

Functional Ecology

Functional impact and trophic morphology of small, sand-sifting fishes on coral reefs

Brodnicke, OB^{*,1}, Hansen, CE^{*,1}, Huie, JM², Brandl, SJ³ & Worsaae, K¹

* Shared first authorship

1 Department of Biology, University of Copenhagen, Universitetsparken 4, 2100 Copenhagen Ø, Denmark

2 Department of Biological Sciences, The George Washington University, Washington, DC 20052, USA

3 Department of Marine Science, The University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, USA

Corresponding author

Ole Bjørn Brodnicke

Universitetsparken 4

2100 Copenhagen Ø

Denmark

Ole.brodnicke@gmail.com

Acknowledgements

Thanks to the Karel F. Liem Bio-Imaging Center at Friday Harbor Labs and Den Blå Planet (National Aquarium of Denmark) for the use of their facilities and equipment. A special thanks to Michael Sweet for counselling on the experimental design and Elisabeth Bjerking for assisting in the experiment execution. Additional thanks to Katherine Maslenikov for providing access to the UW Fish Collection specimen and to Peter R. Møller and Marcus Kragh for assisting with LM and SEM preparations. JMH was supported by a NSF Graduate Research Fellowship (DGE-1746914) and NSF oVert TCN (DBI-1701665).

Conflict of Interest

The authors declare that there are no conflict of interests.

Authors' contributions

All the authors meet all the criteria for authorship defined in the Functional Ecology author guidelines. OBB, CEH and KW conceived the experimental ideas and experimental designs, the later was also guided by SJB; OBB and CEH executed the feeding experiments supervised by KW; Morphological experiments were performed by CEH, JMH, KW; The data was statistically analysed by CEH, OBB SJB; CEH and OBB lead the writing of the manuscript and all authors critically contributed to result interpretation, manuscript drafts and approved the final version for publication.

Data availability statement

The micro computed tomography scans are uploaded and accessible on MorphoSource (<http://n2t.net/ark:/87602/m4/383379> & <http://n2t.net/ark:/87602/m4/433651>).

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/1365-2435.14087](https://doi.org/10.1111/1365-2435.14087)

Abstract

1. Oligotrophic tropical coral reefs are built on efficient internal energy and nutrient cycling, facilitated by tight trophic interactions. In the competition for available prey, some small fishes have evolved to feed on apparently barren sand patches that connect hard-substratum patches in many reef habitats.
2. One strategy for obtaining prey from a particulate matrix is to sift out small prey items from the sediment (often called ‘winnowing’). Yet, the trophic link between small winnowing consumers and their prey are poorly resolved, let alone the morphological specialisations that enable this foraging behaviour.
3. We used aquarium-based feeding experiments to quantify the impact of winnowing by two sand-dwelling goby species (*Valenciennea sexguttata* and *V. strigata*) on meiobenthos abundance and diversity, and examined their actual ingestion of meiobenthos using gut content analysis. To identify potential morphological structures involved in winnowing, we investigated the gobies’ feeding apparatus with electron microscopy (SEM) and micro-computed tomography (micro-CT).
4. After four days of sifting through the sand matrix, the two species significantly reduced meiobenthic prey abundance by $30.7\% \pm 9.2$ SE (*V. sexguttata*) and $46.1\% \pm 5.1$ SE (*V. strigata*), but had little impact on the meiobenthic diversity. The most abundant prey groups (copepods and annelids) experienced the greatest reduction in number, suggesting selection by size, shape and density of prey items. Furthermore, gut content analysis confirmed that winnowing gobies can efficiently separate meiobenthic prey from heavier inorganic particles (sand), likely facilitated by a specialised epibranchial

lobe, pharyngeal jaws and highly abundant papillose taste buds in the oropharyngeal cavity.

5. Our results provide important background on the trophic link between the meiobenthos and winnowing gobies on coral reefs. The revealed specialisations of the goby feeding apparatus facilitate sand-sifting foraging behaviour and access to microscopic prey and an otherwise inaccessible trophic niche. By having evolved a specialised strategy to obtain nutritious and highly abundant prey from seemingly barren sand, we suggest that winnowing gobies act as an important conduit for sand-derived energy to higher trophic levels.

Keywords: Aquaria, functional morphology, Gobiidae, meiofauna, micro-CT, sand eating, substrate sifting, trophic ecology

Introduction

Across all ecosystems, species are interlinked through interactions, either directly or indirectly via intermediate species, thus forming complex food webs through which energy and nutrient flow (Montoya et al. 2006; Thompson et al. 2012). On coral reefs the sources of energy and nutrients are scarce and heterogeneously distributed, with substantial amounts of productivity originating from pelagic or external subsidies (Morais and Bellwood 2019). Meanwhile, local biomass is frequently locked up and is only available through distinct trophic pathways (Wild et al. 2004; de Goeij et al. 2013; Brandl et al. 2019). One pathway appears to be via microscopic, benthic invertebrates which consume benthic autotrophic producers, detritus, and microbes, and are in turn consumed by small, bottom-dwelling ('cryptobenthic') fishes (Kramer et al. 2013b; Giere 2019). The latter group have recently been suggested to play an important role in coral reef energy transfer, as they are highly abundant and major contributors to consumed fish biomass by higher trophic levels on reefs (Ackerman and Bellwood 2000; Depczynski et al. 2007; Brandl et al. 2019). Cryptobenthic fishes are characterized by small adult body size (< 5cm), cryptic behaviour and/or appearance, and a strong association with the benthos (Depczynski and Bellwood 2003; Brandl et al. 2018). They generally feed on abundant microscopic food sources such as filamentous algae or invertebrates (Depczynski and Bellwood 2003; Hernaman et al. 2009; Brandl et al. 2018). Further, by falling prey to larger piscivores in large numbers (Ackerman and Bellwood 2000; Depczynski and Bellwood 2006; Goatley and Bellwood 2016; Brandl et al. 2019), they make these otherwise unavailable resources accessible to a wide range of coral reef consumers (Brandl et al. 2019). Morphological specialisations can enable; efficient and different prey utilisation in sympatric fish species (Fugi et al. 2001; Svanbäck and Eklöv 2003), fine partitioning of dietary niches among reef fishes, including small cryptobenthic species and may promote their efficient utilization of prey (Price et al. 2011; Brandl et al. 2020a; Huie et al. 2020).

Sediment patches are an abundant habitat on coral reefs. While they often seem barren, soft sediment hosts diverse communities of bacteria, microalgae and invertebrates that can act as nutritious prey for consumers if efficiently captured. The sediment interstices trap detritus and the grain surfaces provide substrate for microalgae primary production and productive bacterial communities (Moriarty et al. 1985; Johnstone et al. 1990). This further provides resources for invertebrates, including the often overlooked, but productive and diverse meiobenthos (e.g., including copepods, nematodes, annelids, etc.), defined as fauna able to pass through a 0.5 mm (or 1 mm) sieve and be retained at 44 μ m (Giere 2009). Diversity and abundance of meiobenthos is particularly high in medium coarse and calcareous subtidal sediments, such as coralline sand which can contain more than 1000 individuals per 10 cm² (John et al. 1989; Armenteros et al. 2009; Giere 2009; Semprucci et al. 2013; Sarmiento et al. 2017). Their high abundance, short generation times, high production rates and ability to cycle nutrients in the sediment make them a valuable infaunal prey community for larger organisms (Gerlach 1971; Coull 1990; Schratzberger and Ingels 2018; Ptatscheck et al. 2020). In coastal soft bottom habitats, up to 75% of meiobenthic productivity is translocated to higher trophic levels through predation on sediment by macropredators (Danovaro et al. 2007). Meiobenthos is a particularly important prey source for fish larvae and juvenile fishes (Gee 1989; Spieth et al. 2011; Weber et al. 2018; Ptatscheck et al. 2020) that display an ontogenetic diet shift to bigger prey items as adults (Macneill and Brandt 1990; McCormick 1998). However, some adult fishes, including many species of coral reef gobies, primarily rely on small invertebrates and meiobenthos as a food source even as adults (Hoese and Larson 1994; Henry and Jenkins 1995; Hernaman et al. 2009; Brandl et al. 2018, 2022). Feeding on meiobenthos in sand habitats stands to contribute to energy transfer through the food web from primary producers and detritus to secondary consumers and higher trophic levels (Gerlach 1971; Heip and Herman 1988; Schratzberger and Ingels 2018).

Several fish species have adopted specialized feeding strategies for consuming microscopic organisms living in sediments, exploiting a distinct foraging niche (Carle and Hastings 1982; John et al. 1989; Kramer et al. 2009). While some fish target discrete prey either on the substrate surface or by localising them by excavation, others will simply ingest bulk sediment (Sazima 1986; Krajewski et al. 2006; Tebbett et al. 2022). Winnowing (or sand-sifting) is a specific feeding behaviour in which fishes take mouthfuls of sediment and separate meiobenthos prey items from unpalatable particles in the oropharyngeal cavity. The food items are consumed, while the indigestible materials are expelled through the gill openings. This feeding strategy has evolved several times across bony fishes in both freshwater and marine environments (Drucker and Jensen 1991; Depczynski and Bellwood 2004; López-Fernández et al. 2014). This includes diverse taxa such as surfperch (*Embiotoca jacksoni*) (Drucker and Jensen 1991), the dirt-sifting devilfish (*Satanoperca daemon*) (Weller et al. 2017), the lesser electric ray (*Narcine brasiliensis*) (Dean and Motta 2004), twinstot gobies (*Signigobius biocellatus*) (Hoese and Allen 1977), darter gobies (*Gobionellus boleosoma*) (Carle and Hastings 1982; Gregg and Fleeger 1997), and many more. In Geophagini cichlids, winnowing behaviour is related to specific morphological features such as the presence of an anteroventral expansion of the first gill arch (epibranchial lobe) that is lined with chemosensory cells (López-Fernández et al. 2012, 2014; Weller et al. 2017). Winnowing behaviour is suggested to involve creating currents in the oropharyngeal cavity and the use of pharyngeal jaws to enable prey capture (Drucker and Jensen 1991; Weller et al. 2017). However, the morphological mechanisms that facilitate winnowing across a broader range of fishes and its quantitative impact on meiobenthos in marine sediment are poorly understood.

Many cryptobenthic reef fishes display winnowing behaviour, especially within the order Gobiiformes (Carle and Hastings 1982; Fitzhugh and Fleeger 1985; Hoese and Larson 1994; Brandl et al. 2022). The goby family (Gobiidae) is highly diverse and makes up a

proportionally large fraction of the highly abundant cryptobenthic reef fish on coral reefs (Brandl et al. 2018). In *Valenciennea*, a genus inhabiting sandy or rubble substrates across the Indo-Pacific, winnowing is the main feeding behaviour (Hoese and Allen 1977; Hoese and Larson 1994; Reavis 1997; Froese and Pauly 2021). By exploiting the sandy substrate feeding trophic niche and having high predation-derived mortality rates (Reavis 1997), these fishes potentially link meiobenthic prey to higher trophic levels. Yet, to date, little is known about the foraging behaviour, functional impact, and morphological adaptations that underpin meiobenthic feeding in *Valenciennea*.

The present study aims to uncover the trophic impact of winnowing *Valenciennea* gobies on meiobenthic prey communities and to identify which morphological structures may facilitate their specialised feeding behaviour. We conducted aquarium-based experiments to investigate the impact of the sixspot goby, *Valenciennea sexguttata* (Valenciennes 1837) and the blue band goby, *Valenciennea strigata* (Broussonet 1782) on meiobenthos abundance and diversity, and examined the anatomical structures potentially involved in winnowing. Specifically, we 1) investigated the effect of foraging by the two species on the abundance and diversity of the meiobenthos over time 2) conducted gut content analyses to record prey size and diversity for each goby species to confirm meiobenthos ingestion and prey selectivity, and 3) investigated the feeding apparatus of *V. sexguttata* and *V. strigata* to identify potential morphological adaptations in the two species. In doing so, our study sheds light on the predator-prey dynamics unfolding in coral reef sand habitats, while elucidating some of the organismal adaptations that permit sand-dwelling predators to exploit an abundant but difficult to access food source to contribute to the tight network of trophic linkages on coral reefs.

Materials and methods

Materials

Wild caught specimens of *Valenciennea sexguttata* (n=4) and *V. strigata* (n=4) were obtained from the Danish National Aquarium (Den Blå Planet). The animals were maintained on artificially supplemented coral sediment, in 25 °C, 31 psu seawater with a photoperiod of 10 hours of light and 14 hours of darkness. Total length ranged between 65-86 mm for *V. sexguttata* and 68-91 mm for *V. strigata*. The meiobenthos present in the aquarium coral sediment was assumed to represent a worldwide mix of tropical species brought into the aquarium facilities over time from imported live coral, rock, and megafauna. Prior to the feeding experiments, larger macrofauna (>2 mm) were removed from sediment to eliminate predation by macrofauna on meiobenthos. The granulometry of the aquarium sediment is summarized in Table S1 in supporting information.

Feeding experiments

Experiments measuring the impact of winnowing on meiobenthos were conducted in a separate testing aquarium (218 × 80 × 30 cm in length, width, and height), filled with a 10 cm layer of aquarium sediments containing the resident meiobenthos. We separated the tank into 12 identical arenas (20 x 55 cm) and randomly placed the eight gobies (four of each species) into eight of the arenas (one fish per arena), while leaving four arenas unpopulated as controls. We allowed the gobies to winnow the sediment in their respective arenas for six days. To promote winnowing behaviour, the gobies were starved for two days prior to being placed in the testing tank and were not fed during the experiment. Physical barriers lined each arena to prevent movement of fish and mobile meiobenthos in both water and sand. We also provided PVC pipes as shelter for the gobies. The scope of this experiment did not require ethical approval.

We sampled the meiobenthos community in each of the twelve arenas on day zero, prior to placing the gobies in their respective arenas, and again on day two, four, and six. At each time point, three composite samples covering ~17.2 cm² (composed of three smaller samples

taken to 2 cm depth, Ø: 2.8 cm) were haphazardly collected from each arena and pooled, to account for potential patchiness on meiobenthos. Thus, 36 composite samples were collected on each sampling day, which were processed in the laboratory within 36 hours of collection. The used 2 cm sample depth was based on our preliminary experiment to determine the feeding depth of the two goby species (Fig. S1).

To separate the meiobenthos from the sediment, samples were anesthetized with an aqueous isotonic $MgCl_2$ solution (mixed 1:1 with seawater) for 15 minutes. Afterwards, samples were swirled and suspended organisms were carefully decanted thrice through a cone-shaped, 63 μm cone shaped mesh. The fauna retained in the mesh was suspended in 40 ml of isotonic $MgCl_2$ from which a 10 ml subsample of the meiobenthos (25%) were revitalized in filtered seawater for improved identification and counting using a dissecting microscope. Annelids were separated into permanent meiobenthic Annelida (annelids living their entire life cycle as meiobenthos, herein listed as “Annelida”) and temporary meiobenthic Annelida (= juvenile macrobenthic annelids), which were only found in insignificant numbers (<3%, Table S2). Individuals of Anthozoa and Sipuncula were all classified as temporary meiobenthic groups. Copepods were counted after adding EtOH to pacify them; free-swimming nauplius larvae were ignored. No adult macrofauna were observed in any of the samples.

After conducting the feeding experiments, all gobies were euthanized with an overdose of benzocainum and fixed in 4% formalin. Prior to fixation, we dissected and removed the gastrointestinal tracts of each specimen for a qualitative assessment of the contents. We examined whether *V. sexguttata* and *V. strigata* consumed meiobenthos, and identified the prey items in a semi-quantitative way. We established a prey size range by measuring the smallest and largest prey item from each taxon using ImageJ 2 on images of prey (Rueden et al. 2017).

Statistical analyses

Statistical analyses and data visualisations were performed in R version 4.0.4 (R Core Team 2021). Visualisations were created in *ggplot2* (Wickham 2016) using the *fishualize* color palettes (Schiettekatte et al. 2021). Changes in total meiobenthic abundance (number of individuals per 10 cm²) were explored in relation to the three treatments (*V. sexguttata*, *V. strigata*, and the controls with no fish) over time. Specifically, we performed a generalised linear mixed model (GLMM) with a negative binomial error distribution (Zuur 2009; Harrison et al. 2018) using the “glmer.nb” function (Bates et al. 2015). Treatment and time were included as fixed effects (including their interaction effect), while arena number was included as a random effect to account for repeated sampling over time. Model assumptions were tested with the *DHARMA* package (Hartig 2021). Predictions of the fixed effects on meiobenthic abundance were computed with the “ggpredict” function (Lüdtke 2018) and a Tukey multiple comparison post-hoc test was applied to establish differences in the fixed effects using the “lsmeans” function (Lenth 2016). The abundance changes of the three dominant meiobenthic taxa (copepods, ostracods, and annelids) were also individually assessed using a negative binomial GLMM as described above. The diversity of the meiobenthic community was explored using Shannon’s diversity index (H), which accounts for both species richness and relative abundance. Changes in (H) were using the “lmer” function, since the data were approximately normally distributed (Bates et al. 2015). Principle Coordinate Analyses (PCoA) were performed to visualise the differences in meiobenthic community composition across treatments and sampling days. The ordinations were performed using a Bray-Curtis dissimilarity index applied to the species abundance matrix, calculated with the “vegdist” function in the *vegan* package. The PCoA was computed using the “wcmdscale” function with lingoes correction to avoid negative eigenvalues which distort the ordination (Oksanen et al. 2018). Taxa most likely responsible for observed differences between treatments were analysed by examining Pearson correlations ($|r| > 0.5$) of taxa abundance with canonical axes using the

“envfit” function (Oksanen et al. 2018). Finally, to assess the change in community composition, a multivariate permutational analysis of variance (PERMANOVA) was performed on the dissimilarity matrix with 9,999 permutations using the “adonis” function (Oksanen et al. 2018) and significant results were further investigated with pairwise PERMANOVA using “pairwise.adonis” function (Martinez Arbizu 2017). The data is available on Zenodo repository (Brodnicke et al. 2022).

Morphology

To investigate potential morphological adaptations associated with winnowing behaviour in gobies, we examined the feeding apparatus of the four *V. sexguttata* and four *V. strigata* using light microscopy. Based on the observed morphological similarity, the gill arches and pharyngeal jaws of one representative specimen of both *V. sexguttata* (78 mm TL) and *V. strigata* (91 mm TL) were dissected out and prepped for scanning electron microscopy (SEM). Each sample was post-fixed in 2% osmium tetroxide for 2 hours, rinsed with distilled water, dehydrated through a series of EtOH changes, and then transferred to 100% acetone. Samples were critical point dried (Tousimis Autosamdri-815) and sputter coated with platinum-palladium (JEOL-JFC-2300HR). The gill arches and pharyngeal jaws were examined and photographed with a JEOL-JSM-6335F scanning electron microscope.

We also examined the gross morphology of the oropharyngeal cavity in *V. strigata* using micro-computed tomography (CT) scanning combined with iodine-based contrast-staining to visualize soft tissue (Gignac et al. 2016). Two specimens of *V. strigata* (45 and 101 mm SL) on loan from the University of Washington Fish Collection (UWFC 007439) were soaked in a 3% Lugol’s iodine solution (I₂KI) for one (45 mm specimen) or two weeks (101 mm specimen) prior to scanning. The specimen was scanned with a Bruker Skyscan 1173. The scan was conducted with a voxel size of 6 µm (45 mm specimen) and 13.8 µm (101 mm specimen),

voltage of 65 kV, amperage of 123 μ A, and an exposure time of 1.15 s. We used 3D Slicer with the SlicerMorph extension to visualize and segment the scan (Kikinis et al. 2014; Rolfe et al. 2021).

Results

A total of 3,467 meiobenthic individuals from 14 taxa, spanning 10 phyla, were identified throughout the feeding trials. The three most dominant taxa of the meiobenthic community (copepods, ostracods and annelids) accounted for more than 75 % of all meiobenthic individuals (Table S2).

In the presence of *V. sexguttata* or *V. strigata*, total meiobenthic abundance decreased over time, while increasing in the control treatments (Fig. 1a). The majority of the variability in the model was explained by the two fixed effects and their interaction (marginal $R^2 = 54.2$ %). The GLMM model predictions indicate that the gobies significantly reduced the meiobenthic abundance, with a decrease of $30.7 \% \pm 9.2$ SE and $46.1 \% \pm 5.1$ SE (Tukey's HSD: $P < 0.01$) for *V. sexguttata* and *V. strigata* respectively, after four days. While *V. strigata* reduced meiobenthic abundance more than *V. sexguttata* (Fig. 1a), no statistically significant difference between the two species was detected on any day (Tukey's HSD: $P > 0.05$). For both species, the meiobenthic abundances in their arenas plateaued between days four and six. In the absence of winnowing gobies, the meiobenthic abundance increased by $36.7 \% \pm 13.0$ SE after six days, though this change was not significant (Tukey's HSD: $P = 0.113$). Yet, on day four and six, the meiobenthic abundance in the two goby treatments was significantly lower than in the control (Tukey's HSD: $P < 0.0001$).

Abundance changes for the three most abundant taxa in the sediment (copepods, ostracods, and annelids) showed distinct trends. Copepods were significantly reduced in the first four days of the goby treatments compared to the control (Tukey's HSD: $P < 0.05$). For

annelids, only *V. strigata* treatments showed significant differences compared to the control (Tukey's HSD: $P < 0.0001$). In contrast, ostracod abundance did not decrease in the presence of gobies (Tukey's HSD: $P > 0.05$).

The Shannon diversity index (H) of the meiobenthic community remained relatively constant across time and treatments (Fig. 1b). The two goby species reduced the meiobenthic diversity slightly over time compared to the control, but no significant differences were detected (Tukey's HSD: $P > 0.05$). Only a small fraction of the variability in the model was explained by the fixed effects and their interaction (marginal $R^2 = 6.4\%$) and the random effects (conditional $R^2 = 10.2\%$). However, the PERMANOVA test performed on the dissimilarity matrix (including both species and numbers of individuals) showed that the meiobenthic community composition differed significantly between sampling days ($P < 0.001$), treatments ($P < 0.001$) and time \times treatment interactions ($P < 0.01$). The pairwise PERMANOVA test showed that the controls differed significantly from the goby treatments ($P < 0.001$), with a significant difference on day four between both gobies and the controls ($P < 0.05$), and with no significant difference between the *V. sexguttata* and *V. strigata* treatments ($P > 0.05$). These effects are also reflected in the PCoA ordination (Fig. 2), where the differences in meiobenthic community were mainly driven by abundance changes of copepods, annelids, ostracods, and to lesser degree nematodes (Fig. 2b-d).

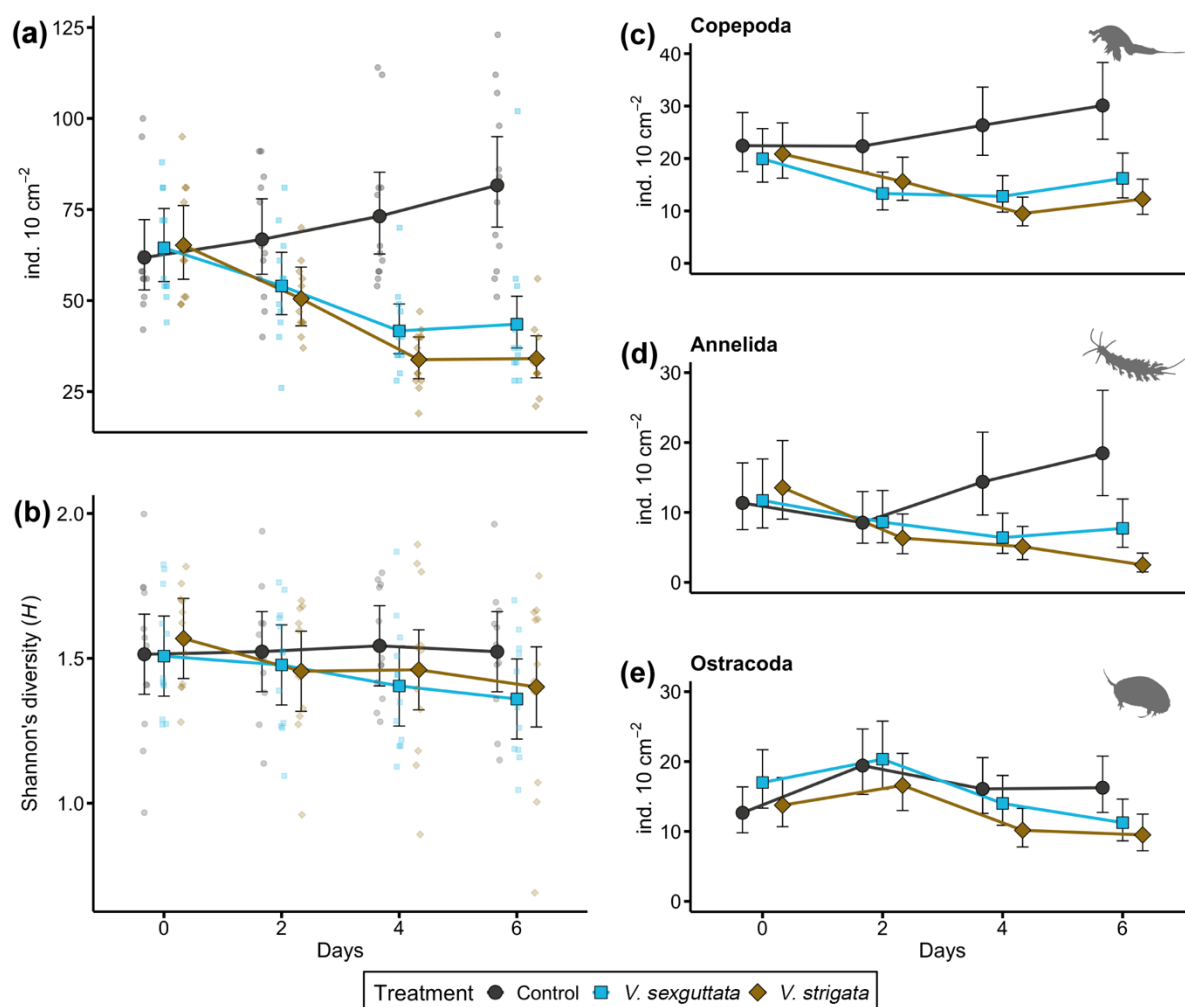


Figure 1. The impact of two winnowing goby species (*V. sexguttata* and *V. strigata*) on total meiobenthos abundance and diversity over six days. Closed symbols show mean predicted marginal effects of time and treatment on (a) abundance (ind. 10 cm⁻²) and (b) diversity (*H*) of the meiobenthic community. Small, transparent symbols represent raw data. The reduction in total meiobenthos is mainly driven by a decrease in two of the three most abundant taxa observed, namely Copepoda (c) and Annelida (d). The goby predators did not visibly affect the abundance of the second most abundant taxa, Ostracoda (e). Note the different y-axis scales for the three taxa. Error bars show 95% confidence intervals.

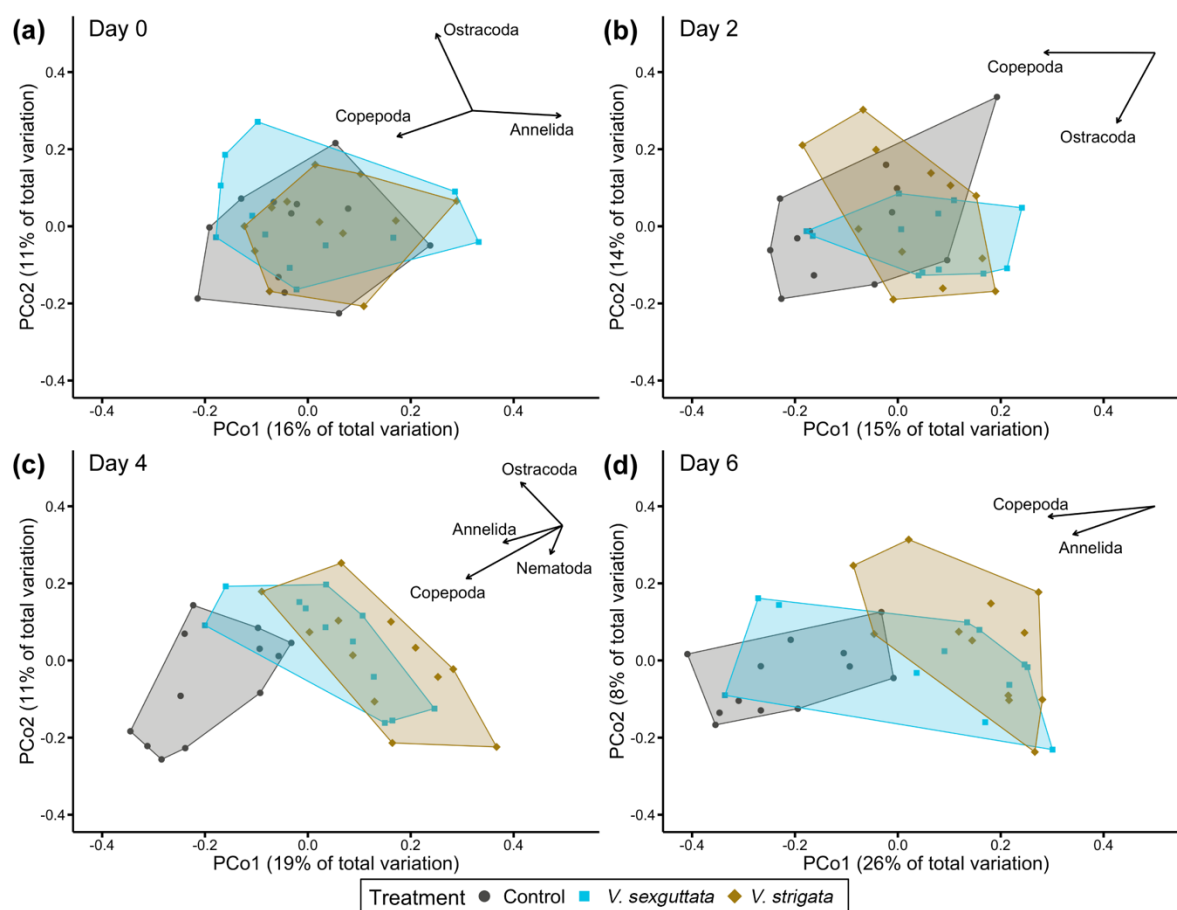


Figure 2. Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity matrix of the meiobenthic community sampled in the three treatments; control (grey), *V. sexguttata* (blue), and *V. strigata* (yellow) across sampling days; (a) day 0, (b) day 2, (c) day 4, and (d) day 6. Treatments are delineated by convex hull polygons. The most influential meiobenthic taxa are represented as vectors ($|r| > 0.5$).

Gut content

The gut contents of *V. sexguttata* ($n = 4$) and *V. strigata* ($n = 4$) confirmed that the gobies were consuming meiobenthos from the sediment (Fig. 3). While not a quantitative analysis, the most common prey in the guts were harpacticoid copepods, ostracods, and halacarids. Smaller sand grains, foraminifera, and filamentous algae were also present in the gut, but none of the otherwise abundant soft-bodied organisms (e.g., Annelida, Platyhelminthes) were detected, likely due to them being rapidly digested and lacking thick identifiable cuticles. *V. sexguttata* ingested food items in the size range of 53-10,400 μm and *V. strigata* in the range of 100-

11,780 μm . The longest prey items were nematodes (9.30-11.78 mm), while copepods were the most abundant prey and ranged from 173 to 1,178 μm in length. Many of the dietary items fell into a similar size range that also includes smaller sand grains (67-777 μm) (Fig. 3).

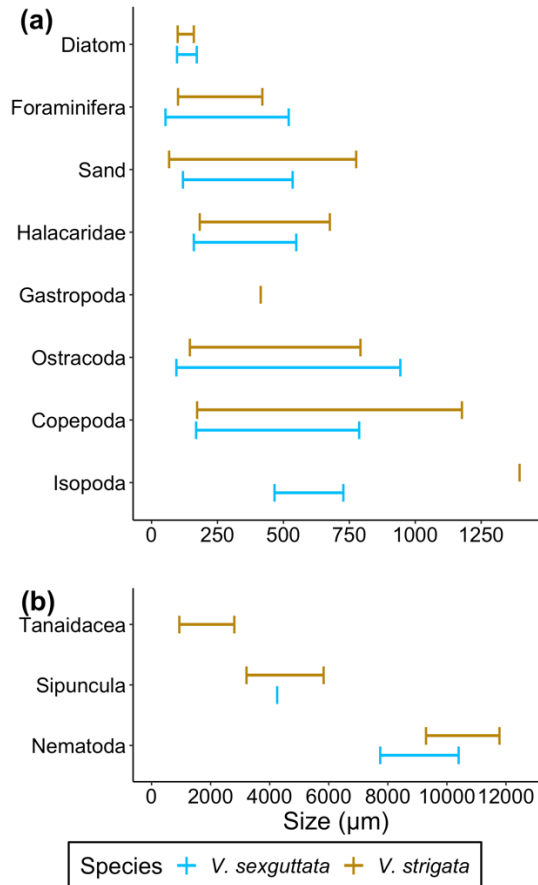


Figure 3. Gastrointestinal content and size ranges of ingested prey and particles of *V. sexguttata* (blue) (n=4) and *V. strigata* (yellow) (n=4). (a) gut items ranges: 50-1,400 μm , (b) larger gut items. Single vertical lines represent prey items occurring once. Note different scales on y-axes.

Morphology

In general, *V. sexguttata* and *V. strigata* shared similar feeding morphologies (Figs. 4; S3); therefore *V. strigata* will be described as the representative example. The micro-CT scans of both specimens revealed the position of the main morphological structures (gill arches, epibranchial lobe, pharyngeal jaws) in the oropharyngeal cavity relative to each other (Figs. 4d; S2a, b). The upper arm of the first gill arch has a notably developed anteroventral laminar

Accepted Article

expansion also called the epibranchial lobe (ebl, Figs. 4a; S3a). The medial side of the first gill arch and in particular the epibranchial lobe possessed several large protruding papillae, each with smaller papillae present at the tips (we hereafter refer to as “papillous lobules” following Fishelson and Delarea (2004)) (Fig. 4c). Chemosensory cells revealed by SEM and identified as taste buds were observed at the tip of each of the smaller papillae (tb, Figs. 4c) and were also present along the length of the gill filaments (Fig S2e). On the first gill arch, gill rakers and papillous lobules were both present (gr, pl, Fig. 4a). Gill rakers of the second and third gill arches were finger-like in shape with presence of papillous lobules with taste buds (Fig. S2c, f).

Papillous lobules with taste buds were highly abundant between the teeth of the large upper and lower pharyngeal jaws of both winnowing species (Figs. 4a, e; S3a, c, g, h). There was also some evidence of mucous glands present on the pharyngeal jaws (Fig. S3h). The pharyngeal teeth differed slightly between species (hooked tips in *V. strigata* and bulbous tips in *V. sexguttata*), but both species possessed primarily tall, thin teeth angled posteriorly with a row of stouter teeth on the posterior margin (Figs. 4b, f; S3a, g). The teeth of the pharyngeal jaws can be tilted horizontally, but only in the posterior direction without damaging the teeth.

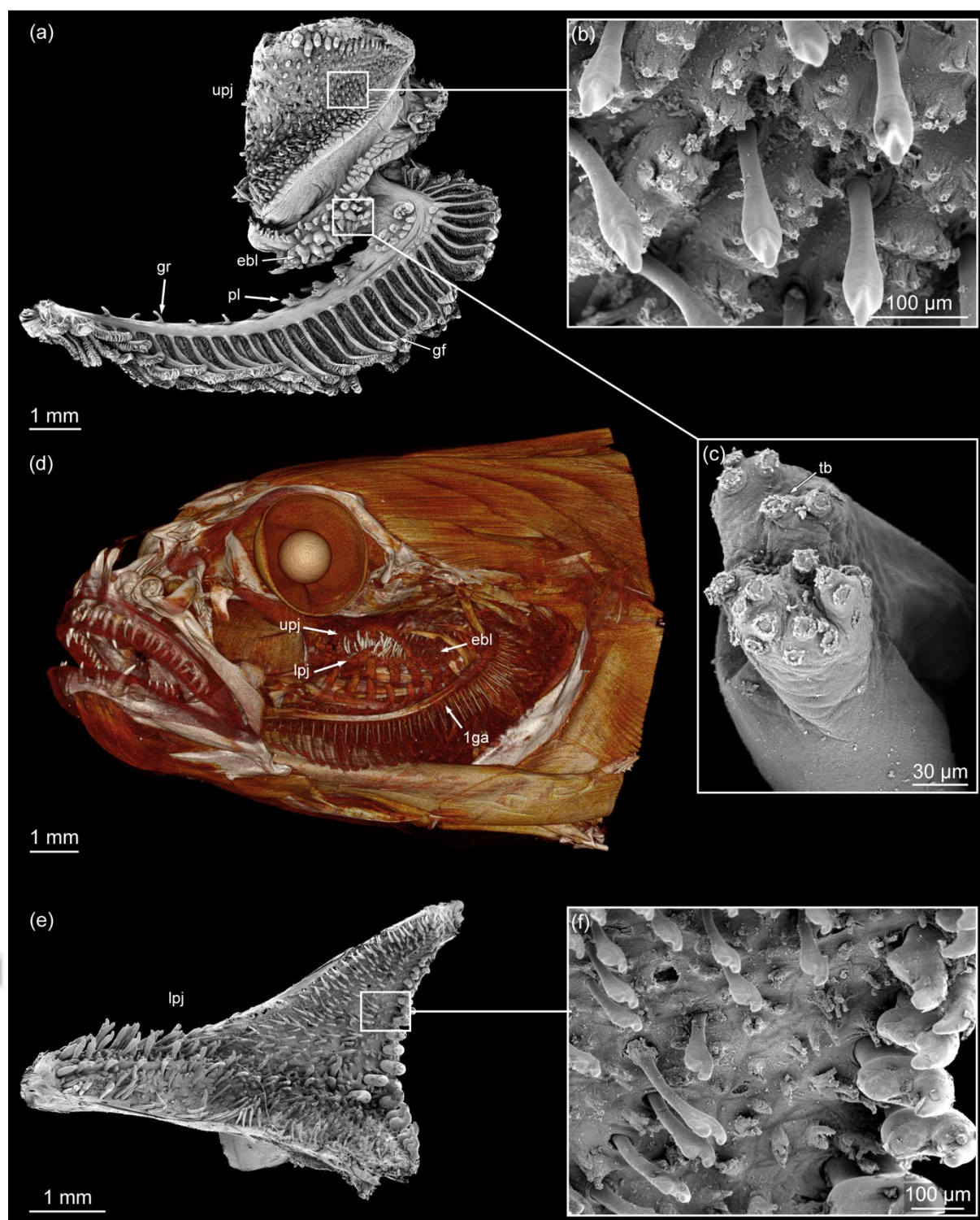


Figure 4. Scanning electron micrographs (a-c, e-f) and computed tomography scan (d) of morphological structures proposedly involved in winnowing in *Valencienna strigata*. (a) 1st gill arch, epibranchial lobe, and upper pharyngeal jaw (lateral view). (b) Close up of upper pharyngeal jaw teeth and intermediate papillous lobules. (c) Close up of papillous lobules with taste buds from the epibranchial lobe. (d) Lateral view of head and gill basket, with the opercula series covering the pharyngeal basket removed. (e) Lower

pharyngeal jaw (left posterior side broken). (f) Close up of lower pharyngeal jaw teeth and small intermediate papillous lobules. upj = upper pharyngeal jaw, lpj = lower pharyngeal jaw, ebl = epibranchial lobe (position only highlighted (d)), gf = gill filament, gr = gill raker, tb = taste bud, pl = papillous lobules and lga = 1st gill arch. For full ct-scans of both individuals see: <http://n2t.net/ark:/87602/m4/383379> & <http://n2t.net/ark:/87602/m4/433651>.

Discussion

Impact of winnowing gobies on meiobenthic communities

Both *Valenciennea sexguttata* and *V. strigata* significantly affect meiobenthic communities. In just four days, the meiobenthic abundance was reduced by ~31% and ~46% by *V. sexguttata* and *V. strigata*, respectively, highlighting the ability of these fishes to efficiently extract microscopic prey from the sand. Furthermore, the qualitative assessment of gut contents supported that the fishes actually ingested meiobenthic organisms as a food source. The revealed impact on meiobenthic abundance is comparable to other fish preying on meiobenthos. The common carp (*Cyprinus carpio*), reduced meiobenthic density by 62% over 32 days in an enclosure cage experiment and *Cyprinus carpio* and *Gobio gobio* had a stronger impact on the meiobenthic community reducing nematode abundance by 82% and 56% (respectively) in two days (Weber and Traunspurger 2014; Weber et al. 2018). Thus, winnowing by *Valenciennea* appears to successfully separate meiobenthic prey from an indigestible, particulate medium.

Copepods and annelids were the most abundant taxa in the sediment of our experiment (Table S2), and both were efficiently removed by the winnowing gobies. These taxa are commonly dominating the meiobenthos communities of coral sand (Armenteros et al. 2009; Semprucci et al. 2013; Sarmiento et al. 2017) and hard-substrate (Kramer et al. 2013a), thus forming a potentially valuable prey source. Diet examinations of wild-caught species of *Valenciennea*, such as *V. longipinnis* and *V. muralis*, confirmed that they predominantly prey

on harpacticoid copepods and other minute crustaceans, reflecting the relatively high abundance of these prey items in coral sand (John et al. 1989; Hernaman et al. 2009; Kramer et al. 2014). However, similar to Hernaman (2009) we attribute the absence of identifiable annelids in the gut content to their lack of thick chitinous cuticles, which cause them to disintegrate rapidly during winnowing, maceration and digestion.

In contrast to abundance, the presence of gobies did not have an impact on the diversity of the meiobenthic community in our study. The lack of change in overall diversity suggests relatively little taxon-specific preference in goby winnowing. Previous work on sand feeding gobies suggests that these ingest a wide range of taxa (Kramer et al. 2009) and do not visually detect prey in the sand (Gregg and Fleeger 1997). This is probably also the case for winnowing gobies. However, some of the most abundant taxa (copepods and annelids) were ingested more than others (ostracods), resulting in the observed differences in community composition. Rather than taxonomic preferences, several lines of evidence suggest that both size and shape of prey items may influence food selection after sediment is ingested (i.e., filtering through the winnowing process). For example, there was a non-significant reduction in ostracod abundance in response to *Valenciennea* predation, even though ostracods were the second most abundant taxa observed in the sediment and fall within the size range of other small prey items in our gut content analyses. This may also be driven, in part, by the resemblance of ostracods to sand grains in shape and potentially in mass-weight-ratio, thus avoiding selection by the gobies that seek to limit ingestion of inorganic material. In contrast, copepods and annelids comprise taxa with elongated body shape and larger mean length (typically >250 μm) (Schmidt-Rhaesa 2020), potentially making them easier targets in the winnowing process. While the artificial setting of our experiments warrant caution in our interpretation, our data suggest that *Valenciennea* are feeding relatively indiscriminately, and their ingestion of prey may be dependent on size, shape and density rather than taxonomy as a selective criterion.

Morphological adaptations to winnowing behaviours

V. sexguttata and *V. strigata* are clearly able to separate meiobenthic prey from similarly sized unpalatable sediment particles. This is achieved through highly specialized feeding structures. Notably the epibranchial lobe on the first gill arch in *Valenciennea* strongly resembles those found in several freshwater winnowing cichlids (López-Fernández et al. 2012, 2014; Weller et al. 2017). The facultative winnowing goby genus *Amblygobius* also has an epibranchial lobe (Hoese and Allen 1977; JMH personal observation), suggesting that this pharyngeal structure is important in the winnowing mechanism, although the exact mechanical function is yet to be explored. The abundant papillous lobules we found on the epibranchial lobe and all but the fourth gill arches in both goby species suggest that these structures aid in sensing and retention of ingested items. Gracile pharyngeal jaws have been a suggested trait of winnowing cichlids (López-Fernández et al. 2012). The delicate and soft parts of the pharyngeal jaws in winnowing gobies likely assist in combing and manipulating ingested material rather than chewing. Finally, the high abundance of hooked pharyngeal teeth may be effective in catching and retaining vermiform meiobenthic prey. Although speculative, the pharyngeal teeth's ability to be tilted in the posterior but not anterior direction may act like a barricade to promote a unidirectional flow of prey items towards the oesophagus, but further investigation is warranted.

The high abundance of taste buds covering most of the feeding apparatus (including pharyngeal jaws) in *V. sexguttata* and *V. strigata*, is uncommon for gobies and emphasises their well-developed taste capacity (Fishelson and Delarea 2004). We hypothesize that the activation of taste buds help the fish determine when prey items are sufficiently separated from indigestible material and when to expel the latter to minimize ingestion of inorganic material. The elevated position of the taste buds on the papillous lobules likely increases their the sensory

capacity and discriminatory ability (Fishelson and Delarea 2004; Elsheikh et al. 2012). In the context of broader foraging behaviours, taste buds may enable detection of sand patches with high abundance of meiobenthos for optimization of foraging efforts in the environment. This is supported by the higher density of *Valenciennea* gobies in areas with high copepod abundance (John et al. 1989), indicating their ability to detect profitable foraging patches. Thus, a well-developed sense of taste may benefit both large-scale selection of foraging areas and territories, and fine-scale selection of food items in the ingested sediment.

In contrast to *Valenciennea*, winnowing freshwater cichlids do not have papillose lobules on the pharyngeal jaw (Weller et al. 2017), suggesting that these structures are not strictly necessary for winnowing. Instead, these lobules may be an exaptation in some goby genera such as *Valenciennea* and *Coryphopterus* (Kramer et al. 2009) and could relate to differences in size, quantity and type of infaunal prey available in the freshwater vs marine sediment. By contrast, the epibranchial lobe may be relatively more important for winnowing since winnowing cichlids have epibranchial lobes, while closely related non-winnowing species lack this structure (López-Fernández et al. 2012, 2014; Arbour and López-Fernández 2013; Novakowski et al. 2016). Thus, while our study adds to the evidence that the epibranchial lobe is of functional significance for winnowing, the specific role of the papillose lobules documented in our study remains to be explored in greater detail.

We observed winnowing gobies to have rapid movement of oral jaws and opercula when feeding, which likely creates an anterior-posterior water flow as described in *S. daemon* and in surfperches (Drucker and Jensen 1991; Weller et al. 2017). In combination with the epibranchial lobe and gill rakers, this creates micro-currents that may facilitate the separation of prey items from sediment particles through mass-weight differences. We hypothesise that the lighter particles remain in suspension and are pushed further into the oropharyngeal cavity by the current where the pharyngeal jaw, epibranchial lobes and gill rakers all aid in capture

and transport towards the oesophagus. Simultaneously, the heavier sand grains likely fall to the bottom of the oropharyngeal cavity to be expelled through the gill openings.

The importance of winnowing gobies in coral reef trophodynamics

The specialized morphology and behaviour of winnowing gobies enable them to exploit an abundant, high-quality prey source (Coull 1999; Giere 2009; Kramer et al. 2013b; Semprucci et al. 2013) that is located in a seemingly barren, featureless habitat. Winnowing gobies belong to a group of general sand feeders, but are distinguished functionally based on how they extract organic material from the sediment (Bellwood et al. 2019). Similar to other cryptobenthic fishes and general sand feeders, which both contribute substantially to fish productivity on coral reefs (Brandl et al. 2018, 2020b, 2020a; Morais and Bellwood 2019), our findings support the role of winnowing gobies in making a minute and highly productive prey source directly available to larger consumers and thus decreasing the loss in energy efficiency through intermediate trophic levels (Eddy et al. 2021). Like other gobies and cryptobenthic fishes, sand-dwelling gobies such as *Valenciennesa* are at high risk of predation with < 1% to 2.3% annual survivorship (Hernaman and Munday 2005; Brandl et al. 2019). In *V. strigata* the main cause of the almost 100% annual mortality was observed to be predation (Reavis 1997). Considering that prey density of meiobenthos can reach 2033 ± 329 individuals per 10 cm^2 of coral reef sand (Semprucci et al. 2013), these winnowing fishes' access an abundant energy source which they "fast-track" to larger predators via rapid growth and high mortality which we propose represents an important ecological function in oligotrophic reefs. Finally, the function of winnowing fishes is likely mirrored in other natural ecosystems beyond coral reefs.

References

- Ackerman J, Bellwood D (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar Ecol Prog Ser* 206:227–237 DOI:10.3354/meps206227
- Arbour JH, López-Fernández H (2013) Ecological variation in South American geophagine cichlids arose during an early burst of adaptive morphological and functional evolution. *Proc R Soc B Biol Sci* 280:20130849 DOI:10.1098/rspb.2013.0849
- Armenteros M, Creagh B, González-Sansón G (2009) Distribution patterns of the meiofauna in coral reefs from the NW shelf of Cuba. *Rev Investig Mar Univ La Habana* 30:37–43
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–109 DOI:10.18637/jss.v067.i01
- Bellwood DR, Streit RP, Brandl SJ, Tebbett SB (2019) The meaning of the term ‘function’ in ecology: A coral reef perspective. *Funct Ecol* 33:948–961 DOI:10.1111/1365-2435.13265
- Brandl S, Quigley C, Casey J, Mercière A, Schiettekatte N, Norin T, Parravicini V, Côté I (2022) Metabolic rates mirror morphological and behavioral differences in two sand-dwelling coral reef gobies. *Mar Ecol Prog Ser* 684:79–90 DOI:10.3354/meps13968
- Brandl SJ, Casey JM, Meyer CP (2020a) Dietary and habitat niche partitioning in congeneric cryptobenthic reef fish species. *Coral Reefs* DOI:10.1007/s00338-020-01892-z
- Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Biol Rev* 93:1846–1873 DOI:10.1111/brv.12423
- Brandl SJ, Johansen JL, Casey JM, Tornabene L, Morais RA, Burt JA (2020b) Extreme environmental conditions reduce coral reef fish biodiversity and productivity. *Nat Commun* 11:1–14 DOI:10.1038/s41467-020-17731-2
- Brandl SJ, Tornabene L, Goatley CHR, Casey JM, Morais RA, Côté IM, Baldwin CC,

- Parravicini V, Schiattekatte NMD, Bellwood DR (2019) Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. *Science* (80-) 364:1189–1192 DOI:10.1126/science.aav3384
- Brodnicke OB, Hansen CE, Huie JM, Brandl SJ, Worsaae K (2022) Data: Functional impact and trophic morphology of small, sand-sifting fishes on coral reefs. <https://zenodo.org/record/6352974#.Yi9WRHrMJJaQ> DOI:10.5281/zenodo.6352974
- Carle KJ, Hastings PA (1982) Selection of meiofaunal prey by the darter goby, *Gobionellus boleosoma* (Gobiidae). *Estuaries* 5:316–318 DOI:10.2307/1351755
- Coull BC (1990) Are members of the meiofauna food for higher trophic levels? *Trans Am Microsc Soc* 109:233 DOI:10.2307/3226794
- Coull BC (1999) Role of meiofauna in estuarine soft-bottom habitats. *Austral Ecol* 24:327–343 DOI:10.1046/j.1442-9993.1999.00979.x
- Danovaro R, Scopa M, Gambi C, Fraschetti S (2007) Trophic importance of subtidal metazoan meiofauna: evidence from in situ exclusion experiments on soft and rocky substrates. *Mar Biol* 152:339–350 DOI:10.1007/s00227-007-0696-y
- Dean MN, Motta PJ (2004) Feeding behavior and kinematics of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea). *Zoology* 107:171–189 DOI:10.1016/j.zool.2004.04.002
- Depczynski M, Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Mar Ecol Prog Ser* 256:183–191 DOI:10.3354/meps256183
- Depczynski M, Bellwood DR (2004) Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Mar Biol* 145:455–463 DOI:10.1007/s00227-004-1342-6
- Depczynski M, Bellwood DR (2006) Extremes, plasticity, and invariance in vertebrate life history traits: Insights from coral reef fishes. *Ecology* 87:3119–3127 DOI:10.1890/0012-9658(2006)87[3119:EPaIV]2.0.CO;2

Depczynski M, Fulton CJ, Marnane MJ, Bellwood DR (2007) Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia* 153:111–120

DOI:10.1007/s00442-007-0714-2

Drucker EG, Jensen JS (1991) Functional analysis of a specialized prey processing behavior: Winnowing by surfperches (Teleostei: Embiotocidae). *J Morphol* 210:267–287

DOI:10.1002/jmor.1052100306

Eddy TD, Bernhardt JR, Blanchard JL, Cheung WWL, Colléter M, du Pontavice H, Fulton EA, Gascuel D, Kearney KA, Petrik CM, Roy T, Rykaczewski RR, Selden R, Stock CA, Wabnitz CCC, Watson RA (2021) Energy flow through marine ecosystems: Confronting transfer efficiency. *Trends Ecol Evol* 36:76–86 DOI:10.1016/j.tree.2020.09.006

Elsheikh EH, Nasr ES, Gamal AM (2012) Ultrastructure and distribution of the taste buds in the buccal cavity in relation to the food and feeding habit of a herbivorous fish:

Oreochromis niloticus. *Tissue Cell* 44:164–169 DOI:10.1016/j.tice.2012.02.002

Fishelson L, Delarea Y (2004) Taste buds on the lips and mouth of some blennioid and gobioid fishes: Comparative distribution and morphology. *J Fish Biol* 65:651–665

DOI:10.1111/j.0022-1112.2004.00475.x

Fitzhugh GR, Fleeger JW (1985) Goby (Pisces: Gobiidae) interactions with meiofauna and small macrofauna. *Bull Mar Sci* 36:436–444

Froese R, Pauly D (2021) FishBase. www.fishbase.org

Fugi R, Agostinho AA, Hahn NS (2001) Trophic morphology of five benthic-feeding fish species of a tropical floodplain. *Braz J Biol* 61:27–33 DOI:10.1590/s0034-

71082001000100005

Gee JM (1989) An ecological and economic review of meiofauna as food for fish. *Zool J Linn Soc* 96:243–261 DOI:10.1111/j.1096-3642.1989.tb01830.x

Gerlach SA (1971) On the importance of marine meiofauna for benthos communities.

Oecologia 6:176–190 DOI:10.1007/BF00345719

Giere O (2009) Meibenthology. Springer Berlin Heidelberg, Berlin, Heidelberg

DOI:10.1007/978-3-540-68661-3

Giere O (2019) Perspectives in meibenthology: Reviews, reflections and conclusions.

Gignac PM, Kley NJ, Clarke JA, Colbert MW, Morhardt AC, Cerio D, Cost IN, Cox PG,

Daza JD, Early CM, Echols MS, Henkelman RM, Herdina AN, Holliday CM, Li Z,

Mahlow K, Merchant S, Müller J, Orsbon CP, Paluh DJ, Thies ML, Tsai HP, Witmer

LM (2016) Diffusible iodine-based contrast-enhanced computed tomography (diceCT):

An emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. J

Anat 228:889–909 DOI:10.1111/joa.12449

Goatley CHR, Bellwood DR (2016) Body size and mortality rates in coral reef fishes: a three-phase relationship. Proc R Soc B Biol Sci 283:20161858 DOI:10.1098/rspb.2016.1858

de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM,

Admiraal W (2013) Surviving in a marine desert: The sponge loop retains resources

within coral reefs. Science (80-) 342:108–110 DOI:10.1126/science.1241981

Gregg JC, Fleeger JW (1997) Importance of emerged and suspended meiofauna to the diet of the darter goby (*Gobionellus boleosoma* Jordan and Gilbert). J Exp Mar Bio Ecol

209:123–142 DOI:10.1016/S0022-0981(96)02682-2

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson

BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and

multi-model inference in ecology. PeerJ (San Fr CA) 6:e4794–e4794

DOI:10.7717/peerj.4794

Hartig F (2021) DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models: The R package DHARMA.

Heip C, Herman MJ (1988) The production of meiofauna. ICES CM 19881L26 1–10

- Henry BA, Jenkins GP (1995) The impact of predation by the girdled goby, *Nesogobius* sp. 1, on abundances of meiofauna and small macrofauna. *J Exp Mar Bio Ecol* 191:223–238
DOI:10.1016/0022-0981(95)00061-U
- Hernaman V, Munday PL (2005) Life-history characteristics of coral reef gobies. II. Mortality rate, mating system and timing of maturation. *Mar Ecol Prog Ser* 290:223–237
DOI:10.3354/meps290223
- Hernaman V, Probert PK, Robbins WD (2009) Trophic ecology of coral reef gobies: Interspecific, ontogenetic, and seasonal comparison of diet and feeding intensity. *Mar Biol* 156:317–330 DOI:10.1007/s00227-008-1085-x
- Hoese D, Allen G (1977) *Signigobius biocellatus*, a new genus and species of sand-dwelling coral reef gobiid fish from the western tropical pacific. *Japanese J Ichthyol* 23:P199-207
DOI:10.11369/jjil1950.23.199
- Hoese DF, Larson HK (1994) Revision of the indo pacific Gobiid fish genus *valenciennea* with description of seven new species. Bishop Museum, Honolulu
- Huie JM, Thacker CE, Tornabene L (2020) Co-evolution of cleaning and feeding morphology in western Atlantic and eastern Pacific gobies. *Evolution (N Y)* 74:419–433
DOI:10.1111/evo.13904
- John J St., Jones GP, Sale PF (1989) Distribution and abundance of soft-sediment meiofauna and a predatory goby in a coral reef lagoon. *Coral Reefs* 8:51–57
DOI:10.1007/BF00301803
- Johnstone R, Koop K, Larkum A (1990) Physical aspects of coral reef lagoon sediments in relation to detritus processing and primary production. *Mar Ecol Prog Ser* 66:273–283
DOI:10.3354/meps066273
- Kikinis R, Pieper SD, Vosburgh KG (2014) 3D slicer: A platform for subject-specific image analysis, visualization, and clinical support. *Intraoperative Imaging and Image-Guided*

Therapy. Springer New York, New York, NY, pp 277–289 DOI:10.1007/978-1-4614-7657-3_19

- Krajewski JP, Bonaldo RM, Sazima C, Sazima I (2006) Foraging activity and behaviour of two goatfish species (Perciformes: Mullidae) at Fernando de Noronha Archipelago, tropical West Atlantic. *Environ Biol Fishes* 77:1–8 DOI:10.1007/s10641-006-9046-z
- Kramer A, Van Tassell JL, Patzner RA (2009) Dentition, diet and behaviour of six gobiid species (Gobiidae) in the Caribbean Sea. *Cybium* 33:107–121
- Kramer MJ, Bellwood DR, Bellwood O (2013a) Emergent fauna from hard surfaces on the Great Barrier Reef, Australia. *Mar Freshw Res* 64:687–691 DOI:10.1071/MF12284
- Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic crustacea on coral reefs: A quantitative survey. *Mar Ecol Prog Ser* 511:105–116 DOI:10.3354/meps10953
- Kramer MJ, Bellwood O, Bellwood DR (2013b) The trophic importance of algal turfs for coral reef fishes: the crustacean link. *Coral reefs* 32:575–583 DOI:10.1007/s00338-013-1009-1
- Lenth R V. (2016) Least-squares means: The R package lsmeans. DOI:10.18637/jss.v069.i01
- López-Fernández H, Arbour J, Willis S, Watkins C, Honeycutt RL, Winemiller KO (2014) Morphology and efficiency of a specialized foraging behavior, sediment sifting, in neotropical cichlid fishes. *PLoS One* 9: DOI:10.1371/journal.pone.0089832
- López-Fernández H, Winemiller KO, Montaña C, Honeycutt RL (2012) Diet-morphology correlations in the radiation of south american geophagine cichlids (perciformes: Cichlidae: Cichlinae). *PLoS One* 7: DOI:10.1371/journal.pone.0033997
- Lüdtke D (2018)ggeffects: Tidy data frames of marginal effects from regression models. *J Open Source Softw* 3:772 DOI:10.21105/joss.00772
- Macneill DB, Brandt SB (1990) Ontogenetic shifts in gill-raker morphology and predicted prey capture efficiency of the alewife, *Alosa pseudoharengus*. *Copeia* 1990:164–171

DOI:10.2307/1445832

Martinez Arbizu P (2017) pairwiseAdonis: Pairwise multilevel comparison using adonis: The R package pairwiseAdonis.

McCormick MI (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar Biol* 132:9–20 DOI:10.1007/s002270050367

Montoya JM, Pimm SL, Solé R V. (2006) Ecological networks and their fragility. *Nature* 442:259–264 DOI:10.1038/nature04927

Morais RA, Bellwood DR (2019) Pelagic subsidies underpin fish productivity on a degraded coral reef. *Curr Biol* 29:1521–1527.e6 DOI:10.1016/j.cub.2019.03.044

Moriarty DJW, Pollard PC, Hunt WG, Moriarty CM, Wassenberg TJ (1985) Productivity of bacteria and microalgae and the effect of grazing by holothurians in sediments on a coral reef flat. *Mar Biol* 85:293–300 DOI:10.1007/BF00393250

Novakowski GC, Cassemiro FAS, Hahn NS (2016) Diet and ecomorphological relationships of four cichlid species from the Cuiabá River basin. *Neotrop Ichthyol* 14:1–10 DOI:10.1590/1982-0224-20150151

Oksanen AJ, Blanchet FG, Kindt R, Legendre P, Minchin PR, Hara RBO, Simpson GL, Solymos P, Stevens MHH, Wagner H (2018) vegan: Community ecology package. *Community Ecol Packag* 1–275

Price SA, Holzman R, Near TJ, Wainwright PC (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol Lett* 14:462–469 DOI:10.1111/j.1461-0248.2011.01607.x

Ptatscheck C, Brüchner-Hüttemann H, Kreuzinger-Janik B, Weber S, Traunspurger W (2020) Are meiofauna a standard meal for macroinvertebrates and juvenile fish? *Hydrobiologia* 847:2755–2778 DOI:10.1007/s10750-020-04189-y

R Core Team (2021) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>.

Reavis RH (1997) The natural history of a monogamous coral-reef fish, *Valenciennaea strigata* (Gobiidae): 2. Behavior, mate fidelity and reproductive success. *Environ Biol Fishes* 49:247–257 DOI:10.1023/A:1007320708862

Rolfe S, Pieper S, Porto A, Diamond K, Winchester J, Shan S, Kirveslahti H, Boyer D, Summers A, Maga AM (2021) SlicerMorph: An open and extensible platform to retrieve, visualize and analyse 3D morphology. *Methods Ecol Evol* 12:1816–1825 DOI:10.1111/2041-210X.13669

Rueden CT, Schindelin J, Hiner MC, DeZonia BE, Walter AE, Arena ET, Eliceiri KW (2017) ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18:529–529 DOI:10.1186/s12859-017-1934-z

Sarmiento VC, Pinheiro BR, De Jesus Flores Montes M, Parreira Santos PJ (2017) Impact of predicted climate change scenarios on a coral reef meiofauna community. *ICES J Mar Sci* 74:1170–1179 DOI:10.1093/icesjms/fsw234

Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *J Fish Biol* 29:53–65 DOI:10.1111/j.1095-8649.1986.tb04926.x

Schiettekatte NMD, Brandl SJ, Casey JM (2021) fishualize: Color Palettes Based on Fish Species: The R package fishualize.

Schmidt-Rhaesa A (2020) Guide to the identification of marine meiofauna. Verlag Dr. Friedrich Pfeil, Munich, Germany

Schratzberger M, Ingels J (2018) Meiofauna matters: The roles of meiofauna in benthic ecosystems. *J Exp Mar Bio Ecol* 502:12–25 DOI:10.1016/j.jembe.2017.01.007

Semprucci F, Colantoni P, Baldelli G, Sbrocca C, Rocchi M, Balsamo M (2013) Meiofauna

associated with coral sediments in the Maldivian subtidal habitats (Indian Ocean). *Mar Biodivers* 43:189–198 DOI:10.1007/s12526-013-0146-7

Spieth HR, Möller T, Ptatscheck C, Kazemi-Dinan A, Traunspurger W (2011) Meiobenthos provides a food resource for young cyprinids. *J Fish Biol* 78:138–149 DOI:10.1111/j.1095-8649.2010.02850.x

Svanbäck R, Eklöv P (2003) Morphology dependent foraging efficiency in perch: A trade-off for ecological specialization? *Oikos* 102:273–284 DOI:10.1034/j.1600-0706.2003.12657.x

Tebbett SB, Siqueira AC, Bellwood DR (2022) The functional roles of surgeonfishes on coral reefs: past, present and future. Springer International Publishing, DOI:10.1007/s11160-021-09692-6

Thompson RM, Brose U, Dunne JA, Hall RO, Hladyz S, Kitching RL, Martinez ND, Rantala H, Romanuk TN, Stouffer DB, Tylianakis JM (2012) Food webs: Reconciling the structure and function of biodiversity. *Trends Ecol Evol* 27:689–697 DOI:10.1016/j.tree.2012.08.005

Weber S, Majdi N, Traunspurger W (2018) Effects of bottom-feeding fish juveniles on the vertical distribution of a meiofaunal community. *Hydrobiologia* 820:215–226 DOI:10.1007/s10750-018-3658-0

Weber S, Traunspurger W (2014) Top-down control of a meiobenthic community by two juvenile freshwater fish species. *Aquat Ecol* 48:465–480 DOI:10.1007/s10452-014-9498-8

Weller HI, McMahan CD, Westneat MW (2017) Dirt-sifting devilfish: winnowing in the geophagine cichlid *Satanoperca daemon* and evolutionary implications. *Zoomorphology* 136:45–59 DOI:10.1007/s00435-016-0335-6

Wickham H (2016) ggplot2: Elegant graphics for data analysis: The R package ggplot2.

DOI:ISBN 978-3-319-24277-4

Wild C, Huettel M, Kluter A, Kremb SG, Rasheed MYM, Jørgensen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428:66–70 DOI:10.1038/nature02344

Zuur AF (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York