

## RESEARCH ARTICLE

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

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## 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 *Valenciennea 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 4 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 an otherwise inaccessible trophic niche of microscopic prey. By having evolved a specialised strategy to obtain nutritious and highly abundant

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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

## 1 | 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 nutrients 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 & Bellwood, 2019). Meanwhile, local biomass is frequently locked up and is only available through distinct trophic pathways (Brandl et al., 2019; de Goeij et al., 2013; Wild et al., 2004). 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 (Giere, 2019; Kramer et al., 2013b). 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 & Bellwood, 2000; Brandl et al., 2019; Depczynski et al., 2007). Cryptobenthic fishes are characterised by small adult body size (<5 cm), cryptic behaviour and/or appearance, and a strong association with the benthos (Brandl et al., 2018; Depczynski & Bellwood, 2003). They generally feed on abundant microscopic food sources such as filamentous algae or invertebrates (Brandl et al., 2018; Depczynski & Bellwood, 2003; Hernaman et al., 2009). Further, by falling prey to larger piscivores in large numbers (Ackerman & Bellwood, 2000; Brandl et al., 2019; Depczynski & Bellwood, 2006; Goatley & Bellwood, 2016), 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 & Eklöv, 2003), fine partitioning of dietary niches among reef fishes, including small cryptobenthic species, and may promote their efficient utilisation of prey (Brandl, Casey, & Meyer, 2020; Huie et al., 2020; Price et al., 2011).

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 (Johnstone et al., 1990; Moriarty et al., 1985). 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 µm (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 1,000 individuals per 10 cm<sup>2</sup> (Armenteros et al., 2009; Giere, 2009; Sarmiento et al., 2017; Semprucci et al., 2013; St. John et al., 1989). 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 (Coull, 1990; Gerlach, 1971; Ptatscheck et al., 2020; Schratzberger & Ingels, 2018). 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; Ptatscheck et al., 2020; Spieth et al., 2011; Weber et al., 2018) that display an ontogenetic diet shift to bigger prey items as adults (Macneill & 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 (Brandl et al., 2018, 2022; Henry & Jenkins, 1995; Hernaman et al., 2009; Hoesé & Larson, 1994). 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 & Herman, 1988; Schratzberger & Ingels, 2018).

Several fish species have adopted specialised feeding strategies for consuming microscopic organisms living in sediments, exploiting a distinct foraging niche (Carle & Hastings, 1982; Kramer et al., 2009; St. John et al., 1989). While some fish target discrete prey either on the substrate surface or by localising them by excavation, others will simply ingest bulk sediment (Krajewski et al., 2006; Sazima, 1986; 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

(Depczynski & Bellwood, 2004; Drucker & Jensen, 1991; López-Fernández et al., 2014). This includes diverse taxa such as surfperch *Embiotoca jacksoni* (Drucker & Jensen, 1991), the dirt-sifting devilfish *Satanoperca daemon* (Weller et al., 2017), the lesser electric ray *Narcine brasiliensis* (Dean & Motta, 2004), twin-spot gobies *Signigobius biocellatus* (Hoese & Allen, 1977), darter gobies *Gobionellus boleosoma* (Carle & Hastings, 1982; Gregg & 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 & 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 (Brandl et al., 2022; Carle & Hastings, 1982; Fitzhugh & Fleeger, 1985; Hoese & Larson, 1994). 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 (Froese & Pauly, 2021; Hoese & Allen, 1977; Hoese & Larson, 1994; Reavis, 1997). 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 (a) investigated the effect of foraging by the two species on the abundance and diversity of the meiobenthos over time, (b) conducted gut content analyses to record prey size and diversity for each goby species to confirm meiobenthos ingestion and prey selectivity and (c) 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.

## 2 | MATERIALS AND METHODS

### 2.1 | 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 hr of light and 14 hr of darkness. Total length ranged between 65 and 86 mm for *V. sexguttata* and between 68 and 91 mm for *V. strigata*. The meiobenthos present in the aquarium coral sediment was assumed to represent a world-wide 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 summarised in Table S1.

#### 2.1.1 | 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 × 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 6 days. To promote winnowing behaviour, the gobies were starved for 2 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 12 arenas on day 0, prior to placing the gobies in their respective arenas, and again on days 2, 4 and 6. At each time point, three composite samples covering ~17.2 cm<sup>2</sup> (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 of meiobenthos. Thus, 36 composite samples were collected on each sampling day, which were processed in the laboratory within 36 hr of collection. The used 2 cm sample depth was based on our preliminary experiment to determine the feeding depth of the two goby species (Figure S1).

To separate the meiobenthos from the sediment, samples were anaesthetised with an aqueous isotonic MgCl<sub>2</sub> solution (mixed 1:1 with seawater) for 15 min. Afterwards, samples were swirled, and suspended organisms were carefully decanted thrice through a 63-µm cone-shaped mesh. The fauna retained in the mesh was suspended in 40 ml of isotonic MgCl<sub>2</sub> from which a 10 ml subsample

of the meiobenthos (25%) was revitalised 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 euthanised 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 ImageJ2 on images of prey (Rueden et al., 2017).

## 2.2 | 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* colour palettes (Schiettekatte et al., 2021). Changes in total meiobenthic abundance (number of individuals per 10 cm<sup>2</sup>) were explored in relation to the three treatments (*V. sexguttata*, *V. strigata* and the controls with no fish) over time. Specifically, we performed a GLMM with a negative binomial error distribution (Harrison et al., 2018; Zuur, 2009) 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 (Lüdecke, 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 assessed using the 'lmer' function, since the data were approximately normally distributed (Bates et al., 2015). Principle coordinate analyses (PCoAs) 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 lingo correction to avoid negative eigenvalues which distort the ordination (Oksanen et al., 2020). 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., 2020). Finally, to assess the change in community composition, a multivariate permutational analysis of variance (PERMANOVA) was performed on the dissimilarity matrix with 9999 permutations using the 'adonis' function (Oksanen et al., 2020), and significant results were further investigated with pairwise PERMANOVA using 'pairwise.adonis' function (Martinez Arbizu, 2017). Data are available on Zenodo repository (Brodnicke et al., 2022).

## 2.3 | 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 hr, rinsed with distilled water, dehydrated through a series of EtOH changes and then transferred to 100% acetone. Samples were critical point dried (Tousimis Autosamdry-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 visualise 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 (I<sub>2</sub>KI) for 1 (45 mm specimen) or 2 weeks (101 mm specimen) prior to scanning. The specimens were scanned with a Bruker Skyscan 1173. The scans were conducted with a voxel size of 6 µm (45 mm specimen) or 13.8 µm (101 mm specimen), voltage of 65 kV, amperage of 123 µA and an exposure time of 1.15 s. We used 3D Slicer with the SlicerMorph extension to visualise and segment the scans (Kikinis et al., 2014; Rolfe et al., 2021).

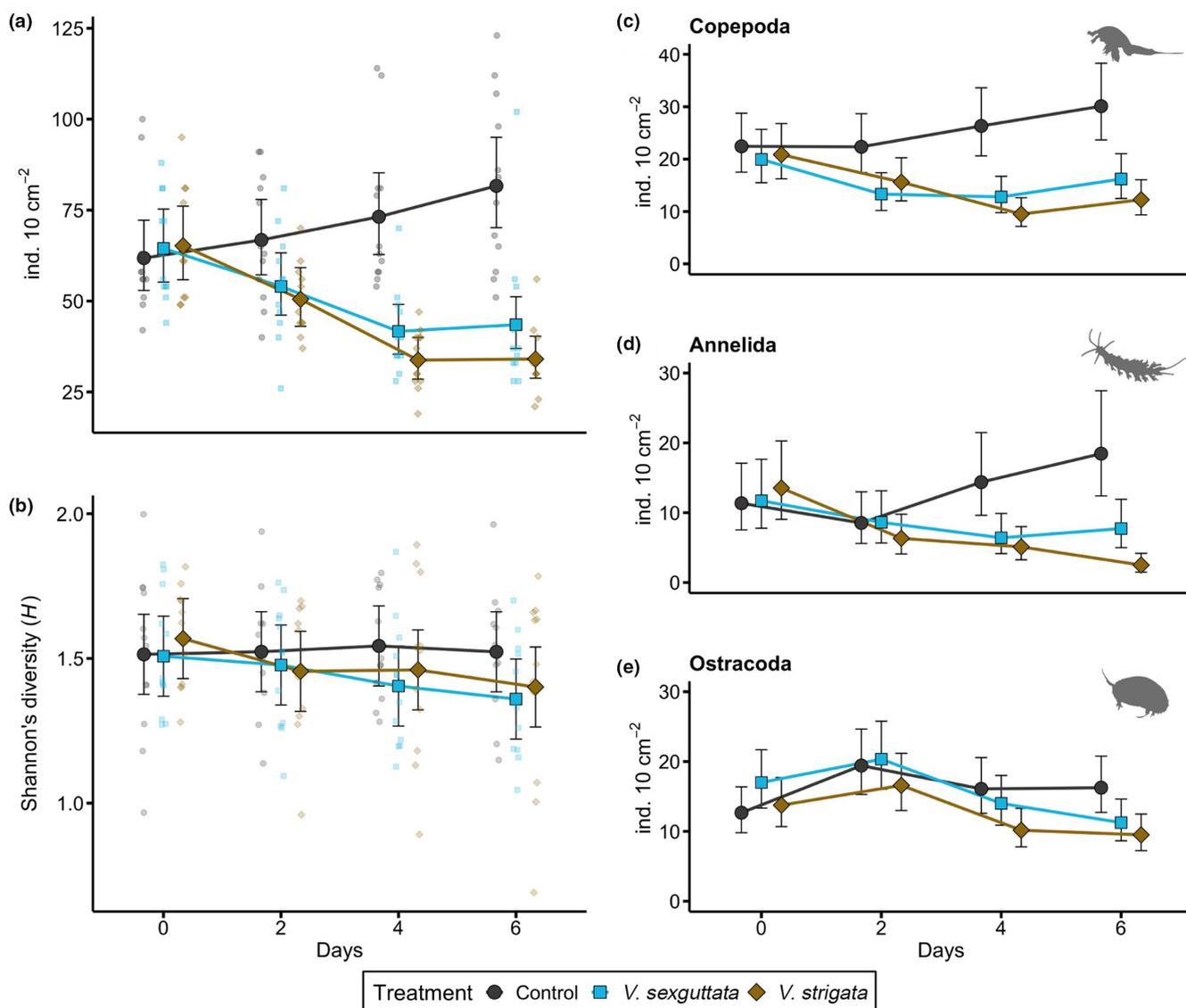
## 3 | RESULTS

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 (Figure 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 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 4 days. While *V. strigata* reduced meiobenthic abundance more than *V. sexguttata* (Figure 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 4 and 6. In the absence of winning gobies, the

meiobenthic abundance increased by  $36.7\% \pm 13.0$  SE after 6 days, though this change was not significant (Tukey's HSD:  $p = 0.113$ ). Yet, on days 4 and 6, 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 4 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:  $p > 0.05$ ).



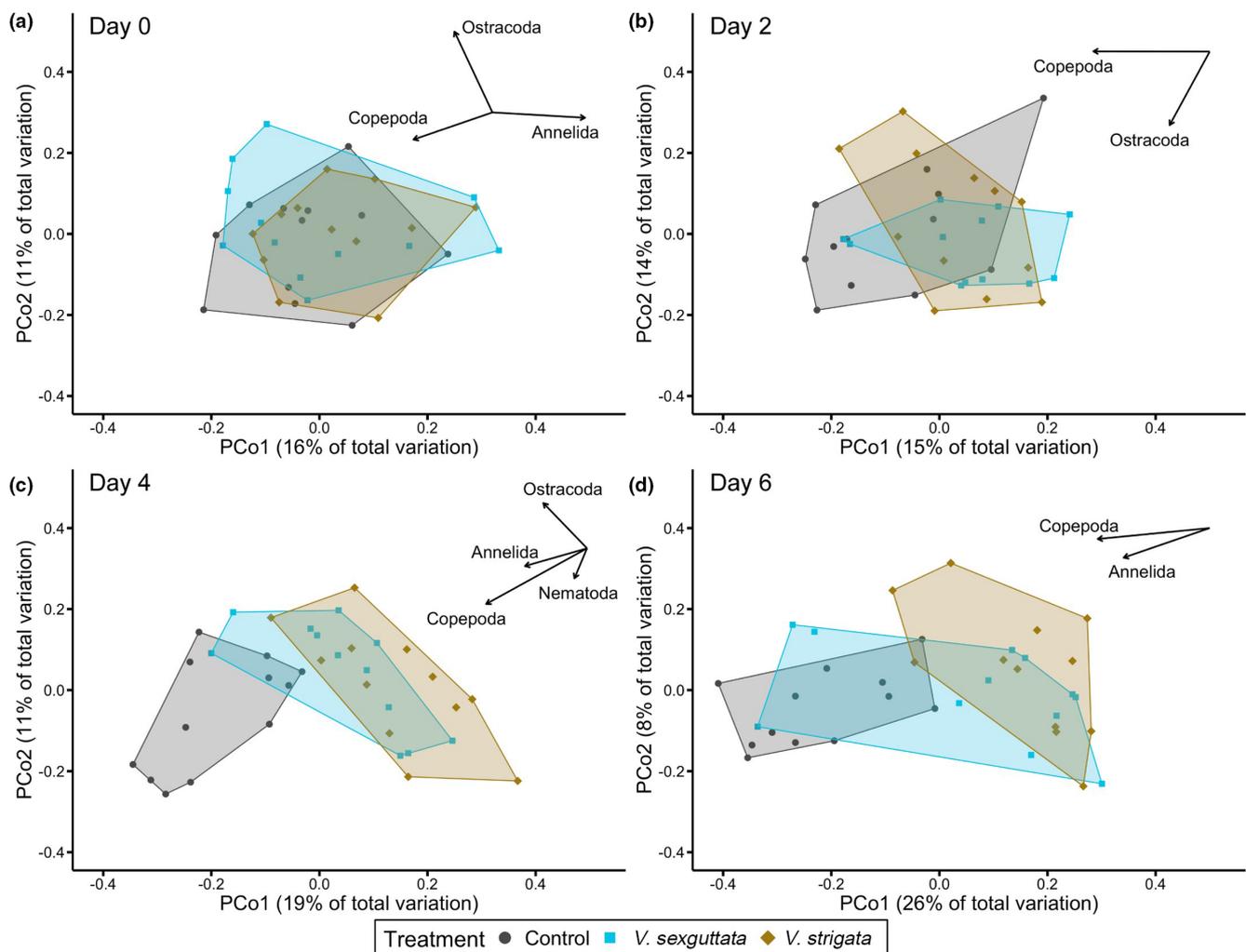
**FIGURE 1** The impact of two winning goby species (*Valencienna sexguttata* and *Valencienna strigata*) on total meiobenthos abundance and diversity over 6 days. Closed symbols show mean predicted marginal effects of time and treatment on (a) abundance (ind. 10 cm<sup>-2</sup>) and (b) diversity ( $H$ ) 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.

The Shannon diversity index ( $H$ ) of the meiobenthic community remained relatively constant across time and treatments (Figure 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 4 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 (Figure 2), where the differences in meiobenthic community were mainly driven by abundance changes of copepods, annelids, ostracods and to lesser degree nematodes (Figure 2b–d).

### 3.1 | 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 (Figure 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  $\mu\text{m}$  and *V. strigata* in the range of 100–11,780  $\mu\text{m}$ . The



**FIGURE 2** Principal Coordinate Analysis (PCoA) based on Bray–Curtis dissimilarity matrix of the meiobenthic community sampled in the three treatments—control (grey), *Valencienna sexguttata* (blue) and *Valencienna 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 ( $|r| > 0.5$ ).

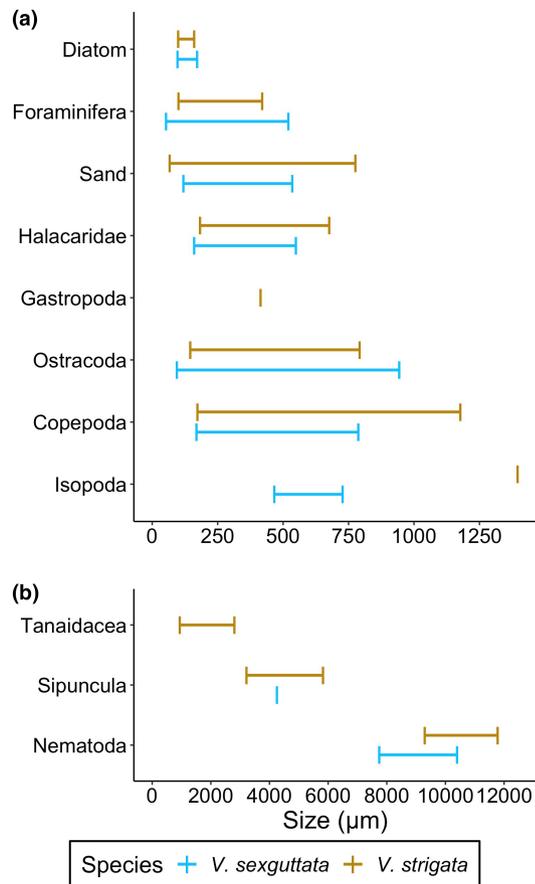


FIGURE 3 Gastrointestinal content and size ranges of ingested prey and particles of *Valencienna sexguttata* (blue;  $n = 4$ ) and *Valencienna strigata* (yellow;  $n = 4$ ). (a) gut items ranges: 50–1,400  $\mu\text{m}$ , (b) larger gut items. Single vertical lines represent prey items occurring once. Note different scales on x-axes.

longest prey items were nematodes (9.30–11.78 mm), while copepods were the most abundant prey and ranged from 173 to 1178  $\mu\text{m}$  in length. Many of the dietary items fell into a similar size range that also includes smaller sand grains (67–777  $\mu\text{m}$ ; Figure 3).

### 3.2 | Morphology

In general, *V. sexguttata* and *V. strigata* shared similar feeding morphologies (Figure 4; Figure 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 (Figure 4d; Figure S2a,b). The upper arm of the first gill arch has a notably developed anteroventral laminal expansion also called the epibranchial lobe (ebl, Figure 4a; Figure 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 (hereafter referred to as ‘papillous lobules’ following Fishelson and Delarea (2004); Figure 4c). Chemosensory cells revealed by SEM and identified as

taste buds were observed at the tip of each of the smaller papillae (tb, Figure 4c) and were also present along the length of the gill filaments (Figure S2e). On the first gill arch, gill rakers and papillous lobules were both present (gr, pl, Figure 4a). Gill rakers of the second and third gill arches were finger-like in shape with presence of papillous lobules with taste buds (Figure 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 (Figure 4a,e; Figure S3a, c, g, h). There was also some evidence of mucous glands present on the pharyngeal jaws (Figure 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 (Figure 4b,f; Figure S3a,g). The teeth of the pharyngeal jaws can be tilted horizontally, but only in the posterior direction without damaging the teeth.

## 4 | DISCUSSION

### 4.1 | Impact of winnowing gobies on meiobenthic communities

Both *Valencienna sexguttata* and *V. strigata* significantly affect meiobenthic communities. In just 4 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 2 days (Weber et al., 2018; Weber & Traunspurger, 2014). Thus, winnowing by *Valencienna* 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; Sarmiento et al., 2017; Semprucci et al., 2013) and hard-substrate (Kramer et al., 2013a), thus forming a potentially valuable prey source. Diet examinations of wild-caught species of *Valencienna*, 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 (Hernaman et al., 2009; Kramer et al., 2014; St. John et al., 1989). However, similar to Hernaman et al. (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 & 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.

## 4.2 | Morphological adaptations to winnowing behaviours

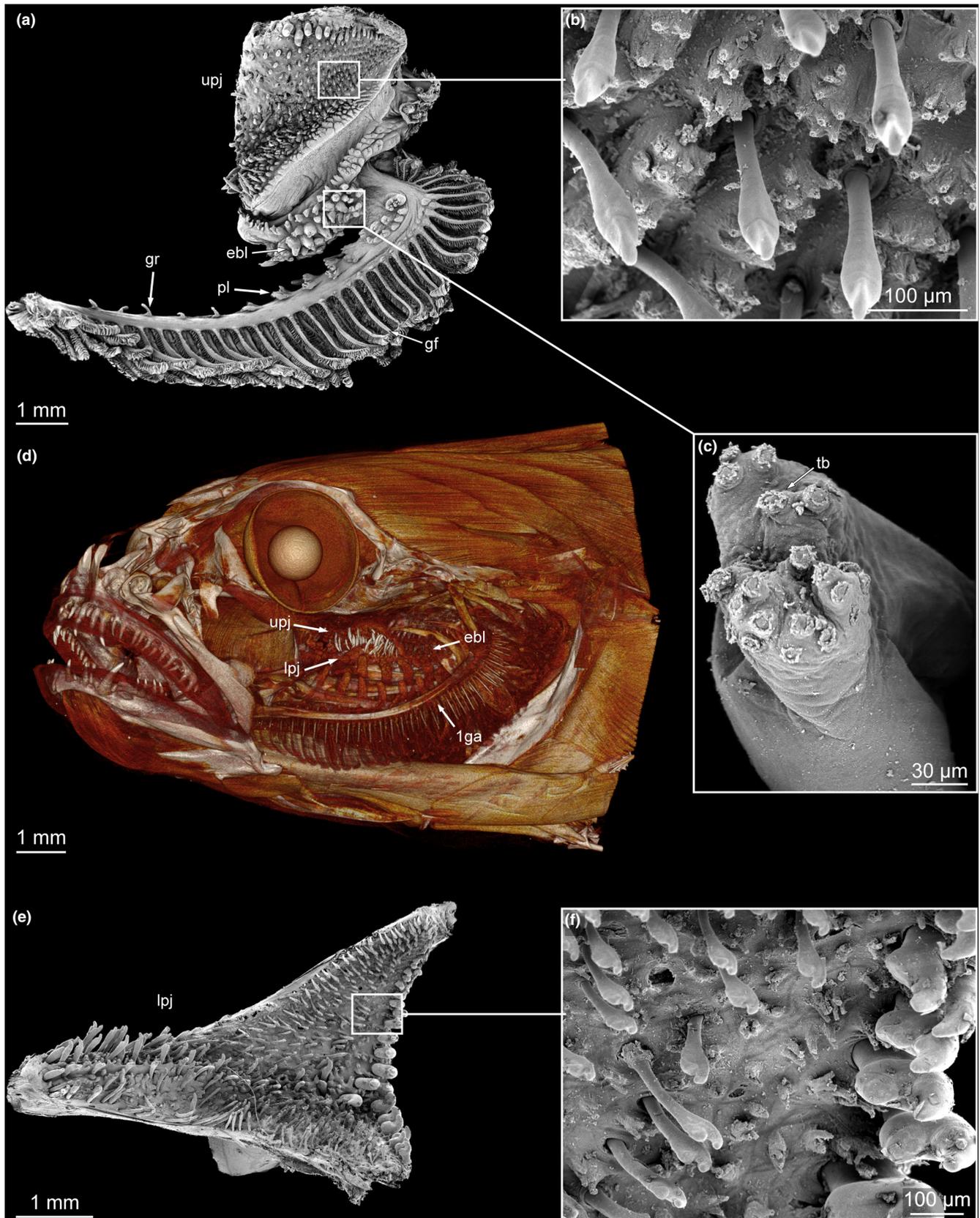
*V. sexguttata* and *V. strigata* are clearly able to separate meiobenthic prey from similarly sized unpalatable sediment particles. This is achieved through highly specialised feeding structures. Notably the epibranchial lobe on the first gill arch in *Valenciennea* strongly resembles those found in 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 & 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 tooth 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 & Delarea, 2004). We hypothesise that the activation of taste buds helps the fish determine when prey items are sufficiently separated from indigestible material and when to expel the latter to minimise ingestion of inorganic material. The elevated position of the taste buds on the papillous lobules likely increases their sensory capacity and discriminatory ability (Elsheikh et al., 2012; Fishelson & Delarea, 2004). In the context of broader foraging behaviours, taste buds may enable detection of sand patches with high abundance of meiobenthos for optimisation of foraging efforts in the environment. This is supported by the higher density of *Valenciennea* gobies in areas with high copepod abundance (St. 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 papillous 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 (Arbour & López-Fernández, 2013; López-Fernández et al., 2012, 2014; Novakowski et al., 2016). Thus, while our study adds to the evidence that the epibranchial lobe is of functional

**FIGURE 4** Scanning electron micrographs (a–c, e–f) and computed tomography scan (d) of morphological structures proposedly involved in winnowing in *Valenciennea strigata*. (a) First 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 1ga = 1st gill arch. For full CT scans of both individuals, see: <http://n2t.net/ark:/87602/m4/383379> and <http://n2t.net/ark:/87602/m4/433651>



significance for winnowing, the specific role of the papillous 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 & 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.

### 4.3 | The importance of winnowing gobies in coral reef trophodynamics

The specialised 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; Brandl, Casey, & Meyer, 2020; Brandl, Johansen, et al., 2020; Morais & 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 *Valenciennea* are at high risk of predation with <1% to 2.3% annual survivorship (Brandl et al., 2019; Hernaman & Munday, 2005). 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  $2,033 \pm 329$  individuals per  $10 \text{ cm}^{-2}$  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.

### AUTHORS' CONTRIBUTIONS

All authors meet all the criteria for authorship defined in the *Functional Ecology* author guidelines; O.B.B., C.E.H. and K.W. conceived the experimental ideas and experimental designs, the later was also guided by S.J.B.; O.B.B. and C.E.H. executed the feeding experiments supervised by K.W.; Morphological experiments were performed by C.E.H., J.M.H. and K.W.; Data were statistically analysed by C.E.H., O.B.B. and S.J.B.; C.E.H. and O.B.B. lead the writing of the manuscript, and all authors critically contributed to result interpretation, manuscript drafts and approved the final version for publication.

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### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

### DATA AVAILABILITY STATEMENT

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

The data for the main figures and statistics are available at <https://zenodo.org/record/6352974#Y19WRHrMJaq> with [10.5281/zenodo.6352974](https://doi.org/10.5281/zenodo.6352974).

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