



Contents lists available at ScienceDirect

## Journal of Experimental Marine Biology and Ecology

journal homepage: [www.elsevier.com/locate/jembe](http://www.elsevier.com/locate/jembe)

## Growth of reef fishes in response to live coral cover

David A. Feary<sup>a,b,\*</sup>, Mark I. McCormick<sup>a</sup>, Geoffrey P. Jones<sup>a</sup><sup>a</sup> ARC Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia<sup>b</sup> United Nations University - International Network on Water, Environment and Health, Dubai International Humanitarian and Aide City, Doha St. Building No. 3, P. O. Box 33328, Dubai, United Arab Emirates

## ARTICLE INFO

## Article history:

Received 3 December 2008

Received in revised form 4 March 2009

Accepted 5 March 2009

Available online xxx

## Keywords:

Coral cover

Coral reef

Coral reef fish

Growth

Physiology

Pomacentridae

## ABSTRACT

Although the global decline in coral reef health is likely to have profound effects on reef associated fishes, these effects are poorly understood. While declining coral cover can reduce the abundance of reef fishes through direct effects on recruitment and/or mortality, recent evidence suggests that individuals may survive in disturbed habitats, but may experience sublethal reductions in their condition. This study examined the response of 2 coral associated damselfishes (Pomacentridae), *Chrysiptera parasema* and *Dascyllus melanurus*, to varying levels of live coral cover. Growth, persistence, and the condition of individuals were quantified on replicate coral colonies in 3 coral treatments: 100% live coral (control), 50% live coral (partial) and 0% live coral (dead). The growth rates of both species were directly related to the percentage live coral cover, with individuals associated with dead corals exhibiting the slowest growth, and highest growth on control corals. Such differences in individual growth between treatments were apparent after 29 d. There was no significant difference in the numbers of fishes persisting or the physiological condition of individuals between different treatments on this time-scale. Slower growth in disturbed habitats will delay the onset of maturity, reduce lifetime fecundity and increase individual's vulnerability to gape-limited predation. Hence, immediate effects on recruitment and survival may underestimate the longer-term impacts of declining coral on the structure and diversity of coral-associated reef fish communities.

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## 1. Introduction

There has been a rapid increase in the extent and severity of both natural and anthropogenic disturbances in both aquatic and terrestrial habitats globally (Watling and Norse 1998; Laurance 1999; Naiman and Turner 2000). A central question, highlighted by such habitat degradation, has been to examine which ecological characteristics render species prone to change (Jiguet et al., 2007; Brook et al., 2008; Isaac et al., 2009). Habitat loss may manifest as direct fluctuations in the associated community's abundance and diversity, through the reduction or loss of suitable resources (i.e. shelter and food) (Andren 1994; Kruess and Tschamtket 1994; Myers et al., 2000). An increasing amount of work, however, is now showing that habitat loss may have substantial effects on the physiological condition of individuals within degraded habitats, with concomitant changes in individual's reproduction, growth and fitness (Homan et al., 2003; Martinez-Mota et al., 2007). Such indirect changes in the demographic mechanisms important in population maintenance and renewal may then have far-reaching, negative effects on both the composition and structure of communities within degraded habitats.

The destruction and degradation of shallow marine habitats is increasing at an unprecedented rate (Alongi, 2002; Duarte, 2002; Lotze et al., 2006) and coral reef ecosystems appear to be particularly vulnerable (Pandolfi et al., 2005; Aronson and Precht, 2006; Pandolfi and Jackson, 2006; Hoegh-Guldberg et al., 2007). While impacts on coral reefs can have direct and immediate consequences for coral biodiversity (Hoegh-Guldberg, 1999; Knowlton, 2001; Pandolfi and Jackson, 2006), the associated fish fauna will often exhibit dramatic changes in structure with reef degradation (Jones and Syms, 1998; Halford et al., 2004; Jones et al., 2004; Graham et al., 2006; Wilson et al., 2006). Some effects may occur immediately in response to coral tissue loss, particularly for corallivorous or obligate coral dwelling species (Syms and Jones, 2000; Halford et al., 2004; Jones et al., 2004). Other effects may not become apparent for several years, perhaps in response to the collapse of the 3-dimensional physical structure on dead reefs (Graham et al., 2006; Wilson et al., 2006). Our understanding of the demographic mechanisms by which coral degradation impact fish communities over different time-scales remains limited.

Longer-term effects of declining coral cover on fish communities may arise through mechanisms that have no immediate effects on demographic rates such as mortality. Sublethal effects in response to a loss of resources, such as reductions in reef fish growth or physiological condition may not be detected for months or years after disturbance. For example, Pratchett et al. (2004) found little change in the population abundance of a small obligate corallivore (*Chaetodon lunulatus*), associated with degraded reefs, 2 years after

\* Corresponding author. United Nations University - International Network on Water, Environment and Health, Dubai International Humanitarian and Aide City, Doha St. Building No. 3, P.O. Box 33328, Dubai, United Arab Emirates. Tel.: +971 4 3753714; fax: +971 4 3686919.

E-mail address: [dfeary@inweh.unu.edu](mailto:dfeary@inweh.unu.edu) (D.A. Feary).

live coral reductions. However, there were significant declines in the physiological condition of populations, likely to have resulted from declines in the quantity and quality of available coral prey (Pratchett et al., 2004).

Previous work investigating the sublethal response of fishes to coral disturbance has focused entirely on obligate corallivores (e.g., Pratchett et al., 2004). While the effects can be substantial, coral-feeders represent a small proportion of coral reef fish communities (Hixon, 2003), with small, coral associated planktivorous damselfish often making up a larger proportion of reef fish assemblages (Sale, 1991). These fishes typically associate with live coral colonies, presumably using them primarily as shelter sites (Holbrook et al., 2000; Holbrook and Schmitt, 2002). Significant declines in damselfish abundance have been observed with live coral loss (Booth and Beretta, 2002, but see Pratchett et al., 2008). However, even for species that exhibit no immediate change in abundance (Feary et al., 2007), reductions in the live coral may theoretically have negative effects on their growth or physiological condition (Jones and Syms, 1998; Jones and McCormick, 2002, Pratchett et al., 2008).

This study examined the response of 2 species of coral associated, planktivorous damselfish to different levels of live coral. Under experimental conditions, the effects of coral cover were tested on short term patterns of persistence, growth and condition of individual fish. The short term response of individuals on degraded habitats was predicted to involve reductions in abundance, growth and/or condition, with lower live coral cover leading to lower persistence on corals and lower fish growth and/or condition. As body size may have also influenced individual's persistence, growth or condition with live coral loss, we also compared these parameters between 2 size classes (juveniles and adults).

## 2. Materials and methods

### 2.1. Study area and experimental design

This study was conducted at Kimbe Bay, West New Britain, Papua New Guinea (5°30'S, 150° 05'E), on the coral associated planktivorous damselfishes, *Chrysiptera parasema* and *Dascyllus melanurus* (Pomacentridae). These two species are commonly associated with branching corals on isolated patch reefs in back-reef habitats in this region and have previously been successfully translocated to patch reefs established for experimental manipulations (Srinivasan, 2003).

A factorial design was used, with 3 levels of coral cover crossed with the 2 fish species. Thirty six live colonies of *Acropora millepora* were translocated to an expanse of sand (5–6.5 m). All colonies were separated by 20 m of open sand. Corals were ~300X200 mm diameter (Total coral volume =  $1/3 \times \pi \times r^2 \times h$  (cm), where  $r$  = radius and  $h$  = height from base of coral); there was no significant difference in coral size among replicates between species and treatments ( $F_{1, 30} = 0.120$ ,  $P = 0.886$ ). Using only locally collected individuals (collected  $\leq 400$  m from the experimental site), 8 individuals of *C. parasema* were stocked on each of 18 randomly selected colonies, while 8 *D. melanurus* individuals were stocked on the remaining 18 colonies. Subsequent emigrants were replaced (approximately 1 individual per colony) until the population on each colony stabilized at 5–6 *C. parasema* and 6–7 *D. melanurus*. Fishes remaining on colonies were then tagged for individual recognition, using subcutaneous injections of colored elastomer *in situ*, and measured to the nearest mm (standard length [SL] and TL) (Malone et al., 1999). Individuals were then categorized into two different size classes (juveniles and adults) using published size class data (*C. parasema*: juveniles  $\leq 21$  mm total length [TL], adults  $> 21$  mm TL; *D. melanurus*: juveniles  $\leq 19$  mm TL, adults  $> 19$  mm TL) (Cole, 2002; Asoh, 2003; Srinivasan and Jones, 2006). There was no significant variation in individual size within each size category (*C. parasema*, juvenile:  $F_{2, 30} = 0.174$ ,  $P = 0.840$ ; adult:  $F_{2, 30} = 0.215$ ,  $P = 0.807$ ; *D. melanurus*, juvenile:  $F_{2, 79} = 3.032$ ,  $P = 0.053$ ; adult:

$F_{2, 79} = 0.073$ ,  $P = 0.929$ ). The ratio of juvenile to adult individuals within colonies was 5 ( $\pm 0.481$ ) to 3 ( $\pm 0.283$ ), with no significant variation in the range of individuals body size within each coral colony between treatments (*C. parasema*:  $F_{2, 84} = 0.309$ ,  $P = 0.735$ ; *D. melanurus*:  $F_{2, 122} = 1.355$ ,  $P = 0.261$ ). This ratio is similar to natural populations in the area (D.A. Feary personal observation).

Each coral colony was then randomly assigned to 1 of 3 treatments: 100% live coral cover ( $n = 12$ ); 50% live coral cover ( $n = 12$ ), and 0% live coral cover ( $n = 12$ ). All colonies were caged with wire-mesh cages and a single crown-of-thorns starfish (COTS) introduced into each coral-reduced treatment. COTS were constrained to feed on selected parts of treatment colonies by attaching rubble to the coral head, limiting the area of coral for the COTS to feed on. Coral loss occurred over 2–4 d, all cages and COTS were then removed; no change in the abundance of focal damselfish was apparent throughout all treatments over this time period. Total degraded coral volume (after COTS disturbance) ( $1/3 \times \pi \times dr^2 \times dh$  (cm), where  $dr$  = degraded radius,  $dh$  = degraded height from base of coral) was measured and coral loss quantified (total live coral volume/ total degraded coral volume \* 100).

Due to logistical difficulties this study could only be conducted for 29 d. After this time all study species were collected, euthanized with an overdose of clove oil, and their total and standard length (TL and SL) measured.

### 2.2. Persistence

We used generalized linear models (GLM) to test for the effects of size class (juvenile, adult) and coral treatment (100%, 50% and 0% live coral) on the relative persistence of individuals over the 29 day test.

### 2.3. Growth

As potential natural growth may differ between adult and juvenile fishes, we analyzed individual growth by comparing the natural log of final and initial size and calculated growth using % change in TL (mm), calculated as:

1.  $\text{Lnlog}(\text{change TL}) = \text{Lnlog}(\text{TL}) \text{ at trial end} - \text{Lnlog}(\text{TL}) \text{ at trial start then,}$
2.  $\% \text{ change TL} = \text{Lnlog}(\text{change TL}) / \text{Lnlog}(\text{TL}) \text{ at trial start.}$

To examine whether there were significant differences in % change TL between size class (juvenile, adult) and treatment (100%, 50%, 0% live coral), a two-way ANOVA was used. All data were arcsine transformed to meet assumptions of normality and homoscedascity. Any significant difference in % change TL within or between factors was examined further using Tukey HSD tests.

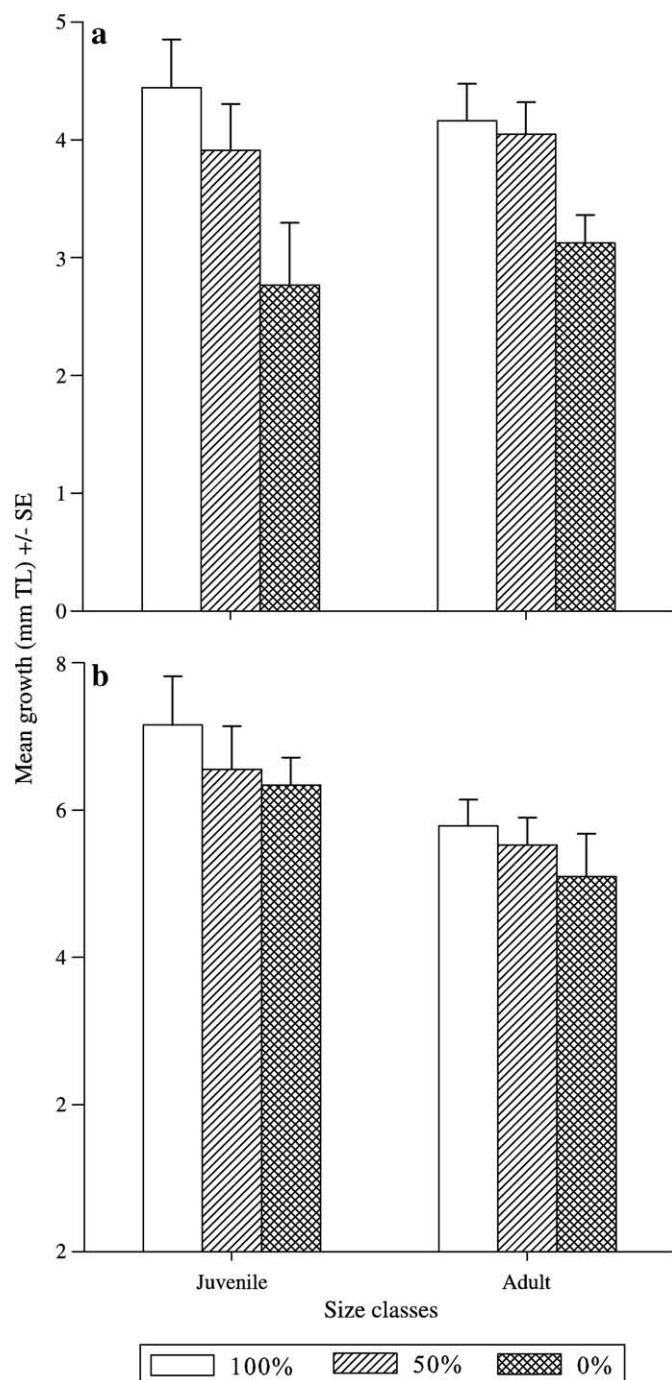
### 2.4. Condition

To determine the influence of coral treatment on the physiological condition of both study species, between size classes, the Fulton's condition factor was calculated. Fulton's condition factor ( $K$ ) was defined as:  $K = \text{WB} * 100 / L^3$ ; where WB is gutted body weight (g) and L is standard length (mm). High  $K$  values indicate a greater body mass for a given length; indicative of individuals with good physiological condition.

To quantify the physiological condition of study species, hepatocyte vacuolation was measured (i.e., the proportion of liver tissues occupied by intracellular vacuoles), which is an indirect measure of total liver lipid stores (Green and McCormick, 1999). A high proportion of liver tissues occupied by intracellular vacuoles are indicative of individuals with high physiological condition (Green and McCormick, 1999). After fixing, hepatic tissues were dehydrated in a graded ethanol series and embedded in paraffin wax. Tissues were sectioned at 5  $\mu\text{m}$  and sections were stained using Mayer's

hematoxylin and eosin. The proportion of vacuoles in hepatic tissues was then quantified using a Weibel eyepiece, recording the proportion of points (out of 42) that intersected hepatocyte vacuoles viewed at 400 magnification. Hepatocyte vacuole counts were repeated 3 times by a single observer without reference to the fish's identity (i.e., blind).

For each condition index, 30 individuals in each size class were examined (10 individuals from each coral treatment) within each study species (using the same individuals as analyzed above). Each condition index was then separately analyzed using two-way ANOVA on 4th root transformed data (to meet assumptions of normality and homoscedasticity).



**Fig. 1.** Mean somatic growth (mm total length [TL]) of (a.) *Chrysiptera parasema* and (b.) *Dascyllus melanurus* individuals over a 29 day experiment between size classes (juvenile, adult) and coral treatments (100%, 50%, 0% live coral).

### 3. Results

There was no significant difference in the persistence of populations between size classes or treatments for either *C. parasema* (Size class:  $P=0.732$ ; Coral treatment:  $P=0.374$ ) or *D. melanurus* (Size class:  $P=0.970$ ; Coral treatment:  $P=0.389$ ), with both study species showing high levels of persistence throughout the trial period. For juvenile sized *C. parasema* individuals,  $86\% \pm 0.04$ ,  $72\% \pm 14.2$  and  $91\% \pm 8.3$  of transplanted individuals survived throughout the 29 day trial period between control, half and full degraded colonies, respectively. Within the adult size class,  $74\% \pm 6.6$ ,  $72\% \pm 13.3$  and  $75\% \pm 8.75$  of transplanted individuals survived throughout the 29 day trial period between control, half and full degraded colonies, respectively. For juvenile sized *D. melanurus* individuals,  $84\% \pm 7.9$ ,  $84\% \pm 5.5$  and  $83\% \pm 12.4$  of transplanted individuals survived throughout the 29 day trial period between control, half and full degraded colonies, respectively. For adult sized individuals of *D. melanurus*,  $73\% \pm 10.3$ ,  $73\% \pm 12.0$  and  $87\% \pm 8.2$  of transplanted individuals survived throughout the 29 day trial period between control, half and full degraded colonies, respectively.

There were significant differences in somatic growth of *C. parasema* individuals among coral treatments ( $F_{2, 73} = 7.989$ ,  $P=0.001$ ) with higher growth for both size classes on the colonies with 100 and 50% coral treatments compared to those with no live coral. Fishes on 0% coral treatments showed approximately 1/4 the growth of those on 100 and 50% coral treatments (Tukey HSD,  $P<0.01$ ) (Fig. 1). Growth on the 100 and 50% coral treatments did not significantly differ from one another. Notably, there was no difference in growth between the two size classes in any of the treatments.

Moderately high variability in somatic growth of *D. melanurus* precluded significant trends within *D. melanurus* among coral treatments ( $F_{2, 102} = 1.175$ ,  $P=0.313$ ). However, there was significantly higher growth for juvenile than adult sized individuals for all coral treatments ( $F_{1, 102} = 26.591$ ,  $P=0.0001$ ) (Tukey HSD,  $P<0.01$ ) (Fig. 1).

A comparison of the physiological condition of both study species suggested that there was little change in individual condition between treatments or size class over the trial period. Within both species there was no significant difference in Fulton's  $K$  value between size class (*C. parasema*,  $F_{1, 83} = 0.78$ ,  $P=0.381$ ; *D. melanurus*,  $F_{1, 119} = 1.96$ ,  $P=0.164$ ) or treatment (*C. parasema*,  $F_{2, 83} = 1.08$ ,  $P=0.345$ ; *D. melanurus*,  $F_{2, 119} = 0.02$ ,  $P=0.982$ ) and hepatocyte vacuolation value between size class (*C. parasema*,  $F_{1, 132} = 0.0005$ ,  $P=0.982$ ; *D. melanurus*,  $F_{1, 86} = 0.001$ ,  $P=0.965$ ) or treatment (*C. parasema*,  $F_{1, 132} = 0.648$ ,  $P=0.524$ ; *D. melanurus*,  $F_{1, 86} = 0.290$ ,  $P=0.748$ ).

### 4. Discussion

This study supports recent work showing that coral loss can have sublethal effects on growth in coral reef fishes (Booth, 1995; Pratchett et al., 2004), and that this extends to fishes that do not rely on coral as a food source. Low levels of live coral significantly reduced the growth of *C. parasema* by up to 25% of those living on undisturbed corals; *D. melanurus* showed a similar strong trend in lower growth with coral loss. Despite such effects on growth, reductions in live coral did not have any short-term effects on either species abundance or physiological condition. Although loss or alteration of habitat can directly affect the growth of fishes, reductions in growth usually correspond with declining quality and/or quantity of feeding resources within the habitat (Sogard, 1992; Gilliers et al., 2006). However, both study species are planktivores, and thus it can be predicted that low coral cover should have had no effect on their food resources.

Both study species utilize live coral colonies for shelter (Srinivasan, 2003), using the colony structure as refuge (Holbrook and Schmitt, 2002). Within this study, algal biomass rapidly filled the interstitial

spaces between coral branches on dead and partially degraded colonies. Non-quantitative behavioral observations taken throughout the study period showed that individuals on partially degraded colonies were more likely to utilize live coral than algal-covered areas of the coral colony. With increases in algal biomass within partially and full-degraded colonies, possible shelter space for residents may have been substantially reduced (Munday, 2001). Such a loss of suitable shelter may have led to an intensification of competition between residents for suitable refugia, increasing resident's physiological stress (McCormick, 2006; Trenzado et al., 2006), reducing individuals' growth rate (Forrester, 1991; Booth, 1995; Munday, 2001).

Within group-forming coral associated fishes, differences in body size between residents may create the potential for highly asymmetrical intraspecific competition for shared resources (Webster and Hixon, 2000; Webster, 2004). Theoretically, such asymmetry in competition can lead to some form of demographic density dependence within the group (Hixon and Jones, 2005). The most common consequence of competitive interactions between residents is lower growth and survival of smaller sized residents (reviewed in Jones, 1991). However, within the present study there was no significant difference in persistence of size classes between coral treatments, within each species, and no difference (i.e., *C. parasma*) or relatively higher levels of growth (i.e., *D. melanurus*) in juvenile than adult individuals between coral loss treatments. Although group size for both species was within the boundaries of natural *in situ* abundance (Srinivasan, 2003), both species can form groups holding 2–3 times more individuals than utilized in the present study. Therefore, within the present research, despite the loss of habitat availability with live coral disturbance, for both species sufficient habitat was available to reduce intraspecific competition for resources between residents. However, on a longer temporal scale, lethal interactions between small and large bodied residents may become density dependent (Holbrook and Schmitt, 2002; Webster, 2004). Increased growth of algal biomass throughout the coral structure, coupled with the growth of resident individuals, may result in increased competition between residents for suboptimal space leading to higher levels of predation on juveniles (e.g., Holbrook and Schmitt, 2002).

Despite the negative effects on growth rate of remaining within disturbed colonies, there was no substantial movement of individuals after coral loss (low emigration occurred when fishes were first placed into corals, though this was thought to be due to handling stress). The majority of small-bodied coral associated fishes show extremely low migration ability, predominantly remaining within the shelter of their host coral colony throughout their lifecycle (Forrester, 1991; Munday and Jones, 1998). For these species, a high level of competition for a limited supply of suitable habitats (Shulman, 1985; Bay et al., 2001) may preclude successful movement of individuals between habitats throughout the reef. In addition, mortality risk may substantially increase with emigration, due to the increased risk of predation when outside of suitable shelter (Holbrook et al., 2000; Stewart and Jones, 2001). Therefore, although reductions in live coral cover may reduce preferred space within colonies for resident fishes, their individual survival, to some extent, may be dependent on their ability to remain in the shelter of a coral colony (Shulman, 1985; Holbrook et al., 2000). We can predict that a trade-off may exist in which the potential benefits of emigrating from degraded to live coral colonies are outweighed by the increased risk of mortality outside of the coral's shelter. An increasing number of studies are finding relatively high levels of resistance to coral decline within coral reef fish assemblages (Pratchett et al., 2004; Feary, 2007). Although coral degradation may be closely followed by species emigration or loss (Pratchett et al., 2006), for fishes closely associated with the coral habitats, persistence in disturbed habitats may dramatically increase their ability to survive disturbance events (Feary, 2007).

Reductions in the growth rate of individuals associated with degraded coral habitats may have substantial effects on the demo-

graphic processes structuring the populations. As attainment of sexual maturity is often size based within group forming animals, factors that cause fluctuations in growth rate (i.e., low live coral for coral reef fishes), may have substantial negative effects on species fecundity by increasing their time to maturity (Sogard, 1992; Booth, 1995). Such changes in maturity may reduce species lifetime gamete production, substantially influencing the replenishment of populations both locally and regionally (Jones et al., 1999, 2004). In addition, variation in growth may indirectly affect species mortality, as individuals remain for longer periods in small, predator vulnerable sizes (Forrester, 1995; Booth and Hixon, 1999). As predator abundance will track prey availability (Stewart and Jones, 2001), we can expect that predator density may increase around disturbed habitats, enhancing predation risk for the associated community. The long-term effects of such increased predation risk may include substantial changes in the abundance, diversity and/or size structure of the resident community (reviewed in Hixon, 1991).

Time lags in the response of the coral associated reef fish community to coral loss may be due to a coupling of adult fishes with the coral reefs physical complexity (Graham et al., 2006). Broad reductions in the structure of reef fish communities may then be linked to the long term physical breakdown of the reef (Lewis, 1998; Syms and Jones, 2000; Graham et al., 2006). However, the present work has shown that reductions in the growth rate of small sized individuals may also explain a phase delay in species response to live coral loss. We can expect that within populations associated with degraded habitats, the loss of live coral will manifest as short term reductions in individual growth rate, mediating any significant numerical response within the population (Jones and McCormick, 2002; Pratchett et al., 2004b). Such reductions in individual growth rate, however, may have negative long-term effects on the population's demographic structure within the habitat, suggesting that a sublethal growth response to live coral loss may play a substantial role in altering the structure of the reef associated fish community within degraded reef systems.

## Acknowledgments

This project was supported by grants from Mahonia Na Dari Research and Conservation Centre, Walindi Plantation Resort and The Nature Conservancy to DAF, a James Cook University Merit Research Grant to MIM and the Australian Research Council Centre of Excellence for Coral Reefs Studies to GPJ. Many thanks to D. Godoy, J. Pickering, B. Ponde, L. Romaso and S. van Dijken for invaluable field assistance, M. Fraser for habitat data and G. Almany and 3 anonymous reviewers for helpful comments. [SS]

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