

# Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient?

SHAUN K. WILSON\*†, NICHOLAS A. J. GRAHAM\*, MORGAN S. PRATCHETT‡, GEOFFREY P. JONES‡ and NICHOLAS V. C. POLUNIN\*

\*School of Marine Science & Technology, University of Newcastle, Newcastle-upon-Tyne NE1 7RU, UK, †Australian Institute of Marine Science, PMB 3, TMC, Townsville, Qld 4810, Australia, ‡Centre of Excellence, Coral Reef Studies, James Cook University, Qld 4811, Australia

## Abstract

Increased frequency of disturbances and anthropogenic activities are predicted to have a devastating impact on coral reefs that will ultimately change the composition of reef associated fish communities. We reviewed and analysed studies that document the effects of disturbance-mediated coral loss on coral reef fishes. Meta-analysis of 17 independent studies revealed that 62% of fish species declined in abundance within 3 years of disturbances that resulted in >10% decline in coral cover. Abundances of species reliant on live coral for food and shelter consistently declined during this time frame, while abundance of some species that feed on invertebrates, algae and/or detritus increased. The response of species, particularly those expected to benefit from the immediate loss of coral, is, however, variable and is attributed to erratic replenishment of stocks, ecological versatility of species and sublethal responses, such as changes in growth, body condition and feeding rates. The diversity of fish communities was found to be negatively and linearly correlated to disturbance-mediated coral loss. Coral loss >20% typically resulted in a decline in species richness of fish communities, although diversity may initially increase following small declines in coral cover from high coverage. Disturbances that result in an immediate loss of habitat complexity (e.g. severe tropical storms), have a greater impact on fishes from all trophic levels, compared with disturbances that kill corals, but leave the reef framework intact (e.g. coral bleaching and outbreaks of *Acanthaster planci*). This is most evident among small bodied species and suggests the long-term consequences of coral loss through coral bleaching and crown-of-thorn starfish outbreaks may be much more substantial than the short-term effects currently documented.

*Keywords:* coral bleaching, ecological versatility, global warming, habitat complexity, resilience, storms

Received 25 April 2006; revised version received 1 June 2006 and accepted 5 June 2006

## Introduction

Natural sources of physical and biological disturbance play important roles in determining the structure and dynamics of ecological communities (e.g. Sousa, 1984; Pickett & White, 1985; Petraitis *et al.*, 1989). The predicted outcomes of variation in the intensity, duration and frequency of disturbances have become important components of ecological theory (Connell, 1978;

Huston, 1979; Wootton, 1998). Coastal marine habitats in particular are exposed to and appear to be susceptible to a wide range of natural disturbances, including storms, temperature fluctuations, rainfall and terrestrial run-off, diseases and outbreaks of predatory echinoderms. Variations in the scale and intensity of these disturbances contribute to the spatial complexity, biodiversity and dynamic nature of these habitats (Harris *et al.*, 1984; Dayton, 1985; Karlson & Hurd, 1993; Short & Wyllie Echeverria, 1996).

The diversity, frequency and intensity of anthropogenic disturbances has been increasing exponentially over the last 100 years, long-term records showing that these are leading to directional changes in the structure

Correspondence: Shaun Wilson, School of Marine Science & Technology, University of Newcastle, Newcastle-upon-Tyne NE1 7RU, UK. tel. +61 7 4753 4117, fax +61 7 4772 5852, e-mail: [skwilson@aims.gov.au](mailto:skwilson@aims.gov.au)

of benthic marine ecosystems (Dayton *et al.*, 1998; Jackson *et al.*, 2001; Hughes *et al.*, 2003). Marine ecologists are alarmed over the extent of past impacts and the predicted loss of coastal habitats, including seagrass beds (Short & Wyllie Echeverria, 1996; Duarte, 2002), kelp forests (Dayton *et al.*, 1998; Steneck *et al.*, 2002), mangroves (Ellison & Farnsworth, 1996; Alongi, 2002) and coral reefs (McClanahan, 2002; Hughes *et al.*, 2003). These structurally complex, yet seemingly fragile marine habitats support a large proportion of the world's shallow marine biodiversity and the full consequences of the declining area and quality of these habitats remain largely unknown.

As most habitats are exposed to multiple disturbances, identifying the role or importance of any one agent of disturbance can be problematic. Disturbance will differ in terms of the spatial scale of impact on habitat, intensity and the magnitude of the effect, duration of individual episodes of disturbance, and temporal frequency of different episodic events (Connell, 1978; Bender *et al.*, 1984). Different kinds of disturbances may impact on one habitat at the same time or at different times, and they may have a range of both common and unique impacts on habitat structure. The current state of a community will be a product of a complex disturbance history, and the impact of any new disturbance will be contingent upon this history and the stage of recovery (Hughes, 1989; Dayton *et al.*, 1998; Jackson *et al.*, 2001). In addition, the timing and frequency of different disturbances may be inextricably linked at different scales of space and time. For example, the mechanical effects of storms may be linked with those of freshwater run-off, salinity changes and sedimentation over short time scales (Jokiel *et al.*, 1993). At the other extreme, global warming has been linked to increasing frequency of storms over several decades (Goldenberg *et al.*, 2001; Webster *et al.*, 2005).

The bulk of the disturbance literature deals either with a single type of disturbance or treats disturbance as a single extrinsic force. However, as the diversity and the relative importance of different disturbances changes, it is important that we unravel their unique, combined and/or synergistic effects. It is increasingly evident that communities susceptible to natural disturbances are even more vulnerable to increasing pressure from anthropogenic factors (Waldichuk, 1987; Glynn, 1994; Short & Wyllie Echeverria, 1996). While the distinctions between 'natural' and 'disturbed' habitats, and between 'natural' and 'anthropogenic' agents of disturbance have become increasingly blurred, we do know that multiple disturbances are changing the nature of shallow water seascapes world-wide. Perhaps the most documented changes are for coral reefs.

Disturbance plays a major role in determining the structure and dynamics of coral reef habitats and may be critical to the maintenance of diversity in these species-rich systems (Connell, 1978; Huston, 1985; Karlson & Hurd, 1993; Jones & Syms, 1998). Disturbances such as crown-of-thorns starfish outbreaks, sea-urchin die-offs, tropical cyclones, terrestrial run-off, coral bleaching and disease can all result in dramatic changes to coral cover and the structure of benthic populations and communities. Long-term data show that coral cover is in decline in many (not all) regions of the world (Hughes, 1994; Gardner *et al.*, 2003; Bellwood *et al.*, 2004) and ecologists have directed their attention towards the causes of and remedies for this decline. The number of publications dealing with disturbance to coral reefs since 1960 show that research and our understanding of these phenomena has increased dramatically over the last 20 years (Fig. 1). The range of disturbance agents that have been studied has increased and the relative attention received by different kinds of disturbance has changed. The publication record (Fig. 1) evidently reflects global decline in reef health over this period (Roberts, 1993), increasing concern over the susceptibility of coral reefs to anthropogenic disturbance in general, and the perception that the relative importance of different threats to coral reefs has changed. While the crown-of-thorns starfish was once seen as the greatest threat (see review by Grigg, 1992), since the 1998 bleaching event that devastated many coral reefs world-wide, the impacts of global warming have become a higher priority.

Even today, most studies on coral disturbance address a single form of disturbance, studies on multiple disturbances being the exception (Fig. 1). However, the long-term decline in coral cover in many regions is often explained by multiple disturbances. For example, the phase-shift from corals to algae in Jamaica has been explained by the sequential and combined effects of cyclone damage, mass mortality of sea urchins and over-fishing of herbivores (Hughes, 1994). Similarly, coastal sedimentation, bleaching and crown-of-thorns starfish have combined to devastate some coastal reefs in PNG (Jones *et al.*, 2004). Different agents of disturbance are likely to have similarities and differences, which when combined, may hasten the collapse of coral reef ecosystems.

The combined forces of nature and human intervention all appear to be distinctly bad for corals, the major habitat-forming organism on coral reefs (Bellwood *et al.*, 2004). However, the effects of different disturbances on corals are also likely to be transferred to other organisms that are reliant on reef habitats. Coral reefs which cover only 0.09% of the ocean area are the habitat of approximately a quarter of all fish species (Spalding

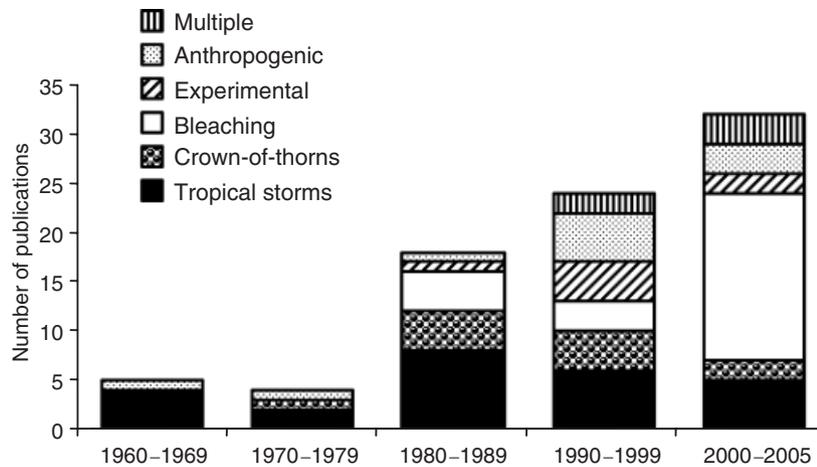


Fig. 1 Temporal distribution of studies documenting response of fish to coral loss from different disturbance types.

*et al.*, 2001) and fishes are the most conspicuous, diverse and well-studied groups of organisms that are closely associated with coral reefs. For the large part, they are dependent on coral reef habitat for vital resources such as food, shelter and living space, the requisites for survival and reproduction (Jones & Syms, 1998). The abundance of individual species and the structural and functional composition of the community should, thus, be very sensitive to disturbance-induced changes in habitat structure. However, reef fish species vary from small species that may be associated with a single coral species to those that may be found almost anywhere on the reef (Williams, 1991; Munday *et al.*, 1997; Munday, 2000). In theory, the susceptibility to disturbance may largely be determined by where most fish lie between the extremes of specialization and versatility (Vazquez & Simberloff, 2002). Disturbances may have a range of effects including the loss, fragmentation and/or degradation of preferred habitat, which may affect fish species in different ways (Caley *et al.*, 2001). In addition, some fishes may be associated with biotic features of the habitat such as corals or sponges (e.g. Bell & Gazlin, 1984), while others are more associated with the topographical complexity of the reef, occupying caves, holes or crevices (e.g. McCormick, 1994). To understand the impacts of habitat-disturbance on fishes we need to understand, not only the specific habitat requirements of the fish, but the ways in which different disturbances affect the biological and physical structure of the substratum.

Developing an understanding of how coral reef fishes respond to habitat loss and degradation is becoming urgent. There has been a proliferation of studies that are showing that reef fish communities are responding to habitat change (see Table 1), and when coral loss has been severe, reef fish biodiversity is in decline (Jones

*et al.*, 2004; Graham *et al.*, 2006). The consequences could be far-reaching. The presence of important functional groups of reef fishes is important for coral reef health (Bellwood *et al.*, 2004), and many fish species are important to local economies and subsistence in the more than 181 countries that have coral reefs (Wilkinson, 2004). In developing theory to apply to the problem, the published literature on the effects of different kinds of disturbances on reef fish communities and resources is fragmentary. As with studies on the effects of disturbance on corals, most studies on fishes have documented the short-term effects of single known disturbance events (Fig. 1). When this subject was first reviewed, based on papers published up until the mid-1990s, few generalizations about different disturbances and their effect on fishes had emerged (see Jones & Syms, 1998). Despite a proliferation of new studies over the last decade, there have been no further attempts to synthesize this information or provide a long-term prognosis for coral reef fish communities in a changing seascape.

In this review, we take a 'bottom-up' approach to understanding the determinants of change and long-term trends in the structure and composition of coral reef fish assemblages. That is, we assess to what degree fish abundance and diversity is determined by the nature of their underlying habitat, and to what degree changes to fish communities are linked to habitat change resulting from different agents of disturbance on coral reefs. We provide a meta-analysis of the empirical data from published papers to address a number of specific questions:

(1) *How does disturbance-induced coral decline affect different fish species, different functional groups of species and fish communities as a whole?* A meta-analysis of existing data is here presented to determine the effect

**Table 1** Details of studies used to assess the affect of coral loss on fish

| Location                          | Disturbance | Time since disturbance | % coral cover |       | Source                               |
|-----------------------------------|-------------|------------------------|---------------|-------|--------------------------------------|
|                                   |             |                        | Before        | After |                                      |
| Iriomote Island, Japan            | Bleaching   | 2 years                | 95            | 0     | Sano (2004)*,†                       |
| Okinawa Island, Japan             | Experiment  | 1 month                | 90            | 0     | Sano <i>et al.</i> (1984)*           |
| Arabian Gulf, Dubai               | Bleaching   | 3 years                | 90            | 22    | Riegl (2002)†                        |
| Kona, Hawaii                      | Storm       | 4 months               | 78            | 37    | Walsh (1983)*                        |
| Chagos                            | Bleaching   | 3 years                | 69–39         | 47–8  | Sheppard <i>et al.</i> (2002)†       |
| Little Trunk reef, GBR, Australia | Experiment  | 1 year                 | 66            | 29    | Lewis (1997, 1998)*,†                |
| Seychelles                        | Bleaching   | 1 year                 | 64–29         | 10–0  | Spalding & Jarvis (2002)*,†          |
| Palm Islands, GBR, Australia      | Bleaching   | 6 months               | 63–16         | 45–1  | Thompson & Malcolm (1999)*,†         |
| Lizard Island, GBR, Australia     | Experiment  | 21 months              | 55            | 43–34 | Syms (1998)*                         |
| Moorea, French Polynesia          | Multiple    | 1 year                 | 51            | 24    | Adjeroud <i>et al.</i> (2002)†       |
| Seychelles                        | Bleaching   | 6 months               | 50–23         | 17–0  | S. Jennings (unpublished)*,†         |
| Ishigaki Island, Japan            | Bleaching   | 1 year                 | 39            | 3     | Shibuno <i>et al.</i> (1999)*,†      |
| Moorea, French Polynesia          | COTS        | 1 year                 | 36            | 16    | Bouchon-Navaro <i>et al.</i> (1985)* |
| Cairns sector, GBR, Australia     | Storm       | 1 year                 | 36–21         | 23–9  | Cheal <i>et al.</i> (2002)*,†        |
| One Tree Island, GBR, Australia   | Bleaching   | 1 year                 | 35–26         | 20–9  | Booth & Beretta (2002)*,†            |
| Tutia reef, Tanzania              | Bleaching   | 6 months               | 33            | 0     | Lindahl <i>et al.</i> (2001)*        |
| Trunk reef, GBR, Australia        | Multiple    | 3 years                | 33            | 3     | Pratchett <i>et al.</i> (in press)*  |
| Trunk reef, GBR, Australia        | Bleaching   | 1 month                | 33            | 15    | Pratchett <i>et al.</i> (2004)*      |
| Lizard Island, GBR, Australia     | COTS        | 3 years                | 31–24         | 14–18 | Pratchett (2001)*                    |
| Lizard Island, GBR, Australia     | Experiment  | 1 year                 | 30–20         | <10   | Syms & Jones (2000)*                 |
| Kimbe Bay, Papua New Guinea       | Multiple    | 3 years                | 30            | 8     | Jones <i>et al.</i> (2004)†          |

\*Studies used in species and functional group analyses.

†Studies used for species richness analysis.

of coral depletion, caused by various disturbances (e.g. severe tropical storms, coral bleaching and outbreaks of the coral feeding crown-of-thorns starfish, *Acanthaster planci*), on coral reef fishes. Specifically, we wanted to assess the extent of impacts of coral decline across entire communities of fishes, as well as identify species and groups of fishes that are disproportionately affected. Our analysis of responses considers the life history and ecology of different fish species, focussing on the diet and habitat requirements of species assigned to different functional groups. The influence of niche specialization on species response to coral decline will also be investigated.

(2) *How do different disturbance types, such as crown-of-thorns starfish, tropical storms and coral bleaching, affect fish communities?* Herein, responses of coral reef fishes to different types of disturbance will be compared. Specifically, we wanted to compare disturbances that directly kill corals (biological) vs. those that, in addition to causing coral mortality, disrupt the underlying reef framework (physical). We compare the response of different functional groups to the two disturbance types. The results will be discussed with reference to the role that habitat complexity plays in determining the structure of fish assemblages, and we examine the longer-term impacts of disturbance.

## Methods

To explore the effects of reduced coral cover, caused by various disturbance events, on coral reef fishes we collated and analysed data from 22 separate studies (Table 1) conducted across six geographic regions, including the Caribbean, Arabian Gulf, Indian Ocean, Indo-Australia Archipeligo, Southern Japan and East Pacific. These 22 studies are in no way exhaustive. Since 1961, there have been at least 84 separate studies that have considered responses of fishes to coral declines caused by different disturbances (Fig. 1). In this review, however, we considered only those studies, which included a temporal component, and repeatedly measured the abundance and/or diversity of fishes during at least part of the disturbance event (preferably, before, during and after the disturbance). Moreover, all studies considered in this review resurveyed fishes within 3 years after the disturbance, as after extended periods postdisturbance recovery of populations, as well as the additional effects of subsequent disturbance events, are likely to confound interpretation of results.

To explore variation in responses of reef fishes to declines in coral cover, we extracted species-level data from 17 studies (Table 1), which documented both changes in the abundance of fishes and changes in coral

cover during specific disturbances. As some disturbances have minimal impact on corals and are unlikely to affect fish abundance (e.g. Syms, 1998; Cheal *et al.*, 2002), we considered only those studies where resulting declines in coral cover were greater than 10%. Furthermore, as many fish species are sparsely distributed and not consistently encountered during studies, we only included data from species where five or more individuals were observed. To account for differences in the initial abundance of fishes, their responses to coral declines were calculated by dividing the proportional change in the abundance of each fish species by the proportional decline in coral cover within the local environment. This metric (change in species abundance divided by change in coral cover) puts greater weighting on studies where small changes in coral cover (e.g. <20%) lead to disproportionate changes in the abundance of fishes, relative to studies where severe large-scale disturbances cause almost 100% coral mortality and there is a corresponding change in fish abundance. As the size of survey areas may also influence estimates of fish abundance, results from each study were weighted by multiplying the change in fish abundance by the natural logarithm of the study area, following Mosquera *et al.* (2000). To detect congruent trends in species responses to coral depletion, the weighed change in fish abundance over coral decline was averaged across multiple studies, and/or multiple locations. Data presented are only for those 55 species for which we had at least four separate records of their responses. Each fish species was also assigned a functional category based on diet or its use of live coral as habitat (coral dwellers).

To further assess the effect of coral depletion on the overall diversity of fish assemblages, data were collated from 12 studies, where initial coral cover varied between 13% and 90%, and subsequent changes in coral cover ranged from a 5% increase to 70% decline (Table 1). In this review, we considered only studies that measured diversity of fishes across a sample area greater than 100 m<sup>2</sup> and included 30 or more species in their analyses, as our purpose is to assess change at large scale across many species. To summarize results from these 12 separate studies, changes in species richness were plotted against percent coral decline. The significance of this relationship was assessed using regression analysis.

The influence of different types of disturbance (e.g. coral bleaching vs. severe tropical storms) on reef fish assemblages was investigated by comparing the mean response of five functional groups. It was not possible to explore variation in the effects of different disturbances on individual species due to a paucity of studies that have considered identical species. The mean response

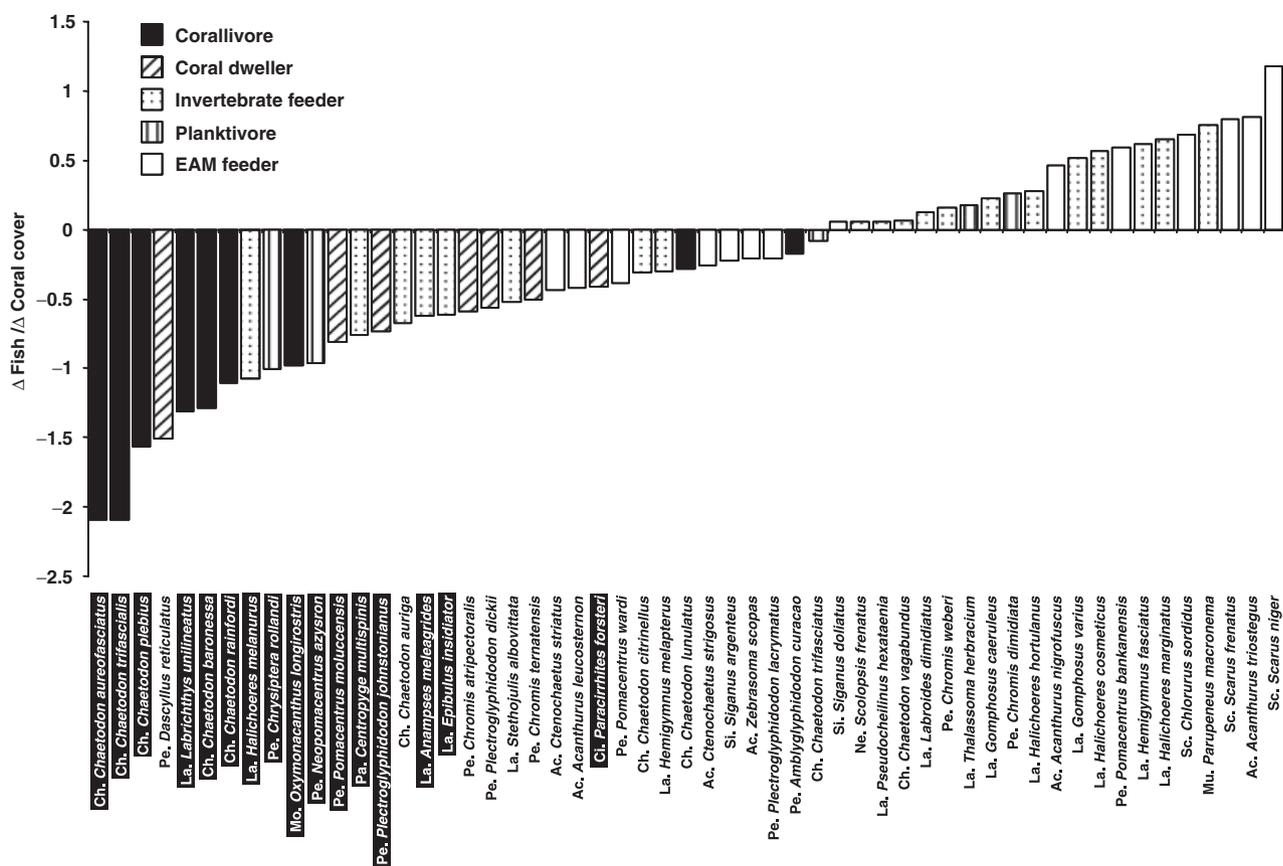
and 95% confidence intervals of each functional group were calculated from the response of all representative fish species. Here, we were particularly interested in comparing biological (e.g. coral bleaching and outbreaks of *A. planci*) vs. physical disturbances (e.g. severe tropical storms). Variation in the effect of biological vs. physical disturbances were analysed using a two-way ANOVA, comparing variation in the effects among functional groups [obligate corallivores, coral dwellers, planktivores, invertebrate feeders and epilithic algal matrix (EAM) feeders] and between biological vs. physical disturbances. Data were tested for homogeneity and normality and if necessary transformed to meet the assumptions of the ANOVA. Tukey's HSD test was used to further investigate significant differences.

## Results and discussion

### *Impact of coral loss on fish species*

The predominant response of fishes following coral depletion caused by acute disturbance events was a net decline in abundance, indicative of increased mortality or relocation of fishes to alternate habitats. Of the 55 species considered, 34 (62%) including representatives from eight different families, exhibited marked declines in abundance following coral depletion. For 16 (29%) of these species, significant declines in abundance were recorded across multiple study locations, even where coral cover declined by as little as 10%. Some fish species increased in abundance after coral decline, however, variation about the mean response by all of these species was high, suggesting increased abundance was not consistent among study locations. High variability in the response of fish species expected to benefit from coral loss may be partially attributed to the limited time available for species to recruit to reefs following disturbance, as most of the studies used in meta-analysis surveyed fish population within 1-year postdisturbance (Table 1). However, within the same short time period the rapid decline in abundance of more than half the fish species investigated demonstrates coral is essential for the survival of many species.

Specific responses of different fishes to coral depletion were largely dependent on their reliance on coral for food or shelter. The affect of coral loss was most severe on obligate coral feeding fishes (Fig. 2). All nine of the corallivore species included in our meta-analysis declined in abundance following coral loss, and corallivorous species accounted for six of the seven most severely affected species (Fig. 2). This functional group is represented by three families; however, it is members of the family Chaetodontidae, genus *Cheatodon* that are the most prominent and



coral bleaching implies live coral *per se* is an important facet of their habitat (Booth & Beretta, 2002). It is possible that live coral confers benefits to coral dwellers other than shelter, such as camouflage or supplementing diet.

An important component of this study was the revelation that some fishes with no apparent reliance on live coral are negatively impacted by declines in coral cover. Of the 20 invertebrate feeding species, all of which do not associate strongly with live coral colonies, eight species exhibited declines in abundance following coral depletion. Further, four of these species consistently declined in abundance in multiple studies conducted across multiple locations. Similarly, small-bodied planktivorous fishes, such as *Neopomacentrus azysron* and *Chrysiptera rollandi*, also declined in abundance following coral loss, suggesting these fishes are in some way reliant on corals, even though they do not consistently seek shelter within live coral colonies like the coral-dwelling damselfishes, *Pomacentrus moluccensis* and *Dascyllus* spp.

While most species of fishes exhibited significant declines in abundance following coral depletion, some fishes actually increased in abundance (Fig. 2). Decreases in coral cover are often associated with increased algal cover, thereby increasing the availability of dietary resources for herbivorous fishes. Accordingly, the abundance of several fish species that feed on algae and associated detrital resources (EAM or EAM feeders) might be expected to increase following perturbations of reef habitats (Sheppard *et al.*, 2002). Contrary to expectations, abundance of seven EAM feeding species declined in response to coral loss, including four of six surgeonfishes (family Acanthuridae; Fig. 2). Furthermore, apparent increases in the abundance of each of the parrotfishes (family Scaridae) and *Acanthurus triostegus*, the surgeonfish with the highest positive response, can be attributed to a large increase of fish at one or two locations. Changes to total 'herbivore' abundance after disturbance are also variable, some studies finding significant increases (e.g. Shibuno *et al.*, 1999; Lindahl *et al.*, 2001; Sheppard *et al.*, 2002), while others failed to detect any difference (e.g. Hart *et al.*, 1996; Riegl, 2002; Sano, 2004). These variable results and the short time period between disturbance and resurveying fish abundance suggest increases in abundances of fish that feed on algae and associated detritus are due to movement of fish rather than population growth. Although most reef fishes are site attached, small-scale patchiness in disturbance and associated changes in resource availability will serve as a powerful force to promote migrations of fishes among habitats or between adjacent reefs (Lewis, 1998). Consequently, EAM feeding fish in areas surrounding disturbed reef

habitats may migrate to damaged areas to exploit increased availability of food.

Although this analysis revealed significant and consistent declines in the abundance of some species and certain functional groups of fishes following coral depletion, responses of fishes were for the most part highly variable. Some species (e.g. *C. lunulatus*) were shown to be negatively impacted by declines in coral cover in some studies, but not others. Further, some species of obligate coral-dwelling fishes consistently decline in abundance following reductions in coral cover, but others (e.g. *Chromis atripectoralis*) do not. We attribute this variation in the responses of fishes to three main factors; (i) the degree to which coral (vs. other factors such as recruitment) may be limiting the abundance of fishes, (ii) specialization vs. versatility in the resource requirements of coral-dependent fishes and (iii) the capacity of fishes to persist despite major reductions in essential resources, which is apparent from sublethal responses (e.g. Pratchett *et al.*, 2004). These three factors will be discussed in turn.

*Resource limitation.* The rate and magnitude of declines in the abundance of fishes following disturbance-induced coral depletion will vary depending on the degree to which coral limits their abundance. For example, common coral-dwelling gobies (e.g. *Gobiodon histrio*) tend to saturate available habitats, such that their abundance is limited by the availability of suitable habitat (Munday *et al.*, 1997). As such, any decline in the availability of habitat immediately and negatively affects their abundance. For obligate coral feeding fishes, however, it is much less clear whether population size is regulated by the availability of coral prey, or by some other factor, such as recruitment or availability of other essential resources (Fowler, 1990; Cox, 1994). Where coral cover is high, and less likely to be limiting, initial declines in the abundance of corallivores (e.g. Pratchett *et al.*, in press). Similarly, for herbivorous fishes, if dietary resources or habitat availability are regulating population size, an increase in population density, following increased algal growth will be reliant on sufficient recruitment. Robertson (1991) demonstrated that abundance of herbivorous surgeonfishes increased rapidly with increased availability of algae in the Caribbean, but recruitment of these species was consistently high. Supply of larval fish and subsequent recruitment are typically variable, both spatially and temporally (Doherty, 1991), and delays are likely to occur before species respond to increased availability of resources. Furthermore, many monitoring studies do not count juvenile fish

(e.g. Halford & Thompson, 1996), and it may take several years to detect population responses to increased resource availability.

Some fish species also settle into specific microhabitats, such as certain coral species (Booth & Wellington, 1998). A decline in coral cover can therefore reduce the abundance of recruits and juveniles that rely on live coral habitat (Lewis, 1998; Booth & Beretta, 2002), potentially influencing future adult population size (Booth & Wellington, 1998). Unfortunately, a paucity of information on the specific habitat requirements of coral reef fish during their early life history make it difficult to assess the impact of coral loss on fish recruitment, although this could explain long term declines in adults with no apparent reliance on live coral.

*Ecological versatility.* The degree to which fishes are specialized or versatile in their use of available resources can have a significant bearing on their response to habitat perturbations (Munday, 2004). Highly specialized species are much more constrained in their distribution and abundance by the availability of specific resources, compared with more versatile species that can exploit a range of resources (MacNally, 1995). Declines in the abundance of a particular resource are likely to have greater impact on species that specialize on it, compared with versatile species that may utilize alternative resources (Munday, 2004). Although most fishes appear highly versatile and opportunistic in their use of available resources (Pratchett *et al.*, 2001; Bellwood *et al.*, 2003), there is increasing evidence that some fishes are highly specialized in their use of certain prey (Pratchett, 2005) and/or habitat types (Munday *et al.*, 1997; Gardiner & Jones, 2005). Munday (2004) demonstrated that among obligate coral-dwelling gobies of the genus *Gobiodon*, more specialized species (i.e. those fishes that occupied fewer coral species) suffered a greater decline in abundance following coral loss and were more susceptible to local extinction. A similar effect may be expected when comparing feeding specialists and generalists. Following coral degradation, Bouchon-Navaro *et al.* (1985) and Pratchett *et al.* (in press) observed dramatic declines in the density of obligate corallivores within a chaetodontid assemblage, resulting in a shift to a community dominated by omnivores and facultative corallivores. Even among obligate corallivores, some butterflyfishes such as *Chaetodon trifascialis* feed only on a few particular coral species, while others such as *C. lunulatus* feed on a wide range of different coral species (Pratchett, 2005). This may explain why *C. trifascialis* is consistently negatively affected by declines in live coral cover, whereas responses of *C. lunulatus* are much more variable (Fig. 2).

Diet and feeding modes also vary among species of fish that feed on the EAM (Choat *et al.*, 2002, 2004) and on invertebrates (Hiatt & Strasburg, 1960; Randall, 1967; Westneat *et al.*, 2005) and as reef disturbance influences the structure of algal (Cheroske *et al.*, 2000) and invertebrate (Moran & Reaka-Kudla, 1991; Dreyer *et al.*, 2005) communities, changes to the availability of algal types or invertebrate species could influence abundance of diet specialists within the EAM and invertebrate feeding groups. For example, McClanahan *et al.* (1999) suggested increased macroalgae cover suppresses feeding and abundance of some 'herbivorous' surgeonfish, a family that displayed highly variable responses to coral decline among species (Fig. 2).

*Sublethal responses.* Fish responses to disturbance and coral loss may be manifest in ways other than absolute changes in abundance. Although the abundance of obligate corallivores may be unaffected by low coral cover, a decline in the availability of dietary resources can lead to a reduction in energy reserves (Pratchett *et al.*, 2004; Berumen *et al.*, 2005) or reduced growth rates (Kokita & Nakazono, 2001). Loss of body condition and reduced growth may allow fish to persist in the short term, but may have longer-term consequences for survivorship and reproductive output (Jones & McCormick, 2002), leading to eventual declines in population size. Reductions in live coral cover may also increase the area over which corallivores forage (Tricas, 1989; Kokita & Nakazono, 2001; Samways, 2005), potentially increasing both intra and interspecific competition which may have further deleterious effects on survivorship. Similarly, an increase in turf algae following coral decline can lead to increased feeding (McClanahan *et al.*, 1999, 2000) and growth rates of EAM-feeding fish (Hart & Russ, 1996), rather than short-term increases in abundance.

Declines in the abundance of fishes from within specific habitats may also be moderated by the ability of fishes to find more suitable habitats. Although implicitly assumed to represent the demise of fish populations, declines in the abundance of fishes following habitat perturbations may reflect the large-scale migration of fishes to nearby and relatively unaffected habitats. The potential for fishes to move to more suitable habitats will depend upon the scale and severity of the disturbance. Reef-wide disturbance, such as that caused by mass coral bleaching, will severely limit the ability of fishes to find alternate habitats, such that these disturbances may appear to have lesser impact on fish abundance compared with smaller-scale disturbances of moderate amplitude.

*Impact of coral loss on species richness*

Changes in the abundance of particular species and functional groups of fishes following declines in coral cover inevitably leads to changes in overall composition and species diversity. High diversity among coral reef fishes may be important because it provides a high degree of functional redundancy, such that declines in the abundance of some species and reduced species richness will not necessarily affect ecosystem processes (Chapin *et al.*, 2000). However, a loss of key species within critical functional groups, or the complete loss of entire functional groups, can have a profound affect on reef resilience (Bellwood *et al.*, 2004). Our meta-analysis has already revealed that extensive coral depletion can potentially lead to the loss of corallivorous and coral-dwelling fishes, although the impact this has on reef ecosystems is equivocal. More pertinent is the response of 'herbivorous' fishes, as increased abundance and feeding of these following coral loss should maintain substratum suitable for coral recovery and, thus, reef resilience (Bellwood *et al.*, 2004). However, we found that abundance of EAM-feeding fishes does not always increase after coral loss and in some circumstances these fishes fail to compensate for increased growth of macroalgae on surfaces previously occupied by corals (Williams *et al.*, 2001) potentially leading to phase shifts.

Studies specifically on changes in the species diversity of fishes following large-scale coral depletion have shown that such disturbances can have broad impacts across a wide range of different fishes and lead to marked reductions in species diversity (e.g. Jones *et al.*, 2004; Graham *et al.*, 2006). Information from 12 independent studies show there to be a negative linear relationship between fish species richness and coral decline ( $r = 0.61$ ,  $F_{1,28} = 16.52$ ,  $P < 0.001$ ; Fig. 3), indicating the severity of species decline is dependant on the degree of coral loss. Interestingly, a reduction in coral cover, particularly when small, can result in an increase in species richness. This is most likely related to an

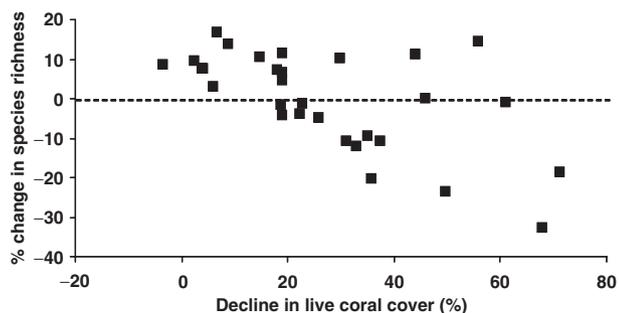


Fig. 3 Relationship between coral decline and species richness of fish assemblages on coral reefs.

increase in habitat heterogeneity, especially when coral cover was initially extensive. Species richness may also be inflated immediately after perturbations, even when coral loss is high, as species reliant on coral may persist for short periods while other species migrate into the area to exploit new resources (Garpe *et al.*, 2006). However, coral loss (>40%) can lead to extensive algal cover of reefs, effectively homogenizing habitat and reducing the number of niches available for fish species, resulting in a decline in species richness. Furthermore, increased frequency of disturbances such as coral bleaching and storms (Hoegh-Guldberg, 1999; Wooldridge *et al.*, 2005), combined with increased fishing pressure and pollution will inhibit reef recovery after disturbances, and coral reef communities may be held in early successional stages, keeping species richness low.

When coral decline is severe, the loss of fish species must extend beyond those species reliant specifically on corals for food or habitat. Fishes with such reliance on corals typically represent a small portion ( $\approx 11\%$ ) of the overall fish community (Jones *et al.*, 2004) and the loss of these groups alone can not account for the overall reduction in the number of fish species following severe coral decline. We have already revealed that coral declines impacted at least four species of invertebrate feeding and two planktivorous species. Although not obligate coral dwellers, these species and many others must benefit from the presence of corals, which may provide refuges from predators, provide suitable substrate for settlement, reduce effects of exposure or have other benefits, such as on prey abundance. Moreover, the full extent of species loss after coral decline is rarely measured, as very small and cryptic fishes are often overlooked in community studies and monitoring programs, yet they may become locally extinct following coral loss (Munday, 2004; Bellwood *et al.*, 2006). These small cryptic fishes may play an important role in reef ecology (Depczynski & Bellwood, 2003; Wilson, 2004) and a concerted effort should be made to include these species in community studies.

*Comparing different types of disturbance*

To this point, we have ignored potential differences in the effects of different types of disturbances (e.g. coral bleaching vs. severe tropical storms), simply assessing the effect of coral depletion on fishes. However, it is important to discern how different disturbances differ in their affects on the biological and physical structure of reef habitats. Severe coral bleaching events and outbreaks of *A. planci* cause widespread loss of live coral tissue (Moran, 1986; Hoegh-Guldberg, 1999) and algal proliferation in the remaining space (McClanahan *et al.*,

2001) without directly modifying the physical structure of the reef, at least in the short term (Sano *et al.*, 1987; Sheppard *et al.*, 2002; Garpe *et al.*, 2006). Conversely, during severe tropical storms (Cheal *et al.*, 2002; Halford *et al.*, 2004) and direct physical perturbations (Lewis, 1997; Syms & Jones, 2000), there is an immediate reduction in both live coral cover and structural complexity of the reef framework. This distinction may be important in teasing apart the impacts of disturbance to fish assemblages. Whereas, live coral may be important for only some species (Öhman *et al.*, 1998) and certain functional groups of fishes (Spalding & Jarvis, 2002), habitat complexity is likely to be important for most fishes (Luckhurst & Luckhurst, 1978; Gratwicke & Speight, 2005). In extreme cases, where very severe or successive disturbances have caused a complete loss of topographical structure, resulting rubble banks support only a very depauperate and low diversity assemblage of fishes (e.g. Sano *et al.*, 1987; Garpe *et al.*, 2006; Graham *et al.*, 2006).

Impacts of physical disturbances are generally much greater than those of biological disturbances ( $F = 4.35$ ,  $P = 0.03$ ), highlighting the importance of topographic complexity and live coral cover in supporting reef fishes (Fig. 4). However, the effects of both biological and physical disturbances varied among the five fish functional groups ( $F = 5.03$ ,  $P < 0.001$ ). Corallivorous and coral-dwelling fishes exhibited greater declines in abundance after disturbance-induced coral declines, compared with all other functional groups (Fig. 4), 95% confidence limits indicating significant reductions due to both biological and structural disturbances (Fig. 4). Of the remaining three functional groups, only planktivores display significant departures from 0 and only in response to structural disturbance (Fig. 4).

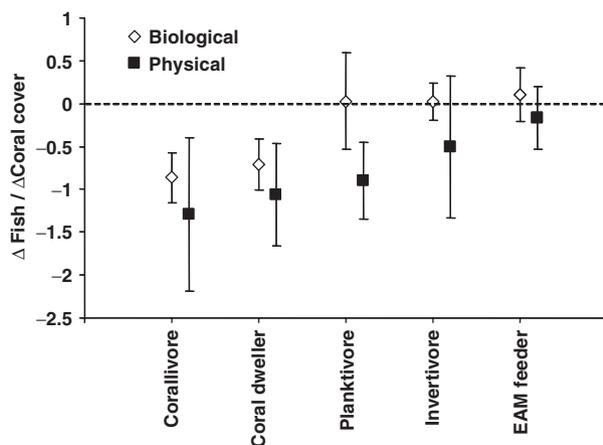


Fig. 4 Mean responses of function fish groups to two types of disturbance. Error bars are 95% confidence intervals calculated from 10 or more observations.

The potential reasons for these differences in response to the two categories of disturbance are many. The importance of the structural matrix of a reef to small-bodied fish is well known (Munday & Jones, 1998), so a loss of structure is likely to have a greater impact on these. This is well demonstrated by the response of planktivorous fish to the two disturbance types. In our analysis, planktivores are predominantly represented by small-bodied pomacentrids that are not reliant on live coral for food or shelter. However, after physical disturbance alters the structural complexity of the reef, reducing the availability of refuges, there is a significant decline in planktivores. Small-bodied prey fish may be depleted by predators on reefs (Graham *et al.*, 2003), and this applies to smaller life history stages of all species (Dulvy *et al.*, 2004b). Consequently, as refuge space from predators is lost, competition over the remaining space and susceptibility to predation may increase (Dulvy *et al.*, 2004b), resulting in greater impacts on a wide range of species from different size ranges and functional groups. It is also likely that many reef fish require structural complexity at the time they settle from the plankton; a time when they are particularly susceptible to predation and competition.

Different disturbances may further vary in their effects due to selective impacts on particular coral species (De'ath & Moran, 1998; McClanahan *et al.*, 2004) or growth forms (De'ath & Moran, 1998; Cheal *et al.*, 2002). For example, both coral bleaching and outbreaks of *A. planci* have disproportionate impacts on different corals, having the greatest effect on *Acropora* spp. and other fast-growing coral species (Marshall & Baird, 2000). This will likely have implications for the follow-on effects of these disturbances on coral reef fishes. For example, certain fishes (including both specialist coral-feeding butterflyfishes and obligate coral-dwelling gobies) have a specific reliance on *Acropora* corals, and will be disproportionately affected by declines in the abundance of these corals during coral bleaching and outbreaks of *A. planci* (Pratchett, 2001; Munday, 2004). These fast growing, habitat forming functional forms of coral are also most susceptible to physical damage through storms (Halford *et al.*, 2004). The importance of them to fish as habitat (Bellwood *et al.*, 2004) is highlighted by the greater declines across the board for this kind of disturbance (Fig. 4).

## Conclusions

Results of this review show that disturbances on coral reefs are broadly differentiated into two groups based on their effects on reef corals, with concomitant differences in the geographic, temporal and taxonomic extent

of their effects on coral reef fishes. On the one hand, declines in live coral cover have direct effects across a fairly narrow range of species, with disproportionate impacts on those fishes that rely on corals for either food or shelter (e.g. Pratchett *et al.*, in press). In contrast, large-scale physical degradation of coral reef habitats affects a wide range of fishes and has profound implications for the ecosystem as a whole (e.g. Sano *et al.*, 1987). Corals are ecosystem engineers par excellence (Jones *et al.*, 1994), playing a key role in the formation of the system, but their susceptibility to changes in the physico-chemical environment and reef community (such as through competition with algae) is evidently a major reason for ecosystem fragility (e.g. McClanahan, 2002).

The data we present shows that removal of coral cover *per se* typically has more limited effects than physical disturbance (Fig. 4), though removal of coral tissues will ultimately lead to erosion of intact skeletons and declines in the physical structure of reef habitats (Sano *et al.*, 1987). Physical disturbances are however, mostly limited in their spatial extent (Cheal *et al.*, 2002; Halford *et al.*, 2004), meaning that undamaged areas remain and can support recovery in impacted areas (Bythell *et al.*, 2000; Halford *et al.*, 2004). In contrast, coral bleaching, which is expected to become more severe and frequent in coming decades (Hoegh-Guldberg, 1999; Sheppard, 2003), may cause degradation throughout entire reef systems (Goreau *et al.*, 2000). The supply of both coral and fish recruits are expected to be diminished, reducing the probability of rapid reef recovery, especially for geographically isolated reef systems (Cowen *et al.*, 2006). Further, shifts in the composition of coral communities towards species and genera that are more thermally tolerant, following bleaching, is also of considerable concern as these species and genera are generally less structurally complex (McClanahan *et al.*, 2004), reducing refuge sites for recruits and prey fishes. If recovery does not occur, the reef structure will become further degraded through biological and physical erosion (Sano *et al.*, 1987; Sheppard *et al.*, 2002). In these circumstances, impacts on fish assemblages may be similar to structural disturbances, such as those caused by storms. In this review, our analyses have focussed on short-term effects of disturbance, and considerable research is still required to elucidate these longer-term effects of disturbances to coral reef ecosystems.

Implications of coral loss for processes which depend on physical habitat are many, including declines in settlement and survivorship of coral reef fishes, and modifying interactions between species. The consequences of coral and habitat degradation for processes such as predation and competition are potentially wide-

ranging. Change in habitat may affect predator and prey populations at species and group levels including that of size, the last as indicated by recent work in the Seychelles (Graham *et al.*, 2006). Understanding of these important spatially-driven processes is severely constrained, partly because experimental manipulations are very limited in their spatial extent (Lewis, 1997; Syms & Jones, 2000), whereas natural disturbances can simultaneously affect 10s–100s km<sup>2</sup> of reefal habitat (Cheal *et al.*, 2002; Halford *et al.*, 2004). Information on most key processes such as recruitment at the level of the whole ecosystem is scarce enough, but we know next to nothing about how these may respond at different temporal and spatial scales.

The findings of this review are not unique to coral reefs, rather the consequences of coral loss are comparable with the effects of habitat degradation in kelp and other ecologically engineered ecosystems. Most notably, reductions in the abundance of dominant habitat forming taxa (e.g. kelp) interrupt trophic pathways and have wide-ranging impacts across a multitude of organisms (e.g. reviews of Williams & Heck, 2001; Witman & Dayton, 2001). Further, such ecosystems appear particularly subject to changes of state (e.g. Steneck *et al.*, 2002). The large-scale dynamics of these system-level phenomena are poorly known. In the cases of kelp and coral reef ecosystems, phase changes are linked to the prevalence of trophic cascades in which echinoderms play a prominent part (e.g. Pinnegar *et al.*, 2000). However, corals, which not only provide the predominant habitat, but form the very foundation of coral reefs, are particularly sensitive to increasing temperature (and many other stressors), making coral reef ecosystems especially vulnerable to global climate change (Donner *et al.*, 2005). Their high species richness, dynamism and evident susceptibility to a range of factors, both natural and anthropogenic, mean that coral reef ecosystems are integral in the development of diversity-stability theory (e.g. Chapin *et al.*, 2000; Cottingham *et al.*, 2001), for example, in relation to concepts of resilience (Bellwood *et al.*, 2004). Large-scale ecology approaches are beginning to use *de facto* (e.g. fisheries; Dulvy *et al.*, 2004a) and management-led manipulations (e.g. Mumby *et al.*, 2006) to elucidate dynamics of the whole ecosystem. There are many issues of the longer-term impacts of system-wide reef degradation that are scarcely studied but deserve far greater scientific attention. Moreover, experimental and observational studies of disturbance must be conducted at greater temporal and spatial scales.

Are there substantial socio-economic implications associated with the vulnerability of coral reef ecosystems to coral loss? The short-term socio-economic implications of reef disturbances appear relatively minor.

For example, in the Seychelles which experienced substantial coral bleaching in 1998, changes in abundance of fishery target species within 2–3 years were driven more by ongoing fishery depletion than any effects of the loss of coral cover (Grandcourt & Cesar, 2003). The indication is that if reversing declines in target species biomass is the objective, then resources should be invested in fisheries management rather than mitigating effects of disturbance or its consequences. However, later effects of disturbance may be substantial. Longer-term degradation of physical reef structure by biological disturbances is much more likely to affect abundances, catch rates and compositions of fishery-target reef species and thus affect livelihoods of those dependent on that exploitation. More pertinently, while there are important alternatives to reef fishing (e.g. pelagic resources), the value of reefs to tourism is potentially far greater than that to fisheries (Pet-Soede *et al.*, 1999). The state of reef coral and fish communities affects tourists' perceptions and their enjoyment of reef recreational diving (e.g. Shafer & Inglis, 2000; Williams & Polunin, 2000), such that widespread degradation of coral reef habitats is likely to have far greater economic consequences for tourism industries, compared with fisheries. Profound systemic changes in the abundance of reef fishes and state of reef habitats are likely to impact local, and in some cases national, revenues derived from recreational uses of coral reefs. There are specific actions that management can take to address specific facets of the tourism value; for example effective marine protected areas may increase abundances of species appreciated by divers (Williams & Polunin, 2000) but the system-wide changes brought about by major disturbance events are far more challenging, both in terms of management and enhancing scientific understanding of their potential effects.

It is clear that the focus now should be on the longer-term impacts of disturbances, particularly those acting at large spatial scale such as coral bleaching. This work should include impacts on biodiversity, fisheries, tourism and resilience. Many current management actions are likely too small for the scale of the impact (Bellwood *et al.*, 2004) and a move towards large-scale, trans-boundary and international management, policy and interventions will be required to offer sustainability in a changing climate.

### Acknowledgments

This work was supported by grants from Leverhulme Trust and Fisheries Society of the British Isles. We would also like to thank D. Pratchett for helping to prepare figures and P. Munday for comments on an early draft.

### References

- Adjeroud M, Augustin D, Galzin R *et al.* (2002) Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Marine Ecology Progress Series*, **237**, 121–131.
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Biological Conservation*, **29**, 331–349.
- Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, **15**, 265–274.
- Bell JD, Harmelin-Vivien M, Galzin R (1985) Large scale spatial variation in abundance in butterflyfishes (Chaetodontidae) on Polynesian reefs. *Proceedings of the 5th International Coral Reef Symposium*, **5**, 421–426.
- Bellwood DR, Hoey AS, Ackermen JL *et al.* (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, **12**, 1587–1594.
- Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, **6**, 281–285.
- Bellwood DR, Hughes TP, Folke C *et al.* (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.
- Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. *Ecology*, **65**, 1–13.
- Berumen ML, Pratchett M, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series*, **287**, 217–227.
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. *Marine Ecology Progress Series*, **245**, 205–212.
- Booth DJ, Wellington G (1998) Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology*, **23**, 274–279.
- Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien ML (1985) Impact of coral degradation on a Chaetodontid fish assemblage (Moorea, French Polynesia). *Proceedings of the 5th International Coral Reef Symposium*, **5**, 427–432.
- Bozec YM, Doledec S, Kulbicki M (2005) An analysis of fish-habitat associations on disturbed coral reefs: chaetodontid fishes in New Caledonia. *Journal of Fish Biology*, **66**, 966–982.
- Bythell JC, Hillis-Starr ZM, Rogers CS (2000) Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series*, **204**, 93–100.
- Caley MJ, Buckley KA, Jones GP (2001) Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology*, **82**, 3435–3448.
- Chapin FS, Zavaleta ES, Eviner VT *et al.* (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.
- Cheal AJ, Coleman G, Delean S *et al.* (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.
- Cheroske AG, Williams SL, Carpenter RC (2000) Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii. *Journal of Experimental Marine Biology and Ecology*, **248**, 1–34.

- Choat JH, Clements KD, Robbins WD (2002) The trophic status of herbivorous fishes on coral reefs I. Dietary analysis. *Marine Biology*, **140**, 613–623.
- Choat JH, Robbins WD, Clements KD (2004) The trophic status of herbivorous fishes on coral reefs II: food processing modes and trophodynamics. *Marine Biology*, **145**, 445–454.
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Cottingham KL, Brown BL, Lennon JT (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, **4**, 72–85.
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science*, **311**, 522–527.
- Cox E (1994) Resource use by corallivorous butterflyfishes (Family Chaetodontidae) in Hawaii. *Bulletin of Marine Science*, **54**, 535–545.
- Dayton PK (1985) The ecology of kelp communities. *Annual Review of Ecology and Systematics*, **16**, 215–245.
- Dayton PK, Tegner MJ, Edwards PB *et al.* (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications*, **8**, 309–322.
- De'ath G, Moran PJ (1998) Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: feeding preferences. *Journal of Experimental Marine Biology and Ecology*, **220**, 107–126.
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series*, **256**, 183–191.
- Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: *The Ecology of Fish on Coral Reefs* (ed. Sale PF) pp. 261–292. Academic Press, San Diego, CA, USA.
- Donner SD, Skirving WJ, Little CM *et al.* (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology*, **11**, 2251–2265.
- Dreyer J, Bailey-Brock JH, McCarthy SA (2005) The immediate effects of Hurricane Iniki on intertidal fauna on the south shore of O'ahu. *Marine Environmental Research*, **59**, 367–380.
- Duarte CM (2002) The future of seagrass meadows. *Environmental Conservation*, **29**, 192–206.
- Dulvy NK, Freckleton RP, Polunin NVC (2004a) Coral reef cascades and the indirect effects of consumer removal by exploitation. *Ecology Letters*, **7**, 410–416.
- Dulvy NK, Polunin NVC, Mill AC *et al.* (2004b) Size structural change in lightly exploited coral reef fish communities: evidence for weak ecological release. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 466–475.
- Ellison AM, Farnsworth EJ (1996) Anthropogenic disturbance of Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. *Biotropica*, **28**, 549–565.
- Findley JS, Findley MT (1985) A search for pattern in butterfly fish communities. *American Naturalist*, **126**, 800–816.
- Fowler AJ (1990) Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. *Marine Ecology Progress Series*, **64**, 39–53.
- Gardiner N, Jones GP (2005) Habitat specialization and overlap in a guild of coral reef cardinalfish (family Apogonidae). *Marine Ecology Progress Series*, **302**, 163–175.
- Gardner TA, Cote IM, Gill JA *et al.* (2003) Long-term region-wide declines in Caribbean corals. *Science*, **301**, 958–960.
- Garpe KC, Yahya SAS, Lindahl U *et al.* (2006) Effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series*, **315**, 237–247.
- Glynn PW (1994) State of coral reefs in the Galapagos Islands: natural vs. anthropogenic impacts. *Marine Pollution Bulletin*, **29**, 131–140.
- Goldenberg SB, Landsea CW, Mestas-Nuñez AM *et al.* (2001) The recent increase in Atlantic hurricane activity: causes and implications. *Science*, **293**, 474–479.
- Goreau T, McClanahan T, Hayes R *et al.* (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology*, **14**, 5–15.
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation*, **30**, 200–208.
- Graham NAJ, Wilson SK, Jennings S *et al.* (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences*, **103**, 8425–8429.
- Grandcourt EM, Cesar HSJ (2003) The bio-economic impact of mass coral mortality on the coastal reef fisheries of the Seychelles. *Fisheries Research*, **60**, 539–550.
- Gratwicke B, Speight MR (2005) Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series*, **292**, 301–310.
- Grigg RW (1992) Coral reef environmental science: truth versus the Cassandra syndrome. *Coral Reefs*, **11**, 183–186.
- Halford A, Cheal AJ, Ryan D *et al.* (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, **85**, 1892–1905.
- Halford AR, Thompson AA (1996) *Visual census surveys of reef fish. Long term monitoring of the Great Barrier Reef Standard Operational Procedure Number 3*. Australian Institute of Marine Science, Townsville, 24pp.
- Harris LG, Ebeling AW, Laur DR *et al.* (1984) Community recovery after storm damage: a case of facilitation in primary succession. *Science*, **224**, 1336–1338.
- Hart AM, Klumpp DW, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Marine Ecology Progress Series*, **132**, 21–30.
- Hart AM, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofusus*. *Marine Ecology Progress Series*, **136**, 25–35.
- Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs*, **30**, 65–127.
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.
- Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. *Ecology*, **70**, 275–279.
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**, 1547–1551.

- Hughes TP, Baird AH, Bellwood DR *et al.* (2003) Climate change, human impacts and the resilience of coral reefs. *Science*, **301**, 929–933.
- Huston MA (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Huston MA (1985) Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics*, **16**, 149–177.
- Jackson JBC, Kirby MX, Berger WH *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–637.
- Jokiel PL, Hunter CL, Taguchi S *et al.* (1993) Ecological impact of a fresh-water “reef kill” in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*, **12**, 177–184.
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Jones GP, McCormick MI (2002) Numerical and energetic processes in the ecology of coral reef fishes. In: *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale PF), pp. 221–238. Academic Press, San Diego, CA.
- Jones GP, McCormick MI, Srinivasan M *et al.* (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences*, **101**, 8251–8253.
- Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology*, **23**, 287–297.
- Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs*, **12**, 117–125.
- Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. *Coral Reefs*, **20**, 155–158.
- Lewis AR (1997) Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Marine Ecology Progress Series*, **161**, 37–50.
- Lewis AR (1998) Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs. *Journal of Experimental Marine Biology and Ecology*, **230**, 91–110.
- Lindahl U, Öhman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: effects of fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin*, **42**, 127–131.
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, **49**, 317–323.
- MacNally RC (1995) *Ecological Versatility and Community Ecology*. Cambridge University Press, Cambridge, UK.
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs*, **19**, 155–163.
- McClanahan TR (2002) The near future of coral reefs. *Environmental Conservation*, **29**, 460–483.
- McClanahan TR, Baird AH, Marshall PA *et al.* (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **48**, 327–335.
- McClanahan TR, Bergman K, Huitric M *et al.* (2000) Response of fishes to algae reduction on Glovers Reef, Belize. *Marine Ecology Progress Series*, **206**, 273–282.
- McClanahan TR, Hendrick V, Rodrigues MJ *et al.* (1999) Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. *Coral Reefs*, **18**, 195–203.
- McClanahan TR, Muthiga NA, Mangi S *et al.* (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs*, **19**, 380–391.
- McCormick MI (1994) Comparison of field methods for measuring surface topography and associations with a tropical reef fish assemblage. *Marine Ecology Progress Series*, **112**, 87–96.
- Moran PJ (1986) The *Acanthaster* phenomenon. *Oceanography and Marine Biology: An Annual Review*, **24**, 379–480.
- Moran DP, Reaka-Kudla ML (1991) Effects of disturbance: disruption and enhancement of coral reef cryptofaunal populations by hurricanes. *Coral Reefs*, **9**, 215–224.
- Mosquera I, Côté IM, Jennings S *et al.* (2000) Conservation benefits of marine reserves for fish populations. *Animal Conservation*, **4**, 321–332.
- Mumby PJ, Dahlgren CP, Harborne AR *et al.* (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, **311**, 98–101.
- Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes. *Environmental Biology of Fishes*, **58**, 355–369.
- Munday PL (2004) Habitat loss, resource specialisation, and extinction on coral reefs. *Global Change Biology*, **10**, 1642–1647.
- Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review*, **36**, 373–411.
- Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series*, **152**, 227–239.
- Öhman MC, Rajasuriya A, Svensson S (1998) The use of butterflyfishes (Chaetodontidae) as bio-indicators of habitat structure and human disturbance. *Ambio*, **27**, 708–716.
- Pet-Soede C, Cesar HSJ, Pet J (1999) An economic analysis of blast fishing on Indonesian coral reefs. *Environmental Conservation*, **26**, 83–93.
- Petraitis PS, Latham RE, Niesenbaum RA (1989) The maintenance of species diversity by disturbance. *Quarterly Review of Biology*, **64**, 393–418.
- Pickett STA, White PS (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- Pinnegar JK, Polunin NVC, Francour P *et al.* (2000) Trophic cascades in fisheries and protected-area management of benthic marine ecosystems. *Environmental Conservation*, **27**, 179–200.
- Pratchett MS (2001) *Dynamics of outbreak populations of crown-of-thorns starfish (Acanthaster planci L.), and their effects on coral reef ecosystems*. PhD Thesis, James Cook University, Townsville.
- Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology*, **148**, 373–382.
- Pratchett MS, Gust G, Goby G *et al.* (2001) Consumption of coral propagules represents a significant trophic link between corals and reef fish. *Coral Reefs*, **20**, 13–17.

- Pratchett MS, Wilson SK, Baird AH (in press) Declines in the abundance of *Chaetodon* butterflyfishes (Chaetodontidae) following extensive coral depletion. *Journal of Fish Biology*.
- Pratchett MS, Wilson SK, Berumen ML *et al.* (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs*, **23**, 352–356.
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, **5**, 665–847.
- Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). *Marine Biology*, **140**, 29–40.
- Roberts CM (1993) Coral reefs: health, hazards and history. *Trends in Ecology and Evolution*, **8**, 425–427.
- Robertson DR (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Marine Biology*, **111**, 437–444.
- Samways MJ (2005) Breakdown of butterflyfish (Chaetodontidae) territories associated with the onset of a mass bleaching event. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, S101–S107.
- Sano M (2004) Short-term effects of a mass coral bleaching event on a reef fish assemblage at Iriomote Island, Japan. *Fisheries Science*, **70**, 41–46.
- Sano M, Shimizu M, Nose Y (1984) Changes in structure of coral-reef fish communities by destruction of hermatypic corals – observational and experimental views. *Pacific Science*, **38**, 51–79.
- 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.
- Shafer CS, Inglis GJ (2000) Influence of social, biophysical, and managerial conditions on tourism experiences within the Great Barrier Reef World Heritage area. *Environmental Management*, **26**, 73–87.
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature*, **425**, 294–297.
- Sheppard CRC, Spalding S, Bradshaw C *et al.* (2002) Erosion vs. recovery of coral reefs after 1998 El Niño: Chagos reefs, Indian Ocean. *Ambio*, **31**, 40–48.
- Shibuno T, Hashimoto K, Abe O *et al.* (1999) Short-term changes in structure of a fish community following coral bleaching at Ishigaki Island, Japan. *Galaxea*, **1**, 51–58.
- Short FT, Wyllie Echeverria S (1996) Natural and human-induced disturbance of seagrasses. *Environmental Conservation*, **23**, 17–27.
- Sousa WP (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.
- Spalding MD, Jarvis GE (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Marine Pollution Bulletin*, **44**, 309–321.
- Spalding MD, Ravilious C, Green EP (2001) *World Atlas of Coral Reefs*. University of California Press, Berkeley, USA.
- Steneck RS, Graham MH, Bouque BJ *et al.* (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, **29**, 436–459.
- Syms C (1998) Disturbance and the structure of coral reef fish communities on the reef slope. *Journal of Experimental Marine Biology and Ecology*, **230**, 151–167.
- Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology*, **81**, 2714–2729.
- Thompson A, Malcolm H (1999) Benthic and fish monitoring of fringing reefs in the Brook, Palm and Rattlesnake Island groups: Status post 1998 coral bleaching event. Technical report: Queensland Parks & Wildlife Service, Australia, pp. 26.
- Tricas TC (1989) Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*. *Animal Behaviour*, **37**, 830–841.
- Vazquez DP, Simberloff D (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *American Naturalist*, **159**, 606–623.
- Waldichuk M (1987) Natural versus anthropogenic impacts. *Marine Pollution Bulletin*, **18**, 143–144.
- Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs*, **2**, 49–63.
- Webster PJ, Holland GJ, Curry JA *et al.* (2005) Changes in tropical cyclone, number, duration and intensity in a warming environment. *Science*, **309**, 1844–1846.
- Westneat MW, Alfaro ME, Wainwright PC *et al.* (2005) Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proceedings of the Royal Society B – Biological Sciences*, **272**, 993–1000.
- Wilkinson C (2004) *Status of Coral Reefs of the World: 2004*. Australian Institute of Marine Science, Townsville, Queensland.
- Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: *The Ecology of Coral Reef Fishes* (ed. Sale PF), pp. 437–474. Academic Press, San Diego, CA.
- Williams SL, Heck KL (2001) Seagrass community ecology. In: *Marine Community Ecology* (eds Bertnes MD, Gaines SD, Hay ME), pp. 317–337. Sinauer Associates, Sunderland, MA, USA.
- Williams ID, Polunin NVC (2000) Differences between protected and unprotected Caribbean reefs in attributes preferred by dive tourists. *Environmental Conservation*, **27**, 382–391.
- Williams ID, Polunin NVC, Hendrick V (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series*, **222**, 187–196.
- Wilson SK (2004) Growth, mortality and turnover rates of a detritivorous blenny. *Marine Ecology Progress Series*, **284**, 253–259.
- Witman JD, Dayton PK (2001) Rocky subtidal communities. In: *Marine Community Ecology* (eds Bertnes MD, Gaines SD, Hay ME), pp. 339–366. Sinauer Associates, Sunderland, MA, USA.
- Wooldridge S, Done T, Berkemans R (2005) Precursors for resilience in coral communities in a warming climate: a belief network approach. *Marine Ecology Progress Series*, **295**, 157–169.
- Wootton JT (1998) Effects of disturbance on species diversity: a multitrophic perspective. *American Naturalist*, **152**, 803–825.