



## Contrasting predation rates on planktotrophic and lecithotrophic propagules by marine benthic invertebrates



Annie Mercier<sup>a,\*</sup>, Emily Joan Doncaster<sup>a</sup>, Jean-François Hamel<sup>b</sup>

<sup>a</sup> Department of Ocean Sciences, Memorial University, St. John's, Newfoundland and Labrador A1C 5S7, Canada

<sup>b</sup> Society for the Exploration and Valuing of the Environment (SEVE), Portugal Cove-St. Philips, Newfoundland and Labrador A1M 2B7, Canada

### ARTICLE INFO

#### Article history:

Received 10 June 2013

Received in revised form 11 September 2013

Accepted 13 September 2013

Available online 3 October 2013

#### Keywords:

Cnidaria  
Echinodermata  
Egg  
Larva  
Mortality  
Offspring

### ABSTRACT

When modeling life-history evolution of marine benthic invertebrates, it has been common to assume constant mortality rate of offspring during the pre-settlement phase and greater propagule vulnerability in the pelagic than in the benthic habitat. However, recent findings have challenged these assumptions, emphasizing the need for further empirical tests. Here we present the results of a multifactorial experimental investigation of predation rates on propagules of various taxa by benthic invertebrates. Planktotrophic and lecithotrophic propagules of echinoderms, cnidarians and annelids (i.e. sea cucumbers, sea stars, sea urchins, corals, sea anemones, jellyfishes, and polychaetes) were tested at various stages of development to examine the effects of ontogeny, size and behavior on predation rates by common filter feeders (mussels, tunicates) and suspension feeders (sea anemones). Overall, propagule survival was positively correlated with their size, although on closer inspection this was essentially due to the size difference between developmental modes (larger lecithotrophic propagules being less vulnerable). A slight inverse relationship between survival and age was detected in both lecithotrophic and planktotrophic propagules; however ingestion rates were not systematically higher on more advanced life stages within prey species due to predator-specific responses to ontogenetic changes. Filter feeders were generally more effective predators than suspension feeders. Tunicates expressed greater selectivity based on size and age of propagules than on their behavior, while the inverse occurred in the two other predators. A combination of factors, i.e. size, buoyancy and chemical defenses, presumably underlie overall higher survival rates in lecithotrophic than in planktotrophic propagules, supporting the hypothesis that the former but not the latter may have evolved due to increased epibenthic predation.

© 2013 Elsevier B.V. All rights reserved.

### 1. Introduction

As the primary or sole motile stage of many benthic taxa, pelagic propagules play a central role in their population dynamics, macroevolution and biogeography. While loss of larvae during development in the water column is believed to be very high (Morgan, 1995; Thorson, 1950), the causes and extent of larval mortality are still not well understood (Cowen and Sponaugle, 2009; Rumrill, 1990). Predation is frequently recognized as a key factor (Pechenik, 1999; Thorson, 1950; Vance, 1973; Young and Chia, 1987), although empirical support remains limited. Experimental studies of differential predation rates on early life stages of benthic taxa aiming to define their main drivers have largely examined predation on feeding (planktotrophic) larvae by pelagic predators (e.g. Johnson and Shanks, 2003; Pennington and Chia, 1984; Pennington et al., 1986; Rumrill et al., 1985), whereas fewer have investigated non-feeding (lecithotrophic) larvae (Iyengar and Harvell, 2001; Lindquist, 1996; Lindquist and Hay, 1996) or benthic predators (Cowden et al., 1984; Lindquist, 1996; Morgan, 1992). This

imbalance might be due to the perception that lecithotrophic propagules are often encapsulated or brooded, overlooking the fact that many are either freely spawned or undergo a free-living stage. Likewise, it is often assumed that pelagic propagules chiefly encounter benthic predators as settlers (Pechenik, 1999; Young and Chia, 1987), even though pelagic propagules of many benthic taxa are negatively or neutrally buoyant.

The above-mentioned literature shows that offspring of benthic invertebrate have evolved a number of morphological (e.g. spines, setae), behavioral (e.g. taxis, escape) and chemical defenses against predation. Less often evoked is buoyancy, which may afford protection against benthic predators by maintaining propagules high in the water column or at the sea surface. Buoyant propagules are generally associated with lecithotrophic development (Strathmann, 1985), which are larger, take more energy per gamete to produce and are thus typically produced in much lower numbers than the smaller planktotrophic propagules (Emlet et al., 1987). In echinoderms and other marine invertebrates, it is largely agreed that the various types of non-feeding larvae evolved from a feeding larva (Nielsen, 2009; Raff, 2008). However, phylogenetic studies recently argued that lecithotrophy is primitive for most groups and was achieved independently multiple times by

\* Corresponding author. Tel.: +1 709 864 2011.  
E-mail address: [amercier@mun.ca](mailto:amercier@mun.ca) (A. Mercier).

the end of the Early Cambrian, and that planktotrophy evolved between the late Cambrian and Middle Ordovician, also independently on numerous occasions (Peterson, 2005). A continuum of nutritional strategies between planktotrophy and lecithotrophy was proposed to be determined by variation in maternal investment, independent of larval morphology, suggesting the possibility of reversible transitions (Herrera et al., 1996; McEdward and Janies, 1997).

Peterson (2005) suggested that the initial exploitation of the pelagic zone by lecithotrophic larvae and the acquisition of planktotrophy both correlate in time with a drastic rise in the number and type of epibenthic suspension feeders in the Early Ordovician. He also proposed that adaptations that protect early embryonic stages from benthic predators are associated with the secondary evolution of lecithotrophy, e.g. the increase in egg size might reduce mortality of early embryos due to positive buoyancy and other mechanisms (Peterson, 2005). Lecithotrophic larvae generally have higher lipid contents than planktotrophic larvae that are neutrally or negatively buoyant (Emlet et al., 1987). Chemical defense may be another potential deterrent (Iyengar and Harvell, 2001). Planktotrophic larvae are often assumed to remain in the water column longer than lecithotrophic larvae and therefore have greater potential for dispersal (and loss). However, several classes of echinoderms do not follow this trend, suggesting that larval nutrition is not systematically tied to pelagic propagule duration (Mercier et al., 2013), and that other evolutionary pressures, such as differential predation, should be explored.

Recent findings have weakened other assumptions that are frequently made when modeling life-history evolution of marine benthic invertebrates, i.e. that there is constant mortality rate of offspring during the pre-settlement phase (independent of size or age), and greater vulnerability in pelagic than benthic habitats. In reality, mortality rates of offspring likely vary in time (throughout development) and space (as they move between different habitats) (Morgan, 1995; Pechenik, 1999). Many of these findings are based on the study of echinoderms which display various forms of lecithotrophic and planktotrophic larvae (Cowden et al., 1984; Emlet et al., 1987; Iyengar and Harvell, 2001; Pennington et al., 1986). They are also common and fairly diverse in many regions, making them easy to collect and maintain under laboratory conditions. Recent evidence has shown that mortality of propagules in echinoderms can be largely influenced by: (1) ontogenetic stage, i.e. the same predator will ingest some life stages and reject others, and different predators will have different preferences (Iyengar and Harvell, 2001); (2) propagule size, i.e. most benthic invertebrate predators prefer younger and small-sized larvae, whereas postlarval fish prefer larger larvae (Allen, 2008); and (3) the nature of predators or habitats, i.e. rates of predation are low in plankton assemblages (Johnson and Shanks, 2003) and higher in the benthic than in the planktonic habitat (Allen and McAlister, 2007). Among the potential caveats to the above-listed findings is the fact that experimental studies on size-specific and habitat-related predation are based on few species with planktotrophic propagules (Allen, 2008; Allen and McAlister, 2007; Johnson and Shanks, 2003). Furthermore, while the results on the respective importance of benthic versus pelagic predation are convincing, they were mainly obtained using flavored agarose baits rather than live propagules, with the exception of tethered megalopa larvae (Allen and McAlister, 2007). As for ontogenetic variations in predator deterrence, they were only rarely investigated in lecithotrophic species (Iyengar and Harvell, 2001).

The present study took an integrative approach in trying to address some of the previous shortcomings. The main goal was to compare acceptance/rejection and ingestion rate by benthic predators (with distinct feeding mechanisms) of propagules from a range of species belonging to three phyla. We primarily aimed to test the hypothesis that lecithotrophic propagules (of broadcast-spawning and brooding species) are less susceptible to benthic predation than planktotrophic counterparts. We also wanted to assess differences in vulnerability to

predation by the various predators based on propagule size, age, stage and behavior between and within these two developmental modes. A corollary of the study examined whether decreased susceptibility (if present) was due to unpalatability (i.e. rejection by predators) or a spatial barrier (e.g. buoyancy). If the physical distance is the only factor preventing benthic invertebrate predators from preying on certain propagules, then these predators should ingest the propagules when contact is induced.

## 2. Materials and methods

This study focused on ubiquitous benthic taxa that co-occur in subtidal habitats of the Northwest Atlantic. The majority is known to spawn in spring and many were shown to engage in simultaneous multispecies breeding events (Mercier and Hamel, 2010).

### 2.1. Collection and maintenance of predators

Three planktivorous species were tested that represent some of the most common sessile marine invertebrates along the coast of eastern Canada. The mussel *Mytilus edulis* (Linnaeus) (7–7.8 cm shell length,  $n = 8$ ), the solitary ascidian, or tunicate, *Halocynthia pyriformis* (Rathke) (3–3.9 cm basal diameter,  $n = 18$ ) and the sea anemone *Metridium senile* (Linnaeus) (3.8–4.6 cm basal disk diameter,  $n = 10$ ) were collected by divers in Logy Bay, Flat Rock and Pouch Cove (southeastern insular Newfoundland;  $\sim 47^{\circ} 40'N$ :  $52^{\circ} 42'W$ ) between 5 and 15 m depth. They were immediately transferred to a 1-m<sup>3</sup> tank supplied with unfiltered running seawater ( $\sim 50 \text{ L h}^{-1}$ ) at ambient temperature under natural photoperiod (large windows supplemented with timer-controlled lights).

For the trials (May–August 2009), specimens of the three species were individually placed in beakers ( $n = 8$ –10 for each species) submerged in a holding tank supplied with running seawater that maintained the temperature around 12 °C (corresponding to ambient temperature in the field). All individuals were left to acclimatize until they resumed their normal feeding/filtering postures. Only individuals firmly anchored to the bottom were used in the trials. Mussels and sea anemones anchored to the substrate on their own, whereas the tunicates were sewn onto fly screen mesh by tying their basal ramifications to the mesh and using small rocks to hold them in an upright feeding position. If an animal moved to the sides of its enclosure, it was gently repositioned on the bottom center and left to acclimatize again before the next run.

### 2.2. Spawning and larval cultures of prey species tested

#### 2.2.1. Planktotrophic oocytes, embryos and larvae

In May 2009, spawning was induced in female sea urchins *Strongylocentrotus droebachiensis* (Muller) ( $n = 4$ ) with 0.5 M potassium chloride (KCl). Spermatozoa were extracted surgically from males, and used for fertilization ( $\sim 500$ –1000 spermatozoa  $\text{mL}^{-1}$ ), which was confirmed by elevation of the fertilization membrane and/or first cleavage. Fertilized oocytes had neutral buoyancy with a slight tendency to deposit on the bottom in still water (coined mixed behavior). With the onset of swimming, neutrally buoyant gastrula stages and pluteus larvae spread evenly throughout the water column.

In June 2009, final oocyte maturation was induced in female sea stars *Asterias rubens* Linnaeus ( $n = 4$ ) using extracted gonad exposed to  $10^{-4}$  M 1-methyladenine. Extraction of spermatozoa and fertilization were carried out as described above. Mature oocytes displayed slightly negative buoyancy (i.e. mixed), while gastrulae and bipinnariae were neutrally buoyant and dispersed throughout the water column.

In May 2009, larvae of the polychaete worm *Alitta* (= *Nereis*) *virens* Sars were developed from a spontaneous spawning; they were collected and placed in culture. Trochophores were neutrally buoyant,

Download English Version:

<https://daneshyari.com/en/article/6304262>

Download Persian Version:

<https://daneshyari.com/article/6304262>

[Daneshyari.com](https://daneshyari.com)