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EFFECTS OF CLIMATE-INDUCED CORAL BLEACHING ON CORAL-REEF FISHES — ECOLOGICAL AND ECONOMIC CONSEQUENCES

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Abstract Global climate change is having devastating effects on habitat structure in coral-reef ecosystems owing to extreme environmental sensitivities and consequent bleaching of reef-building scleractinian corals. Coral bleaching frequently causes immediate loss of live coral and may lead to longer-term declines in topographic complexity. This review identifies coral cover and topographic complexity as critical and distinct components of coral-reef habitats that shape communities of coral-reef fishes. Coral loss has the greatest and most immediate effect on fishes that depend on live corals for food or shelter, and many such fishes may face considerable risk of extinction with increasing frequency and severity of bleaching. Coral loss may also have longer-term consequences for fishes that require live corals at settlement, which are compounded by devastating effects of declining topographic complexity. Topographic complexity moderates major biotic factors, such as predation and competition, contributing to the high diversity of fishes on coral reefs. Many coral-reef fishes that do not depend on live coral are nonetheless dependent on the topographic complexity provided by healthy coral growth. Ecological and economic consequences of declining topographic complexity are likely to be substantial compared with selective effects of coral loss but both coral cover and topographic complexity must be recognised as a critical component of habitat structure and managed accordingly. Urgent action on the fundamental causes of climate change and appropriate management of critical elements of habitat structure (coral cover and topographic complexity) are key to ensuring long-term persistence of coral-reef fishes.

Introduction

The world's climate is constantly changing and has a major influence on all biological processes, species, and ecosystems. Most notably, extreme and rapid shifts in climatic conditions have a pervasive influence on temporal patterns of biodiversity; major episodes of species extinctions (e.g., the end-Permian extinction event) and diversification are strongly associated with periods of rapid climate change (e.g., Sepkoski 1998, Benton & Twitchett 2003). Currently, mean atmospheric temperatures are increasing at a largely unprecedented rate, with concomitant changes in many other climatic variables (e.g., rainfall, incidences of extreme climate events). The current ongoing rate of

Table 1 Exponential increase in research on ecological effects of global climate change within marine and freshwater environments

Decade	Topic of research		
	Climate change	+Ecology	+Marine & freshwater
1972–1979	54	0	0
1980–1989	136	2	0
1990–1999	11,190	1054	17
2000–2007	19,259	2854	123
Total	30,160	3910	140

Note: Data represent numbers of Institute for Scientific Information (ISI) published papers included under each topic (climate change, ecology, and marine and freshwater research) considered hierarchically (records start in 1972).

warming ($\sim 0.02^{\circ}\text{C yr}^{-1}$) is greater than at any time in the last 1000 yr, largely due to anthropogenic activities (Houghton et al. 2001, P.D. Jones & Moberg 2003, Houghton 2005). Atmospheric temperatures have been much higher (up to 10°C warmer) in the geological past, but recent temperature increases follow a long period of relative stability and current climatic conditions have not been experienced for more than 120,000 yr (Houghton 2005). Global warming is also expected to continue for the next century due to continued increases in greenhouse gas emissions and the inertia in the climate system (Houghton et al. 2001).

The effects of climate change on the biology and ecology of organisms are receiving considerable and increasing attention in the scientific literature (Table 1). The most apparent effects of recent climate change are changes in phenology (e.g., altered timing of breeding activities; Walther et al. 2002, 2005, Parmesan & Yohe 2003, Høye et al. 2007) and shifts in the distribution of species (e.g., Thomas et al. 2004, Perry et al. 2005, Poloczanska et al. 2007). Climate change has also been implicated in dramatic shifts in species composition and community structure across a number of important and highly sensitive ecosystems (e.g., arctic, arid, tropical rainforests and coral-reef ecosystems), as well as contributing to species extinctions within these systems (J.H. Brown et al. 1997, Walther et al. 2002, S.E. Williams et al. 2003, Thomas et al. 2004). Thomas et al. (2004) predict that 15–37% of species in terrestrial ecosystems will be “committed to extinction” given a 2.0°C increase in mean global atmospheric temperatures. Impending species losses will not only alter biological diversity but potentially reduce productivity and ecosystem stability, increasing sensitivity to future disturbances and increasing the likelihood of ecosystem collapse (Tilman 2000, Myers & Knoll 2001).

The devastating effects of recent climate change were first recognised and are most pronounced on coral reefs, where there are clear links between increasing ocean temperatures and regional-scale bleaching of scleractinian corals (E.H. Williams & Bunkley-Williams 1990, Glynn 1991, Walther et al. 2002, Parmesan 2006). Climate-induced coral bleaching has caused massive devastation to coral-reef habitats (Hoegh-Guldberg 1999, Wilkinson 2000a) and is predicted to become more frequent and more severe in coming decades (Sheppard 2003, Donner et al. 2005). Scleractinian corals function exceedingly close to their upper thermal limit, at which bleaching may occur when sea temperatures exceed normal local limits by as little as 1.0°C (Jokiel & Coles 1990). The increasing occurrence and importance of climate-induced coral bleaching reflects gradual increases in global sea-surface temperatures, which have increased by 0.6°C in the last century (Lough 2000, Hoegh-Guldberg 2004), bringing baseline ocean temperatures much closer to the maximum thermal tolerances for reef corals. Consequently, naturally occurring thermal anomalies (e.g., El Niño) will

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increasingly exceed thermal tolerances of corals, resulting in more frequent and severe episodes of coral bleaching (Hoegh-Guldberg 1999, Stone et al. 1999).

While linkages between global climate change, thermal stress and coral bleaching have been well studied and are becoming better understood (reviewed by B.E. Brown 1997, Douglas 2003, Hughes et al. 2003, Hoegh-Guldberg 2004), the ecological ramifications of climate-induced coral bleaching for fishes and other coral-reef organisms are only just beginning to become apparent (e.g., G.P. Jones et al. 2004, Aronson & Precht 2006, Graham et al. 2006). Corals (especially, reef-building scleractinian corals) are fundamental to the functioning of coral-reef ecosystems, contributing to primary production, nutrient recycling, and reef growth (Hoegh-Guldberg 2004, Wild et al. 2004). Scleractinian corals are also the primary habitat-forming species (foundation species; Dayton 1972) in coral-reef habitats (e.g., Connell et al. 1997). Removal or destruction of corals will therefore profoundly alter the structure and dynamics of coral-reef habitats, with potentially significant effects on highly diverse assemblages of species that associate with coral reefs (e.g., Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2007). This review considers the effects of climate-induced coral bleaching on coral-reef fishes, which are an important component of coral-reef ecosystems, in terms of both their economic value (Westmacott et al. 2000a) and ecological function (Bellwood et al. 2004, Hughes et al. 2007). More than one quarter of known fish species are strongly associated with coral reefs (Spalding et al. 2001) and will be increasingly affected by ongoing degradation of coral-reef habitats caused or exacerbated by climate-induced coral bleaching (G.P. Jones et al. 2004, Munday 2004a, Pratchett et al. 2006).

This review provides the first comprehensive assessment of effects of climate-induced coral bleaching on coral-reef fishes. Climate-induced coral bleaching has had major effects on the biological and physical structure of coral-reef habitats in recent years (mostly since 1998; e.g., Wilkinson 2000a,b) and numerous studies have documented concomitant changes in the abundance, diversity or composition of fishes (Shibuno et al. 1999, Booth & Beretta 2002, McClanahan et al. 2002a, Spalding & Jarvis 2002, Munday 2004a, Sano 2004, Bellwood et al. 2006a, Garpe et al. 2006, Graham et al. 2006, Pratchett et al. 2006). These studies concur that communities of coral-reef fishes are strongly influenced by changes in habitat structure caused by climate-induced coral bleaching, but there is little consensus on the processes involved or the key aspects of habitat structure that shape communities of coral-reef fishes. This review examines associations between coral-reef fishes and benthic reef habitats and identifies two critical components of habitat structure, namely coral cover and topographic complexity. Changes in the abundance of coral-reef fishes following mass bleaching are contrasted with loss of coral versus declining topographic complexity, emphasising differences in the timing of these effects. These data are also used to forecast future effects of climate-induced coral bleaching on diversity and composition of reef fish assemblages. Notably, many studies have warned of impending waves of species extinctions due to climate-induced degradation of marine and terrestrial habitats (Walther et al. 2002, Thomas et al. 2004). Herein, threatened species of coral-reef fishes are identified based on their susceptibility to coral loss, combined with biological attributes (e.g., restricted geographic range and rarity; McKinney 1997) that exacerbate extinction risk. Finally, economic consequences of expected changes in the abundance, diversity and composition of coral-reef fishes are considered, with a view to adapting management strategies that will minimise economic costs of climate-induced coral bleaching.

Mass bleaching: geographic extent and differential effects

Bleaching is a stress response common among scleractinian and alcyonarian corals, clams and anemones that causes the pigmented symbiotic microalgae (zooxanthellae; Odum & Odum 1955) to be expelled, leaving the animal tissue pale or white (Hoegh-Guldberg 1999). Persistent low levels of natural or 'background' bleaching occur on all coral reefs (E.H. Williams & Bunkley-Williams

Use single quotes
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works

1990) contributing to natural attrition and turnover among corals. However, 'mass bleaching' in which multiple species exhibit unusually high incidences of bleaching tends to reflect extreme environmental stresses (Glynn 1991). Mass bleaching may result from high or low water temperatures, excessive ultraviolet radiation, aerial exposure, reduced salinity, high sedimentation, pollutants, or toxins (E.H. Williams & Bunkley-Williams 1990, Glynn 1991, S.V. Smith & Buddemeier 1992, B.E. Brown 1997, Hoegh-Guldberg 1999). Recent and severe mass bleaching events have primarily resulted from positive thermal anomalies, linked to global climate change (Glynn 1991, Hoegh-Guldberg 1999). In the most extreme example, global mass bleaching in 1998 resulted from severe El Niño conditions (Wilkinson 1998, Stone et al. 1999), combined with the Indian Ocean dipole (Saji et al. 1999), which dramatically increased sea-surface temperatures throughout the tropical Pacific, Indian and Atlantic Oceans (Goreau et al. 2000). Throughout 1998, mass bleaching occurred on an unprecedented geographic scale (Goreau et al. 2000) and effectively 'destroyed' 16% of the coral reefs around the world (Wilkinson 2000a).

The 1998 global mass bleaching was the most devastating and widespread bleaching event ever recorded and contributed greatly to increased acceptance of global climate change as both a real phenomenon and a significant threat to entire ecosystems (Walther et al. 2002). The significance of this event was highlighted by the death of coral colonies that had survived 100–1000 yr of environmental fluctuations and climate change (Hodgson 1999, Goreau et al. 2000). Effects of the 1998 bleaching were nonetheless spatially variable, both at very large (geographic scales; McClanahan et al. 2007a) and very small scales (e.g., between adjacent coral colonies; Marshall & Baird 2000). Coral bleaching was particularly severe on coral reefs in the Indian Ocean, where coral cover declined by an average of 46% following the 1998 bleaching (Hoegh-Guldberg 2004). In contrast, coral bleaching killed only 3% of corals in the south-west Pacific (Papua New Guinea and Australia's Great Barrier Reef [GBR]), although there were isolated incidences of very high (up to 90%) coral mortality (Berkelmans & Oliver 1999). Since 1998, there have been only isolated instances of mass bleaching (e.g., Berkelmans et al. 2004, McClanahan et al. 2007b, Penin et al. 2007) but further mass bleaching on the scale of the 1998 event is inevitable given sustained and ongoing climate change (Sheppard 2003, Hoegh-Guldberg 2004, Donner et al. 2005).

A notable and recurring pattern in the effects of bleaching on coral communities is strong differences in bleaching susceptibilities among coral taxa. Following bleaching, some coral species may become locally extinct while others appear largely unaffected (e.g., Marshall & Baird 2000, Loya et al. 2001, Floros et al. 2004, McClanahan et al. 2004, 2007a). In general, there is a clearly defined hierarchy of bleaching susceptibilities, at least among coral genera (B.E. Brown & Suharsono 1990, Marshall & Baird 2000, McClanahan et al. 2004, 2007a, Figure 1). However, coral bleaching is possibly less selective than some other major disturbances, such as outbreaks of the corallivorous seastar *Acanthaster planci* and storm damage (e.g., Hughes & Connell 1999, Figure 1). Taxonomic differences in susceptibility to bleaching are generally ascribed to physiological and morphological attributes, such as colony integration (Soong & Lang 1992, Baird & Marshall 2002) and tissue thickness (Loya et al. 2001). However, there is also marked intraspecific variation in susceptibility to bleaching, especially during moderate bleaching (Baird & Marshall 2002). Susceptibility to bleaching and subsequent survival of corals may vary according to differences in their depth and habitats (Hoegh-Guldberg & Salvat 1995), history of thermal stresses (Jokiel & Coles 1990, B.E. Brown et al. 2002, McClanahan & Maina 2003), differences in thermal sensitivities of symbionts (Baker 2001) and fine-scale hydrodynamics (Nakamura & van Woesik 2001, McClanahan et al. 2005). Variable responses of coral species to thermal stress both within reefs and across the tropical oceans suggest there is some potential for corals and their endosymbionts to adapt to changing climatic conditions (Douglas 2003, Hughes et al. 2003). It is clear that some corals are extremely resistant to increasing temperatures, rarely showing any visible signs of coral bleaching (Marshall & Baird 2000). Given predicted increases in the severity and frequency

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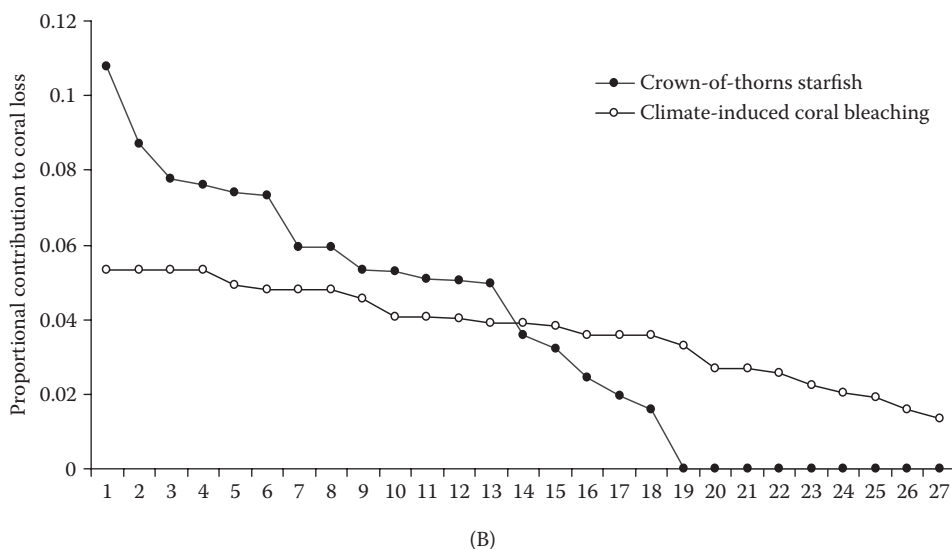
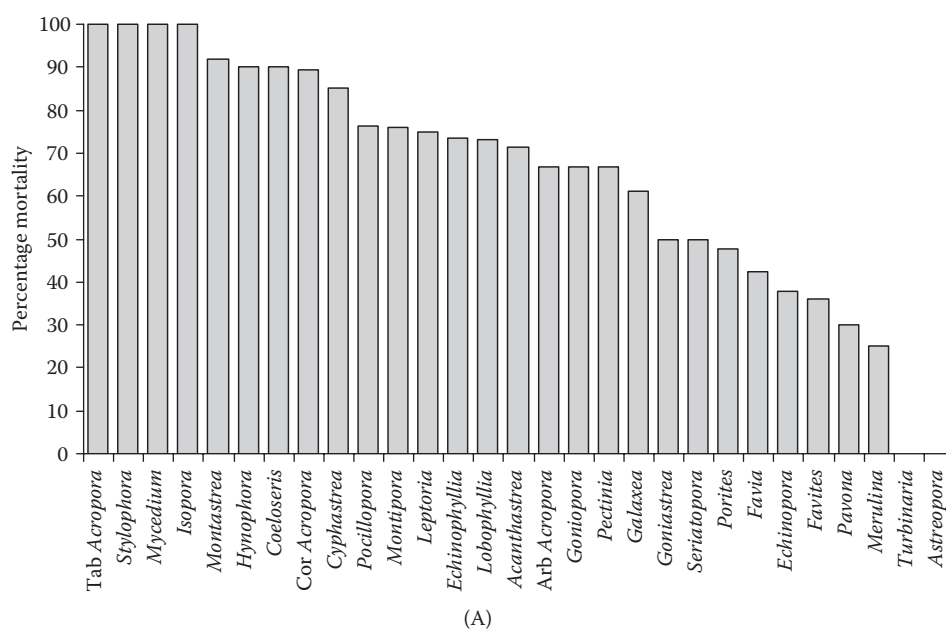


Figure 1 Selectivity of coral disturbances. (A) Variation in bleaching susceptibility among different coral types (genera plus growth forms: Tab, tabular; Cor, corymbose; Arb, arborescent) on the Great Barrier Reef (Marshall & Baird 2000). (B) Selectivity of coral bleaching versus outbreaks of *Acanthaster planci* (Pratchett 2001), showing taxonomic contributions to overall coral loss by each of the worst-affected coral species, where both disturbances caused ~50% decline in overall coral cover. *Note:* Coral rankings also differ between disturbances, so numbers do not refer to a particular coral species.

of coral bleaching, taxonomic differences in susceptibility to bleaching are likely to become a major driver of community structure and species diversity for scleractinian corals (Marshall & Baird 2000, Hughes et al. 2003, McClanahan et al. 2007a), with concomitant influences on the structure and diversity of communities of coral-reef fishes.

Associations between fishes and coral-reef habitats

Coral-reef fishes strongly associate with conspicuous features of habitat structure (e.g., G.P. Jones & Syms 1998, Munday & Jones 1998) but there are opposing schools of thought on the critical aspects of coral-reef habitats. Certain authors (e.g., G.P. Jones 1988, Holbrook et al. 2000, 2002, 2006, Munday 2000, G.P. Jones et al. 2004) consider that live coral cover has a major influence on the distribution and abundance of coral-reef fishes. Accordingly, major changes in the abundance, diversity or composition of fishes have been related to extensive coral loss (D.M. Williams 1986, Sano et al. 1987, G.P. Jones et al. 2004, Munday 2004a, Pratchett et al. 2006). Alternatively, there is considerable correlative evidence linking the abundances and diversity of coral-reef fishes with spatial and temporal variation in topographic complexity (e.g., Luckhurst & Luckhurst 1978, McClanahan 1994, Jennings et al. 1996, Öhman & Rajasuriya 1998, Lawson et al. 1999, Gratwicke & Speight 2005, Garpe et al. 2006, Wilson et al. 2007) and some authors perceive that live coral is largely irrelevant, except in providing habitat diversity and topographic complexity (Sale 1991, Lindahl et al. 2001, Garpe et al. 2006). Ultimately, both coral cover and topographic complexity may be critical elements of coral-reef habitats, although they may influence different components of reef fish assemblages. For example, coral cover is important for specialist fishes that depend on corals for food or shelter (D.M. Williams 1986, Lewis 1997, 1998, Syms 1998, Munday 2000, Pratchett et al. 2006), whereas topographic complexity plays a key role in enhancing diversity of coral-reef fishes (Lindahl et al. 2001, Gratwicke & Speight 2005, Graham et al. 2006).

The relative importance of coral cover versus topographic complexity is critical to understanding the effects of habitat perturbations in coral-reef ecosystems (Wilson et al. 2006). Comparative studies on the effects of habitat perturbations on coral-reef fishes have differentiated between disturbances that affect live coral cover versus topographic complexity (e.g., Sano et al. 1987, Wilson et al. 2006). Disturbances are separated into (1) biological disturbances (e.g., climate-induced coral bleaching, outbreaks of *A. planci*, and coral disease), which kill corals without immediately compromising the integrity of coral skeletons (e.g., Sano et al. 1987, Garpe et al. 2006) and (2) physical disturbances (e.g., severe tropical storms and tsunamis), which break down, displace and/or overturn entire coral colonies, simultaneously reducing both live coral cover and structural complexity (e.g., Cheal et al. 2002, Halford et al. 2004, Baird et al. 2005). Biological disturbances can have severe effects but these effects appear to be limited to fishes that are highly dependent on corals for food or shelter (e.g., D.M. Williams 1986). In contrast, physical disturbances that cause a loss of topographic complexity can have much more wide-ranging effects (e.g., Sano et al. 1987) because many coral-reef fishes that do not depend on live corals are nonetheless dependent on topographic complexity provided by healthy coral growth (e.g., Carpenter et al. 1981, Lawson et al. 1999, Gratwicke & Speight 2005, Glynn 2006). At Iriomote Island, Japan, healthy, diverse and topographically complex coral assemblages were converted to a homogeneous flat plain of unstructured coral rubble (Sano et al. 1987). As a consequence, 47 of 62 species (76%) of fishes completely disappeared and 9 of 15 remaining species exhibited significant declines in abundance. Extirpated species were partly replaced by more generalist species but overall species richness on resulting rubble banks was a fraction (35%) of the species richness recorded in former coral-dominated habitats (Sano et al. 1987). Notably, declines in coral cover and topographic complexity recorded at Iriomote Island were caused by a biological disturbance (outbreaks of *A. planci*). While biological disturbances do not directly affect the structural integrity of coral skeletons, exposed coral skeletons are highly susceptible to physical and biological erosion (Hutchings 1986, Glynn 1997) leading to their eventual (after 4–10 yr) collapse and gradual declines in structural complexity (e.g., Sano et al. 1987, Sheppard et al. 2002). Consequently, longer-term consequences of biological disturbances (including climate-induced coral bleaching) may be analogous to physical disturbances, affecting both live

coral cover and the physical structure of coral-reef habitats (e.g., Sheppard et al. 2002, Garpe et al. 2006, Graham et al. 2006).

Effects of climate-induced coral bleaching on coral-reef fishes

Climate change is rapidly emerging as the single greatest threat to coral-reef fishes (Wilson et al. 2006, Munday et al. 2007, Pratchett et al. 2007). Munday et al. (2007) reviewed direct effects of climate changes (e.g., ocean warming, acidification, sea-level rise) on the reproductive potential and dispersion of coral-reef fishes. Such effects are likely to become increasingly important in the future (Poloczanska et al. 2007). Currently however, the most devastating effects of climate change in coral-reef ecosystems relate to locally severe and geographically extensive episodes of coral bleaching (S.V. Smith & Buddemeier 1992, Goreau et al. 2000, Munday et al. 2007), which significantly alter the biological and physical structure of coral-reef habitats and thereby affect coral-reef fishes (G.P. Jones et al. 2004, Munday 2004a, Pratchett et al. 2006). Until 1998 very few studies had explored the broader ramifications of coral bleaching and associated habitat modification for reef-associated motile organisms (but see Glynn 1985, Tsuchiya et al. 1992). However, major effects of coral bleaching on coral-reef fishes would be anticipated given prior research showing responses of fishes to coral loss and habitat modification caused by outbreaks of *A. planci* (D.M. Williams 1986), severe tropical storms (e.g., W.J. Walsh 1983, Letourneur et al. 1993) and experimental disturbances (Lewis 1997, 1998, Syms 1998).

To assess effects of coral bleaching on coral-reef fishes, this review compiled data from six independent studies (Shibuno et al. 1999, Booth & Beretta 2002, Spalding & Jarvis 2002, Munday 2004a, Sano 2004, Pratchett et al. 2006), which together documented changes in abundance of 116 species of coral-reef fishes in the aftermath of mass bleaching. Densities of fishes were recorded 1–3 yr post-bleaching and compared with densities recorded before the bleaching. Only 45 of 116 fishes exhibited significant changes in abundance, and responses ranged from local extinction to several-fold increases in abundance (Figure 2). Fishes that increased in abundance were mostly dietary and habitat generalist species (e.g., roving herbivores) that appear to move into areas vacated by competitively dominant specialist species (see also Hart et al. 1996). Fishes that exhibited declines in abundance were mostly species that depend on corals for food or shelter and probably died as a direct result of coral depletion (e.g., Kokita & Nakazono 2001, G.P. Jones et al. 2004, Munday 2004a, Pratchett et al. 2006). It is possible that declines in abundance of fishes may result from movement of fishes to unaffected habitats (e.g., W.J. Walsh 1983, Letourneur et al. 1993). However, the potential for coral-reef fishes to find more suitable habitats following extensive coral bleaching may be very limited due to the scale of bleaching (e.g., Berkelmans et al. 2004) relative to potential movement of post-settlement reef fishes (e.g., Chapman & Kramer 2000). Furthermore, competition among coral-reef fishes and priority effects in the occupation of habitats are likely to prevent successful colonisation of displaced individuals (Almany 2003). Fishes in highly degraded habitats are also likely to have experienced a protracted decline in resource availability, leading to reduced physiological condition (Pratchett et al. 2004), which would further limit their ability to outcompete conspecifics and invade new habitats.

The effects of coral bleaching and coral loss on coral-reef fishes may not always be immediately apparent or become manifest through short-term declines in adult abundance. For example, reduced availability of preferred coral prey can have significant but sublethal effects on coral feeding fishes (Kokita & Nakazono 2001, Pratchett et al. 2004, Berumen et al. 2005). Pratchett et al. (2004) showed that there was no short-term decline in the abundance of an obligate coral-feeding butterfly-fish (*Chaetodon lunulatus*) despite a 55% decline in coral cover caused by mass bleaching. However, *C. lunulatus* did exhibit significant declines in physiological condition (Pratchett et al. 2004), which

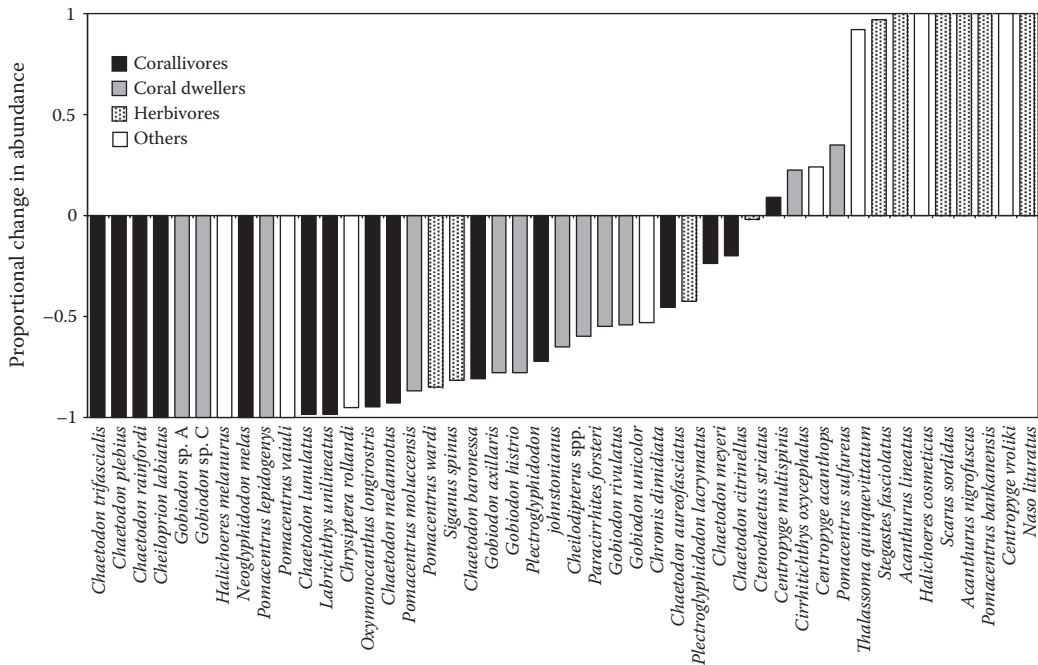


Figure 2 Changes in the abundance of coral reef fishes following climate-induced coral bleaching. Data presented for 45 (of 116) species that exhibited significant changes in abundance following mass bleaching that caused >50% coral loss. Data sources: Shibuno et al. (1999), Booth & Beretta (2002), Spalding & Jarvis (2002), Munday (2004a), Sano (2004), Pratchett et al. (2006).

contributed to reduced survival and eventual population declines (Pratchett et al. 2006). Similarly, reductions in live coral may limit settlement and recruitment for fishes that are otherwise unaffected by coral depletion (Booth & Beretta 2002, G.P. Jones et al. 2004, Osenberg et al. 2006, Feary et al. 2007a,b). Limitations to population replenishment will undoubtedly reduce species abundance but these effects may not be immediately apparent (Feary et al. 2007b).

Several studies have documented extensive declines in the abundance and diversity of coral-reef fishes several years (>3 yr) after climate-induced coral bleaching (e.g., Garpe et al. 2006, Graham et al. 2006). These studies attribute changes in reef fish assemblages to the delayed effect of structural collapse of dead corals, which reduces overall topographic complexity of coral-reef habitats (see also Sano et al. 1987). Many different fishes declined in abundance, including herbivorous fishes (Graham et al. 2006) that might be expected to benefit from the increased abundance of algae following extensive coral loss (Table 2, Figure 3). However, delayed effects of coral bleaching on reef fishes may also be due to either (1) a lack of recruitment by fishes that need coral at settlement (e.g., G.P. Jones et al. 2004), (2) reductions in survivorship and/or reproductive output of fishes that lead to gradual declines in population size (Pratchett et al. 2004) or (3) secondary declines in the abundance of piscivorous fishes due to declines in coral-dependent prey fishes. Consequently, loss of live coral may be as important as declining topographic complexity in protracted effects of coral bleaching on coral-reef fishes (e.g., G.P. Jones et al. 2004, Table 2). Existing studies have never attempted to separate these effects, although there is substantial correlative and indirect evidence that both live coral and topographic complexity are important attributes of coral-reef habitats and strongly affect communities of coral-reef fishes (Carpenter et al. 1981, Lawson et al. 1999, Holbrook et al. 2000, Munday 2000, Garpe & Öhman 2003, Graham et al. 2006). Longer-term effects of coral bleaching on coral-reef fishes are poorly understood, mostly because there are few studies that

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Table 2 Temporal basis of contrasting effects of coral loss versus declines in topographic complexity on coral reef fishes: examples of major families of coral reef fishes affected by coral loss versus declines in topographic complexity during the periods <3 yr and 3–10 yr post-bleaching

	Period	
	<3 yr	3–10 yr
Live coral cover	Chaetodontidae	Labridae
	Gobiidae	Pomacentridae
Topographic complexity	None	Acanthuridae
Scaridae		

have measured changes in the reef fish assemblages >3 yr after bleaching (G.P. Jones et al. 2004, Bellwood et al. 2006a, Graham et al. 2006), and no studies have sampled >10 yr after bleaching.

Loss of live coral

The most immediate and predictable effect of climate-induced coral bleaching is a decline in live coral cover caused by mortality of entire coral colonies as well as partial loss of live tissue for many surviving corals (e.g., Baird & Marshall 2002). Coral loss reduces resources available to coral-dependent fishes, with expected consequences for individual condition (e.g., Kokita & Nakazono 2001, Pratchett et al. 2004) and population size (e.g., Munday 2004a, Pratchett et al. 2006). The important question is what proportion of fishes actually depend on live corals for their long-term persistence. A wide range of associations exist between reef fishes and live corals, from species that depend on live coral for food and habitat (Munday 2002, Pratchett 2005), to species that are rarely associated with live coral and are characteristic of sites with low coral cover (Sano et al. 1984). Current estimates of the proportion of coral-reef fishes with apparent and direct reliance on live corals are 9–11% (G.P. Jones et al. 2004, Munday et al. 2007). Of 1221 coral-reef fishes recorded on the GBR, Munday et al. (2007) estimated that 104 species (9%) have direct and explicit reliance on corals (Figure 4; see also G.P. Jones et al. 2004). These species include (1) corallivorous fishes that feed on live coral tissue (e.g., many *Chaetodon* butterflyfishes; Pratchett et al. 2006), (2) coral-dwelling fishes, including species living entirely within the branches of live coral colonies (e.g., *Gobiodon* coral-gobies; Tsuchiya et al. 1992, Munday et al. 1997, Munday 2004a.), as well as species that shelter within live corals when threatened but otherwise feed above their host coral (e.g., *Dascyllus* damselfishes; Holbrook et al. 2002) and (3) fishes that settle on or near live corals but do not necessarily associate with coral throughout their lives (e.g., many damselfishes; Booth & Beretta 2002, Feary et al. 2007a). Based on these findings, coral loss is expected to affect <12% of coral-reef fishes. However, G.P. Jones et al. (2004) showed that 75% of coral-reef fishes declined in abundance following extensive (90%) coral mortality and habitat modification caused by climate-induced coral bleaching and sedimentation, which might suggest that importance of corals for coral-reef fishes has been underestimated.

It is intuitive that coral-dependent fishes will be significantly and adversely affected by coral bleaching and coral loss. Effects of coral depletion on strongly coral-dependent fishes are nonetheless highly variable. For example, Munday (2004a) examined effects of coral bleaching and coral loss on coral-dwelling gobies. Although all species were obligate coral dwellers and highly dependent on live corals, declines in the proportional abundance of the six species ranged from 50% to 100% (Munday 2004a). Specific responses of coral-dependent fishes may vary according to (1) the extent to which populations are limited by the availability of live coral, (2) their versatility in use

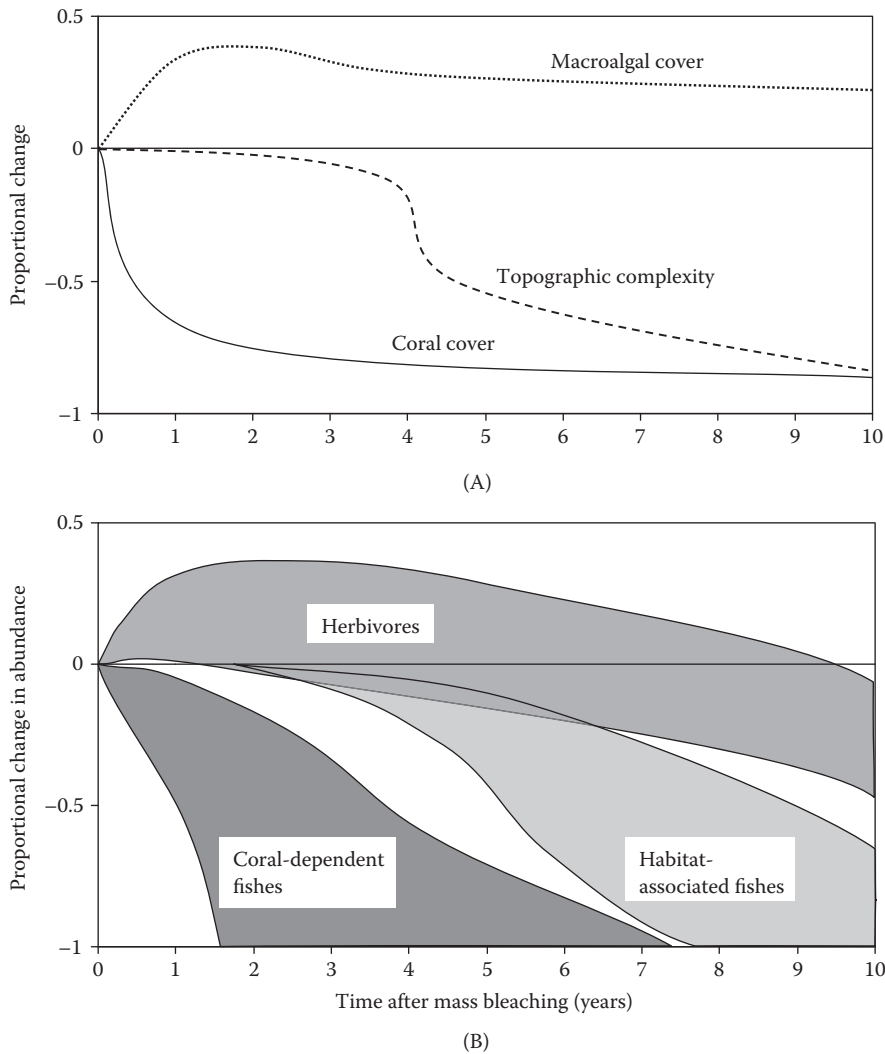


Figure 3 Conceptual diagram of changes in coral reef habitats and fish communities following climate-induced coral bleaching. (A) Timing and magnitude of proportional changes in macroalgal cover, topographic complexity and coral cover. (B) Response envelopes for strongly coral-dependent fishes (e.g., obligate coral-livores), habitat-associated fishes and herbivores.

of alternate resources and (3) the degree to which sublethal responses mitigate or delay declines in abundance (Wilson et al. 2006). Importantly, highly specialised coral-dependent fishes will respond to changes in the abundance of their predominant food or habitat type rather than changes in live coral cover *per se*.

Corallivorous fishes

Corallivorous fishes have the most apparent and direct reliance on live corals (Randall 1974) and are consistently among the worst-affected fishes following extensive coral loss (e.g., Bouchon-Navaro et al. 1985, D.M. Williams 1986, Kokita & Nakazono 2001, Pratchett et al. 2006, Wilson et al. 2006, Figure 2). Worldwide, there are 117 species of coral-reef fishes from 10 families that have been reported to feed, at least in part, on scleractinian corals (A. Cole unpublished data). The most diverse

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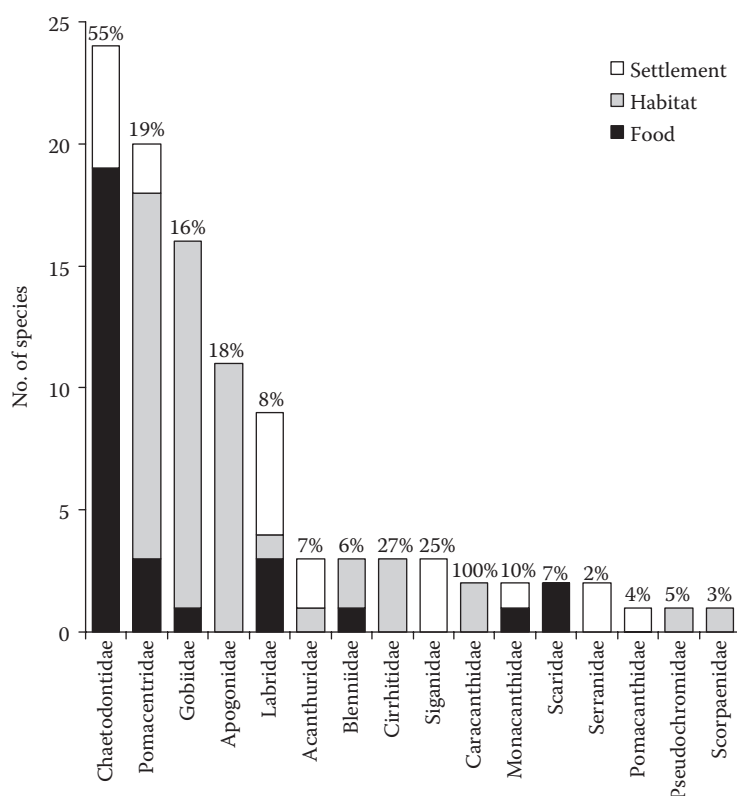


Figure 4 Coral-dependent fishes on the Great Barrier Reef. Numbers indicate percentage of species in each family considered to be coral dependent out of total number of species listed for each family in Randall et al. (1997). Where species used corals for more than one purpose, precedence was given to food, then habitat, and then recruitment.

and best-studied group of corallivorous fishes are the butterflyfishes, family Chaetodontidae (e.g., Tricas 1985, Harmelin-Vivien & Bouchon-Navaro 1983, Harmelin-Vivien 1989, Irons 1989, Sano 1989, Zekeria et al. 2002, Pratchett 2005, 2007a). Other families with significant numbers of coral-feeding species are the Pomacentridae (14 species), Monacanthidae (9 species), Labridae (8 species), Balistidae (7 species), and Tetraodontidae (7 species) (A. Cole unpublished data). Despite this diversity, corallivorous fishes still only account for a small proportion (<5% of species) of the overall diversity of fishes on coral reefs (Spalding et al. 2001). However, live coral may also contribute to the nutritional intake of many fishes that do not feed directly from the surface of corals. For example, many coral-reef fishes opportunistically exploit and derive considerable benefit from feeding on coral gametes (Pratchett et al. 2001, McCormick 2003). Corals also produce large quantities of mucus (e.g., $1.7 \text{ m}^{-2} \text{ day}^{-1}$), which is enriched by trapping organic matter from the water column (Wild et al. 2004) and probably represents a significant input to the trophodynamics of coral-reef ecosystems (Wilson et al. 2003). Many fishes may supplement diets with coral mucus and tissue, which may go undetected because coral tissue is often indistinguishable from exogenous material and partially digested matter in the gut (Zekeria et al. 2002). This situation may be particularly true of many cryptic coral-dwelling species, for which there is limited knowledge of feeding behaviour.

Reduced availability of coral clearly limits the abundance of corallivorous fishes (Carpenter et al. 1981, Bell & Galzin 1984, Bouchon-Navaro et al. 1985, Findley & Findley 1985, Roberts et al. 1988, Öhman et al. 1998, Cadoret et al. 1999, Bozec et al. 2005), although relationships between

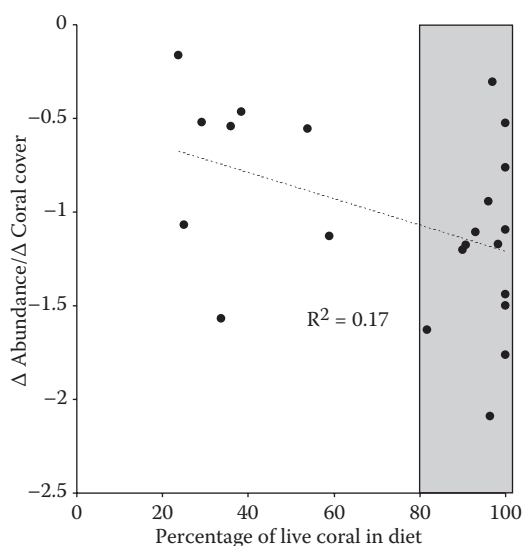


Figure 5 Declines in the abundance of 22 corallivorous fishes following coral depletion versus percentage consumption of scleractinian corals. Data extracted from 17 studies that explored fish responses following climate-induced coral bleaching, outbreaks of *Acanthaster planci*, sedimentation, and experimentally imposed disturbances. Responses (declines in abundance) are standardised for variation in proportional declines of live coral cover, following Wilson et al. (2006). Dotted line indicates line of best fit for the linear relationship between declines in the abundance of butterflyfishes versus proportional consumption of scleractinian corals. Grey shading indicates obligate corallivores.

coral cover and abundance of corallivores are not always apparent (e.g., Bell et al. 1985, Fowler 1990, Kulbicki et al. 2005). Responses of corallivorous fishes to changes in availability of corals are likely to depend on (1) their dependence on corals for food, (2) the severity and extent of coral loss and (3) the extent to which live coral (versus other factors such as recruitment) may be limiting their abundance. The extent to which corallivorous fishes feed on corals (vs. other non-coral prey) is highly variable (e.g., Hobson 1974, Pratchett 2005) and obligate coral feeders are much more affected by coral loss than facultative coral feeders (Bouchon-Navaro et al. 1985, D.M. Williams 1986, Wilson et al. 2006, Pratchett et al. 2006, Figure 5). Facultative corallivores are relatively unaffected by moderate decline in abundance of corals, presumably because they can compensate by increasing intake of non-coral prey. However, corals may represent an important and necessary component of their diet, such that even facultative corallivores are adversely affected by extensive coral loss (Pratchett et al. 2006).

Among obligate coral-feeding butterflyfishes there are marked differences in the range of different corals eaten as well as the proportional consumption of different corals. For example, *Chaetodon trifascialis* is an extreme specialist, which feeds almost exclusively on *Acropora hyacinthus* (Pratchett 2005), whereas *Chaetodon lunulatus* feeds on a wide diversity (up to 52 species) of corals (Berumen et al. 2005, Pratchett 2005). This variability in the dietary habitats of coral-feeding butterflyfishes is likely to influence their reliance on particular corals as well as their responses to different types of disturbances (Figure 6). Like facultative corallivores, highly versatile obligate corallivores can access a greater diversity of prey and may partially compensate for initial depletion of preferred prey resources by increasing intake of alternate prey types (i.e., prey switching; Pratchett et al. 2004) and increasing the area over which they forage (Tricas 1989, Kokita & Nakazono 2001, Samways 2005). Consequently, generalist species may be more resilient to changes in cover and composition of hard corals (e.g., Pratchett et al. 2004), whereas effects of disturbances

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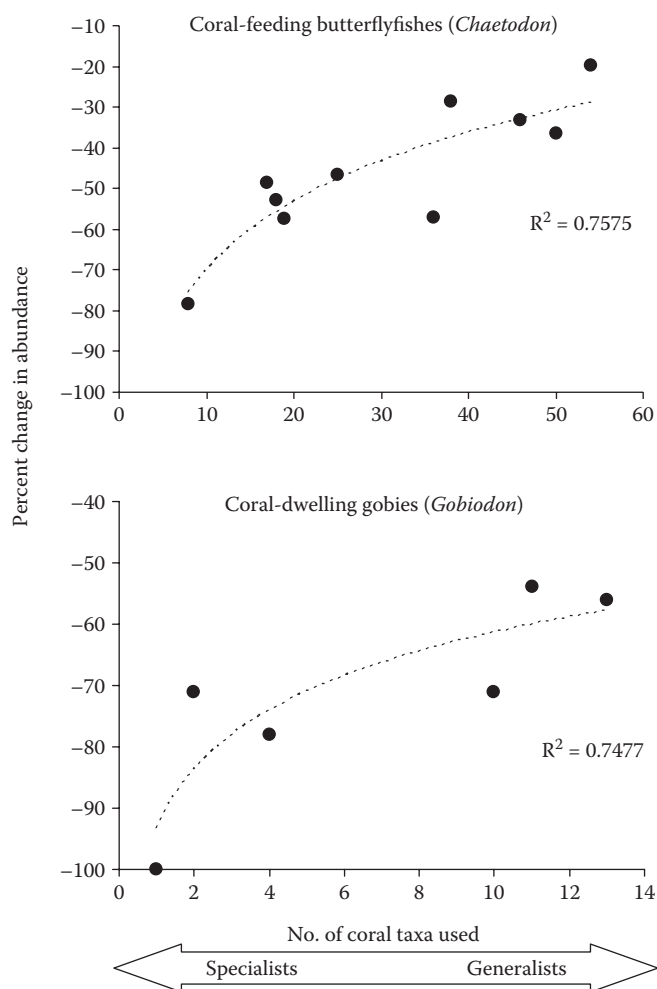


Figure 6 Declines in abundance following severe coral depletion in relation to number of different coral taxa used for strongly coral-dependent reef fishes. Data for coral-feeding butterflyfishes come from Lizard Island, northern GBR, following coral depletion caused by *Acanthaster planci* (Pratchett 2001). Data for coral-dwelling gobies are from Kimbe Bay, where global warming and coastal development caused extensive coral loss (Munday 2004a). Dotted lines indicate line of best fit for logarithmic relationship between declines in the abundance of fish species versus number of coral species that they use.

on specialist species will vary according to changes in abundance of the particular coral species on which they specialise. In Moorea, for example, recurrent disturbances (bleaching, outbreaks of *Acanthaster planci*, and severe storms) throughout the last 25 yr have substantially altered coral composition, causing a transition from *Acropora*- to *Pocillopora*- and *Porites*-dominated coral assemblages (Berumen & Pratchett 2006). Accordingly, local abundance of butterflyfishes that feed predominantly on *Acropora* spp. has declined, whilst *Pocillopora* specialists and more generalist corallivores have proliferated (Berumen & Pratchett 2006).

While dietary composition and specialisation are fundamental in determining responses of corallivorous fishes to coral losses (Pratchett et al. 2006), the range of corals consumed by coral-feeding fishes is known for <25 species (Pratchett 2005). Until recently, very few studies distinguished among coral taxa when documenting diets of coral-feeding fishes. Rather, most studies

(e.g., Harmelin-Vivien & Bouchon-Navaro 1983, Bouchon-Navaro 1986, Sano 1989, Pitts 1991, Zekeria et al. 2002) treated all scleractinian corals as a single prey category and simply distinguished between obligate versus facultative corallivores. The few studies that have explored specific prey preferences (Irons 1989, Tricas 1989, Pratchett et al. 2004, Berumen et al. 2005, Pratchett 2005, 2007a) have shown that corallivorous fishes may be very specialised, consuming only a very small suite of available coral prey. Moreover, dietary preferences of corallivorous butterflyfishes appear to be highly convergent. For example, at Lizard Island (northern GBR) most coral-feeding butterflyfishes feed predominantly on either *Acropora hyacinthus* or *Pocillopora damicornis* (Pratchett 2005), demonstrating significant selectivity for either or both these corals (Pratchett 2007a). These coral species are among the first corals affected during mass bleaching (Marshall & Baird 2000) and are highly susceptible to predation by *Acanthaster planci* (De'ath & Moran 1998, Pratchett 2007b) and displacement during storms (Madin & Connolly 2006), probably explaining why highly specialised butterflyfishes are disproportionately affected during these types of disturbance. *Chaetodon trifascialis*, for example, is often extirpated (100% decline in local abundance) even during fairly moderate (<21%) declines in live coral cover (e.g., Syms 1998). As habitat perturbations become more frequent and more severe, it appears likely that highly specialised obligate coral feeders will be increasingly replaced by much more generalist and facultative corallivores, as has already been demonstrated following recurrent disturbances in Moorea (Berumen & Pratchett 2006).

Coral-dwelling fishes

The majority of coral-dwelling fishes are relatively small in body size and depend on the complex structure provided by live coral colonies for shelter (Munday & Jones 1998). Coral-dwelling fishes comprise two fairly distinct groups. The first group, exemplified by coral gobies (*Gobiodon* spp., *Paragobiodon* spp.), generally remains hidden among the branches of their host coral colonies. This group (also including the crouchers *Caracanthus* spp., the scorpionfish *Sebastapistes cyanostigma* and some hawkfishes, e.g., *Neocirrhites armatus*) live, feed and reproduce within live corals and often remain within a single coral host for the duration of their lives. The second group of coral-dwelling fishes is the species that retreat into live corals at night or when threatened but otherwise remain in close proximity and feed above their specific coral host (e.g., *Eviota* spp., *Pomacentrus* spp., *Chromis* spp., *Dascyllus* spp.). Most coral-dwelling species have small home ranges and individuals often exhibit strong fidelity to a single coral head (Sale 1971, Feary et al. 2007a). Even species that leave their coral habitat to forage across the reef tend to exhibit strong fidelity to their shelter site (Marnane 2000).

Variation in the abundance and composition of scleractinian corals has a major influence on the structure and dynamics of coral-dwelling fishes, although the apparent strength of associations between fishes and corals are taxonomy and scale dependent (G.P. Jones 1991, Sale 1991, Jennings et al. 1996, Munday et al. 1997, Holbrook et al. 2000). While the community structure of fishes on individual coral heads can vary unpredictably from one coral head to another (Sale & Dybdahl 1975, Sale et al. 1994), distinct assemblages of fishes can be consistently found on different species and growth forms of coral (Gladfelter et al. 1980, Ebersole 1985, Tolimieri 1995, Munday et al. 1997, Holbrook et al. 2000, 2002). Suitable coral habitat also appears to be a limiting resource for many coral-dwelling fishes (Holbrook et al. 2000, Schmitt & Holbrook 2000, Munday et al. 2001, Munday 2004b) and the population dynamics of these species often match the population dynamics of their preferred coral habitats (Kuwamura et al. 1994, Munday et al. 1997). For example, even though there are peaks of recruitment among juvenile coral-dwelling gobies, the size of the adult population remains stable and is closely correlated with the number of coral colonies large enough to support a breeding pair (Kuwamura et al. 1994, Hobbs & Munday 2004). When coral colonies decline in abundance there is a corresponding decline in the abundance of coral-dwelling gobies

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(Kuwamura et al. 1994, Munday 2004a). Adult population size is less rigidly controlled by habitat availability in many other coral-dwelling species (Sale 1972, Gardiner & Jones 2005). However, these species still usually decline in abundance following significant declines in coral cover (Lewis 1998, Spalding & Jarvis 2002, G.P. Jones et al. 2004, Wilson et al. 2006), demonstrating that their habitat is in limited supply.

Many coral-dwelling fishes favour coral species from the families Acroporidae (mainly *Acropora* spp.) and Pocilloporidae (*Pocillopora*, *Stylophora* and *Seriatopora*), probably because their complex branching structure provides refuge from predation (Beukers & Jones 1997). On Indo-Pacific reefs, species of *Gobiodon* (Gobiidae), *Paragobiodon* (Gobiidae) and *Caracanthus* (Scorpaenidae) are almost exclusively associated with corals from these two families (Tyler 1971, Patton 1994, Munday et al. 1997). Similarly coral-dwelling damselfishes (Pomacentridae) from the genera *Amblyglyphidodon*, *Chromis*, *Dascyllus*, *Plectroglyphidodon*, and *Pomacentrus* are most commonly associated with acroporid and pocilloporid corals. Numerous *Eviota* and *Bryaninops* species (Gobiidae) occur where there are dense stands of acroporid corals (Larson 1985, 1987, Randall et al. 1997) and *Sebastapistes cyanostigma* (Scorpaenidae) is commonly found among the branches of pocilloporid corals (P. Munday personal observation). Coral-dwelling fishes associate with a variety of other coral taxa, but these too are usually species with a high degree of structural complexity. For example, Gardiner & Jones (2005) found that nine common cardinal-fishes (Apogonidae) exhibited strong association with the branching coral *Porites cylindrica*. Also, *Gobiodon acicularis*, one of the few *Godiodon* species to inhabit non-acroporid corals, lives among dense thickets of *Echinopora* and *Hydnophora* (Munday et al. 1999). Those coral-dwelling fishes that are not associated with complex branching corals are typically well camouflaged and cryptic, such as the elongate gobies of the genus *Bryaninops* that can be found on the stems of black corals and sea whips (Larson 1985, Randall et al. 1997).

Ironically, coral species most frequently used by coral-dwelling fishes are often those that are most susceptible to bleaching (Munday et al. 1997, Munday 2004a, Feary et al. 2007b). Overall, there is high concordance in primary coral preferences of coral-dwelling fishes (particularly for gobies and damselfishes), which means that coral bleaching tends to have a negative effect on a broad suite of coral-dwelling fishes. Despite this broad overlap in habitat preferences, coral dwellers still vary greatly in their ecological versatility, from species that inhabit just one species of coral, to species that use a wide range of available coral types (Munday 2002, Munday et al. 2007). The most specialised species (i.e., those fishes that occupy fewer coral species) appear to suffer greater declines in abundance following coral loss (Munday 2004a, Figure 6). Effects of coral mortality are greatest for highly specialised species because they are not able to adjust their patterns of habitat use as preferred coral habitats become scarcer. In contrast, the more generalist species increase their use of alternative coral species if their primary preferences decline in abundance, which results in less-serious declines in their population abundance (Munday 2004a).

Coral bleaching could further influence local abundance and population structure of coral-dwelling fishes through its effect on habitat patch size. Social group size of some coral-dwelling fishes is correlated with habitat patch size (e.g., Wong et al. 2005, Thompson et al. 2007) and the total number of all coral-dwelling fishes on a coral head often increases in proportion to the coral colony size (Munday et al. 1998). Therefore, communities of older and larger corals can support larger populations of coral-dwelling fishes. Bleaching reduces the average size of coral colonies through mortality of mature corals and this will probably reduce the overall abundance of coral-dwelling fishes (Feary et al. 2007a). Because of the close association between body size and fecundity in most coral-reef fishes, reduction in average coral colony size could also affect reproductive output for species for which the size of dominant breeding individuals is correlated with coral colony size (Kuwamura et al. 1994, Hobbs & Munday 2004).

Coral as settlement habitat

Species that closely associate with live coral as juveniles and adults commonly exhibit strong selection for live coral habitat at settlement (Gutierrez 1998, Öhman et al. 1998, Srinivasan 2007). For these species, larvae often settle directly into adult habitat and may even be cued by resident conspecifics already present in suitable habitat patches (Sweatman 1985, 1988, Booth 1992, Öhman et al. 1998, Lecchini et al. 2005). Many coral-reef fishes also associate with live coral when they first settle to the reef, even if they do not exhibit strong associations with live corals in later life (Booth & Beretta 1994, G.P. Jones et al. 2004, Feary et al. 2007b). These juvenile fishes use live colonies as a settlement cue (Öhman et al. 1998), food source (Harmelin-Vivien 1989) or to provide refuges against predation (M.S. Webster 2002). Widespread reliance on live corals around the time of settlement may explain why the effects of coral loss sometimes extend beyond species known to be coral dependent (Booth & Beretta 2002, Bellwood et al. 2006a). G.P. Jones et al. (2004) estimate that 65% of fishes on coral reefs in Papua New Guinea were preferentially associated with live coral at settlement and observed declines in population abundance of different species closely corresponded with the proportion of juveniles that settled on live coral. Furthermore, Graham et al. (2007b) documented a substantial decline in smaller size classes (<35 cm) of important fisheries species following coral bleaching and ongoing habitat degradation in the Seychelles. These declines in smaller size classes are attributed not only to increased predation and competition following loss of the physical reef structure but also to repeated recruitment failure (Graham et al. 2007b).

For fishes that are only loosely associated with coral habitats, adult survival might be largely unaffected by coral loss but settlement may be reduced (Bouchon-Navaro et al. 1985, Booth & Beretta 2002, G.P. Jones et al. 2004, Feary et al. 2007b, Graham et al. 2007b, Srinivasan 2007). Therefore, eventual declines in adult abundance result from a natural attrition combined with a lack of replenishment. The extent to which settlement failure is reflected in adult abundance depends on the severity and duration of recruitment failure, population turnover and adult longevity (Halpern et al. 2005, Feary et al. 2007b). Declines in the juvenile population will have a strong effect on adult population size if the juvenile population is relatively small compared with the adult population and population size is essentially limited by recruitment. Declines in the juvenile population will have smaller effects on the adult population if they are relatively large compared with the adult populations and there is an oversupply of juveniles available to recruit to the adult population (Halpern et al. 2005). Longevity will also influence how settlement failures affect adult populations because, for long-lived species, occasional good recruitment provides a buffer against intervening periods of little or no recruitment (storage effect; Warner & Hughes 1988), whereas adult populations of short-lived species decline rapidly following settlement failure (Bellwood et al. 2006a, Feary et al. 2007b). For longer-lived species (such as many commercially exploited fisheries species), the time lag between recruitment failure and apparent declines in adult abundance may be decades rather than years (Bellwood et al. 2006a, Graham et al. 2007b). In these cases, effects of recent mass bleachings may not have even begun to become apparent in adult populations of long-lived species.

Loss of topographic complexity

The importance of the physical structure of coral-reef habitats for fishes has been extensively studied and there is strong support for links between topographic complexity and abundance of fishes, biomass and diversity (Risk 1972, Luckhurst & Luckhurst 1978, Sano et al. 1987, Grigg 1994, Friedlander & Parrish 1998). Experiments using non-coral materials to construct artificial reefs of differing complexities (e.g., Caley & St John 1996, Gratwicke & Speight 2005), manipulation of complexity within coral colonies or assemblages (Sano et al. 1984, Lewis 1997, Syms & Jones 2000, Glynn 2006), and comparison of biological versus physical disturbances (Wilson et al. 2006) all indicate that topographic complexity has a major influence on coral-reef fish communities. Habitat

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complexity has an important influence on biotic interactions, such as predation and competition, and has a major influence on the local abundance of coral-reef fishes, especially during the early life stages (Almany 2004, Hixon & Jones 2005). Increased structural complexity moderates predation intensity and competitive interactions, thereby increasing local diversity and abundance of fishes (Hixon & Jones 2005, Lee 2006). Reef habitats with reduced topographic complexity typically support lower fish abundance, fewer species and increased evenness (Syms & Jones 2000, Gratwicke & Speight 2005, Graham et al. 2006). Loss of structural complexity is especially detrimental for small-bodied fishes (including both small species and juvenile phases of larger-bodied species) because these fishes are highly susceptible to predation and often depend on specific microhabitats to evade predators (Hixon & Beets 1993, Beukers & Jones 1997).

Climate-induced coral bleaching kills corals, but leaves the underlying skeleton completely intact (Hoegh-Guldberg 1999). Exposed coral skeletons are then subject to a whole suite of bio-eroding organisms that undermine the structural integrity of these carbonate structures (Hutchings 1986). Over time, coral skeletons of erect branching corals (e.g., *Acropora* and *Pocillopora*) break down into coral rubble (Sheppard et al. 2002, Graham et al. 2006), whereas more robust skeletons of massive corals (e.g., *Porites*) may become dislodged or gradually eroded *in situ* (Sheppard et al. 2002). These processes contribute to long-term declines in structural complexity and can ultimately result in structurally depauperate reef landscapes (e.g., Sano et al. 1987, Sheppard et al. 2002). Successive degradation of reef habitats compounds initial coral losses and significantly extends effects of coral bleaching on coral-reef fishes (e.g., Wilson et al. 2006). On reefs in the Indian Ocean, severe mass bleaching in 1998 and subsequent collapse of 3-dimensional corals have converted complex coral-dominated habitats to areas of flattened carbonate pavement or rubble fields where macroalgae now predominate (Sheppard et al. 2002, Garpe et al. 2006, Graham et al. 2006). Associated with these shifts in benthic habitats, species richness of fishes declined by as much as 50% and while coral-dependent species were disproportionately affected, many other functional groups of fishes, including herbivorous fishes, also disappeared, probably due to declines in topographic complexity (Garpe et al. 2006, Graham et al. 2006, Figure 3). Even where there is no apparent change in the abundance or species richness of fishes, coral loss and reef collapse have caused marked shifts in the community structure of fish assemblages (Bellwood et al. 2006a). In general, fish communities in degraded post-bleaching habitats are characterised by dietary and habitat generalists (e.g., omnivores and detritivores), which replace coral-dependent specialists (Bellwood et al. 2006a, Graham et al. 2006). These post-bleaching fish assemblages may be fairly resilient to future disturbances but are nonetheless undesirable because the loss of entire functional groups (e.g., corallivores and herbivores) may have ramifications for recovery, productivity and ecosystem function (Bellwood et al. 2006a).

Declines in topographic complexity are not a certain consequence of climate-induced coral bleaching. In reef habitats once dominated by erect branching corals (e.g., lagoonal habitats dominated by monospecific stands of staghorn *Acropora*) degradation of structural complexity can be fairly rapid and particularly severe, reducing complex coral habitats to flat rubble banks (e.g., Glynn 2006, Graham et al. 2006). Elsewhere, however, dead corals may remain intact for many years and may become the foundation for new coral growth (e.g., Bellwood et al. 2004, DeVantier & Done 2007). Also, on some reefs (mostly, highly exposed reef slopes) live corals contribute little to overall topographic complexity; rather the inherent complexities within the vertical reef matrix contribute most topographic relief and habitat structure (e.g., Halford et al. 2004). The extent to which reef habitats exhibit declining topographic complexity following widespread coral mortality depends on (1) the fragility of the original coral assemblage, branching corals being more susceptible to collapse than massive corals, (2) the underlying complexity of the reef framework, (3) abundances of bioeroding organisms such as excavating parrotfish (Bellwood et al. 2003) and sea urchins (McClanahan & Shafir 1990) and (4) the extent of physical erosion caused by persistent wave action or acute storms (Madin & Connolly 2006, L.W. Smith et al. 2007).

Persistence and recovery of fish assemblages

The strong linkage between coral-reef fishes and underlying habitat clearly makes them susceptible to climate-induced coral bleaching. However, provided bleaching is sporadic and does not cause 100% mortality of critical coral species, even highly susceptible fish populations may have the potential to persist and recover. For example, Holbrook et al. (2006) show that dramatic declines in fish abundance and diversity may not occur until coral cover is reduced to <10% (see also Wilson et al. 2006). Recovery of fish communities will be expected, provided there are refuge adult populations and recovery of critical aspects of the biological and/or physical structure of these habitats (e.g., Halford et al. 2004). Recovery of fish populations is reliant upon many factors, such as the continual supply of fish recruits (Doherty & Williams 1988) and the ability of fishes to reclaim space occupied prior to temporary disruptions in habitat structure. Pre-emption of space by new species may retard the recolonisation by some previous residents (Almany 2003), although competitive hierarchies can eventually reinstate species as they gradually recruit back to the reef, a process that appears to be particularly important for habitat and feeding specialists (Munday et al. 2001). Clearly however, coral-reef fishes affected by disturbance-mediated changes in coral-reef habitats must be limited by some biological or physical aspect of habitat structure (e.g., live coral cover, topographic complexity, habitat diversity or coral composition) and recovery can only occur after the habitat itself has reverted to a state suitable for settlement and survival of these fishes (Halford et al. 2004). The recovery of specialist species, for example, will be dependent upon renewed abundance of their preferred coral species.

Following major habitat perturbations, and in the absence of any further disturbances, it may take as little as 5 yr for coral cover to return to predisturbance levels (e.g., Halford et al. 2004, Gardner et al. 2005). The time taken for coral cover to increase depends on the severity and extent of coral loss, which dictates the ability of surviving corals to recover, reproduce and reseed affected areas (Hughes & Connell 1999, Riegl & Piller 2003, Golbuu et al. 2007). Importantly, isolated reefs are likely to be more sensitive to declines in viability of local populations, whereas well-connected reefs, such as those along continental margins or large archipelagos, are more likely to be reseeded by larvae from nearby and relatively unaffected populations (Ayre & Hughes 2004). Recovery will be much faster if at least some coral colonies survive the bleaching, as often occurs during mass bleaching (e.g., Baird & Marshall 2002), because growth of surviving corals leads to more rapid increases in coral cover compared with settlement and subsequent growth of new individuals (Connell et al. 1997), whereas local populations of mature corals are the most reliable source of new recruits (Hughes et al. 2000). Where viable source populations are available to initiate recovery, settlement and survival of juvenile corals will also be conditional upon the availability of suitable settlement substrata (Hughes et al. 2007). It is frequently hypothesised that local populations of herbivores play a key role in keeping reef substrata relatively free of both turf-forming and macroalgae, which facilitates the settlement and subsequent survival of coral recruits (Bellwood et al. 2004, Mumby et al. 2006, Hughes et al. 2007, Ledlie et al. 2007). Some herbivores can have negative effects on coral recruitment, either through incidental predation on coral recruits (McClanahan et al. 2005) or by promoting coralline algae that inhibit coral recruitment (Harrington et al. 2004). However, large-scale caging experiments demonstrate that exclusion of large-bodied fishes (analogous to overfishing of herbivorous fishes) leads to extensive growth of fleshy macroalgae, which suppresses fecundity, recruitment and survival of corals (Hughes et al. 2007).

Coral mortality following bleaching provides space on the reef that is rapidly colonised by turf-forming algae (Diaz-Pulido & McCook 2002). On reefs where herbivorous fishes and/or sea urchins are abundant, algal assemblages may remain as cropped turf forms following coral bleaching and coral loss (Aronson et al. 2002, Arthur et al. 2005). However, where grazing pressure is low, or if coral mortality is extensive, local stocks of turf-feeding species may be unable to counter increased

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algal abundance and macroalgal blooms can develop (Ostrander et al. 2000, McClanahan et al. 2001b, I.D. Williams et al. 2001, Diaz-Pulido & McCook 2002, Aronson & Precht 2006), bringing about a phase shift from coral- to macroalgal-dominated reefs. Once established, macroalgae may persist because many of the fish species traditionally expected to target macroalgae feed almost exclusively on epilithic turf-forming algae and avoid larger fleshy thalli (Bellwood et al. 2006b, Ledlie et al. 2007). Furthermore, some species traditionally regarded as herbivorous are actually detritivores (Wilson et al. 2003). Indeed there are relatively few fish species that ingest substantial quantities of macroalgae (Choat 1991, Choat et al. 2002, 2004, Crossman et al. 2005, but see Mantyka & Bellwood 2007) and the presence of macroalgae tends to discourage the presence of many 'herbivorous' fish species (McClanahan et al. 1999, 2000, 2002b). While many herbivorous fishes are important in preventing increasing biomass of macroalgae in coral-reef habitats by intensive grazing of reef substrata, thereby preventing phase shifts (Bellwood et al. 2004, Mumby et al. 2006, Hughes et al. 2007, Ledlie et al. 2007), an entirely different suite of fishes is needed to remove macroalgae once they become established (Bellwood et al. 2006b).

Can you explain your reasoning here. If herbivorous fishes don't eat much macroalgae and macroalgae discourage their presence, how do herbivorous fishes prevent the dominance of macroalgae?

If corals do recover and remain the dominant habitat-forming species on coral reefs, it is still likely that climate-induced coral bleaching will cause significant changes in community structure (Hughes et al. 2003, 2005, McClanahan et al. 2007a). Foremost, increased frequency of mass bleaching is likely to prevent community reassembly of scleractinian corals (West & Salm 2003, Donner et al. 2005). Initial increases in coral cover within highly perturbed habitats are affected by fast-growing, early successional corals (Hughes 1985, Golbuu et al. 2007), whereas recovery of long-lived and slow-growing coral may take 50–100 yr (Done 1988, Fong & Glynn 2000). Fortunately, faster-growing corals (e.g., *Acropora* and *Pocillopora* spp.) contribute most topographic complexity (Sheppard et al. 2002) and are the major corals used by corallivorous and coral-dwelling fishes (e.g., Munday et al. 1997, Pratchett 2005). However, dominance by monospecific stands of coral can lead to competitive dominance and thus reduced diversity within fish assemblages (Graham et al. 2007a). As climate-induced coral bleaching occurs more frequently, recurrent disturbances are likely to cause directional shifts in coral composition (Hughes et al. 2003, McClanahan et al. 2007a). There are two possible outcomes of climate forcing on coral communities. While climate-induced coral bleaching remains an infrequent but catastrophic occurrence, coral communities are likely to be dominated by fast-growing early successional 'weedy' species (*Acropora* spp.), which persist in habitat patches in various states of recovery (e.g., Golbuu et al. 2007). Many faster-growing corals, such as branching *Acropora* and *Pocillopora*, are however highly susceptible to coral bleaching (Marshall & Baird 2000, Loya et al. 2001) and may be unable to persist as bleaching becomes more frequent and more severe. Consequently, coral communities are likely to become dominated by bleaching-resistant species (Hughes et al. 2003, McClanahan et al. 2004, Arthur et al. 2005, McClanahan et al. 2007a), most of which are less structurally complex and rarely used by coral-dwelling or coral-feeding species (Bellwood et al. 2006a, Golbuu et al. 2007, Munday et al. 2007).

Future threats to biodiversity

Perhaps the most significant, and irreversible, consequence of climate-induced coral bleaching on coral-reef fishes will be the extinction of species with associated declines in biodiversity (*sensu* Thomas et al. 2004). Until recently, the occurrence and importance of species losses on coral reefs has been largely overlooked because (1) marine species are generally predicted to be much less prone to extinctions because marine environments are more 'buffered' against environmental change (Carlton 1993), (2) marine species are expected to be less vulnerable to extreme population fluctuations owing to their large geographic ranges (Gaston 1994) and (3) high diversity may confer a degree of functional redundancy by which some species are expendable (Steele 1991). On

Use single quotes here unless 'buffered' is a direct quote from Carlton

the contrary, climate change is already implicated in species extinctions across a wide range of ecosystems (e.g., Fahrig 2001, Walther et al. 2002, Julliard et al. 2003, Thomas et al. 2004), including coral reefs (Hawkins et al. 2000, Dulvy et al. 2003, Munday 2004a). Climate change is greatly altering marine environments and compounding upon direct anthropogenic effects (Roberts et al. 2002, Hughes et al. 2003), causing geographically extensive habitat degradation that simultaneously affects disparate populations of increasingly large-range species. Increasing fragmentation of habitat patches may further limit the potential for remnant populations to repopulate locations where species are extirpated (Hughes et al. 2003, Hughes et al. 2005). It is very likely therefore, that climate-induced coral bleaching will ultimately cause global extinctions of many more coral-reef fishes. Moreover, functional redundancy on coral reefs may have been significantly overstated (e.g., Bellwood et al. 2003). It is also important to separate functional redundancy from response diversity (Elmqvist et al. 2003). If entire groups of fishes all respond to a disturbance in the same way (e.g., if all species are extirpated following climate-induced coral bleaching), then ecological functions will stop irrespective of how many species are fulfilling that role. Thus, functional redundancy in the absence of response diversity will give a false sense of security (Bellwood et al. 2004). Even for groups with high functional redundancy and response diversity, Naeem et al. (1994) suggest that all species are important because the higher the number of species in a community the greater the efficiency of biogeochemical and trophic functions (see also Tilman & Downing 1994).

Despite the potential effects of climate change and widespread habitat degradation, there are few reported incidences of global extinctions of marine species (Dulvy et al. 2003). This is largely attributable to the fact that detecting species extinctions in marine environments is very difficult (Dulvy et al. 2003) and there are no large-scale, phylogenetically controlled datasets on population decline (Munday 2004a), such as those available for terrestrial species. However, extinction risk for individual species may be predicted based on an individual's susceptibility to disturbance and inherent biological properties such as longevity, population dynamics, population size and geographic range (McKinney 1997, Purvis et al. 2000, Dulvy et al. 2003). In terrestrial environments, it is species with small populations, restricted geographic ranges, and limited ecological versatility that are most at risk of extinction from climate change and associated habitat degradation (Owens & Bennett 2000, Julliard et al. 2003). Similarly, in marine systems it is rare, endemic and highly specialised coral-reef fishes that have recently disappeared or are committed to extinction (Hawkins et al. 2000, Munday 2004a). Importantly, species with multiple traits that predispose them to extinction (e.g., restricted geographic ranges and small population size) face a disproportionate risk of extinction (e.g., Y.M. Williams et al. 2006). To assess extinction risk of coral-reef fishes caused or exacerbated by climate-induced coral bleaching, this review attempts to identify species that have restricted ranges, are locally rare and are highly specialised with specific reliance on corals.

Restricted-range coral-reef fishes

Geographic ranges of coral-reef fishes are mostly very large, but vary greatly (Hughes et al. 2002, Bellwood et al. 2005). *Forcipiger flavissimus*, for example, is the most widespread butterflyfish (geographic range of 1.06×10^8 km²) with a circumtropical distribution as well as a very large latitudinal range (from 34°N to 32°S). At the other extreme, there are some coral-reef fishes with extremely small geographic ranges (<1 km²), and these species may be much more susceptible to extinction due to an increased probability that any given disturbance may make the species unviable (Gaston 1998). Several recently discovered coral-dwelling gobies (*Gobiodon* spp.) are currently known from only one site each in Papua New Guinea (Munday et al. 1999). The abundance of one of these species declined precipitously following extensive mortality of its preferred host coral on nearshore reefs, and it may be threatened with extinction due to ongoing habitat degradation throughout its known range (Munday 2004a). There are a relatively large proportion of fishes (up

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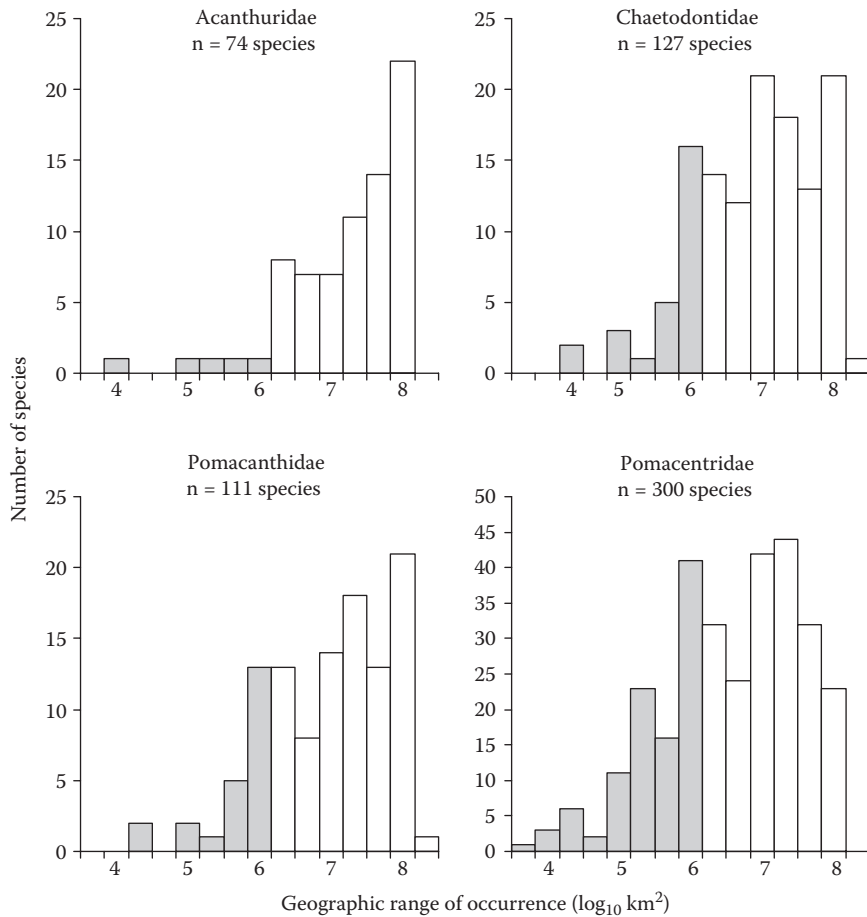


Figure 7 The distribution of geographic ranges ($\log_{10} \text{ km}^2$) for 559 species of nominal coral reef fishes (i.e., does not include deep-water and temperate species) within four major families. Geographic ranges were estimated based on maximum area encompassed within irregular polygons around locations of occurrence, based on data published in Hughes et al. 2002. Grey bars indicate species with geographic ranges $< 8 \times 10^6 \text{ km}^2$.

to 24% of species) with geographic extents restricted to a single reef or region (Figure 7). Hawkins et al. (2000) define restricted-range species as those with ranges $< 80,000 \text{ km}^2$ and estimate that 24% of coral-reef fishes ($n = 1677$ species) fit within this category. However, there are some striking taxonomic differences in patterns of range size (Hughes et al. 2003, Figure 7). Across four of the major families of coral-reef fishes (Acanthuridae, Chaetodontidae, Pomacanthidae and Pomacentridae), 25.6% of species (158/612 species) had geographic ranges $< 80,000 \text{ km}^2$, although the proportion of restricted-range species ranged from $< 7\%$ for the Acanthuridae, 21% for Chaetodontidae and Pomacanthidae and up to 34% for Pomacentridae (Figure 7).

Small range size *per se* does not increase a species susceptibility to climate-induced coral bleaching but means that geographically restricted disturbances can have potentially dire consequences. However, the extraordinary spatial extent of habitat destruction caused by the 1998 global mass bleaching event (Wilkinson 1998) suggests that even large-range species may be threatened by habitat perturbations. Susceptibility of fishes to extinction is probably more dependent upon their geographical location rather than range size (Hawkins et al. 2000, Roberts et al. 2002). Species with restricted geographic ranges that are centred within areas subject to disproportionate effects

of climate change and/or direct anthropogenic disturbances are at much greater risk than similarly restricted-range species located in relatively unaffected locations and/or areas devoid of additional anthropogenic stresses (Downing et al. 2005, Graham et al. 2007a). The severe 1982 El Niño is blamed for the extinction of *Azurina eupalama*, a plankton-feeding damselfish that was endemic to the Galapagos Islands (Jennings et al. 1994). Meanwhile, *A. hirundo*, an ecologically equivalent species persists in the Guadalupe and Revillagigedo islands (Allen 1991).

Rarity in coral-reef fishes

Risk of extinction is intuitively much greater for populations comprising few individuals compared with larger populations. For example, smaller populations are much more likely to become non-viable following stochastic reductions in population size (Gaston 1994). There are many examples of 'rare' coral-reef fishes that are rare not only because they are geographically restricted, but also because they have consistently low local abundance throughout their geographic ranges (G.P. Jones et al. 2002). *Chaetodon bennetti*, for example, is relatively widespread but never common (Allen et al. 1998); mean densities of *C. bennetti* across three geographically separated locations in the southern Pacific (<1 individual ha⁻¹) are an order of magnitude lower than those of the next-rarest species (M. Pratchett & M. Berumen unpublished data). For terrestrial species there is a consistent and often-striking positive relationship between geographic ranges and population abundance (Gaston 1998, Lawton 1999). For coral-reef fishes, however, previous studies have failed to detect any relationship between geographic range size and local abundance (G.P. Jones et al. 2002). For both Chaetodontidae and Acanthuridae, which are the only families of fishes for which there are good data on local abundance of multiple species across geographically widespread locations, there is no apparent relationship between geographic ranges of occurrence and mean abundance (Figure 8). It is possible that restricted-range species are much more common than expected due to historical effects of extinction filtering (Y.M. Williams et al. 2006), by which extant species with restricted ranges have only persisted by virtue of their high abundance. However, despite a generally poor relationship between range size and abundance among reef fishes (G.P. Jones et al. 2002), there are coral-reef fish species that are geographically restricted and locally rare (Figure 8; *Acanthurus polyzona* and *Prionurus punctatus*). Perhaps these species are destined for extinction.

Extreme rarity can predispose a species to extinction but common species are also likely to disappear if they are highly susceptible to particular disturbances. Recurrent disturbances, predicted to result from sustained and ongoing climate change, are likely to have successive and cumulative effects on all susceptible species (S.V. Smith & Buddemeier 1992), irrespective of their geographic range. For example, species of fishes and corals that experienced significant declines in abundance during the 1998 global mass bleaching may become extinct if locally severe and geographically extensive mass bleaching reoccurs within the time required for affected populations to recover. Coral-reef fishes at greatest risk are those that exhibited disproportionate declines in abundance during previous mass bleachings. Thus coral-dependent and highly specialised coral-reef fishes are increasingly likely to be threatened with extinction.

Ecological specialisation

Ecological specialisation increases extinction risk for several reasons. Foremost, specialist species are usually expected to be geographically restricted and locally rare (J.H. Brown 1984), which increases extinction risk. These relationships notwithstanding, specialist species are expected to be disproportionately affected by changes in resource availability, compared with generalist counterparts (Munday 2004a, Pratchett et al. 2006, Figure 6). Both Munday (2004a) and Pratchett et al. (2006) showed that highly specialised coral-dependent species became locally extinct following

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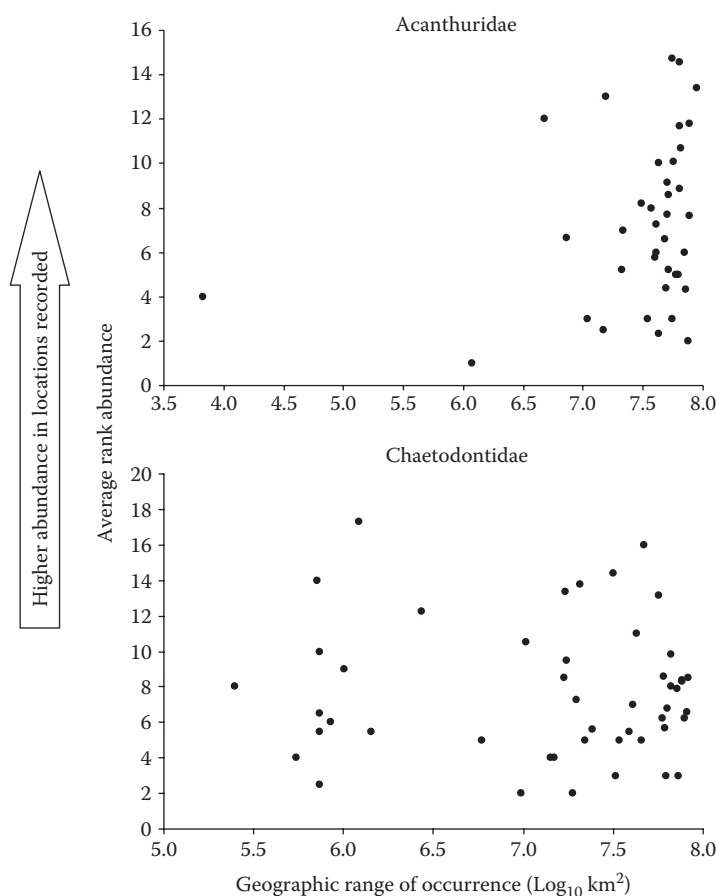


Figure 8 Average rank abundance versus geographic range of occurrence (\log_{10} km²) for coral reef fishes from two distinct families. Rank abundance was calculated across 12–15 geographically separated locations. For Chaetodontidae data were derived from Jones et al. (2002), Khalaf & Abdallah (2005), and Shokri et al. (2005). For Acanthuridae data are from Letourneur et al. (1993) and Hughes et al. (2002).

coral loss caused by mass bleaching. In contrast, more generalist (i.e., ecologically versatile) species were relatively unaffected, presumably because they were able to exploit alternate prey resources as preferred corals were depleted (Pratchett et al. 2004). Notably however, these patterns arise because corals used by specialist species are a subset of corals used by more generalist species, and the coral species most frequently used by coral-dependent fishes are also those most susceptible to bleaching and other disturbances (Munday et al. 1997, Feary et al. 2007b, Srinivasan 2007).

Ecologically equivalent groups of coral-dependent fishes (e.g., corallivorous butterflyfishes and coral-dwelling gobies) might be expected to exhibit some resilience to coral loss because niche-based competition theory would predict that sympatric species each specialise on different coral species (Schoener 1974). Therefore, selective depletion of corals (e.g., during moderate bleaching) would affect some fishes but have limited negative or even positive indirect effects on their competitors. A common pattern, however, is that many species tend to specialise on the same coral resources, possibly because these corals confer higher individual fitness. For example, all nine species of apogonids studied by Gardiner & Jones (2005) preferred to inhabit *Porites cylindrica*.

Similarly, *Acropora nasuta* appears to be a preferred coral habitat for a variety of *Gobiodon* species (Munday et al. 1997, 2001), probably because growth and survival are higher for a range of goby species in this coral (Munday 2001). Specialisation and reliance on a relatively small suite of coral species increased the vulnerability of coral-dwelling species to declines in the availability of those coral resources. To what degree coral-dependent species will shift their resource use if preferred coral habitats decline is unknown (e.g., Pratchett et al. 2004) but it is clear that at least some species are strict specialists that use only a narrow range of coral types (e.g., Munday 2004a) and loss of these habitats will have serious implications for their persistence (Munday 2002).

Ecological theory predicts that specialists should have smaller ranges than generalist species because the distributions of specialist species are more likely to be constrained by the distribution of a few key resources than are the distributions of generalist species that can use a wide range of resources (J.H. Brown 1984). If this relationship holds, highly specialised species may face a 'double jeopardy' of extinction or even a 'triple jeopardy' where specialist species are also rare (Hawkins et al. 2000, Munday 2004a). All the evidence to date suggests that coral-dependent fishes do not, on average, have smaller geographic ranges than other coral-reef fishes, possibly because the coral species used have widespread distributions themselves or because the fishes change their patterns of resource use in accordance with the relative abundance of different coral species in different geographic regions. Both of these alternatives appear likely. *Gobiodon* species A, an extreme specialist that inhabits just one species of coral (*Acropora tenuis*) has a geographic distribution extending from Japan to the southern GBR (Munday et al. 1999). The widespread distribution of its host coral probably contributes to the relatively large geographic range of this coral goby. *Gobiodon histrio*, which has an even larger geographic range, prefers the same suite of coral species at locations separated by thousands of kilometres (Munday 2002). In contrast, *G. quinquestrigatus*, which uses a range of coral species within sites, also changes its pattern of habitat use among geographic locations (Munday 2002). Moreover, G.P. Jones et al. (2002) found no clear relationship between geographic range size and specialisation for either butterfly fishes or anemone fishes. A similar conclusion regarding the relationship between range size and specialisation in anemone fishes was also reached by Ollerton et al. (2007).

Specialist species are also expected to be less common compared with generalist counterparts because their populations are more likely to be constrained by the abundance of specific resources (J.H. Brown 1984). There is some evidence among coral-dependent fishes that specialists have smaller populations than generalists but the pattern is far from consistent. Coral-dwelling gobies that inhabit just one or two coral species tend to have smaller population sizes than generalists and their populations decline more rapidly following loss of preferred habitat (Munday 2004a). In contrast, butterfly fishes that are specialist coral feeders are often locally abundant and can have higher densities than many generalist species (G.P. Jones et al. 2002). For example, *Chaetodon trifascialis* is the most specialised of coral-feeding fishes, feeding almost exclusively on *Acropora hyacinthus* (Pratchett 2005), and yet it is also the most widely distributed of butterflyfish species (Allen et al. 1998) and frequently ranks in the top three most abundant butterflyfishes throughout its geographic range (G.P. Jones et al. 2002). For butterflyfishes generally, there are many species that might be considered to have an increased risk of extinction owing to (1) relatively small geographic ranges, (2) consistently low abundance or (3) extreme dietary specialisation (Figure 9). There are, however, surprisingly few butterflyfishes that face multiple jeopardy of extinction. For example, the only dietary specialist that has a restricted geographic range (<80,000 km²) is *Chaetodon larvatus*, which is the most abundant butterflyfish throughout its range.

Other factors that increase susceptibility to extinction include short lifespan and low intrinsic rates of population growth (Pimm et al. 1988). In many cases, these aspects of population demographics would balance each other, such that short-lived species would be expected to have higher turnover and greater potential for population growth. Consequently, both short-lived and long-lived

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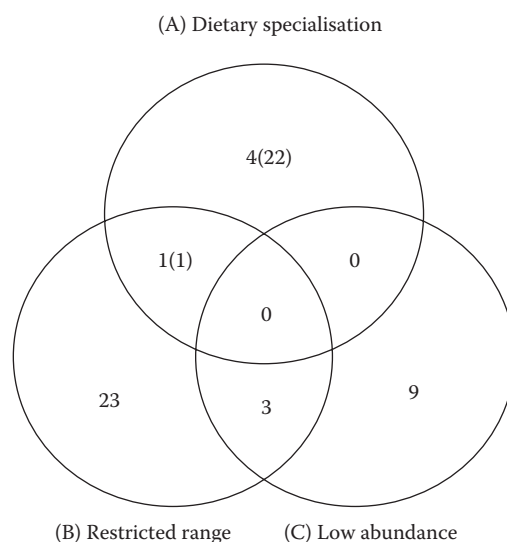


Figure 9 Venn diagram showing the number of Chaetodontidae (of 127 species) facing increased risk of extinction due to (A) dietary specialisation, in that they selectively consume only one or two different coral genera (the numbers in parentheses refer to all obligate coral-feeding species), (B) restricted geographic ranges (<80,000 km²) and/or (C) consistently low abundance.

species may be equally susceptible to extinction due to very different reasons, and identifying outliers in the expected relationship between longevity and population growth might be critical in establishing species-specific extinction risk. Overall, it appears the highly specialised coral-dependent fishes face the greatest risk of extinction from future mass bleaching and associated coral loss, although unexpected extinctions may also arise due to added effects of exploitation and other disturbances (Hawkins et al. 2000, Dulvy et al. 2003). Many highly specialised coral-dwelling fishes are extremely small and cryptic (Munday & Jones 1998, Bellwood et al. 2006a), suggesting that recent mass bleaching and degradation of coral-reef habitats may have already caused numerous, but as yet unappreciated, extinctions (Dulvy et al. 2003).

Socioeconomic consequences

Worldwide, the goods and services that coral reefs provide are estimated to be worth almost U.S.\$30 billion yr⁻¹ (Cesar et al. 2003). Sustained and ongoing climate-induced coral bleaching will significantly diminish the value of these goods and services, resulting in serious consequences for people and even countries dependent on coral reefs (Hoegh-Guldberg 1999, Wilkinson 1999, 2000b, Hughes et al. 2003, Lesser 2004). Coral bleaching has the potential to affect fisheries, the livelihoods and health of fisheries-dependent communities, reef-related and coastal tourism and important ecosystem services provided by reefs (Wilkinson 1999, Westmacott et al. 2000a, McClanahan et al. 2002a, Cesar et al. 2003, Grandcourt & Cesar 2003, Sheppard et al. 2005, Graham et al. 2007b). To date, empirical studies have focused largely on the effects of bleaching on fisheries and tourism, which are the most obvious immediate effects (but see Sheppard et al. 2005).

Fisheries

Coral bleaching has the potential to affect reef and reef-related fisheries through a number of mechanisms: (1) coral mortality or structural loss may cause a decline in the abundance of reef-related

fishes (i.e., those that depend on coral for settlement, feeding, dwelling or are associated with the reef structure), leading to reduced catches of these fishes (Westmacott et al. 2000a, Graham et al. 2007b); (2) highly mobile predatory species, although not directly dependent on reef structures, may decline in abundance following declines in abundance of prey species (Westmacott et al. 2000a); (3) declines in reef fish biodiversity may lead to a reduction in energy transfer to higher trophic levels, which may mean that reefs will support a reduced biomass of higher-order predators (Munday et al. 2007); (4) many fishes can be negatively affected by a high abundance of late-successional algae (McClanahan et al. 2002b) that may dominate after coral mortality; (5) coral mortality may cause a reduction in abundance of some small-bodied ornamental coral-feeding and coral-dwelling fishes, which are valued by the aquarium trade (Wilson et al. 2006) and (6) macroalgae habitats attract some invertebrates (McClanahan et al. 2001a), such that the abundance of some invertebrate feeders may increase (Pratchett et al. 2007). These changes in the relative abundance of targeted species are likely to significantly affect fisheries yields, species composition of catches and the economic value of coral-reef fisheries (Westmacott et al. 2000a). Most likely, catch composition will change even if there is no decline in catch rates, which may reduce the total value of landings (Westmacott et al. 2000a).

Despite potential effects of climate-induced coral bleaching on coral-reef fisheries, no studies have actually shown that total catch, catch composition, or value of fisheries have been affected by severe mass bleaching (McClanahan et al. 2002a, Grandcourt & Cesar 2003). However, detecting definitive effects of coral bleaching on fisheries yields may be very difficult because the confounding effects of overfishing in many locations outweigh any effects that loss of live coral may have on temporal trends in fisheries yields. For example, in Mombasa, Kenya, Westmacott et al. (2000a) found a decline in catch while effort remained the same but concluded that bleaching had no detectable effect because the rate of decline in the fishery was consistent for several years prior to the bleaching. In a longer-term study of Kenyan fisheries (1994–2001), McClanahan et al. (2002a) found that catches of Siganidae overall were reduced by 8% after the bleaching and that catch per fisherman per day decreased 20–30% for Siganidae and Scaridae but they attribute most of this change to a 17% rise in fishing effort over the study period. Likewise, in the Seychelles fishery, low abundance and yield of herbivorous Siganidae post-bleaching was attributed to a prebleaching trend associated with fishing effort (Grandcourt & Cesar 2003). These results reinforce the importance of examining long-term trends, fishing effort and catch composition rather than simply documenting changes in focus parameters immediately before and immediately after punctuated disturbances (Hughes & Connell 1999).

Failure to detect significant effects of climate-induced coral bleaching on coral reef fisheries may also be due to the fact that many fisheries mainly target fishes that are not dependent on coral (e.g., Acanthuridae, Siganidae, Scaridae and various planktonic species) (Bellwood 1988, Goreau et al. 2000, Figure 10). In artisanal fisheries in both Kenya and Papua New Guinea, coral-dependent fishes made up only a very small proportion of the species and individuals caught (Figure 10). Despite major differences in fishing intensity (Cinner & McClanahan 2006), the overwhelming majority of fishes caught in both these fisheries were associated with the reef structure but not explicitly reliant on live corals. There were also significant landings of fishes that are not really dependent on coral reefs but may be caught in the proximity of coral reefs (e.g., Carangidae and Scombridae) (Figure 10). These data suggest that artisanal fisheries may be relatively unaffected by coral loss caused by climate-induced coral bleaching but there could be major consequences associated with the longer-term declines in topographic complexity (Graham et al. 2007b) However, the significant lag between the coral loss and its potential effect on most target fish populations might mask the effects of bleaching on fisheries' catches. Changes in fishing locations or habitats, coincidental with bleaching (Westmacott et al. 2000a), or simultaneous/subsequent disturbances such as cyclones, increased sedimentation, or freshwater run-off (G.P. Jones et al. 2004, Munday 2004a), may also

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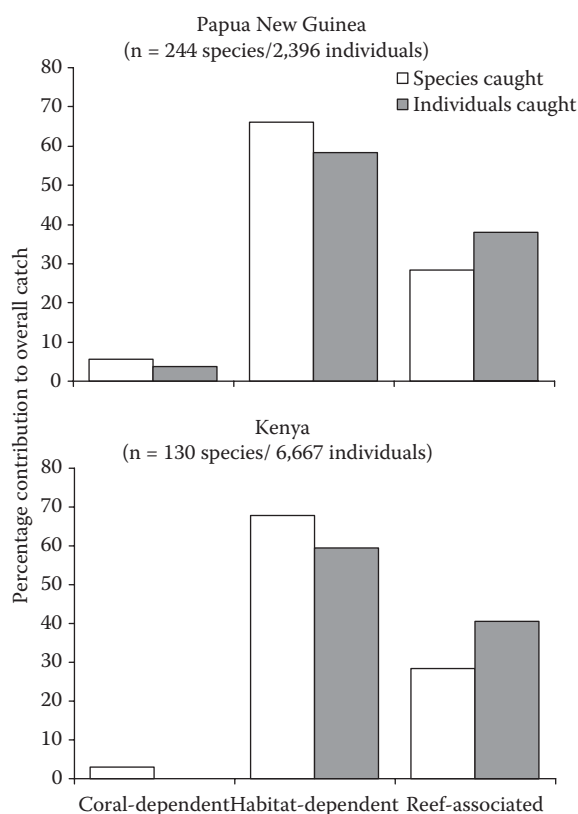
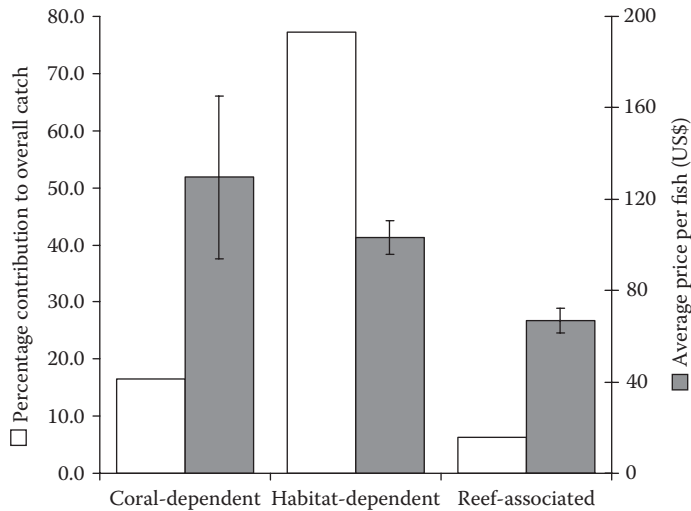


Figure 10 Relative contribution (by species and individuals) of coral-dependent, habitat-dependent, and reef-associated fishes in artisanal fisheries in Papua New Guinea and Kenya. Categories of associations were intended to represent decreasing susceptibility to climate-induced habitat modification on coral reefs. Data were reanalysed from Cinner & McClanahan (2006) and McClanahan & Mangi (2004).

make it difficult to establish the relative importance of different disturbances. Consequently, effects of climate-induced coral bleaching on coral-reef fisheries are likely to be difficult to detect because they are highly protracted and potentially masked by a wide range of other factors.

Economic costs of coral bleaching on coral-reef fisheries may be most apparent in niche fisheries targeting mainly coral-dependent fishes (e.g., aquarium fisheries). The international marine ornamental fish trade is currently worth U.S.\$90–300 million yr⁻¹ (Sadovy & Vincent 2002) and mostly targets small coral-reef fishes such as the Pomacentridae, Chaetodontidae, Monacanthidae and Apogonidae (Kolm & Berglund 2003, Tissot & Hallacher 2003, Lunn & Moreau 2004). Many of these fishes (especially butterflyfishes) are coral dependent and thus highly susceptible to climate-induced coral bleaching. However, it is unclear if or how this fishery might be affected by significant declines in wild populations of coral-dependent fishes. Importantly, aquarium fisheries may opportunistically exploit individuals from a range of targeted species, such that overall catch rates are insensitive to fluctuations in relative abundance of different species. However, the most specialised of coral-reef fishes are often difficult to maintain in aquaria (Allen et al. 1998, Michael 2004) and generally not targeted for the ornamental trade (Allen et al. 1998).

Analyses of the predominant fish species caught for the ornamental trade confirm that relatively few are coral dependent. Of the 124 most expensive ornamental fish species caught around the world, 80% were associated with the habitat structure but only 15% were coral dependent (Figure 11).



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Figure 11 The proportion of fish caught and average price paid per fish for the 124 most expensive species in the ornamental fishery for coral reef fishes categorised as coral-dependent, habitat-dependent and reef-associated. Categories of associations were intended to represent decreasing susceptibility to climate-induced habitat modification on coral reefs. Prices were obtained from the Aquatic Connections aquarium supply retail shop (Sunrise, Florida, USA) website. (see Sadovy & Vincent 2002).

Interestingly, there was significant variation in the average price of fishes within these three groups; the price was highest for coral-dependent species and lowest for non-reef species (Figure 11). This may suggest that the species most susceptible to bleaching are also in high demand, or at least attract greater value. Therefore, climate-induced coral bleaching might be expected to affect total value if not the overall catches of aquarium fishes. Notably, there was a marked decline in the total value of marine aquarium fishes imported into Hong Kong in 1997–1998, driven mainly by decline in the value of imports from Indonesia and the Philippines (Chan & Sadovy 1998). These economic trends are not currently attributed to overriding effects of mass bleaching but to coincidental changes in the national metrics used to record imports of marine aquarium fishes (Chan & Sadovy 1998). However, the recent disappearance of several coral-dependent fishes from aquarium catches (e.g., *Oxymonacanthus longirostris*) has been directly attributed to declines in local stocks following the 1998 mass bleaching (Dulvy et al. 2003).

Tourism

In contrast to the rather inconclusive studies concerning effects of bleaching on coral-reef fisheries, several studies have been able to detect and project the effects of coral bleaching on reef-based tourism (e.g., Westmacott et al. 2000b, Uyarra et al. 2005, Andersson 2007). Bleaching has been found to negatively affect tourism and tourism-related industries by reducing the attractiveness of particular locations or activities for tourists, resulting in a change of either destination or activity and subsequent loss of reef-related revenue (Westmacott et al. 2000b, Uyarra et al. 2005). Tourists' perceptions of changes in coral-reef habitats after bleaching are often limited (except where there has been extensive degradation and extensive loss of fishes) but knowledge of recent bleaching may influence where tourists choose to dive (including snorkelling) on both small spatial scales (i.e., a particular dive site) and large spatial scales (i.e., a particular country or region). In Kenya and Tanzania, >75% of divers avoided dive sites known to be recently bleached (Westmacott et al. 2000a, Andersson 2007). Where user fees exist for access to marine protected areas and areas under

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customary ownership, changes in specific dive site selection may affect revenue generation used for reef management and community development. On a larger scale, bleaching may reduce national and regional economies by influencing the choices of destinations. For example, 19% of Zanzibar, Tanzania, and 30% of Mombasa, Kenya, tourists would change their holiday destination as a result of bleaching (Westmacott et al. 2000a), 80% of tourists visiting Bonaire would be unwilling to return at equivalent cost in the event of coral bleaching (Uyarra et al. 2005) and there was 5–10% decline in the number of tourists visiting Palau subsequent to the 1998 coral bleaching (Graham et al. 2000).

The recreational value of diving in Kenya and Tanzania was no different in 1999 (after widespread bleaching) from 1996 (before the bleaching), suggesting that visitors were still eager to visit and view coral-reef habitats (Westmacott et al. 2000a). However, the divers in 1999 were less experienced than divers in 1996, suggesting that more experienced divers may have chosen to dive in alternative regions that experienced less bleaching. In 1999, estimates of economic losses from diver satisfaction ranged from U.S.\$1.6–4.8 million in Zanzibar (Ngazy et al. 2002). A ‘willingness to pay’ survey of tourists in the Philippines found that individual divers were prepared to pay an average of U.S.\$202 more to dive a ‘pristine’ reef compared with a bleached or degraded reef, whereas snorkellers were willing to pay an additional U.S.\$25 (Cesar 2000).

Overall economic losses attributable to recent climate-induced coral bleaching are staggering, ranging from tens of millions of dollars for a single country to billions of dollars for the Indian Ocean (Wilkinson 1999, Cesar 2000, Westmacott et al. 2000a). For example, changes in destination choice and decreases in consumer surplus (i.e., the value of the dive experience to the diver less the costs of the vacation) resulted in total losses to the Palau tourism industry as high as U.S.\$750,000 over the 2 yr following bleaching (Graham et al. 2000). In the Philippines, recent bleaching is predicted to result in economic losses ranging from U.S.\$6 million to as high as U.S.\$27 million, depending on the time required for reefs to recover (Cesar 2000). The overall economic damages from the 1998 coral bleaching event in the Indian Ocean (over a 20-yr time frame with a 10% discount rate) could be over U.S.\$8 billion; U.S.\$1.4 billion loss of food production/fisheries, U.S.\$3.5 billion loss of tourism revenue, U.S.\$2.2 billion loss of coastal protection and U.S.\$1.2 billion in other services (Wilkinson 1999, Westmacott et al. 2000a).

Managing effects of climate-induced coral bleaching

Managing effects of climate change on coral reefs represents a considerable challenge, especially given that reef managers themselves cannot prevent the predicted increases in sea temperatures and storms that are associated with climate change. However, by reducing other stressors on the reef environment (e.g., overfishing, pollution and sedimentation) reef managers could potentially increase resilience to climate-induced coral bleaching and reduce the likelihood of catastrophic and irreversible changes in habitat structure, as has been suggested by Hughes et al. (2003) and West & Salm (2003). Considerable research is still needed to establish links between management and reef resilience (McClanahan & Maina 2003, G.P. Jones et al. 2004, McClanahan et al. 2005). It seems logical, however, that minimising direct anthropogenic stresses will serve to maximise the capacity of reefs to withstand climate-induced coral bleaching. At the very least, coral communities on reefs with intact fish assemblages and minimal additional stresses will have a greater chance of recovering after bleaching (B.E. Brown 1997, Mumby et al. 2006, Hughes et al. 2007). Accordingly, the objectives of coral-reef management should be 3-fold: (1) eliminate or minimise extrinsic disturbances (pollution and sedimentation, e.g., Orpin et al. 2004), (2) protect threatened and functionally important species (Bellwood et al. 2004) and (3) abolish destructive activities (e.g., blast fishing) that degrade benthic reef habitats (Kaiser et al. 2000, Baird et al. 2005). There are a variety of management tools that may be adaptively employed to achieve these objectives,

including bans on catching particular species, gear restrictions, or prohibiting all extractive activities (McClanahan & Cinner 2007), but their relevance and effectiveness are very context specific, depending on a range of social, economic and cultural factors (McClanahan et al. 2006, Cinner 2007, Cinner et al. 2007). For example, prohibiting all extractive activities within specified areas (no-take areas) may be the best way to ensure minimal levels of protection for heavily exploited species (Russ 2002) but resource users may be more amenable to gear-based bans (McClanahan et al. 2006). Restricting the use of certain gear types (e.g., gill and seine nets that tangle in corals) may also have added benefits of preventing declines in topographic complexity (Kaiser et al. 2000, McClanahan & Cinner 2007).

Marine protected areas that limit or prevent (e.g., no-take areas) extractive activities are considered by many as currently the most effective way to minimise long-term consequences of climate-induced coral bleaching on coral-reef ecosystems (e.g., Westmacott et al. 2000b, Marshall & Schuttenberg 2006a,b). Protecting large areas of reef from fishing helps to preserve the abundance and diversity of exploited fish species (Halpern & Warner 2002, Russ 2002). Where exploited species include important herbivorous fishes, this protection may be fundamental to rapid recovery of coral communities following climate-induced coral bleaching (Bellwood et al. 2003, Hughes et al. 2007). However, marine protected areas must be recognised as a small part of the solution to problems faced by coral reefs because, ultimately, they cannot protect coral-reef ecosystems from extrinsic disturbances (Gray 1997, Boersma & Parrish 1999, G.P. Jones et al. 2004, Hughes et al. 2005). Importantly, marine protected areas encompass only a minor proportion of coral-reef area (Wilkinson 2004) and may detract from effective management of broader-scale issues (Bellwood et al. 2004, Hughes et al. 2005, G.P. Jones et al. 2007). Moreover, marine protected areas benefit exploited species when habitat is degraded (e.g., Hawkins et al. 2006) but the majority of small and potentially threatened coral-reef fishes are not exploited (e.g., Munday 2004a). The greatest threats to marine biodiversity throughout the world occur in coastal zones near to high population densities, where pollution, marine litter, eutrophication, species introductions/invasions, water-shed alteration, and physical alterations of sea margins have contributed to habitat loss, and habitat conversion, with the associated loss of species (Gray 1997). A substantial proportion of the global human population (~8%) now lives within 100 km of coral reefs, and burgeoning populations continue to put pressure on these sensitive ecosystems (Hawkins et al. 2000). This is a particular problem in Indonesia where areas with greatest biodiversity are situated closest to centres of highest human population growth (Gray 1997). If marine biodiversity is to be conserved, better protection and management of coastal zones and catchments, which are rarely included with marine protected areas, are needed.

Beyond simply conserving biodiversity, strategic placement of marine protected areas may be used to protect habitats that support high abundance of particularly threatened and ecologically important coral-reef fishes (Beger et al. 2003, Roberts et al. 2003). Herbivorous fishes, for example, are considered to be important in facilitating recovery of coral communities following extensive mortality (Mumby et al. 2006, Hughes et al. 2007) and preventing phase shifts to highly undesirable algal-dominated habitats (Hughes et al. 2003, Bellwood et al. 2004). Other important species are keystone predators that regulate the deleterious effects of prey species (e.g., McClanahan 2000, Dulvy et al. 2004) or fulfil unique but critical ecological functions (Bellwood et al. 2003). *Balistapus undulatus*, for example, is a major predator on bioeroding sea urchins and is hypothesised, therefore, to have indirect positive effects on coral recruitment and cover (McClanahan 1995, 2000). In some cases, these key species may be deserving of special protection at a global scale (e.g., worldwide bans on exploitation) (Wood 2004). There are already worldwide bans on the exploitation of heavily exploited food fishes, such as *Cheilinus undulatus*, enacted under the 1973 Washington Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Sadovy 2005). Similar levels of protection or *ex situ* conservation may be fundamental

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to preventing the extinction of rare or threatened species (Wood 2004) and functionally important species and groups (Bellwood et al. 2003, 2004).

This review emphasises the importance of both live coral cover and topographic complexity in maintaining diverse communities of coral-reef fishes. As such, live coral cover and topographic complexity need to be recognised as critical components of coral-reef ecosystems and managed accordingly. Branching corals are especially important in providing surface topography, food and habitat for coral-reef fishes (G.P. Jones et al. 2004) but are also highly susceptible to bleaching (Marshall & Baird 2000) and other direct anthropogenic stresses (e.g., destructive fishing practices, McManus et al. 2004). To minimise reductions in structural complexity caused by climate-induced coral bleaching (e.g., Graham et al. 2006), there need to be unequivocal reductions in destructive activities (e.g., blast fishing, seine netting, coral mining and anchor damage) that compromise topographic complexity (McManus et al. 2004). Some reefs have a high level of landscape complexity, such that even after the framework provided by branching corals collapses, caves, crevices and overhangs remain intact (e.g., Halford et al. 2004). The call for the establishment of marine protected areas in habitats that are somewhat resistant to coral bleaching and subsequent physical degradation (e.g., West & Salm 2003, Marshall & Schuttenberg 2006a, Salm et al. 2006) may provide a source of population replenishment for nearby reefs that are damaged by bleaching (Graham et al. 2007a, McClanahan et al. 2007a). However, it is imperative that structural complexity is protected both inside and outside marine protected areas.

The importance of structural complexity also raises the question of engineering increased topographic complexity to retain fish diversity in the likely event of reef collapse. Human intervention in coral-reef recovery is, however, rarely effective on large spatial scales and the exorbitant costs associated with engineering recovery in already degraded reef systems may be better spent on increasing protection of nearby healthy coral systems that will enhance natural recovery processes and ensure the continuity of ecosystem function (Spurgeon & Lindahl 2000, Adger et al. 2005). Habitat management is also important in adjoining habitats, such as mangroves, seagrass meadows, estuaries and coastal wetlands. These habitats are important nursery and juvenile habitats for many coral-reef fishes (Nagelkerken et al. 2000, 2002), some of which, like the rainbow parrotfish, *Scarus gaucamai*, are important grazers (Mumby et al. 2004). Furthermore, these habitats stabilise coastlines, preventing erosion and filtering sediments, nutrients and pollution from terrigenous sources that may exacerbate existing stresses to corals. All coastal habitats are increasingly threatened by terrestrial development, as well as climate change (Roessig et al. 2004, Poloczanska et al. 2007), and require additional protection to prevent their continued loss or degradation.

Conclusions and future directions

This review reveals that habitat structure, particularly coral cover and topographic complexity, plays a critical and probably underappreciated role in structuring reef fish assemblages. Sustained and ongoing climate-induced coral bleaching, which can cause coral loss and reduced topographic complexity, may therefore have profound effects on the abundance, diversity and community structure of coral-reef fishes (e.g., McClanahan et al. 2002a, G.P. Jones et al. 2004, Munday 2004a, Pratchett et al. 2004, 2006, Sano 2004, Bellwood et al. 2006a, Garpe et al. 2006, Graham et al. 2006). Coral loss has unequivocal effects on highly specialised fishes that feed or shelter on live corals but the effects of extensive and lasting coral loss extend well beyond those fishes that are traditionally thought to need live coral (e.g., butterflyfishes, damselfishes and gobies; G.P. Jones et al. 2004). There is also strong evidence that topographic complexity is an important attribute in maintaining species diversity of coral-reef fishes, which is likely to be fundamental in limiting ecological and economic consequences of climate-induced coral bleaching. In general, communities of coral-reef

fishes can recover quickly following temporary reductions in coral cover (e.g., Halford et al. 2004), and may exhibit considerable resilience to climate-induced coral bleaching, as long as the physical structure is not compromised. Here, adaptive management may be critical in preventing declines in topographic complexity and protecting against long-term shifts in the structure of coral communities towards less structurally complex bleaching-resistant corals (e.g., Hughes et al. 2003, McClanahan et al. 2007a). The longer-term consequences of climate change and coral bleaching for coral-reef fishes are far from certain, but reducing direct anthropogenic pressures and improving management of coral-reef habitats are important elements in preventing ecological and economic consequences of declines in the abundance and diversity of coral-reef fishes.

Effects of climate-induced coral bleaching are compounding preexisting pressures from natural and direct anthropogenic stresses (e.g., overfishing, pollution, excess nutrients and disease epidemics) to accelerate and exacerbate widespread degradation of coral-reef ecosystems (Nyström et al. 2000, Jackson et al. 2001, Kleypas et al. 2001, Nyström & Folke 2001, Hughes et al. 2003, Pandolfi et al. 2003). To prevent further declines in the condition of coral-reef habitats, and thereby conserve communities of coral-reef fishes, it is imperative to move beyond traditional reductionist management strategies (e.g., marine protected areas) to implement adaptive and targeted management strategies that recognise individual and critical components of habitat structure (e.g., topographic complexity). This requires an entirely different approach to management, requiring bold decisions to prioritise conservation of critical functional attributes rather than focusing on individual stocks or species. Protection of critical habitat attributes is much more achievable and probably far more effective at providing ecosystem resilience than current efforts aimed at preserving biodiversity.

This review has focused on climate-induced coral bleaching, which until now has been the most apparent and devastating effect of climate change in coral-reef ecosystems. However, the potential effects of climate change on coral-reef habitats and reef fishes are extensive (reviewed by Roessig et al. 2004, Munday et al. 2007, Poloczanska et al. 2007). Global climate change will not only raise the temperature of the oceans but also cause major changes in sea level, hydrodynamic conditions and ocean chemistry (Roessig et al. 2004, Poloczanska et al. 2007). Increasing concentrations of atmospheric carbon dioxide are reducing pH and altering the carbonate-bicarbonate ion balance in the world's oceans (Pelejero et al. 2005). Consequences of these changes for scleractinian corals are weaker skeletons, reduced extension rates and increased susceptibility to erosion (Kleypas et al. 1999, Orr et al. 2005). As ocean acidification undermines the structural integrity of coral skeletons, predicted increases in the frequency and severity of severe tropical storms (Henderson-Sellers et al. 1998, K. Walsh 2004, P.J. Webster et al. 2005) are likely to lead to increased breakage and dislodgement of corals (Madin & Connolly 2006), further affecting topographic complexity and 3-dimensionality of coral-reef habitats. Furthermore, sea-level rise combined with erosion of shallow-water habitats may threaten shallow-water specialists. Increased sea temperatures, reduced ocean acidity and modified circulation patterns could also have significant direct effects on individual performance and population dynamics of coral-reef fishes (Munday et al. 2007). It is hoped appreciation of the likely impacts of climate change on coral-reef fishes will fuel international efforts to take action on climate change, while bold management initiatives are needed to maximise capabilities of coral-reef ecosystems to withstand future and unexpected effects.

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