Interdependence between reef fishes and scleractinian corals

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Abstract. Scleractinian corals are the primary habitat-forming species in healthy, intact coral reef ecosystems. Removal or destruction of corals will therefore, profoundly alter the structure and dynamics of coral-reef habitats, with likely effects across a diverse range of reef fishes. Conversely, many reef fishes are considered fundamental to the structure and resilience of reef ecosystems, such that degradation of coral-dominated habitats may initiate a downward spiral in ecosystem state leading to fundamental shifts in structure and function. This paper explores strong interdependence between reef fishes and scleractinian corals, focusing on the data necessary to establish linked vulnerabilities of fish and coral given increasing incidence of major disturbances. A large and increasing number of studies purport to show strong coral dependence among reef fishes based on strong and positive correlations between local abundance and live coral cover. However, coral cover may explain a very limited portion of spatial structure in the abundance of fishes, even among those species known to depend on live coral (e.g., for food and habitat). This is because coral-dependent fishes may be highly specialized and only use a limited suite of available corals. Also, numerous factors (e.g., local recruitment) may contribute to variation in abundance of fishes among locations with established coral communities, and reliance on corals is really only apparent by documenting changes in the individual abundance and fitness of reef fishes following localized declines in coral cover. Likewise the role of fishes in enhancing coral reef resilience is most apparent during recovery from major disturbances, but it is unclear whether reef fishes (e.g., corallivores) increase or decrease susceptibility of corals to disease and bleaching. This review emphasizes the importance of long-term monitoring, combined with effective experimental studies to establish the linked vulnerabilities of fishes and corals to ongoing disturbances, as well as interdependence between fishes and corals in reef resilience.

Key words: Disturbance, monitoring, resilience, resource specialisation, and vulnerability

Introduction

Coral reef ecosystems are increasingly subject to acute, but often catastrophic, disturbances that cause marked reductions in the abundance of reef-building corals (e.g., Hughes et al. 2003; Hoegh-Guldberg et al. 2007). At the same time, increasing anthropogenic pressure and chronic disturbances are compounding on coral loss, and perhaps more importantly, eroding the resilience (resistance and recovery potential) of coral assemblages that are subject to increasing diversity and incidence of acute disturbances (Hughes et al. 2003). Not surprisingly, therefore, coral cover is declining on most coral reefs (e.g., Bruno and Selig, 2007), and there is a very real threat that coral-dominated reef habitats will become dominated by macroalgae, or other less desirable benthic organisms (Hughes et al. 2010).

Changes in the physical and biological structure of benthic reef habitats are likely to have further, often detrimental, effects on other reef associated organisms, such as coral reef fishes (e.g., Wilson et al. 2006; Pratchett et al. 2008; Hoey & Bellwood 2011). Butterflyfishes from the genus *Chaetodon* (family Chaetodontidae), for example, often feed on hard corals (Pratchett 2005) and will therefore starve and disappear in the absence of sufficient prey corals (Pratchett et al. 2006). Accordingly, spatial variation in the abundance of butterflyfishes is often correlated with hard coral cover (e.g., Cadoret et al. 1999; Pratchett & Berumen 2008), but not always (e.g., Lawton & Pratchett 2012). More importantly, many butterflyfishes exhibit rapid and dramatic declines in abundance following extensive coral depletion (e.g., Pratchett et al. 2006; Graham et al. 2007). Together these data provide a compelling case for strong dependence on live corals. It is unclear, however, what proportion of coral reef fishes are reliant on scleractinian corals, or what would happen if coral reefs become dominated by macroalgae, but this information is critical to predict likely effects of

ongoing coral reef degradation on biodiversity and fisheries productivity.

Declines in biodiversity and abundance of coral reef fishes, especially those that perform critical ecological functions, may further reduce resilience of coral reef ecosystems. Concern regarding the loss of key functional groups on coral reefs mostly centers on herbivorous fishes, and particularly grazing species (Bellwood et al. 2004), which play a critical role in controlling macroalgae that might otherwise limit coral recruitment and recovery (Hughes et al. 2007). Hughes et al. (2007) showed that exclusion of fishes, led to rapid overgrowth of macroalgae. High cover of macroalgae did not directly undermine the local abundance of scleractinian corals, but did prevent ongoing coral recruitment necessary to replenish adult corals lost to bleaching (Hughes et al. 2007). These findings point to the importance of maintaining intact reef fish assemblages, but it is unclear exactly which fishes were important in maintaining low macroalgal cover, and therefore, high coral cover. Strong interdependence between fishes and corals is often assumed, rather than clearly established (Pratchett et al. 2008), and it is likely that the functional importance of some fish and corals has been underestimated.
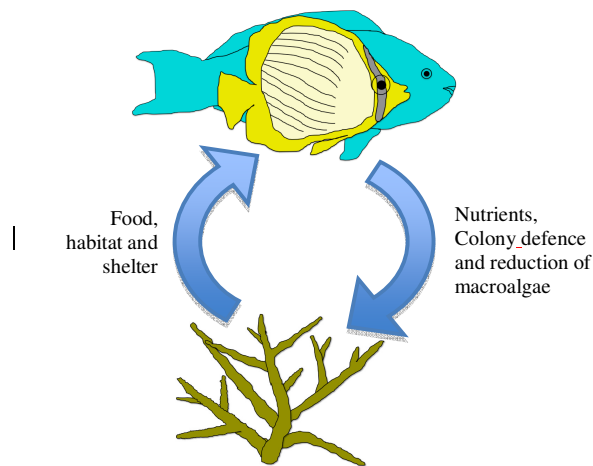

Figure 1: Interdependence between reef fishes and scleractinian corals.

For reef fishes, reliance on corals is often assumed based on either patterns of coral use (e.g., Ohman et al. 1998), or spatial correlations between local abundance and live coral cover (e.g., Bell & Galzin 1984). Neither of these methods conclusively show that fishes are actually dependent on live coral, and therefore vulnerable to declines in abundance of live coral. This data is, however, important in predicting the likely effects of coral loss due to significant and increasing levels of acute and chronic disturbances. Likewise, understanding of the role of fishes in the resilience of coral reef ecosystems is largely based on events after catastrophic coral loss, thereby emphasizing the role of herbivorous fishes in maintaining low cover of macroalgae (Fig. 1), rather than considering potentially beneficial effects of reef fishes in reducing susceptibility of corals to bleaching and disease (e.g., Cole et al. 2009). This paper reviews current evidence for the strong interdependence between reef fishes and scleractinian corals, and proposes key research necessary to improve understanding of linked vulnerabilities to future disturbances.

Establishing coral dependence among fishes
Estimates of the number (or proportion) of species of coral reef fishes that are reliant on corals, and will therefore be adversely affected by extensive coral loss, vary enormously. Of 1221 coral-reef fishes recorded on Australia's Great Barrier Reef, Munday et al. (2008) estimated that 104 species (9%) have direct and explicit reliance on corals either for food or shelter (see also Jones et al. 2004). However, a far greater proportion of fishes exhibit declines in abundance following acute disturbances and extensive coral loss. At Iriomote Island, Japan, for example, 47 of 62 species (76%) of fishes completely disappeared following extensive coral loss caused by outbreaks of crown-of-thorns starfish (*Acanthaster planci*), and 9 of 15 remaining species exhibited significant declines in abundance (Sano et al. 1987). In a meta-analysis of 17 independent studies, Wilson et al. (2006) showed that 62% of reef fishes declined in abundance following a >10% decline in coral cover. Similarly, Pratchett et al (2011b) showed that in 60% (815 out of 1360) of cases from more recently published studies, local abundance of fishes declined following declines in live coral cover. For some species however, such as *Chaetodon trifasciatus*, observed changes in local abundance following extensive coral loss are highly contradictory (Fig. 2), questioning whether these data really capture the reliance of fishes on corals.

Changes in the abundance of fishes following extensive coral loss may be confounded by a number of factors. Mostly, it is unclear whether fishes are responding to the loss of live coral cover per se, or associated changes in the biological and physical habitat structure (Graham et al. 2006; Pratchett et al. 2008). Some authors (e.g., Jones et al. 2004) consider that live coral cover has a major influence on the distribution and abundance of coral-reef fishes, but there is also correlative evidence linking the abundances coral-reef fishes with topographic complexity (e.g., Gratwicke & Speight 2005; Garpe et al. 2006; Wilson et al. 2007). Establishing the importance of live coral for reef fishes is further complicated because the relationship between

abundance of coral-dependent fishes and live coral may be non-linear (Holbrook et al. 2008), such that fishes may be insensitive to all but major changes in live coral cover.

Correlations with live coral cover
For fishes that are strongly reliant on live corals it is expected that variation in coral cover will have a major bearing on patterns of abundance (Lawton & Pratchett 2012). Indeed, numerous studies have found strong links between total hard coral cover and abundance of specific reef fishes, both at small (e.g., Holbrook et al. 2000) and relatively large spatial scales (e.g., Emslie et al. 2010). These associations also tend to be stronger for fishes with a direct reliance on live corals for food (e.g., butterflyfishes) or habitat (coral-dwelling gobies and damselfishes). However, some studies have failed to detect a significant relationship between live coral cover and abundance of fishes, even among species that are seemingly reliant on live corals. Lawton and Pratchett (2012) showed that coral cover explained relatively little (<20%) of the variation in abundance of coral-feeding butterflyfishes across 5 locations in the south Pacific.

Strong positive relationships between coral cover and local abundance of fishes are probably a good indication of strong coral-dependence. However, the lack of any such relationship may mean that either (1) the fishes studied are insensitive to changes in coral cover over the range sampled, or (2) that any effect of coral cover was indiscernible against the backdrop of numerous other factors that may regulate abundance of reef fishes (Lecchini et al. 2003). It is important therefore, to account for differences among habitats, depths, exposure, and other major environmental gradients, when relating variation in abundance of reef fishes to coral cover (Chabanet et al. 1997; Lecchini et al. 2003). It is also important to consider whether fishes are likely to respond to overall changes in live coral cover, or only changes in the abundance of a specific subset of corals that they actually utilize, depending on their degree of resource specialization (Munday et al. 1997).

Resource specialization is rapidly emerging as one of the key determinants of a species' vulnerability to disturbance (McKinney 1997; Munday et al. 2004), and is useful for establishing specific reliance on given resources (e.g., Munday et al. 1997). It is important however, to use measures of specialization that explicitly consider availability of resources (Lawton et al. 2012). Specialization indices that do not consider resource availability cannot distinguish between species that selectively use a restricted subset of available resources versus those that have limited access to different resources. Species that use a

restricted set of resources regardless of availability, (*obligate specialists*; Cornell 1967) are critically dependent upon the few resources used. In contrast, *facultative specialists*, that can modify patterns of prey use according to their availability, are likely to be much less reliant on specific resources, and therefore less vulnerable to disturbances (Lawton et al. 2012b). It is critical however, to consider both susceptibility and recovery potential, to assess the resilience of individual species.

Specialization in coral use has been studied for a range of fishes, and especially gobies (Munday et al. 1997) and butterflyfishes (Pratchett 2005). A comprehensive review of these studies is yet to be completed, but most studies have shown that coral-dependent fishes are specialized, tending to use *Acropora* and *Pocillopora* in preference to other dominant coral genera, such as *Porites* (but see Gardiner & Jones, 2005). These data are important in predicting the consequences of changes in coral communities, which are likely to occur due to selective effects of major disturbances (Hughes et al. 2012). However, there are several groups of coral-dependent fishes (e.g., hawkfishes) for which we still need to quantify habitat specialization.

Responses to coral loss
Reef fishes reliant on live corals would be expected to be significantly and adversely affected by extensive coral loss, with the extent of declines somewhat reflective of coral-dependence. However, there are a great number of reef fishes shown to have declined in abundance following extensive corals loss (Pratchett et al. 2011). Mean responses vary predictably across key functional groups, with corallivores exhibiting strong and consistent declines in abundance following pronounced coral loss, whereas carnivores, herbivores and planktivores exhibit net increases in abundance (Fig. 2). However, within all functional groups, there are some species recorded to go locally extinct (100% decline) following extensive coral loss, and modal responses are generally negative (Pratchett et al. 2011). Effects of coral loss on coral-dependent fishes are also highly variable within species. For example, *C. trifasciatus* has been shown to increase and decrease in abundance during significant declines in live coral cover (Fig 2b). Some studies have actually shown large increases in proportional abundance (300%), probably due to inherent sample error, which has magnified effects in areas where species are naturally rare.

Responses of fishes to coral loss may vary according to the severity of coral loss, the extent to which coral limits their abundance, specialization in coral use, and the specific coral species they use (Pratchett et al. 2008). Also, extensive coral loss may

not necessarily lead to short-term declines in abundance of coral-dependent reef fishes. Rather, reduced availability of live coral can have significant but sublethal effects, such as declines in physiological condition (Pratchett et al. 2004) or recruitment (Graham et al. 2007) which will only become manifest as declines in abundance over protracted periods. Temporal delays in the effects of coral loss are particularly important for long-lived fishes, including many large and commercially important fisheries species (e.g., coral trout). However, longer-term effects (e.g., decadal) of coral loss are poorly understood, mostly because there are few studies that have systematically measured abundance of coral-reef fishes for >10 years following major disturbances (Pratchett et al. 2008).
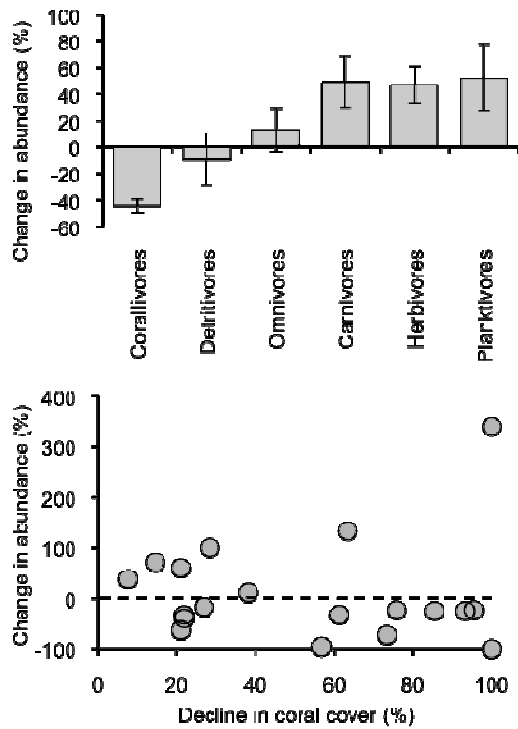

Figure 2: Effects of coral loss on reef fishes, showing A) mean (± SE) responses among key functional groups, and B) variation in responses for a single species of fish, *Chaetodon trifasciatus*. For data sources, see Pratchett et al. (2011)

Effects of fishes on scleractinian corals
The global degradation of coral reef habitats, combined with strong reliance on reef habitat by coral reef fishes, has generated considerable concern over fundamental changes in the structure and function of reef ecosystems (Bellwood et al. 2004). However, aside from the important role of herbivorous fishes in maintaining suitable reef substrates for coral settlement (e.g., Hughes et al. 2007) the functional importance of coral reef fishes is poorly understood.

There are a number of distinct studies that suggest large predatory fishes have an important role in maintaining coral dominated habitats, either by minimizing devastating outbreaks of the crown-of-thorns starfish, *Acanthaster planci* (Dulvy et al. 2004) or by regulating abundance of coral-feeding fishes thought to spread coral disease (Raymundo et al. 2010). However, these studies provide limited support for critical mechanistic links (e.g., that early life-stages of *A. planci* are susceptible to predation, and that butterflyfishes are vectors of coral disease, respectively) necessary to support alleged trophic cascades. Regarding the role of butterflyfishes in coral disease, Cole et al. (2009) actually showed that butterflyfishes may have a beneficial role; intensive feeding by *Chaetodon plebeius* at sites of black band disease on *Acropora muricata* effectively halted progression of the disease, whereas disease bands progressed rapidly in the absence of butterflyfishes.

Coral reef fishes can confer direct benefits to scleractinian corals, including provision of nutrients, removal of sediments, and protection from predators, which can significantly increase coral growth (Holbrook et al. 2011) and survivorship (White & O'Donnell 2010). Holbrook et al. (2011) showed that colonies of *Pocillopora damicornis* inhabited by large social groups of coral-dwelling damselfishes grew much faster due to increased nutrient provisioning. Coral-dwelling fishes may also protect host corals from other corallivores, such as crown-of-thorns starfish (Lassig 1977). This strong mutualism will greatly increase resilience of both fish and corals during major disturbances.

Conclusions
Increased recognition of the range of reef fishes that depend on scleractinian corals, and *vice versa*, has resulted mostly from effective, long-term monitoring (e.g., Graham et al. 2007; Emslie et al. 2010). It is critical therefore, to maintain established monitoring programs, and utilize the data arising to address emerging controversies, such as the importance of live coral for key fisheries species (e.g., coral trout). It is also necessary to complement monitoring studies with experimental tests of coral dependence across a wide range of different reef fishes, including quantification of dietary and habitat specialization.

The utility of monitoring is particularly important in understanding the factors that facilitate rapid recovery and promote resilience among coral reef assemblages. Importantly, strong interdependence between coral reef fishes and scleractinian corals not only leads to linked vulnerabilities, but may also be important in understanding recovery trajectories and resilience of coral reef ecosystems.

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