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Fine sediments suppress detritivory on coral reefs

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Abstract

Increasing sediment inputs are recognised as an important factor leading to coral reef degradation. However, the role of sediments in ecological processes is poorly understood. This study used paired-choice trials to quantify the effects of sediment grain size and chemical composition on feeding by the abundant detritivorous reef fish, *Ctenochaetus striatus*. The size of sediments from algal turfs were also compared to those ingested by reef-dwelling *C. striatus*. Algal turfs containing coarser sediments were preferred by *C. striatus*, while sediment composition (reefal carbonates vs. riverine silicates) had little effect. On the reef, *C. striatus* ingested finer sediments than those present in algal turfs. *C. striatus* appears to prefer algal turfs with coarser sediments as this facilitates ingestion of fine detrital particles, while finer sediments prevent selective feeding on detritus. These findings suggest that fine sediments from terrestrial runoff or dredging may be detrimental to feeding by detritivorous species.

Introduction

Sediments are increasingly associated with coral reef degradation around the world (Fabricius, 2005; Rogers, 1990; Wolanski et al., 2009). On the Great Barrier Reef (GBR), sediment inputs have increased substantially due to coastal land use practices and activities such as dredging (Brodie and Pearson, 2016; Hughes et al., 2015; McCulloch et al., 2003; Neil et al., 2002). This has led to concern about the potential ecological effects of sediments on coral reefs and their inhabitants. While we know that increased sediment inputs may cause coral reef degradation, many of the underlying mechanisms remain unclear. In this study we focus on the role of sediments in algal turfs, the epilithic algal matrix (EAM).

Increased benthic sediment loads within the EAM can suppress herbivory and detritivory on coral reefs (Bellwood and Fulton, 2008; Goatley and Bellwood, 2012; Gordon et al., 2016a). In doing so, sediments may drive a change in the state of the EAM: from palatable, short productive algal turfs (SPATs) to unpalatable, long sediment-laden algal turfs (LSATs). These changes may reduce the resilience of coral reefs (Goatley et al., 2016). However, the total sediment load is not the only consideration; sediment can vary in composition in terms of particle size, chemical composition and organic load. It is important to understand how these disparate chemical and physical properties of sediments modify their impacts on ecological processes.

The chemical composition of sediments differs markedly depending on their source. Sediments produced on reefs are predominantly composed of biogenic carbonates, while those from terrestrial sources are predominantly silicates (Browne et al., 2013; Gordon et al., 2016b; Scoffin, 1992). Terrestrially-derived siliceous sediments and reef-derived carbonates differ in their hardness, ability to adsorb nutrients and solubility, as well as numerous other properties (Gordon et al., 2016b; Nichols, 2009; Scoffin, 1992). As fishes invariably ingest some sediment when feeding on the EAM the varying chemical qualities of inorganic sediments may have markedly different effects on fish feeding.

In addition to the chemical composition of sediments, the basic physical properties of sediments also differ among locations. The grain size distributions of sediments within the EAM also vary

(Goatley et al., 2016; Gordon et al., 2016b; Purcell, 2000), with grain size distributions showing consistent trends among habitats and individual reefs (Gordon et al., 2016b; Purcell, 2000). Variation in EAM sediment grain size distributions is most likely driven by hydrodynamic conditions (Browne et al., 2013; Purcell, 2000; Scoffin, 1992) and local variation in patterns of sediment production and reworking by fishes (Bellwood, 1996; Hoey and Bellwood, 2008). However, fine sediments, in particular, may be transported in from outside sources, especially on inshore reefs (Goatley et al., 2016).

Compared to coarse sediments, which fall out of suspension relatively quickly, finer sediments are more likely to be resuspended, transported to, and deposited on, coral reefs (Fabricius et al., 2016, 2014; Goatley et al., 2016; Wolanski et al., 2008). When suspended in the water column these fine sediments have deleterious effects on coral reef organisms (Fabricius, 2005; Hess et al., 2015; Storlazzi et al., 2015; Wenger et al., 2014). However, fine sediments also have the potential to affect benthic processes, especially when bound within the EAM (Birrell et al., 2005; Clausing et al., 2014).

The grain size of sediments appears to be a key factor that suppresses the feeding of herbivorous/detritivorous fishes on inner-shelf reefs of the GBR (Gordon et al., 2016a). *Scarus rivulatus*, the most abundant herbivorous fish on these reefs, showed a clear preference for fine sediments over coarse, while the composition of sediment (reefal carbonates vs. riverine silicates) did not affect feeding behaviour (Gordon et al., 2016a). Inner-shelf reefs, however, are markedly different to mid- and outer-shelf reefs which have less exposure to terrigenous sediments (Brodie et al., 2012; Fabricius et al., 2016, 2014) and host different communities of herbivorous and detritivorous fishes (Russ, 1984). With the exception of S. *rivulatus*, the majority of herbivorous and detritivorous reef fishes are most abundant on mid- and outer-shelf reefs (Cheal et al., 2012; Johansson et al., 2013; Russ, 1984). The lined bristletooth, *Ctenochaetus striatus*, (Fig. 1a) clearly displays this pattern (Cheal et al., 2012; Russ, 1984), and plays a key functional role in detritivory and in EAM sediment dynamics on these mid- and outer-shelf reefs (Choat et al., 2002a; Goatley and Bellwood, 2010; Wilson et al., 2003). As *C. striatus* is likely to experience less exposure to terrestrial sediments and fluxes of fine sediments this important species may be far more sensitive to these sediment properties than *S. rivulatus*. This raises the question: does *C. striatus* avoid feeding on inner-shelf reefs because of the presence of fine and/or siliceous sediments?

While we understand how some properties of sediment affect herbivory/detritivory on inner-shelf reefs, we currently lack information on the possible mechanistic basis underlying sediment mediated suppression of feeding in herbivorous/detritivorous fishes that commonly occur on mid- and outer-shelf reefs. The aim of the present study, therefore, is to assess the role of sediment grain size and composition (reefal carbonates vs. riverine silicates) on the feeding behaviour of one of the most abundant detritivorous fish species on mid- and outer-shelf reefs, *C. striatus*.

Methods

Outline

The effects of sediment properties on *C. striatus* feeding were assessed using experimental feeding trials and examination of ingested sediments. Two experimental feeding choice trials were performed in aquaria at Lizard Island Research Station (14˚ 40′ S, 145˚ 27′ E), on the mid-shelf of the GBR. Specifically, we examined the effects of inorganic sediment grain size (fine vs. coarse) and composition (reefal carbonates vs. riverine silicates). Finally, to examine if *C. striatus* exhibit particle size selectivity when feeding on the reef, EAM sediment grain sizes from the preferred feeding habitat of *C. striatus* were compared with sediments from the gizzard-like stomach and intestines of *C. striatus* specimens that held feeding territories in the same location.

Feeding preference experiments

C. striatus were caught using barrier nets while on SCUBA at Lizard Island. The average total length of *C. striatus* used in feeding trials was 116.6 ± 6.9 mm (± SE). The fish were individually housed in 90 L containers at Lizard Island Research Station. Fish were acclimated for at least three days to ensure they were accustomed to experimental conditions and were feeding readily. During this acclimation period, fresh EAM-covered rocks and a video camera (GoPro with lights and sound turned off) were added daily to monitor feeding behaviour and to acclimatise fishes to experimental procedures. Trials were only commenced once fish were feeding repeatedly on EAM-covered rocks.

Sediment treatments were prepared following (Gordon et al., 2016a). Reefal sediments in the sediment composition trial and grain size trials were prepared from carbonate sediments from Lizard Island lagoon (14˚ 40′ S, 145˚ 27′ E). River sediments were collected from Ross River estuary, Townsville (19˚ 25′ S, 146˚ 50′ E), which delivers terrestrial sediment directly into the GBR lagoon. Sediments were bleached using hydrogen peroxide (H_2O_2), for more than two weeks to remove organic matter. During this period the sediments were stirred and fresh H_2O_2 was added on a regular basis. Sediment was then dried to a constant weight at 60˚C and sieved through a sieve stack (2000 - 63 µm). Four different sediment treatments were necessary for these experiments. With each treatment using a mass equivalent to 225 g m^{-2}. This sediment load approximates that found naturally within Lizard Island reef crest EAMs (Purcell 2000; Goatley and Bellwood 2012), where *C. striatus* predominantly feeds (Goatley and Bellwood 2010).

To create the different grain size treatments (fine vs. coarse sediments), individual sediment size fractions were weighed out in order to replicate the finest 50 % and the coarsest 50 %, by mass, of Lizard Island reef crest EAM sediment grain size distributions (ESM; Fig. S1a). All grain sizes under 2000 µm were considered sediment (sands, silts and clays; ISO 14688-1:200). The fine treatment comprised grain sizes from < 63 - 500 µm while the coarse treatments comprised grain sizes from (250 - 2000 µm [ESM; Fig. S1a]). Treatments for the sediment composition experiment were created by weighing out individual grain size fractions of river and reef sediments in order to simulate Lizard Island reef crest grain size distributions (ESM; Fig. S1b). Therefore, when comparing different sediment compositions (reefal carbonates vs. riverine silicates) frequency distribution of the sediments was identical, and thus size was factored out as a potential confounding factor.

Experimental process

Treatments were presented to *C. striatus* on natural feeding surfaces (circular 50 cm^2, flat, EAM-covered coral rocks, free of large macroalgae or encrusting organisms) following Gordon et al. (2016a). Prior to use, feeding rocks were cleaned in seawater to remove any sediment and detritus. Two rocks were then placed into each aquarium and a 500 mm length of 90 mm diameter polyvinyl chloride (PVC) pipe was placed over each rock. One treatment for each choice trial (e.g. fine) was then randomly assigned to either the left or the right rock and the companion treatment (e.g. coarse) was then assigned to the remaining rock. The wetted sediment treatments were then poured into the respective pipes and allowed to settle on the rock for more than 17 hours following Gordon et al. (2016a).

At the same time each day, a video camera (GoPro) was placed into each tank, the PVC pipes were removed and a PVC ring was placed over each rock to restrict feeding to the rock surface following Gordon et al. (2016a; Fig. 1b). Feeding activity was then recorded for a minimum of two hours before the camera and rocks were removed. Fishes were only exposed to a given trial (sediment composition or grain size) once. Only one choice trial was performed each day, with trials randomised between trial type and individual fish. There were thirteen replicates for the grain size and fourteen for the sediment composition choice trials.

The video footage was analysed to determine if *C. striatus* exhibited any preferences. In all cases data collection commenced one minute after the fish had taken a bite from the surface of both rocks, which usually took less than two minutes. Data collection then continued for 30 minutes following Gordon et al. (2016a). Three independent metrics were used to asses if the fish exhibited any feeding preferences. The first 'bite rate', assessed the feeding rate of the fishes, i.e. bites from the surface of the rock per minute. The second 'bites rejected', assessed the number of sediment spits (the forceful rejection of sediment from the mouth *sensu* Randall [1955]). To account for differences in total feeding rates on each rock, rejected bites were standardised to percent of total bites on each rock. The third, 'multiple bites', quantified the number of feeding bouts with a single bite compared to the number of feeding bouts with multiple consecutive bites. This assessed if, after taking a single bite, fish were discouraged from feeding on a particular treatment.

Statistical analysis

The differences in bite rates between treatments were analysed using generalised linear mixed-effects models (GLMMs) with a negative binomial error distribution and a log link, to account for non-normality and over-dispersion in the count data (following Brooker et al. [2014]). The percentage of bites rejected and the percentage of feeding bouts with multiple bites were both analysed using GLMMs with a binomial error distribution and a logit link. If over dispersion was detected an observation level random effect was fitted. In all models, treatment (river vs. reef or fine vs. coarse) was coded as a fixed factor, while each fish was treated as a random factor, to account for the paired nature of the choice trials and the subsequent lack of independence. Model fits were assessed using residual plots. All statistical analyses were performed in the statistical software R (R Core Team, 2014) using the *lme4* (Bates et al., 2014) and *nlme* (Pinheiro et al., 2014) packages.

Examination of ingested sediments

Sampling was conducted at Lizard Island reef crest between Palfrey and South Island (ESM; Fig. S2). Within this habitat the reef crest may be categorised into upper, middle and lower zones *sensu* Goatley and Bellwood (2010). In the present study all sampling was conducted from the upper reef crest, where *C. striatus* predominantly feeds (Goatley and Bellwood, 2010). At this site the upper reef crest was dominated by a planar, horizontal reef matrix in approximately 1 – 3 m of water.

To examine the grain size distributions of sediments in the EAM, 56 benthic particulate samples were collected by haphazardly placing a 20 cm^2 PVC ring on a suitable EAM-covered surface and then using an underwater vacuum sampler to remove the particulate material from the EAM (Purcell 1996; Kramer et al. 2012). Suitable EAM surfaces were free of sediment-retaining pits, macroalgae or encrusting organisms, and of low structural complexity (following Purcell [2000]). Only sediments from EAMs on horizontal surfaces ($< 15^\circ$ from horizontal) were sampled, as this is the preferred feeding microhabitat of *C. striatus* (Brandl et al., 2015; Choat and Bellwood, 1985).

After removing sediment from the EAM, samples were transferred into 9 L containers for three hours to allow particulate material > 10 µm to settle (Dyer, 1986). Water was then carefully decanted, leaving at least three hours between decants, until samples could be transferred into 120 ml sample jars. Samples were then decanted and rinsed with freshwater three times, to remove salts, allowing a standard (minimum three hours) settling period between rinses. To standardise samples, they were all wet sieved through a 2 mm stainless steel mesh. All inorganic particulate material under 2 mm was considered sediment (sands, silts and clays; ISO 14688-1:200). To remove organic matter samples were bleached using 30 % hydrogen peroxide, dried, dry sieved through a sieve stack (2000 to 63 µm) and the size fractions weighed, as above, to determine grain size distributions.

Five *C. striatus* were collected from the sampling site, the day after EAM sampling was completed. These specimens were collected using a barrier net while on SCUBA, immediately euthanised (clove oil), placed in an ice water slurry and frozen for later examination. The average total length of specimens was 188 ± 12.6 mm (± SE). The specimens were dissected and all material from the stomach and intestines was processed, separately, in the same manner as described for sediment samples.

Statistical analysis

Sediment grain size distributions were compared between environmental sediment samples and sediments from the stomach and intestines of *C. striatus* using a non-metric multidimensional scaling (nMDS) ordination. This nMDS was based on a non-normalised Euclidean resemblance matrix of standardised data. Subsequently homogeneity of dispersion, between the three sediment categories (environment, stomach and intestines), was assessed using permutational analysis of multivariate dispersions (PERMDISPs), based on deviations from the centroid with 9999 permutations. Pairwise tests were performed using the PERMDISP routine to examine within-factor differences. A one-way analysis of similarities (ANOSIM) based on 9999 permutations, with sediment categories as a factor, was then performed to test for any significant groupings. To examine within-factor differences pairwise tests were performed using the ANOSIM routine. All multivariate analyses were performed in PRIMER V6 PERMANOVA+.

Results

Feeding choice experiments

Sediment grain size

C. striatus exhibited a clear preference for feeding on EAMs containing coarse compared to fine sediments (GLMM; *t* = -2.05, $p < 0.05$; Fig. 2a; ESM; Table S3). The average number of bites on coarse sediments (3.6 ± 0.9 bites min^{-1} [± SE]) was nearly three times higher than on fine sediments (1.3 ± 0.5 bites min^{-1}). *C. striatus* also rejected a significantly higher percentage of bites from algal turfs containing fine compared to coarse sediments (GLMM; $z = 4.56$, $p < 0.0001$; Fig. 2c; ESM; Table S3), with a mean of 18.0 ± 6% of bites rejected from fine treatments and 5.5 ± 2.7% (± SE) for coarse sediments. The mean percentage of feeding bouts with multiple bites was also significantly higher on coarse (60.5 ± 6.5% [± SE]) compared to fine (28.2 ± 8.6%) sediments (GLMM; $z = -2.58$, $p < 0.01$; Fig. 2e; ESM; Table S3). All three metrics suggest that *C. striatus* prefers to feed on EAMs containing coarse sediments.

Sediment composition

C. striatus exhibited no clear preference between river and reef derived sediment, based on the number of bites taken (GLMM; $t = -0.98$, $p = 0.33$; Fig. 2b; ESM; Table S3) or the percentage of feeding bouts with multiple bites (GLMM; $z = -1.22$, $p = 0.221$; Fig. 2f; ESM; Table S3). The percentage of bites resulting in sediment spitting; however, was significantly different with more rejection of siliceous (river) sediment (15.5 ± 7.1% [± SE]) than carbonate (reefal) sediments (3.8 ± 1.5%) (GLMM; $z = 2.42$, $p < 0.05$; Fig. 2d; ESM; Table S3).

Examination of ingested sediments

Sediments from the stomach and intestines of *C. striatus* were generally finer than those from the environment (Fig. 3). Sediments with grain sizes < 250 µm were found in higher proportions in the digestive tract of *C. striatus* while coarser sediments (500 – 2000 µm) were more prevalent in the environment (ESM; Table S4). Although no groupings were statistically significantly different (ANOSIM; Global R = 0.14; no pairwise tests > 0.5), significant differences in the dispersion of sediment grain size distributions were found (PERMDISP: $F_{2,\,63} = 4.50$, $p_{[\text{perm}]} < 0.05$). The grain size distribution of sediments from the intestines of *C. striatus* was significantly more homogenous than those from the stomach ($t = 7.05$, $p_{[\text{perm}]} < 0.01$) as well as the environment ($t = 2.42$, $p_{[\text{perm}]} < 0.05$). There was no significant difference in dispersion between sediments from the stomach and environment ($t = 1.44$, $p_{[\text{perm}]} = 0.20$).

Discussion

C. striatus displayed a clear preference for feeding on EAMs containing coarse sediments but no clear preference for feeding on EAMs with different sediment compositions (silicates vs. carbonates). *C. striatus* are rarely found in areas with high loads of fine sediments (e.g. inner-shelf reefs), instead they are primarily found on mid- and outer-shelf reef crests where sediments are generally coarser (Cheal et al., 2012; Goatley and Bellwood, 2010; Purcell, 2000). It seems incongruous that the intestinal tract of *C. striatus* was found to contain predominantly finer sediments. Yet this is in accordance with previous studies (Choat et al., 2002a; Nelson and Wilkins, 1988). The presence of these finer sediments in the intestinal tract of *C. striatus* is consistent with the gut of *Ctenochaetus* species which have very thin, fragile intestinal walls, which may be damaged by coarse abrasive sediments (Choat, 1991; Jones, 1968). These findings suggest that *C. striatus* are: a) highly selective in their feeding activities; and b) that surface sediment preferences are not matched by sediment ingestion patterns. Indeed, the presence of coarse sediments within algal turfs may facilitate the selective ingestion of fine detrital matter by *C. striatus.*

Coarse sediments tend to be loosely aggregated and less tightly packed within the EAM compared to finer sediments, which can become tightly bound or blanket the EAM (Clausing et al. 2014; Fig. 4a, b). Consequently, while the mass of both sediments may be equal, they tend to interact with the EAM in different ways. Coarse sediments settle with more space between particles compared to finer sediments (Fig. 4a, b). The highly selective manner in which *C. striatus* feed, by using modified, elongate teeth and suction to remove detritus from algal turfs (Purcell and Bellwood, 1993), means that they may be able to feed more selectively on EAMs containing coarse sediments, i.e. maximising ingestion of fine organics (detritus) while minimising sediment ingestion (Fig. 4c). Such feeding behaviour is also likely to lead to the ingestion of the small amounts of fine sediments which associate closely with organic material (e.g. detritus) as they flocculate together (Purcell and Bellwood, 2001; Wilson et al., 2001). Essentially, as coarse sediments are less tightly bound within the EAM, *C. striatus* may be able to feed around them, while tightly bound finer sediments may limit selective feeding. Consequently, where finer sediments predominate fish would have to either ingest or reject all of these fine inorganic sediments when targeting detritus.

It must also be noted that the selective ingestion of small amounts of coarse sediment may be beneficial to *C. striatus*. *Ctenochaetus* first process ingested material in a muscular, gizzard-like stomach (Bellwood, 1996; Choat et al., 2002b) which, as suggested by Crossman et al. (2005), may require coarse sediments as a triturating agent. The selective ingestion of stones/gastroliths, to assist with the processing of material in muscular gizzards, has been extensively studied in birds and dinosaurs (Fritz et al., 2011; Louchart and Viriot, 2011). Therefore, the selective ingestion of small amounts of coarse sediment by *C. striatus* could also contribute to their preference for feeding on EAMs containing these sediments.

Recently, Gordon et al. (2016a) found that the particle size of sediment was a key factor which suppresses feeding by the parrotfish *S. rivulatus*. However, in marked contrast with the present study, initial phase *S. rivulatus* from the inner-shelf of the GBR, preferred to feed on EAMs containing fine, rather than coarse sediments (Gordon et al., 2016a). This contrast in results may be explained by differences in the functional morphologies of the two fishes. *S. rivulatus*, like *C. striatus*, consume detrital aggregates (Choat et al., 2002a), however, the two species exploit this resource in different ways. By using highly modified comb like teeth, *C. striatus* selectively removes fine particulates (detritus and sediments) from algal turfs (Bellwood et al., 2014; Purcell and Bellwood, 1993). In contrast, *S. rivulatus* uses fused teeth to scrape the substratum removing and ingesting the entire EAM, including algae, detritus and sediment (Bellwood and Choat, 1990), a less selective feeding mode. As *C. striatus* can feed selectively, EAMs with coarse sediments are favourable as the fish can actively avoid ingesting the large particles. However, as *S. rivulatus* must ingest all the sediment within the EAM, EAMs containing finer sediments may be preferable due to the less abrasive nature of fine sediments and/or the higher proportion of detrital material associated with finer sediments (Gordon et al., 2016a; Wilson et al., 2003).

Feeding ecology has important implications in our understanding of the ecosystem function of these fishes. Parrotfishes and *C. striatus* both play an important role in sediment dynamics on reefs (Bellwood, 1996; Goatley and Bellwood, 2010; Hoey and Bellwood, 2008; Nelson and Wilkins, 1988). In both taxa the presence of finer sediments in the intestinal tracts, when compared to the environment, has been taken as evidence of particle size reduction, through trituration in the pharyngeal mill of parrotfishes and the muscular stomach of *C. striatus* (Bellwood, 1996; Hoey and Bellwood, 2008; Nelson and Wilkins, 1988). While the process of particle size reduction is widely accepted, conclusive evidence of such processing remains remarkably sparse. Furthermore, selective feeding is also likely to contribute to the higher loads of fine sediments in the guts of these fishes. The fine, homogenous sediments within the intestines of *C. striatus* suggests that they are selectively feeding, sorting, and potentially reducing the size of ingested sediments. However, the relative contribution of selectivity versus particle size reduction cannot be clearly determined from the present study and requires further investigation.

Unexpectedly, *C. striatus* did not exhibit a clear response favouring reef carbonates over terrestrially-derived siliceous sediments. This may be expected in the parrotfish *S. rivulatus*, which lives on inner-shelf reefs that are often exposed to terrestrial sedimentation (Brodie and Pearson, 2016; Fabricius et al., 2016, 2014). However, as *C. striatus* were from the mid-shelf, where high loads of terrestrial sediments are relatively rare (Fabricius et al., 2014), it is unlikely that *C. striatus* was accustomed to feeding on fine silicates. As *C. striatus* rejected a significantly higher percentage of bites taken from EAMs containing river sediments, it appears that *C. striatus* can detect particular qualities of the siliceous river sediments (e.g. their taste or texture). However, regardless of the location fish come from, both the inshore parrotfish, *S. rivulatus*, and the mid- and outer-shelf reef surgeonfish, *C. striatus*, do not exhibit lower feeding rates on siliceous material than on similarly-sized carbonate material. It appears that *C. striatus* does not avoid inner-shelf reefs because of the presence of siliceous sediment *per se*.

It must be noted that our experiments only examined the composition of the inorganic sediment (reefal carboantes vs. riverine silicates). River sediments are often associated with other materials including pollutants and organic material (Fabricius and Wolanski, 2000; Fabricius, 2005; Kroon et al., 2012). These constituents of river sediments can have negative effects on coral reef organisms (Fabricius, 2005; Harrington et al., 2005), although their effects on fishes remains to be determined.

Future studies to examine the combined impacts of other constituents of river sediments are required if we are to understand the full effects of terrestrial sediment on reef ecosystems.

Sediments within algal turfs may be inconspicuous, but they have the potential to impact reef ecosystems and decrease their resilience. While the chemical composition of EAM sediments may not affect the feeding behaviour of herbivorous/detritivorous fishes, the size of particles in these sediments clearly does. However, it appears that different species of fish react to particle sizes in contrasting ways. For *C. striatus*, high loads of finer sediments are likely to prevent them from feeding selectively on detrital matter in the EAM, preventing the species from procuring nutritional resources. However, in small quantities, when associated with detritus, finer sediments are readily ingested. This multifaceted relationship between *C. striatus* and sediment size has shed new light on how finer sediments may reduce the resilience of coral reefs, by altering trophic interactions between a numerically abundant detritivorous fish and the EAM.

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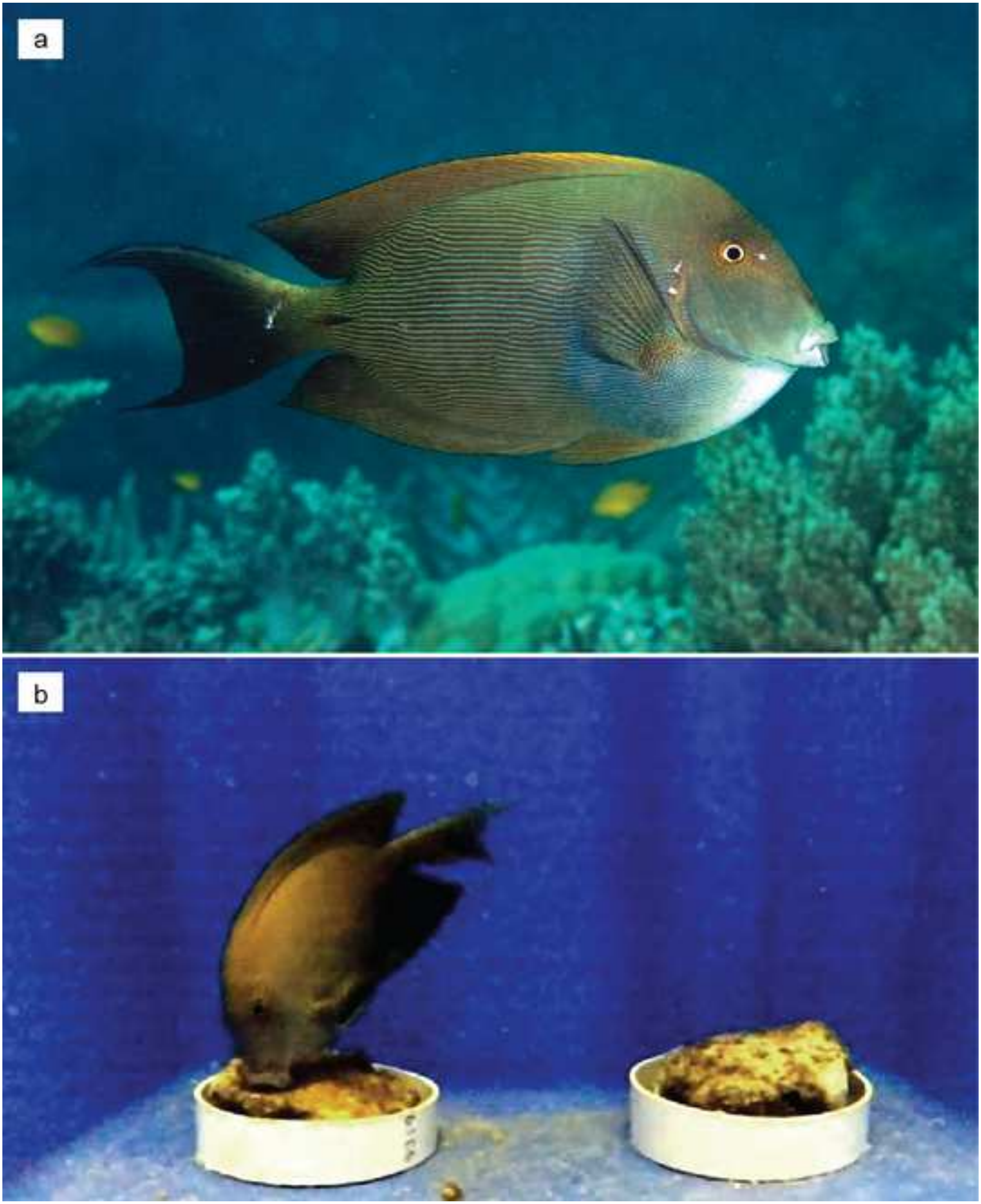
Figure Legends

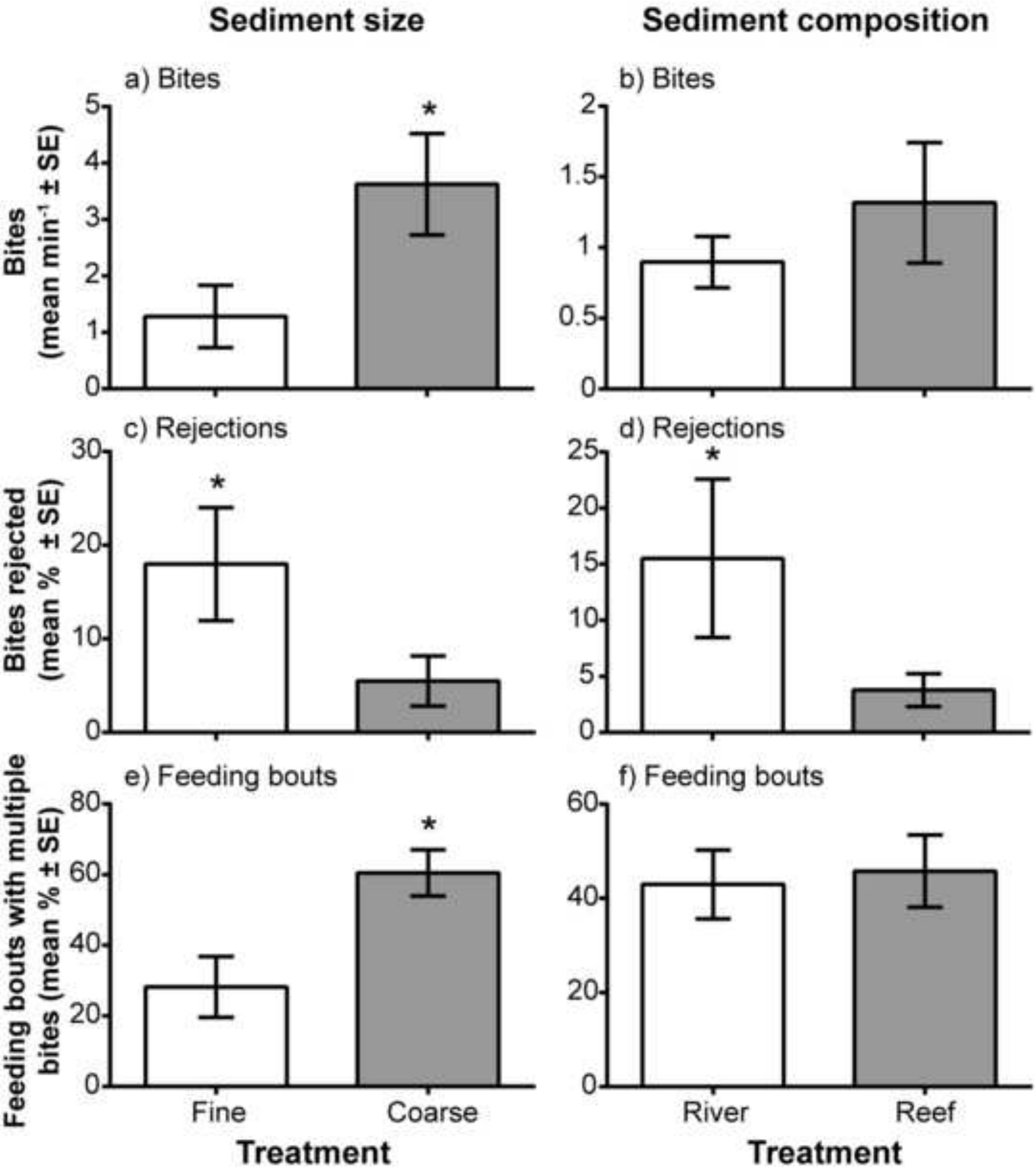
Fig. 1. Photographs of the lined bristletooth, *Ctenochaetus striatus*, a) on the reef (photograph JP Krajewski) and b) during experimental paired-choice feeding trials.

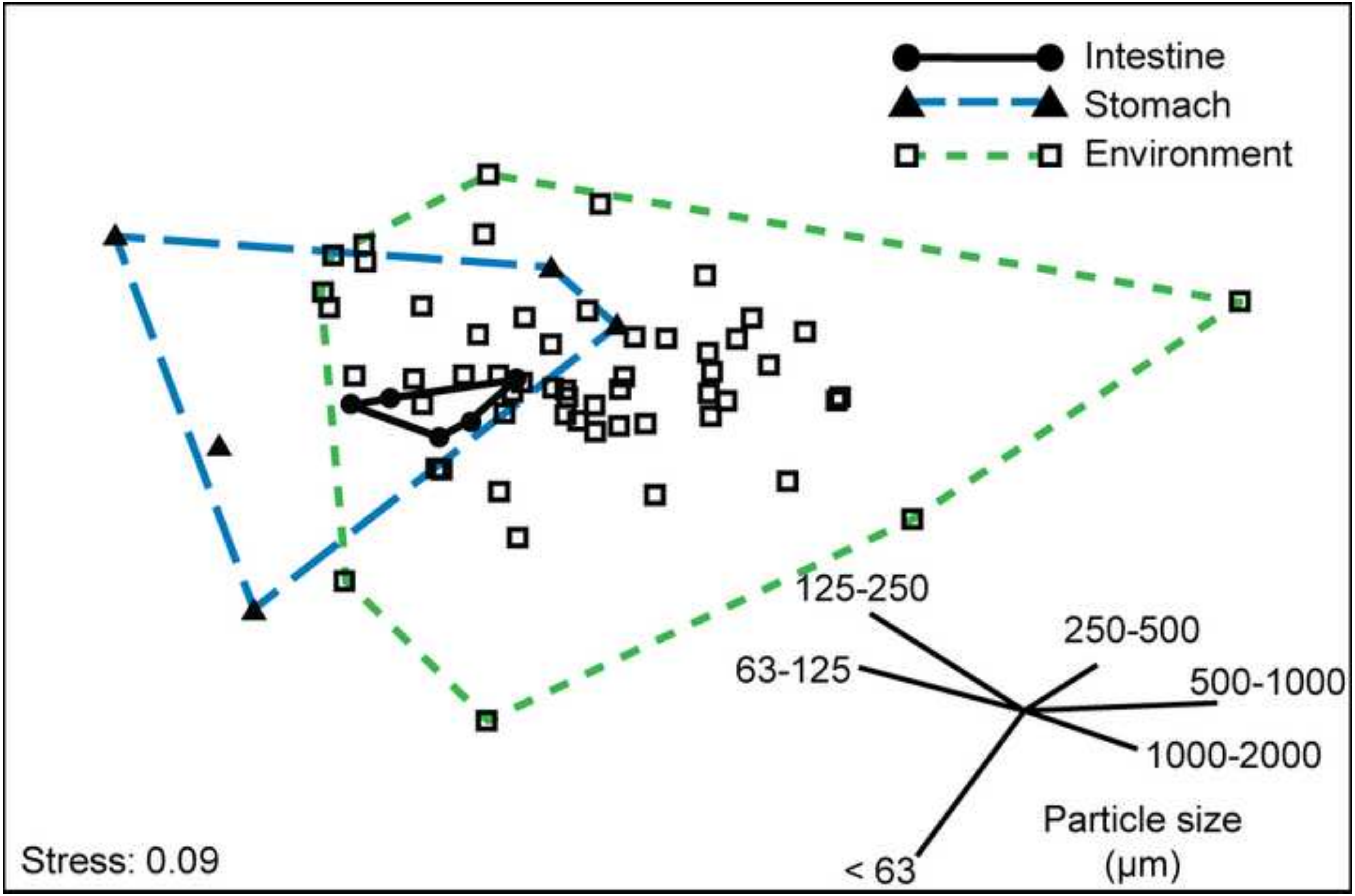
Fig. 2. The mean bite rate (± SE) (a, b), mean percentage of bites rejected (± SE) (c, d) and mean percentage of feeding bouts with multiple bites (± SE) (e, f) taken by *Ctenochaetus striatus* on inorganic sediments of different sizes (fine vs. coarse) and compositions (river vs. reef). * denotes significantly different (GLMM; α = 0.05).

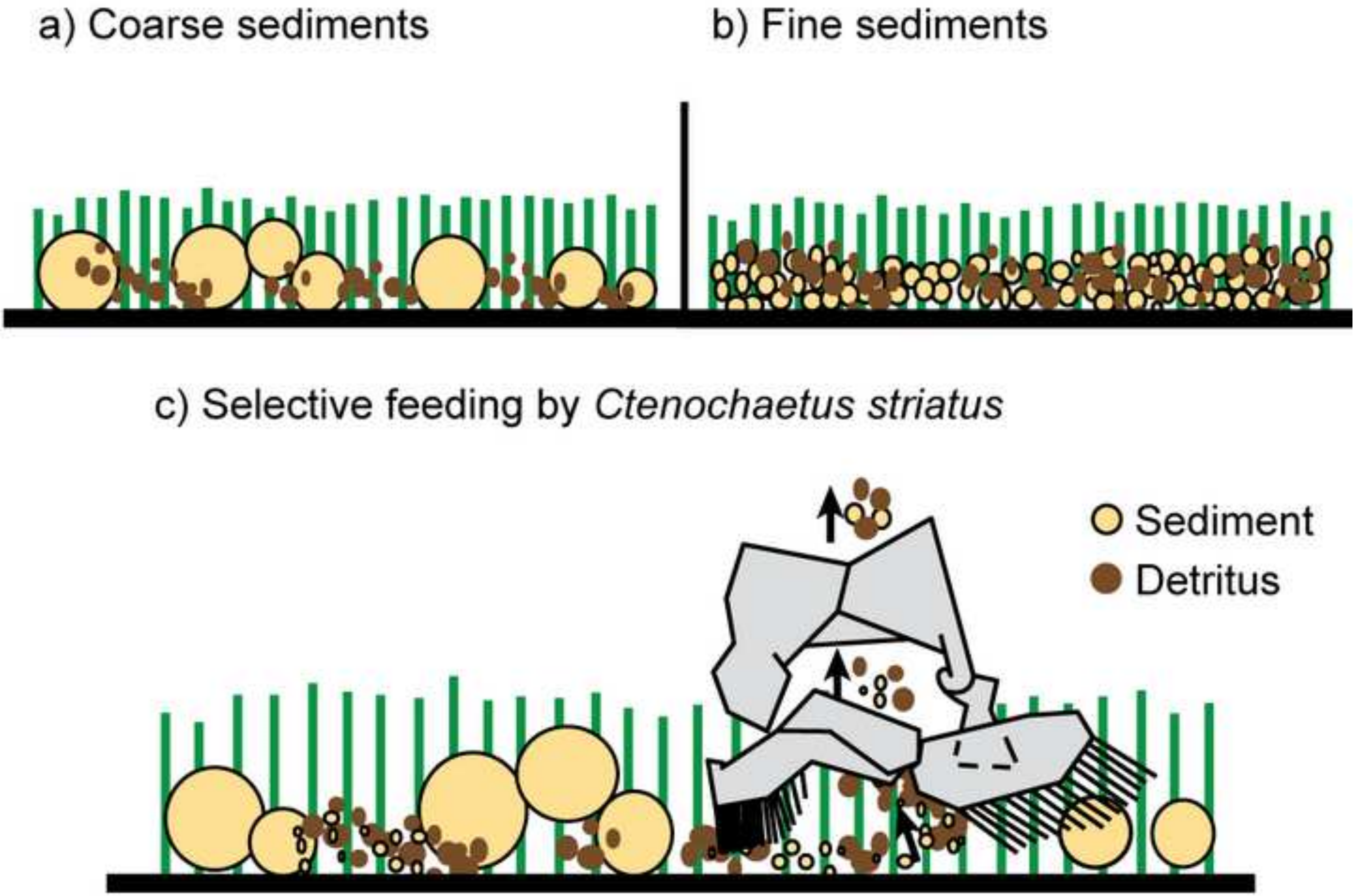
Fig. 3. Nonmetric multidimensional scaling plot of grain size distributions from EAM sediment samples on an upper reef crest at Lizard Island and sediments from the stomach and intestines of *Ctenochaetus striatus* specimens collected from the same location. Vectors represent grain sizes in µm and indicate the source of any differences among samples.

Fig. 4. A schematic figure demonstrating: a) how coarse sediments tend to be loosely bound within algal turfs, which may allow *Ctenochaetus striatus* to feed around them and minimise sediment ingestion. b) Fine sediments may become more tightly bound in algal turfs preventing *C. striatus* from feeding selectively around these sediments. c) *C. striatus* may avoid ingesting coarser sediments when selectively feeding on organic detritus, but in doing so ingests the small amounts of fine sediments which associate closely with this detrital matter on reefs. *C. striatus* jaws redrawn from Purcell and Bellwood (1993), premaxilla (upper jaw) to the left, dentary (lower jaw) to the right. N. B. jaws and algae/particles not to scale; in life the turf is approximately 3 mm high, particles < 2 mm and the jaw gape is 10 – 20 mm (high).


a
b


Sediment size
Sediment composition
a) Bites
b) Bites
Bites (mean min⁻¹ ± SE)
0
1
2
3
4
5
*
0
0.5
1
1.5
2
c) Rejections
d) Rejections
Bites rejected (mean % ± SE)
0
10
20
30
*
0
5
10
15
20
25
*
e) Feeding bouts
f) Feeding bouts
Feeding bouts with multiple bites (mean % ± SE)
0
20
40
60
80
*
0
20
40
60
Fine
Coarse
River
Reef
Treatment
Treatment


Intestine
Stomach
Environment
125-250
250-500
63-125
500-1000
1000-2000
Particle size
(µm)
< 63
Stress: 0.09

a) Coarse sediments
b) Fine sediments
c) Selective feeding by *Ctenochaetus striatus*
Sediment
Detritus