Corallivory in tubelip wrasses: diet, feeding and trophic importance

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This paper describes a 2 month study of the patterns of abundance, feeding pressure, diet and feeding selectivity in corallivorous tubelip wrasses (Labridae), rarely studied, yet widespread and abundant group of corallivores on Indo-Pacific coral reefs. The relative abundance and feeding pressure of corallivorous wrasses and butterflyfishes (Chaetodontidae) in Kimbe Bay, Papua New Guinea, were compared. Overall, tubelip wrasses were more than twice as abundant as corallivorous butterflyfishes and accounted for three times as many feeding bites on corals. The three most abundant tubelip wrasses (yellowtail tubelip *Diproctacanthus xanthurus*, Allen's tubelip *Labropsis alleni* and the tubelip wrasse *Labrichthys unilineatus*) were all obligate corallivores taking >97% of bites from the surface of live corals. *Labropsis alleni* and *D. xanthurus* were highly selective, consuming preferred prey species in proportions significantly higher than expected given their availability. In contrast, *L. unilineatus* was fairly non-selective and consumed most corals in direct accordance with their availability. As coral predators, tubelip wrasses are highly comparable to coral-feeding butterflyfishes in the coral species consumed, range of dietary specialization and their reliance on live coral. Tubelip wrasses, however, may supersede butterflyfishes as the predominant corallivorous family in some Indo-Pacific locations, and coral-feeding tubelip wrasses are likely to be severely affected by coral decline.   © 2010 The Authors

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INTRODUCTION

The ecological role of a species can only be interpreted from an understanding of its distribution, diet and patterns of feeding selectivity (Cox, 1986; Morrison, 1988; Jones, 1992; Bellwood, 1996; Rotjan & Lewis, 2006; Ceccarelli, 2007; Hoey & Bellwood, 2008). Likewise, the effect of ecologically similar species or guilds depends upon the pattern of abundance of guild members, the extent of their dietary specialization and the degree to which they partition habitats and food resources (Bellwood & Choat, 1990; Fox & Bellwood, 2007; Hoey & Bellwood, 2008). These factors also have important implications for how species and guilds respond to changing or degrading environments. Highly specialized species are susceptible to declining

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resources (Reese, 1981; Kokita & Nakazono, 2001; Halford *et al.*, 2004; Jones *et al.*, 2004; Munday, 2004; Pratchett *et al.*, 2006; Feary, 2007), and a guild of specialists with highly overlapping resource requirements are especially susceptible to a loss of a restricted range of resources (Sano, 2004; Gardiner & Jones, 2005).

On tropical reefs, coral-feeding fishes represent one of the most distinctive and most specialized functional groups of coral reef fishes (Randall, 1974). Corallivory is increasingly recognized as an important feeding mode that may affect the structure of coral reef habitats (Neudecker, 1979; Wellington, 1982; Cox, 1986; Rotjan *et al.*, 2006; Pratchett, 2007). As a functional group, specialist corallivores are intricately linked to the corals on which they feed and are the first and worst affected group of reef fishes following major disturbances that result in coral mortality (Reese, 1981; Sano, 2004; Graham *et al.*, 2006, 2009; Wilson *et al.*, 2006). Furthermore, the loss of these corallivores from reef assemblages has important flow-on effects for higher trophic levels; the primary production provided by zooxanthellate corals will be effectively lost from coral-reef food webs (Glynn, 2004). The taxonomic extent of corallivory and the variation in the degree of dietary specialization and overlap has only recently been appreciated (Cole *et al.*, 2008; Rotjan & Lewis, 2006, 2008). Coral-feeding fishes are taxonomically diverse and have been recognized in at least 11 reef-fish families (Cole *et al.*, 2008). Specific dietary composition, however, has been documented for relatively few species, primarily *Chaetodon* butterflyfishes (Irons, 1989; Cox, 1994; Alwany *et al.*, 2003; Berumen *et al.*, 2005; Pratchett, 2005; Graham, 2007). Very little research has been conducted on coral-feeding species from other major families, such as the Tetradontidae, Monacanthidae, Pomacentridae and Labridae, and the extent of dietary specialization and overlap is unknown. The abundance of these other corallivores relative to the more widely studied butterflyfishes (Chaetodontidae) has also seldom been investigated.

The majority of research on corallivory to date has focused on butterflyfishes where it is unusually prevalent and well recognized. Numerous studies across wide geographical ranges have allowed generalizations to be drawn about species-specific behaviour (Birkeland & Neudecker, 1981; Gore, 1984; Cox, 1994; Pratchett, 2005; Graham, 2007; Pratchett & Berumen, 2008). For example, despite high diversity of corals on most reefs (often >150 species), many butterflyfishes tend to feed on a very specific sub-set of available corals (Irons, 1989; Alwany *et al.*, 2003; Berumen *et al.*, 2005; Pratchett, 2005, 2007; Graham, 2007). Even the most generalist coral-feeding butterflyfish, the redfin butterflyfish *Chaetodon lunulatus* Quoy & Gaimard, eats <30% of available coral species (Pratchett *et al.*, 2004). Moreover, there is very high concordance in feeding preferences of coral-feeding butterflyfishes. In the northern Great Barrier Reef, Pratchett (2007) showed that virtually all corallivorous butterflyfishes (11 of 14 species) feed predominantly on either *Acropora hyacinthus* or *Pocillopora damicornis*. Selective feeding on a small number of coral species has important implications for the composition of both coral communities and fish assemblages (Cole *et al.*, 2008). For example, the highly preferred *P. damicornis* is restricted to shallow lagoons in Guam due to the high levels of predation on the reef slope (Neudecker, 1977, 1979). Conversely, declines in preferred coral species can lead to decreased physiological condition (Pratchett *et al.*, 2004; Berumen *et al.*, 2005) and even the localized extinction of corallivorous fishes (Reese, 1981; Kokita & Nakazono, 2001; Wilson *et al.*, 2006). These same conclusions, however, cannot be extrapolated to non-chaetodontid corallivores without first investigating individual

species or genera. Each new corallivorous group represents a unique evolutionary path. As such, these under-studied taxa require detailed dietary and behavioural studies before their relative importance to corallivory can be ascertained. These studies can then be compared with the existing chaetodontid-focused literature to make broader assumptions about the implications of fish predation on corals.

There are several reasons why generalizations about butterflyfishes may not apply to other taxa. Butterflyfishes have fairly distinct feeding behaviour, visually locating and feeding from exposed tentacles of individual polyps, and they derive nutrition mainly from coral tissue (Reese, 1977; Tricas, 1989; Aeby, 2002; Gochfeld, 2004). Corallivorous wrasses, on the other hand, may derive most of their nutrition from coral mucus, rather than the tissue itself. For example, McIlwain & Jones (1997) showed that the tubelip wrasse *Labrichthys unilineatus* (Guichenot) preferentially fed from injured and damaged coral colonies over healthy, intact coral, which, they hypothesized, may be due to increased mucous production and release of olfactory cues by injured colonies. If coral-feeding wrasses feed mostly on coral mucus, it is likely that their patterns of prey preference would be fundamentally different to that of other coral-feeders, targeting those species with highest mucous production.

The role of corallivores can only be interpreted from fundamental information on abundance, feeding pressure, diet and feeding selectivity. The aims of this study were: 1) to examine the distribution and abundance of corallivorous wrasses and compare their relative contribution to corallivory with butterflyfishes and 2) to quantify dietary composition and feeding selectivity for the three most abundant and widespread species of tubelip wrasse, yellowtail tubelip *Diproctacanthus xanthurus* (Bleeker), *L. unilineatus* and Allen's tubelip *Labropsis alleni* Randall. The level of specialization and reliance on coral of corallivorous wrasse was compared with the dietary specialization with published information on butterflyfishes to identify whether coral-feeding wrasses are functionally similar to butterflyfishes.

MATERIALS AND METHODS

Fieldwork was conducted over a 2 month period between October and December 2006 in Kimbe Bay, on the island of New Britain, Papua New Guinea (5° 25′ S; 150° 05′ E). Although little studied, this region is typical of the coral triangle region in terms of the representation of corallivorous fishes (Allen & Munday, 1994). This region experienced a steady decline in coral cover from 66% in 1996 to as low as 7% in 2002 (Jones *et al*., 2004); coral cover has been increasing since then and is currently at 30–40% (unpubl. data). Research focused on three sheltered inshore platform reefs typical of the bay: Matane Walindi, Luba Luba and Hanging Gardens. All three reefs are isolated platform reefs with steep slopes and shallow reef tops, located <1 km from the mainland island of New Britain. The maximum distance between reefs is *c*. 600 m, although they are separated by very deep water (*c*. 180 m) (Holthus, 1994; Holthus & Maragos, 1994). The three reefs were selected for their similarity in size, shape and proximity to the shoreline, and for the purposes of this study were considered one homogenous near-shore reef.

CORALLIVORE ABUNDANCE AND CONTRIBUTION TO CORALLIVORY

Abundances of corallivorous fishes were quantified at four distinct depths: 0, 2, 6 and 10 m below the reef crest. At each depth, the abundance of all corallivorous fishes was quantified along replicate 50 m × 4 m belt transects (following Jones *et al*., 2004). Four

replicate transects were run within each depth zone, laid from haphazardly selected starting points and following depth contours of the reef. The observer waited *c*. 5 min after deploying the transect line to allow the fishes to resume their normal behaviour. Subsequently, one diver swam along the transects and recorded all corallivorous fishes encountered 2 m either side of the tape (following Khalaf & Abdallah, 2005); to eliminate any bias, all counts were performed by the same observer. The near-shore reefs of Kimbe Bay are relatively small platform reefs with steep sides and as such there is a large environmental difference over the 10 m depth range. By sampling a combined area of 800 m^2 at each depth, the variation in fish communities that corresponded with this habitat gradient was adequately captured.

To compare and contrast the functional importance of different fishes as coral predators, *in situ* feeding observations were undertaken. Feeding observations of 15 min were conducted within 16 replicate 2 m × 2 m quadrats established at each of four depths (0, 2, 6 and 10 m below the reef crest), corresponding with transect-based sampling. Each quadrat was positioned in areas with relatively high coral cover (>50% live coral), as the purpose of this study was to quantify relative rates of coral feeding by different fish species and not to extrapolate rates of feeding per unit area. During observations, the total number of bites taken by each corallivorous fish (*L. unilineatus*, *D. xanthurus*, *L. alleni*, southern tubelip *Labropsis australlis* Randall, eastern triangular butterflyfish *Chaetodon baronessa* Cuvier, eight-banded butterflyfish *Chaetodon octofasciatus* Bloch, *C. lunulatus*, Klein's butterflyfish *Chaetodon kleinii* Bloch and the chevroned butterflyfish *Chaetodon trifascialis* Quoy & Gaimard) on any live coral within the quadrat area was recorded. Feeding observations were split evenly between the morning (0800–1200 hours) and afternoon (1200–1600 hours) periods, to reduce any confounding influence of diurnal feeding patterns. Moreover, all feeding observations were completed within a single 10 day period (13 to 23 October 2006).

FEEDING OBSERVATIONS OF CORALLIVOROUS WRASSES

Focal animal sampling with all occurrences was used to assess dietary composition of *L. unilineatus*, *D. xanthurus* and *L. alleni*; this sampling was conducted on 75–144 randomly selected individuals of each species on the exposed fore-reef slope and flat. Based on a pilot study (Cole, 2007), the optimal duration of observations was 4 min during which time each fish was followed at a distance of 1–3 m, while feeding behaviour and dietary composition were recorded. Observations were terminated if the individual disappeared from view or showed any noticeable signs of distress. *Labrichthys unilineatus* is sexually dimorphic, so feeding observations were performed equally (72 observations) on both sexes, but later pooled due to the high similarity. The sexes could not be discerned in either *L. alleni* or *D. xanthurus*. To account for any diurnal variation in feeding rates, approximately equal numbers of observations were conducted during three time periods: morning (0600–1000 hours), mid-day (1000–1400 hours) and afternoon (1400–1800 hours).

In addition to recording dietary composition, several other biological attributes were also recorded such as body size, group dynamics (*e.g.* paired and solitary) and interspecific and intraspecific aggression. Additionally, the condition of the substratum being fed from was also noted as either healthy or damaged. Damaged substratum consisted of broken, bleached or diseased corals, or colonies with conspicuous recent injuries. No account was taken of the potential causes (*e.g.* bleaching, sedimentation or crown-of-thorns starfish) of coral damage and injuries, but the proportion of coral colonies within these categories was generally low (<10%).

Dietary overlap was assessed using Schoener's similarity index (*T*) determined from $T = 1 - 0.5 \sum |Px_i - Py_i|$, where Px_i and Py_i are the proportions of bites on each coral species for species pair *x*, *y*. *T* ranges from 0 to 1; values >0·6 represent species that show very high similarity in diet and are not considered sustainable over ecological time due to the detrimental effects of direct competition over shared resources (Ross, 1986). Conversely, dietary overlap <0·4 indicates that there are major differences in patterns of prey use.

FEEDING SELECTIVITY OF CORALLIVOROUS WRASSES

Feeding selectivity of corallivorous wrasses were assessed by comparing the proportional use of coral consumed (estimated by the number of bites on each species) to their relative availability inside individual feeding territories or home ranges. To determine an individual's feeding range, each fish was followed, and the boundaries of its foraging areas marked with weighted flagging tape. Individual fishes were monitored for at least 30 min; this area was then marked out by laying a measuring tape encompassing all previously marked edge boundaries. These territories were checked randomly throughout the day; if the fish could not be found inside the marked territory, the area was re-observed until the fish was found and its new boundaries were identified and marked.

When the fishes were consistently found foraging inside the marked-out area, feeding selectivity observations began the next day. Feeding observations of 10 min, three times throughout the day, were used to assess feeding selectivity. These feeding observations were conducted in the same way as the 4 min observations; however, they provided a cumulative total of 30 min worth of feeding data per fish.

The availability of prey corals within each feeding territory was estimated using replicate line-point transects (Nadon & Stirling, 2006). Transects were laid every 0·5 m along the longest side of an individual's territory, and the substratum was recorded every 10 cm along each transect. In this way, territories were effectively split up into a 10 cm × 50 cm grid. This method was utilized for *D. xanthurus* and *L. unilineatus* and provided a direct comparison between an individual's diet and its diet choices. This method could not be used for *L. alleni* due to the deeper nature of its feeding ranges and the lack of well-defined foraging areas. For these reasons, *L. alleni*'s dietary selectivity was examined in a broader manner, such that coral prey availability was assessed at the population level. Five 50 m transects were laid and the substratum recorded at 10 cm intervals, to provide a total of 2500 individual points. These transects were run parallel to the reef slope from a haphazardly selected starting point between a depth of 8 and 17 m. The 4 min feeding observations of *L. alleni* at Matane Walindi were pooled and provided a total of 54 replicate feeding observations, which corresponded to the area in which the coral cover was sampled. This allowed a viable comparison between feeding and availability of coral prey.

Feeding selectivity for all species of corallivorous wrasses was analysed using the log-likelihood statistic (X^2_{L2}), calculated through the following formula: $X^2_{L2} = 2 \sum_{j=1}^{n} \sum_{i=1}^{I} u_{ij} \ln\{u_{ij}[E(u_{ij})]^{-1}\}$, where u_{ij} is the proportional use of each prey type (i) by each individual (j), and $E(u_{ij})$ is the expected number of bites taken from prey type i by the jth individual if use is proportional to availability (Manly *et al.*, 1993). Resource selection functions were then used to determine which coral species were consumed more or less frequently than expected (from their availability) by each species of wrasse. Bonferroni-corrected 95% CI were calculated around each selection function. Use was deemed disproportionate (either positively or negatively) to availability if the 95% CI did not contain 1 (Manly *et al.*, 1993).

RESULTS

CORALLIVORE ABUNDANCE AND DISTRIBUTION

A total of nine corallivorous butterflyfishes [*C. baronessa*, *C. lunulatus*, *C. octofasciatus*, ornate butterflyfish *Chaetodon ornatissimus* Cuvier, latticed butterflyfish *Chaetodon rafflesi* (Bennett), *C. trifascialis*, pennant bannerfish *Heniochus chrysostomus* Cuvier and the humphead bannerfish *Heniochus varius* (Cuvier)] and four tubelip wrasses (*L. unilineatus*, *D. xanthurus*, *L. alleni* and *L. australis*) were observed on the study reefs, although most of these species were rarely encountered. Tubelip wrasses were the most abundant corallivores across all depths and had an overall mean ± s.e. density of 16·50 ± 1·59 fish per 200 m², two and a half times higher than that found for the butterflyfish (6·50 ± 0·83 per 200 m²). *Labrichthys*
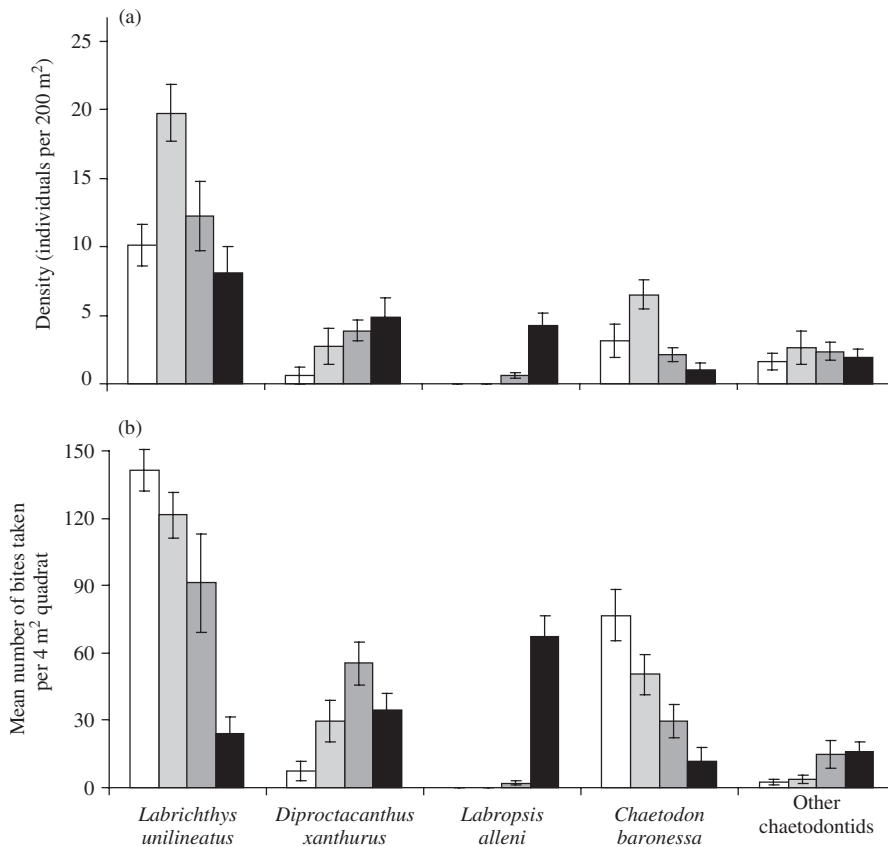
FIG. 1. Comparison of abundance and importance to corallivory of coral-feeding wrasses and butterflyfishes in Kimbe Bay. (a) Mean ± S.E. density of the most common corallivorous species, observed across four depths (☐ 0, ☐ 2, ☐ 6 and ■ 10 m) and (b) mean ± S.E. number of bites taken in 4 m^2 quadrats over 15 min by corallivorous fishes at four depths on near-shore reefs in Kimbe Bay.

unilineatus was by far the most abundant coral-feeding species across all depths. Densities peaked 2 m below the crest with 19.75 ± 1.03 individuals per 200 m^2 (Fig. 1). *Diproctacanthus xanthurus* showed a trend of increasing in abundance with depth and the greatest densities occurred at the deepest zone (10 m) with 4.87 ± 0.68 individuals per 200 m^2. The remaining two tubelip wrasses, *L. australis* and *L. alleni*, were relatively rare and restricted to the deeper zones. Of these two species, *L. alleni* was more abundant with 4.25 ± 1.11 individuals per 200 m^2 in the deepest zone.

Corallivorous butterflyfishes were much lower in abundance than tubelip wrasses. Only one species, *C. baronessa*, was present in any notable numbers, and abundances were highest in the shallows and declined with depth. The highest mean abundance for this species occurred at 2 m below the crest with densities of 6.50 ± 0.53 individuals per 200 m^2 [Fig. 1(a)].

CONTRIBUTION OF WRASSES AND BUTTERFLYFISHES TO CORALLIVORY

Feeding observations conducted within the 64 quadrats yielded a total of 12 447 bites on live scleractinian corals, which equate to a mean ± S.E. feeding rate of 195·9 ± 15·2 bites m^{-2} of live coral h^{-1}. Rates of coral feeding were, however, spatially variable and ranged from 77 to 420 bites per quadrat. Overall, corallivorous wrasses took 74% (9312 bites) of all bites taken inside quadrats.

In terms of bites taken, *L. unilineatus* and *C. baronessa* were the predominant corallivores in the shallow zones, though feeding of both species declined with depth. *Labrichthys unilineatus* was unique in the widespread nature of its coral consumption, as bites were observed in 89% (57/64) of quadrats; furthermore, these seven quadrats with zero bites were all in the deepest zone (10 m). *Labrichthys unilineatus* fed most heavily on the reef flat with a feeding rate of 35·3 ± 2·3 bites per m^{-2} per 15 min, just under twice that observed for *C. baronessa* (19·2 ± 2·8 bites per m^{-2} per 15 min), the second-heaviest feeder in this shallow zone [Fig. 1(b)].

In the deeper zones, other corallivorous species became more prevalent, especially *D. xanthurus* and *L. alleni* [Fig. 1(b)]. *Diproctacanthus xanthurus* was observed to feed across all depths, but feeding activity peaked 6 m below the crest with 13·8 ± 2·4 bites per m^{-2} per 15 min. *Labropsis alleni* was the most prevalent corallivore in the deeper zones (16·8 ± 2·3 bites per m^{-2} per 15 min) and seldom fed in depths <10 m. In contrast to the tubelip wrasses, other corallivorous butterflyfishes (primarily *C. octofasciatus* and *C. lunulatus*) were always a minor contributor to corallivory, although the feeding rate of *C. octofasciatus* did increase slightly with depth. These other chaetodontids, even combined, rarely took >30 bites from within a quadrat.

SPECIES-SPECIFIC DIET PATTERNS OF CORALLIVOROUS WRASSES

In situ feeding observations confirmed that adult individuals of *D. xanthurus*, *L. unilineatus* and *L. alleni* feed almost exclusively from scleractinian corals, with at least 97% of bites occurring on live coral. In addition to hard corals, *D. xanthurus* and *L. alleni* also took a small proportion of their bites from non-coralline sources, mainly cleaning other reef fishes, although *L. alleni* also fed from sponges in small quantities (1·2% of bites).

The range and proportional consumption of different corals varied greatly among the three wrasses. *Labropsis alleni* was the most specialized of the three species, feeding from only 33 species of hard coral, and just over half of all bites were directed towards only two species, *Pavona cactus* (33·75%) and *Anacropora puerto-galerae* (21·8%) (Fig. 2). Dietary overlap between *L. alleni* and other corallivorous wrasses was also very low: $T = 0.25$ and 0.20 for *D. xanthurus* and *L. unilineatus*, respectively.

Diproctacanthus xanthurus and *L. unilineatus* had broad diets compared with *L. alleni* and consumed 46 and 53 coral species, respectively, and also exhibited a much higher dietary similarity ($T = 0.54$). Corals of the genus *Acropora* accounted for just under half of all bites for both species (Fig. 2). *Diproctacanthus xanthurus* tended to actively forage across 26 different *Acropora* species, and never took >6% of its bites from any one species. In contrast, *L. unilineatus* fed from 20 *Acropora*
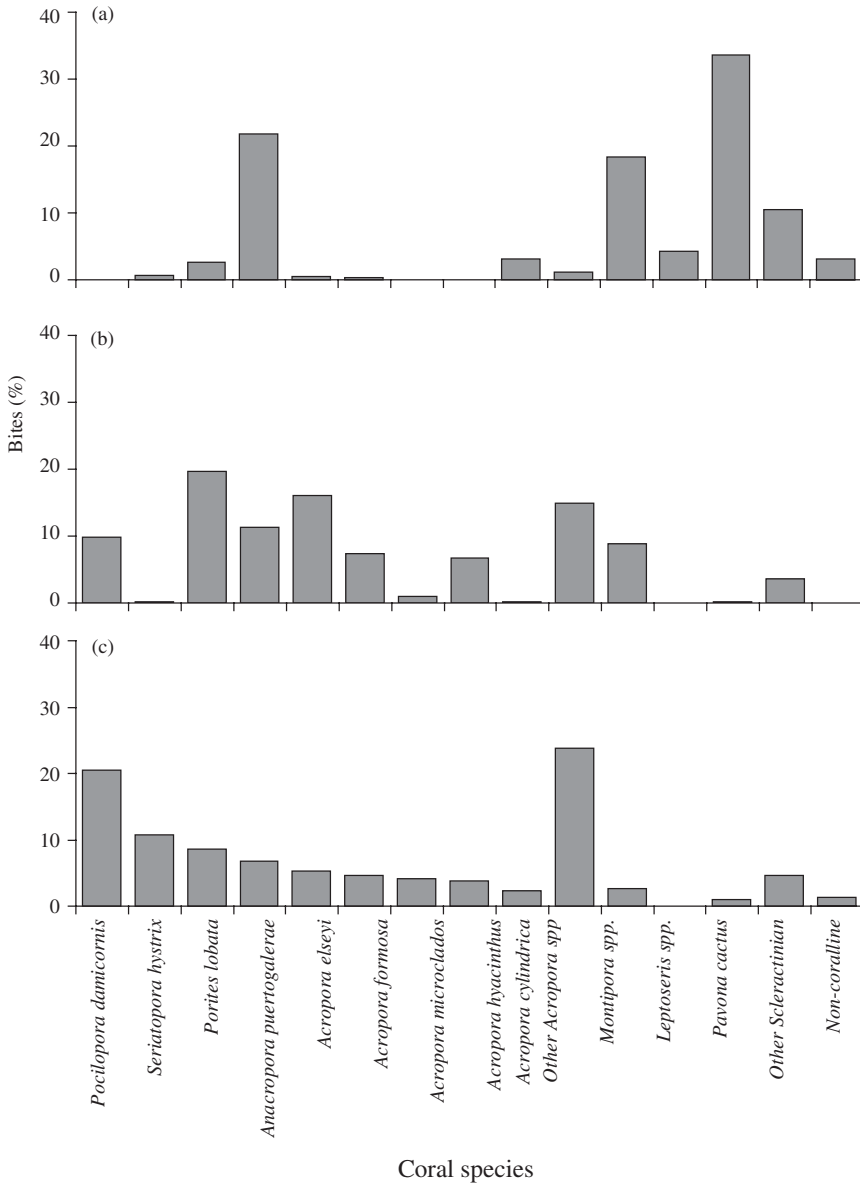
FIG. 2. Per cent consumption of main coral prey for three species of corallivorous wrasse (a) *Labropsis alleni* (total bites = 2378), (b) *Labrichthys unilineatus* (total bites = 4577) and (c) *Diproctacanthus xanthurus* (total bites = 2708).

species; however, feeding was mainly concentrated on *Acropora elseyi* (16·1%), *Acropora formosa* (7·4%) and *Acropora hyacinthus* (6·6%). Despite this similarity, the focal point of each wrasse's diet was very different. *Labrichthys unilineatus* fed most heavily from *Porites lobata* (19·8%), while *D. xanthurus* primarily consumed *P. damicornis* (20·5%) (Fig. 2).

TABLE I. Dietary selectivity of coral-feeding wrasses. The significance of selectivity (P) was ascertained by comparing overall levels of selectivity (χ^2_{L2}) to a χ^2 distribution with $n(I-1)$ d.f., where I was the total number of prey types utilized by each species of wrasse

Species	n	χ^2_{L2}	P
Labrichthys unilineatus	21	$1\cdot79 \times 10^3$	$<0\cdot001$
Diproctacanthus xanthurus	12	$2\cdot68 \times 10^3$	$<0\cdot001$
Labropsis alleni	64	$1\cdot56 \times 10^4$	$<0\cdot001$

The relative utilization of damaged coral by each species also differed dramatically. *Labrichthys unilineatus* fed heavily from damaged sections and took 25% of its bites from these areas. Furthermore, *L. unilineatus* incorporated damaged sections from all species fed from. In contrast, *D. xanthurus* and *L. alleni* were more likely to feed from healthy areas and only 6·4 and 7·0% of bites were taken from injured areas, respectively. When damaged coral was encountered, all three species increased feeding activity, although *L. unilineatus* was the only species that appeared to actively seek out damaged sections.

PATTERNS OF CORAL SELECTIVITY

All three species exhibited significant dietary selection and consumed one or more prey species in proportions greater than expected based on their availability (Table I). *Diproctacanthus xanthurus* and *L. alleni* showed the highest degree of selectivity, consuming preferred prey in much greater proportions than expected. *Labropsis alleni* tended to select for only a few coral species, principally *P. cactus*, *Montipora* species and, to a lesser extent, *Leptoseris hawaiiensis* (Fig. 3). In terms of selectivity, *L. alleni* was inclined to either select or avoid different coral species, and only *A. puertogalerae* was consumed in proportions similar to availability. *Diproctacanthus xanthurus* showed strong positive selection for *A. millepora*, *Seriatopora hystrix* and *P. damicornis* but avoided *P. lobata*, *Montipora* spp. and *Acropora cyclindrica*. *Labrichthys unilineatus* was much less selective. Some positive selection was exhibited for *A. hyacinthus* and *P. lobata* and, conversely, *S. hystrix* and *A. millepora* were avoided. Overall, *L. unilineatus* tended to feed from most species in proportions expected if feeding was largely non-selective (Fig. 3).

DISCUSSION

The present study showed that tubelip wrasses are the primary corallivores on near-shore reefs in Kimbe Bay. Tubelip wrasses were two and a half times more abundant and took three times as many bites on corals compared with coral-feeding butterflyfishes in this region. This was true across all depth gradients, although different tubelip wrasse species were prevalent at each depth. Even when taking into account the larger mean size of butterflyfishes, it appears likely that the total biomass of wrasses is higher. Subsequently, tubelip wrasses are a functionally important component of the corallivore guild in Kimbe Bay, Papua New Guinea. This study also confirmed that species from three different wrasse genera (*D. xanthurus*,
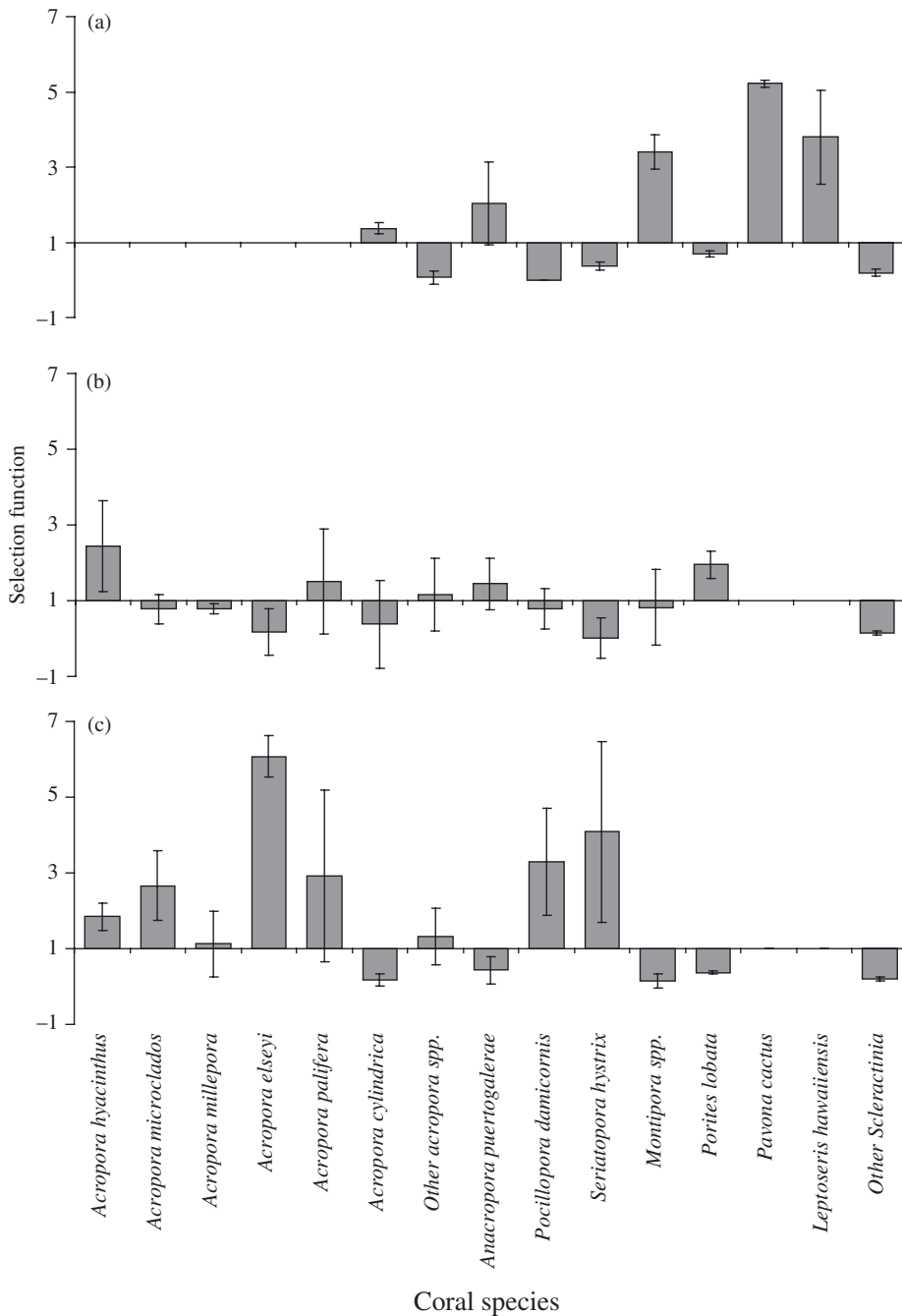
FIG. 3. Dietary selection by coral-feeding wrasses. (a) *Labropsis alleni*, (b) *Labrichthys unilineatus* and (c) *Diproctacanthus xanthurus*. Values are means ± 95% CI. Selection functions >1 indicate that these corals were used more than expected from their availability (*i.e.* selected), while selection functions <1 indicate corals that were avoided. Gaps represent species that were not available to be grazed inside a species' feeding territory.

L. unilineatus and *L. alleni*) are all obligate corallivores as adults. Fishes are considered obligate hard coral-feeders when >80% of their bites are taken from living coral (Cole *et al.*, 2008). At Kimbe Bay, adult tubelip wrasses took between 97 and 100% of bites from scleractinian corals, and, as such, hard coral is clearly an important food resource. The extent of feeding selectivity and overlap among species, however, appears to differ from their more well-known butterflyfish counterparts.

Previous work has shown that obligate corallivorous butterflyfishes can be separated along a continuum from generalists to specialists (Birkeland & Neudecker, 1981; Irons, 1989; Cox, 1994; Alwany *et al.*, 2003; Pratchett, 2005, 2007; Berumen *et al.*, 2005). Specialist feeders are capable of using only a very restricted range of prey species irrespective of abundance and are fundamentally dependent on these prey species for their survival (Irons, 1989; Berumen *et al.*, 2005; Pratchett *et al.*, 2006; Graham, 2007). *Chaetodon trifascialis* is the most specialized corallivorous butterflyfish, feeds almost exclusively on tabular *Acropora* colonies (Irons, 1989; Pratchett, 2005) and is among the most susceptible species to coral depletion (Reese, 1981; Pratchett *et al.*, 2006; Wilson *et al.*, 2006). In comparison, the three species of tubelip wrasse exhibit only minor to moderate levels of dietary specialization; all three species consumed at least 33 different coral species, and major dietary components never accounted for more than a third of their total diet.

Labropsis alleni is the most specialized of the three study species, taking a disproportionate number of bites from the relatively rare corals, *P. cactus*, *Montipora* species and *L. hawaiiensis*. Additionally, the dietary composition of *L. alleni* was very consistent among individuals, despite marked variation in the local abundances of different corals. These data suggest that *L. alleni* has strong and consistent preferences for the aforementioned corals. *Diproctacanthus xanthurus* also showed a moderate degree of dietary specialization and exhibited clear feeding preferences for *Acropora* species, *P. damicornis* and *S. hystrix*. *Diproctacanthus xanthurus* consumes a much wider range of corals compared with *L. alleni* and is capable of altering its diet in response to differences in coral abundances among feeding territories. For example, *P. damicornis* was abundant on the reef crest where it is grazed heavily but on the deeper slope feeding was often directed towards *A. puertogalerae* and staghorn *Acropora* which were the more abundant species at this depth. Of the three wrasse species, the diet composition of *D. xanthurus* was the most similar to that seen in butterflyfishes, with feeding preferences for *Acropora* and *Pocilloporid* corals (Pratchett, 2005, 2007; Berumen *et al.*, 2005).

Generalist feeders typically show large variation in diet composition among individuals and between geographical areas (Birkeland & Neudecker, 1981), reflecting variation in availability of different prey types. *Labrichthys unilineatus* was the least specialized of the three wrasses. This species showed little prey selectivity and fed on most corals in direct proportion to their availability. *Labrichthys unilineatus* is an obligate corallivore throughout its geographical range, although the corals eaten do vary (Sano *et al.*, 1984; McIlwain & Jones, 1997). At Lizard Island, *L. unilineatus* consumed predominantly *A. hyacinthus* and *Montipora* species, which were the most abundant coral species at this study site (McIlwain & Jones, 1997). Similar patterns were observed at Kimbe Bay, where *L. unilineatus* fed predominantly on the most abundant coral species, *P. lobata*. Interestingly, in Kimbe Bay *L. unilineatus* consumed *P. lobata* disproportionately to its availability. These data suggest that *L. unilineatus* is a generalist feeder that specializes on locally abundant coral species.

Specialization differences between corallivorous species have important conse-quences for the survival of these species following disturbance events and subsequent declines in live coral. Highly specialized species that rely on only a small sub-set of available resources (*e.g. C. trifascialis*) are prone to extinction following the loss of these key resources (Munday, 2004; Wilson *et al*., 2006; Munday *et al*., 2008; Pratchett *et al*., 2008). In contrast, coral-feeding generalists are more capable of adapting to changes in the coral community (Pratchett *et al*., 2004, 2006). Of all corallivorous fishes studied to date, *L. unilineatus* appears to be among the most resilient to changes in the coral community. This species is highly adaptable to dif-ferences in the coral community, both between regions and across the reef. This flexibility may partly explain its numerical dominance in Kimbe Bay. It is worth noting that even the most adaptable corallivorous species are still highly dependent on live corals (Pratchett *et al*., 2006). Even *L. unilineatus* has gone locally extinct in several regions following large scale declines in live coral cover following outbreaks of the crown-of-thorns starfish and mass bleaching events (Sano *et al*., 1987; Jones *et al*., 2004; Sano, 2004; Garpe *et al*., 2006; Graham, 2007).

The extent that the disturbance history of Kimbe Bay has influenced the outcome of this study is not known. The low abundance of corallivorous chaetodontids on the study reefs may reflect recent declines in live coral cover, attributable to dual impacts of climate-induced coral bleaching and persistently high levels of sedimentation (Jones *et al*., 2004). Between 1997 and 2002, coral cover in Kimbe Bay declined from *c*. 66% to *c*. 7%. Branching *Acropora* species, which are the preferred prey of many corallivorous fishes (Pratchett, 2007), declined to <2% cover on the crest of near-shore reefs (Jones *et al*., 2004). Abundances of all coral-feeding species were severely impacted, and while some recovery has occurred, densities of corallivores may not have returned to pre-impacted levels. Interestingly, this decline does not appear to have affected corallivorous wrasses to the same degree as chaetodontids. This may have occurred because corallivorous wrasses overall have a lower degree of specialization compared with corallivorous butterflyfishes and were able to adapt their diet to feed on previously unexploited coral species. This implies that generalist species such as *L. unilineatus* are more likely to survive long-term environmental changes.

Another explanation is that coral-feeding wrasses have a much higher recruitment rate, which may facilitate re-colonization following a major disturbance event. In general, larval butterflyfishes are poorly represented in the plankton (Leis, 1989). In a 2·5 year recruitment study, butterflyfishes were found to have some of the lowest recruitment rates on near-shore reefs in Kimbe Bay (Srinivasan & Jones, 2006). In contrast, *L. unilineatus* had a much higher settlement rate, and this may explain the high abundance of this species relative to both other tubelip wrasses and butterflyfishes. In near-shore reefs of Kimbe Bay, the highly specialized butterfly-fish *C. trifascialis* has still not recovered from the declines in coral cover despite recent increases in the abundance of its prey corals. It is possible that corallivorous wrasses, especially the generalist *L. unilineatus*, have partly succeeded corallivorous butterflyfishes in Kimbe Bay. If this is the case, it will have important ramifica-tions for the community structure on future coral reefs, considering the expected regime of increased anthropogenic disturbances. These future coral reefs will prob-ably select for generalist species that have a high flexibility in habitat and prey use.

Labrichthys unilineatus could be further separated from other corallivorous wrasses and from chaetodontids based on the differences in foraging behaviour. The feeding behaviour of *D. xanthurus* and *L. alleni* was consistent with the feeding behaviour detailed by Tricas (1989) for the coral-feeding Multiband butterflyfish *Chaetodon multicinctus* Garrett. Specifically, corals are encountered and then carefully inspected before feeding. Bites on corals are then divided into distinct feeding forays, often comprising multiple bites within any one region of the coral, interspersed with movement to a new part of the coral or an alternative colony (Tricas, 1989). In contrast, *L. unilineatus* rapidly and consistently bites the same exact area of a coral colony and displays little evidence of colony inspection between bites or feeding forays. These differences in foraging behaviour may reflect highly contrasting feeding strategies, whereby the former species feed predominantly on coral tissue (more specifically, exposed tentacles of individual coral polyps), whereas the latter species (*L. unilineatus*) is targeting coral mucus.

Tricas (1989) explains the distinctive feeding behaviour of *C. multicinctus*, which searches the surface of corals between every bite and rarely takes more than a few bites in any one location, in terms of polyp feeding and the retraction of coral polyps. It is likely, therefore, that *D. xanthurus* and *L. alleni* are also searching for specific locations within each coral colony where polyps are extended and are then required to move to an entirely new feeding location. Repeated feeding in the same location must be delayed long enough for polyps to once again become fully extended (Gochfeld, 2004).

Most corallivorous fishes are thought to target coral polyps and thus exhibit highly convergent feeding preferences, leading to the assumption that polyps are the most nutritious component of hard corals. Coral mucus contains a large protein–nitrogen component that results in a carbon to nitrogen ratio comparable with coral tissue (Brown & Bythell, 2005). Additionally, major lipid components of coral mucus are wax esters (particularly cetyl palmitate) and triglycerides. These compounds make coral mucus a relatively rich energy source for those species capable of digesting them (Benson & Muscatine, 1974). Corallivorous fishes have some of the longest intestines of all fishes, particularly mucous feeders (Harmelin-Vivien & Bouchon-Navaro, 1983; Motta, 1988; Elliott & Bellwood, 2003); long digestive tracts facilitate high gut retention times and may allow the digestion of these complex wax esters.

The relative use of damaged *v*. healthy corals may also be explained by coral mucus. *Labrichthys unilineatus* shows a consistent preference for both natural and experimentally damaged coral (McIlwain & Jones, 1997). Corals that are broken, diseased or undergoing partial mortality are under considerable stress. A common stress response by corals is to increase mucous production (Loya & Rinkevich, 1980; Krupp, 1984; Telesnicki & Goldberg, 1995; Wild *et al.*, 2004, 2005). Therefore, by targeting these damaged areas, *L. unilineatus* is most probably focusing on areas that have the highest availability of mucus. This idea is consistent with the lower relative use of damaged corals by *D. xanthurus* and *L. alleni*, which appear to predominantly feed on polyps. This is not to completely discredit the possibility that *L. alleni* and *D. xanthurus* feed on mucus in addition to coral polyps. Feeding intensity of these two species did increase when damaged colonies were encountered; however, the proportion of time spent foraging on damaged areas was considerably lower than that of *L. unilineatus*.

The importance of corallivory as a functional group in coral reef dynamics has traditionally been underestimated (Robertson, 1970; Connell, 1973; Hatcher, 1988). Considering the high number of bites taken (c. 200 m^2 of live coral h^{-1}) by coral-feeding fishes in this study, the transfer of energy up in the food web is likely to be considerable. For example, Glynn (2004) found over 287 links between corals, invertebrate and fish corallivores, and top-level fish predators on low-diversity eastern Pacific Ocean reefs. On higher diversity reefs (*e.g.* Kimbe Bay), the size and number of these links are expected to be even greater.

Tubelip wrasses (*Diproctacanthus*, *Larabicus*, *Labrichthys* and *Labropsis*) are a major group of corallivorous fishes on coral reefs, second only to butterflyfishes (Cole *et al.*, 2008). In addition to the three species considered here, there are at least six other species of tubelip wrasses (Parenti & Randall, 2000) that remain unstudied, although a similar reliance upon hard coral is expected (Lieske & Myers, 2001; Randall, 2005; Froese & Pauly, 2008). The three corallivorous wrasse species investigated in this study are all obligate corallivores as adults and consume a diverse range of coral species. Furthermore, the feeding modes also differed between the three species; *L. alleni* and *D. xanthurus* appear to predominantly target coral polyps and feed in a manner similar to the majority of corallivorous butterflyfishes. In contrast, *L. unilineatus* appears to partition the coral resource on a finer scale and feeds directly from coral mucus. Interspecific variation in prey selectivity among corallivorous wrasses has consequences for explaining both the distribution and abundance of their spatial patterns, and their resilience to disturbance events and declining coral cover. Corallivorous wrasses, as a group, show a broader dietary niche and greater flexibility than the more specialized corallivorous butterflyfishes; however, the ecological role of corallivorous wrasses is probably comparable with that played by butterflyfishes. The ecological effect that the corallivorous functional group has on the coral community is not well understood. Future research needs to focus on a functional group approach and consider the effect that chronic predation by corallivorous fishes as a guild has on the coral community and subsequently coral reef dynamics. Specific areas of future study include the effect of predation on a coral colony's energy budget, its capacity for repair and reproductive output. Further study is needed to ascertain how chronic predation by corallivorous fishes will interact with other anthropogenic stressors to influence the long-term survivorship of coral reef communities.

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