Comparisons made before coral decline were used to assess natural variation in pomacentrid abundance. Calculations for before impact assessment were based on comparing data collected 3 years before disturbance with data 1 year before disturbance at each of the impacted reefs. Regression was used to assess the significance of the relationship between change in species abundance and niche breadth. Fish abundance data were $\log(x + 1)$ -transformed prior to analysis to meet the assumptions of homogeneity of variance and normality, examined using residual plots.

Microhabitat selectivity indices of all species selected for this analysis had strong affinities with live coral as adults. However, two species with strong affinity for live coral, *Plectroglyphidodon dickii* Liénard and *Dascyllus reticulatus* Richardson, were excluded from the analysis as they were of low abundance before COTS outbreaks and occurred on fewer than two of the affected reefs.

Results

WHAT ARE THE MICROHABITAT PREFERENCES OF POMACENTRIDS?

Eight (40%) of 20 adult pomacentrid study species and seven (53%) of 13 juvenile species displayed a preference for live coral (Table 2). This represented 56 and 60% of all adult and juvenile individuals, respectively. All eight of the coral-favouring adult species were strongly associated with branching corals, although only three species were strongly associated with plating corals (Table 2). No species showed a preference for massive or encrusting-type corals, although three species avoided either one or both of these coral growth forms. Juvenile coral favouring pomacentrids were also closely associated with branching corals; however, five species also showed a strong alliance with plate corals (Table 2).

Over 30% of all observed juveniles were found in association with plate corals, which was four times as many as the percentage of adults associated with this microhabitat (Fig. 2). Comparisons of coral-associated adult and juvenile distribution patterns suggest ontogenetic changes in microhabitat use among four of the coral-associated species (Table 3). Significant differences in microhabitat use were driven primarily by a 20–40% increase in the use of plating corals by juvenile *Chromis atripectoralis* Wellander & Schultz, *Pomacentrus lepidogenys* Fowler & Bean and *Pomacentrus moluccensis* Bleeker, while increased use of branching corals by juveniles accounted for small ontogenetic differences in the distribution patterns of *Amblyglyphidodon curacao* Bloch.

Juvenile *Neoglyphidodon melas* Cuvier and *Pomacentrus nagasakiensis* Tanaka were also closely associated with plate corals, although low adult abundance of these species precluded comparisons of adult and juvenile distribution patterns. Niche breadth of all coral-associated juveniles tended to be narrower than in adult conspecifics (Table 3), primarily because such juveniles were rarely seen away from corals.

Selectivity indices of six species of adult pomacentrid suggested a preference for rubble, and two of the rubble-dwelling species preferentially used rubble as juveniles (Table 2). Three

Table 2. Microhabitat use by adult (A) and juvenile (J) pomacentrids

		n	Microhabitat								
			Branching	Plate	Sub massive	Massive	Encrusting	Soft	Dead coral	Rubble	Pavement
% Availability			2.3	5.0	2.1	2.0	3.4	12.8	1.7	17.2	49.7
Coral associated											
<i>Amblyglyphidodon curacao</i>	A	334	23 ⁺	11	4	<1 ⁻	<1 ⁻	20	7	20	13 ⁻
	J	10	61 ⁺	5	0	0	0	33	0	0	0
<i>Amblyglyphidodon leucogaster</i>	A	68	25 ⁺	10	5	0	1	9	9	19	21
	J	10	60 ⁺	0	0	0	0	30	0	0	0
<i>Chromis atripectoralis</i>	A	85	42 ⁺	16	13	2 ⁻	1	9	1	13	3 ⁻
	J	29	45 ⁺	46 ⁺	1	0	0	0	0	0	2 ⁻
<i>Chromis ternatensis</i>	A	38	62 ⁺	6	8	0	2	6	9	2 ⁻	0
<i>Dascyllus reticulatus</i>	A	81	45 ⁺	27 ⁺	16	4	0	1 ⁻	1	0	0
<i>Neoglyphidodon melas</i>	J	56	6	60 ⁺	3	0	0	29	0	0	<1 ⁻
<i>Plectroglyphidodon dickii</i>	A	17	68 ⁺	0	32	0	0	0	0	0	0
<i>Pomacentrus lepidogenys</i>	A	960	9 ⁺	14 ⁺	2	2	2 ⁻	26 ⁺	1	17	25
	J	231	18 ⁺	36 ⁺	4	0	0	22 ⁺	1	7 ⁻	7 ⁻
<i>Pomacentrus moluccensis</i>	A	516	36 ⁺	19 ⁺	14 ⁺	<1	3	10	5	6 ⁻	6 ⁻
	J	197	22 ⁺	59 ⁺	11	0	0	5 ⁻	1	2 ⁻	0
<i>Pomacentrus nagasakiensis</i>	J	51	14	31 ⁺	9	4	0	19	0	9	5 ⁻
No coral association											
<i>Chromis margaritifer</i>	A	63	5	22	3	6	2	21	11	10	19
<i>Chrysiptera rollandi</i>	A	44	0	0	0	0	0	0	0	94 ⁺	6 ⁻
	J	57	1	0	0	0	0	0	1	83 ⁺	15 ⁻
<i>Dischistodus melanotus</i>	A	64	10	3	0	0	0	1 ⁻	2	50 ⁺	34
<i>Neoglyphidodon nigroris</i>	A	414	4	4	<1 ⁻	1	2	8 ⁻	5	33 ⁺	42
	J	32	0	0	0	0	9	8	9	53	21
<i>Neopomacentrus azysron</i>	A	127	7	14	2	1	1	18	2	26	25
	J	41	19	27	0	1	2	15	0	21	13
<i>Plectroglyphidodon lacrymatus</i>	A	351	7	2 ⁻	1 ⁻	0 ⁻	1 ⁻	5 ⁻	16 ⁺	22 ⁺	44
<i>Pomacentrus amboinensis</i>	A	22	15	2	0	0	0	3	3	73 ⁺	3
<i>Pomacentrus bankanensis</i>	A	360	3	4	3	3	1 ⁻	14	5	39	28 ⁻
	J	19	3	0	0	0	0	11	3	62	21 ⁻
<i>Pomacentrus grammorhynchus</i>	A	43	6	0	0	2	3	0	3	47	39
<i>Pomacentrus philippinus</i>	A	252	1	11	2	2	3	26	<1	19	34
	J	23	0	0	0	0	0	0	0	30	70
<i>Pomacentrus wardi</i>	A	411	2	2 ⁻	2	0	<1 ⁻	5 ⁻	4	39 ⁺	45
	J	205	0	4	1	<1	3	3 ⁻	1	37 ⁺	49
<i>Stegastes apicalis</i>	A	300	4	1 ⁻	<1 ⁻	0	5	5 ⁻	10	32	43

Values are percentage of fish observed in each microhabitat. Microhabitats were used significantly more (+) or less (-) than expected by chance considering the proportional availability of each microhabitat based on Bonferroni-corrected confidence intervals around selectivity indices.

species, *Chromis margaritifer* Fowler, *Neopomacentrus azysron* Bleeker and *Pomacentrus philippinus* Evermann & Seale, used microhabitats in proportion to their availability.

DOES MICROHABITAT COVERAGE PREDICT FISH ABUNDANCE?

The percentage cover of coral microhabitats explained significant amounts of variation in the abundance of five of the eight adult coral-associated species (Table 4). However, the amount of variation explained was typically <15%, the exception being the relationship between branching coral and *C. atripectoralis* ($R^2 = 0.35$). The abundance of the two *Amblyglyphidodon* spp. was unrelated to percentage cover of branching coral, although selectivity indices suggested that *Amblyglyphidodon leucogaster* Bleeker and *A. curacao* were associated with branching corals as both adults and juveniles. Abundances of coral-dwelling species with

narrower niche breadths than the two *Amblyglyphidodon* spp. were correlated with habitat availability, suggesting a relationship between specialization and the importance of microhabitat to abundance. However, there was no relationship between niche breadth and correlation coefficients of fish abundance/microhabitat models. Availability of preferred coral microhabitats was generally a poor predictor of juvenile abundance. The only significant relationships were between *C. atripectoralis* and branching coral, and between *N. melas* and plate coral (Table 4). In both cases, availability of microhabitat type accounted for <10% of the variation in juvenile abundance.

HABITAT SPECIALIZATION AND DISTURBANCE

In the absence of disturbances that result in severe coral loss, there was no detectable relationship between niche breadth of coral-associated pomacentrids and changes in their

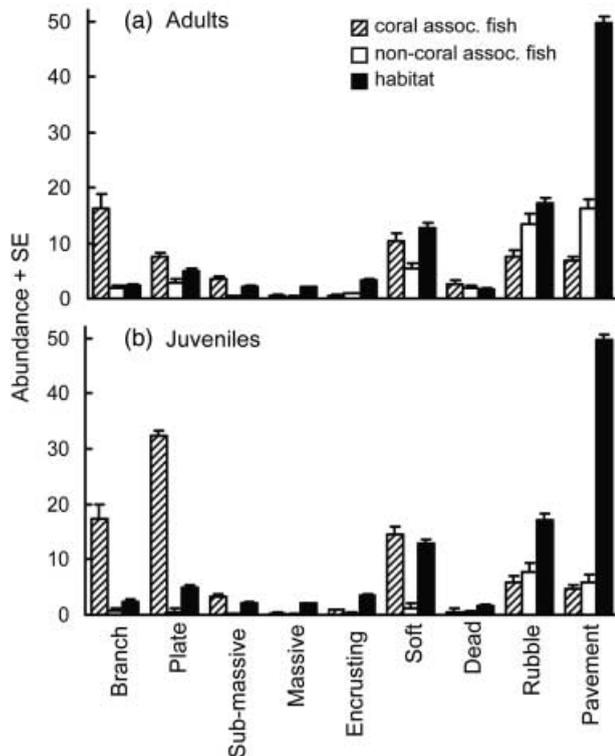


Fig. 2. Distribution and relative abundance of adult and juvenile pomacentrids among habitats. Bars represent mean percentage (+SE) of adult (a) and juvenile (b) fish observed in each microhabitat, calculated from values at each of the 10 reefs surveyed. Pomacentrids are categorized as either coral-associated (cross-hatched bars) or non-coral-associated (white bars) based on information in Table 2. Black bars show mean percentage coverage of each microhabitat type.

abundance ($F_{1,4} = 0.4$, $P = 0.574$; Fig. 3a). However, there was a significant negative relationship between the niche breadth of fish and their mean response to declines in coral cover due to COTS outbreaks ($F_{1,4} = 11.4$, $P = 0.028$; Fig. 3b). Those species with narrow niche breadths and high dependency on coral (*Chromis ternatensis* Bleeker, *C. atripectoralis* and *P. moluccensis*) consistently showed larger declines in abundance following coral loss than pomacentrids with wider niche breadths (*Amblyglyphidodon* spp. and *P. lepidogenys*). On some reefs, abundance of fish with wider niche breadth increased following coral decline, although these changes were not significant when averaged over all reefs. Niche breadth explained 74% of the variation in species' mean response to coral decline.

Table 3. Distribution pattern statistics and niche breadth of adult and juvenile pomacentrids with a preference for live coral

Species	Adult vs. juvenile distribution			Niche breadth	
	χ^2	df	P	Adult	Juvenile
<i>Amblyglyphidodon curacao</i>	4.8	1	0.028	0.59	0.16
<i>Amblyglyphidodon leucogaster</i>	3.6	1	0.058	0.61	0.17
<i>Chromis atripectoralis</i>	15.5	2	<0.001	0.46	0.24
<i>Pomacentrus lepidogenys</i>	78.4	6	<0.001	0.68	0.47
<i>Pomacentrus moluccensis</i>	103.3	7	<0.001	0.36	0.22

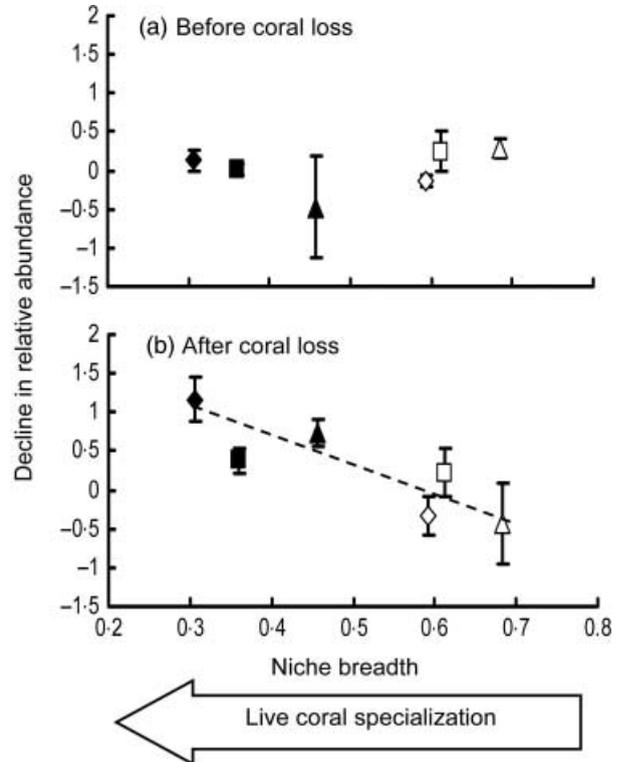


Fig. 3. Relationship between niche breadth and abundance changes of pomacentrids with differing coral dependency: (a) in the absence of coral decline; (b) when *Acanthaster planci* causes severe coral decline. Relative abundance was calculated as the percentage change in fish density divided by change in coral cover. Niche breadth calculated as proportional similarity index (Feinsinger *et al.* 1981). Mean response to change in coral cover and standard errors are calculated from four to seven reefs for each fish species. Pomacentrid species: \diamond , *Amblyglyphidodon curacao*; \square , *A. leucogaster*; \blacktriangle , *Chromis atripectoralis*; \blacklozenge , *C. ternatensis*, \square , *Pomacentrus lepidogenys*; \blacksquare , *Pomacentrus moluccensis*.

Discussion

Resource specialization confers an advantage over generalists within a subset of resources; however, generalists are expected to outperform specialists over a wider range of resources (Caley & Munday 2003). In particular, generalist species should be more resilient to changing resource availability (Vazquez & Simberloff 2002). Consequently, dietary and habitat specialization are strong predictors of response to disturbance by animals in both terrestrial and aquatic systems

Species		Mhab*	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²	<i>P</i>
<i>Amblyglyphidodon curacao</i>	A	Br	0	10.1	4.7	<0.01	1.000
	J	Br	0.2	52.59	0.03	0.03	0.402
<i>Amblyglyphidodon leucogaster</i>	A	Br	0.4	360.8	0.4	0.02	0.480
	J	Br	0	2.57	0.10	<0.01	1.000
<i>Chromis atripectoralis</i>	A	Br	>1000	0.03	0.00	0.35	<0.001
	J	Br	22.6	9.39	0.25	0.09	0.022
	J	Pl	5.0	103.4	0.00	0.02	0.743
<i>Chromis ternatensis</i>	A	Br	6.3	9.53	0.08	0.15	<0.001
<i>Dascyllus reticulatus</i>	A	Br	1.0	19.3	0.35	0.02	0.340
	A	Pl	0.8	78.1	0.00	0.02	0.422
<i>Neoglyphidodon melas</i>	J	Pl	0.7	115.3	0.02	0.07	0.046
<i>Plectroglyphidodon dickii</i>	A	Br	1.6	3.36	0.00	0.14	<0.001
<i>Pomacentrus lepidogenys</i>	A	Br	8.4	193.3	16.2	0.04	0.120
	A	Pl	19.8	11.58	13.81	0.08	0.006
	J	Br	5.1	2437	10.87	0.02	0.624
	J	Pl	0	10.0	14.51	<0.01	1.000
<i>Pomacentrus moluccensis</i>	A	Br	3.6	48.12	2.56	0.08	0.006
	A	Pl	0	9.59	3.95	<0.00	1.000
	A	Sm	0	9.41	3.95	<0.00	1.000
	J	Br	2.7	95.95	4.75	0.02	0.665
	J	Pl	0	9.73	6.17	<0.01	1.000
<i>Pomacentrus nagasakiensis</i>	J	Pl	66.1	0.04	0.34	0.01	0.805

*Preferred microhabitats (Br, branching coral; Pl, plating coral; Sm, submassive coral) based on information in Table 2 for coral-associated species. Model parameters: *a*, asymptotic population levels; *b*, rate of population change with increasing habitat availability; *c*, fish abundance when habitat is absent.

(Swihart *et al.* 2003; Cleary & Genner 2004; Julliard, Jiguet & Couvet 2004; Munday 2004). However the strength of the specialization–disturbance relationship may vary between communities, even when within the same system and subjected to the same disturbance (Taki & Kevan 2007).

We found varying levels of habitat specialization and response to disturbances within a prominent and ecologically important family of reef fish, the Pomacentridae. Some species were strongly associated with coral as both adults and juveniles, while others used a range of microhabitats, many of which were non-coral. Overall, coral dependency within the pomacentrids is high compared with other coral reef fishes, and ≈20% of all pomacentrid species on the GBR rely on coral for food or shelter (Munday *et al.* 2007). This value is lower than our estimate of 40%; however, meta-analysis of studies documenting fish responses to coral loss indicate that the percentage of species declining in abundance exceeds that of known coral dependents (Wilson *et al.* 2006), indicating that other species are somehow reliant on coral.

Reduced abundance of adult fish not known to associate with coral on perturbed reefs may be partially attributed to juveniles' preference for coral habitats (Jones *et al.* 2004). We found that a higher percentage of species and individuals relied on coral microhabitat as juveniles compared with adults, including some not known to associate with hard coral as adults. These findings are consistent with other studies showing strong juvenile associations with live coral in fish with adult conspecifics that do not favour coral habitats (Booth & Beretta 1994; Gutiérrez 1998; Feary *et al.* 2007b).

Loss of live coral and increased algal cover can also result in an overall reduced abundance of fish recruits and a shift to juvenile communities dominated by algae-associated species (Feary *et al.* 2007a, 2007b). Extensive and protracted declines in coral cover may therefore result in changes to adult communities, whereby fish that associate with corals as juveniles decline in abundance, irrespective of their habitat associations as adults.

All coral-dwelling adults displayed a preference for live coral as juveniles. This is partially due to juveniles recruiting to sites occupied by conspecifics (Sweetman 1985; Booth 1992). However, juveniles had a narrower niche breadth than adults and a stronger association with plating corals, suggesting preference for a subset of corals used by adults. Juvenile fish may be better suited to coral plate refuges, as fish tend to choose shelters that match their body size (Hixon & Beets 1993; Friedlander & Parrish 1998), and spaces between branches of plating corals provide better shelter for small juveniles than do larger branching colonies. Importantly, narrow niche breadth of juveniles relative to adults suggests that they are more specialized and therefore more susceptible to disturbance.

Species with ontogenetic shifts in coral preferences may be particularly susceptible to coral loss, as declines in either habitat type will ultimately influence adult populations. Density dependence during early life history regulates demographics at later life stages of some amphibians (Altweg 2003), and availability of juvenile habitat can influence adult populations of reef fishes (Halpern 2004; Mumby *et al.* 2004).

Table 4. Modelled relationship between preferred coral microhabitats (Mhab) of adult (A) and juvenile (J) pomacentrids and their abundance

Models predict that adult abundance will be limited by juvenile habitat when adult habitat size is greater than that of juveniles (Halpern, Gaines & Warner 2005), which is likely for coral-dependent pomacentrid species that have a narrower niche breadth as juveniles.

For pomacentrids, availability of preferred coral microhabitat was, however, a poor predictor of abundance, particularly that of juveniles, suggesting that factors other than microhabitat are more important in determining juvenile abundance. Caselle & Warner (1996) found that microhabitat failed to predict recruitment patterns of coral reef fish at different sites, concluding that physical oceanic processes were more important in determining recruitment patterns at large spatial scales. Microhabitat could, however, predict recruit density at the smaller spatial scale of transects (Caselle & Warner 1996). Poor relationships between the abundance of specialists and their preferred habitat probably reflect the balancing of pre- and postrecruitment processes in driving the recruitment patterns of these fish. At small scales, postrecruitment processes such as habitat selection, predation and competition, and the interaction of these processes with habitat complexity, are dominant (Almany 2004), whereas the abundance of juveniles at larger scales are probably driven by supply rates from the plankton. Thus small-scale dependence of specialist species on live coral suggests that comprehensive coral loss is still expected to have serious consequences for coral-dependent juveniles and ultimately adult abundance of these species.

Although microhabitat availability was a poor predictor of fish abundance at larger scales, niche breadth of microhabitat use provided estimates of habitat specialization that are compatible with the specialization-disturbance hypothesis (Vazquez & Simberloff 2002). As predicted, versatility in resource use improved resilience of coral-dependent species to COTS-mediated coral declines, with more generalist species showing reduced declines in abundance relative to specialists. However, the response of generalist coral-dwelling species was variable, and the abundance of these species occasionally increased. Munday (2004) found that, although the extent of population declines in coral-dwelling *Gobiodon* was related to habitat specialization, abundance of all coral-dwelling species declined following coral loss. Similarly, Pratchett, Wilson & Baird (2006) found that when coral loss was severe, all obligate coral-feeding butterflyfish declined in abundance irrespective of diet breadth. Thus the extent of habitat disturbance may sometimes outweigh differential impacts on habitat or diet specialists.

Habitat specialists are likely to take longer than generalists to recover from disturbances, because the continued absence of these species allows invasion by habitat generalists (Marvier, Kareiva & Neubert 2004), as observed among butterfly communities following extensive forest fires (Charrette, Cleary & Mooers 2006). On coral reefs, this may translate to fish communities dominated by generalist species, which are not reliant on live coral at any stage in their life history, and a higher extinction risk for coral specialists. This prediction is supported by local extinctions of coral specialists (Munday 2004; Graham *et al.* 2006) and an increased proportion of habitat generalists (Bellwood *et al.* 2006) following disturbances.

Our study supports the hypothesis that habitat specialists are at greater risk due to disturbance than are generalists. Analysis of changes to adult fish abundance following coral decline found that highly specialized coral-associated pomacentrids consistently declined in abundance, while the response from generalist habitat-users was more variable and may relate to the severity of the disturbance. A high proportion of pomacentrids are closely associated with live coral, although the type of coral they associate with varies among species and often changes ontogenetically. Importantly, associations with live coral were especially high among juveniles, suggesting that this is a life-history phase more vulnerable to coral loss, which may have serious consequences for future adult stocks.

Acknowledgements

We thank N.A.J. Graham, M.S. Pratchett and T. Done for comments on earlier drafts, the crew of the RV Lady Basten for support in the field, and the long-term monitoring team for collecting data. Financial support from the Leverhulme trust was provided to S.K.W.

References

- Abdo, D., Burgess, S., Coleman, G. & Osborne, K. (2003) *Surveys of Benthic Reef Communities using Underwater Video*. Long-term monitoring of the Great Barrier Reef, SOP no. 9. Australian Institute of Marine Science, Townsville, Queensland, Australia.
- Allen, G.R. (1991) *Damselfishes of the World*. Mergus, Germany.
- Almany, G.R. (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia*, **141**, 105–113.
- Alongi, D.M. (2002) Present state and future of the world's mangrove forests. *Environmental Conservation*, **29**, 331–349.
- Altwegg, R. (2003) Multistage density dependence in an amphibian. *Oecologia*, **136**, 46–50.
- Beck, M.W. (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology*, **76**, 968–980.
- Bellwood, D.R., Hoey, A.S., Ackerman, J.L. & Depczynski, M. (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, **12**, 1587–1594.
- Birkeland, C. (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology*, **69**, 175–185.
- Booth, D.J. (1992) Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. *Journal of Experimental Marine Biology and Ecology*, **155**, 85–104.
- Booth, D.J. & Beretta, G.A. (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs*, **13**, 81–89.
- Brown, J.H. (1984) On the relationship between the abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Bruno, J.F. & Selig, E.R. (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One*, **8**, e711.
- Caley, M.J. & Munday, P.L. (2003) Growth trades off with habitat specialization in coral-dwelling gobies. *Proceedings of the Royal Society B: Biological Sciences*, **270**, S175–S177.
- Caselle, J.E. & Warner, R.R. (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology*, **77**, 2488–2504.
- Ceccarelli, D.M., Jones, G.P. & McCook, L.J. (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: Annual Review*, **39**, 355–389.
- Ceccarelli, D.M., Jones, G.P. & McCook, L.J. (2005) Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs*, **24**, 606–620.
- Charrette, N.A., Cleary, D.F.R. & Mooers, A.O. (2006) Range-restricted, specialist Bornean butterflies are less likely to recover from ENSO-induced disturbance. *Ecology*, **87**, 2330–2337.
- Cheal, A.J., Coleman, G., Delean, S., Miller, I., Osborne, K. & Sweatman, H. (2002) Responses of coral and fish assemblages to a severe but short-lived

- tropical cyclone on the Great Barrier Reef, Australia. *Coral Reefs*, **21**, 131–142.
- Cleary, D.F.R. & Genner, M.J. (2004) Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. *Global Ecology and Biogeography*, **13**, 129–140.
- Dayton, P.K. (1985) The ecology of kelp communities. *Annual Review of Ecology and Systematics*, **16**, 215–245.
- Duarte, C.M. (2002) The future of seagrass meadows. *Environmental Conservation*, **29**, 192–206.
- Dulvy, N.K., Freckleton, R.P. & Polunin, N.V.C. (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters*, **7**, 410–416.
- Feary, D.A., Almany, G.R., Jones, G.P. & McCormick, M.I. (2007a) Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series*, **333**, 243–248.
- Feary, D.A., Almany, G.R., McCormick, M.I. & Jones, G.P. (2007b) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia*, **153**, 727–737.
- Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth. *Ecology*, **62**, 27–12.
- Friedlander, A.M. & Parrish, J.D. (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, **224**, 1–30.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.
- Goldenberg, S.B., Landsea, C.W., Mestas-Núñez, A.M. & Gray, W.M. (2001) The recent increase in Atlantic hurricane activity: causes and implications. *Science*, **293**, 474–479.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. & Robinson, J. (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences, USA*, **103**, 8425–8429.
- Gutiérrez, L. (1998) Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*. *Oecologia*, **115**, 268–277.
- Halford, A.R. & Thompson, A.A. (1996) *Visual Census Surveys of Reef Fish*. Long-term monitoring of the Great Barrier Reef, SOP no. 3. Australian Institute of Marine Science, Townsville, Queensland, Australia.
- Halford, A.R., Cheal, A.J., Ryan, D. & Williams, D.McB. (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, **85**, 1892–1905.
- Halpern, B.S. (2004) Mangroves as a limiting resource for coral reef fish. *Marine Ecology Progress Series*, **272**, 93–98.
- Halpern, B.S., Gaines, S.D. & Warner, R.R. (2005) Habitat size, recruitment and longevity as factors limiting population size in stage-structured species. *American Naturalist*, **165**, 82–94.
- Hiatt, R.W. & Strasburg, D.W. (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs*, **30**, 65–127.
- Hixon, M.A. & Beets, J.P. (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, **63**, 77–101.
- Hoegh-Guldberg, O. (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.
- Holbrook, S.J., Brooks, A.J. & Schmitt, R.J. (2006) Relationships between live coral cover and reef fishes: implications for predicting effects of environmental disturbances. *Proceedings of the 10th International Coral Reef Symposium* (ed. Y. Suzuki, T. Nakamori, M. Hidaka, H. Kayanne, B.E. Casareto, K. Nadaoka, H. Yamano & M. Tsuchiya), pp. 241–249. Japanese Coral Reef Society, Tokyo, Japan.
- Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**, 1547–1551.
- Jones, G.P., McCormick, M.I., Srinivasan, M. & Eagle, J.V. (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences, USA*, **101**, 8251–8253.
- Julliard, R., Jiguet, F. & Couvet, D. (2004) Common birds facing global changes: what makes a species at risk? *Global Change Biology*, **10**, 148–154.
- Lecchini, D. & Galzin, R. (2005) Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology*, **147**, 47–58.
- Manly, B.F., McDonald, L.L. & Thomas, D.L. (1993) *Resource Selection by Animals*. Chapman & Hall, London.
- Marvier, M., Kareiva, P. & Neubert, M.G. (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, **24**, 869–878.
- McKinney, M.L. (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology Evolution and Systematics*, **28**, 495–516.
- Meekan, M.G., Ackerman, J.L. & Wellington, G.M. (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology Progress Series*, **212**, 223–232.
- Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E. et al. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533–536.
- Munday, P.L. (2004) Habitat loss, resource specialisation, and extinction on coral reefs. *Global Change Biology*, **10**, 1642–1647.
- Munday, P.L., Jones, G.P., Sheaves, M., Williams, A. & Goby, G. (2007) Vulnerability of fishes of the Great Barrier Reef to climate change. *Climate Change and the Great Barrier Reef* (ed. J. Johnson and P. Marshall), pp. 357–391. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.
- Pandolfi, J.M., Jackson, J.B.C., Baron, N. et al. (2005) Are U.S. coral reefs on the slippery slope to slime? *Science*, **307**, 1725–1726.
- Pratchett, M.S. (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology*, **148**, 373–382.
- Pratchett, M.S., Wilson, S.K. & Baird, A.H. (2006) Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. *Journal of Fish Biology*, **69**, 1269–1280.
- Pratchett, M.S., Wilson, S.K., Graham, N.A.J., Munday, P.L., Jones, G.P. & Polunin, N.V.C. (in press) Effects of coral bleaching on motile reef organisms: current knowledge and the long-term prognosis. *Coral Bleaching: Patterns, Processes, Causes and Consequences* (eds J. Lough & M. Van Oppen). Springer, Berlin.
- Sano, M., Shimizu, M. & Nose, Y. (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series*, **37**, 191–199.
- Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.
- Steneck, R.S., Graham, M.H., Bourque, B.J. et al. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, **29**, 436–459.
- Sweatman, H.P.A. (1985) The influence of adults of some coral reef fishes on larval recruitment. *Ecological Monographs*, **55**, 469–485.
- Sweatman, H., Abdo, D., Burgess, S. et al. (2003) *Long-Term Monitoring of the Great Barrier Reef*. Status Report 6. Australian Institute of Marine Science, Townsville, Queensland, Australia.
- Swihart, R.K., Gehrig, T.M., Kolozsvary, M.B. & Nupp, T.E. (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions*, **9**, 1–18.
- Taki, H. & Kevan, P.G. (2007) Does habitat loss affect the communities of plants and insects equally in plant–pollinator interactions? *Biodiversity and Conservation*, **16**, 3147–3161.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.
- Travis, J.M. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 467–473.
- Vazquez, D.P. & Simberloff, D. (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *American Naturalist*, **159**, 606–623.
- Webster, P.J., Holland, G.J., Curry, J.A. & Chang, H.R. (2005) Changes in tropical cyclone number, duration and intensity in a warming environment. *Science*, **309**, 1844–1846.
- Wellington, G.M. (1992) Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia*, **90**, 500–508.
- Williams, D.M. (1986) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short term effects of *Acanthaster planci* infestations. *Marine Ecology Progress Series*, **28**, 157–164.
- Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. & Polunin, N.V.C. (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, **12**, 2220–2234.

Received 13 August 2007; accepted 16 October 2007
Handling Editor: Karl Cottenie