

The role of cryptobenthic reef fishes in coral reef trophodynamics

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ABSTRACT: An examination of the trophic status of a cryptobenthic reef fish community from the central Great Barrier Reef was carried out to evaluate the potential role of cryptobenthic fishes in coral reef ecosystems. Using frequency of occurrence data, dietary analyses revealed a diverse range of trophic groups, although detritivory (in 10 out of 16 species and 39.3% of individuals) and carnivory (5 of 16 species and 40.5% of individuals) clearly dominate as trophic modes. Herbivory (1 species; 2.4% of individuals) is only a minor component in the community trophic structure. Of the 18 dietary categories identified, detritus and copepods were the only constituents represented in all 16 species examined. Although the degree of dietary specialization varied among taxa, the 2 most abundant species, *Eviota queenslandica* and *Istigobius goldmanni*, utilised the broadest range of dietary items. Morphology reflected the trophic partitioning among fishes: carnivores were invariably <28 mm total length (TL) and had gut-length ratios (GLRs) of <0.5; detritivores were all >38 mm TL with GLRs generally exceeding >1.0. The trophic composition and numerical strength of the cryptobenthic fish fauna suggests that cryptobenthic reef fishes have the potential to make a significant contribution to reef trophodynamics along a number of trophic pathways. This prompts a re-evaluation of the roles of reef fishes in the functioning of coral reefs, particularly those related to the recycling of primary production through detrital pathways.

KEY WORDS: Detritus · Trophic · Detritivory · Herbivory · Diet · Gobiidae · Assemblages · Ecosystem function

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INTRODUCTION

Despite the knowledge that a significant proportion of coral reef fish assemblages are composed of small, cryptic, benthic fishes, marine ecologists have focused almost entirely on the larger, more conspicuous members of the reef fish community (Sale 1991). This has resulted in a distorted and fragmented picture of reef fishes that is heavily biased towards larger species. Recently, an entire 'cryptobenthic' reef fish assemblage was quantitatively described for a fringing reef system on the Great Barrier Reef (Ackerman & Bellwood 2000, 2002). Cryptobenthic fishes, defined as 'adult fishes of typically <5 cm that are visually and/or behaviourally cryptic, and maintain a close association with the benthos', may be extremely abundant. Estimates of the numerical abundance and species richness of this cryptobenthic community were strikingly

high, with an average of 95 individuals and 36 species in a 10 m² area (Ackerman & Bellwood 2000). This represents approximately 50.1% of individuals and 40.4% of all reef fish species at this location.

Apart from abundances and species richness at a single geographical location, we know very little of the ecology of cryptobenthic reef fish communities. As the standard visual censusing techniques employed in reef fish studies do not adequately census cryptic fishes, it is not surprising that our understanding of this component of the reef fish fauna is so limited. The difficulties involved with accurately sampling and identifying small, cryptic fishes and their omission from non-destructive censusing techniques explain much of the disparity and bias towards the larger, conspicuous fishes (Sale 1981, Bellwood 1996). In the absence of even rudimentary knowledge on most cryptobenthic fishes such as their densities, diets and distribution on

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coral reefs, their role in reef trophodynamics has been assumed to be a minor one (but see Townsend & Tibbetts 2000 and Wilson et al. 2003). Their exclusion from studies focusing on community structure (e.g. Jones & Chase 1975, Sheperd et al. 1992) and trophodynamics in particular, is evident in trophic models focusing on community dynamics and ecosystem energetics (e.g. Christensen & Pauly 1992). These studies rarely acknowledge the absence of cryptobenthic fishes in their analyses.

Despite this obvious gap in our knowledge, the information to date suggests that the cryptobenthic community has the potential to make a significant and substantial contribution to reef ecosystem processes. In particular, their numerical strength has led to the suggestion that this group of fishes may play a significant role in reef trophodynamics, with up to 25% of the energy flow by fishes passing through these taxa (Ackerman & Bellwood 2002). Estimates indicate that this reef fish component constitutes 9.7%, or 20 g m⁻² of overall reef fish biomass (Ackerman & Bellwood 2000), an estimate similar to that recorded for mobile invertebrates on coral reefs (7.5 to 22.3 g m⁻²) (Klumpp et al. 1988, Riddle et al. 1990). It is widely considered that the contribution of cryptobenthic reef fishes to trophic pathways can be largely defined by their consumption of microcrustaceans and their status as prey items for larger reef fishes. Certainly their role as small carnivores is consistent with size-based expectations, as most small fishes are carnivorous, including juvenile herbivores (Choat 1991, Choat & Clements 1998, Wainwright & Bellwood 2002). However, a role in other trophic pathways has been documented, with cryptobenthic fishes in the family Blennidae, for example, accessing and utilising detritus as a major dietary component (Wilson 2000, Wilson et al. 2001a).

To date, no study has examined the trophic status of an entire cryptobenthic reef fish community in a way that permits their role in ecosystem trophodynamics to be evaluated. Without knowledge of the trophic status of this community it is difficult to identify their role in reef processes beyond a role as potential prey for larger taxa. Determining the diets of cryptobenthic fishes is an essential primary step in accurately assessing their potential importance in coral reef trophodynamics, and provides us with an enhanced opportunity to further define the role of reef fish populations in coral reef ecosystems.

In this study therefore, we utilised morphological and gut-content analyses of a range of dominant cryptobenthic reef fish species from the central Great Barrier Reef to assess the trophic status and structure of this community. The specific aims of this study were: (1) to identify the diets of the dominant cryptobenthic species; (2) to examine the extent and nature of dietary

variability within this reef fish community; and (3) to assess their potential role as a functional group in the trophodynamics of a coral reef ecosystem.

MATERIALS AND METHODS

Collections. Collections were undertaken from March to July 2001 at 3 locations on the leeward side of Orpheus Island (18° 35' S, 146° 28' E), central Great Barrier Reef, at depths of 6 to 9 m. We identified 4 distinct habitats (sand and rubble, cave, open reef and soft coral) and sampled them all 7 times at each of the 3 locations (n = 84). Specimens were collected on SCUBA using clove oil and a fine-mesh net (2 mm) covering a basal area of 0.4 m², giving a total sampling area of 33.6 m² (modified after Ackerman & Bellwood 2002). The net was placed in a circle on the substratum, before approximately 125 ml of a 5:1 ethanol: clove-oil mixture was pumped into the netted area for approximately 20 s. The mixture was allowed to sit inside the net for 1 min before the search for anaesthetised fishes began. This short duration reduced the potential for regurgitation of gut contents during anaesthesia. Individuals found in crevices and holes were carefully extracted using plastic cable ties. Fishes were placed in individually labelled clip-seal bags and placed in an ice-water slurry as soon as possible after capture. Individuals were then identified and put into a 10% formalin-seawater solution for 5 d, then transferred into 70% ethanol. Identification of species was confirmed in the laboratory using taxonomic texts (Winterbottom 1985, Winterbottom & Emery 1986, Randall et al. 1997, Meyers 1999), with the exception of *Pleurosicya muscarum*, which was identified by H. Larson (Northern Territory Museum, Australia). Where identification to species level could not be established, forms were denoted Sp. A, Sp. B etc.

Gut-content analysis. The gut contents of 20 individuals from each of the 16 most abundant cryptobenthic species were examined (see Table 1). Of the 320 specimens used, 109 were obtained from previous samples taken from the same locations using comparable techniques (Ackerman & Bellwood 2002). Samples were based exclusively on individuals collected either late in the morning, or in the afternoon.

Gut contents were quantified using methods developed for studies of other small taxa in the families Blennidae (Wilson 2000), Pomacentridae (Wilson & Bellwood 1997) and Apogonidae (Marnane & Bellwood 2002). Total lengths and intestine lengths of each individual were measured to 0.1 mm using vernier calipers. The intestine was opened lengthways and the entire contents removed, then agitated (to prevent stratification) and distributed evenly on a petri dish in

the shape of a square. A transparent sheet with a similar-sized square containing a grid of 100 squares, of which 60 were randomly blacked out, was then placed over the gut contents. The gut content in a single point in each of the 40 transparent squares (top-right corner of each grid square) was identified using a stereomicroscope (40 \times), and recorded. This technique provides a quantitative estimate of gut contents (20 individuals per species \times 40 squares per individual); 18 separate dietary components across a range of trophic groups (carnivores, herbivores and detritivores) were identified (see Table 2). Amorphous (<250 μ m) organic matter (AOM) was assigned to the detritivore food group and is defined as dead organic material lacking any identifiable form or structure (cf. Bowen 1984, Wilson 2000). Species were assigned to trophic categories based on the dominant (>50% mean occurrence) category in their diet.

Statistical analysis. Principal components analysis (PCA) based on a covariance matrix of the occurrence (number of cells occupied) for each dietary category in each species was generated using SPSS (Version 10.0). Linearity was checked using a series of scatterplots and found to be adequate after transformation of the data using $\log_{10}(x+1)$. To evaluate the relationship between diet and 2 morphological attributes, PC1 (describing the main source of variation in diet among species) was plotted against total lengths, and gut-length ratios (total length:gut length), for the 16 species.

RESULTS

A total of 458 individuals from 48 species in 11 families were collected. The 16 most abundant species, selected for gut content analysis, represented 84% of all individuals (Table 1). All but 3 belonged to the family Gobiidae, with gobiids comprising 85% of all individuals. The 3 most abundant species were all gobiids and, collectively, these species made up 51% of all specimens (Table 1).

A diverse range of species-specific dietary preferences was evident (Fig. 1), including specialised carnivores (e.g. *Priolepsis nuchifasciatus* and *Pleurosicya muscarum*), herbivores (*Amblygobius rainfordi*) and detritivores (e.g. *Asterropteryx semipunctatus* and *Ecsenius mandibularis*). Other species, however, including the 2 most abundant species, *Eviota queenslandica* and *Istigobius goldmanni*, appear to utilise a much broader range of dietary items. At the 2 extremes of generalists to specialists, *I. goldmanni* consumed 14 out of a possible 18 dietary components (Table 2), in contrast to *E. mandibularis* which fed on a total of 4 categories, with 1 (AOM) constituting 86% of its diet. The mean number of food categories utilised by all

species was 13.6. AOM and copepods were the only dietary components represented in the diet of all 16 species.

The importance of detritus in the diets of all species is clearly evident (AOM: Fig. 1), ranging from 11% in *Priolepsis nuchifasciatus* to 86% in *Ecsenius mandibularis*, with a mean of 42.6% across all 16 species. Detritus was the dominant dietary component in 10 species (*Assessor macneilli*, *Eviota queenslandica*, *Trimma caesiura*, *Istigobius goldmanni*, *Valenciennea muralis*, *I. decoratus*, *Bathygobius fuscus*, *Amblygobius nocturnis*, *Asterropteryx semipunctatus* and *E. mandibularis*). The other major component, copepods, was dominant in 5 species (*Priolepsis nuchifasciatus*, *Pleurosicya muscarum*, *Eviota* sp. C., *Enneapterygius tutuilae*, and *Trimma striata*) and filamentous algae in only 1 (*Amblygobius rainfordi*). Sediment was found in a total of 12 species, filamentous algae in only 4 species.

PCA of these 16 species and the occurrence of the 18 dietary categories revealed a distinct division of species into 4 dietary groups (Fig. 2). Of these, 3 discrete trophic groups are immediately apparent: detritivory (*Ecsenius mandibularis*, *Amblygobius nocturnis*, *Asterropteryx semipunctatus*, *Istigobius goldmanni*, *Valenciennea muralis*, *I. decoratus* and *Bathygobius fuscus*), carnivory (*Trimma striata*, *Eviota* sp. C., *Pleurosicya muscarum*, *Enneapterygius tutuilae* and *Priolepsis nuchifasciatus*), and herbivory (*Amblygobius rainfordi*). The fourth group located centrally on the

Table 1. Families, species and numbers of individuals sampled for 16 dominant cryptobenthic reef fish species selected for gut-content analysis, and their contribution (%) to total sample (of 458 individuals in 48 species). For gut-content analysis (n = 20 per species), the shortfall was made up from existing collections from same area (Ackerman & Bellwood 2000, 2002). An expanded species list is given in Ackerman & Bellwood (2002)

Species	Family	No.	% of total sampled species
<i>Eviota queenslandica</i>	Gobiidae	154	33.6
<i>Istigobius goldmanni</i>	Gobiidae	47	10.3
<i>Pleurosicya muscarum</i>	Gobiidae	32	7.0
<i>Assessor macneilli</i>	Plesiopidae	19	4.2
<i>Eviota</i> sp. C	Gobiidae	15	3.3
<i>Enneapterygius tutuilae</i>	Tripterygiidae	14	3.1
<i>Trimma caesiura</i>	Gobiidae	13	2.8
<i>Priolepsis nuchifasciatus</i>	Gobiidae	13	2.8
<i>Asterropteryx semipunctatus</i>	Gobiidae	13	2.8
<i>Valenciennea muralis</i>	Gobiidae	11	2.4
<i>Ecsenius mandibularis</i>	Blenniidae	11	2.4
<i>Trimma striata</i>	Gobiidae	10	2.2
<i>Amblygobius rainfordi</i>	Gobiidae	10	2.2
<i>Amblygobius nocturnis</i>	Gobiidae	9	2.0
<i>Istigobius decoratus</i>	Gobiidae	7	1.5
<i>Bathygobius fuscus</i>	Gobiidae	6	1.3
		384	83.9

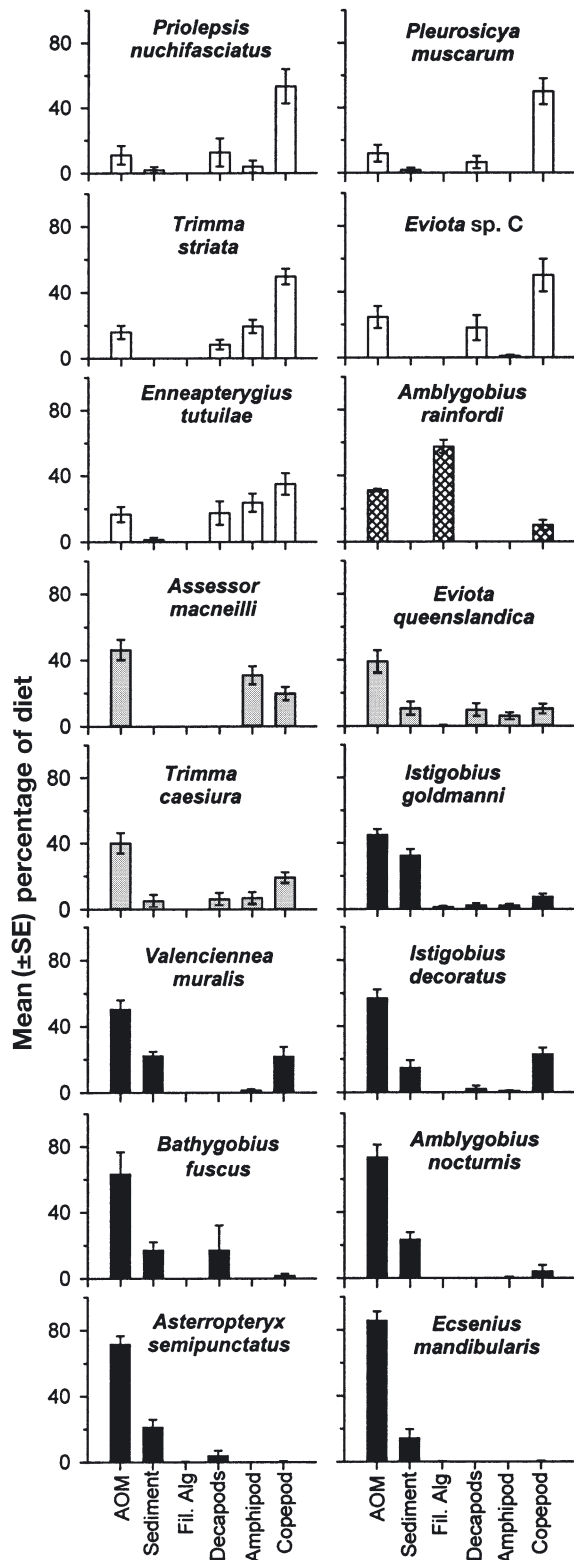


Fig. 1. Distribution of major dietary items in 16 cryptobenthic reef fish species (each species n = 20). White bars: carnivores; cross-hatched: herbivores; grey: generalist feeders; black: detritivores (classified as in Figs. 2 & 3). AOM: amorphous organic matter; Fil. Alg: filamentous algae

biplot (*T. caesiura*, *Eviota queenslandica* and *Assessor macneilli*) indicates that a broad range of dietary items are equally represented in the diets of these species. PC1 explains 57.3% of the variation in diet among species: negative scores correspond to those species that feed heavily on detrital matter (AOM) and sediment. Those with positive scores feed heavily on a carnivorous diet of copepods, amphipods and other crustaceans. PC2 explains 19.6% of the variation, positive scores reflecting a high proportion of filamentous algae in the diet. These results clearly identify AOM and copepods as the dominant dietary components in the cryptobenthic community.

Species-specific trophic patterns identify detritivory as the dominant trophic category among species (7 of the 16 species), followed closely by carnivory (5 of the 16 species: Fig. 1). When taking species abundances into consideration, however, carnivory marginally dominates the trophic structure of cryptobenthic fishes, although the pattern remains similar (Fig. 3), with 39.3% of the diets of all individuals analysed being in the detrital category and 45.0% in the carnivorous category. Subtracting the influence of the numerically dominant *Eviota queenslandica* (33.6% of all individuals collected) changes this trend little, with detrital items averaging 40.5% among individuals and carnivorous items 42.8%. Overall, both detritivory and carnivory are highly represented among both species and individuals within the cryptobenthic reef fish community. Herbivory, represented by just 1 species and

Table 2. Dietary components and their assigned trophic groups. Sediment was quantified and recorded, but not assigned to any trophic group because of its uncertain nutritional value. 'Other' includes echinoderms, fishes, fish scales, tunicates, nematodes, sponges, bryozoans and annelids other than polychaetes. Combined with unidentified material, this category equates to 1.6% of overall dietary assemblage

Dietary components	Assigned trophic group
Amorphous organic matter (AOM)	Detritivore
Sediment	Nil
Gastropods	Carnivore
Bivalves	Carnivore
Copepods	Carnivore
Amphipods	Carnivore
Isopods	Carnivore
Ostracods	Carnivore
Decapods	Carnivore
Polychaetes	Carnivore
Foraminiferans	Carnivore
Filamentous algae	Herbivore
Nonfilamentous algae	Herbivore
Dinoflagellates	Herbivore
Eggs	Carnivore
Diatoms	Herbivore
Other	Nil
Unidentified	Nil

2.4% of individuals, appears to be a minor trophic pathway within this community.

The relationship between diet, as expressed by the score on PC1, and total length, TL (Fig. 4a), and diet and gut-length ratio (gut length:TL) (Fig. 4b) revealed a distinctive and consistent relationship between diet and the 2 morphological parameters. Without exception, species with a carnivorous diet (*Pleurosicya muscarum*, *Enneapterygius tutuilae*, *Priolepsis nuchifasciatus*, *Eviota* sp. C and *Trimma striata*) were small (<28 mm TL) (Fig. 4a) and had small gut length ratios (GLRs) of less than 0.5 (Fig. 4b). At the other extreme, detrital feeders (*Istigobius goldmanni*, *Asterropteryx semipunctatus*, *Valenciennesa muralis*, *Ecsenius mandibularis*, *Amblygobius nocturnus*, *Bathygobius fuscus*, and *I. decoratus*) were larger, at least 38 mm TL (Fig. 4a), with GLRs of ≥ 1.0 (Fig. 4b). *E. mandibularis*, a detrital specialist (85.5% of diet) showed the most extreme GLR (2.9) of all the species examined. Exceptions to this general relationship existed in the TLs of 2 generalist feeders, *T. caesiura* and *Assessor macneilli* (Fig. 4a), and the GLR's of 2 detritivores, *V. muralis* and *I. goldmanni* (Fig. 4b), reflecting the generalist dietary habits of these 4 species (cf. Fig. 1). *Amblygobius rainfordi*, the only herbivore, had the longest TL of all species examined; however, its GLR was markedly smaller (<0.9) than that of the detritivores.

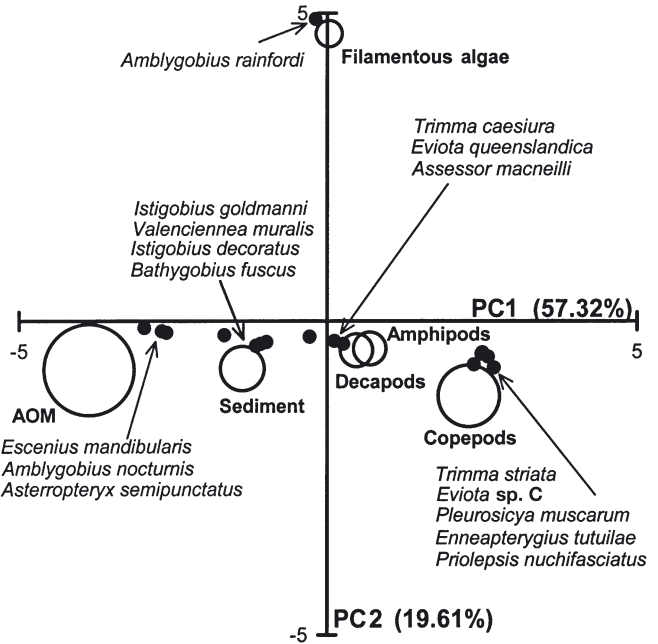


Fig. 2. Principal components biplot based on dietary composition of 16 cryptobenthic species selected for gut-content analysis; (●) position of taxa. Analysis is based on all 18 dietary categories (Table 2); (○, varying sizes) 6 dominant food-category vectors; circle diameters scaled (square-root transformation) to indicate proportional importance of various dietary categories among all individuals in the 16 species

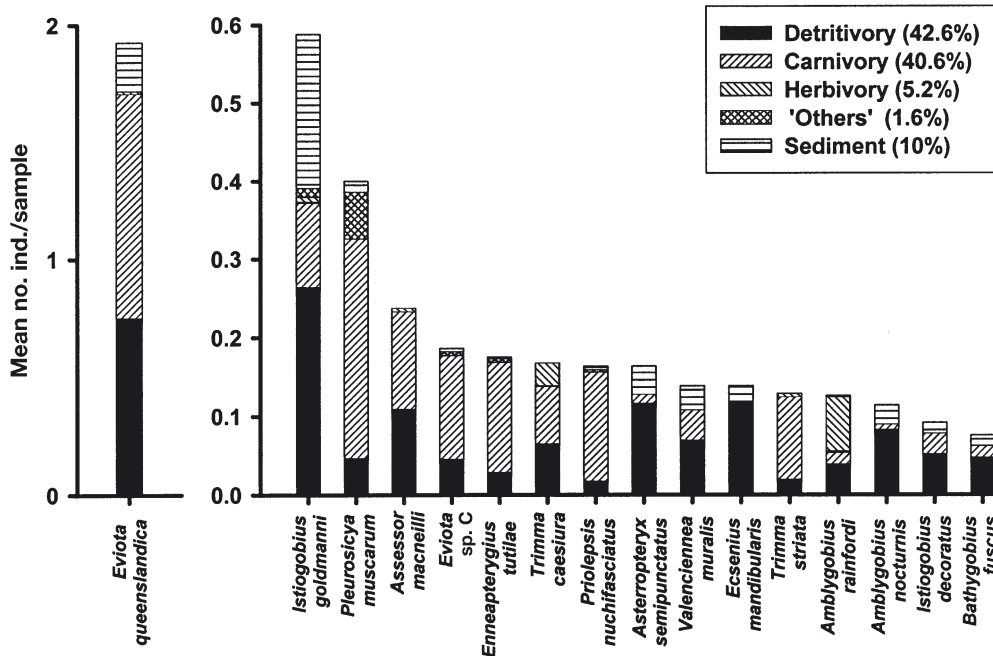


Fig. 3. Mean number of individuals caught per sample (n = 80 samples) and their trophic composition based on 18 different food categories (Table 2). 'Others' includes both unidentified material and a range of minor dietary items. Sediment included to indicate proportion of largely inorganic material ingested. Percentages in key indicate mean importance of each major trophic category among the 16 species. Note different scale for *Eviota queenslandica*, indicative of its dominant status within the cryptobenthic reef fish community

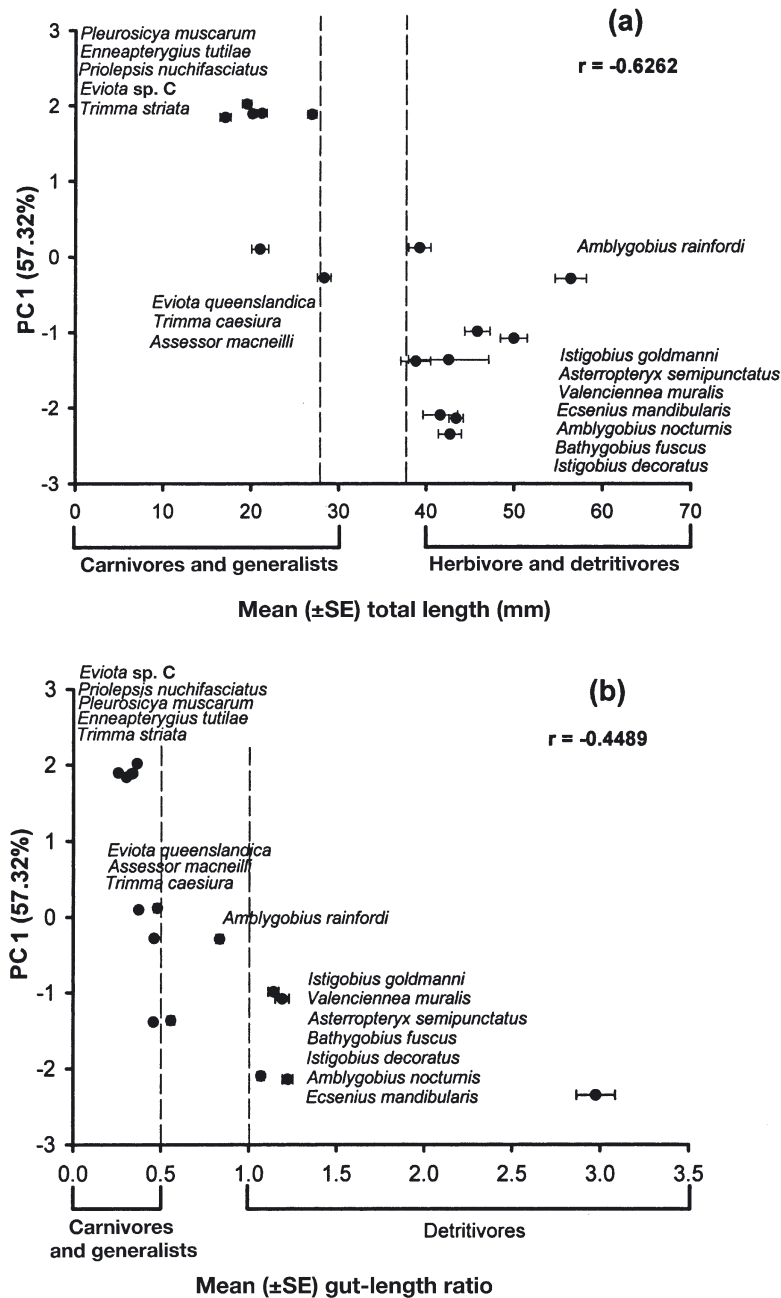


Fig 4. Diet, expressed by PC1 scores (Fig. 2) describing major source of variation in diets among species versus (a) mean (\pm SE) total length (mm), and (b) mean (\pm SE) gut length ratio (gut length:total length). Species names (top to bottom) correspond with data points from left to right

DISCUSSION

The diets of cryptobenthic species were surprisingly diverse, encompassing a full range of trophic food groups. Despite the presence of a wide range of dietary items in the intestines of most species, detritus followed by copepods overwhelmingly dominated the diets of the 16 species examined. The presence of

detritus as the dominant constituent is striking. The diets of small benthic fishes from a diverse range of ecosystems have long been thought to be restricted to micro-invertebrates (Targett 1981, Angermeier 1982, St. John et al. 1989). The role of detritus and detritivores has received relatively little attention, particularly in the marine environment. For this cryptobenthic reef fish community, however, the high detrital presence within and among species clearly identifies detritus as an important food source for small reef fishes.

Despite invertebrates offering the highest yield in terms of energy and nutritional requirements (Bowen et al. 1995, Choat & Clements 1998), detrital feeding offers some clear advantages that are likely to be of benefit to small reef fish species. The abundant and widespread distribution of detritus is chief amongst these (see Purcell & Bellwood 2001), offering a dependable food source that requires limited foraging, movement and handling, thereby reducing energy expenditure and minimising the risk of predation. Similarly, in comparison to an algal-based diet, detritus offers both increases in protein nutrient quality (Wilson & Bellwood 1997, Crossman et al. 2001) and relative ease of assimilation (D'Avanzo & Valiela 1990). In addition, smaller particle sizes (Choat & Clements 1998, Wilson 2000), lower incidences of refractory material (Bowen 1984), and a reduction in the concentration of anti-herbivore secondary metabolites (Hay & Fenical 1988, Wilson et al. 2003) are likely to further enhance the ingestion and assimilation rates of detritus and boost its nutritional value per unit weight.

Although this study clearly identifies the potential for detritivory to be a significant trophic mode for cryptobenthic reef fishes, a predominantly detritivorous diet may also present a number of challenges. For example, detritivores must overcome the difficulties associated with the large proportion of inorganic and indigestible material typically found in detrital aggregates (Purcell & Bellwood 2001). Consequently, strategies such as increased ingestion and throughput rates, selection for nutritionally rich detritus, or highly efficient nutrient assimilation rates may be a pre-requisite to the successful utilisation of detritus as a sole or principal dietary constituent. Although estimates of consumption rates for detritivorous fishes are limited (but see Klumpp & Polunin

1990), many herbivorous fish species are known to increase their consumption by prolonging feeding bouts or reverting to occasional carnivory to supplement any nutritional shortfalls (Mundahl & Wissing 1987, Horn 1989). In the case of the cryptobenthic community, diets based predominantly on detritus are invariably nutritionally enhanced with invertebrates to some degree.

In considering the diets of small fishes, a number of scale-related issues need to be taken into consideration. Small size may impose limitations on the range of dietary categories available to the cryptobenthic reef fish community. For example, the mechanical strength needed to tear algal thalli from the substratum may exclude most small fishes from herbivory. Decreased motility may also reduce their potential to exploit rarer or more patchily distributed food resources. Furthermore, because both growth and metabolic rates scale allometrically relative to decreasing body size (McNab 1983, Griffiths 1992), relative energy requirements and growth rates are much higher in smaller vertebrates (Miller 1996), and the capacity for fat reserves limited or non-existent (Webster 1974). Under these conditions, a close association with a predictable, ubiquitous and abundant food supply that is easy to procure would be a considerable advantage. Detritus appears to fill this role for the cryptobenthic reef fish community in our study. It is present not only within the epilithic algal matrix (*sensu* Wilson & Bellwood 1997) on hard substrata, but also on soft sediments. This permits a greater range of habitats to be exploited as foraging areas by species capable of utilising detritus as a significant food resource.

Previous studies suggest that nutrient quality and food selectivity are correlated and, as such, are likely to influence selectivity in the diet of particular organisms (Hughes 1980, Moriarty 1982, Bruggemann et al. 1994). From a theoretical point of view, detritivory appears to be a logical feeding mode for small reef fish species and is consistent with the results found in this study. In contrast, herbivory provides an altogether more demanding set of challenges for small reef fishes, including the difficulties involved with the digestion of intact cellular tissue, procurement of algae, and the presence of secondary metabolites. The only herbivore found among the cryptobenthic community examined in this study, *Amblygobius rainfordi*, with an average total length of 56 mm (smallest 45.4 mm TL) may define the lower size-limit for a herbivorous marine vertebrate and represents the smallest documented adult size for a herbivorous marine fish (*cf.* Horn 1989, Choat 1991).

We found a clear relationship between diet and 2 morphological attributes—total length and gut-length ratio. Of the species examined, total length was

longer and gut-length ratios considerably higher in detritivores than in either generalist feeders, carnivores, or the sole herbivore. Gut-length ratios, in particular, are strongly correlated with diet, with a lengthening of the gut being associated with an apparent shift from carnivory towards detritivory. This correlation conforms to a previously described relationship between diet and gut length in fishes (Horn 1989, Carrasson & Matallanas 1994). Ontogenetic shifts from a carnivorous to a herbivorous (Montgomery 1977, Bellwood 1988), or detritivorous (Zismann et al. 1975, Gerking 1994) diet, has long been associated with an increase in gut length ratios. Documented trends for fish species rank planktivores, carnivores, omnivores, and herbivores in order of increasing gut-length ratios (Elliott & Bellwood *in press*). In the cryptobenthic fish community examined, it appears that detritivores appear after herbivores in this continuum. The clear relationship between gut length and diet in cryptobenthic fishes strongly suggests that detritus is a staple component of the diet of cryptobenthic fishes, as the appropriate morphological modifications are present for its efficient digestion and assimilation.

The key to maximising nutrient uptake in smaller detritivorous reef fish species may rely on the simple morphology provided by the gut. The passage of digestibles through a long, yet comparatively narrow gut provides an increased opportunity for higher rates of assimilation. The maintenance of close contact between ingesta and intestinal walls throughout the entire alimentary tract may provide a means of maximising nutrient uptake. An alternate hypothesis explaining highly efficient assimilation rates within simple gut morphologies is provided by Tibbetts (1997) for the herbivorous species *Arrhamphus sclerolepis krefftii*. In this species, digestion, transportation and subsequent absorption of nutrients takes place across a mucous layer which sheathes the entire gut contents, bypassing normal surface area to volume restrictions. A similar mucous layer is seen in many of the cryptobenthic species. These simple digestive strategies may help explain the prevalence and success of detritivores in the cryptobenthic community, although further research in this area is certainly warranted.

It is now known that detritus is a major component in the diets of numerous reef fishes, including pomacentrids (Wilson & Bellwood 1997), blennies (Wilson 2000, Wilson et al. 2001a,b), acanthurids and scarids (Choat et al. 2002) and now, it appears, gobies. Many terrestrial and freshwater systems are based on detritus as the foundation for food webs, with detritivory constituting the most significant trophic pathway for the recycling of primary productivity (Bowen 1983, Baird & Ulanowicz 1993, Hairstone & Hairstone 1993). This raises the question as to whether detrital pathways

might be of comparable importance on coral reefs. Modelling studies suggest that 59 to 69% of primary productivity on coral reefs is processed through detrital-based food webs and that detritivory exceeds herbivory by an overwhelming factor of 10:1 in fringing reef areas (Arias-Gonzalez et al. 1997). The high incidence of detritivory and the skewed detritivore:herbivore ratio in the cryptobenthic reef fish community combined with the recent studies of larger taxa (Wilson & Bellwood 1997, Choat et al. 2002, Wilson et al. 2003) suggests that detritivory on reefs may approach these modelling predictions.

It must be noted that we define detritus based on the presence of at least 50% detritus (AOM) in the diet. The ability of these species to assimilate this material and the extent to which they rely on detritus as a dietary constituent remains to be determined. Nevertheless, it is highly likely that this detritus represents a significant source of nutrients for these species. It has been demonstrated that detritus on coral reefs is potentially as nutritious as algae (Wilson & Bellwood 1997, Purcell & Bellwood 2001, Wilson 2000, 2002, Crossman et al. 2001, Wilson et al. 2003), that several species preferentially select this detrital material (Purcell & Bellwood 1993, Wilson & Bellwood 1997, Wilson 2000, Wilson et al. 2003), and that in some species the detritus is assimilated and represents a major dietary constituent (Wilson et al. 2001a,b, Choat et al. 2002). In at least 1 cryptobenthic species, *Salarias patzneri*, detritus is the principal food resource (Wilson 2000, Wilson et al. 2001a,b). The data herein suggests that this may be the rule rather than the exception for many cryptobenthic reef fishes.

The evidence presented in the present study helps to clarify the role of cryptobenthic reef fish communities in reef trophodynamics and ecosystem function. Previously it was assumed that their role was restricted to the transfer of energy along a single carnivorous trophic pathway (as predators of small crustaceans and prey for piscivores). Our cryptobenthic reef fish community appears to be primarily composed of detritivores, although it also contains species with a range of other trophic modes. The numerical abundance of these fishes and their theorised role as prey for larger reef fishes implies that the cryptobenthic reef fish community is a major and important contributor to several trophic pathways, including the recycling of primary productivity through detrital pathways. Determination of the spatial organisation and demographic patterns of this community will further clarify the relative importance of their contribution and is the next logical step in quantifying the role of this community in reef ecosystem function. The question of which trophic reef fish group dominates the harvesting of primary production on coral reefs has been raised by several

authors (Wilson & Bellwood 1997, Choat & Clements 1998, Crossman et al. 2001, Purcell & Bellwood 2001, Choat et al. 2002, Wilson et al. 2003). Central to this question is the role of the cryptobenthic reef fish community. With their numerical abundance, rapid growth, high turnover rates, and the high incidence of detritus in their diets, cryptobenthic reef fishes lend further weight to the suggestion that detritivory is a major trophic pathway on coral reefs. In this system, cryptobenthic fishes offer an unseen and previously overlooked link in coral reef trophodynamics.

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