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Review



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Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes

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Mucous-mesh grazers (pelagic tunicates and thecosome pteropods) are common in oceanic waters and efficiently capture, consume and repackage particles many orders of magnitude smaller than themselves. They feed using an adhesive mucous mesh to capture prey particles from ambient seawater. Historically, their grazing process has been characterized as non-selective, depending only on the size of the prey particle and the pore dimensions of the mesh. The purpose of this review is to reverse this assumption by reviewing recent evidence that shows mucous-mesh feeding can be selective. We focus on large planktonic microphages as a model of selective mucus feeding because of their important roles in the ocean food web: as bacterivores, prey for higher trophic levels, and exporters of carbon via mucous aggregates, faecal pellets and jelly-falls. We identify important functional variations in the filter mechanics and hydrodynamics of different taxa. We review evidence that shows this feeding strategy depends not only on the particle size and dimensions of the mesh pores, but also on particle shape and surface properties, filter mechanics, hydrodynamics and grazer behaviour. As many of these organisms remain critically understudied, we conclude by suggesting priorities for future research.

1. Introduction

Particles in the ocean exhibit striking diversity in size, shape and chemistry [1,2]. If and how grazers select particles from this mixed assemblage influences food web structure and carbon flux [3,4]. Some of the more abundant marine grazers use mucous meshes to capture prey—a process considered to have minimal potential for dietary selection [5–7]. Here, we review recent developments in the literature that collectively portray mucous-mesh feeding as a more selective process than historically assumed.

Although mucus-based feeding mechanisms have independently evolved in multiple animal classes, this review is restricted to 'large planktonic microphages' [8] (pelagic tunicates and thecosome pteropods) because of their important, yet understudied, roles as benthic–pelagic links and key species in the planktonic food web [4,8,9]. All of these animals use mucous filters with large surface areas to maximize particle capture rates (figure 1a). We use the term 'mucous-mesh grazers' throughout, although the term 'grazers' is used loosely, because some taxa are omnivorous rather than strictly herbivorous [10–15].

Although mucous-mesh grazers tend to be overlooked—with the majority of species distributed far offshore—their ecological impacts are pronounced. Not only does their feeding process typify a mechanistic interaction between small particles and mucus, they also occupy a unique role in the ocean food web. While the consumer–prey size ratio for heterotrophic filter-feeding plankton ranges from approximately 5 : 1 to 100 : 1 [16], mucous-mesh grazers can achieve ratios greater than 10 000 : 1 (figure 1a). This makes them uniquely capable of short-circuiting the microbial loop and providing a more efficient linkage in the trophic chain [8,17,18].

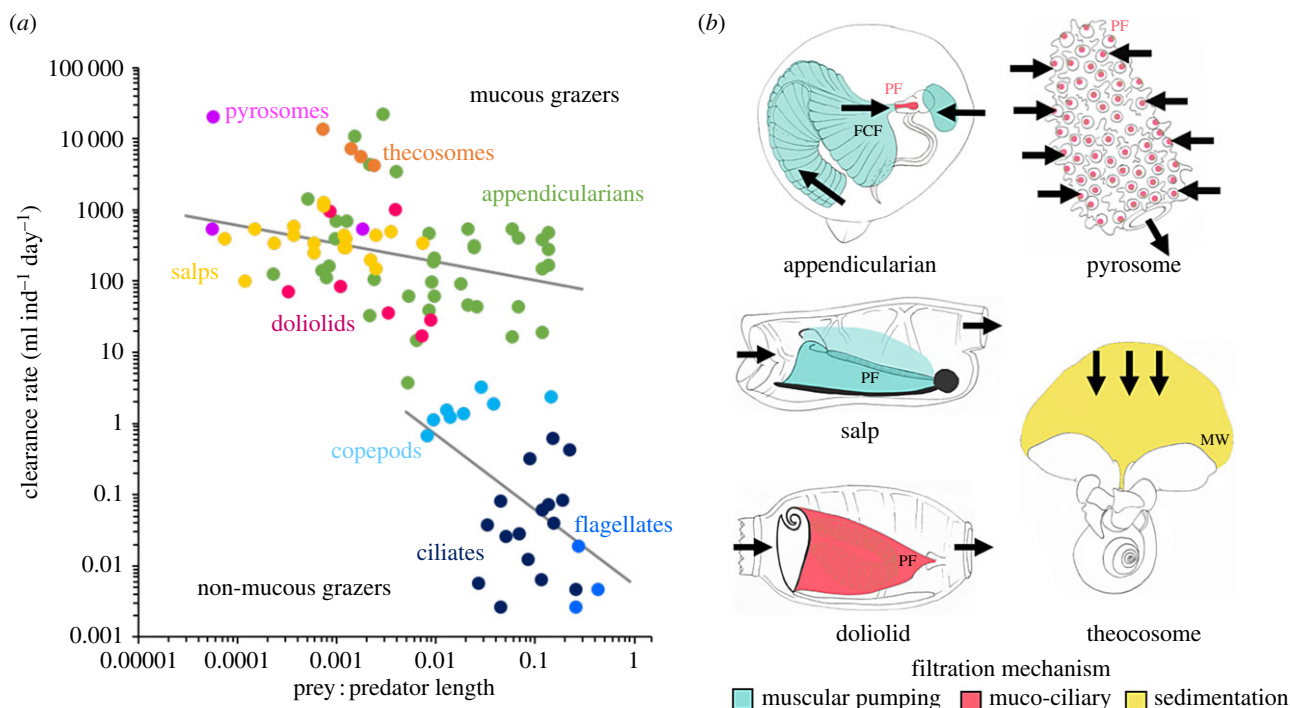


Figure 1. Mucous-mesh grazing: (a) clearance rates of mucous-mesh grazers and other common, non-mucus microphagous grazers versus prey-to-predator length (electronic supplementary material, table S1). (b) Schematic showing location of the mucous mesh for different grazers. The mucous mesh is highlighted according to the mechanism used to drive flow through or across the mesh. (b) IF, inlet filter; FCF, food-concentrating filter; PF, pharyngeal filter; MW, mucous web. Drawings by Caitlyn Webster. (Online version in colour.)

Below, we highlight important differences in the hydrodynamics and filtration mechanics of each of the three groups of mucous-mesh grazers. Next, we summarize the different ways these organisms impact ocean biogeochemical cycling. Then we review the passive and behavioural mechanisms by which mucous-mesh grazers can selectively feed. Equal weight is not given to all taxa because some are less studied than others, owing to patchy or episodic distribution, difficulties with handling, laboratory maintenance or observations of feeding [11,18,19]. We conclude by suggesting future research directions to help remedy these gaps.

2. Mucous-mesh grazers

(a) Appendicularians

Tunicates in the class Appendicularia feed using an external cellulose and mucus filtration apparatus (the house) and an internal mucus filter (the pharyngeal filter) (figure 1b). Sinusoidal beating of the muscular tail drives flow into the house and through the food-concentrating filter, which, for *Oikopleura dioica*, concentrates particles through serial adhesion and detachment in coordination with the tail beating [20]. After being conveyed through the food-concentrating filter, fluid and suspended particles move through the buccal tube and into the mouth, where they are captured on the pharyngeal filter for ingestion (figure 1b). Appendicularians discard and build new houses at species-specific rates, ranging from two to 40 houses per individual per day [21].

(b) Thaliaceans

The tunicate class Thaliacea includes three orders—Salpida, Doliolida and Pyrosomida—that all feed by secreting a mucous mesh that moves posteriorly towards the oesophagus, where it is rolled into a mucus string by cilia and ingested

[22]. Salps and doliolids are barrel-shaped zooids that pass water from an afferent siphon out through an efferent siphon (figure 1b). Salps achieve high filtration rates [23] and produce swimming wakes through muscular contraction (figures 1b and 2) [28]. The feeding current of doliolids is achieved through ciliary beating (figure 1b) [29,30]. Pyrosomes are permanently colonial, with zooids held side by side in a gelatinous tunic [31]. Like salps and doliolids, the individual zooids have an afferent and efferent siphon. The tubular colonies move slowly by the continuous expulsion of fluid through the individual efferent siphons and out of a common aperture (figure 1b) [32].

(c) Thecosome pteropods

Thecosomes are a holoplanktonic order of gastropods that feed using a large external mucous web suspended above the animal (figure 1b) [12,33]. Their molluscan foot has been modified into a wing-like appendage. Unlike tunicates, thecosomes are not true filter-feeders because they do not generate feeding currents; instead, they cease swimming and attain near or complete neutral buoyancy [12], passively entrapping suspended particles via ‘flux feeding,’ a variant of passive ambush feeding (figure 1b) [33,34]. Motile organisms also can be trapped by swimming into the web [10–12]. After prey capture, thecosomes ingest the web by pulling it into the pharynx [19,35].

3. Ecological impacts

Mucous-mesh grazers are uniquely capable of capturing a wide range of particle sizes, and filtering water at high rates (figure 1a). Because mucus is adhesive, the mesh can capture particles smaller than its pores through hydrosol filtration mechanisms [9,27,33,36,37]. Although mucous-mesh grazers were once considered a trophic ‘dead end’ because of their high water content and consequently low to moderate caloric value

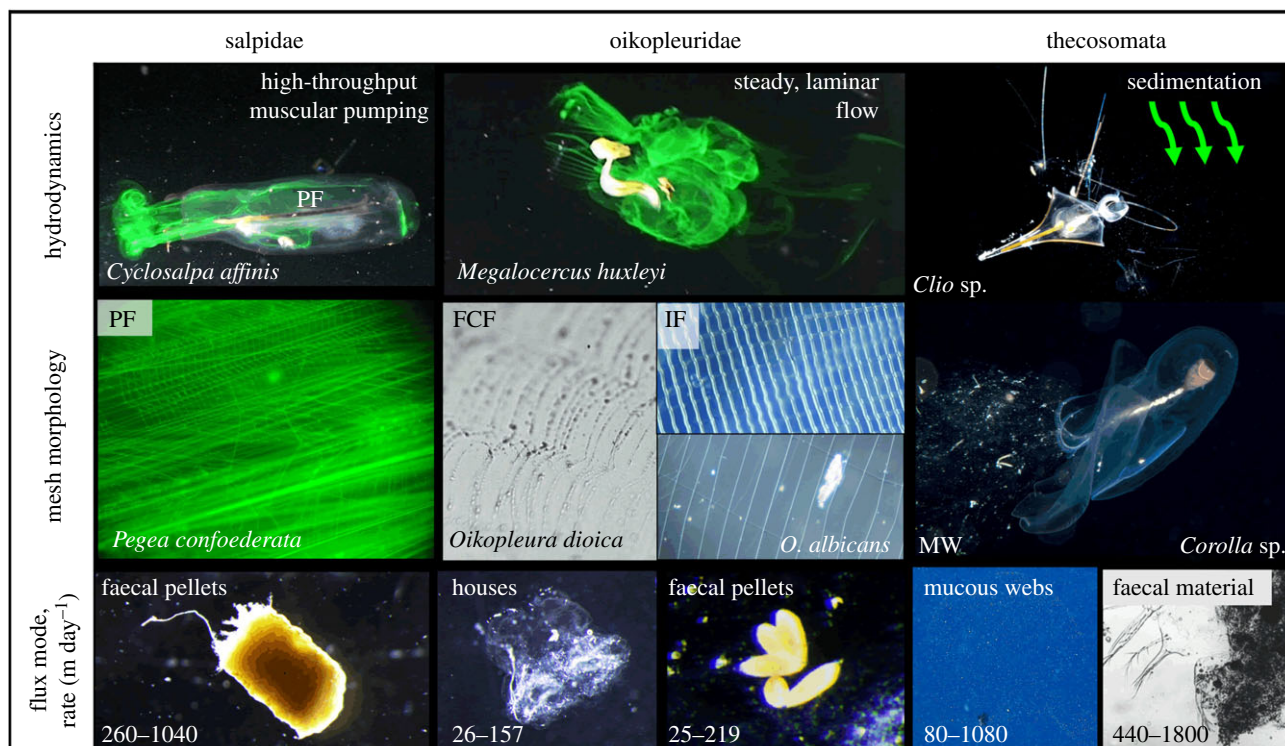


Figure 2. Hydrodynamics, mesh morphologies, and flux of mucous-mesh grazers. PF: pharyngeal filter; FCF: food-concentrating filter; IF: inlet filter prior- (top) and post-inflation of the house (bottom); MW: mucous web. Photographs courtesy of: Linda Ianniello for *Clio* sp. and *Corolla* sp., S. Bush for Peralidae mucous web, © 2008 MBARI, Ron Gilmer for *Cavolinia uncinata* faecal material [10]. Salpidae flux rates based on the faecal pellets of *Pegea confoederata* [24]; Oikopleuridae flux rates based on *Oikopleura dioica* faecal pellets [25] and houses [26]; Thecosomata flux rates based on the mucous webs of *Limacina retroversa* [27] and faecal material of *Corolla spectabilis* [9]. (Online version in colour.)

per unit volume [38], they can have relatively high carbon and protein per unit dry mass; as such, they may represent a valuable food source, particularly at times of prey scarcity [39,40]. Mucous-mesh grazers are increasingly recognized as prey for higher trophic levels (figure 3). Thaliaceans [18,41–44], appendicularians [45,46] and pteropods [11,47,48] contribute a significant proportion of the diet for several fish species and as such can provide a more expedited trophic link to fisheries production [8].

Mucous-mesh grazers also influence the marine particle field through their production of mucous aggregates that contribute to the downward flux of organic matter, sinking at rates ranging from 80 to 800 m day^{-1} (figure 2) [27,49]. Discarded appendicularian houses and thecosome webs contain accumulated pico- and nano-plankton [50–52]. They can also serve as microhabitats with elevated levels of heterotrophic bacterial growth and remineralization [53–56]. Because many of these mucous aggregates can fluoresce and luminesce [57], both visual feeders and non-visual flux-feeders consume them [15,52,58–62] (figure 3).

All mucous-mesh grazers sequester biogenic carbon through production of faecal pellets that sink at high rates (figure 2) [63], except those of doliolids, which are not as compact [64]. Faecal pellets tend to contain more refractory carbon than discarded feeding structures, but can also be a food source for other zooplankton [65]. Only pteropods produce pseudofaeces, composed of mucus and rejected food particles (figures 2 and 3) [58].

Abundance of some mucous-mesh grazers can be pulsed. As these episodic populations die, the carcasses contribute to 'jelly-falls,' which provide particulate organic matter to the seabed [66]. Pyrosomes and salps are important contributors to jelly-falls, and doliolids and pteropods may also contribute to a lesser-known extent [67–69] (figure 3).

4. Selective grazing using mucous meshes

We define selective feeding as 'an imbalance between the proportion of prey types in a predator's diet and the proportion in the environment' [70]. Defining selectivity for appendicularians is complicated by the distinction between the preferential ingestion of certain particles by the animal and the differential retention of particles by the house (figure 4), although both processes can affect ambient particle size spectra and composition [71]. We review physical selection mechanisms that depend on the properties of the particles and mechanisms that depend on grazer behaviour (figure 4). Although this framework suggests these mechanisms are discrete, in many cases the selection process depends on the interaction between particle properties and a behavioural response.

5. Physical selection mechanisms

(a) Size

Mucous-mesh grazers feed in a low Reynolds number environment with thick viscous boundary layers because of the fine mucous-mesh fibres [34]. Within this viscous regime, all mucous-mesh grazers exhibit mechanical, size-dependent selection (figure 1) with a lower limit of particle retention (set in part by the dimensions of the filter pores), and an upper limit that is set by the diameter of the mucous mesh or the animal's mouth (electronic supplementary material, table S2). The upper and lower limits of particle retention vary considerably by species (figure 1), but all appear to capture submicron particles with imperfect (less than 100%) efficiency [9,27,36,72–76]. Despite this, cells in the picoplankton size range (0.2–2 μm) can still constitute an important contribution to the energetic demands of these organisms [36].

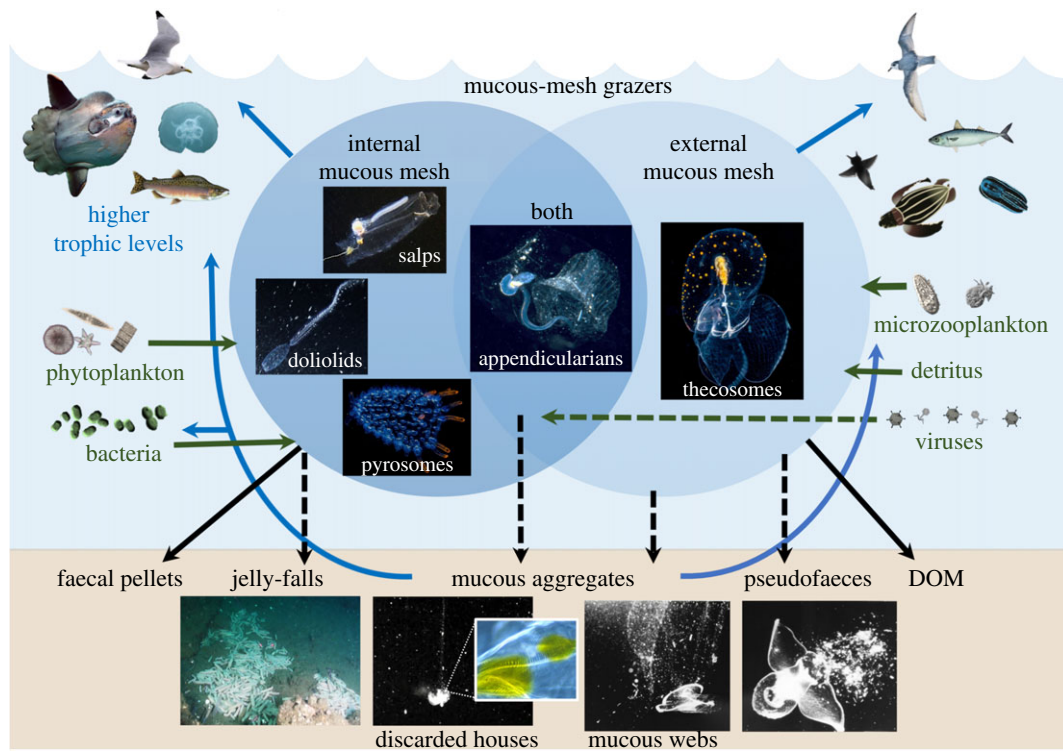


Figure 3. Contributions of mucous-mesh grazers to the ocean food web. Arrows show common flux pathways (solid line) and pathways unique to a specific group (dashed line), including jelly-falls (*Pyrosoma atlanticum*, courtesy of S. Marion), appendicularian houses (inset shows fluorescent inclusions in the house rudiment of *Oikopleura albicans*), mucous webs and pseudofaeces (*Corella calceola* from Gilmer [12], courtesy of R. Gilmer). Pyrosome and thecosome photographs courtesy of Mike Bartick; appendicularian photograph courtesy of Linda Ianniello. (Online version in colour.)

The effective pore size of the mesh is inconstant, depending upon environmental conditions and animal behaviour—for example, through mesh clogging, which can depend upon the ambient particle size and concentrations, or the mucus translational speed, which may affect mesh stretching (electronic supplementary material, table S2). While the mucous filters of tunicates are usually arranged in a rectangular mesh pattern (figure 2) [36,77], the pores of pteropod webs are more irregular [51]. We evaluate the differential size retention patterns by each taxon.

Although historically appendicularians have been assumed to feed non-selectively [5,6,78], we argue that this is a misrepresentation, because the house necessarily causes size-dependent selection by preventing some particles from being ingested [71,79]. For most species of appendicularians, size-dependent selection first occurs at the inlet filter, which excludes large particles (approx. 15–54 μm , depending on the species) from entering the house [80,81]. Spinous particles, such as *Trichodesmium* or foraminifera, as well as large dinoflagellates and diatoms, detritus and metazoans are often excluded [50,80,81]. These particles may or may not remain associated with the house when it is discarded, depending on how strongly they adhere to the filter and whether or not they are dislodged during tail arrests and associated back-flushing of the filters [82–84]. Some appendicularians lack inlet filters and thus the dimensions of the incurrent openings are the only limitation on the size of particles that may enter the house [80]. In addition to inlet filters, *Fritillaria borealis* can exclude large particles (greater than 30 μm) by arresting them against the anterior wall of the tail chamber and ejecting them from the house [83].

In Oikopleurids, size-dependent selection then occurs at the food-concentrating filters on which smaller particles are more likely to remain stuck [5,20,85,86]. After conveyance through the food-concentrating filter, particles reach the

pharyngeal filter, which has a left-skewed retention efficiency curve that declines below approximately 3 μm for larger species (*O. vanhoeffeni*) [87,88] and approximately 1–2 μm for smaller species (*O. dioica* and *F. borealis*) [89]. However, gut content analysis and experiments with live prey indicate that appendicularians can consume small bacteria and large viruses (less than 0.3 μm) [90–92]. *Oikopleura dioica* can even filter viruses (160–180 nm) at rates comparable to those of larger algae (2–50 $\text{ml}^{-1} \text{ind}^{-1} \text{day}^{-1}$) [92].

The pharyngeal filter of thaliaceans appears less efficient at retaining small particles than does that of appendicularians. Experimental evidence shows that many species of salps retain particles less than 2–4 μm with less than 100% efficiency [93,94], with only approximately 15% efficiency of 1.0 μm particles [73], although mathematical models predict higher retention of smaller particles through hydrosol mechanisms [36]. Experimental results show *Pegea confoederata* can ingest particles down to 0.5 μm and mathematical modelling suggests it may capture particles as small as 0.05 μm through hydrosol mechanisms, but only at less than 2% efficiency [36].

The size-retention patterns of doliolids and pyrosomes remain less clear [77]. Evidence from chemostats [74], mesocosms [75], incubations [95] and faecal pellet analysis [96] indicates doliolids can capture submicron free-living bacteria (0.2 μm) with unknown efficiency. Measurements of the mesh of the pyrosome *Pyrosoma atlanticum* [97] suggest submicron particle capture is likely (electronic supplementary material, table S2). The only study to date on size selectivity of pyrosomes showed favourable selection of particles greater than 10 μm [76]. The smallest cells identified in *P. atlanticum* faecal pellets were 3–5 μm phytoplankton [72], but a recent study hypothesized that a swarm of *P. spinosum* was sustained by high densities of *Synechococcus* and flagellates approximately 1–3 μm [98].

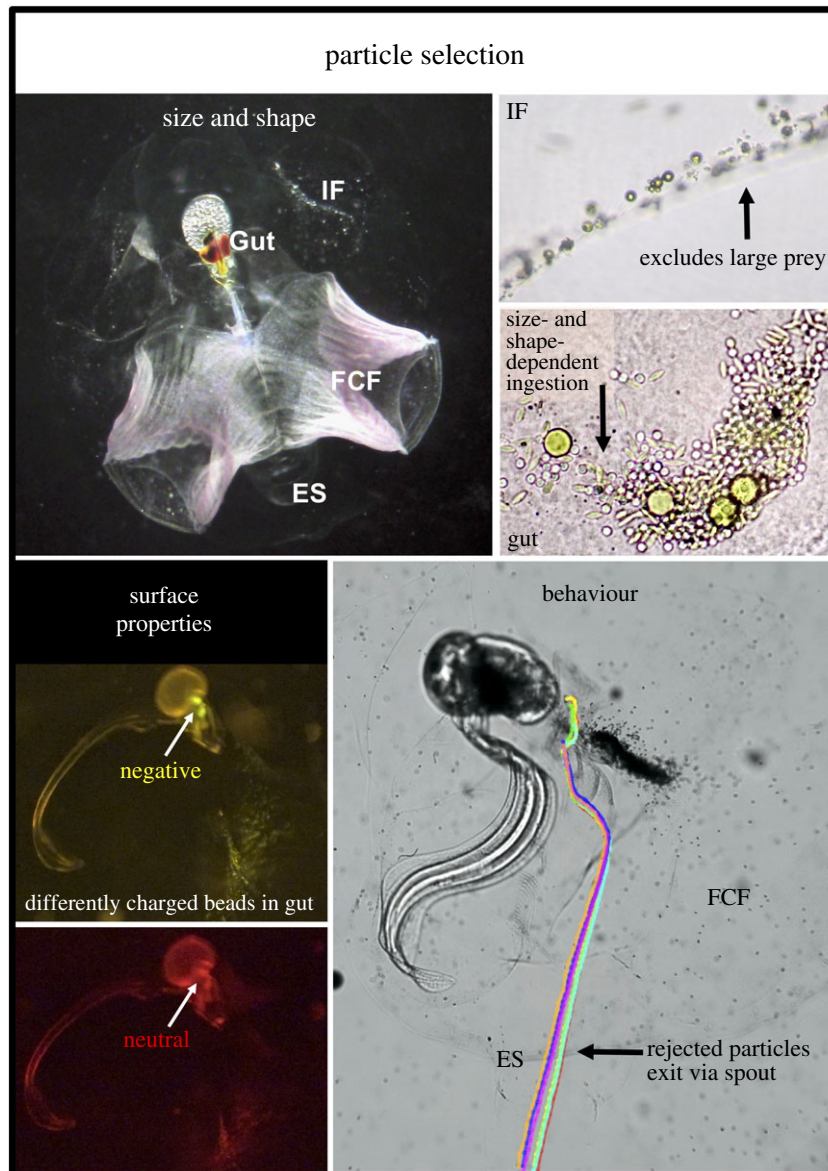


Figure 4. Physical and behavioural particle selection mechanisms of mucous-mesh grazers using the appendicularian *Oikopleura dioica* as a model. The inlet filters (IF) exclude large and spinous prey from entering the house. Small particles, such as the red carmine dye, are more likely to adhere to the food-concentrating filter (FCF). Both of these filtration processes determine what reaches the pharyngeal filter and gut. Surface properties, such as charge, influence particle interactions with the mucous filters (courtesy of A. Karim). Particles rejected by behavioural mechanisms (shown by coloured tracks) can exit the house via the exit spout (ES). (Online version in colour.)

Thecosomes capture a wide range of particles, including small copepods, diatoms, dinoflagellates, coccolithophores, protozoans, detritus and bacteria [35,51,99]. The upper size limit for particle capture is set by the maximum dimensions of the tract used to transport the web to the mouth, which is in the range of 200–800 μm [51]. Clearance of small particles (less than 1 μm) may be facilitated by particle aggregation in mucus produced during spawning, or by direct capture through adhesion to the mucous web [27,51].

(b) Shape

Filter-feeding is defined as ‘feeding by passing the surrounding water through structures that retain particles mainly according to size and shape’ [100]. Despite this, only two studies have explicitly examined the effect of shape on selectivity by mucous-mesh grazers; both focused on appendicularians. In one, the minimum diameter of ellipsoidal particles was the key variable for determining how cells were grazed by *O. dioica* [71]. In another, retention by *O. dioica*

depended on algal cell shape, algal concentration, and whether the animals were fed a monoculture or a mixed algal suspension [101]. A smaller alga with projecting spines was often retained on the inlet filters and blocked the entry of the larger particles into the house [101]. A few other studies have suggested that appendicularians may exhibit reduced ingestion of spinous prey [50,85,102]. Otherwise, the effects of particle shape on selection remain largely overlooked in spite of the abundance of non-spherical particles in the ocean.

(c) Surface properties

A growing body of work calls for a re-evaluation of the role of particle surface properties in dietary selection in the ocean. Surface properties, including charge [103–105], biochemical coatings [106] and hydrophobicity [103,105,107–109] affect particle retention by suspension-feeders. Understanding how surface properties affect selection by mucous-mesh grazers requires a biochemical characterization of both the grazer’s mucus and the prey particles. Although gastropod mucus has

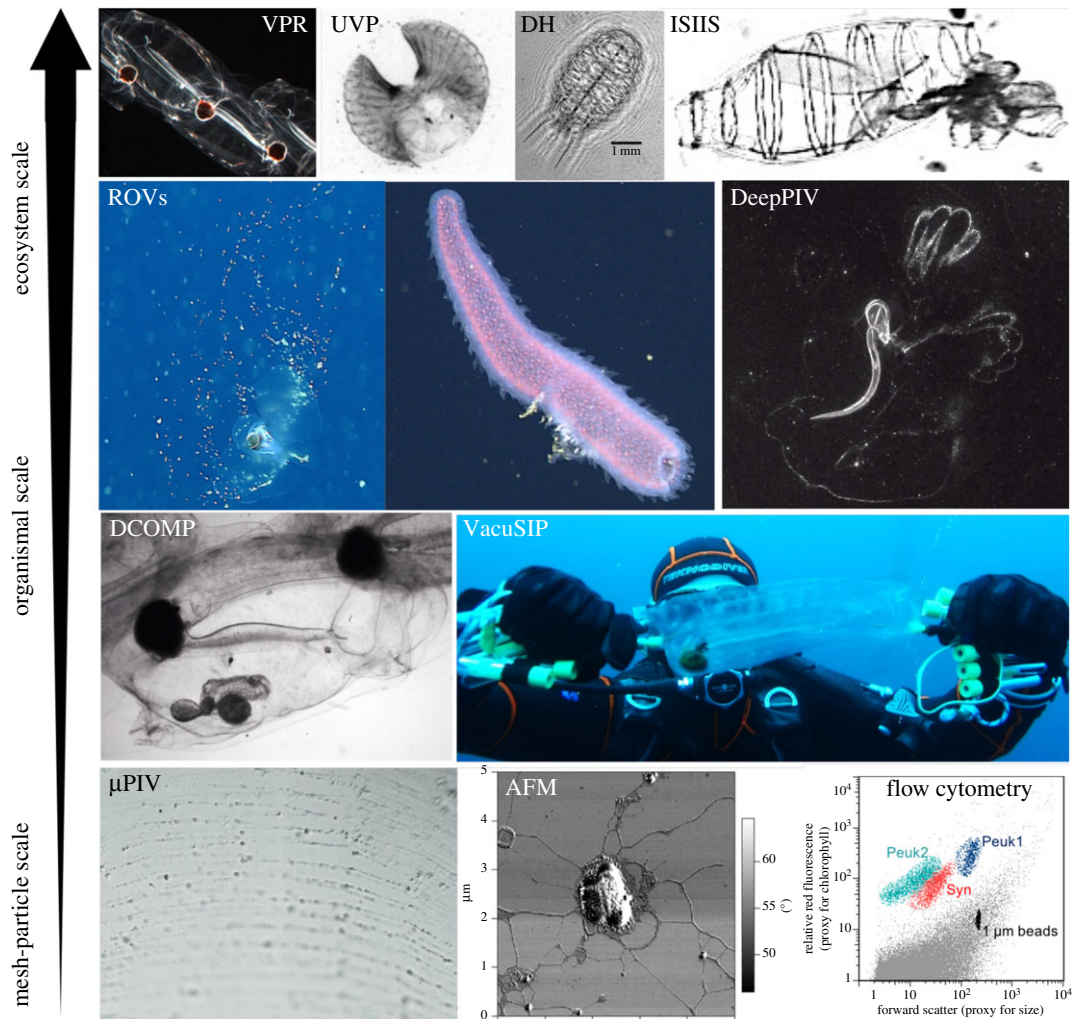


Figure 5. Future directions for investigating feeding by mucous-mesh grazers at different spatial scales. Mesh-particle scale techniques: micro-scale particle image velocimetry (μ PIV) [127]; atomic force microscopy (AFM) topographic image of two conjoint *Synechococcus* cells surrounded by a gel matrix (courtesy of F. Malfatti [128]); flow cytometry cytogram showing prey particles (Syn: *Synechococcus*, Peuks: picoeukaryotes) from pyrosome gut contents (courtesy of A. Thompson). Diver-operated methods: Diver Controlled Observation and Measurement of Plankton (DCOMP) (*Weelia cylindrica*); VacuSIP (courtesy of A. Dadon-Pilosof). Remotely operated systems: remotely operated vehicles (ROVs) (Pteropod © 2008 MBARI, courtesy of S. Bush; *Pyrosoma atlanticum* © 2014 MBARI); DeepPIV (*Bathochordaeus stygius*, courtesy of K. Katija). Towed systems: video plankton recorder (VPR) (*Salpa aspera*, courtesy of C. Davis [129]); underwater vision profiler (UVP) (appendicularian house, courtesy of L. Stemmann [130]); digital holography (DH) (*Thalia democratica*, courtesy of N. Loomis [131]); *In situ* Ichthyoplankton Imaging System (ISIIS) (budding doliolid, courtesy of M. Schmid [132]). (Online version in colour.)

been characterized—consisting of protein–polysaccharides, often with negatively charged acidic carbohydrates—the mucus of pteropod webs has not [110]. Benthic tunicate mucous meshes also contain acidic mucopolysaccharides and mucoproteins [77,111], but the molecular compositions of pelagic tunicate meshes appear to be quite distinct [112].

Despite the high likelihood that particle surface properties play a role in dietary selection, only one study to date has examined this in mucous-mesh grazers. *Oikopleura albicans* removed cyanobacteria, but had null or low retention of the similarly sized SAR 11 heterotrophic bacterial clade [108]. Cell surface hydrophobicity was invoked as a probable mechanism for the observed retention patterns because the SAR 11 clade had a lower hydrophobic interaction chromatography index than other bacterial phylotypes measured [108].

6. Behavioural selection mechanisms

Among mucous-mesh grazers, appendicularians exhibit the greatest array of behavioural mechanisms for selection of

particles (figure 4). At least three particle rejection mechanisms exist: (i) secretion of the pharyngeal filter may cease, causing particles to exit via the spiracles [113]; (ii) the spiracles can create a flow reversal when undesirable particles contact sensory hairs on the lips, rejecting individual particles out of the mouth or buccal tube [20,82,114–116]; (iii) the lower lip can cover the mouth, causing bulk particles to be rejected non-selectively via ‘pipe-smoking’ [113,114,117], possibly in response to satiation at high particle concentrations (greater than 20 000 cells ml^{-1}) [118].

Thaliaceans have a limited array of behavioural selection mechanisms [119]. The different classes have a sensory structure—some shared and some unique—to respond primarily to mechanical and chemical stimuli [120]. Doliolids and salps can perform a ‘crossed reflex’ to reject food, swimming backwards to prevent large objects from entering the pharynx [29,121,122]. Doliolids can also arrest the cilia of the gill bars when large or noxious particles contact the mouth, crushing spinous cells into smaller pieces by cyclically reversing the mucus cord prior to ingestion [29]. Pyrosomes can also arrest the gill cilia in response to large particles [120].

Only a few field observations have been made of thecosomes feeding [12,51,58]. Like thaliaceans, thecosomes have a behavioural response that allows them to dislodge excessive food particles through vigorous beating of the wings [51], but production of pseudofaeces is their primary mechanism for behavioural selection of particles. The ciliary pathways on the mantle lining, footlobes and wings sort and reject prey particles prior to ingestion [35]. Rejected material mixes with mucus (pseudofaeces) and is transported away from the mouth and web by cilia on the footlobes [35].

Swimming is an additional mechanism for behavioural selection by appendicularians, pteropods and some thaliaceans. After ingesting a web, thecosomes can either swim to a new location to secrete a new web, or may set sequential webs in the same location [12]. By regulating the speed of the tail beat, cultured *O. dioica* may move through different particle environments and select favourable patches to dwell [82]. *Oikopleura dioica* swim more at low particle concentrations and reduce tail beat frequency at high particle concentrations—a behavioural mechanism that reduces the negative effects of high food concentrations [118]. House abandonment may be an additional response to an undesirable particle field [5].

7. Future directions

Mounting evidence overturns the paradigm that mucus-mesh grazers are non-selective and instead shows that mesh morphology, behaviour, hydrodynamics and particle properties play important roles in determining particle selection. Further advances will yield a more informed understanding of selective processes and the consequences for food-web dynamics and particle export.

Culture advancements have been made for the pteropod *Limacina helicina* [123] and the appendicularians *O. dioica* [124] and *F. borealis* (JM Bouquet 2017, personal communication). Earlier efforts to culture salps [125] and doliolids [126] have not been replicated; still, continued developments in culture techniques could allow for more detailed observations at the level of feeding structures and controlled feeding incubations.

The fragile nature of mucous-mesh grazers has hampered previous efforts to study them. The most promising tools allow for undisturbed observations in the field, including diver-operated, towed and remotely operated systems (figure 5). Most recently, the filtration rates [133] and size selectivity [134] of giant appendicularians were quantified with DeepPIV, and efforts are underway to investigate the selectivity of salps using the VacuSIP technique [135] coupled with Next Generation Sequencing (A Dadon-Pilosof 2017, personal communication) (figure 5). Many of these systems allow for quantification of non-uniform selection on natural prey assemblages at the same time that they allow for visualizations of the particular mechanisms driving selection.

Understanding the mechanisms of selection by mucous-mesh grazers is particularly important in the context of changing ocean conditions. Climate change may impact mucous-mesh grazers through various means, including ocean temperature, density gradients, pH, nutrient distributions, and changes in primary production, cell size or morphology [136–138]. A better understanding of the selectivity of mucous-mesh grazers is a prerequisite to predicting how their grazing impact may shift under changing ocean regimes. For example, if ambient particle size spectra shift, measurements of size-driven selection will inform how particles will be differentially grazed. Ultimately, such interactions can have significant ramifications for ocean food-web dynamics and biogeochemical cycling.

Data accessibility. This article has no additional data.

Authors' contributions. K.R.S. and K.R.C. conceived of the review. K.R.C. led the writing of the manuscript. K.R.S. and F.L. helped in the drafting and revising of the article. All the authors gave their final approval for publication.

Competing interests. We declare we have no competing interests.

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