



Ontogenetic variation in photosensitivity of developing echinoderm propagules



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ABSTRACT

Swimming behaviours and sensory abilities of early pelagic stages play a prominent role in the life history and ecology of sessile/sedentary benthic species, with implications for settlement, recruitment and dispersal. Light is a particularly important driver of navigational behaviour in the ocean, as a signal of key habitat characteristics (e.g., depth, shelter). Work to date on phototaxis has largely focused on planktotrophic larvae that feed during development, and much less on the larger lecithotrophic larvae that rely on maternal provisions (yolk). It remains unclear how responses to light might differ among ciliated propagules of different sizes and nutritional modes. The present study explored if/how phototactic responses are modulated by ontogeny (from embryo to larva), nutritional mode and light colour (wavelength) in ciliated propagules using four co-occurring species of echinoderms: the sea stars *Asterias rubens* and *Crossaster papposus*, the sea urchin *Strongylocentrotus droebachiensis* and the sea cucumber *Cucumaria frondosa*. Two types of behavioural responses to stimuli (white, red, and blue light) were examined: 1) taxis when the light stimulus was placed at one end of the chamber (net movement towards or away from the light stimulus) and 2) activity level, using a suite of swimming metrics, under uniform illumination. All four species consistently displayed some level of photosensitivity to white light and responses varied intra- and interspecifically. When the stimulus was red or blue light, planktotrophs modified their phototactic responses in a species- and stage-specific manner, while lecithotrophs generally displayed responses without a clear net direction. Swimming speeds displayed stage and species-specific variation under constant red or blue light, but swimming trajectories were consistently straighter under red light, resulting in greater displacement. Taken together, the results suggest that propagules of species with different life-history strategies respond to light stimuli in distinctive stage-wise manners. Interestingly, ontogenetic patterns were not conserved within nutritional modes or taxa. Further investigations of species-specific responses to light might help clarify its roles, in combination with factors such as buoyancy and gravity, in the ecology of propagules of benthic invertebrates.

1. Introduction

Light patterns undergo marked vertical changes in the ocean, in that light intensity is reduced (Dickey et al., 2011) and longer wavelengths (700–650 nm, red) are rapidly filtered out (McFarland, 1986) with increasing depth. The combination of these two features produces a multi-faceted gradient that organisms can detect and respond to (Nilsson, 2009). As such, light is an important driver of behaviour and vertical distribution in marine species (Jékely, 2009; Jékely et al., 2008; Taylor, 1984; Thorson, 1964). For benthic species with a complex pelagobenthic life history (whereby intermediate larval forms develop in the water column before returning to the benthos), the naturally-occurring light gradient in the ocean can act as an orientation cue to help

propagules detect where they are in the water column and to direct larvae towards settlement sites for the completion of metamorphosis and recruitment (Thorson, 1964). Knowledge of sensory behaviour from an ontogenetic perspectives can, therefore, shape our understanding of small-scale and large-scale species distributions (Anil et al., 2010).

Studies on swimming behaviour of marine propagules in response to light cues have been conducted in all major phyla, chiefly at the larval stage. Marine larvae are diverse in form (e.g., ciliated or bearing swimming appendages) and nutritional mode (planktotrophic, relying on external nutrients during development vs. lecithotrophic, yolk-sustained), but share the ability to respond to light during development (Jékely, 2009; Jékely et al., 2008; Thorson, 1964). Basal phyla, such as Porifera (lecithotrophic) and Cnidaria (mainly lecithotrophic), have

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simple ciliated ellipsoid larvae that alter their swimming patterns in response to light of variable intensity and colour (e.g. Porifera, Collin et al., 2010; Leys et al., 2002; Leys and Degnan, 2001; Cnidaria, Holst and Jarms, 2006; Mundy and Babcock, 1998; Svane and Dolmer, 1995). In sponge larvae, the apical cilia flex in the presence of light, generally resulting in photonegative swimming behaviour (Collin et al., 2010). Planula larvae of cnidarians display more variable responses, showing either photonegative or photopositive behaviour depending on light colour and other environmental factors (Mundy and Babcock, 1998). In addition, the swimming behaviours and eventual settlement patterns of planulae have also been shown to be affected by light cues in several species (Pizarro and Thomason, 2008; Svane and Dolmer, 1995; Tran and Hadfield, 2013).

In more derived phyla, studies of phototactic responses have so far centered on planktotrophic larvae, and often excluded the obligatory non-feeding early embryonic stages. Ciliated planktotrophic larvae of Mollusca (Barile et al., 1994; Miller and Hadfield, 1986), Annelida (Butman et al., 1988; McCarthy et al., 2002; Young and Chia, 1982b), Bryozoa (Wendt, 2000) and Echinodermata (Pennington and Emlet, 1986) display species-specific patterns of phototaxis that often vary from intermediate to pre-competent larval stages. Patterns of phototaxis are particularly well described among larvae of Arthropoda that possess swimming appendages (Latz and Forward, 1977; Shirley and Shirley, 1988).

Phototactic behaviours in all types of planktotrophic propagules are often presumed to be related to feeding habits and positioning in the water column (e.g., vertical position of barnacle larvae, *Verruca floridana* and *Paralepas pedunculata*, is controlled by light intensity and ontogeny; Bingham and Young, 1993). Photosensitivity may also assist the settlement phase and ensure recruitment into the adult population (Jékely, 2009).

Knowledge of propagule photosensitivity in lecithotrophic species belonging to derived phyla is quite limited, with the exception of phototaxis among tadpole larvae (phylum Urochordata; McHenry and Strother, 2003; Svane and Dolmer, 1995; Svane and Young, 1989; Vazquez and Young, 1998). Overall, phototactic behaviours in phyla with representatives that may develop through either ciliated lecithotrophic or planktotrophic larvae (e.g., Echinodermata) require further attention. Key questions include: Do pelagic lecithotrophic propagules in mixed-mode phyla possess the same degree of sensory ability as planktotrophic propagules and, if so, does it vary with ontogeny?

The present study explores the responses of four species of echinoderms (across three taxonomic classes) to light of various colours throughout early ontogeny, from newly-hatched embryo to late larva. The underlying hypotheses were that: (1) all echinoderm propagules would exhibit behavioural responses to light (of varied colour); (2) these responses would shift with early ontogeny, independently of nutritional mode; but (3) planktotrophic larvae would be generally more sensitive to light cues, since they are reported to utilize light cues to facilitate feeding and daily vertical movements in the water column (Pennington and Emlet, 1986). Phototactic responses to light of different colour/wavelength (white, red, blue) were characterized based on two aspects of swimming behaviour: (i) taxis (net movement towards/away from a light stimulus) and (ii) swimming metrics under uniform light intensity (increase/decrease in speed, more/less straight paths). The focus was on *how* propagules were swimming under different light colours, as speed alone may not be a robust measure of behaviour in weakly swimming ciliated propagules (Hansen et al., 2010; Montgomery et al., 2017). Echinoderms provide a useful framework for studies of phototaxis, as photosensitive cells have been identified in the planktotrophic larvae of one of the five extant classes, and such larvae display taxis in response to light. However, studies of phototaxis in echinoderms have focused primarily on shallow-water adults (e.g., ophiuroids, Hendler, 1984; asteroids, Yoshida and Ohtsuki, 1968; Yoshida et al., 1984; echinoids, Adams, 2001; Domenici et al., 2003; Yoshida et al., 1984), although phototaxis in the deep sea has

also been reported in one species of echinoid (Salazar, 1970). Assessments of phototaxis in echinoderm larvae are less common, and historically have overlapped with studies of vertical migration patterns (Fox, 1925; Haney, 1988; Pennington and Emlet, 1986; Roy et al., 2012) or settlement preferences in late-stage planktotrophic larvae (Metaxas et al., 2008; Mladenov and Chia, 1983). To our knowledge, no studies of phototaxis or sensory behaviour exist for any lecithotrophic echinoderm larvae. In addition, previous studies of phototaxis have traditionally focused on a single species, whereas comparative studies of species with different development patterns and phylogenies are scarce.

2. Materials and methods

2.1. Species collections and maintenance

Asterias rubens (5–10 cm radius), *Crossaster papposus* (5–10 cm radius), *Strongylocentrotus droebachiensis* (5–8 cm test diameter), and *Cucumaria frondosa* (15–20 cm contracted body length) were collected by SCUBA between 10 and 20 m depth along the Avalon Peninsula in Southeastern Newfoundland (eastern Canada; 46.640416 N, – 52.686534 W). Individuals were housed in 375-L tanks provided with running seawater ($\sim 60 \text{ L h}^{-1}$) at ambient temperatures ranging from 0 to 5 °C, and a natural photoperiod where light intensities ranged daily from 5 to 450 lx (mean = 300 lx; Mercier and Hamel, 2010, Montgomery et al., 2017).

2.2. Spawning and culture maintenance

This study was undertaken in the spring of 2014 and 2015, during the natural spawning periods of the focal species (Mercier and Hamel, 2010). Gonads of *A. rubens* were surgically collected from mature females and were treated with a solution of 0.1 μM 1-Methyladenine to promote final oocyte maturation (Dorée et al., 1976). Spawning was initiated in *S. droebachiensis* by injecting 1–2 mL of 0.5 mol L⁻¹ KCl into the coelomic cavity (Meidel and Yund, 2001). Fertilization of mature oocytes was performed using a dilution ($\sim 10,000$ spermatozoa mL⁻¹; Byrne et al., 2010) in both *A. rubens* and *S. droebachiensis* as this was the optimal concentration to promote 80–90% fertilization success, and reduce the potential for polyspermy. Gametes from a minimum of five females and three males were used to generate cultures. Fertilized oocytes of *C. papposus* and *C. frondosa* were collected following natural spawning events involving multiple males and females, by gently skimming them from the surface of the tanks (as they are positively buoyant).

Propagules were cultured in natural seawater, at the ambient temperature of the spawning season and early development. Standard rearing techniques were used for each species (*A. rubens* and *S. droebachiensis*, Meidel et al., 1999; *C. frondosa* and *C. papposus*, Hamel and Mercier, 1996, Montgomery et al., 2017). Lecithotrophic propagules of *C. papposus* and *C. frondosa* were raised at 1–3 °C (1.5-L vessels, approx. 0.1 L h⁻¹ flow-through conditions). Propagules of *A. rubens* were obtained a little later in the spring when the ocean temperature was higher; these cultures were maintained at 10 °C (static conditions). Once feeding larval stages were reached (4-armed 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; Meidel et al., 1999, Montgomery et al., 2017). 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 parameters so they were pooled for subsequent analyses.

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