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TEMPORAL VARIATION IN CYPRID QUALITY AND JUVENILE GROWTH CAPACITY FOR AN INTERTIDAL BARNACLE

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Abstract. Implicit in past studies of recruitment is the assumption that all new recruits possess the same capacity for juvenile growth, and that observed variation in juvenile growth and survival is due entirely to spatial and temporal variation in food availability, magnitude of physical stresses, and intensity of competition and predation. We set out to determine if daily larval cohorts of the barnacle *Semibalanus balanoides* differ in mean physiological quality and, therefore, in their potential for recruiting to adult populations. To assess larval physiological quality, we measured the organic content of nonfeeding cyprid larvae attaching on five dates (10–15 d intervals) during the 1995 recruitment season. Juvenile physiological quality was determined by monitoring the growth, under controlled laboratory conditions, of individuals attaching on seven dates (3–15 d intervals) during the same season. Both cyprid organic content and juvenile growth capacity differed significantly among daily cohorts. We suggest that variation in cyprid organic content may explain previous observations of temporal variation in cyprid metamorphic success and early juvenile mortality and further suggest that variation in juvenile growth capacity contributes to differences in recruitment success of daily cohorts.

Key words: barnacles; cyprid metamorphosis; juvenile growth capacity; juvenile growth vs. larval organic content; larval physiological quality; recruitment; *Semibalanus balanoides*.

INTRODUCTION

For marine invertebrates with planktonic larvae, the most important forces determining recruitment to adult populations include larval mortality (Morgan 1995) and early juvenile mortality due to predation, competition, and physical stress (Foster 1971, Menge 1976, Bertness 1989, Raimondi 1990, Gosselin and Chia 1995). Past studies of recruitment and models of marine invertebrate reproductive patterns (e.g., Vance 1973) have assumed that all recruits possess the same capacity for juvenile growth, and that observed variation in juvenile growth and survival is due entirely to spatial and temporal variation in food availability (Bertness et al. 1991), the magnitude of physical stresses (Foster 1971, Gosselin and Chia 1995), and the intensity of competition (Connell 1961, Bertness 1989) and predation (Menge 1976, Paine 1976, Gosselin and Chia 1995). However, studies of several barnacle species, including *Semibalanus balanoides*, have revealed that metamorphic success and early post-metamorphic survival in the field are dramatically low (Connell 1961, Wethey 1985, Raimondi 1990, Gosselin and Qian 1996) and differ considerably among daily larval cohorts

(Wethey 1985, Raimondi 1990) even when external factors acting at the time of attachment, such as predation and physical stress, appear not to vary. A possible explanation for this variation in survival is that the physiological quality of attaching larvae and resulting juveniles varies over time. Laboratory studies have revealed that limiting the amount of food provided to invertebrate larvae can result in lower larval energy stores and reduced metamorphic success (West and Costlow 1987), and that extension of larval life reduces the energy reserves of nonfeeding larvae (Lucas et al. 1979, Jaeckle 1994) and results in lower metamorphic success and reduced juvenile growth under controlled laboratory conditions (Lucas et al. 1979, Woollacott et al. 1989, Pechenik et al. 1993). Food limiting planktotrophic larvae in the laboratory can also result in reduced rates of post-metamorphic growth (Pechenik et al. 1996). Particularly for sessile intertidal invertebrates, slow juvenile growth results in inferior competitive abilities (Connell 1961, Bertness 1989); this could also increase mortality by prolonging the period of susceptibility to predation before a size refuge is reached (Connell 1961, Paine 1976, Miller and Carefoot 1989). Evidence that food limitation and extended larval periods can reduce larval and juvenile quality, as well as the recent demonstration of larval food lim-

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itation in the field (Fenaux et al. 1994), suggests that larval experiences other than predation may have an impact on recruitment by reducing the physiological quality of attaching larvae and thereby influencing metamorphic success and juvenile growth rate.

The objectives of this study were (1) to determine if daily cohorts of nonfeeding cyprid larvae of the barnacle *Semibalanus balanoides* differ in physiological quality, by measuring the total organic content of newly attached cyprids, and (2) to determine if juvenile growth capacity (measured under controlled laboratory conditions) varies among cohorts attaching throughout a recruitment season. In this report, we define "attachment" as adhesion to a substrate and "metamorphosis" as the conversion of cyprids to juvenile barnacles.

MATERIALS AND METHODS

Daily attachment of *Semibalanus balanoides* cyprids to 12 plexiglass plates (5 × 7 cm) was monitored in the field at Nahant, Massachusetts USA on seven dates during the 1995 recruitment season between March and May. All plates were covered with safety-walk tape (Product number 7740, 3M Company, Saint Paul, Minnesota, USA) to provide a rough surface for cyprid attachment. To promote larval attachment, a thin film of conspecific adult extract was pipetted onto six tape-covered plates and allowed to dry overnight for deployment the following day. Adult barnacle extract contains "settlement factor," consisting of heat-stable glycoproteins that stimulate attachment of barnacle cyprids (Larman et al. 1982). Conspecific extract was prepared by homogenizing field-collected adults in distilled water. The resulting liquid was centrifuged at $120 \times 10^3 \text{ m/s}^2$ for 5 min and the supernatant was decanted, boiled for 10 min and centrifuged at $120 \times 10^3 \text{ m/s}^2$ for 10 min (Rittschof et al. 1984). The final supernatant was passed through a 1.2- μm filter and then diluted with distilled water to a final protein concentration of 50 $\mu\text{g/mL}$ and frozen in 50-mL aliquots at -20°C . Six additional plates (controls) were coated with a thin film of 0.45 μm filtered seawater and were also allowed to dry overnight before deployment in the field. Each day, 12 new plates were anchored 1.8 m above mean low water in a protected channel (a site where adult and juvenile *S. balanoides* are abundant) at Nahant, Massachusetts, and retrieved after two high tides (24 h).

To determine if the physiological quality of attached cyprids differed among daily cohorts, the individual organic content of 90 newly attached cyprids collected from the field on five dates ($n = 13\text{--}20$ cyprids per date) over 7 wk was measured using a modified dichromate oxidation technique (McEdward and Carson 1987; L. McEdward, *personal communication*). Cyprid lengths were measured to the nearest 0.1 μm and each

cyprid was rinsed in distilled water (for ≈ 5 s) before being individually incubated in 1 mL of 85.5% phosphoric acid solution (15 min at 100°C) to remove excess chloride. Each cyprid was then oxidized with 1 mL of 0.04% acid dichromate (3.3 mL of 0.3% potassium dichromate diluted to 25 mL with sulfuric acid) for 15 min at 100°C . Samples were diluted to 10 mL with distilled water, after which 0.5-mL aliquots from each sample were combined with 4.5 mL of cadmium iodide starch reagent (Parsons et al. 1984) and allowed to stand at room temperature (22°C) for 20 min. Each 5-mL sample was then diluted to 10 mL with distilled water and examined spectrophotometrically at 575 nm. The organic content of each sample was determined by comparison with glucose standards (0–20 μg glucose).

On seven dates over 7 wk, the positions of another 188 newly attached cyprids were mapped and individual cyprid lengths were measured to the nearest 0.1 μm . To assess juvenile growth capacity, metamorphosed juveniles were fed the flagellated protist *Dunaliella tertiolecta* (5×10^4 cells/mL) in the laboratory for 7 d with daily changes of 0.45- μm filtered seawater at 16°C . Fifty of the 188 individuals experienced severe crowding during the 7-d growth study and were excluded from the study; maximum basal diameters of the remaining 138 uncrowded juveniles ($n = 11\text{--}33$ animals per date) were measured 2 d and 7 d after they were brought to the laboratory.

The outcome of interactions among sessile organisms competing for space is often controlled by differences in growth capacity; we therefore chose to examine absolute growth rather than proportional growth. Because cyprid organic content and juvenile growth rate are influenced by initial cyprid size, we used analysis of covariance to test for significant effects of attachment date and treatment (conspecific extract vs. seawater) using cyprid length as a covariate. No interactions were significant ($P > 0.1$). Treatment and date of attachment were considered fixed effects. Data for cyprid organic content and juvenile growth rate were transformed by taking the square root of the sum ($X + 0.5$) to achieve homoscedasticity (Bartlett test, $P > 0.05$ after transformation) before using ANCOVA (Zar 1984).

RESULTS

ANCOVA results revealed that cyprid organic content was significantly influenced by attachment date ($F_{4,78} = 20.6$, $P < 0.001$; Fig. 1a) and cyprid length ($F_{1,78} = 32.89$, $P < 0.001$) but not by treatment (conspecific extract vs. seawater; $F_{1,78} = 1.08$, $P = 0.3$). The variation in cyprid organic content among the five daily cohorts was mainly due to the dramatically low organic content of the cohort attaching on 13 April (Fig. 1a).

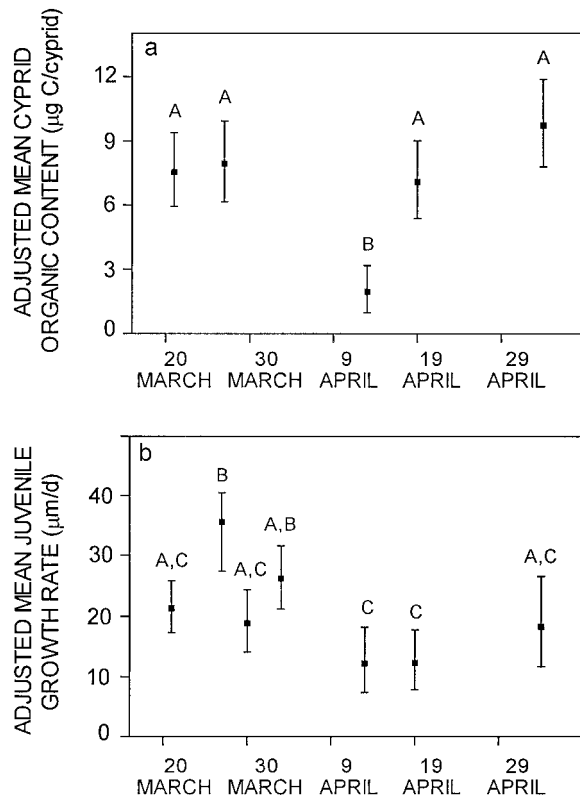


FIG. 1. ANCOVA results for field-collected *Semibalanus balanoides*. (a) Cyprid organic content (adjusted least-squares mean) of newly attached barnacles ($n = 11\text{--}33$ cyprids per date). (b) Juvenile growth rate (adjusted least-squares mean) of barnacles reared under controlled laboratory conditions ($n = 13\text{--}20$ animals per date). Bars indicate 95% confidence intervals. Sample means showing the same capital letter are not significantly different at $P < 0.05$ (GT2 test following ANCOVA).

Juvenile growth rate was also significantly influenced by attachment date ($F_{6,123} = 10.62$, $P < 0.001$; Fig. 1b) and initial cyprid length ($F_{1,123} = 64.55$, $P < 0.001$) but not by treatment ($F_{1,123} = 0.29$, $P = 0.59$). The cohort attaching early in the season, on 27 March, had the highest adjusted mean growth rate ($35.59 \mu\text{m/d}$), at least 2.5 times the adjusted mean growth rate of individuals attaching toward the end of the recruitment season on 13 April ($12.24 \mu\text{m/d}$) and 19 April ($12.37 \mu\text{m/d}$). The adjusted mean growth rate of the 27 March cohort was also more than twice that of the cohort attaching on 30 March ($18.9 \mu\text{m/d}$), indicating that important variation in growth capacity can occur over very short time scales. In general, individuals attaching earlier in the recruitment season grew faster under controlled conditions in the laboratory than individuals attaching later in the season.

Mean juvenile growth rate was not significantly cor-

related with mean cyprid organic content ($r^2 = 0.262$; $F_{1,3} = 1.064$, $P = 0.378$), though the power to detect a correlation was not great.

DISCUSSION

Our results appear to be the first to demonstrate that cyprid organic content and juvenile growth capacity of *Semibalanus balanoides* vary considerably among individuals recruiting to a particular population on different days within a single reproductive season. We do not know whether cyprid organic content and juvenile growth rates also vary among cohorts attaching on the same day at different locations along the coast. However, our results do suggest that, at any one location, cyprids arriving on different days may exhibit dramatic differences in recruitment success due to underlying differences in the physiological quality of individuals making up the cohorts.

The variation observed among cohorts may have resulted from the influence of several factors, none of which necessarily operates exclusively. Temporal variation in the organic content of newly attached cyprids could reflect temporal differences in the quantity (West and Costlow 1987, Fenaux et al. 1994) and quality (Moyses 1963) of food available to the feeding naupliar stages that precede the nonfeeding cyprid stage. Alternatively, they could reflect differences in the length of time cyprids have postponed their metamorphosis (Lucas et al. 1979, Pechenik et al. 1993, Jaeckle 1994). Both food limitation and prolonged larval life have been shown to alter metamorphic success and rates of juvenile growth and development for a variety of marine invertebrate species in laboratory studies (Lucas et al. 1979, West and Costlow 1987, Woollacott et al. 1989, Qian et al. 1990, Pechenik et al. 1993, Pechenik et al. 1996). Variation in larval quality and early juvenile growth capacity could also be due to variation in the quality of eggs produced by adults (George 1990). Finally, variation in physiological quality among cohorts recruiting on different days could have a genetic basis (Bertness and Gaines 1993), with cohorts arriving at different times during the recruitment season originating from different geographic populations or being produced by genetically different individuals within a single population.

Regardless of which factors or combination of factors play a role in determining larval quality, our data demonstrate that daily cohorts of *Semibalanus balanoides* (1) can differ significantly in mean cyprid organic content, which may explain previous field observations of dramatic temporal variation in cyprid metamorphic success and first-day post-metamorphic survival (Connell 1961, Wetthey 1985, Raimondi 1990, Gosselin and Qian 1996); and (2) differ dramatically in juvenile growth capacity. Because growth rates play a large role

in determining vulnerability to predation (Connell 1961, Paine 1976, Miller and Carefoot 1989) and dislodgement (Connell 1961, Petraitis 1983) as well as in the outcome of competitive interactions (Connell 1961, Bertness 1989), such differences in growth capacity may ultimately result in considerable variation among daily cohorts in survival and recruitment success.

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LITERATURE CITED

- Bertness, M. D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* **70**: 257–268.
- Bertness, M. D., and S. D. Gaines. 1993. Larval dispersal and local adaptation in acorn barnacles. *Evolution* **47**:316–320.
- Bertness, M. D., S. D. Gaines, D. Bermudez, and E. Sanford. 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* **75**:91–100.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* **31**:61–104.
- Fenaux, L., M. F. Strathmann, and R. R. Strathmann. 1994. Five tests of food-limited growth of larvae in coastal waters by rates of development and form of echinoplutei. *Limnology and Oceanography* **39**:84–98.
- Foster, B. A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. *Marine Biology* **8**:12–29.
- George, S. B. 1990. Population and seasonal differences in egg quality of *Arbacia lixula* (Echinodermata: Echinoidea). *Invertebrate Reproduction and Development* **17**:111–121.
- Gosselin, L. A., and F. S. Chia. 1995. Characterizing temperate rocky shores from the perspective of an early juvenile snail: the main threats to survival of newly hatched *Nucella emarginata*. *Marine Biology* **122**:625–635.
- Gosselin, L. A., and P. Y. Qian. 1996. Early post-settlement mortality of an intertidal barnacle: a critical period for survival. *Marine Ecology Progress Series* **135**:69–75.
- Jaekle, W. B. 1994. Rates of energy consumption and acquisition by lecithotrophic larvae of *Bugula neritina* (Bryozoa: Cheilostomata). *Marine Biology* **119**:517–523.
- Larman, V. A., P. A. Gabbott, and J. East. 1982. Physicochemical properties of settlement factor proteins from the barnacle *Balanus balanoides*. *Comparative Biochemistry and Physiology* **72**:329–338.
- Lucas, M. I., G. Walker, D. L. Holland, and D. J. Crisp. 1979. An energy budget for the free-swimming and metamorphosing larvae of *Balanus balanoides* (Crustacea: Cirripedia). *Marine Biology* **55**:221–229.
- McEdward, L. R., and S. F. Carson. 1987. Variation in egg organic content and its relationship with egg size in the starfish *Solaster stimpsoni*. *Marine Ecology Progress Series* **37**:159–169.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**: 355–393.
- Miller, K. M., and T. H. Carefoot. 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. *Journal of Experimental Marine Biology and Ecology* **134**:157–174.
- Morgan, S. G. 1995. Life and death in the plankton: larval mortality and adaptation. Pages 279–321 in L. McEdward, editor. *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, Florida, USA.
- Moyle, J. 1963. A comparison of the value of various flagellates and diatoms as food for barnacle larvae. *Journal du Conseil pour l'Exploration de la Mer* **28**:175–187.
- Paine, R. T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858–873.
- Parsons, T. R., Y. Maita, and C. M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, New York, New York, USA.
- Pechenik, J. A., K. Hammer, and C. Weise. 1996. The effect of starvation on acquisition of competence and post-metamorphic performance in the marine prosobranch gastropod *Crepidula fornicata* (L.). *Journal of Experimental Marine Biology and Ecology* **199**:137–152.
- Pechenik, J. A., D. Rittschof, and A. R. Schmidt. 1993. Influence of delayed metamorphosis on survival and growth of juvenile barnacles *Balanus amphitrite*. *Marine Biology* **115**:287–294.
- Petraitis, P. S. 1983. Grazing patterns of the periwinkle and their effects on sessile intertidal organisms. *Ecology* **64**: 522–533.
- Qian, P. Y., L. R. McEdward, and F. S. Chia. 1990. Effects of delayed settlement on survival, growth, and reproduction in the spionid polychaete, *Polydora ligni*. *Invertebrate Reproduction and Development* **18**:147–152.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs* **60**:283–309.
- Rittschof, D., E. S. Branscomb, and J. D. Costlow. 1984. Settlement and behavior in relation to flow and surface in larval barnacles, *Balanus amphitrite* Darwin. *Journal of Experimental Marine Biology and Ecology* **82**:131–146.
- Vance, R. R. 1973. More on reproductive strategies in marine benthic invertebrates. *American Naturalist* **107**:353–361.
- West, T. L., and J. D. Costlow. 1987. Size regulation in the crustacean *Balanus eburneus* (Cirripedia: Thoracica). *Marine Biology* **96**:47–58.
- Wetthey, D. S. 1985. Local and regional variation in settlement and survival in the littoral barnacle *Semibalanus balanoides*: pattern and consequences. Pages 194–202 in P. G. Moore and R. Seed, editors. *The ecology of rocky coasts*. Hodder and Staughton, London, England.
- Woollacott, R. M., J. A. Pechenik, and K. M. Imbalzano. 1989. Effects of duration of larval swimming period on early colony development in *Bugula stolonifera* (Bryozoa: Cheilostomata). *Marine Biology* **102**:57–63.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.