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# Trade-offs associated with dietary specialisation in corallivorous butterflyfishes (Chaetodontidae: *Chaetodon*)

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**ABSTRACT**

Increasing dietary specialisation is an inherently risky strategy because it increases a species' vulnerability to resource depletion. However, risks associated with dietary specialisation may be offset by increased performance when feeding on preferred prey. Though rarely demonstrated, highly specialised species are expected to outperform generalists when feeding on their preferred prey, whereas generalists are predicted to have more similar performance across a range of different prey. To test this theory, we compared growth rates of two obligate coral-feeding butterflyfishes (*Chaetodon trifascialis* and *C. plebeius*) maintained on exclusive diets of preferred versus non-preferred prey. In the field, *C. trifascialis* was the most specialised species, feeding almost exclusively on just one coral species, *Acropora hyacinthus*. *Chaetodon plebeius* meanwhile, was much less specialised, but fed predominantly on *Pocillopora damicornis*. During growth experiments, *C. trifascialis* grew fastest when feeding on *A. hyacinthus* and did not grow at all when feeding on less preferred prey (*P. damicornis* and *Porites cylindrica*). *Chaetodon plebeius* performed equally well on both *A. hyacinthus* and *P. damicornis* (its preferred prey), but performed poorly when feeding on *P. cylindrica*. Both butterflyfishes select coral species that maximise juvenile growth, but contrary to expectations, the more specialised species (*C. trifascialis*) did not outperform the generalist (*C. plebeius*) when both consumed their preferred prey. Increased dietary specialisation, therefore, appears to be a questionable strategy as there was no evidence of any increased benefits to offset increases in susceptibility to disturbance.

Keywords: Feeding selectivity; Resource selection; Growth rates; Coral reef fishes; Ecological versatility

## Introduction

A natural trade-off exists between a species' level of specialisation and the ability of that species to cope with fluctuations in resource availability (Munday 2004). In general terms, increased ecological versatility should reduce a species' extinction risk, but increased specialisation should yield greater fitness when preferred resources are available. In reality, most organisms do exhibit some degree of dietary specialisation, using a much narrower range of prey types than are actually available (Fox and Morrow 1981). Foraging theory predicts that selectivity should increase where there are tangible benefits derived from feeding on specific prey (Stephens and Krebs 1986). Although some species have been shown to be very specialised (e.g., Toft 1995; Bean et al. 2002; Moore et al. 2005) and trade-offs have been explored among a species' foraging choices (e.g., Aeby 2002; Brown and Kotler 2004), few studies have shown that the specific range of prey used by specialised species contributes directly to greater fitness compared to generalist species. Measuring potentially subtle increases in fitness during an individual's lifetime is often difficult (Perry and Pianka 1997), but further understanding differing levels of dietary specialisation among closely related sympatric species will greatly advance our understanding of processes underlying biodiversity (Smith 1979; Irschick et al. 2005).

Specialists benefit from feeding on specific prey presumably because they feed or assimilate energy more efficiently when limiting the range of prey ingested (Schoener 1971). If so, we expect that specialists would outperform generalist counterparts when feeding on their most preferred prey. For example, the specialist woodrat *Neotoma stephensi* more effectively neutralises dietary toxins compared to its more generalist counterpart, *Neotoma albigula*, (Sorensen et al. 2004) which greatly increases assimilation efficiency when feeing on toxic

plants (Dearing et al. 2000). Generalists, meanwhile, are expected to have more similar performance across a range of different resources, providing insurance against fluctuations in resource availability, as was explicitly shown for two species of locusts (*Locusta migratoria*, a grass specialist, and *Schistocerca gregaria*, a more generalist herbivore) fed on manufactured diets with varying nutrient balance (Raubenheimer and Simpson 2004; see also Schoener 1971; Dill 1983; Jones et al. 2002; Munday 2004).

Among coral-feeding butterflyfishes (*Chaetodon*: Chaetodontidae) sympatric species often exhibit highly contrasting levels of dietary specialisation. Highly specialised species, such as *C. trifascialis*, ingest an extremely limited range (<1%) of available coral species (Irons 1989; Pratchett 2005). Correspondingly, the more specialised species appear highly susceptible to depletion of preferred prey corals (Pratchett et al. 2006). More generalist species, such as *Chaetodon lunulatus*, consume a wide range of coral species (Berumen et al. 2005; Pratchett 2005), and can withstand major alterations in prey availability through prey-switching (Pratchett et al. 2004).

To test whether specialist species outperform more generalist counterparts when feeding on preferred prey, we compared growth rates for two species of butterflyfishes maintained on exclusive diets of preferred versus non-preferred prey. This experiment was conducted using small (<5cm TL) juvenile butterflyfishes, where rapid somatic growth is expected both to be highly responsive to food availability and to have a major influence on lifetime fitness (Berumen 2005). Notably, predation on juvenile butterflyfishes is strongly size-dependent (e.g., Almany 2004), so faster growth will increase survivorship. Moreover, maturation in butterflyfishes is based on size, rather than age (e.g., Tricas and Hiramoto 1989), so increased growth will lead to earlier maturation, presumably increasing lifetime

reproductive output. We predict that corallivorous butterflyfishes grow most rapidly when given exclusive diets of highly preferred corals, implicitly assuming that fishes selectively consume prey in the field that maximise individual fitness. We also predict that more specialised species will grow faster compared to generalist counterparts when both species consume their most preferred prey.

## Materials and methods

The study species, *C. trifascialis* and *C. plebeius*, were selected for their relative abundance as both juveniles and adults at Lizard Island (14°40'S, 145°27'E), northern Great Barrier Reef, Australia, where this study was conducted. *Chaetodon trifascialis* is very common and widespread throughout the Indo-West Pacific, ranging from the Red Sea to French Polynesia (Allen et al. 1998; Kuiter 2002). Similarly, *C. plebeius* is common throughout the South Pacific, ranging from Western Australia to French Polynesia and from southern Japan to New South Wales (Randall 2005).

Both *C. trifascialis* and *C. plebeius* are obligate hard-coral feeders (Pratchett 2005). The pronounced preference of *C. trifascialis* for its coral prey, *Acropora hyacinthus,* is conspicuous and well-documented (Irons 1989; Pratchett 2005). *Chaetodon plebeius* consumes mostly corals of the genera *Acropora* and *Pocillopora* with a preference for *P. damicornis* (Pratchett 2005). We measured dietary specialisation for *C. trifascialis* and *C. plebeius* based on field observations conducted for 70 randomly selected adult individuals from shallow reef areas in exposed locations at Lizard Island. Replicate fishes were observed for three minutes, recording the range of coral species consumed and the number of bites taken from each different coral species. Dietary specialisation was assessed based on the number and evenness

(Shannon-Weiner *J*) of different corals consumed. Lower numbers and evenness of different corals consumed indicate increasing dietary specialisation.

Dietary selectivity was determined by comparing the proportional use of different prey types with the proportional availability of different coral prey in the local environment. Data on dietary availability was collected using 10-m line intercept transects (n = 40), along which the relative abundance of all hard- and soft-corals, as well as other sessile invertebrates was recorded. The degree of dietary selectivity exhibited by *C. plebeius* and *C. trifascialis* was quantified using log-likelihood statistics, following Berumen et al. (2005). The resulting value of $X^2_{L2}$ was then compared to the chi-squared distribution with n(*I*-1) degrees of freedom to determine the significance of selectivity exhibited by *C. plebeius* and *C. trifascialis*. Resource selection functions (Manly et al. 1993) were used to determine which coral species were used more or less frequently than expected based on their relative abundance (Manly et al. 1993). Selection functions significantly greater than 1 indicated that corals were consumed more than expected from their availability, indicating prey types that are preferred, while selection functions significantly less than 1 indicated that corals were consumed significantly less than expected, indicating prey types that are avoided.

Controlled feeding experiments were conducted using juveniles (fishes < 50mm total length) of both *C. plebeius* and *C. trifascialis* collected from reefs around Lizard Island. Fishes were randomly allocated to one of 36 individual aquaria (32 x 20 x 16cm) with flow-through seawater (2L / min), and then randomly allocated exclusive diets of one of three different species of common branching corals (*A. hyacinthus, Pocillopora damicornis,* or *Porites cylindrica*). Fishes in each aquarium were provided with a minimum of 100cm$^2$ of live coral, which was replaced at least every three days to ensure fish had access to healthy coral tissue.

Corals were not observed to show signs of stress during the experiment. Replicate fish of each species were given one of the three different coral diets. For *C. plebeius*, five individuals were maintained on a diet of *A. hyacinthus*, four on *P. cylindrica*, and five on *P. damicornis*. For *C. trifascialis*, five individuals were maintained on a diet of *A. hyacinthus*, six on *P. cylindrica*, and six on *P. damicornis* Growth of fishes was scored as change in whole body weight and total length from the start to end of the experiment. Body weight of fishes was measured to the nearest 0.1g by placing fishes in a known weight of water, and total length measured to the nearest 0.1mm using electronic callipers. Rates of change in length were compared among diet using ANOVA separately for each species; the same was done for rates of change in weight.

**Results**

*Chaetodon trifascialis* and *C. plebeius* both exhibited a high degree of dietary specialisation, feeding on <25% (38/152) of available coral species and completely avoiding a whole range of relatively common coral species, including *Porites cylindrica*. *Chaetodon trifascialis* was the most specialised species, feeding on only 16 different coral species from two different families (Acroporidae and Pocilloporidae) (Fig. 1). Dietary evenness for *C. trifascialis* was very low ($J = 0.23$) where 88% (2,065/ 2,347) of bites were taken from a single coral species, *Acropora hyacinthus*. By comparison, C. *plebeius* consumed 38 different corals from 7 families. Moreover, dietary evenness for *C. plebeius* was relatively high ($J = 0.72$) and only 32% of bites were taken from the most frequently used coral species, *Pocillopora damicornis* (Fig. 1).

Both *C. plebeius* and *C. trifascialis* exhibited significant selectivity in their patterns of feeding in field observations (Table 1). *Chaetodon plebeius* selectively consumed a total of 8 different corals, including *P. damicornis*, *A. hyacinthus*, *Montipora* spp., and others (Table 1)

but was never seen to consume *Porites* spp. *Chaetodon trifascialis*, meanwhile, was an order of magnitude more selective than *C. plebeius* (Table 1), consuming *A. hyacinthus* to the exclusion of almost all other scleractinian corals. Like *C. plebeius*, *C. trifascialis* was never seen to consume *Porites* spp. even though these corals were the third most abundant of the scleractinian coral groups used in this analysis. Juveniles of *C. plebeius* and *C. trifascialis* were found in close association with *P. damicornis* and *A. hyacinthus*, respectively.

Butterflyfishes exhibited marked differences in juvenile growth rates when fed on exclusive diets of one of three different coral species (Table 2). *Chaetodon trifascialis* grew fastest (0.053 mm/day ± 0.020 SE and 5.39 X $10^{-3}$ g/day ± 1.87 X $10^{-3}$ SE) when feeding on *A. hyacinthus*, and rapidly lost weight when maintained on alternate diets of *P. damicornis* and *P. cylindrica* (Figs. 2 & 3). Individuals exclusively fed *P. cylindrica* fared worst, with 2/6 fish actually dying during the experiment despite regular feeding rates. (As growth rates are calculated on a per-day basis, this does not complicate our analyses.) Marked differences in growth occurred despite constant and consistent bite rates. Daily observations confirmed that juvenile *C. trifascialis* were actively feeding in all aquaria and there was no difference in bite rates recorded (3.12 bites per minute ± 0.59 SE) for individuals feeding on different coral prey (ANOVA, P = .369, F = 3.74, df = 2/14).

Juvenile *C. plebeius* grew fastest (0.051 mm/day ± 0.029 SE and 8.48 X $10^{-3}$ g/day ± 3.01 X $10^{-3}$ SE) when feeding on *P. damicornis*, though growth rates were not significantly different from individuals fed on *A. hyacinthus*. When feeding on either *A. hyacinthus* or *P. damicornis*, daily growth of *C. plebeius* was very similar to the growth rate recorded for *C. trifascialis* feeding on *A. hyacinthus* (Figs. 2 & 3). As with *C. trifascialis*, *C. plebeius* fared poorly on an exclusive diet of *P. cylindrica*. *Chaetodon plebeius* given *P. cylindrica* fed at

similar rates (3.19 bites per minute ± 0.65 SE) to individuals fed on *P. damicornis* and *A. hyacinthus*, but continued to lose weight throughout the course of the experiment. All fishes (*C. trifascialis* and *C. plebeius*) maintained on exclusive diets of *P. cylindrica* became notably emaciated and there was evident contraction along the lateral line, resulting in "negative" growth.

## Discussion

This study shows that fishes (*C. plebeius* and *C. trifascialis*) perform best on exclusive diets of their preferred prey. By maximising juvenile growth, fishes are expected to have higher survivorship and greater lifetime reproductive output, supporting the notion that dietary specialists select prey that maximise lifetime fitness (Stephens and Krebs 1986). *Chaetodon trifascialis* is among the most specialised of all animal foragers (Pratchett 2005), and this study demonstrates, for the first time, that *C. trifascialis* benefits greatly from feeding exclusively on its preferred prey, *A. hyacinthus*. However, *C. trifascialis* did not grow faster than the more generalist species, *C. plebeius*, when both species fed exclusively on their preferred prey (*A. hyacinthus* and *P. damicornis*, respectively). Increased dietary specialisation appears to be a questionable evolutionary strategy for *C. trifascialis* because there is no apparent fitness benefit that outweighs the increased susceptibility to disturbance and resource depletion (Berumen and Pratchett 2006a; Wilson et al. 2006).

Specialisation and generalisation are a continuum of ecological versatility and significant trade-offs are associated with these alternate strategies (MacNally 1995). Even if a specialist gains a greater benefit from resource specialisation, they sacrifice some degree of resilience to changes in resource availability as they become increasingly dependent on a restricted range of resources (Munday 2004). Both *C. trifascialis* and *C. plebeius* are among

the more specialised species of coral-feeding butterflyfishes, and are accordingly highly susceptible to resource depletion (Pratchett et al. 2006). However, *C. trifascialis* is more often and disproportionately affected by disturbances to coral reef habitats than *C. plebeius* (Wilson et al. 2006). More generalist species have a greater capacity to exploit alternate prey resources during moderate or selective disturbances and thereby withstand temporary reductions in availability of preferred prey resources (Pratchett et al. 2004). It is clear however, that coral reef ecosystems are increasingly subject to disturbances (e.g., climate-induced coral bleaching) that have significant impacts at unprecedented spatial scales (Hoegh-Guldberg 1999; Hughes et al. 2003). Such disturbances have the greatest and most immediate effects on highly specialised species, but even generalist species are significantly impacted by large-scale and devastating impacts of global climate change (Pratchett et al. 2006; Wilson et al. 2006). In extreme cases, highly coral-dependent fishes have already gone extinct (e.g., Munday 2004) further exacerbating the increasing biodiversity crisis (Jenkins 2003).

Increases in foraging or assimilation efficiency are expected to form the basis for increasing dietary specialisation (e.g., Moore et al. 2005). It is possible that *C. trifascialis* feeds more efficiently than *C. plebeius*, even though this is not apparent from juvenile growth rates. Increasing specialisation may yield tangible benefits only under field conditions (e.g., reducing predation rates) or only during the adult life-phase (e.g., increasing reproductive output) and substantial research still needs to be undertaken before ruling out a sound basis for increasing specialisation. It is also interesting that *C. trifascialis* and *C. plebeius* tend to favour different corals. In butterflyfishes, similar morphological specialisations do not correspond to similar dietary specialisations (Motta 1988), but other factors may be influencing feeding behaviours. While competitive exclusion (Berumen and Pratchett 2006b) may play a role in

prey selection, subtle partitioning of the convergent diets of coral-feeding butterflyfishes (Pratchett 2005) may be partly responsible for the ability of *C. plebeius* to perform equally well on different coral prey. Further study of the coral-feeding fishes in this genus will offer an ideal opportunity to advance our understanding of how specialisation evolves (sensu Irschick et al. 2005).

The nutritional bases for feeding preferences in coral-feeding butterflyfishes remain poorly understood. For the two species in our study, *P. cylindrica* clearly appears to be a poor resource. As we cannot distinguish whether bites were on polyps, interpolyp tissue, or mucus, we are unable to rule out the possibility that these species are mechanically restricted in ingestion of material, a potential cause of the poor health of fish fed this coral. Although some species of *Porites* are known to have short-term inducible defences against predation by butterflyfishes (Gochfeld 2004), a more generalist coral-feeding butterflyfish, *C. lunulatus*, actively selects *Porites* at Lizard Island (Berumen et al. 2005). Further investigation of con-generic variations in ability to utilise this prey are warranted. Behavioural interactions, notably territoriality, may play a significant role in the observed feeding preferences of the two species in this study (Berumen and Pratchett 2006b). *Chaetodon trifascialis* is typically a dominant competitor (Irons 1989) and may have become so adapted that it is effectively constrained to this prey type. *Chaetodon plebeius* is subordinate to *C. trifascialis at Lizard Island (Berumen and Pratchett 2006b)* and may have subsequently specialised on an alternate resource. Feeding preferences are also likely shaped by complex interactive effects of nutrients in coral prey (sensu Raubenheimer and Simpson 2004), which deserve further study.

In conclusion, this study confirms that dietary specialists have a greater disparity in performance on preferred versus non-preferred prey compared to more generalist counterparts.

However, the more specialised feeder (*C. trifascialis*) did not outperform the more generalist species (*C. plebeius*) when both species exclusively consumed their preferred prey. This study is one of very few that has considered the evolutionary and ecological basis of dietary versatility (see Ferry-Graham et al. 2002), and substantial work is still needed in this area. Importantly, interspecific variation in ecological versatility appears fundamental to the coexistence of species, and understanding the mechanisms underlying specialisation will greatly enhance our ability to address biodiversity patterns and trends (Irschick et al. 2005).

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**Fig. 1** Proportional consumption (mean percentage ± S.E.) of 10 different coral taxa by a) *Chaetodon plebeius* and b) *Chaetodon trifascialis* at Lizard Island, Great Barrier Reef, Australia. Dietary composition was determined using 3-min feeding observations conducted for 70 individuals of each fish species.

**Fig. 2** Daily rates of change in total length (mm) (± S.E.) for two *Chaetodon* species maintained on exclusive diets of one of three corals (category axis) for an average of 26 days. Lowercase italicised letters represent intraspecific homogeneous subsets identified by Tukey's HSD *post-hoc* test.

**Fig. 3** Daily rates of change in weight (g) (± S.E.) for two *Chaetodon* species maintained on exclusive diets of one of three corals (category axis) for an average of 26 days. Lowercase italicised letters represent intraspecific homogeneous subsets identified by Tukey's HSD *post-hoc* test.

**Table 1** Dietary selectivity and prey preferences of two *Chaetodon* species at Lizard Island, Australia. The significance of selectivity was ascertained using the chi-square statistic ($X^2_{L2}$) (following Berumen et al. 2005), while selection functions were used to test whether certain prey types were used more or less than expected (following Manly et al. 1993). "+" indicates prey that were used disproportionately more than expected from their availability (selected); "-" indicates prey that were used less than expected (avoided); "U" indicates prey that were never used (strongly avoided); blank cells indicate prey that were used in approximate accordance with their availability (neither selected or avoided).

| Species | $X^2_{L2}$ | P | Carbonate Pavement | *Acropora digitifera* | *Acropora hyacinthus* | *Acropora intermedia* | *Acropora millepora* | *Acropora tenuis* | Other *Acropora* | *Montipora* spp. | *Pocillopora damicornis* | *Goniastrea retiformis* | *Porites lobata* | Other Scleractinia | *Lobophytum* spp. | Other Alcyonaria | Non-coral Invertebrates |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Availability (% cover) of prey category | | | 70.56 | 1.43 | 5.64 | 0.21 | 0.15 | 0.22 | 1.03 | 1.16 | 1.36 | 0.62 | 1.36 | 9.58 | 0.44 | 1.39 | 0.46 |
| *C. plebeius* | $1.29\times10^{04}$ | <0.001 | - | + | + | + | + | | + | + | + | + | U | | U | U | U |
| *C. trifascialis* | $1.37\times10^{05}$ | <0.001 | - | | + | + | | | + | U | | U | U | - | U | U | U |

**Table 2** ANOVA results comparing intraspecific changes in length and weight for two species of *Chaetodon* butterflyfish on three diets in a feeding experiment. Homogenous subsets identified by Tukey's HSD *post-hoc* test are shown in Figs. 2 and 3.

| | **F** | **df** | **p** |
|---|---|---|---|
| *C. plebeius* - change in length | 7.80 | 2/11 | 0.008 |
| *C. plebeius* - change in weight | 19.00 | 2/11 | < 0.001 |
| *C. trifascialis* - change in length | 13.67 | 2/14 | < 0.001 |
| *C. trifascialis* - change in weight | 18.72 | 2/14 | < 0.001 |

**Fig. 1**

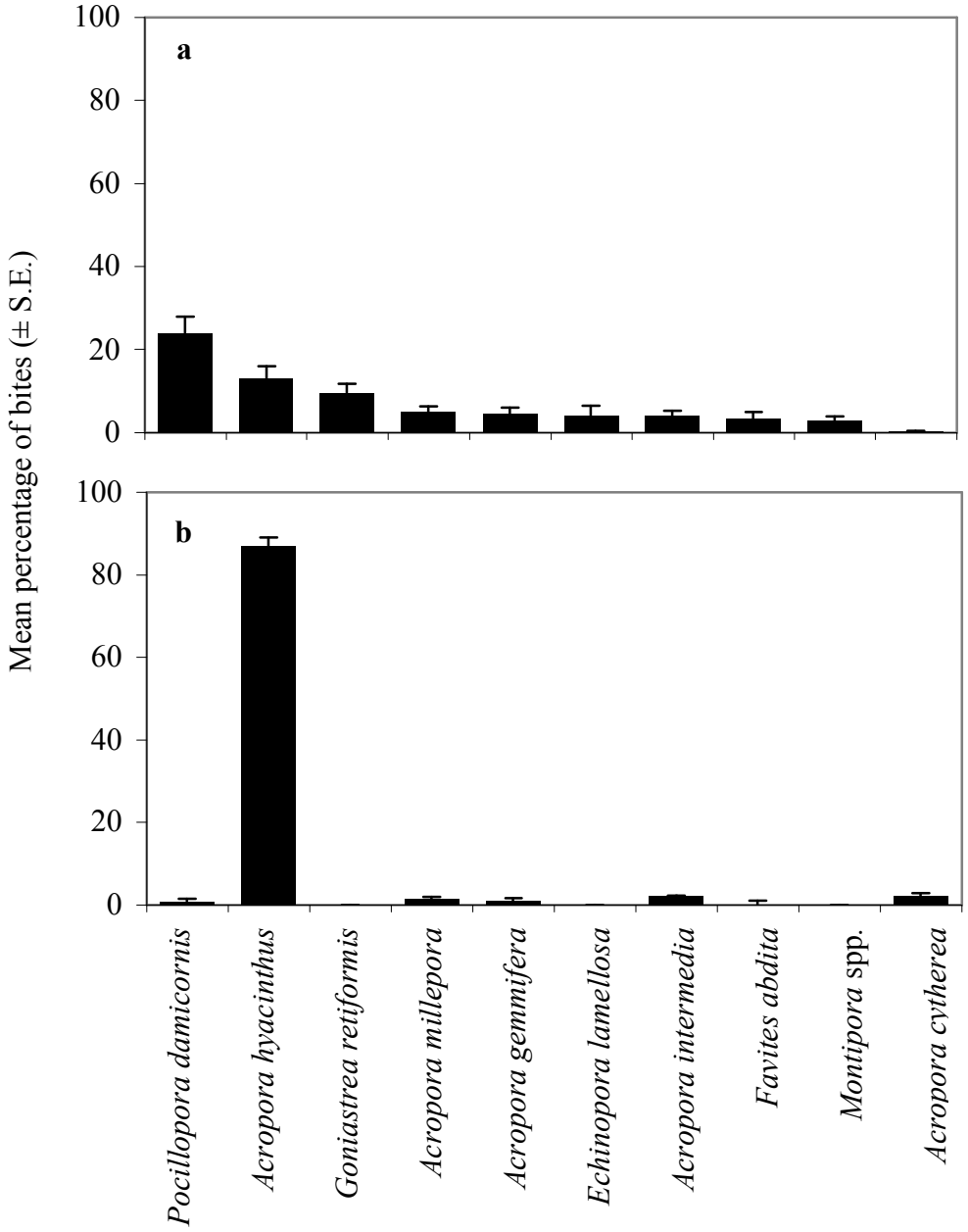

a
b
100
80
60
40
20
0
Mean percentage of bites (± S.E.)
Pocillopora damicornis
Acropora hyacinthus
Goniastrea retiformis
Acropora millepora
Acropora gemmifera
Echinopora lamellosa
Acropora intermedia
Favites abdita
Montipora spp.
Acropora cytherea

**Fig. 2**

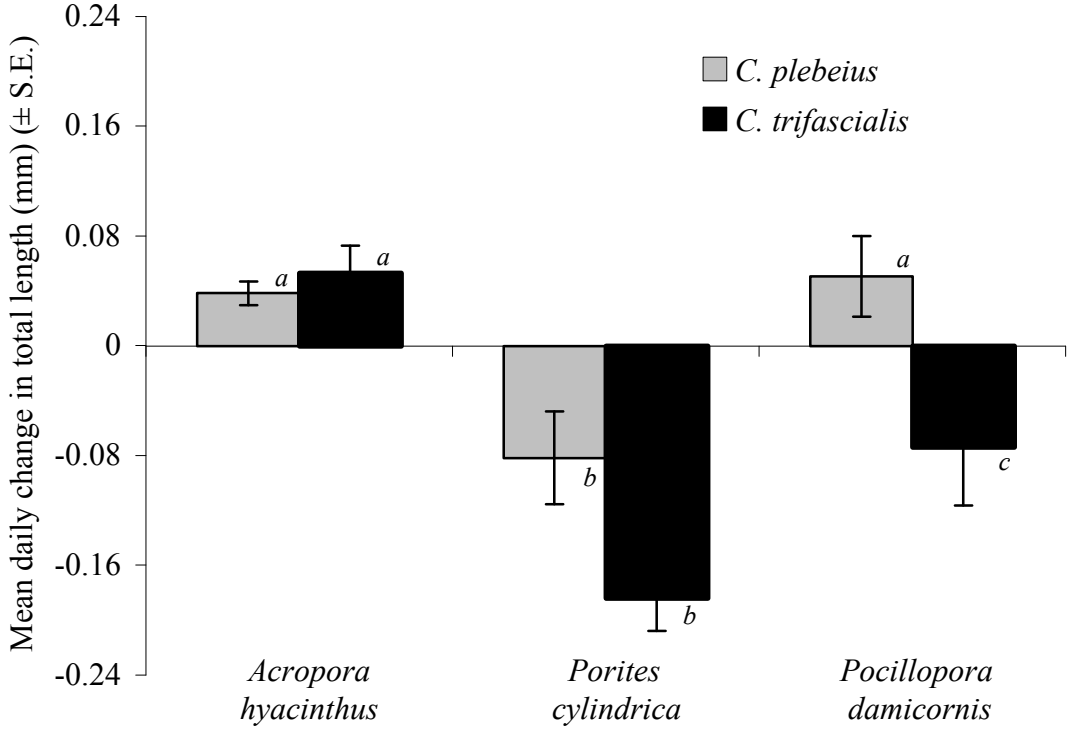
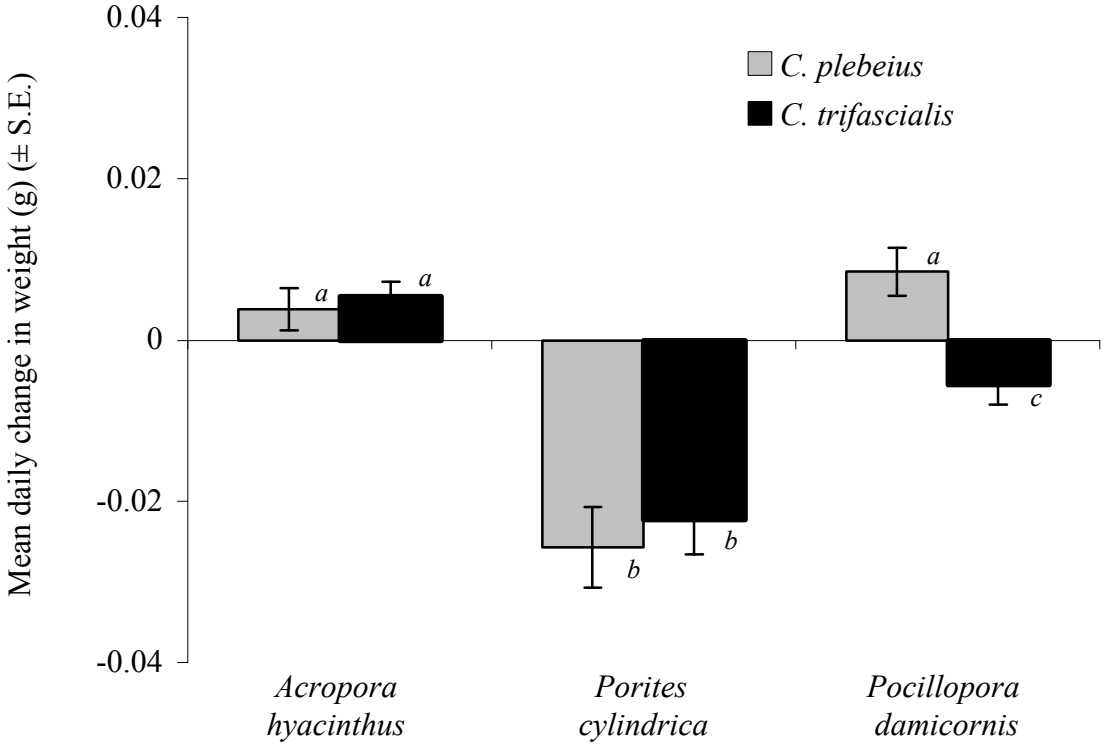

0.24
0.16
0.08
0
-0.08
-0.16
-0.24
Mean daily change in total length (mm) (± S.E.)
C. plebeius
C. trifascialis
a
a
b
b
a
c
Acropora hyacinthus
Porites cylindrica
Pocillopora damicornis

**Fig. 3**


0.04
0.02
0
-0.02
-0.04
Mean daily change in weight (g) (± S.E.)
C. plebeius
C. trifascialis
a
a
b
b
a
c
Acropora hyacinthus
Porites cylindrica
Pocillopora damicornis