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Review

Gelatinous larvacean zooplankton can enhance trophic transfer and carbon sequestration

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Larvaceans are gelatinous zooplankton abundant throughout the ocean. Larvaceans have been overlooked in research because they are difficult to collect and are perceived as being unimportant in biogeochemical cycles and food-webs. We synthesise evidence that their unique biology enables larvaceans to transfer more carbon to higher trophic levels and deeper into the ocean than is commonly appreciated. Larvaceans could become even more important in the Anthropocene because they eat small phytoplankton that are predicted to become more prevalent under climate change, thus moderating projected future declines in ocean productivity and fisheries. We identify critical knowledge gaps and argue that larvaceans should be incorporated into ecosystem assessments and biogeochemical models to improve predictions of the future ocean.

Highlights

Larvaceans are among the most widespread gelatinous organisms of the zooplankton and have extraordinary growth rates, on the same time scale as that of their protozoan prey.

Climate change is expected to favour picoplankton and the microbial loop. Larvaceans can directly feed on the smallest plankton, leading to a competitive advantage. This 'larvacean shunt' could counteract elongated food chains that are projected for our future ocean.

Larvaceans produce marine snow that might sustain carbon export in a future ocean where primary producers are smaller.

Larvaceans are food for many fish and invertebrate species, indicating their importance in trophic transfer. They may be especially important to mesopelagic fish, indirectly increasing carbon sequestration due to these fishes' production of faecal pellets at depth.

Larvaceans are important for repackaging particles, thereby accelerating carbon export and sequestration.

Larvaceans are abundant gelatinous zooplankton with a unique biology

Global change is leading to a reorganisation of food-web structure and functioning. **Gelatinous zooplankton** (see Glossary), especially **jellyfish**, have recently gained considerable attention, linked to an undesirable ecosystem state during their blooms that can negatively impact higher trophic levels [1]. Gelatinous zooplankton are pelagic and share the characteristics of a soft, translucent body texture. But they include groups with different evolutionary histories and ecological roles, they feed at a range of trophic levels, and they vary in their carbon content by two orders of magnitude. Gelatinous zooplankton include **pelagic tunicates** with **larvaceans**, doliolids, pyrosomes, and **salps**, as well as comb jellies (ctenophores) and true cnidarian jellyfish. Pelagic tunicates, distributed throughout the worlds' oceans, are filter-feeders that prey on the smallest food particles by passing large volumes of water through sheets of mucus [2]. Of all gelatinous zooplankton, pelagic tunicates of the class Larvacea are often the most abundant after copepods (crustaceans) from tropical [3] to polar [4] ecosystems (Box 1). Larvaceans show body sizes and carbon weights similar to those of copepods [5,6], but it is their **secondary production** potential that makes them truly remarkable. Larvaceans have faster **growth rates** and much shorter **generation times** than copepods (Box 2). In combination with their ability to feed on the smallest organisms in the oceans, larvaceans can shunt energy from the microbial loop to fish, particularly to **mesopelagic fish** [7,8]. Additionally, larvaceans build themselves a '**house**' that consists of a set of filters (Box 1). The houses accumulate carbon, are regularly discarded, and represent an important contribution to the carbon cycle. These characteristics make larvaceans critical to our understanding and modelling of how climate change impacts marine ecosystems. Despite their potentially major role in marine ecosystems, with many experiments documenting their importance (e.g., [2,5]), larvaceans have been largely ignored in biogeochemical and ecosystem models. Their inclusion could help project changes in fish biomass and carbon cycling under

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climate change. It is therefore timely to review the role of larvaceans in marine ecosystems. In this review, we first detail several key roles played by larvaceans, then we describe their potential response to climate change in the Anthropocene with implications for marine systems, and finally we identify important questions to further understand their importance in the future ocean.

Major roles of larvaceans in marine ecosystems

Larvaceans sustain higher trophic levels

The common perception that larvaceans are relatively unimportant to higher trophic levels is partly a consequence of their underestimation in classical gut-content analysis due to their rapid digestion [9,10]. Common databases used by ecologists, fish biologists, and modellers reinforce this point: an analysis of the diets of 35 000 fish species in FishBase returns only 55 fish species that eat larvaceans, and an analysis of the 85 000 marine species in SeaLifeBase reports only seven nonfish species eating larvaceans. This has led to the impression that gelatinous zooplankton, including larvaceans, transfer little carbon up the food-web [1]. However, multiple lines of evidence confirm that larvaceans are important prey items for many marine species, including commercially important fish.

In a review of the predators of larvaceans, Purcell *et al.* [11] found that they are consumed by >80 invertebrate species, including chaetognaths, ctenophores, jellyfish, and copepods, as well as by >350 vertebrates, mainly fish. Calanoid copepods, for example, can exert a significant predation control on larvacean populations by feeding on their eggs and early life stages, which are in the same size range as their other prey such as ciliates [12] (Figure 1). At times, larvaceans represent

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Box 1. What are larvaceans?

Larvaceans are translucent, free-swimming, highly-specialised, holoplanktonic, pelagic tunicates [87]. The name 'larvacea' refers to the close similarity of their adults with the tunicate tadpole larvae. Larvacea is a class synonym for Appendicularia, but it is preferred to avoid confusion with the genus name *Appendicularia.*

The larvacean body comprises a trunk, usually 0.5–4 mm long, when adult, with a much longer tail (Figure I). Giant larvaceans found in the mesopelagic zone (e.g., *Bathochordaeus spp.*) have total lengths of 40 mm [45].

The class Larvacea (synonyms: Appendicularia, Copelata) has 68 species in three families (Oikopleuridae, Fritillariidae, Kowalevskiidae). Species number is grossly underestimated, especially for mesopelagic [68] and cosmopolitan species due to cryptic diversity [69]. There are more warm-water than cold-water species.

Larvaceans are found in coastal and oceanic waters of all oceans, primarily in near-surface waters but also at mesopelagic and hadal depths [53]. At night, spawning aggregations can occur in surface waters [86]. Density is independent of chlorophyll concentration (Figure II).

Larvaceans reproduce sexually and are sequential hermaphrodites, although one species, *Oikopleura dioica*, has separate sexes. The generation time of *O. doica* is short, varying from 1 day at 27–29°C [77] to 16 days at 10°C [88]; 50–500 eggs are produced [5,86].

The tail is used to generate the feeding current and also provides locomotion for escape sprints (maximum 75 mm/s outside their house) or upward swimming for spawning (average 47 mm/s) [86]. Larvaceans inside their houses are slow and thus are common prey [11].

Feeding, house production, and carbon export

Larvaceans secrete a delicate house of cellulose and mucopolysaccharides [89] around themselves like a bubble that supports a network of filters. This house is about seven times longer than the animal trunk [47] and is usually destroyed during sampling. Larvaceans optimise their food intake by using different filters within the house to concentrate bacteria and picophytoplankton, using their tail as pump[ii]. The fine filters can quickly become clogged. *O. dioica* has up to three house rudiments on the trunk, and it discards its house every 3–4 h at 12°C [46], up to 40 houses/day [27]. Fritillariid larvaceans can deflate their house, swim away, and reinflate it within seconds [90]. Discarded houses, together with heavy faecal pellets and trapped food particles, help to export carbon, but are also consumed by many predators.

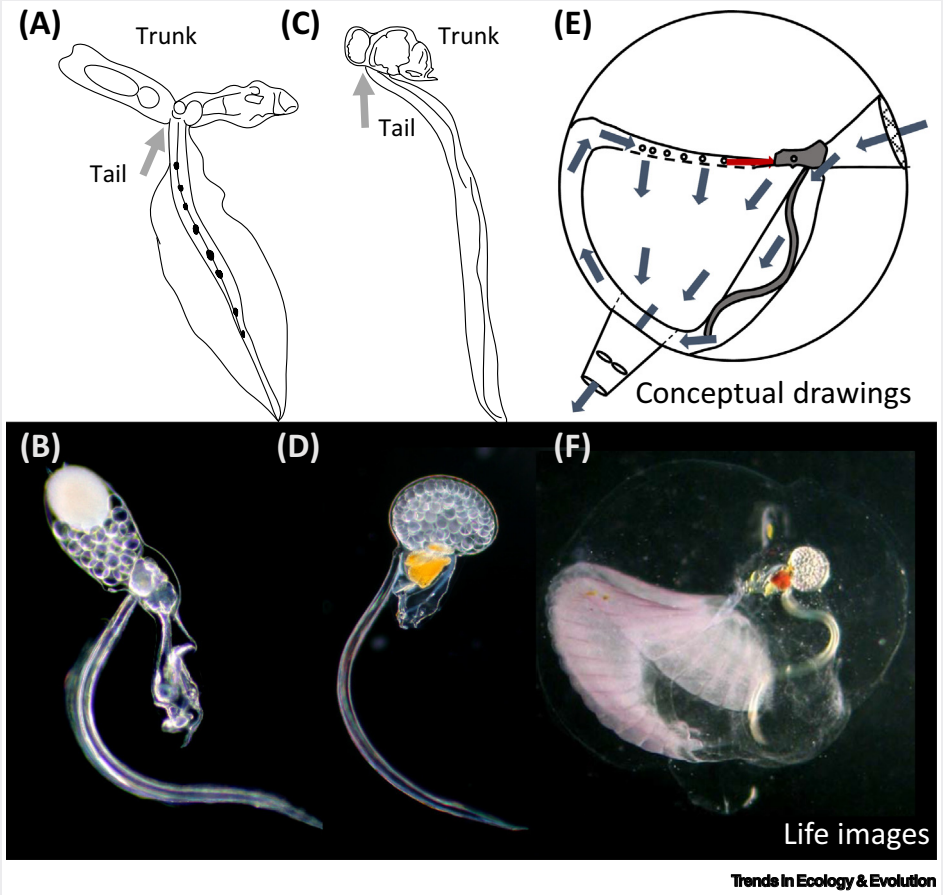

Figure I. Morphological characteristics of two larvacean families (A,B): Fritillariidae with (B) *Fritillaria borealis* (hermaphrodite with eggs/sperm) and (C–F) *Oikopleuridae*, with (D) *Oikopleura dioica* (mature female), and (E,F) the Oikopleuridae house. Arrows indicate water flow (blue) and the junction between tail and trunk (grey) which represents an identification characteristic. Image credit for (B,D): Anne Aasjord.

>90% of the diet of pelagic fish species such as pink salmon (*Oncorhynchus gorbuscha*) [13] and are an important prey item for commercial species such as Atlantic mackerel (*Scomber scombrus*), Atlantic herring (*Clupea harengus*), and Atlantic butterfish (*Peprilus triacanthus*) [14]. An analysis of 450 000 fish stomachs along the US West Coast confirmed that pelagic tunicates, including larvaceans, are widely consumed by fish [15]. Some fish species prefer larvaceans, with positive selection confirmed for larvae and adults of several mesopelagic fish species [7,8,16–18], larvae of different tuna species [10,19], and adult polar cod (*Boreogadus saida*) [20]. Bjørdal *et al.* [21] found that as mackerel expanded poleward with warming in the North Atlantic, juvenile mackerel fed predominately on larvaceans, and they were the second most important prey item for adults. Similarly, environmental warming has induced a diet shift in walleye Pollock (*Theragra chalcogramma*), with five times more larvaceans in their diet in warm (2001–2011) rather than cold (1989–2000) periods [22].

In addition to larvaceans themselves, their discarded carbon-rich houses are often consumed by zooplankton such as copepods [23], euphausiid larvae [23], and fish [24,25], sometimes even

Glossary

***Bathochordaeus*:** a larvacean genus often referred to as 'giant larvaceans'. Living below the productive surface layer, they can reach gigantic house diameters of up to 2 m and could be important for repackaging marine snow and in carbon sequestration.

Biological pump: carbon export mediated by biological processes and biota in the ocean. It is responsible for ocean CO_2 uptake by exporting photosynthetically fixed carbon from the surface ocean.

Carbon export/sequestration: the process of carbon leaving the sunlit surface layers and entering the deep ocean. Once exported from surface layers, its return may take years to centuries, or it could be sequestered and stored in sediments for millennia. Carbon is typically exported as faecal material, dead bodies, or shells, but in the case of larvaceans discarded houses can be important.

Diel vertical migration (DVM): diel (daily) vertical migration between deep and surface waters to avoid predation.

Gelatinous zooplankton: soft-bodied or translucent organisms belonging to evolutionary and ecologically distinct groups that have varying carbon contents.

Generation time: time taken for an organism to complete its life cycle. For larvaceans, the minimum time from fertilised egg to new spawning adult is 24 h, of the same order as that of their protozoan prey.

Growth rate: the rate at which an animal increases its body mass. It is generally referenced to its initial weight at the start of the growth period and expressed as carbon increase in percentage per day.

House: external filter structure, unique to larvaceans, used to feed on the smallest plankton, including viruses. Houses are regularly discarded, forming marine snow.

Jellyfish: transparent macrozooplankton with low carbon content from the phylum Cnidaria.

Larvaceans: gelatinous zooplankton feeding on picoplankton and larger particles via an external filter, called a house. Competing taxonomic schema have used Larvacea, Appendicularia, and Copelata as synonyms. Larvaceans are split into three families.

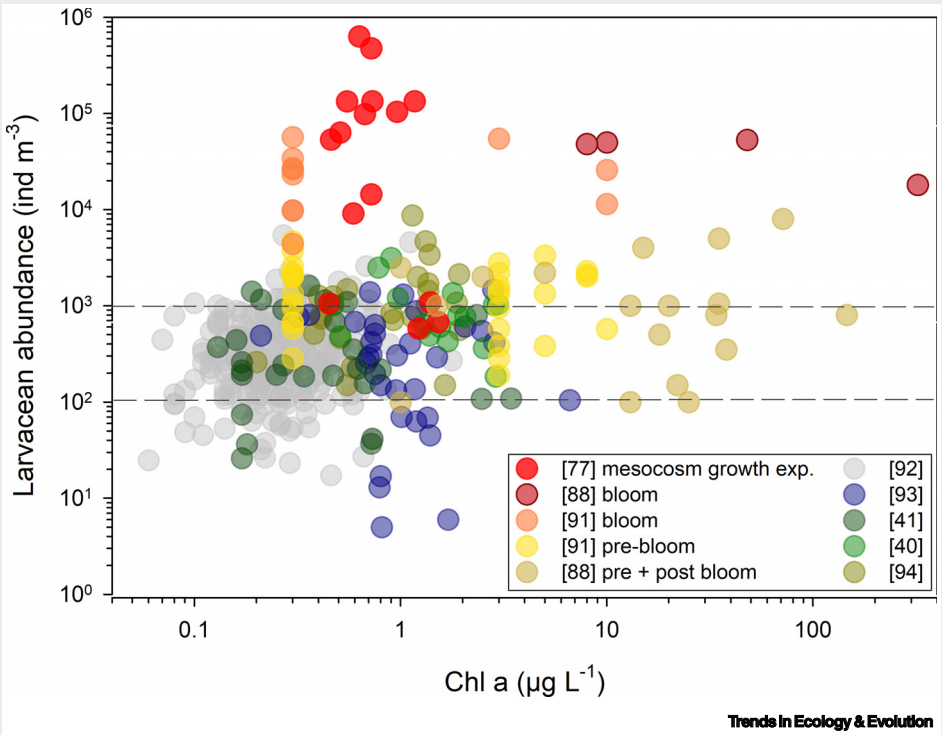

Figure II. Selective compilation of larvacean abundances versus chlorophyll (Chl) concentrations. Hatched box indicates commonly observed abundances, while dark red [88] and orange [91] depict bloom abundances, and light red mesocosm growth experiments [77]. Abbreviation: ind, individuals. See also [40,41,92–94].

Marine snow: detritus sinking in the water column that exports carbon from surface to deeper waters. This carbon is remineralised through respiration, eaten, fragmented, or sequestered.
Mesopelagic fish: small fish living in the mesopelagic zone (200–1000 m), exhibiting extensive diel vertical migration.
Pelagic tunicates: holoplanktonic marine organisms with a rubbery, translucent outer coat. They feed on small prey, grow quickly, and exhibit population outbreaks. Taxonomically, they include the class Larvacea (= Appendicularia) and the class Thaliacea with the orders Salpida, Doliolida, and Pyrosomida, all within the phylum Chordata.
Picoplankton: single-celled plankton with body sizes of 0.2–2 µm. Very abundant globally, they are expected to thrive under climate change and play a critical role in marine food-webs and carbon cycles. Includes eukaryotic protists and bacteria.
Salps: barrel-shaped, colony-forming pelagic tunicates that feed on small plankton and produce fast-sinking faecal pellets and carcasses. Some exhibit diel vertical migration. Colonies can reach >30 m in length.
Secondary production: biomass produced by heterotrophic organisms that consume primary producers. It includes the biomass produced through growth, reproduction, and other products (e.g., houses) of organisms, and feeds other animals.
Trophic transfer: the amount of matter or energy that moves from one trophic level to the one above it.

selectively [23]. The carbon content of a newly secreted house, without attached particles, represents ~15% of the body carbon of the animal [26]. Considering that several houses are produced per day (Box 1), house production corresponds to an expenditure of 75–220% of an individual's biomass per day [27]. Houses also accumulate food particles, faecal material, and detritus, adding many times an individual's biomass in trapped food particles to the discarded houses [26]. Thus, houses alone contribute substantial amounts of carbon, both as food for higher trophic levels and as source of **marine snow** for downward export.

Larvaceans are more nutritious as food than other gelatinous zooplankton. Typically, larvaceans have a carbon content (5% of wet weight) that is ten times higher than that of cnidarians (jellyfish 0.5%), 100 times higher than lobate ctenophores (comb jellies, 0.05%) and six times higher than salps (0.8%) [5,6]. With their relatively high carbon content, larvaceans are more similar to copepods (9.5%) and fish (10%) [6,28] than to other gelatinous zooplankton.

The 'larvacean shunt' short-circuits traditional food-webs

The ability of larvaceans to feed upon the smallest phytoplankton cells [2,29–31], heterotrophic bacteria [31], and even some viruses [32] means that they can access prey unavailable to most crustacean zooplankton such as copepods and krill (Figure 1). While similar in body size to copepods, larvaceans have prey-to-predator size ratios equivalent to a baleen whale eating krill (Figure 1) [33–35]. Although the smallest particles are cleared with lower efficiencies [31,33], heterotrophic bacteria constitute ~20% of the diet of larvaceans [31], and they can remove >60% of the **picoplankton** standing stock per day [36]. Larvaceans can thus 'short-circuit' the

Box 2. Larvacean abundance, growth, and secondary production

Abundance

Several large-scale studies suggest that larvaceans are the second most abundant zooplankton group [4,72], after copepods. Based on 659 samples using a 100-μm mesh net around Australia, Richardson *et al.* [3] found larvaceans were the second most abundant zooplankton group, averaging 10% of the abundance of copepods. Reanalyses of the Continuous Plankton Recorder (CPR) database [95] show that, globally, larvaceans make up ~7.1% of all zooplankton, and 8.2% of copepods, while around Australia larvaceans make up 14.2% of all zooplankton, and 19% of the abundance of copepods. In the Pacific Arctic, net samples show that larvaceans represent ~31% of the total zooplankton abundance [72]. Larvaceans are also more abundant and ubiquitous than other filter-feeding gelatinous zooplankton such as salps, doliolids, and pyrosomes (Figure I), which are patchy in their distribution [87].

Growth

Larvaceans grow faster than any other metazoan on a carbon-specific basis (Figure II). Zooplankton growth rate exhibits a strong allometric relationship with biomass, with larvaceans consistently above the mean relationship. Their growth rate is an order of magnitude faster than that of copepods and cnidarians, two orders of magnitude faster than that of euphausiids, and generally faster than the growth rates of other gelatinous filter-feeding zooplankton such as salps and doliolids. Although orders of magnitude larger in size, growth rates of larvaceans often rival those of the unicellular flagellates and ciliates. Larvacean growth rates are also relatively insensitive to food limitation, because they can access picoplankton and bacteria that are ubiquitous [96], and thus their prey concentration is generally satiating [31] (Figure II). This contrasts with most other mesozooplankton, which are often food-limited. Their consistently fast growth rates enable them to quickly build up biomass and outcompete other zooplankton groups.

Secondary production

Their relatively high abundances and fast growth rates mean that larvaceans make a substantial contribution to ocean productivity (secondary production). Larvaceans can exceed copepod production by two to five times [37,41], and their houses represent an additional source of production [27], including the food and faecal material trapped within discarded houses. Therefore, the role of larvaceans in the ecosystem is much greater than that represented by their somatic production alone [75], fuelling trophic transfer and carbon sequestration. Hence, larvacean production, rather than their abundance, reveals the true ecosystem importance of larvaceans.

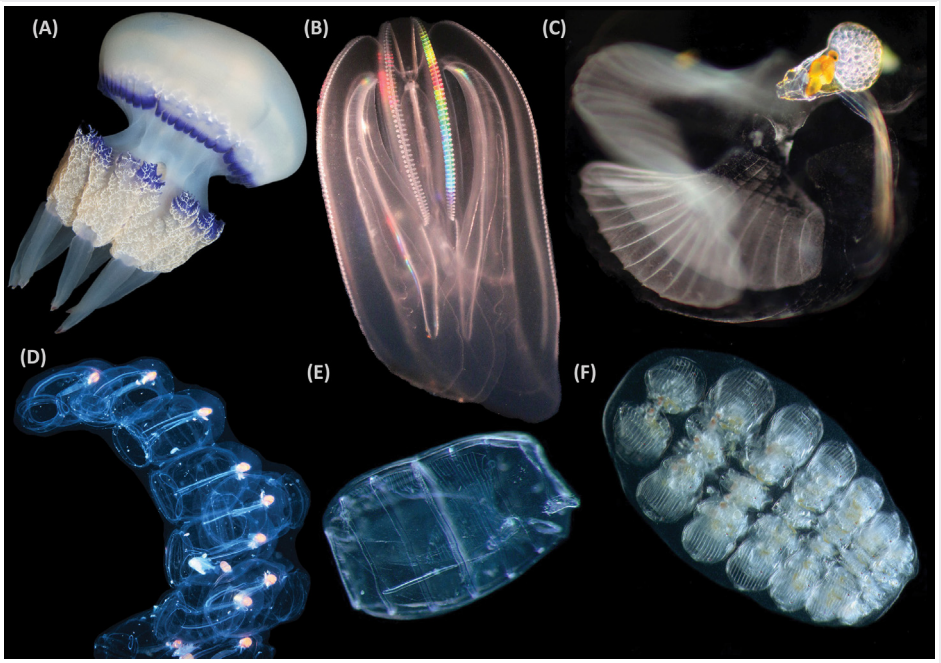

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Figure I. Gelatinous zooplankton (GZ) groups. GZ combine the phyla (A) Cnidaria (including true jellyfish), (B) Ctenophora (comb jellies), and (C–F) pelagic Tunicates within the classes (C) Larvacea and (D–F) Thaliacea with (D) salps, (E) doliolids, (F) pyrosomes. Image credits: (A) Fabrizio Marcuccio, (C) Anne Aasjord.

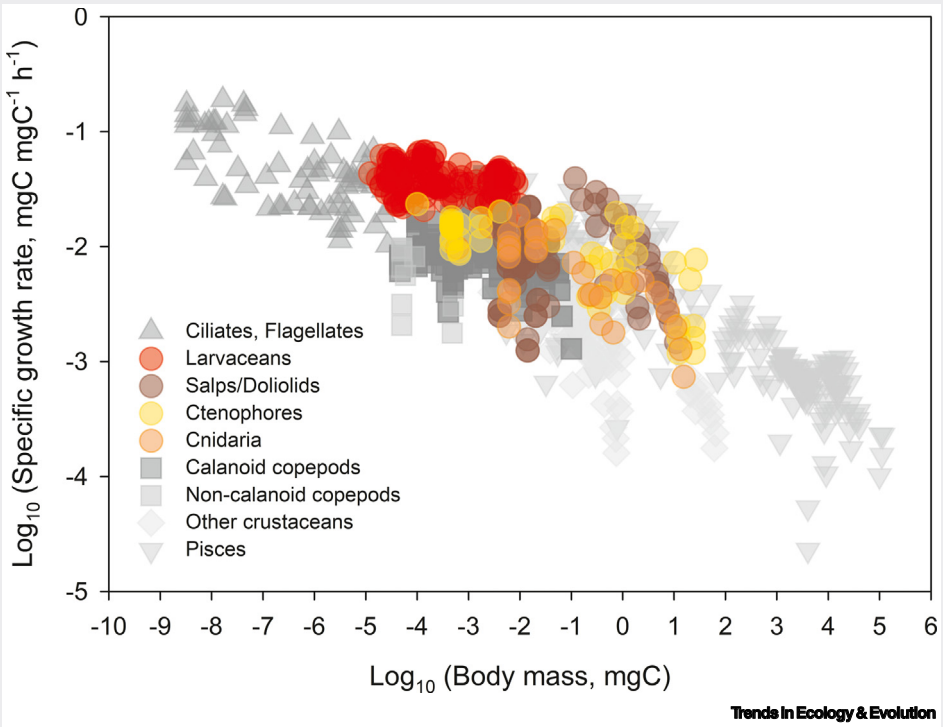


Figure II. Specific growth rates of marine life, corrected to 15°C, covering protists to fish (grey) and gelatinous zooplankton (GZ) (coloured), including larvaceans (red). From [97] supplemented with GZ data from [5,74,98].

'traditional' crustacean-dominated food-web of copepods and krill, efficiently transferring energy from the microbial loop directly to the mesozooplankton size range, where they can then be ingested by fish (e.g., [21,22]). Larvaceans' secondary production estimates can exceed that of crustacean zooplankton [37], especially when small phytoplankton dominate, as is common over most offshore, tropical, and oligotrophic regions [37–41]. The ability of larvaceans to shorten food chains is called the 'larvacean shunt' (Figure 1).

Larvacean houses and the biological pump

Larvaceans play a unique yet underappreciated role exporting carbon from the surface ocean. The **biological pump** includes the passive sinking of various particles such as phytoplankton, marine snow, faecal material, and carcasses, and is further facilitated by the active migration by zooplankton and mesopelagic fish with carbon release at depth (Figure 2A). The biological pump ensures that oceans keep absorbing CO_2 by continually removing photosynthetically fixed carbon from the surface ocean to its interior, sequestering carbon for years to centuries, and thereby regulating the pace of climate change [42,43]; without it, atmospheric CO_2 would be twice as high [42].

Larvaceans build themselves a 'house' that consists of a set of filters to concentrate and feed on the smallest plankton components (Box 1). Discarded larvacean houses are an important source of marine snow [23] and thus key contributors to the biological pump. Houses not remineralised by bacteria or consumed by predators in surface waters exit the sunlight zone aided by their rapid sinking rates. Houses can sink with velocities of up to 300 m/day for surface-dwelling species [44]

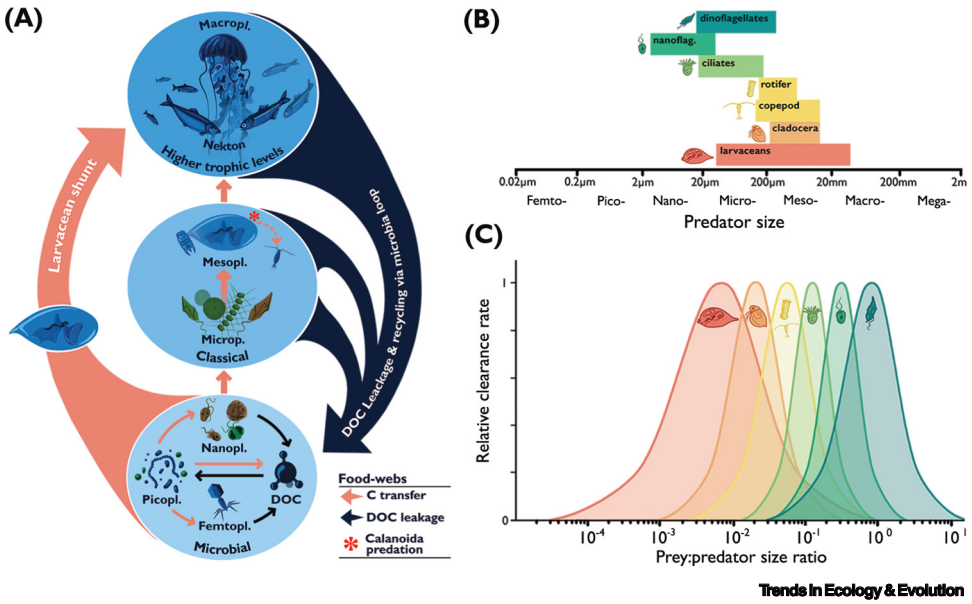
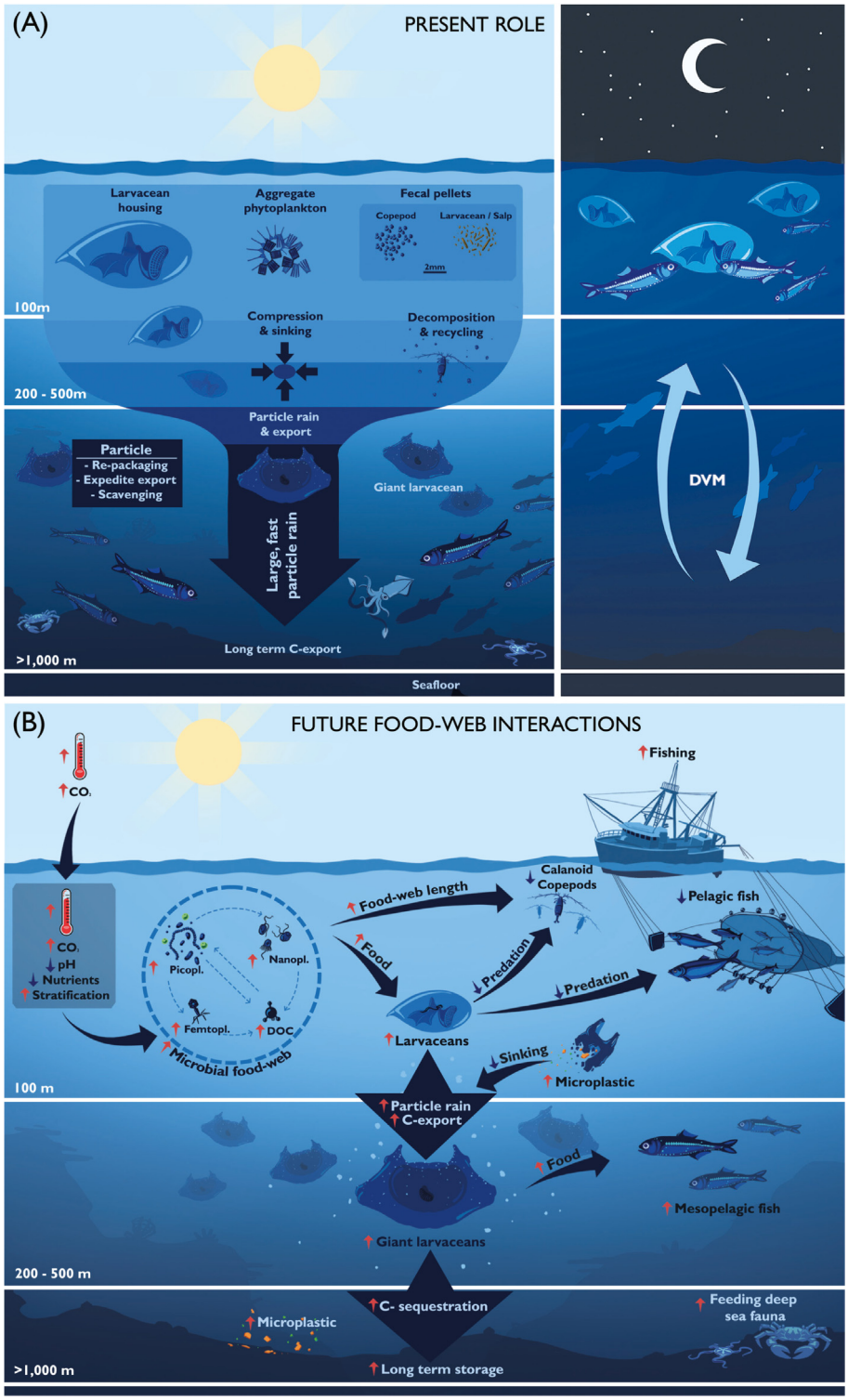


Figure 1. Planktonic trophic relationships with (A) a conceptual food-web including the larvacean shunt, (B) predator sizes, and (C) prey-to-predator size ratios. (A) Pathways illustrating general energy flows in marine environments, including selected gelatinous zooplankton groups, with feeding interactions indicated by orange arrows and autotrophic (green), mixotrophic (brown), and heterotrophic (blue) food-web members, differentiated into microbial and classical food-webs as well as higher trophic levels. The neglected larvacean shunt (left) shortcuts the classical food-web channelling energy from the microbial food-web to higher trophic levels, including different life stages of fish (larval, juvenile, adults). Predation by calanoid copepods counteracts this shortcut [12] as they consume young larvaceans and their eggs, with >5.5 calanoids/l suggested to limit population outbursts [12]. All biological processes leak dissolved organic carbon (DOC), fuelling the microbial food-web (blue arrow). The larvacean shunt links DOC back to higher trophic levels. (B) Size ranges of primary predators covering protists to larvaceans in the ocean along with (C) their relative clearance rate as a function of prey-to-predator size ratios (modified from [33,34] with permission). Larvaceans can feed on organisms >10 000 times smaller than themselves, similar to Baleen Whales eating krill. While respiration is usually related to organism carbon weight (hence body size), feeding and filtration are more strongly correlated with the wet weight of an organism [99], including their feeding apparatus. Given that the house diameter is typically seven times the trunk length [47], the predator-to-prey size ratio is even more extreme (140 000:1). The enlarged house makes larvaceans more vulnerable to visual predators [11].

and 800 m/day for deeper-living, mesopelagic ones [45]. In a temperate ecosystem along the northwest coast of the USA, abandoned houses are exported from surface waters within 2–3 h, with their standing stock turned over four to five times per day [46]. Although houses leak particles during sinking and deflation [47], they remain carbon-rich and can contribute up to 83–100% of the carbon flux to the seafloor, equivalent to an export of 1200 mgC/m^2/day [48,49].

Larvaceans living in the twilight zone of deeper waters (mesopelagic, 200–1000 m) can further accelerate **carbon export/sequestration**. In particular, larvacean species of the genus ***Bathochordaeus***, often referred to as 'giant larvaceans' (Box 1), repackage marine snow into larger fast-sinking particles due to their large houses of up to 2 m in diameter [45]. Giant larvaceans are distributed from the base of the epipelagic throughout the mesopelagic zone, with peak abundance at ~200 m depth [50]. Giant larvaceans can feed on particles of 10–600 µm [35], they clear large water volumes, and thus they concentrate considerable amounts of carbon. *In situ* experiments document average filtration rates of 1000 l/individual/day (maximum 1830 l/ind/d), representing the highest filtration rates for any zooplankton [50]. Giant larvaceans in the California Current Ecosystem have the potential at times to clear the entire 200 m depth layer (between 100 and 300 m depth) in <2 weeks, while on average it is grazed



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within 500 days [50]. Further, Robison *et al*. [51] found that the carbon export of giant larvacean houses was high, with 7.6 gC/m^2/y off California, which matched the missing carbon demand of the benthic community [52]. Hence, discarded larvacean houses can nourish deep-sea biota and help export carbon from surface waters, although its magnitude remains highly uncertain (Figure 2). So far, most of our knowledge about giant mesopelagic larvaceans is based on the California Current Ecosystem, but large larvaceans and deep-dwelling giant larvacean species are widespread [53].

Larvaceans in the Anthropocene

Multiple lines of evidence suggest that larvaceans are likely to be favoured with climate change, with profound repercussions for **trophic transfer** and carbon cycling.

'Larvacean shunt' in a warmer ocean

Climate change is projected to cause a 4–11% decrease in global marine net primary production by 2100 (relative to 2006–2015), in a low- and high-emission future, although there could be much greater declines in some areas [43,54]. Concomitant with this decline in primary production, the abundance of small phytoplankton cells is expected to increase relative to larger phytoplankton cells because of increased stratification and nutrient limitations [55–58]. Similar trends of smaller primary producers during warmer conditions were observed from paleo data over the past 65 million years [58,59], a response further supported by experiments [57,58] and field observations [60]. Globally, however, declines in phytoplankton biomass could be offset by a projected increase in the contribution from faster-growing picoplankton such as *Prochlorococcus* and *Synechococcus* [55,61], which could benefit the larvacean shunt.

Larvaceans can consume prey <1 μm – including *Prochlorococcus* [31], the most widespread picoplankton genus – whereas other filter-feeders such as salps cannot [62]. Therefore, under climate change, the 'salp shunt' could be less efficient than the 'larvacean shunt' in warm-water areas where *Prochlorococcus* is expected to dominate the picoplankton biomass [61]. A model resolving nine zooplankton groups, including larvaceans, showed that a shift towards smaller primary producers led to only a slight increase in food-web length and a potential competitive advantage for larvaceans [39]. Hence, larvaceans could moderate the impacts of smaller phytoplankton on the trophic position of fish by stabilizing food chain length [39].

Carbon export in a warmer ocean

The common paradigm is that climate change with increasing temperatures, enhanced stratification, and nutrient limitation will shift primary production towards smaller phytoplankton [55,58,61] which will reduce the carbon export and thereby the biological carbon pump [43]. However,

Figure 2. Major ecosystem contributions of larvaceans (A) now and (B) in the Anthropocene. (A) Present role of larvaceans. Marine snow primarily arises from larvacean houses, phytoplankton aggregates, and faecal pellets that are impacted by physical (compression, sinking) and biological (decomposition, fragmentation, recycling) processes. Marine snow sinking below 200 m is likely to be sequestered to the deep sea. Giant larvaceans in the mesopelagic can further repackage marine snow into large, fast-sinking particles, providing carbon that feeds deep-sea communities. **Diel vertical migration (DVM)** by mesopelagic fish that feed upon larvaceans in surface waters at night [7] further increases indirect and direct carbon flux. In the future: (B) climate change stressors (warming, higher CO_2, lower pH) with subsequent decreased nutrients (increased stratification) are expected to favour picoplankton and the microbial loop [58], changing food-web interactions. As a consequence, larvaceans could profit due to their competitive advantage in directly utilising small prey and their positive population responses to warming and low pH [100]. However, expected reduced predation from calanoid copepods and pelagic fish due to longer food-webs and increased fishing-mortality could enhance larvacean densities. This translates to higher marine snow production, increased carbon export/sequestration, and provides food for mesopelagic organisms. Larvaceans could also transport microplastic to the deep sea [35], but microplastic changes buoyancy and could decrease sinking speed and carbon export. Increase: red up arrow; decrease: blue down arrow. Schematic not to scale.

larvaceans might complicate this picture. Field data have documented that picoplankton is exported [63,64] and that despite a shift towards smaller phytoplankton, carbon export at depth can remain unchanged [64]. Such sustained export was hypothesised to be a result of a grazer community that shifted towards gelatinous plankton [64]. A recent climate model comparison highlighted that models disagree whether or not there will be a net particulate organic carbon (POC) export by 2100 [65]. We also challenge the unconditional acceptance of the reduced export paradigm, as larvaceans might provide a feedback loop to counteract negative climate change impacts on food-web structure, leading to sustained fish production and carbon sequestration; this deserves further investigation. While surface POC export is important, carbon sequestration is also governed by processes occurring in the mesopelagic [42] where 70–85% of the POC flux is recycled [66]. Increased prevalence of larvaceans in both surface and deeper layers due to climate change could offset projected changes in the biological pump. The addition of larvaceans in ecosystem and biogeochemical models is needed to help solve this question.

Key research is needed to quantify the role of larvaceans

Filling basic knowledge gaps combining traditional and new technology

One reason why larvaceans remain neglected is that estimating their abundance is difficult and often biased with the use of large-meshed nets (Box 2). Net samples also integrate over long distances, averaging over a patchy environment, and often destroy fragile specimens beyond recognition, especially deep-living ones. Advances in *in situ* imaging systems [67] now allow for larger water volumes to be analysed that better represent the entire zooplankton community, including fragile larvaceans and their houses, and record their spatial heterogeneity. Including traditional net samples in *in situ* imaging surveys will further allow for species identification [68] and molecular analyses [69] to confirm species identifications of damaged animals or describe species that are new to science [68]. With the advent of innovative field-based tools – including next-generation sequencing [69], new *in situ* imaging [67], and underwater robots with video and laser-based analyses systems [29] – we are entering a new era of underwater sampling and understanding [70] for larvaceans.

Another reason for the underrepresentation of larvaceans is the belief that they are only warm-water taxa; however, they can be important components in both subpolar and polar waters [71–73] as well as in oligotrophic and eutrophic regions [37,41,74]. Notably, high-latitude species are large-bodied but can still consume small particles [30]. Their seasonal occurrence and often high abundance at ice-edge blooms and in upwelling areas supported by high primary production demonstrate that larvaceans can also consume some of the same particle sizes typically exploited by crustacean zooplankton [34,71,72]. This is suggested to lead to direct competition, especially as larvaceans have been shown to attain much higher community biomasses than copepods during periods [71,72]. A better consideration of larvaceans in highly productive polar waters is overdue.

Finally, field studies are currently biased towards abundance measurements. But larvaceans grow so quickly that even at relatively modest abundances they can make a substantial contribution to secondary production [37,41] and carbon export [75]. Researchers need to move beyond a focus on abundance data alone to consider secondary production as more important than simple standing stock estimates, and explicitly consider their house production as well. Note: Secondary production can also be approximated from species abundances, sizes, and environmental data such as temperature and chlorophyll [41,74].

Evaluating the importance of larvaceans in supporting mid-water fish biomass

It is being debated how the large populations of mesopelagic fish are sustained in the open ocean [76]. One hypothesis is that they are supported by a higher-than-expected trophic transfer

efficiency [76]. If correct, one key mechanism could be the 'larvacean shunt' and direct feeding of mesopelagic fish on larvaceans and their discarded houses containing a large variety of food items from viruses to ciliates. Measurements are needed of the amount of carbon that is transferred via the 'larvacean shunt' through the direct feeding by fish on both larvaceans and their discarded carbon-rich houses. This will require growth experiments with different larvacean species (e.g., [5,37,77]) and estimation of their house production (e.g., [26,27]). Additionally, a more realistic representation of carbon content of discarded houses in different ecosystems is needed, which requires *in situ* collection of large-sized particles: for example, via remotely operated vehicles for offshore waters [29] or scuba diving in coastal areas [46]. Mesopelagic fish have been shown to select for larvaceans during night foraging in surface waters [7,8,16–18]. Though difficult with mesopelagic fish, we need controlled feeding experiments in the laboratory to establish functional response curves and digestion times in order to assess the importance of larvaceans as food for fish. As larvaceans are not food-limited in oligotrophic oceans (Box 2) [74], and the production of larvaceans can exceed copepod production in oligotrophic waters by several times [37,41], larvaceans could be an important but so far unrecognised food source to sustain (especially) mesopelagic fish and tuna. Focused research on the 'larvacean shunt' could illuminate how mesopelagic fish, squid, and tuna stocks in oligotrophic waters are supported.

Quantifying the role of larvaceans in the biological pump

A key gap in our understanding of the carbon cycle is that estimated particle export from the upper ocean is only 30–50% of that needed to sustain midwater animals [78], suggesting that our current models miss critical carbon pathways [42]. Larvaceans could help to resolve this disparity. Currently, larvaceans are ignored in the biological pump; of the 21 primary biological feedback loops in the Earth's climate [79], three feedback cycles involve phytoplankton and none involves zooplankton.

Currently, larvacean houses are underestimated by conventional sediment traps [75], hampering our understanding about the contribution of larvaceans to the biological pump. Improved measurements of larvacean house production and sinking rates are needed (e.g., see [26,44,47]). Combining remotely operated vehicles and *in situ* experiments can be used to estimate house production, sinking, and feeding rates on different particle size ranges especially of large-sized larvacean species, as documented by experiments in the California Current Ecosystem [29,35,50]. Despite the growing evidence of the importance of discarded larvacean houses for direct carbon export [50,51], their magnitude and spatial variation remain uncertain. Furthermore, an open question is whether small or large larvacean species contribute more to carbon export. Due to the extraordinary production of larvaceans (Box 1), changes in the abundance and community composition of phytoplankton can quickly translate into high larvacean abundances (see Figure II in Box 2), with consequent high marine snow formation that further fuels the biological pump [46]. Larvaceans have diverse roles in both active and passive vertical carbon transport, and their climate response is a key uncertainty in the biological pump [65]. Filling this knowledge gap is important, as even small changes in the efficiency of the biological pump can have large climate impacts [80,81].

Incorporating larvaceans in models

Despite the extraordinary growth and production of larvaceans (Box 2), and their active and passive transport of carbon in the biological pump (Box 1), they are rarely included in biogeochemical or ecosystem models. There are several ways that the inclusion of larvaceans in such models could be increased. First, it is important to convince modellers that larvaceans are a key component of the carbon cycle, and that there is sufficient information available to model them. In recent years, there has been an increase in functional complexity for phytoplankton in models (e.g., [55,61]) and in zooplankton [39,82]. Many models that already include gelatinous zooplankton

focus on cnidarian jellyfish [83], but only a few include larvaceans [82,84], which currently miss key processes such as house formation. Second, the entire size range of larvaceans – including the giant mesopelagic species – should be included in models (Box 2). For example, Luo *et al*. [82] included only larvaceans <3 mm in length, missing larger surface-dwelling and deep-water species. Third, model validation against empirical abundance and biomass data from nets should be undertaken with care. For example, net data are often sourced from the COPEPOD database[i], which is often standardised to a mesh size of 330 μm [82] and could thus miss most larvaceans (Box 2). This valuable dataset could be better standardised using statistical models (e.g., [84]), or researchers could use data sources that more appropriately report larvacean abundances (e.g., [41,72,85]). Fourth, many models use a single common parameter value for all zooplankton processes such as grazing or temperature dependence [81], rather than different ones for different zooplankton groups. Although this is sometimes necessary because of the lack of information, there are many physiological data available for larvaceans (e.g., [2,5,26,27,30,31,35,37,38,44,51,75,77,86]). Fifth, as the fastest-growing multicellular animals (see Figure II in Box 2), assessing modelled against observed growth rates for larvaceans is critical to ensure that model ingestion and assimilation parameters are reasonable (see [84] for an example). Lastly, many models assume a common sinking rate for plankton detritus (for phytoplankton, zooplankton carcasses, zooplankton faeces, larvaceans), despite observations that the sinking rate of gelatinous detritus is much faster than that of other detritus [45,47,48,51]. In short, future models have considerable scope for better modelling the role of larvaceans.

Concluding remarks

This review highlights the understudied but important role of larvaceans in supporting fisheries and regulating the biological pump. Novel avenues are suggested to incorporate this fascinating group into future research initiatives and modelling exercises. Larvaceans are an abundant mesozooplankton group in the ocean, have extraordinary growth rates, short-cut the food-web to feed higher trophic levels, and sequester carbon. Technological innovations hold great promise for elucidating the role of larvaceans in the oceans (see Outstanding questions). To understand how climate change impacts marine ecosystems, it is now time for larvaceans and other gelatinous zooplankton to be widely recognised as key members of the marine ecosystem, so that we can assess their potential to counteract the negative impacts of climate change and thus sustain ocean productivity and carbon sequestration in the future.

Outstanding questions

How do larvacean abundance and species composition respond to climate change, and how does this impact biological carbon pump efficiency and harvest consequences of epipelagic and mesopelagic fish in the future?

How does the abundance of larvaceans and their houses change across environmental gradients? Can we standardise investigation efforts using small-meshed nets and combine this with *in situ* imaging? What are the distribution patterns of mesopelagic larvaceans globally, and do oxygen minimum zones impact their depth distribution?

To what extent do larvaceans provide a feedback loop to counteract negative climate change impacts on food-web structure to sustain fish production and carbon sequestration? What are the feeding rates and digestion times of larvaceans for different fish species?

What are the key physiological rates of mesopelagic larvaceans?

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Declaration of interests

No interests are declared.

Resources

[i]www.st.nmfs.noaa.gov/copepod

[ii]https://youtu.be/L1wFb_ShW7k

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