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Dawn Vaughn

Jonathan D. Allen

College of William and Mary, jdallen@wm.edu

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SYMPOSIUM

The Peril of the Plankton

Dawn Vaughn^{1,2,*†} and Jonathan D. Allen^{2,‡}

^{*}Department of Biology, University of Washington, Seattle, Washington 98195-1800, USA; [†]Friday Harbor Laboratories, University of Washington, 620 University Road, Friday Harbor, Washington 98250-9299, USA; [‡]Biology Department, College of William and Mary, PO Box 8795, Williamsburg, VA 23187-8795

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¹Present address: Purdue University, Department of Entomology, 901 West State Street, West Lafayette, Indiana 47907-2089. E-mail: dawnvaughn@purdue.edu

²These individuals contributed equally to the work described here and should be considered joint first authors.

Synopsis The pelagic environment is characterized by unevenly distributed resources and risks. Such unpredictability presents adaptive challenges to diverse planktonic organisms including the larvae of benthic marine invertebrates. Estimates of mortality during planktonic development are highly variable, ranging from 0% to 100% per day. Predation is considered a significant source of this mortality, but what explains the variability in estimates of the mortality of marine invertebrate larvae? While differential exposure of larval prey to predators may explain these widely variable estimates, adaptations that reduce vulnerability of marine larvae to predators may also be important. Although there are excellent reviews of predation upon larvae and of larval mortality and defenses, nearly 15 years have elapsed since these topics were formally reviewed. Here, we highlight recent advances in understanding the behavioral, chemical, and morphological defenses that larvae possess and assess their effectiveness in reducing the risk of predation. While recent work confirms that larval mortality is generally high, it also demonstrates that larvae can reduce their risk of predation in several ways, including: (1) temporarily escaping the benthos during vulnerable early stages, (2) producing chemical compounds that reduce palatability, (3) possessing morphological defenses such as spines and shells, and (4) exhibiting induced defensive responses whereby larvae can alter their behavior, morphology, and life histories in the presence of predators. Taken together, these studies indicate that marine invertebrate larvae possess a sophisticated suite of defensive phenotypes that have allowed them to persist in the life cycle of benthic invertebrates for eons.

Introduction

Planktonic larvae are a persistent feature in the life cycle of marine invertebrates. The origins of marine larvae date back to at least the Ordovician and likely back to the middle-late Cambrian, more than 500 mya (Signor and Vermeij 1994; Peterson 2005). The colonization of the pelagic zone by marine planktonic organisms, including marine invertebrate larvae, may have been driven by high levels of predation in the benthic zone (Peterson 2005) and in turn may have contributed to the Cambrian explosion (Butterfield 2001). While attempts to reconstruct ancient ecological and evolutionary events are extremely valuable and the potential contribution

of predation on marine invertebrate larvae to some of these events is intriguing, neontologists have yet to sufficiently describe the current ecological interplay between marine invertebrate larvae and their predators. Without a sufficient understanding of present-day ecological interactions between larvae and their predators, we have little hope of understanding ancient ones. We therefore focus our attention in this article on the role of predation on plankton in the maintenance of larvae in marine invertebrate life cycles.

The role of predation in structuring planktonic communities has long been recognized, primarily in freshwater habitats (Brooks and Dodson 1965). The

title of our article reflects the influence of classical work on the structure of planktonic communities (Hutchinson 1961). More recent studies of the role of predation in maintaining diverse assemblages of phytoplankton, zooplankton, and fish have confirmed Hutchinson's hypothesis that equilibrium is rarely reached in these habitats [reviewed by (Scheffer et al. 2003)] and suggest that predation on plankton results in chaos within communities (Doveri et al. 1993). Recent studies in planktonic dynamics are reviewed elsewhere (Roy and Chattopadhyay 2007) and are beyond the scope of this review; however, the individual predator-prey interactions described in the following pages should be useful for scaling these interactions to the community level.

All reviews of the role of predation on planktonic marine invertebrate larvae build upon the seminal work of Thorson who believed that the greatest loss of freely-spawned eggs occurred after fertilization and before settlement (Thorson 1946). Of the possible factors responsible for this loss, Thorson concluded that predation during the larval stage was the most important source of larval mortality (Thorson 1950). Decades later the role of predation in the mortality of marine invertebrate larvae was revisited in several important reviews (Young and Chia 1987a; Rumrill 1990; Morgan 1995); however, each of these more recent reviews is now at least 15 years old and none focuses on descriptions of larval defensive mechanisms. Young and Chia (1987) and Rumrill (1990) provided excellent and comprehensive reviews of estimates of larval mortality derived from theory, laboratory observations, and field techniques. Morgan (1995) re-evaluated the claims of Thorson (1950) and others that predation is the primary source of larval mortality. Morgan (1995) and Rumrill (1990) were more conservative than Thorson (1950) was in assessing the role of planktonic predation, concluding that losses due to poor fertilization success, physiological stress, starvation, offshore transport, and predation after settlement in the benthic zone are major additional sources of mortality.

Since 1995 no review has focused exclusively on predation on the planktonic larvae of marine invertebrates. At least one, more general, review of larval biology has highlighted the need for increased understanding of the vulnerability of larvae to both planktonic and benthic predators (Pechenik 1999). Similarly, a review of biophysical models of larval transport concluded that quantification of larval mortality remains poor and suggested increased efforts to sample populations of larvae in the field (Metaxas and Saunders 2009). Such

recommendations echo those made 20 years earlier (Rumrill 1990). Rather than repeat these clear calls for increased efforts in the collection of data, the goal of our review is to update recent approaches to estimating larval predation as a factor in the life histories of marine invertebrates and to describe advances in our understanding of the abilities of larvae to defend themselves against predators through a suite of chemical, morphological, and behavioral defenses.

Estimates of larval predation

Over the past 20 years, few studies have advanced our knowledge of the magnitude of larval predation in the field and those that have been published present extremely different estimates. Rumrill (1990) cited daily mortality rates ranging from 2% to 100%. More recent estimates of daily mortality suggest a similarly broad range of 0% (Johnson and Shanks, 2003) to 90% (Allen and McAlister, 2007). The most consistent pattern in estimates of larval mortality is one of high variability across methodologies, investigators, taxa, geographic locations, and temporal windows. Is this variability real or are some (or all) of these estimates simply inaccurate? In this section, we review the most recent methods for estimating larval mortality and address questions of their accuracy.

Laboratory estimates

Laboratory estimates of larval mortality are commonly encountered in the literature. While providing insight into the ability of larvae to avoid a particular type of predator, these estimates often occur under highly restrictive conditions and almost certainly overestimate absolute rates of predation. Overall, we suggest that these types of studies are best considered as means of identifying and testing the effectiveness of larval defense mechanisms (Purcell et al. 1991; Fabricius and Metzner 2004) rather than a gage of absolute levels of predation.

One of the most important advances in laboratory studies of larval predation is the recognition that the presence of background plankton can greatly reduce or even eliminate predation (Johnson and Shanks 1997). The presence of background plankton serves at least two functions in reducing larval predation: (1) providing an alternative food source and (2) potentially obscuring larvae from predators (Johnson and Shanks 1997). Density of prey can strongly affect measures of mortality rate in laboratory experiments (Rumrill and Chia 1984), and at the low densities (1 larva/L) usually associated with more natural conditions, larval mortality due to predation may

be negligible (Johnson and Shanks 1997). However, our understanding of the distribution of larvae in nature is generally poor and further research is needed before we can determine the natural densities of larvae and their predators. For example, if larvae disperse as passive particles they may become more dilute as development proceeds (Emlet 1986) but at other times nearshore oceanographic processes may dramatically alter larval concentrations or the concentrations of predators (Shanks et al. 2003; Menden-Deuer 2008; Shanks and Shearman 2009). These nearshore processes may be more important in determining larval distributions than are larger-scale patterns of upwelling and downwelling currents (Shanks and Shearman 2009).

Advances have also been made in estimates of the susceptibility of larvae to predation at settlement, including instances of cannibalism by adults (Andre et al. 1993; Tamburri and Zimmer-Faust 1996; Pechenik et al. 2004). Observations of cannibalism at settlement are not new (Timko 1979; Young 1988), but there has been a surge in interest in the effects of adult suspension feeders on settling larvae, particularly as they relate to cannibalism among gregarious species (Lehane and Davenport 2004; Alfaro 2006; Troost et al. 2008a 2008b). The results of these laboratory and field studies suggest that larval stages of some marine invertebrates are susceptible to intense predation and cannibalism at settlement (Troost et al. 2009), but as with estimates of larval mortality during planktonic development, the magnitude of predation at settlement varies considerably from <5% (Tamburri et al. 2007) to >77% (Porri et al. 2008). Whether benthic suspension feeders regularly influence the settlement of larvae either directly through predation or indirectly by influencing habitat choice by larvae remains unknown (Grosberg 1982). While previous work suggests that effects of benthic communities on settling larvae are negligible (Young and Gotelli 1988; Young 1989), they may occasionally be severe (Porri et al. 2008). Some recent work, however, corroborates earlier findings that larvae are not deterred from settling in established communities although these effects may vary widely across taxa (Bullard et al. 2004). Clearly estimating larval mortality at settlement is an area ripe for additional research.

Field estimates

Field estimates of larval mortality could provide more direct assessments of planktivory on marine invertebrate larvae (Young and Chia 1987b; Morgan 1995; Metaxas and Saunders 2009) but

have proved logistically challenging. Citations of the rare studies that track larval predation *in situ* are consistently followed by pleas for further work (Olson and McPherson 1987; Rumrill 1990). While the monitoring of larval cohorts in the field may be the best way to obtain accurate estimates of larval mortality (Metaxas and Saunders 2009), few recent studies have attempted this feat. In a rare example of successful monitoring of larval cohorts, Lamare and Barker (1999) estimated instantaneous rates of mortality (M) of -0.164 day^{-1} for larval sea urchins derived from a mass spawning event in a relatively isolated fjord [$M = \ln(N_0/N_t)/-t$; where M = instantaneous mortality, N_0 = initial number of larvae, N_t = number of larvae after a time interval t]. Similarly, Pedersen (2008) repeatedly sampled a large area of Danish estuaries and found larval mortality rates of 85.2–97.6% with estimates of instantaneous mortality rates of -0.10 to -0.32 day^{-1} for bivalves and -0.09 to -0.23 day^{-1} for polychaetes. In a third study, Tapia and Pineda (2007) used a vertical life-table approach (Aksnes and Ohman 1996) to estimate instantaneous rates of mortality of -0.329 and -0.232 for two species of barnacles. A benefit of the vertical life-table approach is reduced uncertainty of loss due to horizontal transport versus mortality. This approach requires that recruitment rates and durations of stages are well known (Aksnes and Ohman 1996), which may not always be possible (e.g., several estimates by Tapia and Pineda [2007] violated these assumptions and were excluded from analysis). Despite any methodological compromises, these recent estimates of planktonic mortality are similar to the average mortality rates reported by Rumrill (1990) for free-living planktonic larvae ($M = -0.247$). Additional studies that use similar methods for estimating larval mortality are still needed to broaden the number of taxa and habitats surveyed.

As discussed above, one limitation to traditional methods of estimating predation by monitoring of larval cohorts is that researchers cannot distinguish between mortality and removal of larvae due to advection away from the study site or successful recruitment to the benthos. A possible solution, and one that has gained popularity among researchers, is to tether larvae *in situ* and measure predation upon them across habitats. These studies primarily focus on crustaceans because of their large size and the ability to adhere them to monofilament line using cyanoacrylate glue. Using such tethering techniques to assess predation on spiny lobster postlarvae, Acosta and Butler (1999) found that the phase of the lunar cycle and the position of larvae relative

to the surface significantly affected survival rates, with the lowest rates occurring near the surface during the new moon (i.e., when light levels were lowest). Similar types of tethering approaches have shown that for small zooplankton (but not larval stages *per se*) there is wide spatial variation in the risk of predation across benthic habitats (Bullard and Hay 2002) and between benthic and planktonic habitats (Motro et al. 2005).

Results from tethering experiments also demonstrate that planktivory can vary seasonally with highest risks in the summer and early fall and lowest risks during the winter and spring (Bullard and Whitlatch 2008). In a study focused directly on assessing relative risks of planktivory for invertebrate larvae, Allen and McAlister (2007) showed that tethered crab megalopae were more likely to be consumed on the benthos than in the water column. These differences were exaggerated when trials were run at night, with a loss rate of >90% in a 2-h window for benthic megalopae. A similar pattern of increased mortality on the benthos was found when agarose baits flavored with the eggs, embryos, and larvae of several species of marine invertebrates were tethered in the same study site (Allen and McAlister 2007). These results suggest that, while the risk of mortality may be high for the planktonic larvae of marine invertebrates, the relative risk of development in the plankton may be low when compared with benthic alternatives. In the absence of any extraembryonic parental care (e.g., brooding; egg capsules), planktonic development, despite its inherent risks, may be seen as making the best of a bad situation. This is certainly not a new conclusion (Pechenik 1979; Strathmann 1985; Rumrill 1990), but it is one that is increasingly well supported.

In addition to tethering experiments, there have been other innovative methods employed to assess predation on larval invertebrates. We report here two examples of studies incorporating novel methods (with contradictory results) that we hope will inspire ecologists interested in larval forms to think 'outside the jar' and adopt new field methods for assaying larval predation. First, Johnson and Shanks (2003) deployed large-volume (123 L) corrals into the field and used the assemblage of plankton captured within those corrals to assess rates of predation on marked larvae of echinoids, gastropods, and bivalves. When larvae were introduced at densities similar to those reported from the literature ($0.4\text{--}1.0\text{ L}^{-1}$) and background plankton was included, predation was non-existent. Even when potential predators were seeded into the corrals, predation on echinoid and gastropod larvae was consistently low or, more generally,

entirely absent, with only a single pluteus being consumed during nine echinoid runs and two gastropod runs. Predation rates were higher, but still relatively low (mean $M = -0.012$ for nine trials) for bivalve veligers (Johnson and Shanks 2003). These results suggest that planktonic mortality rates for marine invertebrates may be vastly overestimated. However, the corral experiments did not consider predation by larger planktivores such as fish and pelagic cnidarians.

In a second example of innovative field research, Holzman and Genin (2003) examined predation on zooplankton (including larvae at natural densities) by nocturnal fish. In this experiment, predatory fish were enclosed in cages within plankton nets and their diet was measured directly through analysis of gut contents as well as indirectly by comparing the composition of plankton captured in nets with and without fish. Zoeae and megalopae were some of the most abundant taxa consumed by these predatory fish (Holzman and Genin 2003). Abundances of smaller zooplankton (<1 mm) were not compared but these prey were likely to be too small to be consumed by the highly selective focal fish (*Apogon annularis*). Taken together these studies suggest that the heterogeneity of predators may strongly drive measurements of planktonic mortality *in situ*. When large predators on zooplankton are present (e.g., blooms of gelatinous zooplankton), rates of larval mortality may be high while in the absence of gelatinous zooplankton and planktivorous fish mortality may be near zero.

The results above emphasize the importance of identifying the most significant predators on marine invertebrate larvae. Despite increasing confirmation that larvae are lost to predators (as can be estimated from the monitoring of larval cohorts or from tethering experiments), the identification of predators and assessments of the relative impact of different predators on larval populations remains unknown. For example, Costa et al. (2009) surveyed the gut contents of 43 fish species in an estuarine system and found species-specific variation in overall consumption of brachyuran larvae and in the stages of brachyurans consumed (zoeae, megalopae, and juveniles). While there is evidence that larvae are readily preyed upon by diverse groups of predators in the laboratory (Pennington et al. 1986), for nearly all species of marine invertebrates little is known of the diversity and relative importance of predators in nature. More basic research via either analysis of gut contents or through mesocosm and field experiments (such as those described above) are desperately needed to fill this void.

Modeling estimates

While empirical data are typically in short supply for estimating the peril of the plankton, modeling of planktonic mortality rates has potential for increasing our understanding of larval ecology. There have been few advances in modeling of planktonic mortality, although biophysical oceanographic models generally include larval mortality as one component (reviewed by Metaxas and Saunders 2009). However, it is increasingly recognized that better empirical estimates of larval mortality are needed to improve models of recruitment and transport of larvae (Pineda et al. 2009). As discussed above, original approaches are desperately needed to break new ground and improve estimates of larval mortality.

In a recent example of an innovative approach, Pechenik and Levine (2007) combined field, laboratory, and simulation studies to estimate planktonic mortality rates in two species of larval gastropods. They argued that slow-growing larvae are more vulnerable to predators than are fast-growing larvae. That is, if planktonic predation is a significant selective factor, average growth rates should increase as larvae get larger due to the selective removal of slowly growing genotypes. Using field-caught larvae, they demonstrated that large larvae did, indeed, grow faster. Computer simulations then confirmed that the increased mean growth rates of larger larvae could be explained by the selective removal (via predation) of slow-growing larvae. The combination of several techniques (field collection of study-animals, controlled laboratory rearing, and computer simulations) allowed these researchers to provide new insights into the rates and consequences of planktonic mortality.

Larval defenses

The effectiveness of any defense depends upon traits of the predators, the prey, and the environment. The marine planktonic environment is characterized by unevenly distributed resources and risks, including exposure to diverse predators with different modes of attack (Pinel-Alloul 1995; Seuront et al. 2001; Genin et al. 2005). Predators encountered by embryos and larvae during ontogenetic migrations from the benthos to the plankton represent a wide range of taxa that can be divided into two basic groups: pelagic invertebrates and fish. Fundamental differences in detection, capture, and ingestion of prey distinguish these two groups of planktivores. For instance, pelagic invertebrates, including cnidarians, ctenophores, chaetognaths, polychaetes, and adult and larval crustaceans detect prey via

hydromechanical signals (Feigenbaum 1991; Morgan 1992, 1995). Once detected, prey are captured with diverse appendages (e.g., tentacles, paired maxillipeds, grasping bristles or hooks) and consumed. In contrast, many planktivorous fish use vision and buccal suction to detect, capture and ingest prey (Lazarro 1987), although at low levels of light some fish use mechanoreception in detection of prey (Holzman and Genin 2003). In addition to the considerable taxonomic and functional diversity of predators, the distribution of organisms in the sea is highly heterogeneous. This heterogeneity influences the complex spatial and temporal interactions of predators and prey and presents fundamental challenges to the microscopic inhabitants of the marine planktonic environment.

Size- and stage-dependent vulnerability to planktivores

Given the diversity of planktivores and an array of methods of detecting prey and of mechanisms of feeding, the risk of predation likely varies with size, developmental stage, and behavior of the embryonic and larval prey (Pechenik 1999). An early study testing the vulnerability of sand dollar embryos and larvae to planktivorous invertebrates and fish reported that the rate of predation by each predator species was not constant across different stages of prey (Pennington et al. 1986). Stage-specific vulnerability of polychaete embryos and larvae was also documented during direct encounters with predaceous invertebrates and fish (Pennington and Chia 1984). The development of setae enhanced survival of the larval worms (Pennington and Chia 1984). Differential mortality of planktonic embryos and larvae in each of these studies can be attributed to developmental changes in behavior and morphology of prey, but in some cases reflect important differences in the traits of predators (i.e., mechanism of prey detection, prey preference, and feeding mode).

More recently, Allen (2008) demonstrated that both size and age affect mortality rates of marine planktonic larvae. Half-sized sand dollar larvae, resulting from experimental reductions in egg size, experienced lower mortality than did full-sized sibling larvae when each were offered as prey to a suite of four predaceous invertebrates. However, a species of planktivorous fish consumed greater numbers of full-sized larvae and showed no preference for prey based on larval age (Allen 2008). Taken together, the results of Pennington and Chia (1984), Pennington et al. (1986), and Allen (2008), challenge the

assumption of constant mortality rates during planktonic development.

In addition to increasing awareness that the risk of predation can vary (1) throughout planktonic development, and (2) with the traits of prevailing predators, there is increasing evidence that larvae are not hapless victims adrift in the sea (Morgan 1995). While larval shells, spines, and setae have long been attributed a defensive function (Wilson 1929; Foxon 1934), until recently few experimental tests had demonstrated the antipredatory adaptations of marine larvae. Recent demonstrations of the effectiveness of proposed larval defenses suggest that larvae are well-adapted for survival in the plankton and that marine larvae defend themselves chemically, morphologically, behaviorally, and through combinations of these defenses. Moreover, some larvae are capable of altering their defensive phenotypes in response to fluctuations in predation risk. Below we highlight recent advances in understanding the chemical, morphological, behavioral, and inducible defenses exhibited by marine larvae and assess their effectiveness in reducing predation risk.

Chemical defenses

In the past 15 years, awareness of chemical defenses in larvae has grown tremendously [see (Lindquist 2002) for a recent review] as has the recognition of the importance of chemical signals in the plankton more generally (Pohnert et al. 2007). Recent work demonstrated that taxonomically diverse larvae, representing a variety of developmental modes, possess chemical defenses that effectively reduce predation by one or more predators (e.g., Lindquist and Hay 1995; Harvell et al. 1996; McClintock and Baker 1997; Bullard et al. 1999). In some cases, predators learn to avoid chemically defended larvae with aposomatic coloration and larvae frequently survive encounters with predators after ingestion and rejection (Young and Bingham 1987). When chemically defended larvae are ingested, Lindquist and Hay (1995) reported significant reductions in the fitness of predators. For example the anemone *Aiptasia pallida*, exhibited an 80% reduction in growth and a 40% reduction in asexual reproduction when fed a diet including <2% of a chemically-defended ascidian larva. Reductions in the growth and reproduction of predators that are unable to discriminate chemical defenses may indirectly improve the chances of survival for chemically-defended larvae by reducing the abundance of this class of predators (Lindquist and Hay 1995). Chemical defenses, when present, can

therefore influence the survival of both planktonic prey and their predators.

It is currently unclear how widespread chemical defenses are among marine invertebrate larvae. In a survey of temperate meroplankton, Bullard et al. (1999) found that only 0.2% of the total number of larvae in the water column were chemically-defended. In contrast, 34% of the total larvae in the assemblage possessed morphological defenses, suggesting that chemical defenses are rare relative to morphological ones. However, it is possible that production of chemical defenses and the production of large numbers of offspring represent separate solutions to the problem of the peril of the plankton. The production of chemical compounds likely incurs a significant energetic cost. Species lacking defensive compounds may produce significantly more offspring that compensate for reduced or absent chemical defenses, which may explain why chemically-defended meroplankton are seemingly rare. Given this potential bias, additional work is needed to determine the frequency of species exhibiting chemical defenses rather than the number of individual larvae possessing chemical defenses.

To estimate the prevalence of chemical defenses during early life stages of marine invertebrates, we surveyed the literature for studies that tested for the presence of chemical compounds in marine invertebrate eggs, embryos, and larvae. We selected studies that tested chemical defenses directly by isolating putative defensive compounds as well as indirectly by assaying palatability of eggs, embryos, larvae or their extracts. Across 22 studies, 64% of species (63/98) were reported to exhibit chemical defenses during at least one developmental stage (egg, embryo, or larva) that was effective against at least one potential predator (Appendix 1). Using this survey, we then categorized species by developmental mode: planktotrophic, lecithotrophic, brooded, or encapsulated. Embryos and larvae that are derived from brooded or encapsulated eggs were included in the brooded/encapsulated categories regardless of their developmental mode (planktotrophic or lecithotrophic) as larvae. Offspring that are not brooded or encapsulated during early development were classified as planktotrophic or lecithotrophic. We did not account for any potential sampling bias of the studies we surveyed, although there is certainly an uneven distribution of species across taxonomic groups (e.g., 36/98 species were Echinoderms) and developmental modes (e.g., 5/98 species were classified as encapsulated). Our survey determined that of the species tested thus far 50% of planktotrophic species ($n=20$) and 58.6% of

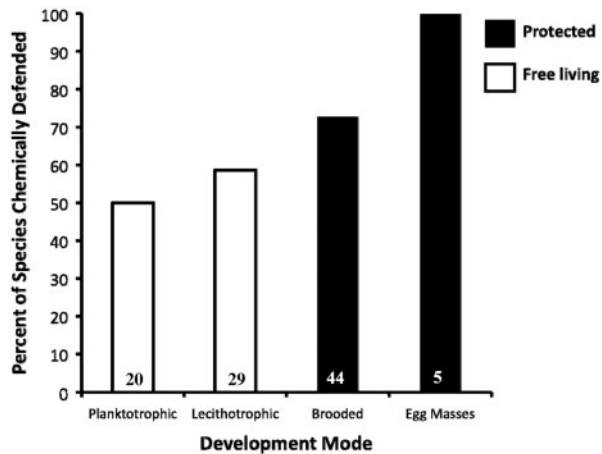


Fig. 1 The frequency of chemical defenses in marine invertebrates with different developmental modes. Bars represent the percent of species found to be chemically-defended against at least one predator during at least one developmental stage. Open bars represent offspring derived from broadcast spawning. Closed bars represent offspring that are brooded or encapsulated for all or part of their development. Data were taken from 22 studies covering 98 species. See Appendix 1 for more details.

lecithotrophic species ($n=29$) were chemically-defended, compared with 72.7% of brooded species ($n=44$) and 100% of encapsulated species ($n=5$) (Fig. 1). Overall, 55% of eggs, embryos, and larvae from broadcast-spawning species were reported to exhibit chemical defenses while 75.5% of eggs, embryos, and larvae from species that brood or encapsulate their embryos were chemically-defended.

The frequency of species possessing chemical defenses (55–75%) is considerably higher than the abundances estimated above (0.2%; Bullard et al. 1999). This may represent a bias toward publication of only positive results. The discrepancy may also result from the large numbers of crustacean larvae found in planktonic assemblages, none of which are known to be chemically-defended. Therefore, while larval chemical defenses may be widespread among species of marine invertebrates, predators may only rarely encounter them. Despite these possible biases, the frequency of chemical defense appears to be higher for protected developers relative to free-spawners. This observation supports the hypothesis of Lindquist and Hay (1996) that large, conspicuous larvae of marine invertebrates (such as are commonly released by brooders) are more likely to be chemically-defended than are smaller, more numerous larvae typically produced by broadcast spawners. Interestingly, among broadcast spawners the likelihood of chemical defenses in species with planktotrophic versus lecithotrophic development was similar (50 versus 58.6%, respectively). A natural

extension of Lindquist's and Hay's (1996) hypothesis is that within broadcast spawners the frequency of chemical defenses would be higher in the larger, more visible, more lipid-rich, and morphologically nondescript lecithotrophs. Support for this pattern has been found in the larvae of Antarctic marine invertebrates (McClintock and Baker 1997). The similar frequency of chemical defenses in planktotrophic and lecithotrophic larvae, and the taxonomic bias within certain reproductive modes in our survey (43% of brooded species surveyed were ascidians and 70.5% of these were chemically-defended), leads us to call for broader surveys of chemical defenses that include broadcast spawners from chemically rich taxa (e.g., solitary ascidians) and larvae from underrepresented lophotrochozoan phyla (e.g., nemerteans, bryozoans, and brachiopods). Despite these taxonomic limitations, it is clear that many larvae from at least 11 phyla possess chemical defenses against predators.

While the taxonomic distribution of chemical defenses remains uncertain, there is increasing evidence that the production of chemical compounds can change dramatically during ontogeny. For example, after release from brooding adults the planktotrophic larvae of *Streblospio benedicti* increase the concentration of halogenated metabolites several fold (Cowart et al. 2000). In a related study, several echinoderm species were found to be consistently unpalatable to predatory fish across all developmental stages tested, although when multiple predators were included in the analysis there was a significant decline in palatability as development progressed [(Iyengar and Harvell 2001); see comments below on the importance of assaying multiple predators]. Looking across the entire life cycle, Lopanik et al. (2006) have shown that the larvae of the bryozoan *Bugula neritina* possess significantly higher concentrations of unpalatable secondary metabolites (bryostatins) than do juveniles or adults and that this decline is significant within 1 day of metamorphosis. While these results suggest that free-living larval stages tend to increase chemical defenses during development, Harvell et al. (1996) reported that chemical defenses of gorgonian larvae decreased significantly during major developmental transitions. Without further tests encompassing broader taxonomic groupings, the generality of these patterns remains unknown.

In addition to broadening surveys of chemical defenses across ontogenetic stages, several studies have demonstrated that chemical defenses are not effective against all predators. Therefore, predators' choice of prey is crucial for interpretations of the effectiveness of larval defenses. For example, McClintock and

Baker (1997) showed that pieces of a nudibranch egg mass were unpalatable to a seastar predator, but ingested at similar rates as controls (krill-flavored alginate pellets) by a sea anemone and an amphipod. Similarly, the larvae of the gorgonian *Eunicea mammosa* were unpalatable to the Caribbean wrasse but readily ingested by the Caribbean damselfish (Lindquist and Hay 1995). These results suggest that the effectiveness of chemical deterrents varies both across broad categories of predators (e.g. invertebrates versus fish) and within a relatively narrow category of predator (e.g., planktivorous fish). Whenever possible, future studies of chemical defense should identify and assay multiple species of ecologically relevant predators.

Morphological defenses

Early inferences about larval defense were based on both structure and behavior. Garstang noted that larval gastropods respond to predators by withdrawing into their shell and shutting the apertural opening with an opercular door (Garstang 1929). These observations suggested that defensive behavioral responses, coupled with the armor of the larval shell, disrupt predation. It has since been established that diverse marine larvae possess defensive structures—such as shells, spines, and setae—that are effective against a wide range of planktivores (see reviews by Young and Chia 1987; Rumrill 1990; Morgan 1995).

Larval shells not only function as the first line of defense against predators, but the damaged shells of some gastropod veligers are rapidly repaired

following sublethal attempts at predation (Hickman 2001). The ability to withstand direct encounters with planktivores and to repair damage following failed attacks may be a significant means of reducing larval mortality. The larval shell may even enhance survival following capture and ingestion by planktivores, with evidence that some shelled larvae can pass unharmed through the guts of some suspension- and deposit-feeding predators (Mileikovsky 1974; Purcell et al. 1991).

Larval spines and setae, like larval shells, can enhance survival of marine larvae during encounters with planktivores. In an experimental investigation of the adaptive significance of spination in crab zoeae, Morgan (1989) concluded that spines are an antipredatory defense against small, gape-limited fish (Fig. 2A). Zoeal spines are quickly regenerated with successive molts and reduce subsequent attacks by experienced planktivorous fish who learn to detect and reject spined zoeae (Morgan 1989). Like spines and setae, the spicule-laden arms of larval echinoids suggest a defensive function. Mechanical measurements on the arm rods of echinoid larvae support this proposed function because the fenestrated skeletal rods are stiffer than required to support the arms against currents when swimming (Emler 1983). Nevertheless, results from laboratory experiments testing for a defensive function of the larval arms of echinoids are equivocal. While later stage echinoid larvae (prism and pluteus stages) with well-developed skeletons appeared to be less vulnerable to predators than are younger stages that lack skeletons

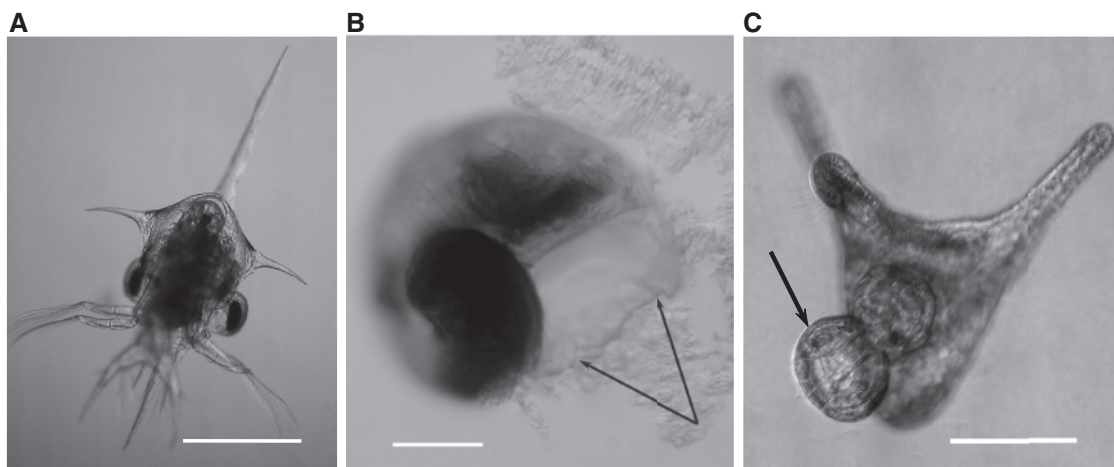


Fig. 2 (A) Zoea of rock crab with flared spines and appendages. Scale = 1 mm. (B) Veliger of a periwinkle snail. Arrows indicate damage along the edge of the shell aperture following a sublethal attack by predatory larval crabs. Scale = 100 μ m. (C) Pluteus of a sand dollar in the process of cloning. The arrow indicates a bud on the aboral surface of the primary larva that will subsequently be released as a gastrula-like individual. Scale = 100 μ m. Photo credits: D. Vaughn. [Veliger (B) from Vaughn, *Ecology*, 88(4) 1030–9, 2007; Cloning pluteus (C) from Vaughn and Strathmann, *Science*, 319:1503, 2008.]

(Pennington et al. 1986), the decreased vulnerability may be attributed to behavioral avoidance of predators rather than to skeletal protection with the development of ciliary arrest and reversal at the late prism stage (Rumrill et al. 1985). Moreover, the development of a skeleton does not appear to protect larval echinoids from ingestion by crab zoeae (Rumrill and Chia 1984). Further research is needed to confirm whether the skeletal arms protect larval echinoids during encounters with predators.

Predator-induced morphological defenses

Much of the research describing morphological defenses of marine planktonic larvae and their effectiveness in reducing the risk of predation was conducted >20 years ago. A focus of recent research considers the ability of larvae to respond to fluctuating risks during planktonic development through induced protective changes in their defensive morphologies. To date, predator-induced defenses have been reported in animals, plants, and microbes across multiple trophic levels in all major ecosystems (Tollrian and Harvell 1999; Vos et al. 2004; Vos et al. 2006; Van Der Stap et al. 2007; Van Donk 2007). Despite the pervasiveness of predator-induced defenses, reports of such responses in marine zooplankton, including marine planktonic larvae, had been limited to induced behaviors (e.g., diel vertical migration [DVM], reduced activity, power strokes, and jumps) to avoid or escape predatory encounters (Bollens and Frost 1989; Neill 1990; Fields and Yen 1997; Cohen and Forward 2005). The lack of studies documenting predator-induced changes in the defensive morphology of marine zooplankton is surprising, given the number of such reports in other prey organisms. Rarity of induced morphological defenses in marine zooplankton, such as the development of longer spines or stronger shells, would imply a difference in predation risk compared to those experienced by other aquatic and terrestrial organisms, whereas the presence of such plasticity would imply that risks are modified by developmental responses.

A series of recent experiments tested for the presence or absence of predator-induced morphological defenses in marine planktonic larvae, including the veliger larvae of an intertidal gastropod and the pluteus larvae of a sand dollar. When exposed to stimuli from zoeae of 'Cancer' crabs, veligers developed smaller apertures and rounder shells than did cohort veligers reared in the absence of stimuli (Vaughn 2007). Zoeae access the soft-bodied larval snails by peeling back the shell from the aperture (Fig. 2B), suggesting that a smaller apertural opening

may make predation more difficult. Pair-wise predation trials determined that veligers with the induced changes in their shells had greater survival than predator-naive veligers during short-term exposure to zoeae (Vaughn 2007).

Exposure to stimuli from fish (external mucus) induced an unusual response in larval sand dollars: cloning (asexual reproduction) with the development and release of embryo-like buds from the aboral surface of early stage plutei (Fig. 2C) (Vaughn and Strathmann 2008). Budded individuals developed into small larvae that appeared to develop no differently than embryos arising from fertilized eggs. The small size of the cloned sand-dollar larvae suggested a defense against visual predators such as fish that exhibit size-selective predation. Subsequent laboratory experiments determined that the smaller cloned plutei are less vulnerable than full-sized sibling larvae when offered as prey to two species of planktivorous fish (Vaughn 2010), and that successful cloning (the production of two larvae from one larva) is influenced by maternity (Vaughn 2009). Increased numbers of larvae resulting from successful cloning could increase the number of plutei; however, this would not likely reduce risk through predator saturation because larvae of most species are scarce relative to other co-occurring zooplankton (Strathmann 1996). Thus, reduced size rather than increased numbers may be the adaptive and ecologically significant response of larval sand dollars to predators (Vaughn 2010).

Taken together, these studies provide a first demonstration of predator-induced changes in the defensive morphology of some marine planktonic larvae (and marine zooplankton more generally) and suggest that developmental responses can mediate risks associated with planktonic development. At present, it is not known whether predator-induced morphological defenses are as common in marine zooplankton and planktonic larvae as documented in prey organisms in other environments. In some cases, the responses of marine planktonic larvae to predators were both unexpected and previously undocumented in any other environment. For example, apart from sand-dollar plutei, there are no other examples of cloning and reduced size as an inducible defense, although such defenses may occur when developmentally feasible and when safety lies in smaller size. Cloning in larval sand dollars and reduced size as a consequence of cloning indicate that in some cases larvae can adjust their size based on experience in the plankton, using cues unavailable to mothers on the sea floor.

These studies also raise a number of important questions about the specificity of stimuli and effectiveness of responses in marine planktonic larvae including: how widespread, varied and effective are predator-induced defenses in marine planktonic environments? How reliable are chemical stimuli as cues to continued risk? And, does a defense against one predator increase vulnerability to other predators (as might be expected for small, cloned larvae)? More generally, these results also suggest that studies of predation using laboratory reared and thus predator-naïve larval prey may overestimate mortality from predators.

The decline of studies testing for morphological defenses in marine planktonic larvae, and the recent findings that some marine larvae develop better-defended morphologies when exposed to stimuli from planktivores, should generate a renewed interest in the effect of defensive morphologies on larval mortality and survival. Testing for the effectiveness of larval defenses and plasticity of defenses is not difficult and may be timely in light of increasing reports of the potentially significant impact of invasion by exotic predators on native prey in the marine realm (Freeman and Byers 2006; Hidalgo et al. 2007; Edgell and Neufeld 2008). Moreover, additional research in this area will further our understanding of the evolutionary and ecological contexts that favor selection for permanent defenses versus defenses that are developmentally plastic.

Behavioral defenses

There is considerable evidence that marine larvae and other marine zooplankton respond to the threat of predation through defensive behaviors. In some cases, similar suites of morphological defenses and behaviors have evolved in diverse taxa. For instance, the setae of larval polychaetes, the spines of larval crabs, and the skeletal arms of larval echinoids all flare when touched, making the larvae larger and more difficult to ingest (Emlet 1983; Pennington and Chia 1984; Morgan 1989). Likewise, the flexing of the bodies of some marine larvae (e.g., larval polychaetes and crabs) can suddenly increase the size of the larvae (Wilson 1929; Pennington and Chia 1984; Morgan 1989).

Defensive behaviors that allow zooplankton to escape or evade predators include power strokes, jumps, and tail flicks (Fields and Yen 1997; Jackson and MacMillan 2000), negative rheotaxis (Singarajah 1969; Pennington and Emlet 1986; Jackson and MacMillan 2000), movement from areas of decreased light intensity (shadow response) (Forward and

Rittschof 2000; Cohen and Forward 2003; Cohen and Forward 2005) and early swimming of echinoid blastulae that decrease encounters with benthic predators (McDonald 2004). Some crab and polychaete larvae are also reported to cease movement, thereby avoiding detection by predators (Pennington and Chia 1984; Morgan 1989).

Perhaps the best-documented predator-induced behavioral responses are large-scale migrations of zooplankton that avoid areas of high risk of predation. Taxonomically diverse groups of zooplankton can change their vertical and horizontal distributions in response to habitat-specific predation risk, often over the course of a day or tidal cycle. DVM, during which zooplankton migrate from shallow depths at night to greater depths during the day, is a widespread phenomenon in the world's oceans (Hays 2003). While there are numerous possible explanations for this behavior (e.g., avoidance of exposure to ultraviolet radiation, metabolic advantage, tidal stream transport to and from offshore nursery grounds), there is considerable support that DVM reduces the risk of predation by visually-hunting predators (Bollens and Frost 1989; Neill 1990; Bollens et al. 1992; Forward and Rittschof 2000; Cohen and Forward 2003; Cohen and Forward 2005; Metaxas and Burdett-Coutts 2006). Reverse vertical migration, with zooplanktonic prey occurring in surface waters during the day and at depth at night, is elicited by the presence of predatory invertebrates (Ohman et al. 1983; Gliwicz 1986).

Experimental investigations of predator-induced migrations in crustacean larvae demonstrate that short-term exposure to stimuli from predatory fish and ctenophores (i.e., external mucus) activates photoresponses involved in DVM for avoidance of planktivores (Forward and Rittschof 1999; Forward and Rittschof 2000; Cohen and Forward 2003). Some crab larvae and freshwater cladocerans also migrate horizontally from areas of high risk (Christy 1982; Morgan 1987; Burks et al. 2002). In a recent study, Metaxas and Burdett-Coutts (2006) found that although sea-urchin plutei changed their vertical distribution and avoided encounters with ctenophore predators, gastropod veligers did not, suggesting that predator-induced migratory behaviors may not have evolved in all phyla (Metaxas and Burdett-Coutts 2006).

While there is increasing evidence that some marine larvae alter their distributions in response to predation risk, Fossheim and Primicerio (2008) tested whether the size of marine zooplankton (adults and larvae), as an indicator of their vulnerability to predators, correlated with adaptive choices

of habitat depth. According to habitat-choice theory, zooplanktonic prey should choose a depth that maximizes food intake while minimizing the risk of predation (Sih 1998; Lima 2002). Because body size affects competitive ability and the vulnerability of zooplankton (including marine planktonic larvae; see Allen 2008), it can also influence adaptive choice of depth (Woodson et al. 2005). As predicted, marine zooplankton were reported to be vertically distributed in ways that balanced between foraging and size-dependent risk of predation (Fossheim and Primicerio 2008), which in the case of marine larvae, can change over ontogeny (Allen 2008). Like prey, predators also exhibit behaviors assisting the exploitation of resources (Sih 1998). Many planktivores modify their movements in response to mechanical and chemical stimuli, suggesting that individual-level behaviors of predators may drive community-level characteristics (Grünbaum 2001; Menden-Deuer and Grünbaum 2006).

Summary

A fundamental question for organismal biologists is why complex life cycles and the larval forms associated with them have been maintained in most metazoan phyla. Over the past three decades, a convincing argument has been made that larvae are maintained in marine invertebrate life cycles as a vehicle for safe migration into the plankton (Strathmann 1985; Strathmann 1993; Strathmann 2007). An assumption of this argument is that the risk of mortality is greater for benthic than for planktonic embryos (Pechenik 1979; Strathmann 1985). However, as summarized in this review, there is strong evidence that predation during planktonic development is variable, non-random, and frequently high. In response, marine larvae have evolved a sophisticated suite of chemical, behavioral, morphological, and inducible defenses that reduce vulnerability to predators encountered during planktonic development. Despite considerable research aimed at determining the relative importance of predation in the maintenance of planktonic developmental stages, significant hypotheses remain to be fully tested (Strathmann 2007).

A number of future research objectives will increase our understanding of the risks of planktonic development. The first is to determine species-specific planktonic mortality rates rather than generalizing across or averaging among groups. Empirical data describe a continuum of planktonic development spanning a range of egg sizes and nutritional requirements [reviewed by (Allen and Pernet 2007)]

that may best be explained by determining species-specific rates of growth and mortality (Strathmann 1985). To meet this objective requires a coordinated program including: (1) field observations to identify predator and prey abundances and estimate encounter rates, and (2) laboratory and mesocosm experiments to estimate the capture efficiency of particular predators across prey life stages. Another underexplored, but crucial, avenue of research are studies that investigate density-dependent mortality rates for larvae and juveniles. The concept of density dependent mortality is not new (Strathmann 1974), but to our knowledge data substantiating this hypothesis are limited. In one of the few studies to directly estimate density-dependent effects on larval growth, Strathmann (1996) found that larvae are at such low densities in the field that they are unlikely to compete for resources within species. In nature, density-dependent predation may be similarly unlikely if larvae occur only rarely, but few data exist to test this possibility and we echo prior calls for stronger empirical evidence to support or refute this hypothesis (Strathmann 1996).

Finally, we believe that further research is needed to estimate mortality rates for unprotected or minimally protected benthic embryos, thereby providing an excellent opportunity to compare the risk of predation during benthic and planktonic development. Taxonomically diverse marine organisms including some ascidians, echinoderms, and copepods develop from unprotected benthic embryos [references in (Strathmann 2007)]. Comparisons of predation risk experienced by unprotected benthic embryos with that experienced by similarly unprotected but closely related planktonic embryos will permit biologists interested in larval ecology to assess the effectiveness of encapsulation as a means of deterring predation. If predation is found to be consistently higher for unprotected benthic embryos this will provide strong support for Strathmann's (1985; 1993; 2007) hypothesis of ontogenetic migration into the plankton as a way to minimize benthic predation, however perilous that migration may be.

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Appendix 1 Distribution of chemical defenses across taxa and developmental modes^a

Taxa	Development mode ^a	Stage assayed	Predator tested	Chemical defense?	References
Annelida					
Polychaeta					
<i>Capitella</i> sp.	Brooded	Larvae	Metabolite assay	Yes	Cowart et al. 2000
	Lecithotrophic	Larvae	Metabolite assay	Yes	Cowart et al. 2000
<i>Eupolymnia nebulosa</i>	Encapsulated	Egg masses	Fish	Yes	Martin et al. 2000
	Planktotrophic	Larvae	Hermit Crabs	Yes	Martin et al. 2000
<i>Hydroides dianthus</i>	Planktotrophic	Larvae	Fish	Yes	Connaughton et al. 1994
<i>Sabellaria cementarium</i>	Planktotrophic	Larvae	Bivalve, Ascidian	No	Cowden et al. 1984
<i>Serpula vermicularis</i>	Planktotrophic	Larvae	Bivalve, Ascidian	No	Cowden et al. 1984
<i>Streblospio benedicti</i>	Brooded	Larvae	Metabolite assay	No	Cowart et al. 2000
	Planktotrophic	Larvae	Metabolite assay	Yes	Cowart et al. 2000
	Brooded	Larvae	Metabolite assay	Yes	Cowart et al. 2000
	Lecithotrophic	Larvae	Metabolite assay	Yes	Cowart et al. 2000
Arthropoda					
Crustacea					
<i>Pollicipes polymerus</i>	Planktotrophic	Larvae	Bivalve, Ascidian	No	Cowden et al. 1984
Unidentified barnacle	Planktotrophic	Larvae	Four predators	No	Bullard et al. 1999
Unidentified crab	Planktotrophic	Larvae	Four predators	No	Bullard et al. 1999
Unidentified shrimp	Planktotrophic	Larvae	Four predators	No	Bullard et al. 1999
Bryozoa					
Gymnolaemata					
<i>Bugula neritina</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1996
Chordata					
Asciidiacea					
<i>Aplidium stellatum</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996
			Anthozoan	No	Lindquist 1996
<i>Aplidium constellatum</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996
			Anthozoan	No	Lindquist 1996
<i>Clavelina oblonga</i>	Brooded	Larvae	Fish	No	Young and Bingham 1987
<i>Clavelina lepadiformis</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Cystodytes dellechiaiei</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Didemnum molle</i>	Brooded	Larvae	Fish	Yes	Olson 1983
<i>Diplosoma spongiforme</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Ecteinascidia herdmanni</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Ecteinascidia turbinata</i>	Brooded	Larvae	Fish	Yes	Young and Bingham 1987
<i>Eudistoma carolinensis</i>	Brooded	Larvae	Anthozoan	No	Lindquist 1996
<i>Eudistoma olivaceum</i>	Brooded	Larvae	Fish	Yes	Young and Bingham 1987
<i>Lissoclinum patellum</i>	Brooded	Larvae	Fish	No	Olson and McPherson 1987
<i>Podoclavella moluccensis</i>	Brooded	Larvae	Fish	Yes	Davis and Butler 1989
<i>Polysyncraton lacazei</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Pseudodistoma crucigaster</i>	Brooded	Larvae	Four predators	Yes	Tarjuelo et al. 2002
<i>Sigilina signifera</i>	Brooded	Larvae	Fish	Yes	Lindquist et al. 1992
<i>Trididemnum solidum</i>	Brooded	Larvae	Fish	Yes	Lindquist et al. 1992
Cnidaria					
Anthozoa					

(Continued)

Appendix 1 Continued

Taxa	Development mode ^a	Stage assayed	Predator tested	Chemical defense?	References		
<i>Agaricia agaricites</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Briareum abestinum</i> -E	Brooded	Eggs	Three predators	Yes	Harvell 1986		
			Embryos	Three predators	Yes	Harvell 1986	
				Larvae	Three predators	Yes	Harvell 1986
				Larvae	Anthozoan	Yes	Lindquist 1996
<i>Briareum abestinum</i> -U	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Eunicea mammosa</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Eunicea tourneforti</i>	Lecithotrophic	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	No	Lindquist 1996		
<i>Erythropodium caribaeorum</i>	Lecithotrophic	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Plexaura flexuosa</i>	Lecithotrophic	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Plexaurella dichotoma</i>	Lecithotrophic	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	No	Lindquist 1996		
<i>Porites astreoides</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Pseudoplexaura porosa</i> -A	Lecithotrophic	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Pseudoplexaura porosa</i> -B	Lecithotrophic	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	No	Lindquist 1996		
<i>Siderastrea radians</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Sinularia polydactyla</i>	Lecithotrophic	Embryos	Fish	Yes	Slattery et al. 1999		
		Larvae	Fish	Yes	Slattery et al. 1999		
Hydrozoa							
<i>Eudendrium carneum</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
<i>Corydendrium parasiticum</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996		
			Anthozoan	Yes	Lindquist 1996		
Echinodermata							
Asteroidea							
<i>Acanthaster planci</i>	Planktotrophic	Eggs	Fish	Yes	Lucas et al. 1979		
<i>Acodontaster conspicuus</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990		
<i>Acodontaster hodgsoni</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990		
<i>Bathybiaster loripes</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990		
<i>Crossaster papposus</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001		
<i>Diplasterias brucei</i>	Brooded	Embryos	Fish	Yes	McClintock and Vernon 1990		
			Three predators	Yes	McClintock and Baker 1997		
<i>Gomophia egyptiaca</i>	Lecithotrophic	Larvae	Nine predators	Yes	Yamaguchi 1974		
<i>Henricia leviuscula</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001		
		Larvae	Fish	Yes	Iyengar and Harvell 2001		

(Continued)

Appendix 1 Continued

Taxa	Development mode ^a	Stage assayed	Predator tested	Chemical defense?	References
<i>Leptasterias</i> sp.	Brooded	Eggs	Five predators	Yes	Iyengar and Harvell 2001
<i>Lophaster gaini</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990
<i>Macroptychaster accrescens</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990
<i>Mediaster aequalis</i>	Lecithotrophic	Eggs	Five predators	No	Iyengar and Harvell 2001
<i>Notasterias armata</i>	Brooded	Eggs	Fish	Yes	McClintock and Vernon 1990
<i>Odontaster validus</i>	Planktotrophic	Eggs	Fish	No	McClintock and Vernon 1990
<i>Perknaster fuscus</i>	Lecithotrophic	Eggs	Fish	Yes	McClintock and Vernon 1990
		Embryos	Three predators	Yes	McClintock and Baker 1997
		Larvae	Three predators	Yes	McClintock and Baker 1997
<i>Pisaster ochraceus</i>	Planktotrophic	Larvae	Bivalve, Ascidian	Yes	Cowden et al. 1984
<i>Porania antarctica</i>	Planktotrophic	Eggs	Fish	Yes	McClintock and Vernon 1990
<i>Psilaster charcoti</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990
		Embryos	Three predators	Yes	McClintock and Baker 1997
		Larvae	Three predators	Yes	McClintock and Baker 1997
<i>Solaster dawsoni</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
<i>Solaster endeca</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
<i>Solaster stimsoni</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
		Larvae	Three predators	Yes	Iyengar and Harvell 2001
Unidentified	Planktotrophic	Larvae	Four predators	Yes	Bullard et al. 1999
Echinoidea					
<i>Abatus nimrodi</i>	Brooded	Embryos	Fish	No	McClintock and Vernon 1990
<i>Abatus shackeltoni</i>	Brooded	Embryos	Fish	No	McClintock and Vernon 1990
<i>Ctenocidaris perrieri</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990
<i>Dendaster excentricus</i>	Planktotrophic	Larvae	Bivalve, Ascidian	Yes	Cowden et al. 1984
<i>Sterechinus neumayeri</i>	Planktotrophic	Eggs	Three predators	No	McClintock and Baker 1997
		Larvae	Anthozoan	No	McClintock and Baker 1997
<i>Strongylocentrotus franciscanus</i>	Planktotrophic	Larvae	Bivalve, Ascidian	Yes	Cowden et al. 1984
<i>Strongylocentrotus purpuratus</i>	Planktotrophic	Larvae	Bivalve, Ascidian	Yes	Cowden et al. 1984
Holothuroidea					
<i>Bathylotes moseleyi</i>	Lecithotrophic	Eggs	Fish	No	McClintock and Vernon 1990
<i>Cucumaria fallax</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
		Larvae	Fish	Yes	Iyengar and Harvell 2001
<i>Cucumaria miniata</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
		Larvae	Four predators	Yes	Iyengar and Harvell 2001
<i>Cucumaria piperata</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
<i>Eupentacta quinquesemita</i>	Lecithotrophic	Eggs	Five predators	Yes	Iyengar and Harvell 2001
<i>Parastichopus californicus</i>	Planktotrophic	Eggs	32 predators	Yes	McCuen 1984
<i>Psolus chitonoides</i>	Lecithotrophic	Eggs	32 predators	Yes	McCuen 1984
Hemichordata					
Enteropneust					
Unidentified	Planktotrophic	Larvae	Four predators	No	Bullard et al. 1999
Mollusca					
Gastropoda					
<i>Hexabranhus sanguineus</i>	Encapsulated	Egg masses	Fish	Yes	Pawlik et al. 1988
<i>Lottia scutum</i>	Lecithotrophic	Larvae	Bivalve, Ascidian	No	Cowden et al. 1984
<i>Tritoniella belli</i>	Encapsulated	Egg masses	Three predators	Yes	McClintock and Baker 1997

(Continued)

Appendix 1 Continued

Taxa	Development mode ^a	Stage assayed	Predator tested	Chemical defense?	References
Nemertea					
Anopla					
Unidentified	Planktotrophic	Larvae	Four predators	Yes	Bullard et al. 1999
Phoronida					
Unidentified	Planktotrophic	Larvae	Four predators	No	Bullard et al. 1999
Porifera					
Demospongiae					
<i>Adocia tubifera</i>	Brooded	Larvae	Fish	No	Lindquist and Hay 1996
			Anthozoan	No	Lindquist 1996
<i>Callyspongia vaginalis</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1992
<i>Calyx podatypa</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
<i>Isodictya setifera</i>	Brooded	Eggs	Three predators	Yes	McClintock and Baker 1997
<i>Monanchora unguifera</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1992
<i>Mycale laxissima</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
<i>Niphates digitalis</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1996
<i>Pseudoceratina crassa</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1996
<i>Ptilocaulis spiculifera</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1996
<i>Tedania ignis</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	Yes	Lindquist 1996
<i>Ulosa ruetzleri</i>	Brooded	Larvae	Fish	Yes	Lindquist and Hay 1996
			Anthozoan	No	Lindquist 1996
<i>Ectyoplasia ferox</i>	Encapsulated	Egg masses	Fish	Yes	Lindquist and Hay 1996
<i>Xestospongia muta</i>	Encapsulated	Egg masses	Fish	Yes	Lindquist and Hay 1996

^aTaxonomic designations are based on Pechenik (2010). Offspring were scored as chemically defended if at least one predator was deterred from feeding on them.