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Crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes

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Summary

Expert opinion was canvassed to identify crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes. Scientists that had published three or more papers on the effects of climate and environmental factors on reef fishes were invited to submit five questions that, if addressed, would improve our understanding of climate change effects on coral reef fishes. Thirty-three scientists provided 155 questions, and 32 scientists scored these questions in terms of: (i) identifying a knowledge gap, (ii) achievability, (iii) applicability to a broad spectrum of species and reef habitats, and (iv) priority. Forty-two per cent of the questions related to habitat associations and community dynamics of fish, reflecting the established effects and immediate concern relating to climate-induced coral loss and habitat degradation. However, there were also questions on fish demographics, physiology, behaviour and management, all of which could be potentially affected by climate change. Irrespective of their individual expertise and background, scientists scored questions from different topics similarly, suggesting limited bias and recognition of a need for greater interdisciplinary and collaborative research. Presented here are the 53 highest-scoring unique questions. These questions should act as a guide for future research, providing a basis for better assessment and management of climate change impacts on coral reefs and associated fish communities.

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Introduction

Coral reefs are among the most diverse of all ecosystems and provide goods and services to millions of people (Moberg and Folke, 1999). However, coral reefs are also highly vulnerable to the effects of climate change. Survival of scleratinian corals, the prominent builders of reef habitat, is threatened by sustained increases in sea surface temperatures (SST), which cause coral bleaching (Glynn, 1996; Brown, 1997; Hoegh-Guldberg, 1999), increase the severity of tropical storms (Webster et al., 2005) and may be linked to outbreaks of coral disease (Harvell et al., 1999; Harvell et al., 2002; Bruno et al., 2007). Furthermore, rapidly increasing levels of atmospheric CO_2 and the consequent acidification of the marine environment can reduce the growth of coral skeletons and their capacity to contribute to reef accretion (Kleypas et al., 1999; Hoegh-Guldberg et al., 2007; De'ath et al., 2009). These climate change-associated stressors are contributing to declines in coral cover at regional scales (Gardner et al., 2003; Bellwood et al., 2004; Bruno and Selig, 2007) and are fundamentally altering the benthic composition of coral reef habitats.

Sustained changes to the composition of reef benthos have major implications for reef-associated communities. One of the most widely studied of these communities are the reef fishes, owing to their importance as a protein source for human societies living close to tropical coastlines (Pauly et al., 2002; Bell et al., 2009) and their functional ecological roles on reefs (Bellwood et al., 2004). Recent reviews have focused on the effects of habitat disturbance on coral reef fishes (Jones and Syms, 1998; Wilson et al., 2006), some specifically addressing the influence of coral bleaching (Pratchett et al., 2008; Pratchett et al., 2009). In addition, Munday et al. present a holistic prediction of climate change impacts on coral reef fishes, considering both the indirect effects associated with changes to habitat and oceanic currents as well as the direct effects on fish physiology and demographics (Munday et al., 2008a). Here we present a list of research questions that, if addressed, will advance our understanding of how climate change will affect reef fishes and improve the capacity of managers to mitigate such impacts.

Materials and methods

A comprehensive range of research objectives was obtained by inviting scientists to submit five questions that represented feasible research projects and information gaps on climate change impacts on coral reef fishes. Each of the invited scientists had considerable expertise on the topic, having authored or co-authored three or more papers on the effects of environmental parameters, such as habitat and temperature on coral reef fishes. Of the 43 scientists invited to contribute, 33 provided 155 questions. This represented expert opinion from people working in 10 countries and 23 institutions, conducting research in all oceans. The majority of these institutions were universities; however, there were also participants from resource management agencies, research and non-government organisations.

To assess the breadth of knowledge canvassed and how this may have influenced the distribution and evaluation of questions, each scientist was asked to identify their areas of research interest relevant to climate change impacts on coral reef fishes. The same research areas were used to categorise the posed questions. As both the research interests of scientists and questions covered multiple topics, both researchers and questions could be assigned to more than one category.

Contributing scientists were then asked to evaluate the quality of all of the submitted questions. Questions were placed in a random order and scientists asked if each question: (i) identified a gap in our current knowledge base, (ii) was achievable, (iii) was of broad ecological scope (applicable to multiple species and coral reefs globally), and (iv) was of high priority needing to be answered immediately. Each of these question attributes was rated as: very low, low, medium, high, or very high, which corresponded to a score between 1 and 5. Of the scientists that submitted questions, 31 provided scores for all 155 questions. In addition, one scientist that did not submit questions completed the survey (see Table S1 in supplementary material).

Results

More than 70% of scientists identified community dynamics, habitat associations, diversity and distribution patterns of reef fish as areas of research interest (Fig. 1). By contrast, less than 20% of contributors listed physiology, productivity and disease as research interests. Scientists' interests influenced the type of questions proposed, with a positive correlation detected between the number of scientists interested in a topic and the number of questions presented on that topic ($F_{1,11}$=4.47, P=0.05, R^2=0.29). However, scientists tended to score questions from different topic areas evenly, suggesting research background did not unduly bias assessment of question quality (Fig. 2). The median response for questions within all categories was 'high' with respect to identifying knowledge gaps and 'medium' with respect to achievability. Question scope and priority were also similar between categories, although studies on fish disease and behaviour were considered to be of slightly lower scope and priority. These results suggest that although there are relatively few researchers working on topics like physiology of coral reef fish, most recognise that more work is required in these areas. Physiological studies in particular are identified as high priority, and a comparatively high level of achievability suggests scientists believe we already have the ability to address many of these questions. Importantly, a greater knowledge of reef fish physiology will underpin ecological understating and improve management capacity. Clearly there is a need for more interdisciplinary studies and greater collaboration between scientists of different research backgrounds and expertise if we are to progress our understanding of climate change effects on reef fishes.

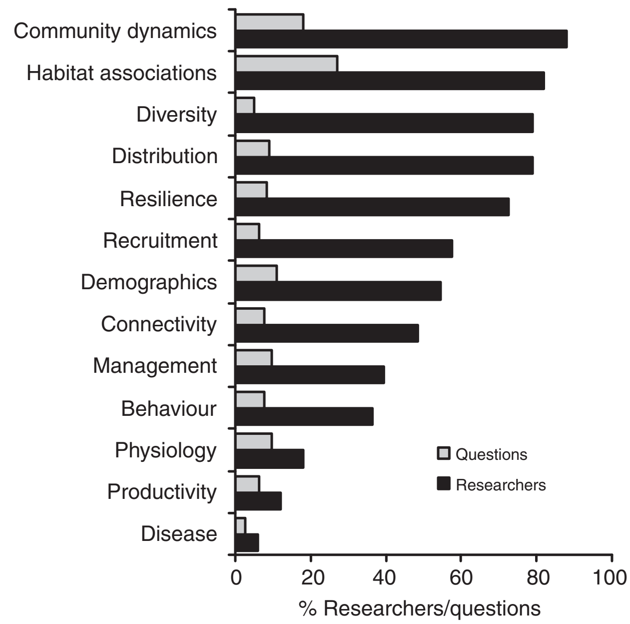

Fig. 1. Research interests of 33 scientists and categorisation of the 155 questions they posed to improve understanding of climate change impacts on coral reef fish.

The final list of 53 questions represents a comprehensive and refined list of objectives that should steer future research. Only questions that the majority of scientists classified as 'high' or 'very high' in terms of identifying a knowledge gap were included whereas questions the majority deemed of 'low' or 'very low' achievability, scope or priority were excluded. In some cases, the same question was posed by multiple scientists, although phrasing of questions differed between scientists. For example, 10 scientists asked how changes in oceanic currents will alter connectivity and recruitment patterns of fish. All 10 of these questions were given median ranks of 'high' in terms of identifying a knowledge gap and scope and 'medium' scores in terms of achievability. Thus, scientists believe our understanding of how climate change affects currents and connectivity is rudimentary but they also realise that these questions are not easily addressed. The standard scoring of similar questions also indicates that scientists were not overly influenced by question phrasing. Nonetheless, there were slight differences in the overall score of similar questions, and where there was replication the

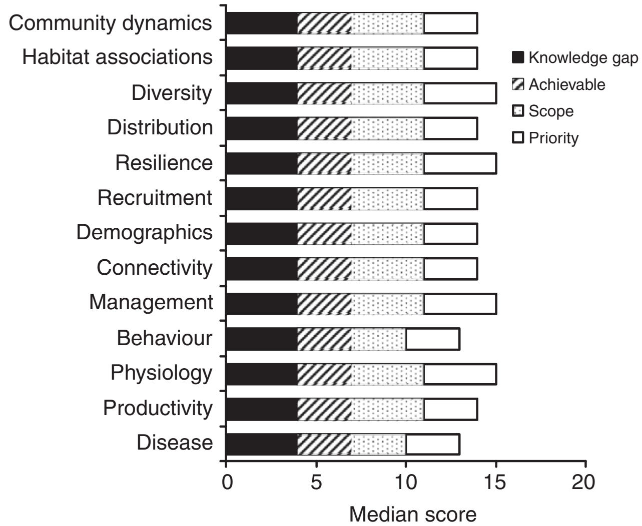

Fig. 2. Median score of questions from 13 research areas. Each question was scored from 1 to 5, where 1 represented very low and 5 very high.

question with the highest overall score was retained. If questions were subtly different (e.g. assessing temporal *vs* spatial trends) information was amalgamated to create a single question. Questions are presented below under the research areas used to classify them although, as previously mentioned, some questions transcend a single topic and could be placed under multiple headings.

Habitat associations, community dynamics and diversity of fishes

(1) While it is clear that fish species that specialise on corals for food or habitat are impacted by coral mortality (Wilson et al., 2006; Pratchett et al., 2008) the effect of coral loss on other fish species, particularly cryptic and rare species, is poorly understood (but see Bellwood et al., 2006). How does coral mortality influence the capacity of a wide range of fish populations, with differing life-history traits, to persist?

(2) Sublethal changes in the condition of reef fish associated with live coral cover have been observed weeks to months after live coral reductions (e.g. Pratchett et al., 2004; Feary et al., 2009). How do sublethal effects vary between species? Are juveniles more susceptible than adults? What are reliable metrics to measure sublethal impacts of climate change on fish?

(3) Very few studies have documented the effects of coral recovery on the short-, medium- and long-term structure of the fish communities (but see Halford et al., 2004; Berumen and Pratchett, 2006). How dependent on coral is the post-disturbance recovery process of fish communities? How will recovery rates of reefs and fish vary due to different disturbance types, e.g. bleaching *vs* storm damage? Which fish species are diagnostic markers of reef regeneration?

(4) Losses in live coral and structural complexity have been shown to cause losses in fish diversity and abundance (Jones et al., 2004; Graham et al., 2006; Wilson et al., 2006); however, little is understood regarding a loss of functional diversity in the fish assemblage or how such a loss may affect coral recovery potential. How is fish functional diversity impacted on degraded coral reefs and how does this interact with benthic recovery dynamics?

(5) It has been shown that different genera of corals vary in their susceptibility to climate change (Baird and Marshall, 2002). Unless rapid adaptation takes place, shifts in coral species dominance will occur (Riegl and Purkis, 2009), most likely away from branching species to more massive and encrusting species. How will this shift in ecosystem engineers, potentially across wide geographical scales, affect reef fish communities? Can we develop a model of what reef fish communities will look like in 10, 25 or 50 years?

(6) What effects will ocean acidification have on coral habitats and how will this affect reef fishes? Much of the work in this domain has focused on the effects of bleaching, due to the historically greater awareness of the issue, but acidification may be the stronger, more critical, impact on habitats and hence on fishes.

(7) Climate change appears to be a major driver leading to the loss of structural complexity on reefs (Alvarez-Filip et al., 2009), which may alter the diversity and composition of fish communities (Sano et al., 1987; Graham et al., 2006). Some reef-associated fish species exhibit a non-linear relationship with structural complexity (Pittman et al., 2009). Do species-specific threshold effects exist beyond which structure no longer supports certain species? What ecological processes and aspects of fish behaviour do loss of structural complexity affect?

(8) Herbivorous fishes often increase in abundance following extensive coral loss (Wilson et al., 2006; Pratchett et al., 2008; Pratchett et al., 2009). At the same time metabolic rate and consumption are expected to increase with temperature, until optimum or threshold temperatures are exceeded (Munday et al., 2008b). How will the rate of feeding and erosion by herbivorous fish (and other bioeroders) be affected by increasing temperatures? To what extent will this process hasten the rates of reef erosion and loss of structural complexity?

(9) Collapse in the physical matrix of the reef following coral mortality has been shown to cause a reduction in the abundance of smaller size classes of large-bodied reef fish (Graham et al., 2007) (Wilson et al., 2010). What are the long-term implications of this for ecological function and fishery resources?

(10) Coral reefs are often a component of a larger ecological system, which incorporates elements such as seagrass, mangroves and algal beds. Changes in temperature, sea level and storm dynamics are likely to affect all of these habitats, the interactions between them and the interactions with terrestrial habitats (e.g. erosion). As many fish undertake ontogenic and trophic migrations between habitats (Nagelkerken et al., 2000; Mumby et al., 2004), how will changes in the composition and cover of habitats adjacent to coral reefs influence fish behaviour, recruitment and abundance?

(11) Much of our focus on coral reef degradation has related to the loss of live coral, and associated structural complexity, and an increase in algal cover. Many other alternate states have been identified, such as those dominated by soft corals, sponges or corallimorphs (Norström et al., 2008). These changes are likely to influence those species that directly rely on these resources (e.g. species that feed directly on soft corals or sponges). How will such changes influence the overall diversity and functioning of reef fish communities?

(12) Climate change could result in increased incidence of disturbances, such as severe storms, or changes may be more gradual, such as gradual declines in pH. Low-level, but persistent, disturbances can still drive changes in community structure (e.g. Berumen and Pratchett, 2006). How does the speed, acuteness or severity of a disturbance influence the resulting fish communities?

(13) How will short- and long-term organic productivity on coral reefs be affected by bleaching? Moreover, as increased water temperature will affect rates of metabolism, digestion and growth, how will this influence the rate at which energy flows through food webs and the productivity of reef fish, particularly species targeted by fishers?

Fish physiology

(14) Can fishes adapt to changing temperature and pH regimes? How will the rate of change in temperature, CO_2 and acidity affect fishes' abilities to adapt? Our understanding of the ability of marine fishes to adapt to rapid environmental change is rudimentary. Many fishes have large geographical ranges spanning a temperature gradient at least as large as projected increases in average SST; therefore, some capacity for adaptation to higher temperatures should be possible, especially in high latitude populations currently living at the lowest temperatures (Munday et al., 2008a). By contrast, there is likely to be much less capacity to adapt to rapid increases in ambient CO_2 (Munday et al., 2009b).

(15) How do fish communities respond to interactions or synergies among various climate change-associated environmental drivers (e.g. rise in temperature, ocean acidification)? Are synergistic effects of SST rise and ocean acidification predicted by their independent effects? Similarly, how does the interaction between habitat degradation and fishing or other anthropogenic pressures affect fish?

(16) Ocean warming and acidification can have a direct effect on coral reef fish (Munday et al., 2008a) and may play an increasingly important role in structuring communities (Poloczanska et al., 2007). How do the direct effects of climate change on fish populations and communities compare with the indirect effects, typically mediated through habitat alteration? Are there other effects associated with climate change (e.g. harmful algal blooms) that may become increasingly important in structuring fish communities?

(17) Recent research has identified an optimal temperature for the damselfish *Acanthachromis polyacanthus*, beyond which growth declines, especially if resources are limited (Munday et al., 2008b). What is the typical optimal temperature for coral reef fishes, and is it likely to be exceeded given sustained ongoing climate change? To what extent are larger and commercially important reef fishes (e.g. *Plectropomus* spp.) affected by projected changes in temperature?

(18) The effects of increased levels of dissolved CO_2 and reduced ocean pH on non-calcifying marine species are poorly understood. Although some research indicates that fishes are tolerant to relatively small increases in CO_2 (Ishimatsu et al., 2008; Munday et al., 2009a), one recent study found that elevated CO_2 exacerbated the effects of increased water temperatures on the aerobic performance of two reef fish species (Munday et al., 2009d). How will performance be affected across a broad spectrum of reef fish species, life stages and genotypes? How will this affect reproductive performance, growth and survival of fishes?

(19) Increasing acidification of marine waters will reduce calcification (mostly aragonite) of marine organisms (Kleypas et al., 1999). What impact will this have on the development of calcified parts of fish, such as otoliths? Could the aragonite be replaced by vaterite or calcite as found in otoliths of some stressed fish?

(20) What are the physiological thresholds at which the functional behaviour and demographics of an animal is compromised or become decoupled? For example, *Pomacentrus ambionensis* adults can sustain 34°C but reproduction is reduced and eggs fail to survive at 31°C (Gagliano et al., 2007).

(21) Animal physiological processes and the maintenance of homeostasis are strongly influenced by temperature and pH. Gametes and embryos have the most poorly developed homeostatic mechanisms. How will increased water temperature and acidification influence gamete viability, performance (e.g. sperm activity) and fertilisation success?

(22) The intrinsic capacity to withstand stressful conditions varies among reef fish species (Gagliano et al., 2009; Nilsson et al., 2009). But how are intrinsic physiological capacities shaped by ecological demands? How similar is the physiological capacity to deal with stress among members of the same functional group or species with comparable life-history traits?

Population demographics of fishes

(23) Because fish are poikilotherms and their metabolic rates are driven by ambient environmental conditions, temperature has a potentially large impact on growth rate and yield. How will growth rates of fishes and fisheries productivity change with respect to temperature shifts?

(24) The upward trend in water temperature could have either a positive or negative effect on the reproductive success of reef fishes that use temperature to cue breeding (Munday et al., 2008a). How will increased temperature affect the reproductive timing/season of marine fishes and the subsequent development, survival and behaviour of larvae?

(25) Parental effects strongly influence the links between ontogenetic stages in a fish's life cycle (McCormick and Gagliano, 2009). Recent studies show that these links are disrupted through maternal stress (McCormick, 1998; McCormick, 2006). How will habitat degradation influence maternal stress and offspring quality, and how will this link influence the size of the population effectively breeding and the number of larvae that replenish local populations?

(26) What would the effect of plastic or inherited life-history changes be on the role of fishes in the community and their role as an extracted marine resource? There are a range of demographic and life-history characteristics that may covary with ecological and anthropogenic effects, and a relatively sound theory of the direction in which variables such as age and size at maturity, mortality, growth and reproduction trade-offs are likely to change (Stearns, 1992). In coral reef fishes understanding these characteristics is made more complicated by the large number of hermaphroditic species in functionally and economically important groups.

(27) Research suggests that food availability becomes limiting to population processes in low latitudes (Jones and McCormick, 2002). If increased temperature increases metabolism, how will the energetic requirements be met at low latitudes? If food is limited, what life process will be traded-off against metabolism?

(28) Life-history theory suggests that in order to maximise reproductive fitness, females will adopt either one of two tactics: investing greater amounts of energy into producing a large quantity of offspring, or producing fewer offspring but investing greater amounts of energy to each individual (Stearns, 1992; Einum and Fleming, 2000). Theory suggests that the allocation strategy adopted depends upon the predictability of the environment (Marshall and Uller, 2007). Will species-specific allocation strategies developed over long time frames be sufficiently flexible to adapt to rapid environmental change, and what are the ramifications of this potential mismatch for recruitment success?

(29) Many coral reef fishes undergo sex change, and the ratio of males and females strongly influences the social organisation of populations. Recent studies have shown that the identity of the individuals that become males (i.e. individuals with highest fitness) depends upon their characteristics at hatching and in the larval phase (Walker et al., 2007) (M.I.M., personal observation). How will climate change influence fitness of early life-history stages and how will this affect social organisation of fish populations.

(30) Which species are really specialists? Theory (Vazquez and Simberloff, 2002) and limited empirical data (e.g. Munday, 2004; Berumen and Pratchett, 2008; Pratchett et al., 2008; Wilson et al., 2008) suggest specialist species are more susceptible to disturbance

than generalists. However, the characterisation of reef fish as specialists and generalists is still unclear. There needs to be a detailed and multi-factorial assessment made of the plasticity in resource use inherent in reef fish.

Resilience of reefs and fishes

(31) Are fishes necessary to maintain coral-dominated systems? There is a general assumption that reefs without fishes decline. But this is often an all-or-none scenario and, beyond herbivores, few groups have been shown to have a significant role in supporting coral reefs. Herbivores may represent a crucial functional group (Bellwood et al., 2004; Mumby, 2006) but are there any others? Which of the fishes on a reef are drivers *vs* passengers (*sensu* Walker et al., 2004), and to what extent are drivers vulnerable to climate change? What physical and biological attributes make some reefs more resilient to disturbance than others?

(32) Habitat degradation caused by coral bleaching is recognised as a major threat to coral reef fishes. Following widespread coral mortality the dead coral skeletons are rapidly colonised by algal turfs, subsequently increasing the algal production per unit area. The ability of the reefs, and hence fish communities, to reassemble following disturbance may be dependent on herbivorous taxa compensating for this increased algal production. What are the thresholds for this positive feedback? Is there a critical biomass of grazing taxa beyond which the reef will start to shift to later successional stage algae? Does this relationship vary spatially? Do any particular taxa play a disproportionately important role in this process?

Connectivity and recruitment of fishes

(33) Water temperature has a significant effect on the growth rate and other life-history traits of pelagic fish larvae (Sponaugle and Pinkard, 2004; Sponaugle et al., 2006). Fish grow faster in warmer water but may settle when smaller and be more susceptible to predation. Faster growth and earlier settlement will potentially reduce larval connectivity among reefs by reducing pelagic larval duration (O'Connor et al., 2007). How will changing water temperature affect the physiological condition and survival of fish larvae settling onto reefs?

(34) Faster growth of larval fish must be supported by higher rates of food intake. In food-limited environments, this has the potential to detrimentally alter recruitment patterns to reef populations (Munday et al., 2009c). How will productivity and availability of oceanic food resources to larval fish be affected by climate change?

(35) Reliable estimates of oceanic currents' response to global warming, at spatial scales relevant to larval dispersal, are urgently needed to better predict the impacts on connectivity among reef fish populations (Munday et al., 2009c). To what extent will current hydrodynamic regimes persist in a warmer climate, and how much will they need to change to affect larval delivery? How will changes in dispersal and connectivity affect fish assemblages within marine protected areas (MPA)? Will MPA designs need to be modified?

(36) Coral mortality attributable to climate change may increase the distances between habitat patches and reduce the 'target' size for larval fish attempting to recruit back to reefs (Munday et al., 2009c). How may loss and fragmentation of reef habitats impair connectivity?

(37) Some fish species recruit to live coral but have no apparent affinity with coral during later life-history stages (e.g. Feary et al., 2007). This may partially explain why the diversity and abundance of reef fish declines after extensive coral mortality (Jones et al., 2004). Most work on juvenile habitat associations of coral reef fish has focused on a few families (e.g. pomacentrids), and there is a need to assess coral specialisation among a broader range of juvenile fish. What other fish recruit to live coral?

(38) What is the role of habitat attributes, such as structural complexity and habitat diversity, for fish recruitment? How will climate-related changes in these habitat attributes influence the settlement, subsequent survival and regional geographical distribution of a wide range of species?

(39) Larval fish may be attracted to reefs through chemical cues (e.g. Atema et al., 2002). How will increased coral bleaching and perturbation on reefs change the 'chemical' environment? Will warmer or more acidic waters increase the rate at which chemical cues break down? How will this affect orientation of pelagic fish larvae?

Fish disease

(40) Could an increase in SST facilitate the role of pathogens (abundance, activity, etc.) interacting with fish, as found with *Vibrio* spp. in Mediterranean gorgonian and tropical corals?

Fish behaviour

(41) Elevated CO_2 [1000 p.p.m. (parts per million)] impairs the ability of clownfish larvae to distinguish olfactory cues from preferred settlement sites (Munday et al., 2009b) and to avoid the chemical cues of predators (Dixson et al., 2010). What other species are similarly affected, and at what levels of CO_2 do behavioural responses manifest? How might this impact future recruitment patterns?

(42) Little is known beyond small-bodied specialised species of fish, regarding how far fish move to escape coral bleaching events (i.e. loss of local habitat) (Samways, 2005; Feary, 2007). Corals can survive in so called 'depth refuges' below thermal thresholds during a bleaching event (Sheppard and Obura, 2005). To what extent do a wide range of reef fishes move, both horizontally and with depth, during a bleaching event, and is such a strategy successful?

(43) A recent study has found that bleaching and coral death leads to changes in phenotypic selection of fishes (McCormick, 2009). How will changes in selective mortality impact the range of phenotypic and behavioural traits of fishes entering the reproductive life stages? These shifts in the nature of mortality may have impacts on the fundamental links between life-history stages and the evolution of life-history strategies (Podolsky and Morany, 2006).

(44) Selection of settlement habitat by olfactory cues may be influenced during early development by acidification (Munday et al., 2009b) but it is currently unclear how other behaviours that require olfactory information may be disrupted. Given the recent finding that chemical alarm cues play an important role in risk assessment and the learning of the identity of predators on coral reefs (Larson and McCormick, 2005; McCormick and Manassa, 2008), how will modified olfactory sensitivity impact predator recognition and predator–prey interactions?

Distribution patterns of fish

(45) Changes in environmental conditions are expected to facilitate colonisation of species in marginal areas, particularly at higher latitudes (Cheung et al., 2009). On some reefs this will affect invasion *vs* extinction processes, with subsequent modifications in the relative dominance of exotic *vs* native species within local fish communities. Which species are most likely to be affected, to what extent will they be affected and how may research institutes collaborate better to monitor shifts in species ranges?

(46) Following extensive habitat loss and changes in environmental conditions local extinctions are inevitable (Munday,

2004). But will local extinctions extend out to regional or even wider-scale extinctions?

(47) At what spatial and temporal scales should correlative and experimental studies address potential climate change effects? There is a broad need to place climate change studies into a suitable temporal and spatial context. Clearly fish assemblages have existed in a fluctuating environment with oceanic oscillations on temporal scales from a few years (e.g. El Niño/La Niña) to multi-decadal regime shifts and longer (e.g. Chavez et al., 2003). Is it sufficient to restrict studies to small areas without considering the larger effects? How relevant are short-term laboratory experiments?

(48) Much reef/climate research has focused on the potential impact of gradual increases in climate-related factors (temperature, acidification, etc.) but changes in the nature of irregular but dramatic climatic events such as El Niño/La Niña have the potential for rapid broad scale effects. For example, El Niño/La Niña events have been shown to synchronise reef fish population dynamics over large spatial scales (Cheal et al., 2007) but the synchronising mechanisms during these events are unclear. Which aspects of El Niño/La Niña cycles are capable of driving broad scale changes in fish communities? How will forecast changes in these major climatic events effect fish populations over large areas?

(49) Spatial variations in coral reef fish assemblages are apparent at regional (Atlantic–Caribbean/Indian/Pacific oceans) and even local scales. Similarly, the effects of climate change will vary over large and small spatial scales. Geographically which fish communities are most susceptible to climate change? Will the impact on community variables (species richness, density, trophic structure, etc.) vary geographically?

Management of fishes

(50) What are our goals: coral-dominated reefs, high fish biodiversity, attractive coral dwelling species, resilience or food security? Can we assume that any of these are correlated or causally linked and if so why? For example, one interpretation of recent evidence (Sandin et al., 2008) is that reefs with top predators are healthier or more resilient than reefs without top predators, and that this means that top predators are essential for ecosystem processes. An alternative interpretation is that reefs that are healthy are also able to retain sharks, i.e. sharks are an indication of, not a requirement for, healthy reefs. How can we separate correlation from causation? If climate change leads to a loss of species does this matter? What is the primary focus of our concern, the fishes, certain types of fishes or their ecological roles?

(51) Is there more we can do to manage climate change impacts on fish and coral reefs than just reduce greenhouse gas emissions? How might we 'enhance reef resilience'? Do existing management strategies contribute to the resilience of reef fish to climate impacts? If so, do they do so beyond just enhancing overall ecosystem resilience? Do no-take areas contribute to reef resilience, make no realistic difference or are they overwhelmed by the effects of climate stressors?

(52) Millions of people rely on coral reef fish for food and livelihoods. How will climate change affect coral reef fisheries? Other than reducing fishing pressure, what can we do to sustain reef fisheries?

(53) Global climate change will impact on human population and socio-economic processes, through population migration, food security, resource availability, etc. These changes will require new approaches for coral reef management and governance (Mumby and Steneck, 2008). How will these modifications in management and governance practices affect fish communities, and how important will they be relative to other physical and biological effects of climate change?

Conclusion

Climate change is already having significant impacts on coral reef ecosystems and coral reef fishes (Pratchett et al., 2008; Pratchett et al., 2009; Munday et al., 2008a; Wilkinson, 2008), and will continue to do so as temperatures increase and oceans become more acidic. Because some of the most dramatic consequences of climate change are yet to occur, there is significant potential for many unknown effects. Yet we currently know enough to anticipate some of these changes and, more importantly, to identify the most pressing (and tractable) research directions to help better address the impacts of climate change in the coming years and decades. The aforementioned questions provide a framework to progress our knowledge of climate change-related effects on fish and fisheries. Although such a process is always evolving, and new pressing research questions may arise through unexpected change in identifying and ultimately filling the above research gaps, we hope to acquire the knowledge necessary to best mitigate the impacts of climate change on reef fish assemblages. Moreover, although we have focused on the effects of climate change on coral reef fishes, many of the posed questions are applicable to other organisms and systems and may act as a general guide for research on climate change.

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References

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M. and Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. Biol. Sci,* **276,** 3019-3025.

Atema, J., Kingsford, M. J. and Gerlach, G. (2002). Larval reef fish could use odour for detection, retention and orientation to reefs. *Mar. Ecol. Prog. Ser.* **241**, 151-160.

Baird, A. H. and Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **237**, 133-141.

Bell, J. D., Kronen, M., Vunisea, A., Nash, W. J., Keeble, G., Demmkea, A., Pontifex, S. and Andréfouët, S. (2009). Planning the use of fish for food security in the Pacific. *Mar. Policy* **33**, 64-76.

Bellwood, D. R., Hughes, T. P., Folke, C. and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* **429**, 827-833.

Bellwood, D. R., Hoey, A. S., Ackerman, J. L. and Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Glob. Chang. Biol.* **12**, 1587-1594.

Berumen, M. L. and Pratchett, M. S. (2006). Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* **25**, 647-653.

Berumen, M. L. and Pratchett, M. S. (2008). Trade-offs associated with dietary specialization for corallivorous butterflyfishes (Chaetodontidae: *Chaetodon*). *Behav. Ecol. Sociobiol.* **62**, 989-994.

Brown, B. E. (1997). Coral bleaching: causes and consequences. *Coral Reefs* **16**, S129-S138.

Bruno, J. F. and Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* **8**, e711.

Bruno, J. F., Selig, E. R., Casey, K. S., Page, C. A., Willis, B. L., Harvell, C. D., Sweatman, H. and Melendy, A. M. (2007). Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol.* **5**, e124.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E. and Niquen, M. C. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**, 217-221.

Cheal, A. J., Delean, S., Sweatman, H. and Thompson, A. A. (2007). Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology* **88**, 158-169.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R. and Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* **10**, 235-251.

De'ath, G., Lough, J. M. and Fabricius, K. E. (2009). Declining coral calcification on the Great Barrier Reef. *Science* **323**, 116-119.

Dixson, D. L., Munday, P. L. and Jones, G. P. (2010). Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* **13**, 68-75.

Einum, S. and Fleming, I. A. (2000). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* **54**, 628-639.

Feary, D. A. (2007). The influence of resource specialization on the response of reef fish to coral disturbance. *Mar. Biol.* **153**, 153-161.

Feary, D. A., Almany, G. R., Jones, G. P. and McCormick, M. I. (2007). Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* **153**, 727-737.
Feary, D. A., McCormick, M. I. and Jones, G. P. (2009). Growth of reef fishes in response to live coral cover. *J. Exp. Mar. Biol. Ecol.* **373**, 45-49.
Gagliano, M., McCormick, M. I. and Meekan, M. G. (2007). Temperature-induced shifts in selective pressure at a critical developmental transition. *Oecologia* **152**, 219-225.
Gagliano, M., Dunlap, W. C., de Nys, R. and Depczynski, M. (2009). Ockham's razor gone blunt: coenzyme Q adaptation and redox balance in tropical reef fishes. *Biol. Lett.* **5**, 360-363.
Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A. and Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science,* **301**, 958-960.
Glynn, P. W. (1996). Coral reef bleaching: facts, hypotheses and implications. *Glob. Chang. Biol.* **2**, 495-509.
Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P. and Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proc. Natl. Acad. Sci. USA* **103**, 8425-8429.
Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Robinson, J., Bijoux, J. P. and Daw, T. M. (2007). Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* **21**, 1291-1300.
Halford, A. R., Cheal, A. J., Ryan, D. and Williams, D. B. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, **85**, 1892-1905.
Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., Lipp, E. K., Osterhaus, A. D. M. E., Overstreet, R. M. et al. (1999). Emerging marine diseases-Climate links and anthropogenic factors. *Science* **285**, 1505-1510.
Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S. and Samuel, M. D. (2002). Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158-2162.
Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshwater Res.* **50**, 839-866.
Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K. et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737-1742.
Ishimatsu, A., Hayashi, M. and Kikkawa, T. (2008). Fishes in high-CO_2, acidified oceans. *Mar. Ecol. Prog. Ser.* **373**, 295-302.
Jones, G. P. and McCormick, M. I. (2002). Numerical and energetic processes in the ecology of coral reef fishes. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. P. F. Sale), pp. 221-238. Academic Press: San Diego, CA.
Jones, G. P. and Syms, C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. *Aust. J. Ecol.* **23**, 287-297.
Jones, G. P., McCormick, M. I., Srinivasan, M. and Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA* **101**, 8251-8253.
Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J., Langdon, C. and Opdyke, B. N. (1999). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118-120.
Larson, J. K. and McCormick, M. I. (2005). The role of chemical alarm signals in facilitating learned recognition of novel chemical cues in a coral reef fish. *Anim. Behav.* **69**, 51-57.
Marshall, D. J. and Uller, T. (2007). When is a maternal effect adaptive? *Oikos* **116**, 1957-1963.
McCormick, M. I. (1998). Behaviorally induced maternal stress in a fish influences progeny quality by a hormonal mechanism. *Ecology* **79**, 1873-1883.
McCormick, M. I. (2006). Mothers matter: crowded reefs lead to stressed mothers and smaller offspring in marine fish. *Ecology* **87**, 1104-1109.
McCormick, M. I. (2009). Behaviourally mediated phenotypic selection in a disturbed coral reef environment. *PLoS One.* **4**, e7096.
McCormick, M. I. and Gagliano, M. (2009). Carry-over effects-the importance of a good start. In *Proceedings of the 11th International Coral Reef Symposium*, pp. 305-310. Florida, USA: Nova South Eastern University.
McCormick, M. I. and Manassa, R. (2008). Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs* **27**, 105-113.
Moberg, F. and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* **29**, 215-233.
Mumby, P. J. (2006). The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol. App.* **16**, 747-769.
Mumby, P. J. and Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.* **23**, 555-563.
Mumby, P. J., Edwards, A. J., Arias-Gonzalez, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L., Renken, H. et al. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**, 533-536.
Munday, P. L. (2004). Habitat loss, resource specialisation, and extinction on coral reefs. *Glob. Chang. Biol.* **10**, 1642-1647.
Munday, P. L., Jones, G. P., Pratchett, M. S. and Williams, A. J. (2008a). Climate change and the future for coral reef fishes. *Fish Fish.* **9**, 261-285.
Munday, P. L., Kingsford, M., O'Callaghan, M. and Donelson, J. M. (2008b). Elevated temperature restricts growth potential of the coral reef fish *Acanthochromis polyacanthus*. *Coral Reefs* **27**, 927-931.
Munday, P. L., Donelson, J. M., Dixson, D. L. and Endo, G. G. K. (2009a). Effects of ocean acidification on the early life history of a tropical marine fish. *Proc. R. Soc. Lond. B* **276**, 3275-3283.
Munday, P. L., Dixson, D. L., Donelson, J. M., Jones, G. P., Pratchett, M. S., Devitsina, G. V. and Doving, K. B. (2009b). Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. USA* **106**, 1848-1852.
Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L. and Lambrechts, J. (2009c). Climate change and coral reef connectivity. *Coral Reefs* **28**, 379-395.
Munday, P. L., Crawley, N. E. and Nilsson, G. E. (2009d). Interacting effects of elevated temperature and ocean acidification on the aerobic performance of coral reef fishes. *Mar. Ecol. Prog. Ser.* **388**, 235-242.
Nagelkerken, I., van der Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hoft, T. and den Hartog, C. (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar. Coast. Shelf Sci.* **51**, 31-44.
Nilsson, G. E., Crawley, N., Lunde, I. G. and Munday, P. L. (2009). Elevated temperature reduces the respiratory scope of coral reef fishes. *Global Change Biol.* **15**, 1405-1412.
Norström, A. V., Nyström, M., Lokrantz, J. and Folke, C. (2009). Alternative states on coral reefs: beyond coral macroalgal phase shifts. *Mar. Ecol. Prog. Ser.* **376**, 295-306.
O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P. and Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl. Acad. Sci. USA* **104**, 1266-1271.
Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R. and Zeller, D. (2002). Towards sustainability in world fisheries. *Nature* **418**, 689-695.
Pittman, S. J., Costa, B. and Battista, T. (2009). Using Lidar bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *J. Coastal Res.* **53**, 27-38.
Podolsky, R. D. and Morany, A. L. (2006). Integrating function across marine life cycles. *Integr. Comp. Biol.* **46**, 577-586.
Poloczanska, E. S., Babcock, R. C., Butler, A., Hobday, A. J., Hoegh-Guldberg, O., Kunz, T. J., Matear, R., Milton, D., Okey, T. A. and Richardson, A. J. (2007). Climate change and Australian marine life. *Oceanogr. Mar. Biol.* **45**, 409-480.
Pratchett, M. S., Wilson, S. K., Berumen, M. L. and McCormick, M. I. (2004). Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs,* **23**, 352-356.
Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinner, J. E., Bellwood, D. R., Jones, G. P., Polunin, N. V. C. and McClanahan, T. R. (2008). Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. *Oceanogr. Mar. Biol.* **46**, 251-296.
Pratchett, M. S., Wilson, S. K., Graham, N. A. J., Munday, P. L., Jones, G. P. and Polunin, N. V. C. (2009). Coral bleaching and consequences for motile reef organisms: past, present and uncertain future effects. In *Coral Bleaching: Patterns, Processes, Causes and Consequences* (eds M. J. H. van Oppen and J. M. Lough), pp. 139-158. Berlin, Heidelberg: Springer-Verlag.
Riegl, B. M. and Purkis, S. J. (2009). Model of coral population response to accelerated bleaching and mass mortality in a changing climate. *Ecol. Model.* **220**, 192-208.
Samways, M. J. (2005). Breakdown of butterflyfish (Chaetodontidae) territories associated with the onset of a mass bleaching event. *Aquat. Conserv.* **15**, S101-S107.
Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Freidlander, A. M., Konotchick, T., Malay, M., Maragos, J. E., Obura, D. et al. (2008). Baselines and degradation of coral reefs in the northern Line Islands. *PloS One* **3**, e1548.
Sano, M., Shimizu, M. and Nose, Y. (1987). Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar. Ecol. Prog. Ser.* **37**, 191-199.
Sheppard, C. and Obura, D. (2005). Corals and reefs of Cosmoledo and Aldabra atolls: extent of damage, assemblage shifts and recovery following the severe mortality of 1998. *J. Nat. Hist.* **39**, 103-121.
Sponaugle, S. and Pinkard, D. R. (2004). Impact of variable pelagic environments on natural larval growth and recruitment of the reef fish *Thalassoma bifasciatum*. *J. Fish Biol.* **64**, 34-54.
Sponaugle, S., Grorud-Colvert, K. and Pinkard, D. (2006). Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Mar. Ecol. Prog. Ser.* **308**, 1-15.
Stearns, S. C. (1992). *The Evolution of Life Histories.* Oxford University Press: New York.
Vasquez, D. P. and Simberloff, D. (2002). Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am. Nat.* **159**, 606-623.
Walker, B., Holling, C. S., Carpenter, S. R. and Kinzig, A. (2004). Resilience, adaptability, and transformability in social-ecological systems. *Ecol. Soc.* **9**, 5.
Walker, S. P. W., Ryen, C. A. and McCormick, M. I. (2007). Rapid larval growth promotes sex change and growth acceleration in a protogynous hermaphrodite, *Parapercis snyderi* Jordan & Starks 1905. *J. Fish Biol.* **71**, 1347-1357.
Webster, P. J., Holland, G. J., Curry, J. A. and Chang, H. (2005). Changes in tropical cyclone number and intensity in a warming environment. *Science* **309**, 844-1846.
Wilkinson, C. (2008). *Status of Coral Reefs of the World: 2008.* Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Center.
Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P. and Polunin, N. V. C. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Glob. Chang. Biol.* **12**, 2220-2234.
Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. C. and Sweatman, H. P. A. (2008). Habitat utilization by coral reef fish: implications for specialists *vs* generalists in a changing environment. *J. Anim. Ecol.* **77**, 220-228.
Wilson, S. K., Fisher, R., Pratchett, M. S., Graham, N. A. J., Dulvy, N. K., Turner, R. A., Cakacaka, A. and Polunin, N. V. C. (2010). Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* In press.