



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



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ARTICLE INFO

Article history:

Received 10 June 2013

Received in revised form 11 September 2013

Accepted 13 September 2013

Available online xxxx

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.

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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

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