

Ontogenetic shifts in swimming capacity of echinoderm propagules: a comparison of species with planktotrophic and lecithotrophic larvae

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Abstract While developmental strategies can modulate the dispersal and recruitment of marine benthic species, the significance and drivers of propagule motility throughout ontogeny remain incompletely understood. Species with lecithotrophic (non-feeding) development are rarely studied, despite their predominance in some taxa, including echinoderms. Quantification of the swimming capacity (i.e. speed and trajectory) of early life history stages and its variability with environmental factors is required to improve the ability to predict population connectivity and assess trade-offs associated with complex life histories. In general, lecithotrophic larvae of echinoderms are ascribed weak swimming abilities relative to planktotrophic larvae, although explicit measures are scarce. Here, we explored selected metrics of swimming capacity in four co-occurring species of North Atlantic echinoderms displaying different types of pelagic development: planktotrophs represented by the sea star *Asterias rubens* and the sea urchin *Strongylocentrotus droebachiensis*, and lecithotrophs represented by the sea star *Crossaster papposus* and the sea cucumber

Cucumaria frondosa. Swimming was characterized in still water based on the horizontal speed and path straightness of early life-history stages, from late blastula (hatched embryo) to late-stage larva. We tested the hypotheses that swimming capacity of propagules increases with progression through developmental stages and with increasing seawater temperature. Swimming speed increased with ontogeny in two of the four species (*A. rubens* and *C. papposus*) and with temperature in all species, although the effects of temperature were not uniform across life stages. The fastest swimming speeds across all species and temperatures were recorded in lecithotrophic propagules (i.e. max speed 1.2 mm s⁻¹ in the brachiolaria of *C. papposus*), whereas propagules of species with planktotrophic development displayed faster relative speeds (body lengths s⁻¹). Relative speeds increased with temperature in all tested species except *C. papposus*. Swimming paths typically increased in straightness from early to later developmental stages, and also became straighter with increased temperature in most species, except in *C. papposus* where they became more circular and complex. In general, planktotrophic and lecithotrophic propagules had similar swimming capacities when tested at the same level of increased temperature, though several stage-specific differences were detected; propagules of species with planktotrophic development had greater relative speeds at the gastrula stage and greater path-corrected speeds at the larval stage. Swimming paths and swimming speeds were similar between propagules of species with planktotrophic development and lecithotrophic development, suggesting that phylogenetically conserved, ontogenetic patterns of swimming capacity (seen here between two sea stars) may supersede the contribution of larval nutritional mode.

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Introduction

Marine animals have evolved diverse developmental strategies that not only shape their reproductive success but also determine their settlement, recruitment and dispersal potential (Thorson 1949; Pechenik 1999). Biphasic life histories, with sessile or sedentary adults and pelagic propagules (embryos and larvae), are common among benthic species (Strathmann 1993; Pechenik 1999). Pelagic larvae can be broadly characterized based on their nutritional requirements during development as either planktotrophic/feeding or lecithotrophic/non-feeding (Poulin et al. 2001). Propagules of species with planktotrophic development are typically smaller and neutrally or negatively buoyant, whereas pelagic lecithotrophic propagules are usually larger and positively buoyant (Chia et al. 1984; Emler 1994).

Though size varies greatly due to development mode (e.g. propagule diameter varying by as much as 15-fold), all species with a planktonic stage share non-feeding embryonic stages that have the ability to swim using cilia or muscular contraction (Emler 1983; Staver and Strathmann 2002; Moore 2003). Overall, species with ciliated propagules are classified as “weakly swimming” (e.g. echinoderms, molluscs; $<1\text{--}10\text{ mm s}^{-1}$) relative to those that rely on appendages and muscles for propulsion (e.g. polychaetes, crustaceans; $>5\text{--}30\text{ mm s}^{-1}$; Grunbaum and Strathmann 2003; Strathmann and Grünbaum 2006). While the swimming speeds of ciliated propagules are generally lower than currents, even small modifications (e.g. two-fold increase) can influence small-scale interactions with the benthos that may modulate capture of food, encounters with predators, settlement and ultimately, recruitment (Gross et al. 1992; Abelson and Denny 1997; North et al. 2008).

Propagule locomotion is primarily controlled by morphology and the mechanics of propulsion (Clay and Grunbaum 2010). Therefore, changes in morphology and behaviour that occur throughout ontogeny are expected to influence the swimming abilities of propagules. There is compelling evidence that even the most basal taxa (Porifera, Cnidaria) are sensitive to abiotic and biotic cues (Pawlik 1992; Tamburri et al. 1996; Leys et al. 2002). Yet, several authors have noted a scarcity of stage-specific studies of swimming capacity, particularly in response to environmental conditions (Metaxas 2001; Metaxas and Saunders 2009; Morgan 2014). Comparative studies involving more than one species are also extremely rare.

Many studies that examine the motility of marine ciliated propagules have focused on one or two species to assess the combined influence of flow and swimming on vertical positioning of larvae in the water column for the purpose of estimating transport over medium to large spatial scales (m to km-Metaxas 2001; Metaxas and Saunders

2009; Sameoto et al. 2010; Roy et al. 2012b). Studies of propagule swimming mechanisms in species with planktotrophic development have been conducted mainly in Mollusca (e.g. Arshavsky et al. 1993; Childress and Dudley 2004) and Echinodermata (e.g. Emler 1983; Strathmann and Grunbaum 2006). Small-scale studies of horizontal swimming (or including horizontal components) are prevalent in some phyla (e.g. Porifera, Maldonado 2006; Annelida; Butman et al. 1988) but relatively limited in others (e.g. Mollusca, Chan et al. 2013; Echinodermata; Mogami et al. 1988; McDonald 2004; Chan 2012). In phyla with different nutritional modes, studies that quantify the motility of lecithotrophic propagules are scarce (McEuen and Chia 1991; Emler 1994; Kelman and Emler 1999). This is especially true in Echinodermata where lecithotrophy is predominant (estimated as 68% of all species, Uthicke et al. 2009). Addressing this will be of particular importance in temperate and cold-water ecosystems where species with lecithotrophic propagules developing in the plankton are equally abundant to species with planktotrophic propagules (Marshall et al. 2012).

Pelagic lecithotrophic echinoderm propagules have been ascribed weak swimming capacities, based on the assumption that their large size and positive buoyancy can impede swimming (Emler 1994). The absence of feeding could exert a strong influence on swimming behaviour in lecithotrophic propagules, which are not constrained by dependence on external sources of nutrition and generally experience less predation; either through morphological incompatibility (Mercier et al. 2013a) or through predator rejection (Iyengar and Harvell 2001). The few studies dedicated to locomotion in ciliated propagules of lecithotrophic echinoderms have documented swimming in a sea star (*Pteraster tesselatus*, $1.0\text{--}1.7\text{ mm s}^{-1}$; Kelman and Emler 1999), a sea cucumber (*Psolus chitonoides*, 1.4 mm s^{-1} ; McEuen and Chia 1991), a brittle star (*Ophioderma brevispinum*, 0.3 mm s^{-1} ; Webb 1989) and discussed the general constraints of cilia band placement to swimming potential (Emler 1994). Positively buoyant propagules may swim with or against the buoyant force (Emler 1994), which makes assessment of “vertical” swimming capacities complicated in lecithotrophs. However, the combination of buoyancy and swimming in *P. tesselatus* and *P. chitonoides* was shown to generate vertical movement that was faster than reported in planktotrophic echinoderms (McEuen and Chia 1991; Kelman and Emler 1999).

In an effort to provide explicit comparisons between developmental strategies and generate novel empirical data of potential use for dispersal and connectivity models, we explored the swimming capacity of embryos and larvae in four common and co-occurring species of North Atlantic echinoderms; planktotrophs represented by the sea star *Asterias rubens* and the sea urchin *Strongylocentrotus*

droebachiensis, and lecithotrophs by the sea star *Crossaster papposus* and the sea cucumber *Cucumaria frondosa*. An initial study was conducted to gather species-specific data and test the hypothesis that swimming capacity increases with ontogenetic development at the scale of the propagule. We hypothesized that swimming speed would increase chronologically from early to late developmental stages due to changes in propagule size, shape and competency. Because temperature is known to influence swimming of ciliated propagules through the physiology of larvae and the viscosity changes of water (Podolsky and Emlet 1993; Kashenko 2007; Chan et al. 2011), we also tested the hypothesis that stage-wise swimming capacity would be positively correlated with temperature. Finally, we tested the assumption that planktotrophs exhibit greater swimming capacity than lecithotrophs under similar conditions (Chia et al. 1984; Emlet 1994). Differences in morphology among these propagule types is likely to affect swimming.

Materials and methods

Animal collections, maintenance and spawning

Adults of *A. rubens* (5–10 cm radius), *C. papposus* (5–10 cm radius), *S. droebachiensis* (5–8 cm test diameter), and *C. frondosa* (15–20 cm contracted body length) were collected by SCUBA between 10 and 20 m depth in South-east Newfoundland (eastern Canada). Specimens of all species were housed in 375-L tanks provided with flow-through seawater ($\sim 60 \text{ L h}^{-1}$) at ambient temperatures ranging from 0 to 5 °C, salinities ranging from 34 to 36, light intensities ranging daily from 5 to 450 lx (mean = 300 lx) and natural photoperiod (see Mercier and Hamel 2010 for details).

This study was undertaken in spring 2014, during the natural spawning periods of the focal species (Mercier and Hamel 2010). Cultures of *C. papposus* and *C. frondosa* were started following natural spawning events in February and March, by gently skimming the positively buoyant fertilized oocytes from the surface of the tanks. Cultures of *A. rubens* and *S. droebachiensis* were started in May. Though experimental trials were conducted at different times for each species, utmost care was taken to ensure continuity of experimental protocols across life stages and species. Gonads of female *A. rubens* were surgically collected from mature individuals and were treated with a solution of 0.1 μM 1-MA to promote final oocyte maturation (Dorée et al. 1976). Spawning was initiated in *S. droebachiensis* by injecting 1–2 mL of 0.5 M KCl into the coelomic cavity (Meidel and Yund 2001). A minimum of three males and five females were used to generate cultures with sufficient genetic diversity. Fertilization of mature oocytes was

performed using a dilution of $\sim 10,000$ spermatozoa mL^{-1} as per Byrne et al. 2010 in both *A. rubens* and *S. droebachiensis* as this was an optimal concentration to promote 80–90% fertilization success and reduce the potential for polyspermy.

Embryos and larvae (generally referred to as propagules) were cultured under conditions chosen to reflect the ambient temperature experienced in nature during the spawning season and early development. Standard rearing techniques were used for each species (Meidel et al. 1999 for *A. rubens* and *S. droebachiensis*; Hamel and Mercier 1996 for *C. frondosa* and *C. papposus*). Propagules of *C. papposus* and *C. frondosa* were raised in 1.5-L vessels at 1–3 °C (matching the ambient conditions during natural spawning) and $\sim 0.1 \text{ L h}^{-1}$ flow-through conditions. Propagules of *A. rubens* were obtained a little later in the spring when the ocean temperature was higher; the cultures were performed at 10 °C (static conditions). Once feeding larval stages were reached (pluteus *S. droebachiensis*, late bipinnaria *A. rubens*), cultures were fed with a commercial mix of algae (Phytofeast Live, Reef Nutrition) at a density of 1000 cells mL^{-1} (concentration per Meidel et al. 1999). Planktotrophs consistently spent proportionally less time in the embryonic phase (11% in *A. rubens*; 13% in *S. droebachiensis*) than the lecithotrophs (57% in *C. frondosa*, 53% in *C. papposus*) relative to total development time (from egg to final larval stage). All trials were performed on propagules obtained inside the same breeding season. In the case of multiple spawning events in the same season (only relevant for *C. frondosa*), cohorts were tested separately; however, there were no statistical differences among tested locomotory and morphological parameters so they were pooled for subsequent analyses.

Experimental protocols

Developmental stages were tested when $\sim 80\%$ of individuals in culture had reached that stage (Gemmill 1914, 1920; Hamel and Mercier 1996; Meidel et al. 1999). Focal stages included the late blastula and gastrula of all species, early brachiolaria in *A. rubens*, four-armed pluteus in *S. droebachiensis*, brachiolaria in *C. papposus*, and early pentactula in *Cucumaria frondosa* (see Table S1 for stage-specific details). Early time points in the most advanced larval stages (e.g. early brachiolaria, four-armed pluteus) were favoured over pre-competent forms to minimize the potential influence of settlement appendages on swimming that may occur during transition between the pelagic and benthic phases (near settlement). To this effect, early pentactulae of *C. frondosa* were tested prior to the emergence of the primary podia, as this results in a shift from swimming to crawling. Though *S. droebachiensis* passes through later-stage plutei forms before undergoing metamorphosis,

four-armed pluteii were chosen here as this is the stage commonly used by investigators working on other aspects of larval swimming in this species (e.g. under turbulent flows, Roy et al. 2012b).

Swimming capacity metrics were measured at temperatures representative of ambient culture conditions, 1–3 °C for *C. papposus* and *C. frondosa* and 10 °C for *A. rubens* and *S. droebachiensis*, as well as an elevated temperature of 15 °C. Selected temperatures were within the natural range of each species [*A. rubens* 5–20 °C, Saranchova and Flyachinskya 2001; Villalobos et al. 2006; *S. droebachiensis* 0–24 °C, Roller and Stickle 1994; (Pearce et al. 2005); *C. frondosa* 0–15 °C, (Hamel and Mercier 1996); *C. papposus* 0–15 °C, (Reitzel et al. 2004)]. Experimental temperature values were confirmed prior to each trial using a glass thermometer ($n=3$ measurements per trial).

A light intensity of 300 lx was selected, as this represented the mean ambient light level experienced by the propagules in culture vessels and represents mid-range light intensity measured in the surface waters of coastal Newfoundland during spring and summer (10–1100 lx; Puvanendran and Brown 1998). A Fuloon 12 V 5050 RGB light emitting diode (LED) lamp was used for all experimental trials, set directly over the experimental vessel to avoid a light gradient that could promote phototaxis in the horizontal plane. During the short duration of the trial, all propagules appeared to stay in the upper half of the experimental vessel. Background shade (white or black) did not affect swimming speed at any developmental stage (as determined during preliminary experiments) so white backgrounds were used to enhance propagule visibility during monitoring.

At the commencement of each trial, propagules were gently transferred into small glass dishes (6–10 cm diameter, 2 cm high) and allowed to swim undisturbed for 5 min. This time frame was sufficient for propagules to recover from the transfer procedure and return to normal swimming behaviour as per preliminary experiments. Following the acclimation period, video recordings were taken for 5 min (30 fps, Olympus TG-1 Camera) and the resulting footage was later analysed with the software ImageJ (see method below). Three replicate trials were performed for each stage in each species resulting in a total of 15–30 individual propagules per stage per species. The effect of replicate was statistically tested (see below) to ensure differences among life stages were not obscured by temporal replication.

As an environmental control, recordings were also taken of unhatched propagules (early developing embryos) to correct for any passive surface drift that may occur from convection currents. Unhatched propagules (still inside the fertilization envelope) are useful in this capacity because they are comparable to newly hatched blastulae in size and buoyancy, but they are not motile (devoid of cilia).

Therefore, it can be assumed that any displacement of non-motile embryos is purely due to background water movements in the horizontal plane. These mean drift currents were very small (0.001–0.01 mm s⁻¹) and were negligible (<5%) at all stages except the blastula of *A. rubens*, in which passive displacement could represent up to 15% of the total horizontal displacement.

Particle tracking and swimming capacity metrics

The MOSAIC particle tracking algorithm in ImageJ [<http://mosaic.mpi-cbg.de/?q=downloads/imageJ>] was used to analyse swimming at each tested life stage (Chenouard et al. 2014). The 2D horizontal paths of swimming propagules were exported as x - y coordinates and converted into displacement data over one second intervals for the duration of the trials. We acknowledge that measuring only the horizontal component of swimming in propagules of species with planktotrophic development can be an underestimation of their true swimming capacity, however, lecithotrophic propagules are buoyant. Therefore, only trials in the horizontal plane can minimize the buoyancy and gravity effects, allowing for meaningful conclusions about nutritional mode differences. Propagules were excluded from the analysis if they collided with each other, or with the edge of the dish. For all treatments, natural drift speeds obtained from unhatched propagules were subtracted from mean speeds to account for passive movement.

Four metrics were used to quantify swimming capacity. (1) Mean absolute speed (mm s⁻¹) was calculated as an average of distance travelled per 1-s interval over the length of the trial. Absolute speed is the most commonly reported metric of swimming in the literature and provides a standard for comparisons. (2) Mean relative speed was calculated as the mean number of body lengths travelled per second (BL s⁻¹), where body length was the longest axis in asymmetrical propagules measured from images (Epp and Lewis 1984). Standardizing speed by size to generate relative speed is useful for making comparisons among propagules of different sizes and shapes, such as the ones in this study. (3) Net-to-gross displacement ratio (NGDR) was calculated as the average ratio between net (displacement) and total distance travelled over 20 s intervals for the duration of the trial. NGDR is a measure of path complexity where values close to 1 indicate a relatively straight path and values near 0 indicate a complex path (Metaxas 2001). NGDR values typically plateaued before the end of swimming trials. (4) Path corrected speed (PCS, mm s⁻¹) was calculated to incorporate the influence of swimming speed and path on propagule movement, allowing for holistic comparisons among stages and species. PCS was obtained by multiplying swimming speed by the path straightness index as a proxy for mean displacement per unit of time.

Statistical analysis

For each species, a nested analysis of variance (ANOVA) was used to test the effect of life stage and replicate trials on all propagule swimming metrics under ambient conditions: mean absolute speed, mean relative speed, net-to-gross displacement ratio and path corrected speed, within species. For this analysis, replicate was nested within stage. Two-way ANOVA was used to test the combined effect of increased temperature and stage on the four metrics of propagule swimming capacity for each species. The same test was used for interspecific comparisons of swimming metrics and stages at 15 °C. Tukey's post hoc tests were conducted on statistically significant ANOVA models. All statistical analyses were conducted and assumptions verified using SigmaPlot statistical software at $\alpha=0.05$.

Results

Swimming capacity throughout ontogeny under ambient conditions

Swimming speed

Among propagules of species with planktotrophic development, absolute swimming speed increased significantly from one developmental stage to the next in *A. rubens* ($F_{2,38}=34.4$, $p<0.01$; Fig. 1a), whereas it plateaued at the gastrula stage in *S. droebachiensis* ($F_{2,56}=10.1$, $p<0.01$; Fig. 1b). On average, the brachiolaria of *A. rubens* exhibited the fastest absolute swimming speed (0.48 mm s^{-1}), representing a tenfold increase compared to the blastula (0.04 mm s^{-1}), whereas values were more constant ($0.19\text{--}0.34 \text{ mm s}^{-1}$) among life stages of *S. droebachiensis*.

Among lecithotrophic propagules, mean absolute swimming speed increased significantly with ontogeny in *C. papposus* ($F_{2,43}=33.3$, $p<0.01$; Fig. 1c) but not in *C. frondosa* ($F_{2,43}=1.9$, $p=0.17$; Fig. 1d). On average, the fastest swimming stage in *C. papposus* was the late larval stage (brachiolaria), with an absolute swimming speed of 0.78 mm s^{-1} . In contrast, the fastest stage of *C. frondosa* was the gastrula; with an absolute swimming speed of 0.21 mm s^{-1} .

When accounting for body length, relative swimming speed increased with ontogeny in *A. rubens* from 0.25 to 1.50 BL s^{-1} ($F_{2,38}=21.8$, $p<0.01$; Fig. 1e) but decreased in *S. droebachiensis* from the blastula/gastrula (1.20 BL s^{-1}) to the pluteus stage (0.30 BL s^{-1} ; $F_{2,56}=39.3$, $p<0.01$; Fig. 1f). Relative swimming speed in *C. papposus* increased significantly from 0.20 to 0.70 BL s^{-1} ($F_{2,43}=15.5$, $p<0.001$; Fig. 1g) but remained stable at $0.20\text{--}0.30 \text{ BL s}^{-1}$ in *C. frondosa* ($F_{2,43}=3.0$, $p=0.064$; Fig. 1h).

Swimming trajectories

Among planktotrophs, net-to-gross displacement ratio (NGDR) increased significantly with ontogeny in *A. rubens* (from 0.57 to 0.81 , Fig. 1i; $F_{2,38}=5.1$, $p=0.015$) and in *S. droebachiensis* (from 0.28 to 0.63 , Fig. 1j; $F_{2,56}=4.1$, $p=0.028$). Paths visibly became straighter in both species with each successive life stage (Fig. 2a, b). Similar increases in NGDR with ontogeny were detected in the lecithotrophs *C. frondosa* ($0.52\text{--}0.75$, Fig. 1l; $F_{2,43}=3.4$, $p=0.049$) and *C. papposus* ($0.44\text{--}0.82$, Fig. 1k; $F_{2,43}=8.9$, $p<0.001$). Paths also visibly straightened in the late life stages of both species, although the pattern was more evident in *C. papposus* (Fig. 2c, d).

Path corrected speed (PCS)

When both speed and path straightness (NGDR) were combined quantitatively, PCS did not exhibit uniform ontogenetic trends among planktotrophs; it increased with each sequential life stage in *A. rubens* (from 0.02 to 0.39 mm s^{-1} , Fig. 1m) but plateaued after an increase from blastula to gastrula in *S. droebachiensis* (from 0.05 to 0.19 mm s^{-1} ; Fig. 1n). PCS also followed different ontogenetic trends among lecithotrophs. In *C. papposus*, PCS increased from the blastula to the brachiolaria ($0.07\text{--}0.64 \text{ mm s}^{-1}$; Fig. 1o). In contrast, PCS did not change with ontogeny in *C. frondosa* ($0.09\text{--}0.11 \text{ mm s}^{-1}$, Fig. 1p).

Effective displacement (horizontal) over a 1-hour period can be estimated using PCS. This provides a general method of comparison under standard conditions. The highest effective displacement among tested propagules was 2.3 m h^{-1} , in the brachiolaria of *C. papposus*. The next highest values were 1.4 and 0.7 m h^{-1} , in the brachiolaria of *A. rubens* and the gastrula of *S. droebachiensis*, respectively. Effective displacement was consistent among life stages of *C. frondosa* with values around 0.3 m h^{-1} .

Temperature effects on propagule swimming capacity

A within-stage analysis in the planktotrophs showed that propagules of *A. rubens* and *S. droebachiensis* responded slightly differently to increased water temperature. In *A. rubens*, only relative swimming speed increased significantly when propagules were tested at 15 °C ($p=0.014$). In contrast, absolute swimming speed (Fig. 3a, $p<0.01$), relative swimming speed (Fig. 3b, $p=0.026$) and path corrected speed (Fig. 3d, $p=0.032$) were higher for *S. droebachiensis* propagules exposed to 15 °C. No differences in the NGDR index of path straightness were detected for either species (Fig. 3c).

At the within-stage level in lecithotrophs, not all tested propagules of *C. papposus* and *C. frondosa* responded the

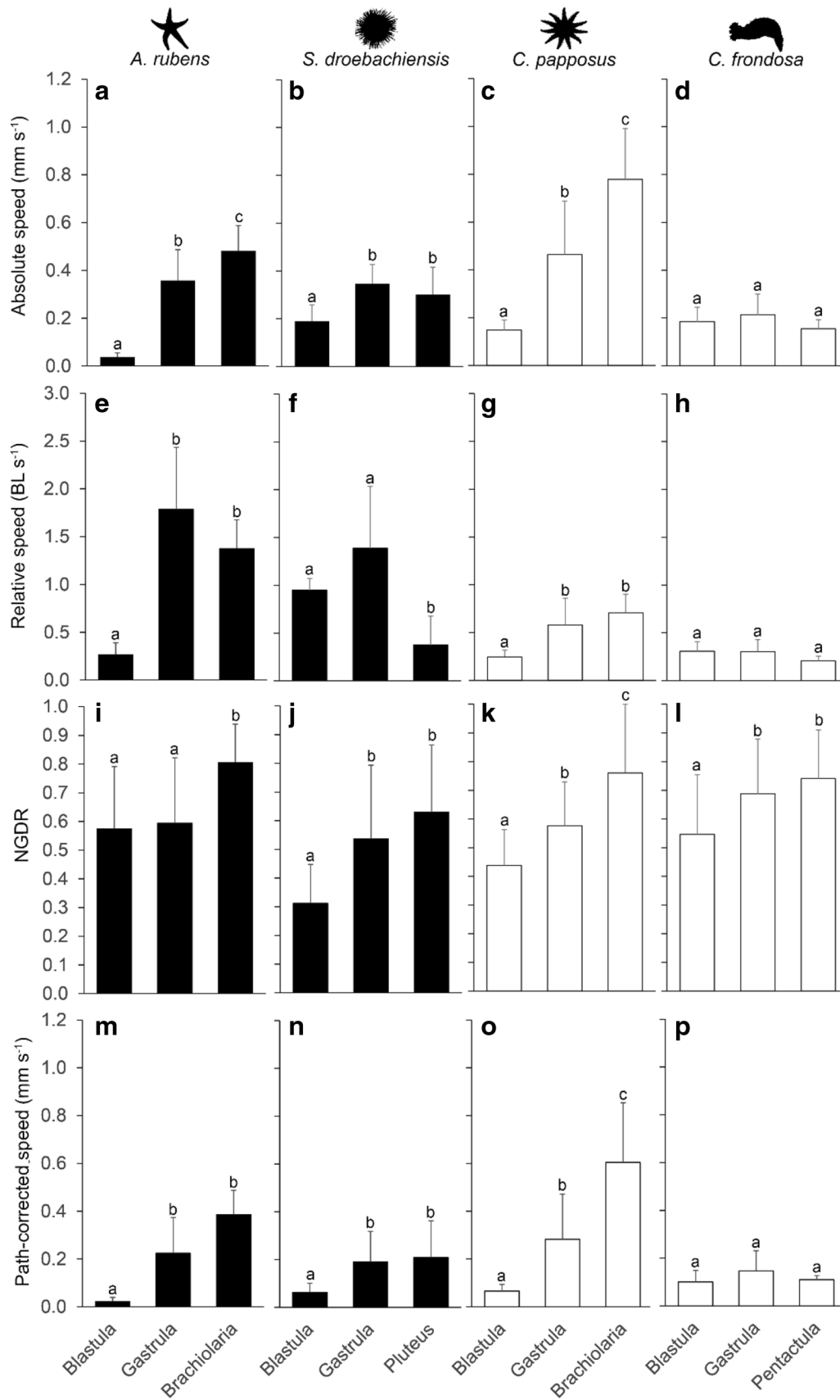


Fig. 1 Swimming capacity of echinoderm propagules under ambient conditions. **a, e, i, m** *A. rubens* at 10 °C; **b, f, j, n** *S. droebachiensis* at 10 °C; **c, g, k, o** *C. papposus* at 1–3 °C; **d, h, l, p** *C. frondosa* at 1–3 °C. Black bars (left panels) represent planktotrophic species and white bars (right panels) represent lecithotrophic species. NGDR = net-to-gross displacement ratio. Values reported are means \pm SD, $n=10$ –15 individuals per stage. Letters over the bars indicate statistically significant differences (see Tables S2, S3 for details and statistical results)

same to the increase in water temperature. While absolute speed, relative speed and PCS of *C. frondosa* propagules (Fig. 3e, f, h) increased significantly ($p < 0.01$) at 15 °C, the NGDR index of path straightness (Fig. 3g, $p < 0.01$) and PCS (Fig. 3h, $p = 0.011$) of *C. papposus* decreased significantly.

Overall, in interspecific comparisons across developmental modes, planktotrophs and lecithotrophs had similar absolute swimming speeds at 15 °C ($F_{3,6} = 0.007$, $p = 0.93$, Table S4). The fastest recorded speeds, across all species and temperatures, remained for the brachiolaria stage of *C. papposus* (1.2 mm s^{-1}). Gastrulae of planktotrophic species exhibited faster relative speeds than gastrulae of lecithotrophic species (1.65 BL s^{-1} faster, $F_{2,6} = 56.73$, $p < 0.001$), but no other differences in relative speeds were detected. Planktotrophs also had slightly higher path corrected speeds at the larval stage (0.07 mm s^{-1} faster, $F_{2,6} = 5.43$, $p = 0.033$). No differences in NGDR were detected among the development modes at any stage ($F_{3,6} = 2.28$, $p = 0.13$).

Discussion

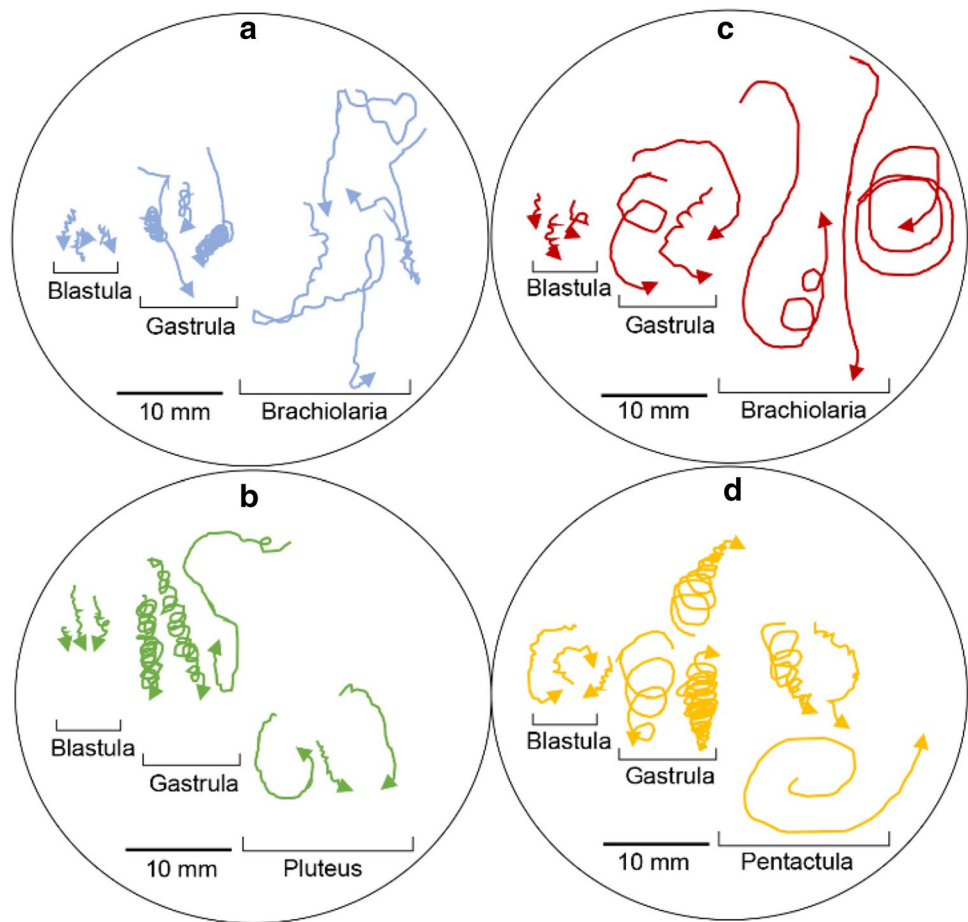
The active swimming behaviours of pelagic propagules are believed to serve various roles, i.e. prevent larvae from sinking, facilitate access to micro-environments, gas exchange and enhance settlement near the benthos (Clay and Grünbaum 2011). Speeds in the range of 0.1–30.0 mm s^{-1} have previously been reported for ciliated propagules from basal taxa, such as Porifera (Maldonado 2006) and Cnidaria (Mileikovsky 1973; Harii et al. 2002), as well as more derived taxa such as Bryozoa (Wendt 2000), Mollusca (Chia et al. 1984) and Echinodermata (Chia et al. 1984; Podolsky and Emlet 1993). Direct comparisons of swimming speed across studies are complicated by inherent differences in life stage and nutritional mode of focal propagules, experimental scale/conditions and direction of displacement (e.g. vertical swimming rates can be influenced by gravity, buoyancy and flow). Results for echinoderms to date have chiefly been obtained for late-stage ciliated larvae of species with planktotrophic development, either in still-water vertical columns (Metaxas 2001; Metaxas and Saunders 2009), under various flow regimes (Roy et al. 2012b) or combining data from both horizontal and vertical planes

(Rebolledo and Emlet 2015). Planktotrophic propagules have been in focus partly because they are easy to culture under laboratory conditions (Wray et al. 2004), they are commonly used in aquaculture (Mos et al. 2011; Liu et al. 2016; Loor et al. 2016) and their cilia serve both as feeding and locomotory structures (Strathmann 1971; Strathmann and Grunbaum 2006). Previous reports of swimming speeds in the bipinnaria of *A. rubens*, and plutei of *S. droebachiensis* and *Dendraster excentricus* are similar to swimming speed values measured in this study at comparable stages, i.e. 0.1–0.5 mm s^{-1} (McDonald 2012; Roy et al. 2012b; Civelek et al. 2013). Increases in swimming speed with increasing water temperature were also reported, i.e. 0.2–0.5 mm s^{-1} in *S. droebachiensis* (Daigle and Metaxas 2012).

The present multi-species study of swimming capacity showed that the absolute swimming speeds of planktotrophs and lecithotrophs were surprisingly similar when tested under respective ambient conditions, and at uniform higher temperatures across all stages. On the other hand, planktotrophs typically displayed faster relative swimming speeds (body lengths s^{-1}) than lecithotrophs, particularly at the gastrula stage, which is more fusiform in the latter than in the former. While this shape may have evolved to reduce projected area and drag of lecithotrophic gastrulae, similar to the faster swimming speeds seen among cyprid versus nauplius larvae in crustaceans (Walker 2004), it apparently does not completely offset the effects of large size. The higher relative speeds of *A. rubens* and *S. droebachiensis* gastrulae could relate to increased risk of epibenthic predation, previously documented in embryonic stages of planktotrophs (Mercier et al. 2013a). Though faster swimming larvae may encounter more predators (Gerritsen and Strickler 1977), the combination of complex paths and fast swimming speeds may allow gastrulae to escape after an encounter with predators as not all predators may be able to track a chaotically swimming propagule.

Relative speeds and other metrics of swimming capacity were similar among the focal species at early embryonic stages (late blastula), despite marked differences in propagule length (0.2–0.3 vs. 0.6–0.8 mm). Relative speeds were higher among late-stage planktotrophs, but the brachiolaria of *C. papposus* displayed on average faster absolute speeds than all other tested life stages and species under ambient and 15 °C conditions. This was in stark opposition to our initial hypothesis that the propagules of planktotrophic species would swim faster than those of lecithotrophic species in the horizontal plane. Over the past 20 years, other assumptions about lecithotrophic propagules have been revisited; they were recognized to disperse as far (Young et al. 1997) and spend as long in the pelagic region as planktotrophs (Mercier et al. 2013b), and have greater control over settlement site selection (Marshall and Keough

Fig. 2 Swimming paths of echinoderm propagules under ambient conditions. **a** *A. rubens* at 10 °C; **b** *S. droebachiensis* at 10 °C; **c** *C. papposus* at 1–3 °C; **d** *C. frondosa* at 1–3 °C. Paths represent typical swimming trajectories of propagules over 300 s and are scaled relative to size of the circle (arena)



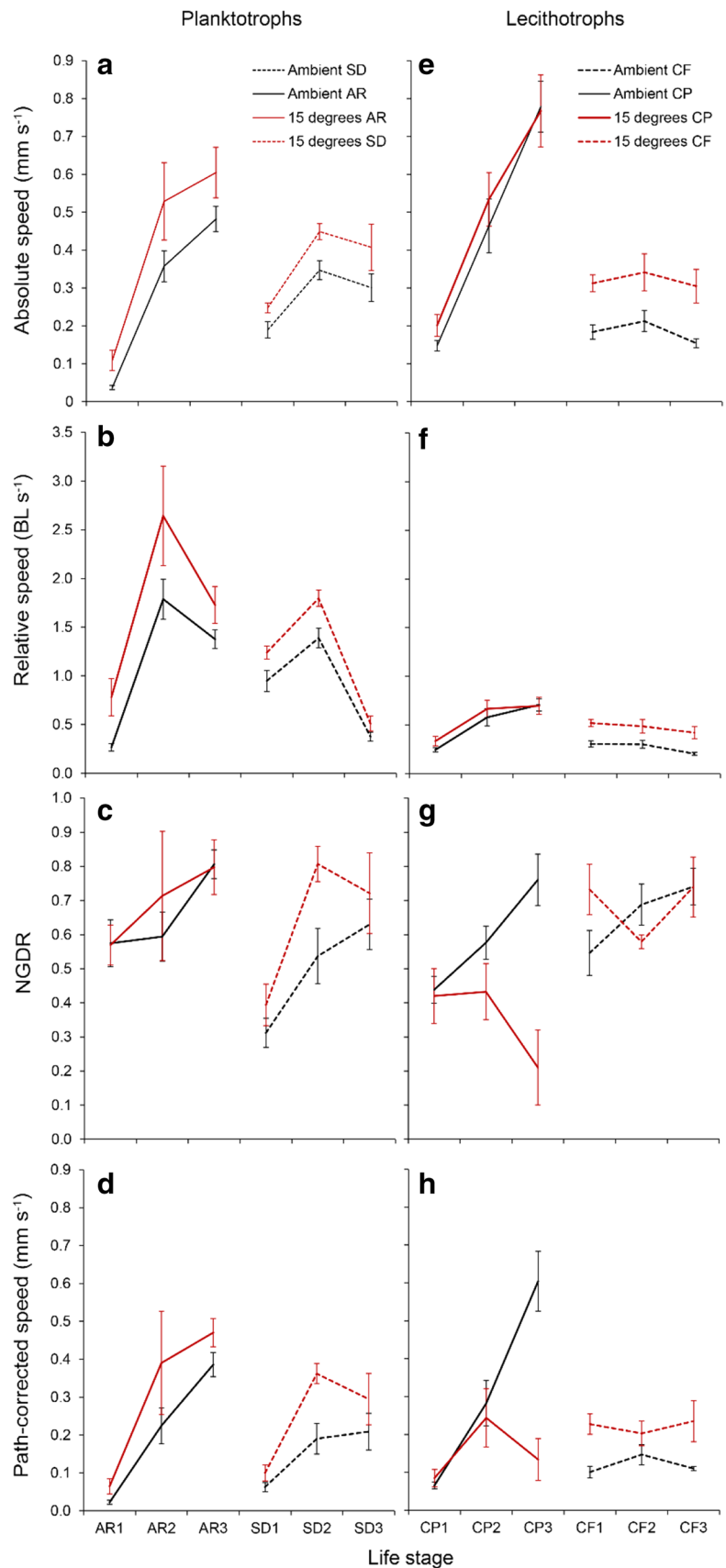
2003). Models have also revealed that positively buoyant propagules, such as most lecithotrophic larvae, can disperse further from adult habitats than neutrally buoyant or passive particles (Koehl 2007).

Even though absolute and relative swimming speeds varied, changes in swimming trajectories with progression through ontogeny were conserved across all four species. Propagules transitioned from circular swimming patterns in embryonic stages to expansive rectilinear paths that covered more ground per unit of time in more advanced larval stages. Overall, lecithotrophic propagules tended to swim with more complex paths than planktotrophs. This may provide an advantage by allowing these propagules to encounter less predators relative to planktotrophs, but without the cost of not finding as much food; a challenge faced primarily by planktotrophs (Visser and Kjørboe 2006). Generally, propagule paths displayed both clockwise and counter clockwise loops throughout the trials, which reflects the variability reported in ciliated propagules of echinoderms (Chia et al. 1984). A capacity to change the direction of rotation while swimming emerged in sea star larvae, i.e. the brachiolaria of *A. rubens* and *C. papposus*. Such an ability was previously described as a backflip, representing body

flexion rather than changes in cilia beating direction or speeds (Strathmann 1971).

Effective horizontal displacement (based on path corrected speed) in the order of 0.5–2.5 m h⁻¹ were recorded here, which may seem limited relative to locally strong mixing and currents; however, the fact that active propulsion has been maintained by pelagic propagules indicates that it serves a purpose. Dispersive abilities in planktotrophs are at least partially controlled by their position in the water column during development (Sameoto et al. 2010; Roy et al. 2012b). In contrast, most pelagic lecithotrophic propagules remain in the upper meters of the water column during much of their development, as a consequence of their positive buoyancy (Emler 1994). The similarity of swimming trajectories among tested planktotrophs and lecithotrophs in the horizontal plane could be evidence of phylogenetically conserved patterns of locomotion that supersede nutritional mode differences. Complex paths that cover both horizontal and vertical planes (as seen in planktotrophs) could expose propagules to different currents and flow environments as greater pelagic surface area is covered between path end points than relatively straighter paths (Chan 2012). In contrast, rectilinear (straight) trajectories

Fig. 3 Swimming capacity of echinoderm propagules under ambient conditions (*black lines*) and warm conditions (*red lines*). Trial temperatures (in °C) are indicated to the right of each line. *Left panels* show planktotrophic species (**a–d**) and *right panels* show lecithotrophic species (**e–h**). Lines indicate mean values for each life stage ($n = 5–15$ individuals per stage). Species names and numbers indicate life stages: 1 blastula, 2 gastrula, 3 a more advanced larval stage that is species-specific (see Fig. 1 and Table S1). *NGDR* net-to-gross displacement ratio. Table S5 provides detailed ANOVA results. *Error bars* indicate standard error



in both horizontal (seen here) and vertical planes could promote rapid access to areas of different flow regimes at small scales (cm to m), especially near the benthos (Walters et al. 1999).

The path corrected speeds were the highest for the brachiolaria of *A. rubens* and *C. papposus*, a life stage designed for substrate selection and settlement (Barker 1977; Byrne and Barker 1991). Furthermore, the increasingly rectilinear swimming trajectories exhibited by the larval stages of most species studied here could correspond to the onset of an exploration phase documented in several competent and pre-competent larvae of echinoderms (Barker 1977; Byrne and Barker 1991; Hamel and Mercier 1996). The importance of swimming trajectories to understanding swimming behaviour in the water column and near the benthos close to settlement has also been confirmed in lecithotrophic coral larvae (Pizarro and Thomason 2008). Together, these findings suggest that speed alone may not be a reliable predictor of swimming capacity in benthic invertebrate propagules, and that swimming trajectories need to be also considered.

While some recent studies have opted to parameterize marine propagules as passive particles for model simplification (e.g. Salama et al. 2013; Myksvoll et al. 2014; Wood et al. 2014; Fenberg et al. 2015), the value of stage-specific and species-specific capacities and behaviours is increasingly being emphasized (Robins et al. 2013; Morgan 2014; Pringle et al. 2014). However, efforts are still challenged by the difficulty of modelling dispersal <2 m above the sea floor, by incomplete understanding of ontogenetic changes in locomotory abilities and fundamental buoyancy/shape differences between species with planktotrophic or lecithotrophic propagules (Metaxas and Saunders 2009; Robins et al. 2013), and the relative scarcity of data on lecithotrophic propagules. These gaps in methodology and knowledge have limited the development of biophysical dispersal models with universal applicability.

Propagule dispersal has two components: passive dispersal as a result of large-scale oceanographic processes (e.g. currents, fronts, mixing) and active dispersal as a result of swimming behaviours (e.g. movement changes, taxis). We acknowledge that the swimming data generated here is unlikely to inform large-scale dispersal phenomena of these species. However, active swimming by propagules may impact the outcome of dispersal predictions at smaller scales. Interestingly, relatively subtle speed changes (e.g. doubling) were shown to alter dispersal predictions (on scales of m to km) more strongly in weakly swimming ciliated propagules than other larval types (e.g. Robins et al. 2013; Morgan 2014). To this effect, horizontal swimming speeds of propagules may interact with currents and facilitate predictions of vertical as well as horizontal displacement of propagules. Swimming speed data collected here

are similar to those previously reported for echinoderm propagules and may be useful to modellers as a starting point, after accounting for fundamental composition and buoyancy differences between planktotrophic and lecithotrophic propagules. Navigation of pelagic ciliated propagules over various spatial scales is currently incomplete (Scheltema 1986; Kingsford et al. 2002), warranting further investigation of the drivers and mechanisms of shifts in their swimming trajectories.

Propagule swimming and behavioural patterns may be driven primarily by location (pelagic development) since the need to detect and avoid unfavourable environments is a ubiquitous selective pressure, independent of nutritional mode and morphology. The degree of propagule sensitivity to abiotic factors (salinity, light, and temperature) and biotic cues in the water column has been well studied in planktotrophs such as *A. rubens* and *S. droebachiensis* (Metaxas 2001; Roy et al. 2012a; Civelek et al. 2013). However, similar studies have not yet been conducted with lecithotrophic echinoderm propagules, although numerous studies exist for other lecithotrophic propagules in Porifera and Cnidaria (Holst and Jarms 2006; Jacobs et al. 2007; Collin et al. 2010). The use of small-scale studies (including detailed examinations of swimming mechanisms and sensory responses) in concert with large-scale population-based studies could help improve our understanding of the persistence of benthic marine animals with diverse types of pelagic development.

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Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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