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REPORT

Effects of juvenile coral-feeding butterflyfishes on host corals

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Abstract Corals provide critical settlement habitat for a wide range of coral reef fishes, particularly corallivorous butterflyfishes, which not only settle directly into live corals but also use this coral as an exclusive food source. This study examines the consequences of chronic predation by juvenile coral-feeding butterflyfishes on their specific host corals. Juvenile butterflyfishes had high levels of site fidelity for host corals with 88% (38/43) of small (<30 mm) juveniles of *Chaetodon plebeius* feeding exclusively from a single host colony. This highly concentrated predation had negative effects on the condition of these colonies, with tissue biomass declining with increasing predation intensity. Declines were consistent across both field observations and a controlled experiment. Coral tissue biomass declined by 26.7, 44.5 and 53.4% in low, medium and high predation intensity treatments. Similarly, a 41.7% difference in coral tissue biomass was observed between colonies that were naturally inhabited by juvenile butterflyfish compared to uninhabited control colonies. Total lipid content of host corals declined by 29–38% across all treatments including controls and was not related to predation intensity; rather, this decline coincided with the mass spawning of corals and the loss of lipid-rich eggs. Although the speed at which lost coral tissue is regenerated and the long-term consequences for growth and reproduction remain unknown, our findings indicate that predation by juvenile butterflyfishes represents a chronic stress to these coral colonies and will have negative energetic consequences for the corals used as settlement habitat.

Keywords Corallivore · Chaetodontidae · Settlement · Chronic stress · Coral condition · Tissue biomass

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Introduction

Scleractinian corals are the foundation species of tropical reef ecosystems (Jones et al. 1994), providing the structural habitat that facilitates the colonisation and continued survival of reef fish populations (Graham et al. 2006; Munday et al. 2008; Pratchett et al. 2008a). Reef fishes benefit from the complex branching structure of many scleractinian corals in three main ways: corals provide critical settlement cues (Danilowicz 1996; Öhman et al. 1998; Feary et al. 2007), living space (Harmelin-Vivien 1989; Pratchett et al. 2008b; Wilson et al. 2010) and increased survivorship by reducing predator-induced mortality (Beukers and Jones 1997; Holbrook and Schmitt 2002; Coker et al. 2009). The close association of many reef fishes with live corals is largely a mutualistic relationship (Liberman et al. 1995). While reef fishes benefit from increased survival, the corals that provide this habitat also benefit from increased growth rates and tissue condition and enhanced reproductive output (Meyer and Schultz 1985a; Liberman et al. 1995; Holbrook et al. 2008).

Corals live in an oligotrophic environment, with dissolved nutrients rapidly dispersed by water motion (Holbrook et al. 2008). Coral-dwelling fishes represent an important source of ammonium, nitrogen and phosphorous for host colonies (Meyer and Schultz 1985b), with levels of ammonium significantly elevated in the interior spaces of *Pocillopora eydouxi* colonies occupied by damselfishes

compared to colonies without inhabitants (Holbrook et al. 2008). This local enhancement of nutrients has measurable benefits for corals, with nubbins of *P. eydouxi* growing at a 50% faster rate when coral-dwelling damselfish were present (Holbrook et al. 2008). Likewise, colonies of *Stylophora pistillata*, which were used as habitat by the damselfish *Dascyllus marginatus* grew significantly faster, had higher skeletal weight and subsequently had a higher reproductive output over a 13-month period compared to adjacent colonies that did not host damselfish (Liberman et al. 1995).

The benefits of fishes to corals have been well established (Meyer and Schultz 1985a; Liberman et al. 1995; Holbrook and Schmitt 2005; Holbrook et al. 2008), however, it is unknown whether the beneficial aspects of this relationship extends to corallivorous fishes. Corallivorous fishes use the coral directly as a source of food (reviewed by Cole et al. 2008) and are highly dependent on coral resources for survival, being the first and most affected group of fishes following disturbances that result in major declines in coral abundance (Wilson et al. 2006; Pratchett et al. 2006, 2008a). Butterflyfishes (F: Chaetodontidae) account for just over half of all coral-feeding fishes (Cole et al. 2008) and typically feed by removing individual coral polyps or tissues without harming the underlying corallite (Tricas 1989; Cole et al. 2010). Adult butterflyfishes forage over relatively wide home ranges taking multiple bites from a single colony before moving on to the next one, a pattern that is repeated continuously throughout the day (Tricas 1989). Adult butterflyfishes can remove up to 3 g of coral tissue each day, and the majority of this predation is directed towards *Acropora* and *Pocillopora* corals (Pratchett 2005; Cole et al. 2011). This constant predation is expected to act as a chronic drain on a coral colony's energy reserves and is likely to outweigh the benefits provided by other fishes that live within the colony but do not feed upon the coral.

During the summer recruitment season, juvenile butterflyfishes are a common feature of coral reefs throughout the Indo-Pacific, with finely branched corals providing important settlement habitat for these fishes (Harmelin-Vivien 1989; Fowler et al. 1992; Pratchett et al. 2008b; Wilson et al. 2010). These juveniles settle directly into live coral and begin feeding upon coral immediately following settlement (Harmelin-Vivien 1989). The potential effects that juvenile coral feeders have on the corals they inhabit have yet to be quantified and will depend to a large extent on the number of juveniles present and the duration that these juveniles reside within the one coral colony. It is possible that juvenile butterflyfish spend only a limited amount of time (days) residing in any one colony, although any large distance movements during this early-juvenile stage will expose them to a very high risk of predation (Doherty and Sale 1986; Heinlein et al. 2010). If juveniles are site attached, they have the potential to consume a significant proportion of coral tissue and exert a large energetic cost upon the colonies used as settlement habitat. Alternatively, this chronic consumption may be offset by the beneficial aspects of enhanced supply of nutrients (e.g. ammonium) (Meyer and Schultz 1985b; Holbrook et al. 2008), resulting in a neutral or positive outcome for the health and condition of the coral colony.

This study aims to quantify the effect that juvenile coral-feeding butterflyfish have on the condition of corals that are used as settlement habitat, by measuring changes in the condition of host corals (specifically, tissue biomass and total lipid content) following experimentally induced recruitment. The study species, *Chaetodon plebeius,* recruits in high numbers throughout the austral spring and summer on mid-shelf reefs of the Great Barrier Reef (Fowler 1990; Pratchett et al. 2008b). At Lizard Island, *C. plebeius* uses a wide range of settlement corals, but was most frequently observed recruiting to *Acropora spathulata*, a coral that is relatively common and is representative of the close branching, corymbose morphology that is used by the majority of coral-feeding fishes during settlement (Pratchett et al. 2008b; Cole 2010). This study also assessed fidelity of newly settled butterflyfishes to their host corals, allowing a quantitative evaluation of feeding impacts by juvenile fish.

Methods

Site fidelity and foraging area of juvenile butterflyfish

This study was conducted between September and December 2009, at Lizard Island (14° 40′ S, 145° 27′ E), in the northern section of the Great Barrier Reef, Australia. To determine whether the foraging area of juvenile *C. plebeius* changes with size, we conducted 5-min observations in which both the microhabitat used within the colony and the total area over which the juvenile foraged was recorded. Three broad categories were used to differentiate microhabitat use: inside the branch structure of the colony, among the upper third of branches and across the colony's tips with minimal use of the branching structure of the colony. The edges of the foraging area were marked with flagging tape during the observation, and the area was calculated by dividing the foraging area into simple geometric shapes. Most of the smaller individuals (<30 mm) did not leave the coral colony that they were first observed in, in which case their foraging area was taken as the planar area of the coral colony, using the equation $SA = (d_1/2) \times (d_2/2) \times \pi$, where d_1 and d_2 are the diameter of the two longest sides of the colony (following Hall and

Hughes 1996). During the observations, we also recorded the coral species inhabited, the total number of coral colonies visited and the distance from the last colony fed from. Observations were conducted at reefs in the lagoon and back-reef habitats of Lizard Island with observations pooled across all sites. As a consequence of the small size and fast movements of small juveniles within the coral colony, it was not possible to accurately record the number of feeding bites taken during an observation, but it was evident that all juveniles fed at very high rates upon their host coral. Following each focal observation, the juvenile was captured using clove oil (following Munday and Wilson 1997), and total length was measured to the nearest mm. Observations on juvenile butterflyfish spanned a size range of 12-50 mm, divided into 5 size classes: <20, 20.1–30, 30.1–35, 35.1–40 and 40.1–50 mm. Between 16 and 23 observations were made for each size class. To confirm the accuracy of our observations on foraging area and to ensure that small juveniles were not limiting their movements due to a diver effect during observations, ten colonies that hosted small juveniles were tagged and checked daily for 10 consecutive days to ensure that the same juveniles were present. On each of these occasions, the same-sized individuals and number of juveniles were present in each of the 10 colonies on each day.

Separate one-way ANOVAs were used to test for differences in foraging area and the number of coral colonies fed from by different size classes of juveniles. Residual plots were used to ensure ANOVA assumptions were met. To improve normality, our estimates of foraging area were $\log_{10}(x+1)$-transformed. Tukey's HSD post hoc test was then used to identify where differences among group means occurred.

Effect of predation by *C. plebeius* juveniles on colony condition

The effects of chronic predation by newly settled butterflyfish on the condition of coral colonies were assessed based on comparisons between naturally inhabited and uninhabited corals, as well as an experiment that manipulated the densities of juvenile butterflyfishes on colonies of *A. spathulata*. In late October 2009, we compared the total lipid content and tissue biomass per unit area between 20 colonies of *A. spathulata* which had no juvenile butterflyfish, and 20 colonies with at least one late-stage juvenile (>30 mm) and up to a total of five juvenile *C. plebeius* living within its branches. The mean density of juvenile *C. plebeius* was 2.75 (±0.25) fish.colony^{-1}. To limit confounding factors, the only other residential fishes on these colonies were coral-dwelling gobies. To standardise the environmental conditions experienced by these colonies, we chose control colonies of a comparable size, located within 10 m of the experimental colony at the same depth. Four branches (length of 6–8 cm) were removed from each of these colonies and fixed in 10% phosphate-buffered formalin. Two of the branches were used to measure total lipid content and two were used to calculate tissue mass per unit area. Before fixing, the surface area of two branches was determined using the aluminium foil method (Marsh 1970); the weight of this foil (x) was converted to surface area (y) using the calibration relationship $y = 288.4 \times x - 0.295$. After fixation, all four branches were decalcified in 5% formic acid for 24 h, followed by 10% formic acid until all skeletal material had been dissolved. Samples were dried overnight at 55°C and weighed to three decimal places. Tissue mass per unit area was determined by dividing the dried weight of each branch by the surface area of each branch and then combining to obtain a colony mean (following Anthony and Fabricius 2000). The remaining two branches were submerged for 24 h in a 2:1 chloroform/methanol solution to extract the lipids. These samples were then re-dried at 55°C and re-weighed. Total lipid content of each branch was then taken as the weight lost during the extraction, with total lipid content presented as a percentage of the original tissue biomass (following Ward 1995). Separate one-way ANOVAs were used to examine differences in tissue biomass per unit area and total lipid content between colonies hosting juvenile butterflyfish and those without juveniles. Total lipid content was arcsine transformed to meet ANOVA assumptions.

The density of juvenile coral feeders was manipulated on 32 previously unoccupied colonies of *A. spathulata* at two back-reef sites around Lizard Island: Osprey Inlet and Station Reef. The size of each of these colonies was measured along the two longest diameters at right angles to each other. These diameters were used to calculate the planar surface area of each colony. Colonies were assigned to one of four treatments ($n = 8$): control, low, medium and high predation intensity. Coral colony size did not differ significantly between our 4 treatments (ANOVA, $F_{3,27} = 0.56$, $P > 0.05$). As juvenile coral feeders rarely move between coral colonies when small, we used the density of *C. plebeius* as a proxy for predation intensity. Four density levels were used: control (no juveniles), low (less than one juvenile per 1200 cm^2), medium (1 juvenile per 650–900 cm^2) and high (1 fish per 250–500 cm^2); these densities correspond to approximately 1–2, 2–3 and 3–5 fish.colony^{-1} for our low, medium and high treatments. This experiment was started on 29 October and ended on 8 December.

Juvenile *C. plebeius* between 12 and 21 mm (total length) were caught using clove oil and hand nets and maintained under aquarium conditions for 24 h before being randomly allocated to one of the three density

treatments. These corals were checked daily, and if any fish were missing, a new juvenile was added to maintain the treatment density. It was rare (<5% of juveniles) for a juvenile to go missing after the first 48 h. To limit the impact of branch removal on a coral colony's energetics and integrity of the branching structure, only two branches were removed from each colony at the beginning of the experiment; one was used to estimate tissue biomass per unit area and the other to determine total lipid content. A further four branches were taken 41 days later to quantify any changes to tissue biomass (two branches) and total lipid content (two branches) using the same techniques as described in the natural comparison of colonies. A repeated measures ANOVA was used to examine whether any changes in tissue mass per unit area and total lipid content corresponded with predation intensity. Residual plots were examined to validate ANOVA assumptions of normality and homogeneity of variance. Tukey's multiple comparison tests were then used to identify where differences occurred.

Variation in tissue mass and lipid content within a colony

To determine whether the within-colony variance in total lipid content and tissue thickness is larger than our among-colony variance, we sampled 10 branches from each of four colonies of *A. spathulata*. Five branches were used to determine tissue mass per unit area and five were used to calculate total lipid content. Branch position within a colony was standardised by taking branches from the central section of the colony with a minimum distance of 5 cm from the colony margins. Both the variance in tissue mass (ANOVA, $F_{3,12} = 88.81$, $P < 0.05$) and total lipid content (ANOVA, $F_{3,12} = 108.65$, $P < 0.0001$) was greater among colonies than the variation in tissue mass (ANOVA, $F_{4,12} = 0.123$, $P < 0.05$) and lipid content (ANOVA, $F_{4,12} = 2.139$, $P < 0.05$) among branches within a colony. There was a maximum of 11% variation between the five branches sampled, as such we felt confident that our experiment would not be confounded by removing only two branches at the beginning and four at the end of our experiment.

Results

Site fidelity and foraging area of juvenile butterflyfish

The foraging area of juvenile *C. plebeius* differed significantly between size classes (ANOVA, $F_{4,86} = 172.14$, $P < 0.0001$) and showed a general increase with increasing size of each fish (Fig. 1). Likewise, as foraging area increased; there was also a significant increase in the number of colonies preyed upon (ANOVA, $F_{4,86} = 48.62$, $P < 0.0001$). Smaller juveniles (<30 mm) were extremely site attached with 88% (38/43) of these juveniles foraging within only one coral colony. Foraging area increased rapidly for larger juveniles with a fivefold increase (0.43 ± 0.11 vs 1.95 ± 0.19 m^2) between medium and large juveniles, with a further fourfold increase to 7.5 m^2 (± 0.91) for very large juveniles. Very large juveniles also fed from significantly more coral colonies (Tukey's HSD $P < 0.0001$) (Fig. 1). Feeding upon multiple colonies was only observed in 9.3% (5/43) of observations upon smaller juveniles (<30 mm TL) compared to 87.5% (42/48) of larger juveniles (>30 mm). When smaller juveniles did feed from multiple colonies, they travelled less than 10 cm. Furthermore, the smallest juveniles (<20 mm) were always observed down inside the branches of the host coral, typically inhabiting the lower two-thirds of the branch, whereas larger juveniles (>30 mm) tended to forage across the top of the colony itself and only used the top section of branches as shelter when threatened.

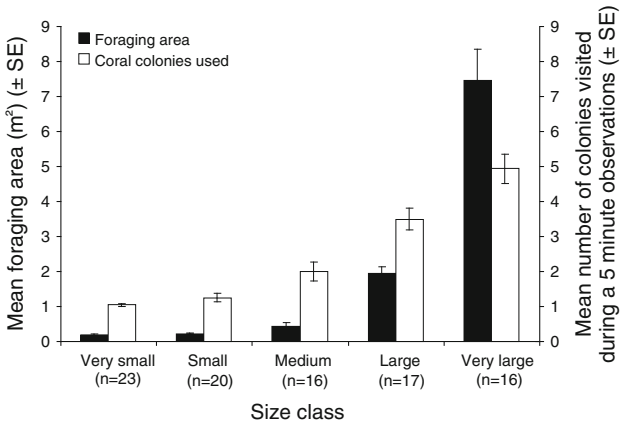

Fig. 1 Foraging area size (m^2) and the number of coral colonies fed from during a 5-min observation for 5 size classes of juvenile *Chaetodon plebeius*; very small (<20 mm), small (20.1–30 mm), medium (30.1–35 mm), large (35.1–40) and very large (40.1–50 mm)

Effect of predation by *C. plebeius* juveniles on colony condition

Colonies of *A. spathulata* that were naturally occupied by *C. plebeius* had significantly (ANOVA, $F_{1,38} = 38.43$, $P < 0.0001$) lower tissue biomass per unit area compared to colonies that did not host juveniles. Occupied colonies had 41.7% lower tissue biomass compared to unoccupied colonies, however, no difference (ANOVA, $F_{1,38} = 1.13$, $P > 0.05$) in total lipid content was detected between the two groups (Fig. 2).

Experimental manipulations, whereby juvenile *C. plebeius* were moved to previously unoccupied colonies, confirmed that declines in tissue biomass were attributable

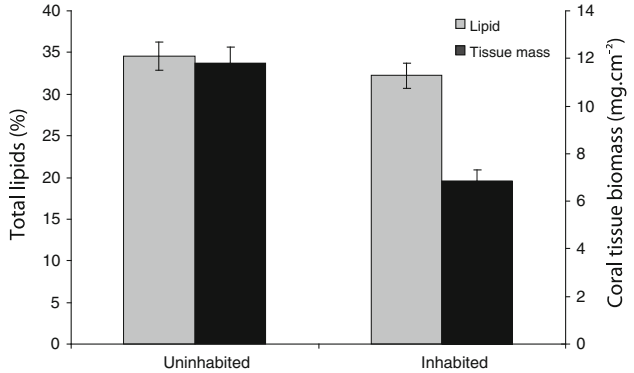

Fig. 2 Total lipid content (%) and tissue biomass (mg cm^{-2}) of *Acropora spathulata* colonies that were naturally inhabited by juvenile *Chaetodon plebeius* and those that were uninhabited. Values are the means and standard errors

Table 1 Repeated measures ANOVA-comparing (a) tissue mass and (b) total lipid content of *Acropora spathulata* colonies exposed to 4 levels of predation intensity: control (no juveniles), low (less than one juvenile per 1200 cm^2), medium (1 juvenile per 650–900 cm^2) and high (1 fish per 250–500 cm^2)

Source of variation	d.f	*F*	*P*
(a) Tissue mass			
Intensity	3	38.379	<0.0001
Reef	2	0.338	NS
Time	1	319.057	<0.0001
Reef × intensity	6	1.967	NS
Time × reef	1	0.309	NS
Time × intensity	3	16.241	<0.0001
Time × reef × intensity	3	0.407	NS
Error	24		
(b) Total lipid content			
Intensity	3	0.323	NS
Reef	2	1.652	NS
Time	1	85.89	<0.0001
Reef × intensity	6	2.631	NS
Time × reef	1	0.13	NS
Time × intensity	3	0.261	NS
Time × reef × intensity	3	0.124	NS
Error	24		

to feeding by resident fishes (Table 1). Increasing predator density caused a corresponding decline in tissue mass of 26.7, 44.5 and 53.4% under low, medium and high predation intensity over the course of this experiment (Fig. 3). In comparison, tissue mass in the control treatment declined by 16.1%. A significant (Table 1) decline in total lipid content of 29–38% occurred across all treatments at both reefs during this experiment (Fig. 3). Declines in lipid content were independent of predation intensity, and there

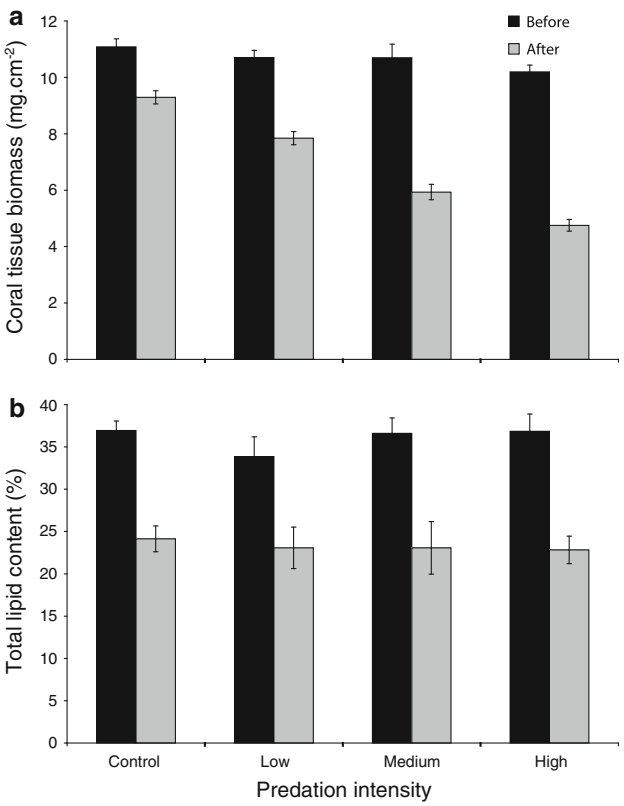

Fig. 3 Mean tissue biomass (mg cm^{-2}) and total lipid content (%) of *Acropora spathulata* colonies subjected to different predation intensities: control (no juveniles), low (less than one juvenile per 1200 cm^2), medium (1 juvenile per 650–900 cm^2) and high (1 fish per 250–500 cm^2) by juvenile *Chaetodon plebeius*. Values are the means and standard errors of the two reefs; Osprey Inlet and Station reef combined

was no significant interaction between time and predation intensity (Table 1).

Discussion

This study confirms that coral-feeding butterflyfishes show very high site fidelity to the coral colonies in which they initially settle (Fowler 1989; Pratchett et al. 2008b). Juvenile butterflyfishes direct their entire feeding effort towards their settlement coral and only begin to expand their foraging area when total length exceeds 30 mm. Predation by juvenile butterflyfishes has negative consequences on tissue biomass but not total lipid content. Tissue biomass per unit area declined with increasing predation intensity in both our natural comparison and our experiment. Tissue biomass is an important measure of coral condition, with declines linked to a stressed state (Szmant and Gassman 1990; Barnes and Lough 1999; Fitt et al. 1993, 2000; Anthony and Fabricius 2000). Stress caused by experimentally shading colonies of *Porites*

cylindrica, for example, resulted in an 80% reduction in tissue growth rates over a 2-month period, while the combination of high suspended particulate matter and shade resulted in negative tissue growth (Anthony and Fabricius 2000). Likewise, Barnes and Lough (1999) documented a linear decline in tissue thickness of massive *Porites* colonies across four sites of increasing levels of sedimentation.

In our study, total lipid content of all corals declined relatively evenly (29–38%) at both sites independently of predation intensity. This was most likely a consequence of the corals spawning midway through our experiment. At Lizard Island, the mass spawning of corals occurs 2–7 days after the full moon in November (Baird et al. 2002). Coral propagules are composed of 50–70% lipids and represent a significant energetic investment by coral colonies (Richmond 1987; Arai et al. 1993; Leuzinger et al. 2003). Similar declines in lipid content of corals following spawning have been observed in previous studies (Ward 1992, 1995; Leuzinger et al. 2003; Anthony 2006; Harii et al. 2007). Total lipid content declined by 20–45% for *Acropora valida* following mass spawning on the central GBR in 2002 (Anthony 2006).

As a consequence of the mass spawning event and the loss of egg and sperm bundles, the overall weight of coral tissue for a given area also declines. In our study, all treatments experienced a decline in tissue biomass per unit area. However, our control colonies experienced a much lower decline in tissue biomass than the three predation treatments (Fig. 3). A small component of this decline in tissue biomass can be explained by the loss of coral reproductive material, while the remaining decline is caused by the increase in predation intensity. The data from our natural comparison also supports this conclusion. In these colonies, branch samples were taken prior to the mass spawning event, and no difference in total lipid content was detected between colonies inhabited by juveniles and those without juveniles. However, colonies that were occupied by juvenile butterflyfish had a 41% lower tissue mass per unit are compared to unoccupied colonies (Fig. 2). This congruency in the decline in tissue biomass between our experiment and natural comparison provides strong evidence that the decline in total lipid content is a consequence of coral reproduction and the loss of lipid-rich eggs, while the decline in tissue biomass is a consequence of chronic predation by juvenile butterflyfish. This implies that feeding by juveniles alters the quantity of coral tissue available, but not the nutritional quality.

Predation by juvenile butterflyfishes is a significant energetic cost for the corals they inhabit, with no evidence of the positive benefits observed in other studies, such as where coral-dwelling damselfish increased the growth and condition of host colonies (Meyer and Schultz 1985a; Liberman et al. 1995; Holbrook et al. 2008). The mechanism that causes these benefits in other studies, nutrient enhancement through fish metabolism, should also be present in this study as juvenile butterflyfish live within the branch structure and produce ammonia and other nutrients similar to coral-dwelling damselfish (Meyer and Schultz 1985b; Holbrook et al. 2008). This suggests that the negative consequences of chronic tissue consumption outweigh the benefits of enhanced nutrient supply. Alternatively, the small size of juvenile butterflyfish could mean that the amount of ammonia produced is minor compared to larger-bodied damselfish (e.g. Holbrook et al. 2008). Furthermore, to avoid confounding our experiments, we used colonies that did not have resident damselfish living within their branches. In colonies that also host planktivorous damselfish, nutrient supply and overall colony growth rates will be higher and would be expected to mitigate some of the negative effects on tissue biomass that were observed in our study (e.g. Holbrook et al. in press).

All of the feeding effort of small juveniles (<30 mm) is concentrated entirely upon their host colony, and when this is compounded daily over a 6–8-week period, the loss of tissue from these colonies will be considerable. The actual amount of coral tissue consumed by juveniles remains unknown, although assuming that individual fishes consume approximately 12% of their body weight in coral tissue each day, we expect it to be in the range of 0.01–0.10 g of coral tissue per day for juvenile butterflyfishes (12–30 mm TL) (sensu Cole et al. 2011). Thus, coral consumption by juveniles, especially in high densities, represents a large drain on an individual colony's energy reserves. The decline in tissue biomass observed in this study with increasing predation intensity could result from a situation where the speed at which coral tissue is being consumed outweighs the regenerative capacity of the corals. Even a slight imbalance between consumption and regeneration would be compounded as these juveniles grew and consumed more tissue each day. The reduction in tissue biomass observed in this study may be the proximal cue for juvenile coral-feeding butterflyfishes (30–35 mm) to begin to expand their foraging area.

Tissue biomass has also been shown to vary seasonally, peaking in spring before steadily declining during the summer as sea water temperatures increase (Fitt et al. 2000). Our study was performed in the austral spring that corresponds to the period when coral tissue biomass is expected to be at its peak (Fitt et al. 2000). As such, the relatively rapid (42 day period) declines in tissue biomass observed in our study may have significant consequences for the energetics and survival of these colonies during the summer months. To regain tissue biomass, these colonies will need to invest energy into the regeneration of lost tissue. The speed that tissue can be regenerated is currently

unknown, but is not likely to occur until after the juvenile butterflyfishes have outgrown their host colony and begin to forage across a larger area. If lipid reserves are utilised in regeneration, these colonies will enter the potentially more stressful summer period with reduced energy reserves. As such, these colonies may have limited capacity to cope with additional stressors and potentially a higher susceptibility to mortality following a coral bleaching event (Anthony et al. 2009).

This study has identified clear negative effects for corals that act as settlement and growth habitat for juvenile butterflyfishes. Coral-feeding juveniles recruit in large numbers throughout the spring and summer months (Zekeria et al. 2006; Pratchett et al. 2008b), and it is not uncommon to observe 4–7 juvenile butterflyfishes co-habiting within the same colony. As such, coral-feeding juveniles are likely to represent a chronic, but seasonal, stress on coral colonies. The effects of coral-feeding butterflyfishes on individual colonies is also likely to interact with and compound other natural and anthropogenic disturbance events (e.g. mass bleaching events), which lead to increasing coral loss throughout the world (Nyström and Folke 2001; Hoegh-Guldberg et al. 2007; Anthony et al. 2009; Pratchett et al. 2008a). Moreover, declines in the abundance of suitable settlement colonies will likely cause increases in the densities of juvenile butterflyfishes settling within any one colony. The results will be further stress on these colonies, while any increase in energy used in regeneration will have implications for future growth, reproductive output and resilience to environmental change.

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References

Anthony KRN (2006) Enhanced energy status of corals on coastal, high-turbidity reefs. Mar Ecol Prog Ser 319:111–116

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol 252:221–253

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Funct Ecol 23:539–550

Arai I, Kato M, Heyward A, Ikeda Y, Iizuka T, Maruyama T (1993) Lipid composition of positively buoyant eggs of reef building corals. Coral Reefs 12:71–75

Baird AH, Marshall PA, Wolstenholme J (2002) Latitudinal variation in the reproduction of *Acropora* in the Coral Sea. Proc 9th Int Coral Reef Symp 1:385–389

Barnes DJ, Lough JM (1999) *Porites* growth characteristics in a changed environment: Misima Island, Papua New Guinea. Coral Reefs 18:213–218

Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114: 50–59

Coker DJ, Pratchett MS, Munday PL (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. Behav Ecol 20:1204–1210

Cole AJ (2010) Cleaning to corallivory: ontogenetic shifts in feeding ecology of tubelip wrasse. Coral Reefs 1:125–129

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish Fish 9:286–307

Cole AJ, Pratchett MS, Jones GP (2010) Corallivory in tubelip wrasses: diet, feeding and trophic importance. J Fish Biol 76: 818–835

Cole AJ, Lawton RJ, Pratchett MS, Wilson SK (2011) Chronic coral consumption by butterflyfishes. Coral Reefs. doi: 10.1007/s00338-010-0674-6

Danilowicz BS (1996) Choice of coral species by naive and field-caught damselfish. Copeia 1996:735–739

Doherty PJ, Sale PF (1986) Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4:225–234

Feary DA, Almany GR, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153:727–737

Fitt WK, Spero HJ, Halas J, White MW, Porter JW (1993) Recovery of the coral *Montastrea annularis* in the Florida keys after the 1987 Caribbean "bleaching event". Coral Reefs 12:57–64

Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45:677–685

Fowler AJ (1989) Description, interpretation and use of the microstructure of otoliths from juvenile butterflyfishes (family Chaetodontidae). Mar Biol 102:167–181

Fowler AJ (1990) Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. Mar Ecol Prog Ser 64:39–53

Fowler AJ, Doherty PJ, Williams DMB (1992) Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. Mar Ecol Prog Ser 82:131–141

Graham NA, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. Proc Natl Acad Sci USA 103:8425–8429

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963

Harii S, Nadaoka K, Yamamoto M, Iwao K (2007) Temporal changes in settlement, lipid content and lipid composition of larvae of the spawning hermatypic coral *Acropora tenuis*. Mar Ecol Prog Ser 346:89–96

Harmelin-Vivien ML (1989) Implications of feeding specializations on the recruitment processes and community structure of butterflyfishes. Environ Biol Fish 25:101–110

Heinlein JM, Stier AC, Steele MA (2010) Predators reduce abundance and species richness of coral reef fish recruits via non-selective predation. Coral Reefs 29:527–532

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737

Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 83:2855–2868

Holbrook SJ, Schmitt RJ (2005) Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. Coral Reefs 24:67–73

Holbrook S, Brooks A, Schmitt R, Stewart H (2008) Effects of sheltering fish on growth of their host corals. Mar Biol 155: 521–530

Holbrook SJ, Schmitt RJ, Brooks AJ (in press) Indirect effects of species interactions on habitat provisioning. Oecologia. doi: 10.1007/s00442-011-1912-5

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Leuzinger S, Anthony K, Willis B (2003) Reproductive energy investment in corals: scaling with module size. Oecologia 136:524–531

Liberman T, Genin A, Loya Y (1995) Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. Mar Biol 121:741–746

Marsh JA (1970) Primary productivity of reef-building calcareous red algae. Ecology 51:255–263

Meyer JL, Schultz ET (1985a) Tissue condition and growth rate of corals associated with schooling fish. Limnol Oceanogr 30: 157–166

Meyer JL, Schultz ET (1985b) Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol Oceanogr 30:146–156

Munday PL, Wilson SK (1997) Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis,* a coral reef fish. J Fish Biol 51:931–938

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:1–25

Nyström M, Folke C (2001) Spatial resilience of coral reefs. Ecosystems 4:406–417

Öhman MC, Munday PL, Jones GP, Caley MJ (1998) Settlement strategies and distribution patterns of coral-reef fishes. J Exp Mar Biol Ecol 225:219–238

Pratchett MS (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. Mar Biol 148:373–382

Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of *Chaetodon* butterflyfishes following extensive coral depletion. J Fish Biol 69:1269–1280

Pratchett MS, Berumen ML, Marnane MJ, Eagle JV, Pratchett DJ (2008a) Habitat associations of juvenile versus adult butterflyfishes. Coral Reefs 27:541–551

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR (2008b) Effects of climate-induced coral bleaching on coral-reef fishes- Ecological and economic consequences. Oceanogr Mar Biol Annu Rev 46:251–296

Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93:527–533

Szmant AM, Gassman NJ (1990) The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8:217–224

Tricas TC (1989) Prey selection by coral-feeding butterflyfishes: strategies to maximize the profit. Environ Biol Fish 25:171–185

Ward S (1992) Evidence for broadcast spawning as well as brooding in the scleractinian coral *Pocillopora damicornis*. Mar Biol 112:641–646

Ward S (1995) The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 187:193–206

Wilson SK, Graham NA, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biol 12:2220–2234

Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary RA, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. PLoS ONE 5(12):e15185. doi:10.1371/journal.pone.0015185

Zekeria ZA, Weertman S, Samuel B, Kale-ab T, Videler JJ (2006) Growth of *Chaetodon larvatus* (Chaetodontidae: Pisces) in the Southern Red Sea. Mar Biol 148:1113–1122