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Abstract: This study documented temporal variation in the abundance of butterflyfishes at Trunk Reef, on the central Great Barrier Reef, Australia, from May 2000 to March 2005. During this period, live coral cover declined by >90%, mostly due to severe coral bleaching. There were no short-term changes (within 4 months) in the abundance of butterflyfishes following initial declines in live coral cover. However, surveys conducted in 2005 revealed significant declines in the abundance of *Chaetodon baronessa*, *C. lunulatus*, *C. trifascialis*, *C. plebeius* and *C. rainfordi*, all of which are obligate hard-coral feeders. In contrast, there was no significant change in the abundance of *C. auriga*, *C. aureofasciatus*, *C. citrinellus*, *C. melannotus*, or *C. vagabundus*, which are much less reliant on scleractinian coral for food. Clearly, extensive coral depletion, such as that caused by severe coral bleaching, can have a major effect on the abundance of butterflyfishes. Specific responses of butterflyfishes varied according to their reliance on hard corals for food and their ability to utilise alternate prey types.

1 Declines in the abundance of *Chaetodon* butterflyfishes
2 (Chaetodontidae) following extensive coral depletion.

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9

10 **Running headline:** Butterflyfish responses to coral depletion

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1 **ABSTRACT**

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3 This study documented temporal variation in the abundance of butterflyfishes at
4 Trunk Reef, on the central Great Barrier Reef, Australia, from May 2000 to March
5 2005. During this period, live coral cover declined by >90%, mostly due to severe
6 coral bleaching. There were no short-term changes (within 4 months) in the
7 abundance of butterflyfishes following initial declines in live coral cover. However,
8 surveys conducted in 2005 revealed significant declines in the abundance of
9 *Chaetodon baronessa*, *C. lunulatus*, *C. trifascialis*, *C. plebeius* and *C. rainfordi*, all of
10 which are obligate hard-coral feeders. In contrast, there was no significant change in
11 the abundance of *C. auriga*, *C. aureofasciatus*, *C. citrinellus*, *C. melannotus*, or *C.*
12 *vagabundus*, which are much less reliant on scleractinian coral for food. Clearly,
13 extensive coral depletion, such as that caused by severe coral bleaching, can have a
14 major effect on the abundance of butterflyfishes. Specific responses of butterflyfishes
15 varied according to their reliance on hard corals for food and their ability to utilise
16 alternate prey types.

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18 Key words: *Acanthaster planci*, Bleaching, Coral Reef Fishes, Disturbance, Dietary
19 specialisation, Resource depletion.

INTRODUCTION

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The loss of habitat via both natural and anthropogenic disturbances plays a major role in structuring coral reef communities. Sessile benthic communities on tropical coral reefs are subject to frequent and often catastrophic disturbances, such as severe tropical storms, freshwater plumes, unseasonal temperature extremes, and infestations of the coral eating crown-of-thorns starfish *Acanthaster planci* L. (Brown, 1997; Hughes & Connell, 1999). These acute, but increasingly frequent disturbances, are compounding upon chronic effects of more direct anthropogenic influences (over-fishing, pollution, and coastal development) causing marked reductions in the abundances of sessile invertebrates, especially scleractinian (“hard”) corals (e.g., Connell, 1997, Ostrander *et al.*, 2000; Hughes *et al.*, 2003; Bellwood *et al.*, 2004). More than 30% of coral reefs throughout the world are already severely degraded and corals on 60% may be lost by 2030 (Hughes *et al.*, 2003). Changes in the physical and biological structure of benthic reef habitats are likely to have further, often detrimental, effects on other reef associated organisms, particularly coral reef fishes. Several studies have documented significant declines in the abundance of fishes, and even localised extinctions, following extensive depletion of hard coral, especially among those species which rely on coral for food or shelter (e.g., Sano *et al.*, 1987; Lewis, 1997; Jones & Syms, 1998; Kokita & Nakazono 2001; Booth & Berretta 2002; Munday, 2004).

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Among those fishes with the greatest reliance on hard corals are butterflyfishes from the genus *Chaetodon* (family Chaetodontidae), many of which feed on hard corals (Anderson *et al.*, 1981; Harmelin-Vivien & Bouchon-Navaro, 1983; Pratchett,

1 2005). Spatial variation in the abundance of butterflyfishes is often strongly correlated
2 with hard coral cover (Öhman *et al.*, 1998; Cadoret *et al.*, 1999; Bozec *et al.*, 2005),
3 indicating a close association between butterflyfishes and coral prey. This is further
4 reinforced by studies (e.g., Lewis, 1997; Bouchon-Navaro *et al.*, 1985; Williams,
5 1986; Halford *et al.*, 2004) showing temporal changes in the abundance of
6 butterflyfishes following significant increases or decreases in hard coral cover.
7 Moreover, butterflyfishes have been promoted as indicators of reef health (Hourigan
8 *et al.*, 1988; Crosby and Reese, 2005), whereby declines in the abundance of
9 butterflyfishes may provide an early warning of stresses to reef corals and overall
10 habitat degradation. However, specific responses of butterflyfishes to changes in hard
11 coral cover vary greatly among species and also among studies (Bouchon-Navaro *et*
12 *al.*, 1985; Williams, 1986). Different butterflyfishes vary in the extent to which they
13 are reliant on hard corals due inter-specific differences in their broad dietary habitats
14 (Pratchett 2005). While most butterflyfishes feed on scleractinian corals, the
15 proportional consumption of scleractinian corals (versus soft-corals, gorgonians or
16 other benthic prey items) varies among species, ranging from 100% for obligate hard-
17 coral feeders down to 0% for some motile invertebrate feeders (Pratchett, 2005). Even
18 among obligate hard-coral feeders, the extent to which coral cover (versus recruitment
19 rates or availability of other resources) limits population size may vary in time and
20 space (Cox, 1994).

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22 Among coral-feeding butterflyfishes there are also marked differences in the
23 range of different corals eaten as well as the proportional consumption of different
24 corals (Cox, 1994; Pratchett, 2005). For example, *Chaetodon trifascialis* Quoy and
25 Gaimard 1825 is an extreme specialist, which feeds almost exclusively *Acropora*

1 *hyacinthus* Dana 1846 (Pratchett, 2005). *Chaetodon lunulatus* Quoy and Gaimard
2 1825 meanwhile, feeds on a wide diversity (up to 52 species) of different corals
3 (Berumen *et al.*, 2005; Pratchett, 2005). This variability in the dietary habitats of
4 coral-feeding butterflyfishes is likely to influence their reliance on particular corals, as
5 well as their responses to different types of disturbances. For highly specialised
6 species the availability of specific prey would be critical to their survivorship, and
7 may ultimately limit their abundance. In contrast, the distribution and abundance of
8 more generalist species would be less constrained by prey availability. As such,
9 generalist species may be much more resilient to changes in cover and composition of
10 hard corals (e.g., Pratchett *et al.*, 2004), whereas effects of disturbances on specialist
11 species will vary according to the particular coral species on which they specialise.
12 Notably, different corals vary in their susceptibility to specific disturbances (Marshall
13 & Baird, 2000; Baird & Marshall 2002), such that different disturbances (e.g., coral
14 bleaching versus outbreaks of *A. planci*) may vary in their effects on highly
15 specialised butterflyfishes.

16
17 The purpose of this study was to explore changes in the abundance of
18 butterflyfishes following extensive coral depletion on the Great Barrier Reef (GBR),
19 Australia, caused by severe coral bleaching. This study follows-on from a previous
20 study (Pratchett *et al.*, 2004), which reported no decline in the abundance of the
21 obligate coral-feeding butterflyfish, *C. lunulatus*, within 4 months after significant
22 declines in live coral cover at Trunk Reef, in the central GBR. There was however, a
23 noticeable decline in the physiological condition of *C. lunulatus* from before and
24 immediately after the bleaching event, which may have led to subsequent reductions
25 in survivorship (Pratchett *et al.*, 2004). Consequently, further surveys of butterflyfish

1 assemblages were conducted at Trunk Reef several years after the bleaching event,
2 testing for long-term changes in abundance. This study examined changes in the
3 abundance of *Chaetodon* butterflyfishes over 5 years, from 18 months before the
4 bleaching event to 3 years post-bleaching. Variation in the abundance of individual
5 species was examined in light of their specific feeding preferences, following
6 Pratchett (2005). Previous studies (Bouchon-Navaro *et al.*, 1985; Williams, 1986;
7 Sano *et al.*, 1987) identified a significant link between the broad dietary habits of
8 butterflyfishes and their susceptibility to coral depletion, whereby obligate coral-
9 feeders are more likely to decline in abundance following major habitat perturbations,
10 compared to facultative or non-coral feeders. However, inter-specific differences in
11 the specific feeding preferences and dietary specialisations of *Chaetodon*
12 butterflyfishes have only recently been documented (Pratchett, 2005), and may
13 account for significant variation in the effects of coral depletion on different
14 butterflyfish species.

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METHODS

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18 This study was conducted at Trunk Reef (18°17'S, 146°53'E), in the central
19 section of the Great Barrier Reef (GBR), Australia. Trunk reef is a large (ca. 125km²)
20 submerged reef, located ~120km north of Townsville. This reef, like many throughout
21 GBR, was subject to extensive and wide-spread coral bleaching during the summer
22 (November – March) of 2001-02 (Pratchett *et al.*, 2004). For this study, local
23 assemblages of both scleractinian corals and butterflyfishes were examined in May
24 2000 (18 months before the bleaching), in March 2002 (towards the end of the
25 bleaching event), and in March 2005 (3 years after the bleaching). Sampling was

1 conducted on the shallow reef crest (2-3m water depth), at three randomly selected
2 sites along the exposed (south-east) side of Trunk Reef. All sites were non-
3 overlapping and independent, but were very similar in their physical structure, aspect,
4 and exposure to prevailing south-east trade winds.

5
6 Live cover and generic composition of scleractinian corals was quantified
7 using replicate 10-m line-intercept transects at each site. Transects were delineated
8 using fibreglass tapes laid parallel to the reef crest and positioned a few metres apart.
9 Ten replicate transects were sampled at each of three different sites in May 2000,
10 March 2002 and March 2005, giving a total of 90 transects. On each transect, every
11 colony lying directly beneath the transect tape was identified to genus and its
12 intercept length measured to the nearest centimetre. Variation in total live cover of
13 scleractinian coral was analysed using a two-factor nested ANOVA (sites nested
14 within sampling occasions) based on arcsine transformed estimates of total coral cover
15 from each transect.

16
17 Densities of butterflyfishes on the reef crest at Trunk reef were quantified
18 using visual surveys conducted along 50-m transects. All adult butterflyfishes
19 observed within 2-m either side of transect line were counted and recorded to species.
20 All transects were positioned within 10-m of the edge of the reef crest, following the
21 natural contours of the reef. Five replicate transects were conducted at each of three
22 sites in May 2000, March 2002 and March 2005, giving a total of 45 transects. A total
23 of 15 species of butterflyfishes were recorded across all 45 transects, but five of these
24 species (*Chaetodon ephippium* Cuvier 1831, *Chaetodon lineolatus* Cuvier 1831,
25 *Chaetodon lunula* Lacepede 1802, *Chaetodon rafflesi* Bennett 1830, and *Chaetodon*

1 *unimaculatus* Bloch 1787) were recorded on only 1-2 different transects and were thus
2 excluded from subsequent analyses. The remaining 10 species (*C. lunulatus*,
3 *Chaetodon auriga* Forsskål 1775, *Chaetodon aureofasciatus* Macleay 1878,
4 *Chaetodon baronessa* Cuvier 1829, *Chaetodon citrinellus* Cuvier 1831, *Chaetodon*
5 *melannotus* Bloch & Schneider 1801, *Chaetodon plebeius* Cuvier 1831, *Chaetodon*
6 *rainfordi* McCulloch 1923, *C. trifascialis*, and *Chaetodon vagabundus* Linnaeus
7 1758) included representatives from three different trophic categories; i) obligate
8 hard-coral feeders (*C. aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. plebeius*, *C.*
9 *rainfordi*, and *C. trifascialis*), which feed almost exclusively on scleractinian corals,
10 ii) facultative coral feeders (*C. citrinellus*, and *C. melannotus*), which feed largely on
11 scleractinian corals but supplement their diets with alcyonaceans or other benthic
12 prey, and iii) non-coral feeders (*C. auriga* and *C. vagabundus*), which rarely consume
13 scleractinian corals but feed mostly on motile benthic invertebrates, following
14 Pratchett (2005).

15

16 Temporal variation in the abundance of butterflyfishes was analysed using a
17 two-factor nested ANOVA (sites nested within sampling occasions). Separate
18 analyses were conducted for each of the 10 most abundant species, to explore
19 individual responses to severe coral depletion. To account for inflated type-I error
20 rates arising from running multiple tests on non-independent data, Bonferroni
21 corrected alpha levels were used to assess the significance of ANOVA results,
22 following Sokal & Rohlf (1987). Raw data was log-10 transformed prior to analyses
23 to improve homogeneity of variances, and Tukey's post-hoc test was used to compare
24 changes in abundance of each species over the two consecutive time periods (May
25 2000 - March 2002 and March 2002 - March 2005).

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RESULTS

Live coral cover declined by >90% on the reef crest at Trunk Reef during this study, from 33.4% ($\pm 1.3SE$) in May 2000, down to just 3.2% ($\pm 0.8SE$) in March 2005. Observed declines in total cover of scleractinian (all species pooled) were highly significant (ANOVA, $df = 2/6$, $p < 0.001$), and very consistent among sites (ANOVA, $df = 6/81$, $p > 0.05$). A significant proportion of observed coral mortality occurred between May 2000 and March 2002 (Fig. 1), associated with extensive coral bleaching in late 2001 (Pratchett *et al.*, 2004). During this time, there were significant declines in live cover of *Acropora*, *Porites* and *Montipora*, but relatively little change in any other coral taxa (Fig. 2). However, many of the coral colonies surveyed in March 2002 (including *Acropora*, *Porites*, *Goniastrea*, *Stylophora* and *Isopora*) though still alive, did exhibit conspicuous signs of coral bleaching.

Between March 2002 and March 2005, live coral cover declined by a further 78%, from 15.0% ($\pm 1.4SE$) coral cover in March 2002 down to 3.2% ($\pm 0.8SE$) in March 2005. Marked declines in live cover were seen across virtually all coral genera, except *Pocillopora* (Fig. 2). Several genera (*Montipora*, *Favia*, *Seriatopora* and *Isopora*) completely disappeared from the reef crest at Trunk Reef by March 2005, while several others (*Porites*, *Goniastrea* and *Stylophora*) persisted only as small remnants of previously, much larger coral colonies. Consequently, the coral assemblage on the reef crest at Trunk Reef underwent a significant shift during the study, from an assemblage with high generic richness (20 different genera) dominated by *Acropora* and *Porites*, to an assemblage with relatively low generic richness (only

1 9 genera) and only *Acropora* and *Pocillopora* represented in reasonable abundance.
2 There was not however, any noticeably decline in topographical complexity, as dead
3 corals remained intact in March 2005.

4
5 Despite significant declines in live coral cover between May 2000 and March
6 2002, there was little corresponding decline in the abundance of butterflyfishes on the
7 reef crest at Trunk Reef (Fig. 1). Mean densities of butterflyfishes recorded in May
8 2000 were $19.46 (\pm 1.24SE)$ fishes per $200m^2$ (per transect), and were only slightly
9 lower ($17.93 \pm 0.66 SE$ fishes per $200m^2$) in March 2002. Moreover, there was little
10 change in the individual abundance of any of the 10 most abundant species over this
11 period (Table 1). In contrast, mean densities of butterflyfishes declined by 73%
12 between March 2002 and March 2005, down to $4.86 (\pm 1.24SE)$ fishes per $200m^2$ in
13 March 2005 (Fig. 1). Overall declines in the abundance of butterflyfishes were highly
14 significant (ANOVA, $df = 2/6$, $p < 0.01$), and consistent across replicate sites
15 (ANOVA, $df = 6/34$, $p > 0.05$). Significant declines in the abundance of
16 butterflyfishes were driven mainly by marked reductions in the abundance of *C.*
17 *lunulatus* and *C. baronessa*, while *C. trifascialis*, *C. plebeius*, and *C. rainfordi* had
18 disappeared entirely by March 2005 (Fig. 3). Mean densities of *C. lunulatus*, which
19 was the dominant butterflyfish recorded at Trunk Reef in May 2000 and March 2002,
20 declined by 97%, from $7.27 (\pm 0.80SE)$ fishes per $200m^2$ in March 2002, to just 0.20
21 $(\pm 0.11SE)$ fishes per $200m^2$ in March 2002.

22
23 Species of butterflyfishes which exhibited significant declines in abundance at
24 Trunk Reef (*C. baronessa*, *C. lunulatus*, *C. plebeius*, *C. rainfordi* and *C. trifascialis*)

1 were all obligate hard-coral feeders. Each of these species exhibited significant
2 declines in abundance, which were apparent across all sites (Table I). Meanwhile,
3 there was no significant change in the abundance of facultative coral feeders (*C.*
4 *citrinellus* or *C. melannotus*) or non-coral feeders (*C. auriga* and *C. vagabundus*)
5 during the study (Table I). There was a noticeable decline in the abundance of *C.*
6 *melannotus* between March 2002 and March 2005 (Fig. 3), but ANOVA and Tukey's
7 post hoc tests revealed that this was not significant. Similarly, mean densities of *C.*
8 *aureofasciatus* declined from 0.73 (± 0.30 SE) individuals per 200m² in May 2000,
9 down to 0.33 (± 0.23 SE) in March 2002, but this change in abundance was not
10 statistically significant (Table I).

11

12 DISCUSSION

13

14 Climate induced coral bleaching represents one of the most significant and
15 increasingly prevalent sources of coral mortality (Hoegh-Guldberg, 1999). In 2001-02,
16 coral bleaching caused widespread and very extensive mortality of scleractinian corals
17 throughout the Great Barrier Reef (Berkelmans *et al.*, 2004) and was the primary
18 factor responsible for declines in hard coral cover at Trunk Reef between May 2000
19 and March 2002 (Pratchett *et al.*, 2004). Coral bleaching may also have been
20 responsible for subsequent declines in hard coral cover after March 2002; many of the
21 corals surveyed in March 2002 were very pale in colour and may have later died as a
22 direct result of bleaching (*sensu* Baird & Marshall, 2002). Baird and Marshall (2002)
23 showed that coral mortality may occur up to 40 weeks after initial signs of bleaching.
24 However, additional coral mortality may also have resulted from infestations of *A.*
25 *planci* at Trunk Reef in 2003-2004 (Sweatman *et al.*, 2004).

1

2 Declines in live cover of different coral genera at Trunk Reef mostly
3 correspond with differences in bleaching susceptibilities of corals, reported by
4 Marshall and Baird (2000). All corals are susceptible to bleaching at some level, but
5 certain taxa, such as *Acropora*, *Isopora*, *Seriatopora*, *Stylophora*, and *Pocillopora* are
6 much more prone to bleaching (Marshall & Baird, 2000), and die very quickly once
7 bleached (Baird & Marshall, 2002). At Trunk Reef in 2001-02 bleaching of hard coral
8 was very severe; nearly all corals exhibited conspicuous signs of bleaching, including
9 some genera (e.g. *Porites*) often resilient to bleaching, and it appears likely that most
10 of these colonies subsequently died. One notable exception was the genus
11 *Pocillopora*. Despite being highly susceptible to coral bleaching, live cover of
12 *Pocillopora* declined very little between May 2000 and March 2002, and showed no
13 change between March 2002 and March 2005 (cf. *Seriatopora* and *Stylophora*). This
14 may suggest that coral mortality recorded between March 2002 and March 2005 is
15 primarily attributable to feeding activities of *A. planci* (cf. delayed affects of coral
16 bleaching) because *Pocillopora* spp. are mostly immune to attack from *A. planci*, due
17 to symbionts (specifically, *Alpheus* shrimps and *Trapezia* crabs) which defend the
18 coral (Glynn, 1974; Pratchett, 2001).

19

20 Corresponding with marked declines in coral cover, this study revealed
21 significant declines in the abundance of several *Chaetodon* butterflyfishes, which are
22 almost certainly related to coral depletion. While this study did not control for the
23 effects of coral depletion, butterflyfishes are reasonably long-lived (Berumen, 2005),
24 and in the absence of habitat perturbations, exhibit little or no inter-annual variation in
25 abundance (Halford *et al.*, 2004). Moreover, only obligate coral feeding butterflyfishes

1 (*C. lunulatus*, *C. baronessa*, *C. trifascialis*, *C. plebeius*, and *C. rainfordi*) declined in
2 abundance, whereas facultative coral feeders (*C. citrinellus* or *C. melannotus*) and
3 non-coral feeders (*C. auriga* and *C. vagabundus*) were ostensibly unaffected by
4 reductions in coral cover at Trunk Reef. This finding is corroborated by several
5 previous studies (e.g., Bouchon-Navaro *et al.*, 1985; Williams, 1986), which
6 suggested that observed declines in the abundance of corallivorous butterflyfishes
7 were due to starvation and subsequent mortality, resulting from a lack of coral prey.
8 Alternatively, declines in the abundance of coral-feeding butterflyfishes may have
9 resulted from migration of fishes to different habitats (e.g., lagoonal or back-reef
10 habitats) with higher cover of live corals. However, given the widespread impacts of
11 climate induced coral bleaching (Berkelmans and Oliver, 1999), combined with reef-
12 wide infestations of *A. planci* (Sweatman *et al.*, 2004), the likelihood of finding more
13 appropriate habitats would have been very low.

14
15 Despite extensive declines in the abundance of live coral, there was one
16 obligate coral feeding butterflyfish, *C. aureofasciatus* that did not decline in
17 abundance from May 2000 and March 2005. *Chaetodon aureofasciatus* is widely
18 reported to feed on scleractinian corals, and has been categorised as an obligate hard-
19 coral feeder (Pratchett, 2005). However, in addition to feeding on scleractinian corals,
20 *C. aureofasciatus* does eat a range of non-coral prey, mostly zooanthids (Pratchett,
21 2005). Increased consumption of non-coral prey may have enabled *C. aureofasciatus*
22 to persist following extensive depletion of its usual coral prey. Prey switching has
23 been documented previously among generalist butterflyfishes (Pratchett *et al.*, 2004),
24 and is fundamental in delaying or mitigating effects of prey depletion. As such,
25 generalist coral feeders (i.e., those species that can eat a wide range of different coral

1 species) were expected to be less susceptible to disturbances compared to more
2 specialist species, as was shown for obligate coral-dwelling gobies (Munday, 2004).
3 However, there was no evidence of this; *C. trifascialis*, which is the most specialist
4 corallivorous butterflyfish (Pratchett, 2005), and *C. rainfordi*, which is an extreme
5 generalist (Pratchett, 2005), were similarly affected by severe coral depletion at Trunk
6 Reef. While moderate disturbances may have a disproportionate impact on specialist
7 species (e.g., Munday, 2004), extensive depletion of live corals (across all taxa)
8 appears to affect all coral-feeding butterflyfishes, irrespective of their dietary
9 preferences. The only butterflyfishes that endured extensive coral depletion were those
10 species capable of feeding on non-coral prey (i.e., facultative coral feeders and non-
11 coral feeders).

12

13 While coral-feeding butterflyfishes are highly dependent on scleractinian
14 corals, effects of coral depletion on the abundance of these fishes took several years to
15 manifest. This suggests that mortality of butterflyfishes following depletion of prey
16 resources is very slow, and may involve secondary processes. For example, in their
17 weakened state, butterflyfishes may be increasingly susceptible to predation and
18 disease. Long-term declines in the abundance of butterflyfishes may also arise due to
19 recruitment failure. While facultative corallivores and non-coral feeders (e.g., *C.*
20 *auriga*, and *C. melannotus*) settle in distinct shallow reef environments, obligate
21 coral-feeding butterflyfishes (e.g., *C. trifascialis*) settle directly into hard corals in
22 habitats with high cover of scleractinian corals (Harmelin-Vivien 1989; M. Pratchett,
23 unpublished data). Therefore, extensive coral depletion may limit recruitment success
24 of obligate corallivores, but not facultative corallivores and non-coral feeders.
25 Alternatively, initial declines in the abundance of hard corals may have had limited

1 influence on the abundance of butterflyfishes, and it is only when coral cover drops
2 below some critical level that butterflyfish populations can no longer be sustained
3 (Cox, 1994). The apparent stability of the butterflyfish assemblage immediately after
4 severe coral bleaching, in March 2002, suggests that there was still sufficient coral
5 prey to sustain existing populations of hard-coral feeders . However, there were
6 significant declines in the physiological condition of *C. lunulatus* apparent after initial
7 declines in hard coral cover (Pratchett *et al.*, 2004), which may have affected their
8 subsequent survivorship and/ or reproductive output. As such, the dramatic declines in
9 the abundance of coral-feeding butterflyfishes between March 2002 and March 2005
10 may have been a delayed response to the initial bleaching event. Further reductions in
11 coral cover, due to infestations of *A. planici*, are also likely to have contributed to these
12 declines.

13

14 Results of this study suggest that extensive coral bleaching, caused by severe
15 coral bleaching and localised infestations on *A. planici*, led to significant declines in
16 the abundance of butterflyfishes. Importantly however, butterflyfishes did not respond
17 immediately to significant reductions in live coral cover, indicating a poor ability to
18 provide early warning of changes in coral health (*cf.* Hourigan *et al.*, 1988; Crosby
19 and Reese, 2005). Moreover, only obligate coral feeding butterflyfishes (*C. lunulatus*,
20 *C. baronessa*, *C. trifascialis*, *C. plebeius*, and *C. rainfordi*) declined in abundance,
21 whereas facultative coral feeders and non-coral feeders were ostensibly unaffected by
22 reductions in coral cover. Further inter-specific differences in the responses of
23 butterflyfishes (i.e., among coral-feeding species) were expected, due to differences in
24 their specific feeding preferences and dietary specialisation. However, depletion of

1 hard corals was so extreme (down to 3.2% coral cover in March 2005) that all coral-
2 feeding butterflyfishes virtually disappeared. Recovery of these butterflyfish
3 populations will be very much dependent on recovery of coral assemblages, which is
4 likely to take at least five years (Halford *et al.*, 2004) and only if there are no other
5 disturbance events in the meantime.

6

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Table I. Two factor ANOVA to test for variation in the abundance of butterflyfishes among years, and among sites within years. Tukey's post-hoc test was used to assess significance of changes in the abundance of butterflyfishes within each of two distinct sampling periods. Significance was based on Bonferroni corrected p-values ($\alpha_{0.05} = 0.01$), “↓↑” indicate direction of change (NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Trophic group and species	Among years (df = 2/6)	Among sites (df = 6/36)	Tukey's post-hoc test	
			2000 –2002	2002 –2005
Obligate hard-coral feeders				
<i>Chaetodon aureofasciatus</i>	NS	NS	NS	NS
<i>Chaetodon baronessa</i>	↓***	NS	↓*	↓***
<i>Chaetodon lunulatus</i>	↓***	NS	NS	↓***
<i>Chaetodon plebeius</i>	↓***	NS	NS	↓**
<i>Chaetodon rainfordi</i>	↓**	NS	NS	↓**
<i>Chaetodon trifascialis</i>	↓**	NS	NS	↓**
Facultative hard-coral feeders				
<i>Chaetodon citrinellus</i>	NS	NS	NS	NS
<i>Chaetodon melannotus</i>	NS	NS	NS	NS
Non-coral feeders				
<i>Chaetodon auriga</i>	NS	NS	NS	NS
<i>Chaetodon vagabundus</i>	NS	NS	NS	NS

1 **Fig. 1.** Mean \pm S.E. percentage cover of scleractinian corals (■, n = 30 transects) and
2 mean \pm S.E. densities of butterflyfishes (○, n = 15 transects) at Trunk Reef in May
3 2000 (before the bleaching), March 2002 (during the bleaching), and in March 2005
4 (three years post-bleaching).

5
6 **Fig. 2.** Mean \pm S.E. percentage cover of major coral genera in May 2000 (□, n = 30
7 transects), March 2002 (■, n = 30 transects), and in March 2005 (■, n = 30 transects).
8 Less abundant genera (*Acanthastrea*, *Astreopora*, *Cyphastrea*, *Favites*,
9 *Gardineroseris*, *Goniopora*, *Leptastrea*, *Leptoseris*, *Lobophyllia*, *Montastrea*, and
10 *Psammocora*) were pooled together and considered as a single category (Other
11 scleractinians).

12
13 **Fig. 3.** Mean \pm S.E. densities of butterflyfishes in May 2000 (□, n = 15 transects),
14 March 2002 (■, n = 15 transects), and in March 2005 (■, n = 15 transects). Species are
15 ordered in decreasing abundance in May 2000.

Fig. 1

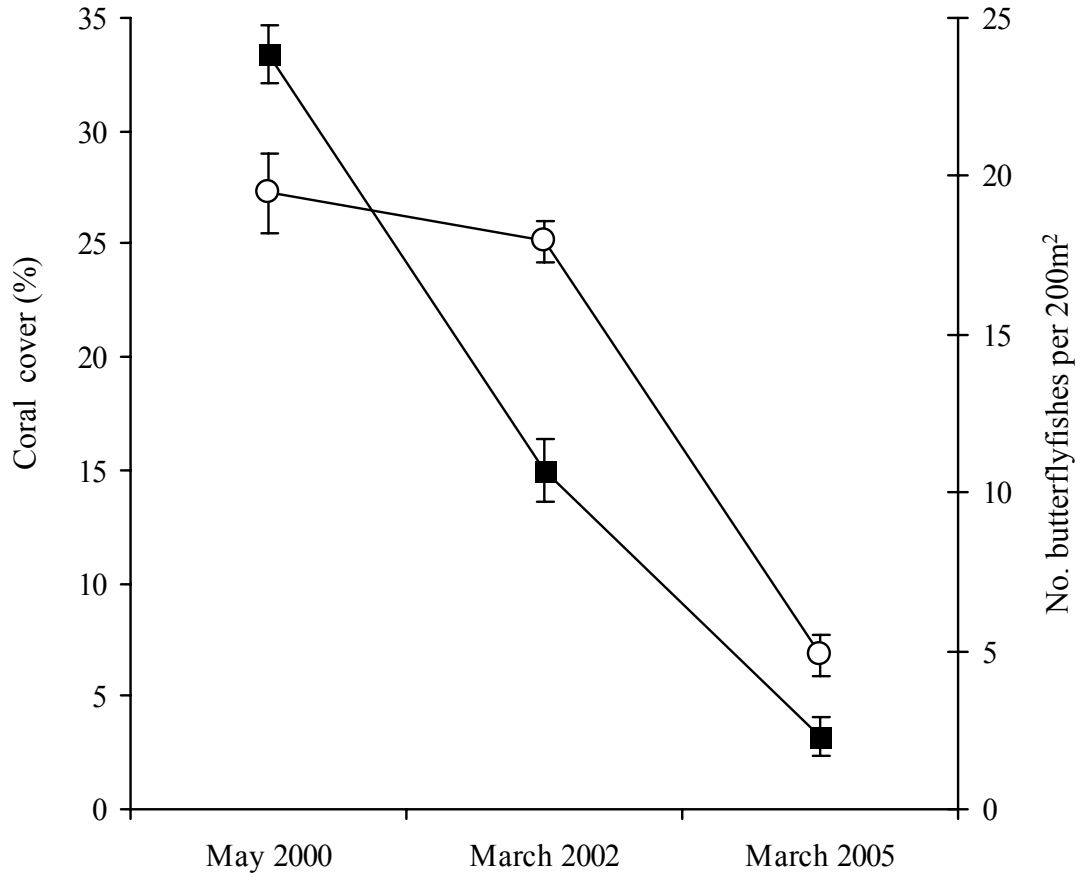


Fig. 2

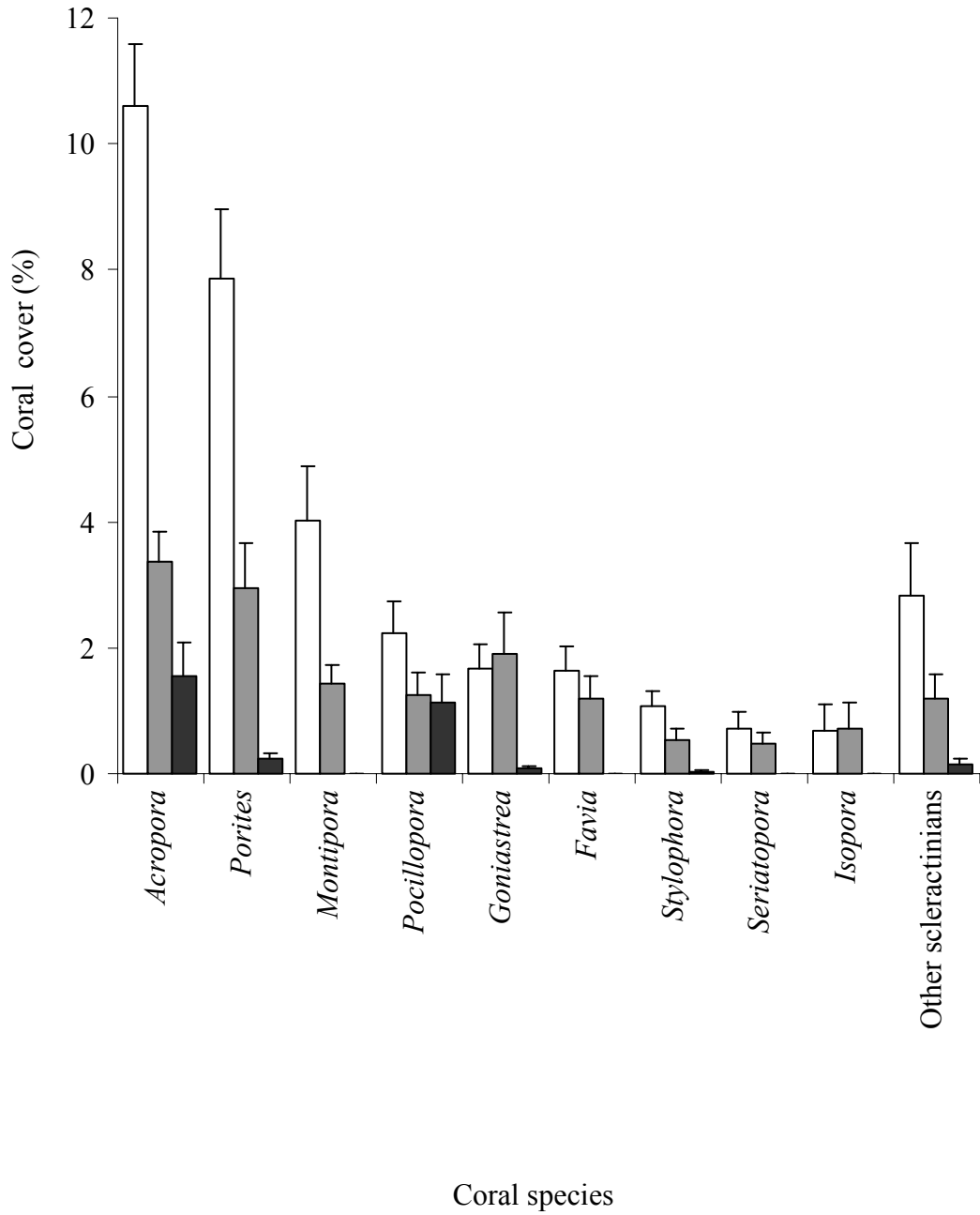
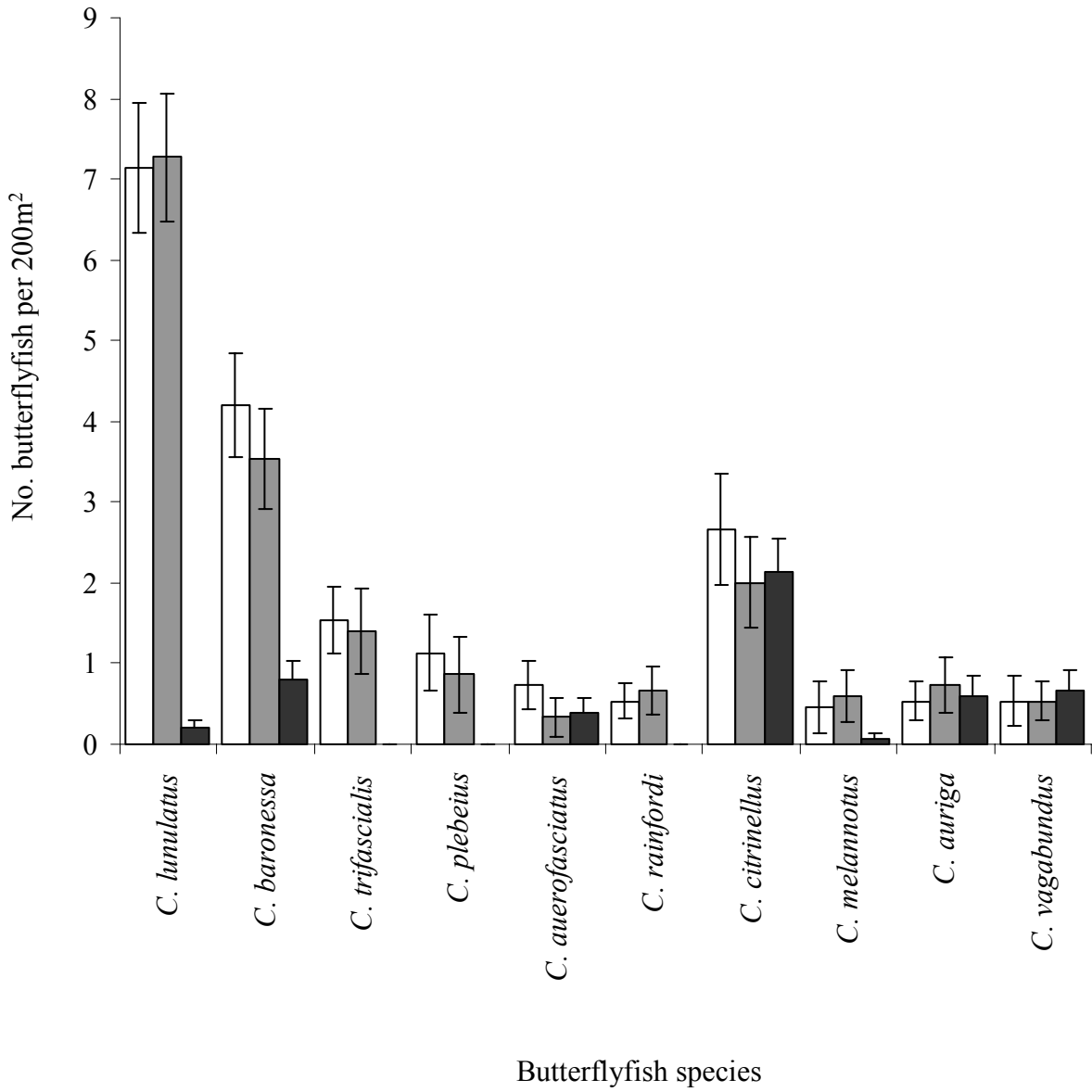


Fig. 3





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February 1st, 2005

Dr. John. F. Craig,
Editor for *Journal of Fish Biology*
Whiteside, Dunscore, Dumfries
DG2 0UU, Scotland

Dear Dr. Craig,

Please find enclosed my manuscript entitled "Declines in the abundance of *Chaetodon* butterflyfishes (Chaetodontidae) following extensive coral depletion" which has been revised in accordance with requirements for the journal.

Specific changes include:

- i) Header removed, and footer reformatted to show only page number
- ii) Line numbers included throughout the manuscript and figure captions
- iii) Specific p-values (eg., $p=0.09$) have been replaced with either $p>0.05$, $p<0.05$, $P<0.01$ or $p<0.001$
- iv) Title page reformatted following Bozec et al. 2005 J. Fish Biol. 66: 966-982.
- v) All paragraphs indented (except Abstract and first paragraph of the Introduction)
- vi) All references to tables in roman numerals (eg., Table I not Table 1).
- vii) Figure captions simplified following Bozec et al. 2005 J. Fish Biol. 66: 966-982, and now include keys to figures
- viii) Legends removed from figures.

I hope this manuscript now meets requirements for publication in *Journal of Fish Biology*. Please advise of any further changes required.

Sincerely,

A handwritten signature in black ink, appearing to read 'M. Pratchett', is written over a light blue circular stamp.

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