

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

by AMY L. MORAN

Newly settled or hatched juveniles of marine benthic invertebrates generally experience very high mortality. Juvenile mortality can profoundly affect adult populations, but little is known about how individual variation in juvenile quality affects performance. Several recent studies have demonstrated that differences in size, larval nutrient stores, or larval feeding history can strongly affect the performance (measured as growth and survivorship) of juveniles. Additional research suggests that the strength of the effect of juvenile size on performance may be mediated by variation in environmental stress in the intertidal, a habitat characterized by strong fluctuations in abiotic factors. The major sources of juvenile snail mortality are likely to differ in intertidal and subtidal habitats; abiotic stresses related to exposure, such as desiccation, are important in the intertidal but far less severe in subtidal environments. Previously observed trends in hatching or settlement size between intertidal and subtidal species from three gastropod taxa may be due to differing selective regimes acting on initial juvenile size.

© COPYRIGHT 1999 Society for Integrative and Comparative Biology(SICB)

INTRODUCTION

The intertidal environment, the zone between high and low water surrounding the world's oceans, supports a rich and unique biota consisting almost entirely of marine organisms. Intertidal organisms are exposed to air on a daily basis, and so must avoid or tolerate environmental stresses rarely encountered in the subtidal. These stresses include fluctuating salinity, extreme temperatures, desiccation, wave action, and solar radiation, all of which are characterized by considerable temporal and spatial variation (Connell, 1975; Vermeij, 1978; Nybakken, 1996; Raffaelli and Hawkins, 1996; Helmuth, 1998). The distributions of many intertidal organisms span gradients of these stresses, and such taxa provide a unique opportunity for observing organisms' responses to environmental stress. Numerous morphological and physiological adult characters have been correlated with physical parameters, including height above sea level (e.g., Foster, 1971; Connell, 1975; Takada, 1996), wave exposure (e.g., Dayton, 1971; Etter, 1989, 1996; Trussell, 1997) and heat/ desiccation stress (e.g., Haven, 1971; Williams and Somero, 1996; Roberts et al., 1997).

Environmental gradients in the intertidal also provide a useful opportunity to examine the relationship between habitat and life history (Etter, 1989). One fundamental component of life-history theory is offspring size. Many models of life-history evolution assume that large offspring have higher individual fitness and reflect greater maternal investment than small offspring. However, neither assumption is universally supported (reviewed in Roff, 1992; Steams, 1992). For example, egg size does not necessarily predict maternal investment in marine invertebrates (McEdward and Carson, 1987; McEdward

and Coulter, 1987). Likewise, the relationship between offspring size and fitness (or fitness-related performance parameters) is not always positive and can be affected by variation in the environment (for terrestrial and freshwater systems; Capinera, 1979; Berven and Chandra, 1988; Williams, 1994; Fox and Mousseau, 1996). The intertidal zone, because of its rich biota and extensive environmental variation, is an excellent system for examining offspring performance in contrasting habitats. Compared to adults, little is known about the ecology of early juveniles among benthic marine invertebrates, perhaps because the small size and cryptic distribution of many taxa during the juvenile period make experimental manipulation difficult (Gosselin and Chia, 1995b).

Recent studies of marine taxa have examined size-dependent performance of newly-recruited juveniles by directly manipulating juvenile size and quality either physically or through larval diet, or by using taxa with considerable natural variation in juvenile size. In this review I will briefly address factors affecting mortality of juvenile benthic invertebrates, and discuss methodologies for investigating the relationship between the size at which juveniles first enter the benthic environment, performance, and variation in habitat quality. I will also compare results of laboratory and field experiments, and discuss whether these two types of studies are likely to provide concordant results. Finally, I will compare environmental factors that may be influencing initial juvenile size in intertidal and subtidal habitats, and suggest avenues for future research on the role of juveniles in the life-history evolution of benthic marine organisms.

JUVENILE MORTALITY IN THE MARINE BENTHOS

Mortality levels during the juvenile period are of considerable interest because they can strongly affect adult population size and distribution (Connell, 1985;

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

Rowley, 1989; Keesing and Halford, 1992; Osman and Whitlatch, 1995; Pfister, 1996). Many intertidal benthic organisms produce large numbers of small offspring (Thorson, 1946) that experience high early mortality (reviewed by Gosselin and Qian, 1997; Hunt and Scheibling, 1997); twenty of the 30 studies reviewed by Gosselin and Qian (1997) reported field mortality rates of greater than 90%. Juvenile survivorship is thought to improve with age, a phenomenon attributed to increases in size and a corresponding reduction in vulnerability to desiccation, predation or other factors (Foster, 1971; Spight, 1975, 1976b; Garrity and Levings, 1984; Cobb and Wahle, 1994; Gosselin, 1997). Juvenile mortality rates are highly variable in time and space, probably due to the variable nature of factors determining mortality including environmental quality, predation, settlement density, and interactions among these variables (Keough and Downes, 1982; Young and Chia, 1984; Keough, 1986; Rowley, 1990; McShane, 1991; Smith and Herrnkind, 1992).

In intertidal habitats, both juveniles and adults face abiotic stresses such as desiccation, insolation and ultraviolet exposure, wave action, and fluctuations in temperature and salinity, as well as biotic factors including predation, competition and starvation. The most important elements regulating juvenile survival in intertidal habitats are thought to be desiccation (Underwood, 1979; Gosselin and Chia, 1995a) and predation (Gosselin and Chia, 1995a). In sub-tidal habitats, in contrast, exposure-related abiotic intertidal stresses are largely absent. Major sources of juvenile mortality in sub-tidal environments are likely to include biotic factors such as predation, food availability and disease (Keesing and Halford, 1992). The relative importance of these mortality factors is not well understood, and equally important is determining whether or not this very high juvenile mortality is indiscriminate with respect to juvenile phenotype.

INITIAL JUVENILE SIZE AND PERFORMANCE IN THE MARINE BENTHOS

A major focus of life-history biology is understanding the relationship between offspring size and fitness (reviewed by Stearns, 1992; Roff, 1992). Because fitness is often difficult to measure, a common approach is to instead measure performance in a parameter thought to be a major component of fitness (Arnold, 1983, 1988). Some frequently-chosen parameters include survival (e.g., Ferguson and Fox, 1984; Kirk, 1997) and growth rate or developmental time (e.g., Fox, 1994; Williams, 1994; Brunkow and Collins, 1996). The early juvenile stages of marine invertebrates appear to be very vulnerable to mortality (Gosselin and Qian, 1997), and the extent to which juvenile characters such as initial size can affect

mortality and growth has been the focus of several recent studies.

Marine invertebrates generally enter the marine benthos either through metamorphosis, settling from the plankton, or through hatching from benthic egg capsules or brooding adults. Recent research suggests that growth and survivorship may be linked to the size at which juveniles first enter the benthos (= "initial juvenile size") in some taxa. Jarrett and Pechenik (1997) demonstrated that both organic content and growth capacity differed significantly among five cohorts of field-settled barnacles reared as juveniles in the laboratory. An important implication of this study was that growth of field-settled juveniles varied even when juvenile habitat was held constant; therefore, variation in larval quality might affect juvenile growth or survivorship in the field (Jarrett and Pechenik, 1997). In another study, Emlet and Hoegh-Guldberg (1997) compared growth and survivorship of juvenile sea urchins whose lipid stores (and therefore size) were experimentally manipulated through centrifugation of early embryonic stages. Their study demonstrated that larger, more lipid-rich juveniles grew faster and lived longer in the laboratory than lipid-reduced juveniles. Experiments comparing the performance of lipid-reduced and control juveniles have been recently repeated in the field with similar results (R. B. Emlet and B. A. Miller, unpublished data).

In a third ongoing study, Emlet (unpublished data) produced barnacle larvae of different sizes at settlement by rearing larvae on different food regimes. High-food (large) individuals exhibited higher post-settlement performance in terms of both growth and survivorship than low-food (small) individuals, in the laboratory and the field. Each of the above studies of urchins and barnacles supports the hypothesis that variation in larval nutrient reserves affects juvenile performance, via its effect on juvenile size, organic content, or other aspects of juvenile quality.

Other studies have examined the effect of offspring size on performance using natural variation in initial juvenile size of intertidal gastropods. Many gastropod species with nonplanktonic development exhibit considerable variation in hatching size among clutches and localities (Spight, 1976a, b; Rivest, 1983; Strathmann, 1987; Etter, 1989). Variation in hatching size is in many cases attributed to "nurse egg feeding," in which embryos feed on nondeveloping eggs during encapsulated development. Hatching size is regulated by the number of nurse eggs consumed during development (Rivest, 1983). The ratio of nurse eggs to embryos varies both within and among capsules and clutches, and the resultant variation in size

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

at hatching can be considerable (Fig. 1, for *Nucella ostrina* (formerly known as *N. emarginata* (northern))--see Palmer et al., 1990 and Marko, 1998)).

[Figure 1 ILLUSTRATION OMITTED]

Laboratory studies suggest that large hatching size may confer survival advantages on intertidal gastropods. In the laboratory, large snail hatchlings are more starvation-resistant than small hatchlings (Rivest, 1983; Moran, 1997). Likewise older (and therefore larger) juvenile snails are more resistant to desiccation (Gosselin, 1997), and laboratory studies suggest that large hatchlings are less susceptible to predators (Spight, 1976b; Rivest, 1983; Gosselin, 1997). Additional laboratory studies have demonstrated that large hatchlings grow faster than small hatchlings (Rivest, 1983; Moran, this manuscript). In a laboratory study performed in 1996-1997, I compared growth rates of large (shell length 1.50 [+ or -] 0.07 mm) and small (1.11 [+ or -] 0.03 mm) sibling hatchlings from six clutches of the gastropod species *Nucella ostrina*. Hatchlings were fed ad libitum and measured over 65 d; large hatchlings grew significantly faster than small hatchlings (ANOVA, $F = 33.86$, $df = 5$, P [is less than] 0.001), and small hatchlings took [is greater than] two weeks to reach the initial hatching size of their larger siblings (Fig. 2).

[Figure 2 ILLUSTRATION OMITTED]

Results of laboratory studies suggest that large hatching size should confer performance advantages in the field, particularly under adverse conditions (Spight, 1976b; Etter, 1989; Gosselin, 1997). In agreement with laboratory studies, larger hatchlings were found to grow faster than small hatchlings in the field (Moran, 1997; in preparation). This pattern may be attributable to improved feeding by large hatchlings (e.g., Palmer, 1990), or to greater nutrient stores; large *N. ostrina* hatchlings represent a much greater maternal investment than small hatchlings (Moran, 1997; in preparation). Large hatchlings were also more likely to survive (recovery was used as an index of survivorship) in the field than small hatchlings, although the effect of size on survivorship varied and was not always significant (Moran, 1997; in preparation). These studies suggest that the outcome of experiments testing the relationship between offspring size and performance in the intertidal (or other variable environments) may depend strongly on local conditions at the time the experiment is performed.

The research summarized up to this point for urchins, barnacles and snails implies a substantial advantage of large initial juvenile size. While this advantage is generally

observed in the laboratory (e.g., Spight, 1976b; Rivest, 1983; Emler and Hoegh-Guldberg, 1997; Emler and Miller, in preparation), laboratory results are not universally transferable to the field. Therefore, future tests of size-dependent offspring performance should be examined in the context of environmental variation. This approach may demonstrate how environmental variability changes the relationship between initial juvenile size and performance, a question of particular interest in highly variable environments such as intertidal habitats.

SELECTION IN INTERTIDAL VS. SUBTIDAL ENVIRONMENTS

Many models of life-history evolution assume that offspring size is optimized by the action of natural selection, which balances the benefits of large offspring size with trade-offs between offspring size and other life-history characters such as parental fecundity (reviewed in Stearns, 1992). One important model, first developed by Shine (1978) and further elaborated by Sargent et al. (1987) and Nussbaum and Schultz (1989), predicts that life histories should evolve to minimize the time spent at the most vulnerable stages. Under these models, an increase in juvenile mortality relative to embryonic mortality should result in lengthened embryonic development and increased offspring size. If juvenile survivorship is positively affected by offspring size, then selection for juvenile size will be yet stronger. In marine environments, early juvenile mortality can be highly variable in both time and space (Hunt and Scheibling, 1997). The importance of initial juvenile size is likely to be variable as well, due to spatial or temporal variation in mortality factors that act in a size-dependent fashion (e.g., predation; Gosselin, 1997).

Sources of juvenile mortality are likely to differ considerably between subtidal and intertidal habitats, and this may lead to different selective regimes for initial juvenile size in the two environments. In the intertidal, sources of mortality include both abiotic stresses and biotic factors. While the relative importance of these elements is likely to vary both temporally and spatially, overall the greatest sources of mortality in intertidal habitats appear to be desiccation and predation (Underwood, 1979; Gosselin and Chia, 1995a). In subtidal habitats, in contrast, abiotic stresses related to emersion are not an issue, leaving biotic stresses as the primary candidates for sources of juvenile mortality (Keesing and Halford, 1992).

The initial size of juveniles is correlated with adult habitat in some marine snails (Spight, 1976b; Perron, 1981; Etter, 1989), and two authors have noted a trend towards subtidal species having larger initial juvenile sizes than their intertidal relatives. Spight (1976b) noted that among

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

the family Muricidae, species living subtidally or on coral reef flats hatched larger than species living on oyster reefs or rocky intertidal surfaces. Perron (1981) also noted that size at settlement was correlated with habitat type among Indo-Pacific members of the genus *Conus*, and that metamorphic sizes of species from subtidal habitats tended to be larger than those of intertidal species in this genus. A preliminary compilation of data from the literature suggests this interspecific trend may be present in the family Buccinidae as well (shown in Fig. 3). At present it is difficult to suggest adaptive scenarios to explain differences in initial juvenile size between subtidal and intertidal habitats, because the relationships among size, performance and mortality factors have yet to be characterized in a range of marine habitat types. One possibility, however, is that size differences may be attributable in part to contrasting causes of juvenile mortality in intertidal and subtidal environments.

[Figure 3 ILLUSTRATION OMITTED]

In low intertidal and subtidal environments, biotic factors such as predation may be relatively greater causes of juvenile mortality than in intertidal habitats where abiotic stresses are strong (Phillips, 1969; Vermeij, 1972, 1978; Connell, 1975; Underwood, 1979; Kneib, 1987; Gosselin and Chia, 1995a). Predation on juvenile stages in subtidal habitats might favor large initial juvenile size because larger snails are likely to better resist crushing predators (Spight, 1976b; Vermeij and Currey, 1980; Rivest, 1983; Vermeij, 1987; Juanes, 1992; Scheibling and Hatcher, 1997), and juveniles that are initially larger are likely to grow faster and spend less time in potentially more vulnerable size classes (Rivest, 1983). While abiotic factors in intertidal habitats, such as desiccation stress or wave action, may be size-selective as well (Spight, 1976b; Etter, 1989; Gosselin, 1997), such factors are highly variable over small spatial and temporal scales (see references in Introduction). Highly variable and unpredictable juvenile mortality is likely to create an environment that is not strongly offspring-size-selective, and that favors parental investment in smaller and more numerous offspring (Begon et al., 1996, and references within).

Based on our present limited understanding of the selective forces acting on initial juvenile size in the marine benthos, this (or any) interpretation of size patterns observed in different habitats must be made with caution. One reason for caution is that while intertidal habitats are certainly more variable in many parameters than subtidal habitats (see Introduction), mortality factors such as predation on juveniles can be seasonally and spatially variable in subtidal habitats as well (Sheibling and

Hatcher, 1997). Clearly, more research is needed to contrast the predictability, severity and size-selectivity of intertidal and subtidal environments for newly-recruited juveniles.

Likewise, patterns in initial juvenile size may be attributable to a number of selective factors besides predation; other potentially size-selective factors such as substrate type, juvenile food sources or abundance, prey size, and competition are likely to vary with depth (Perron, 1981; Elner and Raffaelli, 1980; Raffaelli and Hughes, 1987). Another complicating factor in interpreting patterns of initial juvenile size in gastropods is that datasets for muricids and buccinids do not distinguish among tropical and temperate faunas, which may differ in initial juvenile size for reasons unrelated to depth. Finally, these data include only interspecific comparisons, and have not been evaluated in a phylogenetic context. However, the presence of larger initial juvenile sizes in subtidal representatives of three separate taxa suggests this pattern may be robust to phylogenetic analysis when the relationships among taxa are known.

The relationships among habitat, selection and initial juvenile size are likely to be highly complex and variable, and it may be unrealistic to pursue a universal explanation for life-history differences between invertebrates living in intertidal and subtidal habitats. However, several testable hypotheses are generated. First, do selective forces acting on initial juvenile size vary between intertidal and subtidal habitats? Intraspecific experiments comparing the performance of large and small settlers or hatchlings of species that inhabit both subtidal and intertidal habitats would aid in understanding the relationships among initial juvenile size, performance and environment in benthic marine systems. Second, is mortality of juvenile invertebrates more variable and less predictable in intertidal than subtidal habitats? And thirdly, is predation pressure in fact greater subtidally than intertidally on early life history stages of marine invertebrates? Insights into each of these questions could be obtained by comparing mortality patterns and predation rates on newly settled or hatched juveniles of benthic invertebrate species that inhabit both intertidal and subtidal environments.

SUMMARY AND CONCLUSIONS

High mortality during earliest juvenile development is a characteristic of the life-histories of many benthic marine invertebrates (Gosselin and Qian, 1997). Recent studies demonstrate that differences in size, larval nutrient stores, or larval feeding history can strongly affect the performance (growth and survivorship) of juveniles. Two implications of these findings are that (1) adult population

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

structure is likely to be affected by overall juvenile quality, via the effect of juvenile quality on mortality during early life-history stages; and (2) because juvenile quality can affect performance and juvenile mortality is generally high, selection may be strong on characters that enhance juvenile quality.

The major sources of juvenile snail mortality are likely to differ in the intertidal and subtidal; abiotic stresses related to exposure to air, such as desiccation, are important in the intertidal but largely absent in the subtidal, and biotic factors such as predation may be relatively more important selective agents in subtidal habitats. Trends in the initial size of juveniles observed in three different gastropod groups suggest that initial juvenile size is greater subtidally than intertidally in some taxa. Size differences among gastropod hatchlings or settlers in intertidal and subtidal environments may be due in part to differing selective regimes acting on initial juvenile size.

ACKNOWLEDGMENTS

I thank K. Martin and R. Strathmann for organizing the symposium and inviting me to participate. Discussion with and comments from R. Emlet, L. Gosselin, P. Marko, R. Strathmann, and one anonymous reviewer greatly improved the manuscript, as did discussions with other symposium participants. I am grateful to R. Emlet and B. Miller for permission to cite their data in preparation. Some of the research described in this manuscript was performed as part of my dissertation work at the Oregon Institute of Marine Biology, and was supported by grants from Sigma Xi, the American Museum of Natural History, and NSF Grant IBN-9396004 to R. Emlet.

REFERENCES

- Arnold, S. J. 1983. Morphology, performance and fitness. *Amer. Zool.* 23:347-361.
- Arnold, S. J. 1988. Behavior, energy and fitness. *Amer. Zool.* 28:815-827.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology--individuals, populations and communities.* Blackwell Science Ltd., Cambridge, MA.
- Berven, K. A. and B. G. Chandra. 1988. The relationship among egg size, density and food level on larval development in the wood frog (*Rana sylvatica*). *Oecologia* 75:67-72.
- Brunkow, P. E. and J. P. Collins. 1996. Effects of individual variation in size on growth and development of larval salamanders. *Ecology* 77:1483-1492.
- Capinera, J. L. 1979. Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* 114:350-361.
- Cobb, J. S. and R. A. Wahle. 1994. Early life history and recruitment processes of clawed lobsters. *Crustaceana* 67:1-25.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In M. L. Cody and J. M. Diamond. (ed.), *Ecology and evolution of communities*, pp. 460-490. Belknap Press of Harvard University Press, Cambridge, MA.
- Connell, J. H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* 93:11-45.
- Dayton, P. K. 1971. Competition, disturbance and community organization: the provision of and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41:351-389.
- Elner, R. W. and D. G. Raffaelli. 1980. Interactions between two marine snails, *Littorina rudis* Maton and *Littorina nigrolineata* Gray, a predator, *Carcinus maenas* (L.), and a parasite, *Microphallus similis* Jagerskiold. *J. Exp. Mar. Biol. Ecol.* 43: 151-160.
- Emlet, R. B. and O. Hoegh-Guldberg. 1997. Effects of egg size on postlarval performance: experimental evidence from a sea urchin. *Evolution* 51(1): 141-152.
- Etter, R. J. 1989. Life history variation in the intertidal snail *Nucella lapillus* across a wave-exposure gradient. *Ecology* 70:857-1876.
- Etter, R. J. 1996. The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *J. Exp. Mar. Biol. Ecol.* 196: 341-356.
- Ferguson, G. W. and S. F. Fox. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: Its causes and evolutionary significance. *Evolution* 38:342-349.
- Fioroni, V. P. 1988. Die Prosobranchier-Entwicklung mit Nahreiern. *Zool. Anz.* 221:201-247.
- Foster, B. A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. *Mar. Biol.* 8:12-29.

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

Fox, C. W. 1994. The influence of egg size on offspring performance in the seed beetle, *Callosobruchus maculatus*. *Oikos* 71:321-325.

Fox, C. W. and T. A. Mousseau. 1996. Larval host plant affects fitness consequences of egg size variation in the seed beetle *Stator limbatus*. *Oecologia* 107:541-548.

Garrity, S. D. and S. C. Levings. 1984. Aggregation in a tropical neretid. *Veliger* 27:1-6.

Gosselin, L. A. 1997. An ecological transition during juvenile life in a marine snail. *Mar. Ecol. Prog. Ser.* 157:185-194.

Gosselin, L. A. and E.-S. Chia. 1995a. Characterizing temperate rocky shores from the perspective of an early juvenile snail: The main threats to survival of newly hatched *Nucella emarginata*. *Mar. Biol.* 122:625-635.

Gosselin, L. A. and F.-S. Chia. 1995b. Distribution and dispersal of early juvenile snails: Effectiveness of intertidal microhabitats as refuges and food sources. *Mar. Ecol. Prog. Ser.* 128:213-223.

Gosselin, L. A. and P.-Y. Qian. 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146:265-282.

Haven, S. B. 1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in central California. *Veliger* 13: 231-248.

Helmuth, B. S. T. 1998. Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 68:51-74.

Hunt, H. L. and R. E. Scheibling. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 155: 269-301.

Jarrett, J. N. and J. A. Pechenik. 1997. Temporal variation in cyprid quality and juvenile growth capacity for an intertidal barnacle. *Ecology* 78: 1262-1265.

Juanes, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Mar. Ecol. Prog. Ser.* 87:239-249.

Keesing, J. K. and A. L. Halford. 1992. Field measurements of survival rates of juvenile *Acanthaster planci*: techniques and preliminary results. *Mar. Ecol. Prog. Ser.* 85:107-114.

Keough, M. J. 1986. The distribution of a bryozoan on seagrass blades: settlement, growth and mortality. *Ecology* 67:846-857.

Keough, M. J. and E. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia (Berlin)* 54:348-352.

Kirk, K. L. 1997. Egg size, offspring quality and food level in planktonic rotifers. *Freshwat. Biol.* 37: 515-521.

Kneib, R. T. 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68: 379-386.

Marko, P. B. 1998. Historical allopatry and the biogeography of speciation in the prosobranch snail genus *Nucella*. *Evolution* 52:757-774.

McEdward, L. R. and S. F. Carson. 1987. Variation in egg organic content and its relationship with egg size in the starfish *Solaster stimpsoni*. *Mar. Ecol. Prog. Ser.* 37:159-169.

McEdward, L. R. and L. K. Coulter. 1987. Egg volume and energetic content are not correlated among sibling offspring of starfish: implications for life-history theory. *Evolution* 41:914-917.

McShane, P. E. 1991. Density-dependent mortality of recruits of the abalone *Haliotis rubra* (Mollusca; Gastropoda). *Mar. Biol.* 110:385-389.

Moran, A. L. 1997. Size, form, and function in the early life histories of the gastropod genera *Littorina* and *Nucella*. Ph.D. Diss., University of Oregon, Eugene.

Nussbaum, R. A. and D. L. Schultz. 1989. Coevolution of parental care and egg size. *Am. Nat.* 133:591-603.

Nybakken, J. W. 1996. *Marine biology: An ecological approach*. Benjamin Cummings, Merlo Park, California.

Osman, R. W. and R. B. Whitlatch. 1995. Predation on early ontogenetic life stages and its effect on recruitment into a marine epifaunal community. *Mar. Ecol. Prog. Ser.* 117:111-126.

Perron, F. E. 1981. Larval biology of six species of the genus *Conus* (Gastropoda: Toxoglossa) in Hawaii, USA. *Mar. Biol.* 61:215-220.

Palmer, A. R. 1990. Predator size, prey size, and the scaling of vulnerability: Hatchling gastropods vs. barnacles. *Ecology* 71:759-775.

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

- Palmer, A. R., S. D. Graydon, and D. S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of northeastern Pacific *Nucella*. *Veliger* 33:325-338.
- Pfister, C. A. 1996. The role and importance of recruitment variability to a guild of tide pool fishes. *Ecology* 77:1928-1941.
- Phillips, B. F. 1969. The population ecology of the whelk *Dicathais aegrota* in western Australia. *Aust. J. Mar. Freshwat. Res.* 20:225-265.
- Raffaelli, D. and S. Hawkins. 1996. *Intertidal ecology*. Chapman and Hall, New York.
- Raffaelli, D. G. and R. N. Hughes. 1978. The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. *J. Anim. Ecol.* 47:71-83.
- Rivest, B. R. 1983. Development and the influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia, Buccinidae). *J. Exp. Mar. Biol. Ecol.* 69:217-241.
- Roberts, D. A., G. E. Hofmann, and G. N. Somero. 1997. Heat-shock protein expression in *Mytilus californianus*: Acclimatization (seasonal and tidalheight comparisons) and acclimation effects. *Biol. Bull.* 192:309-320.
- Roff, D. A. 1992. *The evolution of life histories: Theory and analysis*. Chapman and Hall, New York, NY.
- Rowley, R. J. 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a sea urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? *Mar. Biol.* (Berlin) 100:485-494.
- Rowley, R. J. 1990. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a kelp bed and sea urchin barrens: a comparison of growth and mortality. *Mar. Ecol. Prog. Ser.* 62:229-240.
- Sargent, R. C., P. D. Taylor, and M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. *Am. Nat.* 129:32-46.
- Scheibling, R. E. and B. G. Hatcher. 1997. Microhabitat refuges and risk of predation for two species of trochid gastropod (*Trochus histrio* and *Tectus pyramis*) at the Houtman Abrolhos, Western Australia. In F. E. Wells (ed.), *The marine flora and fauna of the Houtman Abrolhos Islands, Western Australia*, p. 159-176. Western Australia Museum, Perth.
- Shine, R. 1978. Propagule size and parental care: The "safe harbor" hypothesis. *J. Theor. Biol.* 75:417-424.
- Smith, K. N. and W. E. Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): Influence of size and shelter. *J. Exp. Mar. Biol. Ecol.* 157:3-18.
- Spight, T. M. 1975. On a snail's chances of becoming a year old. *Oikos* 26:9-14.
- Spight, T. M. 1976a. Hatching size and the distribution of nurse eggs among prosobranch embryos. *Biol. Bull.* 150:491-499.
- Spight, T. M. 1976b. Ecology of hatching size for marine snails. *Oecologia* 24:283-294.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Strathmann, M. F. 1987. *Reproduction and development of marine invertebrates of the northern Pacific coast*. University of Washington Press, Seattle.
- Takada, Y. 1996. Vertical variation in fecundity of the intertidal gastropod *Monodonta labio* caused by different growth rates between tidal zones. *Ecol. Res.* 11:371-379.
- Thorson, G. 1946. *Reproduction and larval development of Danish marine bottom invertebrates*. Medd. Komm.dansk. Fisk-og. Havunders, Ser. Plankton 4:1-52.
- Trussell, G. C. 1997. Phenotypic plasticity in the foot size of an intertidal snail. *Ecology* 78:1033-1048.
- Underwood, A. J. 1979. *The ecology of intertidal gastropods*. *Oceanog. Mar. Biol. Ann. Rev.* 16:111-210.
- Vermeij, G. J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecology* 53:693-700.
- Vermeij, G. J. 1978. *Biogeography and adaptation--patterns of marine life*. Harvard University Press, Cambridge, Massachusetts.
- Vermeij, G. J. 1987. *Evolution and escalation--an ecological history of life*. Princeton University Press, Princeton, New Jersey.
- Vermeij, G. J. and J. D. Currey. 1980. Geographical variation in the strength of thaidid snail shells. *Biol. Bull.* 158:383-389.

Size and Performance of Juvenile Marine Invertebrates: Potential Contrasts Between Intertidal and Subtidal Benthic Habitats(1).

Williams, T D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev.* 68:35-59.

Williams, E. E. and G. N. Somero. 1996. Seasonal-, tidal-cycle- and microhabitat-related variation in membrane order of phospholipid vesicles from gills of the intertidal mussel *Mytilus californianus*. *J. Exp. Biol.* 199:1587-1596.

Young, C. M. and F.-S. Chia. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. *Mar. Biol. (Berlin)* 81:61-68.

Corresponding Editor: Paul Verrell

AMY L. MORAN(2,3)

(1) From the Symposium Aquatic Organisms, Terrestrial Eggs: Early Development at the Water's Edge presented at the annual meeting of the Society for Integrative and Comparative Biology, 3-7 January 1998, at Boston, Massachusetts.

(2) E-mail: moran@fhl.washington.edu Present address of A. L. Moran is University of Washington, Friday Harbor Laboratories, 620 University Road, Friday Harbor, WA 98250.

University of Oregon, Oregon Institute of Marine Biology,
P.O. Box 5389, Charleston, Oregon 97420