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Larval nutritional mode and swimming behaviour in ciliated marine larvae

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Review

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Abstract

Swimming propagules (embryos and larvae) are a critical component of the life histories of benthic marine animals. Larvae that feed (planktotrophic) have been assumed to swim faster, disperse farther and have more complex behavioural patterns than non-feeding (lecithotrophic) larvae. However, a number of recent studies challenge these early assumptions, suggesting a need to revisit them more formally. The current review presents a quantitative analysis of swimming speed and body size in planktotrophic and lecithotrophic propagules across five major marine phyla (Porifera, Cnidaria, Annelida, Mollusca and Echinodermata). Results of the comparative study showed that swimming speed differences among ciliated propagules can be driven by taxonomy, adult mobility (motile vs sessile) and/or larval nutritional mode. On a phylogenetic level, distinct patterns emerge across phyla and life stages, whereby planktotrophic propagules swim faster in some of them, and lecithotrophic propagules swim faster in others. Interestingly, adults with sessile and sedentary lifestyles produce propagules that swam faster than the propagules produced by motile adults. Understanding similarities and differences among marine propagules associated with different reproductive strategies and adult lifestyles are significant from ecological, evolutionary and applied perspectives. Patterns of swimming can directly impact the dispersal/recruitment potential with incidence on the design of larval rearing methods and marine protected areas.

Introduction

Benthic marine animals have evolved a diversity of morphological and behavioural adaptations to overcome the need for dispersal, development and recruitment. Planktonic embryos and larvae (propagules) evolved as a means to offset some of these challenges. These propagules have the capacity to swim autonomously using cilia and/or muscular elements and often possess complex behavioural responses to environment cues. Autonomous locomotion allows propagules to gather food (for feeding), regulate vertical position, avoid predators/non-ideal conditions and select a specific settlement site (Chia *et al.*, 1984).

Swimming speeds are relatively easy to quantify and are a useful starting point for intra- and inter-specific comparisons. To date, the bulk of swimming speed studies have been conducted in phyla with multiple types of larval nutritional mode (e.g. Mollusca, Annelida, Echinodermata) but they have mainly focused on propagules with planktotrophic (feeding) development. Previously reported speed values for planktotrophic and lecithotrophic ciliated propagules range widely between 0.1 and 30.0 mm s^{-1} in species of Porifera (Maldonado, 2006), Cnidaria (Mileikovsky, 1973; Harii *et al.*, 2002), Mollusca (Chia *et al.*, 1984) and Echinodermata (Podolsky & Emlet, 1993). In contrast, propagules that use muscular elements or appendages to swim have speeds in the range of 30–300 mm s^{-1} (e.g. Arthropoda; Chia *et al.*, 1984).

While reviews have examined the swimming patterns of planktotrophic larvae (Mileikovsky, 1973; Chia *et al.*, 1984; Koehl & Reidenbach, 2007), and have compared the dispersal potential of propagules of different nutritional modes (Mercier *et al.*, 2013), no study has ever explicitly explored the locomotory differences between ciliated planktotrophic and lecithotrophic propagules across multiple phyla. The term 'propagules' is used here when embryos and larvae are both being considered. Focusing on ciliated propagules (i.e. that use cilia for locomotion) is valuable from an evolutionary perspective since some form of ciliation is present across the propagules of diverse marine phyla and life stages. Similarly, the intersection of larval nutritional mode, swimming speed and size has not been examined across multiple phyla, leaving many questions unanswered including: do certain types of ciliated propagules swim faster? The relationship between larval swimming speeds and adult mobility also has not been explored, despite the potential for intriguing trade-offs between the need for dispersal and larval provisioning.

To address these uncertainties and tease out some of the potential drivers, we conducted a meta-analysis using propagule swimming speed data from the literature examined through the lens of propagule size, larval nutritional mode, and adult mobility.

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Materials and methods

We gathered swimming speed data of pelagic ciliated propagules (embryonic and larval stages of species with larvae that use cilia for locomotion) across six of the main marine phyla (Porifera, Cnidaria, Annelida, Mollusca, Echinodermata, Bryozoa; N = 118 records, see Table A1 for raw data) from the scientific literature to compare phylum-based differences among larval nutritional modes. For example, taxa with appendaged or muscular larvae (e.g. Arthropoda, Urochordata) were not included. Poriferans (sponges) only possess lecithotrophic larvae (Ereskovsky, 2010), and propagules of cnidarians (corals and sea anemones) are mainly lecithotrophic, with only few known planktotrophic representatives (e.g. Schwarz *et al.*, 2002). In contrast, Bryozoa, Annelida, Mollusca and Echinodermata are among the phyla comprised of a diverse mixture of species with planktotrophic and lecithotrophic larvae (Table A1).

Metrics collected included: phylum, adult mobility level, larval nutritional mode, as well as size (length of longest axis) and swimming speed (mm s^{-1}) for the given stage (Table A1). Life stages ranged from embryonic (blastula/gastrula) to competent larval forms (e.g. urchin pluteus), although the vast majority of the records involved larvae (>90%). Taxonomic classification was confirmed using the World Registry of Marine Species (WoRMS). Adult mobility level was defined as *motile* (exhibiting frequent movement or migration), *sedentary* (capable of movement but doing so less commonly) or *sessile* (permanently fixed for the majority of their life) modified from the standard terminology proposed by Costello *et al.* (2015). The nutritional mode of larvae was defined as *planktotrophic* or *lecithotrophic* based on the classification presented by Poulin *et al.* (2001) and Carrier *et al.* (2017). Propagule size (µm) was defined as the mean length of the longest axis; this value represents Feret diameter in spherical propagules. All speeds used in the analysis were absolute speeds and were not standardized to body size. Wherever possible, horizontal swimming speeds (mm s^{-1}) were used, but these data were not always reported in the literature. When multiple swimming directions were reported, the fastest reported speed was used (e.g. among upward and downward swimming speeds).

Two-way ANOVA and Factorial Analysis of Mixed Data (FAMD) were used to test the relationship among all collected metrics. Statistical analyses were performed in Sigma Plot and R statistical software.

Results

Phylum is a greater driver of swimming speed than larval nutritional mode

Lecithotrophic and planktotrophic propagules across the whole dataset had mean absolute swimming speeds of 3.72 ± 0.65 mm s^{-1} and 1.22 ± 0.18 mm s^{-1}, respectively (Table 1, Figure 1; ANOVA $P = 0.009$). Lecithotrophic propagules generally swam faster than planktotrophic counterparts in those phyla with multiple nutritional modes, including Annelida (2.84 ± 0.64 *vs* 1.44 ± 0.21 mm s^{-1}), Bryozoa (4.60 ± 0.61 *vs* 1.9 mm s^{-1}), Echinodermata (0.49 ± 0.15 *vs* 0.40 ± 0.07 mm s^{-1}) and Mollusca (1.71 ± 0.25 *vs* 1.50 ± 0.43; Figure 1). Phyla that rely exclusively or predominantly on lecithotrophy (Porifera, Cnidaria) had faster average propagule swimming speeds (11.04 ± 3.77 and 2.83 ± 0.57 mm s^{-1}, respectively) than the other phyla under study (Annelida, Mollusca, Echinodermata, Bryozoa; overall mean = 1.4 mm s^{-1}).

Porifera and Echinodermata stood out at opposite ends of the propagule-swimming-speed spectrum when a follow-up FAMD analysis was performed (Table 2). In particular, planktotrophic propagules of echinoderms swam slower on average than all other propagules ($P < 0.001$; Table 2); whereas poriferan propagules (all lecithotrophic) swam faster than other tested propagules (FAMD $P < 0.001$; Table 2). Poriferan propagules were also much larger than planktotrophic echinoderm propagules (mean size 571 ± 68 *vs* 267 ± 35 µm). Lecithotrophic echinoderm larvae are also large (mean size 705 ± 66 µm), however, they do not even come close to reaching the speeds displayed by poriferan larvae (0.49 ± 0.15 *vs* 11.04 ± 3.77 mm s^{-1}).

Patterns of swimming speed between lecithotrophic and planktotrophic propagules were not consistent across phyla when differences within life stages were considered. Lecithotrophic annelid trocophores and late trocophores, echinoderm brachiolariae, and bryozoan cyphonautes larvae swam faster on average than their planktotrophic counterparts (Figure 2). Lecithotrophic mollusc trocophores, and echinoderm embryos swam at similar speeds to planktotrophic equivalents (Figure 2). Lastly, lecithotrophic mollusc veligers and annelid metatrocophores swam slower than planktotrophic equivalents (Figure 2).

Table 1. Mean length/diameter and swimming speed summarized across the two larval nutritional modes and five phyla featured in the dataset (see Table A2 for raw data)

Factor	Mean length (mm ± SE)	Mean absolute swimming speed (mm s^{-1} ± SE)
Nutritional mode		
Planktotrophic (P)	263 ± 25	1.22 ± 0.18
Lecithotrophic (L)	597 ± 61	3.72 ± 0.65
Adult mobility		
Motile	332 ± 30	1.14 ± 0.22
Sedentary	272 ± 60	2.73 ± 0.87
Sessile	664 ± 102	4.63 ± 1.17
Phylum		
Porifera	(L) 571 ± 68[a]	11.04 ± 3.77
Cnidaria	(L) 755 ± 113[a]	2.83 ± 0.57
Annelida	(L) 340 ± 60	2.84 ± 0.64
	(P) 305 ± 62	1.44 ± 0.21
Bryozoa	(L) 202 ± 18	4.60 ± 0.61
	(P) 400[b]	1.9[b]
Echinodermata	(L) 705 ± 66	0.49 ± 0.15
	(P) 267 ± 35	0.40 ± 0.07
Mollusca	(L) 216 ± 32	1.71 ± 0.25
	(P) 168 ± 22	1.5 ± 0.43

[a]Phylum Porifera is entirely lecithotrophic, Phylum Cnidaria is mainly lecithotrophic with a few planktotrophic representatives (Schwarz *et al.*, 2002).
[b]Only one swimming speed record of planktotrophic Bryozoa could be located.

Adult motility level correlates with larval nutritional mode and swimming speed

When all phyla were considered together, species with sessile and sedentary adults produce faster swimming larvae on average than species with motile adults (4.63 ± 1.17 and 2.73 ± 0.87 *vs* 1.14 ± 0.22 mm s^{-1}; ANOVA, $P < 0.001$; Table 1). This pattern was particularly noticeable among sessile species like sponges, corals and bryozoans that produced fairly large, fast swimming larvae, relative to other phyla in the dataset like Echinodermata, that have motile adults (Figure 3). Propagules from sessile and sedentary adults also swam faster within those phyla containing

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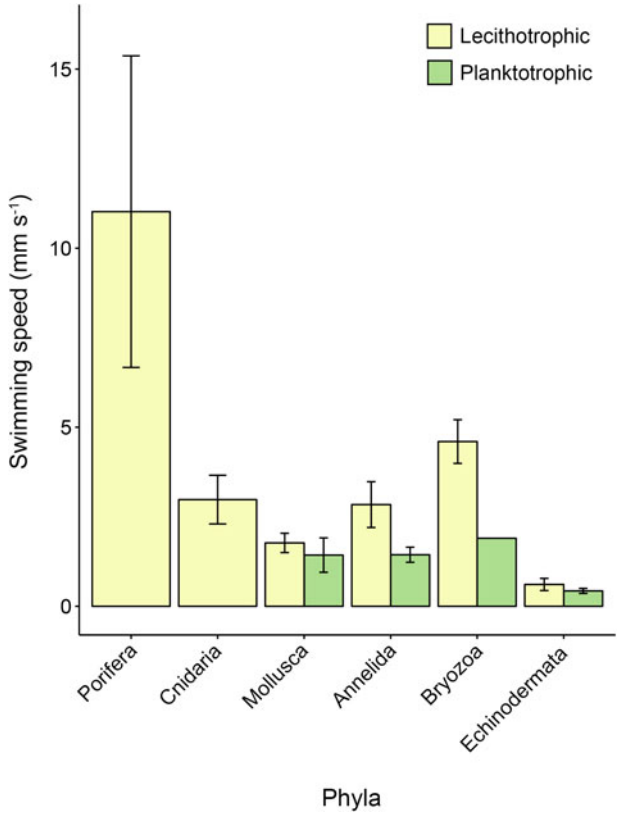


Fig. 1. Mean propagule swimming speed (mm s^{-1} ± SE) varies among phyla and larval nutritional modes. Phylum Cnidaria and Porifera only have one bar as these taxa only have one larval nutritional mode. Error bars are present where more than one record per phylum and category were available. See Table A1 for raw data.

a mix of adult mobility types, such as Annelida, Cnidaria and Mollusca, although speed data for cnidarians with motile adults (e.g. hydro- and scyphozoan medusae) are scarce in the literature (Figure 3), and insufficient to generate a solid statistical comparison.

Swimming speed scales with size in planktotrophic, but not in lecithotrophic propagules

When all phyla were considered together, planktotrophic propagules were smaller than lecithotrophic propagules (263 ± 25 *vs* 597 ± 61 µm); although this difference was mainly driven by lecithotrophic poriferans and echinoderms that were larger on average than all other types of propagules (Table 1). No definitive relationship between propagule size and swimming speed was seen among planktotrophic and lecithotrophic propagules (Figure 4). However, lecithotrophic propagules appeared to have a greater capacity for faster swimming speeds, as the majority of the speed values for lecithotrophic propagules were higher than for planktotrophic counterparts of the same size (Figure 4, ANCOVA, $P < 0.001$).

Discussion

Swimming speeds of ciliated marine propagules clearly varied with phylogeny, though differences between larval nutritional modes emerged when life stages were considered individually. Differences also emerged among propagules produced by adults with sessile/sedentary lifestyles *vs* those with more mobile ones.

On a phylogenetic level, the biggest differences in mean swimming speeds in the dataset was found between poriferan and echinoderm propagules. On average, poriferan propagules swam

Table 2. Summary of results from an FAMD testing the relationship among phylum, propagule size, adult activity level, larval nutritional mode and propagule swimming speed in the dataset

Hierarchical clusters		*P*-value
1	Echinodermata	<0.001
	Annelida	<0.001
	Mollusca	<0.001
	Planktotrophic	<0.001
	Motile Adults	<0.001
	Size < Mean	<0.001
	Speed < Mean	<0.001
2	Porifera	<0.001
	Bryozoa	<0.001
	Cnidaria	<0.001
	Lecithotrophic	<0.001
	Sessile Adults	<0.001
	Size > Mean	0.015
	Speed > Mean	<0.001

10–12× faster than planktotrophic and lecithotrophic echinoderm propagules. This difference may be a result of propagule size and chemical composition differences (e.g. relative amounts of protein, lipid and calcified elements) between these two taxa. Poriferan propagules are a simple prolate spheroid shape and therefore may experience less drag or fluid interactions than other propagule shapes. Planktotrophic echinoderm larvae (and some late-stage lecithotrophic echinoderm larvae) use a completely different morphological strategy than poriferans; they often possess calcified elements and appendages that modulate their density and interaction with fluid and may constrain their swimming abilities (Grünbaum & Strathmann, 2003; Strathmann & Grünbaum, 2006). Interestingly, the gastrula of many planktotrophic and lecithotrophic species (e.g. Annelida, Mollusca, Echinodermata) are similar in shape to poriferan propagules (spheroid) and are also uniformly ciliated with cilia of similar length (~20–25 µm; Strathmann, 1971; Chia *et al.*, 1984; Maldonado, 2006). However, these gastrulae swim at much slower speeds, which suggests that variability in other features such as ciliary beating rates, buoyancy and energy usage could be at play. Some larval types can also supplement their ciliary movements with muscular contractions (e.g. some segmented annelid larvae; Chia *et al.*, 1984) but this addition is usually seen in older, more complex larval forms. Clearly there is something unique about the swimming mechanics of sponge larvae that deserves further attention.

Swimming speed differences between planktotrophic and lecithotrophic propagules were not consistent when life stages were considered individually. Most lecithotrophic versions of the considered life stages swam similarly, or faster than their planktotrophic equivalents (e.g. annelid and molluscan trochophores among others). Only planktotrophic late-stage annelid and mollusc larvae swam faster than the lecithotrophic counterparts, possibly due to the presence of complex ciliation patterns that enhance swimming capacity, or the precursors to muscular swimming in late-stage annelid larvae. Taken together, these data challenge the sometimes-held belief that lecithotrophic larvae experience constraints to their locomotion from their large size and generally positive buoyancy (Emlet, 1991, 1994) and are in line with recent studies that test planktotrophic and lecithotrophic

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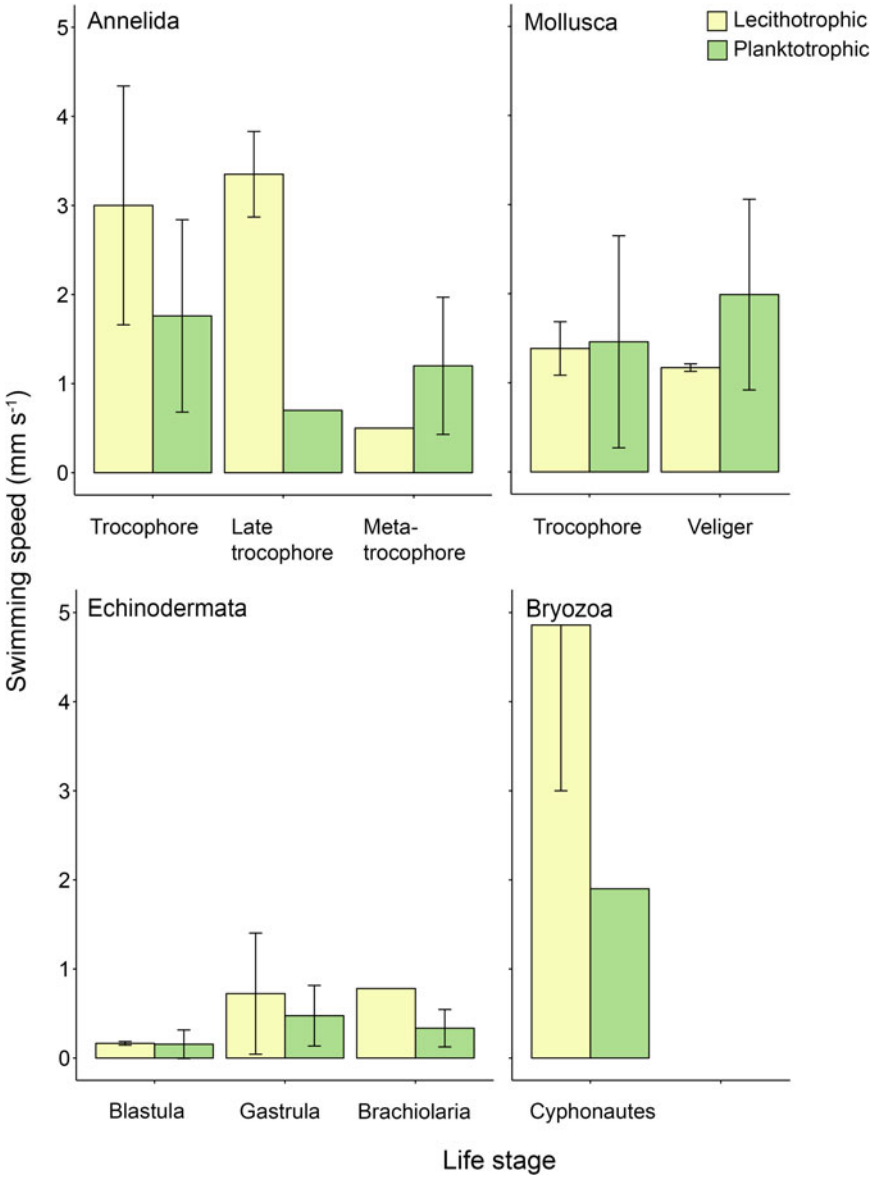


Fig. 2. Mean propagule swimming speed (mm $s^{-1} \pm SD$) of specific life stages varies with nutritional mode. Taxa and life stages presented here had both planktotrophic and lecithotrophic representatives in the dataset. Error bars are present where more than one record per phylum and category were available. See Table A1 for raw data.

propagules together under similar conditions (Krug & Zimmer, 2004; Mercier *et al.*, 2013; Montgomery *et al.*, 2017, 2018). In fact, lecithotrophic propagules swim as fast as planktotrophic propagules even in species that display poecilogony (mixed modes of development) like the nudibranch *Alderia modesta* (Krug & Zimmer, 2000; Krug & Zimmer, 2004). Species with mixed modes of development provide an interesting system to further examine nutritional mode differences without potential phylogenetic constraints; they can be found in Annelida, Mollusca, and Echinodermata, with notable examples including the gastropod *Alderia modesta* (Krug & Zimmer, 2000), the polychaete *Capitella capitata* (Butman *et al.*, 1988) and the sea star *Henricia lisa* (Mercier & Hamel, 2008).

It emerged that the majority of benthic species with fully sessile adults (in phyla Porifera, Cnidaria and Bryozoa) that have ciliated pelagic propagules are lecithotrophic. Exceptions to this include some bryozoan taxa (e.g. order Cheilostomata, Hayward, 1985) that produce long-lived planktotrophic larvae, and some anthozoan planulae (Cnidaria) that ingest symbiotic zooxanthellae while swimming in the plankton (e.g. Schwarz *et al.*, 2002). The predominance of lecithotrophy among sessile marine invertebrates raises many questions, including how larval nutritional mode, adult mobility and larval behaviour might be linked. If we compare across phyla (e.g. Porifera to Echinodermata), propagules from sessile adults clearly swim faster. This pattern also appears to be conserved among sessile adults within Bryozoa using the limited data available in the literature; planktotrophic propagules swam with average speeds of 19 mm s^{-1} *vs* 34–49 mm s^{-1} among lecithotrophic propagules (data from Chia *et al.*, 1984; Wendt, 2000). Interestingly, the pattern also seems to hold in phyla with sedentary (rather than fully sessile) adults, where propagules produced by sedentary adults tend to swim faster than propagules produced by motile adults (e.g. Mollusca and Annelida), though this was not supported statistically.

Maternal reserves likely facilitate radical shape changes during metamorphosis and the construction of morphological features prior to feeding at the juvenile stage (e.g. external skeleton, polyps, choanocytes), which may explain the predominance of lecithotrophy among species with sessile adults. Sessile species also have high specificity and sensitivity to certain settlement cues at the advanced larval stage (Mundy & Babcock, 1998; Leys *et al.*, 2002). The consequences of deviating from standard patterns of larval behaviour and settlement are also likely higher for sessile organisms given the fact that they have limited opportunities to get it right (Raimondi & Morse, 2000). In contrast, species with motile adults probably do not experience the same pressure to settle in ideal conditions as they can migrate and relocate post

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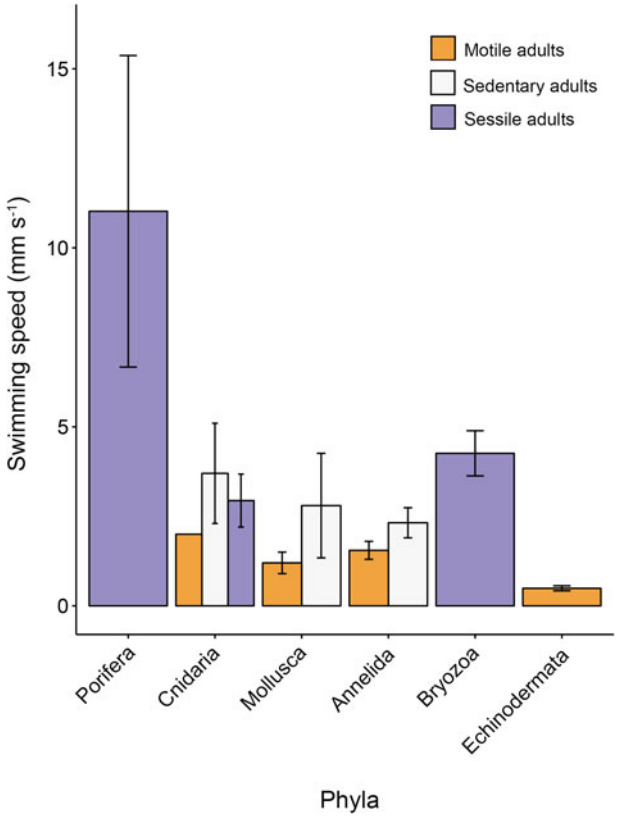


Fig. 3. Mean propagule swimming speed (mm s^{-1} ± SE) varies with taxa and level of adult mobility. Sessile adults are incapable of movement, sedentary adults have the capacity to move but do so rarely and motile adults move readily and often. Error bars are present where more than one record per category were available. See Table A1 for raw data.

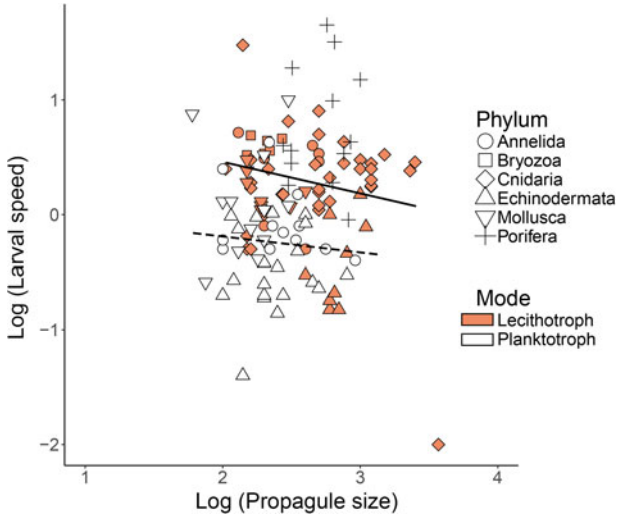


Fig. 4. Larval swimming speed (mm s^{-1}) *vs* propagule body size (μm) in lecithotrophic and planktotrophic larvae of various phyla (Porifera, Cnidaria, Mollusca, Annelida, Echinodermata, Bryozoa) on $\log_{10}$ scales. Log scales were used to examine scaling relationships across a wide range of propagule sizes and speeds. Points represent mean values for individual species. Symbols depicting the various phyla are either solid/open to indicate the lecithotrophic/planktotrophic larval feeding mode (except for Porifera, which is fully lecithotrophic and identified with +). N = 66 total. The solid lines show regression results. Planktotrophs: $y = -0.017x - 0.25$, $R^2 = 0.01$; Lecithotrophs: $y = -0.26x + 0.97$, $R^2 = 0.02$.

settlement. Thus, the production of faster moving, lecithotrophic propagules by sessile adults, relative to motile adults, could enable sessile adults to overcome some of the constraints associated with a sessile lifestyle, such as the need for dispersal, settlement specificity and the energetic costs of metamorphosis.

The present study suggests that the swimming capacity of planktotrophic propagules may be more constrained by size than that of lecithotrophic propagules, since swimming speeds scaled with size in planktotrophic but not lecithotrophic propagules in the dataset. This may be explained by the fact that planktotrophs generally experience greater change in size during their development than lecithotrophs. For instance, planktotrophic propagules of the green sea urchin, *Strongylocentrotus droebachiensis*, range in size from 150 μm as embryos to 1000 μm as fully competent larvae (Meidel *et al*., 1999). In contrast, lecithotrophic propagules of the Australian sea urchin, *Heliocidaris erythrogramma*, range in size from 300 μm as embryos to 600 μm as competent larvae (Emlet & Hoegh-Guldberg, 1997). This size change of nearly 7 times in planktotrophs *vs* 2 times in lecithotrophs may place additional size-based locomotory constraints on the former, as cilia in feeding larvae are thought to be arranged to maximize feeding, not swimming (Strathmann & Grünbaum, 2006).

Swimming speeds may be affected by something other than size in lecithotrophic propagules, which do not require external nutrition to complete metamorphosis, typically do not undergo daily vertical migration during development and often are positively buoyant, which causes them to float to the top of the water column following spawning. To this effect, propagule form and behaviour could therefore influence swimming in conjunction with nutritional mode along with the need to disperse more effectively (e.g. dispersal constraints of sessile adults). Refining our understanding of the morphology and swimming speeds of different types of propagules will help improve the reliability of dispersal models and other predictive means for population management (e.g. marine protected area planning) by highlighting the importance of considering different larval features and ultimately identifying new model parameters.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315418001091.

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