OFFSPRING SIZE AND PERFORMANCE IN VARIABLE ENVIRONMENTS: FIELD STUDIES ON A MARINE SNAIL

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Abstract. This study links offspring size and energetic content to offspring performance (measured as growth and survivorship) in the intertidal gastropod *Nucella ostrina* and examines the effect of hatching size on performance at different times of year and in contrasting environments. The relationships between individual hatchling size and organic content were compared both within and among clutches of *N. ostrina.* Hatchling size was positively, significantly, and predictively correlated with hatchling organic content both within and among clutches, demonstrating that hatching size could be reliably used as an indicator of maternal investment. The slope of the relationship between hatchling size and organic content varied between clutches, suggesting intrapopulation variation in embryonic growth geometry. In field outplants, hatching size always had a positive and significant effect on growth, and small hatchlings took approximately one month to reach the initial size of their larger siblings. More large hatchlings than small hatchlings were recovered in every experimental outplant. The effect of hatching size on recovery was not significant in short (9 d) outplants, but recovery of large hatchlings was significantly greater than recovery of small hatchlings in two out of three long-term (36 or 54 d) outplants. Overall recovery was lower in the summer, the long-term outplant in which size did not significantly affect recovery. In experiments testing the relationship between hatching size and survivorship in two environments that differed in degree of sun exposure, size significantly and positively affected recovery in the more shaded habitat (with higher overall recovery) but not in the sun-exposed environment. Thus, larger hatching size in *N. ostrina* results in (1) increased hatchling growth, (2) considerably shortened time to maturity, and (3) higher survivorship. However, the advantage of large hatching size was decreased under more severe environmental conditions, those which resulted in higher overall hatchling mortality. Contrary to predictions, poor environmental conditions may not be more likely to select for large offspring size in intertidal habitats: during periods of high heat stress, mortality may be largely random with respect to size.

Key words: environmental variability; marine snail; Nucella ostrina; *offspring performance; offspring size; Oregon (USA); rocky intertidal.*

INTRODUCTION

A fundamental principle of life-history theory is the presence of a trade-off between the size and number of offspring a female produces (Lack 1947, Vance 1973, Smith and Fretwell 1974, Brockelman 1975, Kaplan and Cooper 1984, McGinley et al. 1987, Sinervo 1990, Levitan 1993). This trade-off is driven by energetic, physiological, and morphological constraints on the total reproductive output of an individual (Drent and Daan 1980, Godfray 1987) that preclude an increase in offspring size without a corresponding decrease in offspring number (Stearns 1992). The number and size of offspring in a given clutch is considered to reflect the optimizing action of natural selection, that balances the advantages of high fecundity with the benefits of producing higher quality, larger offspring

(Smith and Fretwell 1974, Sinervo 1990). A great deal of evidence supports the presence of trade-offs in offspring size and number within and among numerous taxa, although exceptions are common (see Stearns 1992 for review).

Two important assumptions underlying the hypothesized trade-off between size and number of offspring are that (1) offspring fitness increases with offspring size (Smith and Fretwell 1974), and (2) offspring size and organic content are positively correlated, such that large offspring predictably represent a greater maternal investment than small offspring (McEdward and Carson 1987). The first assumption, that fitness of individual offspring increases with size, is widely held but not universally supported by empirical evidence (reviewed by Stearns 1992, Williams 1994, Hare and Cowen 1997). Important fitness components such as growth and survivorship are not always correlated with offspring size (e.g., Wicklund and Karlsson 1984, Trabanino et al. 1989, Ruohomäki et al. 1993), and in some cases small offspring exhibit relatively higher survivorship (e.g., Cowen and Houde 1990, Litvak and Leg-

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gett 1990, Kaplan 1992, Marañón and Grubb 1993, Tejedo 1993). Deviations from the expected effect of offspring size have been attributed to spatial or temporal variation in environmental quality (Capinera 1979, Yuma 1986, Berven and Chadra 1988, Lyimo et al. 1992), and it is thought that the benefits of large size are reduced under benign environmental conditions (Spight 1976b, Ferguson and Fox 1984, Williams 1994, Fox and Mousseau 1996, Fox 1997).

The second assumption, that larger size represents higher per-offspring investment, is not often directly tested and is violated within some taxa in which the relationship between offspring size and organic content is weak or absent (e.g., seastars, McEdward and Carson 1987, McEdward and Coulter 1987; fish, Niciu and McEdward 1994). This suggests that offspring size cannot be a priori assumed to accurately reflect resource content or maternal investment but must be tested within a given species or population (McEdward and Carson 1987, McGinley and Charnov 1988). If large offspring do not represent higher levels of maternal investment than small offspring in a given taxon, then an important implication is that the life history of that taxon cannot be predicted to evolve in a context of tradeoffs between size and maternal investment.

Because particular taxa may violate one or both of the above assumptions, and because environment can influence the relationship between offspring size and performance, interpretations of life history patterns that assume the presence of a size–number trade-off may be misleading. Neither assumption has been adequately tested in the rocky intertidal environment, which because of its rich biota and well-defined environmental stress gradients has been the focus of many seminal ecological and evolutionary studies. Marine benthic organisms exhibit a tremendous variety of life-history modes both within and among taxa, and therefore are particularly well suited to studies of life-history evolution (Thorson 1946, Strathmann 1985).

Patterns of mortality during the juvenile period are of considerable interest because they are thought to strongly affect adult population size and distribution in intertidal habitats (Connell 1985, Rowley 1989, Osman and Whitlatch 1995, Pfister 1996, Gosselin and Qian 1997, Hunt and Scheibling 1997). A question of increasing interest is, to what extent do cohorts of higher quality or larger juveniles result in greater recruitment into adult populations (Basch 1993, Emlet and Hoegh-Guldberg 1997, Hare and Cowen 1997, Pechenik et al. 1998, Pechenik 1999)? Little is presently known about the role of offspring size in determining juvenile performance or structuring benthic marine communities, possibly because (1) the minute size of juveniles and the complexity of their natural habitat makes field manipulations difficult (Gosselin and Chia 1995b), and (2) complex natural environmental conditions are difficult to simulate in the laboratory.

In this study, we used hatchlings of the intertidal gastropod *Nucella ostrina* (previously *Nucella emarginata*; see Palmer et al. 1990, Marko 1998) to test several assumptions of life-history theory in the laboratory and field. We first determined that hatching size of *N. ostrina* juveniles is strongly correlated with hatchling organic content, and therefore size can be used as a proxy for maternal investment. Next, we outplanted large and small hatchlings intertidally to examine the effects of hatching size on growth and survivorship. Finally, we outplanted hatchlings at two neighboring intertidal sites that experienced different temperature regimes to determine whether the effect of hatching size on survivorship could vary under measurably different, but environmentally realistic, thermal regimes. Results of these experiments suggest that while increased maternal investment in *N. ostrina* improves offspring performance under some conditions, the relationships among offspring performance, maternal investment and environment may not always meet the predictions of life history theory.

METHODS

Study species

The marine gastropod species *Nucella ostrina* (Gastropoda: Prosobranchia) is a common intertidal-zone snail that ranges from Alaska to Half Moon Bay, California (see Plate 1). The biology of this species has been well studied. Both juveniles and adults feed on barnacles and mussels and live in the mid- to high-intertidal zones. Female *N. ostrina* reproduce year-round in Oregon (Seavy 1977), laying multiple clutches of between 4 and 20 benthic egg capsules. Capsules contain between 1 and 33 embryos, and offspring hatch as metamorphosed ''hatchling'' juveniles (Spight 1976a). During prehatching development embryos feed on nurse eggs (nondeveloping or unfertilized eggs), thereby growing from an egg size of 190 μm to hatching sizes of between 0.9 and 2.3 mm, measured as the maximum dimension of the shell (Spight 1976a, Palmer 1990). Hatching size is determined by the number of nurse eggs consumed during development, and the ratio of nurse eggs to developing embryos varies among capsules within a clutch in a haphazard manner (Spight 1976a, Rivest 1983). The total number of ova within capsules is fairly constant, but some capsules contain only a few (1–4) embryos while others contain >30 (Spight 1976a). Therefore, embryos within some capsules divide the nurse egg supply among many siblings, and consequently hatch at smaller sizes than embryos which have fewer capsulemates. Hatching size variation is not attributable to competition between capsulemates, because even when there are many embryos (>30) per capsule, hatching size variation is small (Spight 1976a). Thus, intraclutch hatching size variation is most likely due to a haphazard distribution of embryos between capsules in a clutch (resulting in between-capsule variation in the number of nurse eggs

available for consumption), rather than to differences in developmental rate, composition, vigor, competitive ability, or other confounding factors that might affect post-hatching performance.

Mortality of *Nucella* hatchlings is high. Estimates of mortality made from measurements of adult fecundity and size distributions of juveniles and adults suggest that 90–99% of *N. ostrina* juveniles die in the first year after hatching (Spight 1976*b*), and in a congeneric species (*N. lapillus*) only 1–2% survive the first two months of life (Feare 1970). Sources of mortality in the field are largely unknown, but field manipulations have established that microhabitat is very important; juvenile mortality is close to 100% if juveniles are deprived of cover (Gosselin and Chia 1995*b*). Potentially important biotic and abiotic sources of mortality include predation, desiccation, starvation, salinity and dislodgment by wave action (Underwood 1979, Pechenik 1982, Rivest 1983, Etter 1989, Gosselin and Chia 1995*a*), all of which may exert considerable selective pressure on early life-history traits.

Hatching size is likely to affect hatchling fitness, because large size is thought to confer added resistance to physiological stresses (heat and desiccation), predation, and starvation (Spight 1976*b*). To date these assumptions have not been tested in the field, but laboratory studies generally support the idea that large hatching size is advantageous. Large *N. ostrina* hatchlings consume a wider range of prey sizes than small hatchlings (Palmer 1990), and some predators have been demonstrated to selectively consume smaller hatchlings or juveniles in the laboratory (Spight 1976*b*, Rivest 1983, Gosselin 1997). Large *Nucella* hatchlings survive longer periods of desiccation stress than small hatchlings (Etter 1989), and desiccation resistance continues to increase as snails grow (Gosselin 1997). Large hatchlings both grow more and survive longer under starved conditions in the laboratory (Moran 1997), and large hatchlings exhibit a considerable growth advantage when hatchlings are fed ad libitum in the laboratory (Moran 1999). The superior performance of large snail hatchlings in laboratory experiments suggests that large hatching size will be advantageous under most natural conditions (Spight 1976*b*, Rivest 1983, Etter 1989).

Relationship between hatching size and organic content

To determine the relationship between shell length (a simple and nondestructive measurement) and organic content, clutches at the point of hatching (''ripe'') were collected from three rocky intertidal sites (Gregory Point, Cape Arago [GP]; Coos Head, Charleston [CH]; Boathouse Dock, Oregon Institute of Marine Biology [BHD]). The three sites were all were wave-exposed, west-facing outer coastline, and were within 5 km of each other (CH and BHD were only 200 m apart). Clutches were judged to be ripe if all snails

PLATE 1. Seven *Nucella ostrina* adults on barnacle-covered intertidal rock. Snails are approximately 1.5 cm in shell length.

within the egg capsule had metamorphosed from larvae to juveniles, and the ''capsule plug,'' which seals the capsule hatching pore while embryos are developing, had begun to dissolve. Three clutches from BHD and CH were examined in their entirety, and 10 clutches from GP were subsampled from clutches used in field experiments. Each hatchling was measured for maximum shell length (apex of the shell to the tip of the siphonal canal) to the nearest 10 μm under a Wild dissecting microscope equipped with an ocular micrometer.

Organic content of individual hatchlings was measured in one of two ways. For three clutches, organic content was measured with the potassium dichromate wet oxidation (PDWO) method of Parsons et al. (1984), as modified by McEdward and Carson (1987) with some additional modifications (Moran 1997). Organic content of other clutches was estimated as ash-free dry mass (AFDM). Each hatchling was washed five times with distilled water to remove salts and dried at 80°C to a constant mass (>6 d). The dry mass of each hatchling and pan was recorded and pans and snails were ashed in a muffle furnace at 450°C for 4 h. To obtain AFDM, the ashed mass was subtracted from the dry mass for each snail and pan. Because PDWO and AFDM gave equivalent estimates of total organic content (Moran 1997), results of the two methods are reported together.

To determine the relationship between shell length and organic content of older juveniles, 27 small (1.7– 7 mm shell length) subadult snails were collected at Gregory Point, Cape Arago, on 2 April 1997 and the AFDM of each measured.

Size-dependent growth and survivorship in the field

To determine whether hatching size affected juvenile performance in the field, hatchlings from field-col-

lected ripe clutches were outplanted to the field and sampled over time. Five similar experiments were outplanted at BHD using ripe clutches collected from BHD and CH; these two sites were very similar to each other in wave exposure, thermal exposure, and snail densities, and were separated by ~200 m including a 100 m stretch of sandy beach.

Capsules were opened with fine dissecting scissors and hatchlings gently washed out with a Pasteur pipet. The very smallest (<0.9 mm) and largest (>2 mm) hatchlings were discarded. The remaining hatchlings were rinsed through a series of four graded Nitex screens, and 15 snails were randomly chosen from the largest and smallest mesh screens. Because pilot studies using entire clutches suggested that the effects of size might be subtle, we used only ''large'' (1.40–1.8 mm) and ''small'' (1.0–1.23 mm) size classes from each clutch. The mean size of large and small hatchlings varied somewhat among clutches, but within each clutch size classes differed by at least 0.3 mm shell length. Outplanted hatchlings were marked for 12 h with a solution of Calcein (Sigma-Aldrich, St. Louis, Missouri, USA), a nontoxic label that creates a permanent mark at the growing edge of the shell that is visible viewed under blue light with a yellow filter set (Moran 2000). Calcein was used to both identify experimental animals and measure growth.

Each group of 30 marked, sibling hatchlings was outplanted to the field on removable 13 × 13 cm Astroturf (Monsanto, Dalton, Georgia, USA) panels seasoned in the field for at least 5 mo. Each panel contained abundant hatchling food and cover (small and large barnacles, mussels, algae, etc.). Panels were edged by 15-cm segments of PVC pipe and bolted to the substrate. PVC edges were coated with Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA), a nontoxic, sticky barrier that provided an effective deterrent to hatchling movement (Moran 1997). Barriers were refreshed every 2 d in the field or as necessary. Hatchlings were transported to the field in Eppendorf tubes filled with seawater, then gently transferred to panels with a Pasteur pipet and washed with seawater until all had attached to panel surfaces.

Experimental outplants were performed at BHD in 1995–1996. The first pair of experiments (outplants 1A and 1B) consisted of two 9-d outplants in the fall of 1995, using 15 large and 15 small hatchlings from each of five clutches. Each clutch was placed on a separate Astroturf panel in the field for 9 d, after which panels were retrieved and recovery and shell growth were measured. Because hatchlings' shell length increased relatively little in 9 d, growth in outplants 1A and 1B was measured as shell added from the Calcein mark to the new growth margin of the aperture along the second shell rib, a more sensitive method than length increase for measuring shell growth.

A second pair of outplants (outplants 2A and 2B) both compared growth and recovery of 15 large and 15 small sibling hatchlings from each of five panel-clutches over a longer interval. In these experiments, hatchlings were outplanted for a total of 36 d in the spring (outplant 2A) and summer (outplant 2B) of 1996. Panels were retrieved at 9-d intervals and survivorship and increase in shell growth were measured.

The fifth experiment (outplant 3) was over twice as large, consisting of 15 large and 15 small hatchlings from each of 12 clutches, and was not repeated. Panels from outplant 3 were retrieved at 9 d intervals for a total of 54 d in the fall of 1996. Outplants 2A, 2B, and 3 were terminated when total recovery was lower than 20% of the original number outplanted. Growth in outplants 2A, 2B, and 3 was measured as the difference between original shell length, measured from the Calcein mark, and the new shell length.

At each sample date in each experiment, panels were brought into the laboratory and washed repeatedly with a high-pressure freshwater spray. The washings were filtered through a 600-μm screen and immediately placed in seawater. Hatchlings were never visibly damaged by this procedure and were very active after being returned to seawater. The original size class of each individual (large or small) could be readily determined via the Calcein mark (see Moran 2000). Recovery percentage was calculated by dividing the number of each size class found at each sampling interval by the original number (15) in each group. Laboratory processing of panels was time consuming, so panels and hatchlings were kept in the laboratory for 1–3 d (depending on number of panels and weather conditions) before being returned to the field. While in the laboratory, panels and hatchlings were kept at 4°C to limit growth and metabolism (adult *N. ostrina* do not grow at temperatures below 6°C; Seavy 1977). Temperatures below 4°C occur frequently during the winter on the Oregon Coast, and maintaining hatchlings at this temperature had no visible effects on behavior or survival. After processing, panels were returned to their original position in the field and hatchlings were replaced as described above.

Size-dependent hatchling growth and survivorship under contrasting field conditions

To determine whether local habitat conditions affected size-dependent performance of *Nucella ostrina* hatchlings, newly collected hatchlings were outplanted to locations that differed considerably in degree of sun exposure. Experimental outplants were performed on either side of an intertidal surge channel at Coos Head, Oregon, immediately inside the mouth of Coos Bay. This site experienced considerable wave action in both winter and summer, and summer temperature and salinity conditions were oceanic (Oregon Institute of Marine Biology dock daily records). The surge channel was ~1.8 m wide, 2 m deep, and 4 m long, and the two long, parallel sides faced ENE (''east-facing side'') and WSW (''west-facing side''), respectively. The open

end of the surge channel faced NNW and the SSE end backed on a ~20 m cliff. Both sides of the surge channel were sandstone, and the east-facing side had noticeably reduced cover of barnacles, algae, and mussels relative to the west-facing side. *Nucella ostrina* adults and egg capsules occurred on both sides. Preliminary observations suggested that because of shading from the cliff to the SSE of the surge channel, the east-facing side received the greatest amount of sun exposure.

Because we could not find enough ripe clutches at BHD/CH immediately prior to initiating this experiment, all clutches used in the surge channel outplants were collected at GP (a longer stretch of rocky shoreline that was qualitatively very similar to GP/CH in wave exposure, snail density, and thermal regime), and hatchlings were removed from their capsules and sorted into size classes. Fifteen randomly chosen large and small hatchlings from each of 14 clutches were marked with Calcein for 12 h and measured for total shell length. Each of the 14 marked clutches was randomly assigned to one seasoned 13 × 13 cm Astroturf panel. Hatchlings were transferred to the panels as in the other experiments. After all hatchlings had attached, panels were randomly assigned to one of two groups, east-facing or west-facing. The rock substrate was locally cleared of barnacles and mussels, and the seven east-facing and seven west-facing panels were bolted to the sandstone at ~2 m above the 0 tide level on opposite sides of the surge channel, directly across from each other (~1.8 m apart). Panels within each side were 5–10 cm apart. Each panel was surrounded by Tanglefoot, refreshed at 2-d intervals or as necessary.

To measure temperature as an index of desiccation stress on both sides of the surge channel during experimental outplants, two Optic StowAway thermistors (Onset Inc., Bourne, Massachusetts, USA) were bolted to the substrate at the same height as panels on each side of the surge channel. To avoid greenhouse effects on thermistor temperature, a half round of grey PVC pipe, open at both ends and with several holes bored in it for ventilation, was bolted to the rock on top of but not touching the thermistors. Thermistors were therefore shaded and open to outside air/water at all times. Thermistors were programmed to record the ambient temperature at 5-min intervals for the duration of each experiment. To determine whether temperatures recorded by the thermistors were equivalent to actual panel temperatures and whether temperature varied over the surface of the panels, temperatures were taken on three consecutive low tides at three positions within each panel using a VWR thermocouple temperature probe (VWR Scientific, Bridgeport, New Jersey, USA). Temperatures recorded with the probe were then compared to the Optic StowAway thermistor readings for the same time and date.

These methods were repeated in two outplants (outplants 4A and 4B) in the summer of 1997. Panels and hatchlings in the first outplant (4A) were in the field

TABLE 1. Regression equations, squared *r*, and *n* for the relationship between organic content (μg) and shell length for three complete field-collected clutches (A, B, C), these three clutches combined (D), hatchlings subsampled from ten additional field-collected ripe clutches (E–N) and older juveniles collected in the field.

Clutch	Regression equation	r^2†	n
A	$\log y = 1.43x + 0.03$	0.88	45
B	$\log y = 2.44x - 1.46$	0.80	47
C	$\log y = 1.31x + 0.21$	0.80	51
D (A + B + C)	$\log y = 1.69x - 0.39$	0.68	143
E	$\log y = 1.56x - 0.11$	0.82	24
F	$\log y = 0.78x + 0.83$	0.41	24
G	$\log y = 1.45x - 0.07$	0.57	24
H	$\log y = 1.61x - 0.08$	0.86	23
I	$\log y = 1.47x - 0.01$	0.66	22
J	$\log y = 1.82x - 0.42$	0.86	24
K	$\log y = 1.12x + 0.37$	0.69	24
L	$\log y = 1.53x - 0.18$	0.88	24
M	$\log y = 0.89x + 0.63$	0.76	22
N	$\log y = 1.12x + 0.43$	0.84	24
Wild juveniles	$\log y = 0.29x + 1.81$	0.96	28

† All r^2 are significant at the $P < 0.001$ level.

for a total of 26 d and were sampled at day 3, day 9, and day 27. One panel from the west-facing side was ripped off the rock by wave action and lost between days 9 and 27 of outplant 4A. In the second outplant (4B), panels were in the field for a total of 18 d and were sampled at day 9 and day 18. During sampling, panels were brought into the laboratory and hatchlings were measured for growth and survivorship.

ANALYSES

All data used in paired and multiple-sample tests were initially examined for normal distribution with a one-sample Kolmogorov-Smirnov test with Lilliefors option in Systat (SPSS 1996) and Cochran's test for homogeneity of variance. If data did not meet the assumptions of equal variance and normal distribution, the appropriate nonparametric test was used except where noted otherwise.

Organic content.—The relationship between hatchling length and hatchling organic content was estimated with a linear, ordinary least-squares (OLS) regression of organic content in μg on shell length (SigmaPlot 5.0 for Windows [SPSS 1999]). Because of the probable curvilinear relationship between length and organic content, *y* data (organic content) were log-transformed prior to analysis (Zar 1996). Although a reduced major axis (RMA) regression can be more appropriate than OLS regression for estimating the relationship between two sets of measurements (McArdle 1987), data for these experiments were analyzed with OLS because we were interested in the predictive power of the relationship and we know of no method for calculating prediction intervals around RMA regressions. In addition, given the high *r* values in this study (see Table 1) the difference between slopes calculated by OLS and RMA regression analyses would be small (Seim and Sather

1983). To estimate the value of hatching length as a predictor of organic content, 95% prediction intervals were calculated around each regression using the formula from Zar (1996:334), which calculates the 95% confidence intervals around a single value of y at a given x value. If the prediction intervals did not overlap for the largest and smallest snails in a regression, hatching size was considered to have predictive value for that clutch (McEdward and Carson 1987).

Field outplants.—Percent recovery of large and small hatchlings on the final day of each single-site field outplant were arcsine transformed and compared using a paired Student's t test, with large and small siblings paired within clutch. To determine whether there was a significant trend towards greater recovery in all the experiments, the direction of differences (''+'' if more large hatchlings were recovered, ''−'' if a greater number of small hatchlings were recovered) was compared among experiments using a one-tailed sign test. Growth of large and small hatchlings was compared using a two-factor, mixed-model ANOVA with initial hatching size (L or S) as a fixed factor, clutch as a random factor, and growth as the dependent variable. Because of zero recovery in some groups (either large or small size classes from individual clutches) at the end of each outplant, growth of large and small hatchlings was compared on the last day of each experiment in which individuals were recovered from all groups: day 18 of outplants 2A and 2B, and day 27 of outplant 3.

Due to time constraints, growth was only measured at day 9 of the first of the two-site field outplants (4A). Growth was analyzed using a three-factor, mixed-model ANOVA with initial hatching size as a fixed factor, clutch as a random factor nested within side, side as a fixed factor, and growth on day 9 as the dependent variable. Recovery in both two-site field experiments (4A and 4B) was first analyzed with paired Student's t tests comparing arcsin-transformed percent recoveries of large and small hatchlings within side of the surge channel. Arcsin-transformed paired percent recovery data were normally distributed in all but two of the eight groupings (large and small hatchlings from each of two sides in two experiments), small hatchlings from the east-facing side of outplant 4A (Lilliefors test, $P < 0.05$) and large hatchlings from the west-facing side of outplant 4B (Lilliefors test, $P < 0.05$). T tests are quite robust to departures from normality particularly when tests are two-tailed and sample sizes are equal (Zar 1996, Underwood 1997).

If one side had substantially higher overall recovery than the other, the magnitude of the difference between large and small hatchling recoveries on the high-recovery side might be inflated relative to the low-recovery side even if there were no greater proportional advantage of size on the high-recovery side. Therefore, to determine whether the effect of size on recovery varied between the two sides of the surge channel, we compared relative recoveries of large and small hatchlings by calculating an index, PD_L, that standardized for different recoveries across panels, sides, and experiments.

PD_L is the proportionals deviation of recovery of large hatchlings from the mean percentage recovery of large and small hatchlings within each panel:

$$PD_L = (\%R_L - \%R_{\bar{x}})/\%R_{\bar{x}}$$

where $\%R_L = \text{Recovery}_L/15$ (percentage recovery of larges), $\%R_S = \text{Recovery}_S/15$ (percentage recovery of smalls), and $\%R_{\bar{x}} = (\%R_L + \%R_S)/2$ (mean percent recovery of larges and smalls).

PD_L describes the relative advantage of large size on a given panel independent of total recovery on that panel, thus standardizing for different total recoveries among panels (and among sites and experiments). PD_L ranges between 1 and −1; positive values indicate large hatchlings had higher recovery than small hatchlings on a given panel, and negative values indicate more small hatchlings were recovered. To test for side effects, we performed a two-way ANOVA using side (east- or west-facing) as a fixed factor, outplant (4A or 4B) as a random factor, and the PD_L of each panel as the dependent variable.

Although PD_L is derived from a percentage, arcsine-transformation was not appropriate because some values were negative. Likewise, sample sizes were close to equal and arcsine transformation of binomial data for ANOVA is inadvisable unless there is a greater than five-fold difference between the smallest and the largest sample sizes (Zar 1996:282). Three of the four data groupings were normally distributed without transformation (Shapiro-Wilk test, $P > 0.19$), the fourth (east-facing, outplant 4B) was only marginally non-normal (Shapiro-Wilk, $P = 0.0405$), and ANOVA is robust to small deviations from normality when sample sizes are equal. Variances were homogeneous without transformation (Cochran's $C = 0.477$, $P = 0.259$).

RESULTS

Relationship of hatching size to organic content and maternal investment

All three field-collected clutches exhibited a positive and significant relationship between organic content and shell length (Fig. 1a–c; Table 1, clutches A–C). For each of the three clutches 95% prediction intervals for the largest and smallest snails were nonoverlapping, indicating that a single large hatchling could be predicted, at the 95% confidence level, to have a higher organic content than a single small hatchling from these clutches (Fig. 1a–c). There was also a significant and positive relationship between organic content and shell length when data from all three clutches were combined and analyzed with an ordinary least squares (OLS) regression (Table 1d), and 95% prediction intervals indicated that this relationship had predictive value as
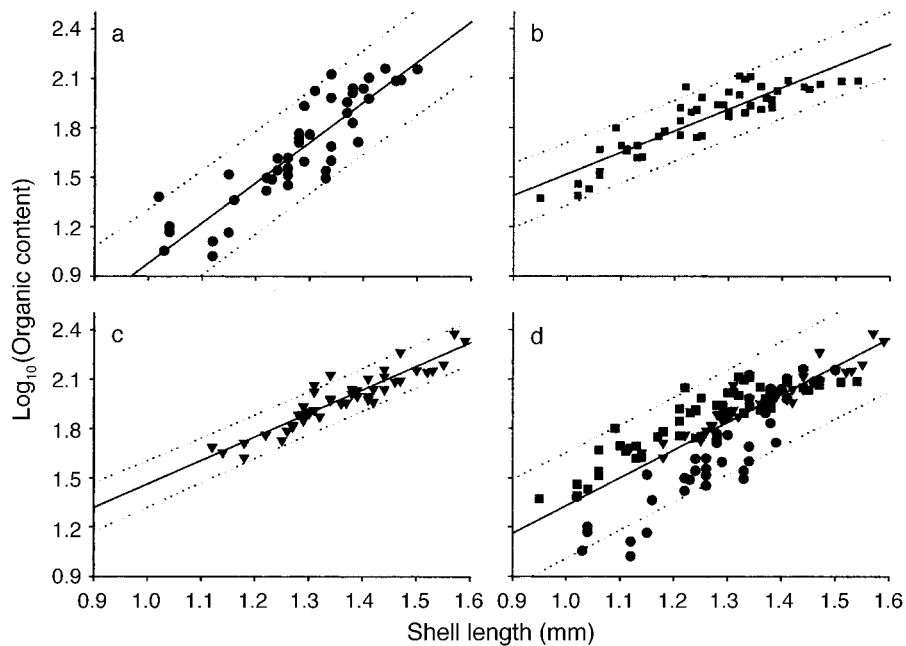
FIG. 1. Log_{10} organic content plotted against shell length (a, b, c) for individual hatchlings from three field-collected ripe clutches and (d) for combined hatchlings from all three clutches. Symbols in (d) are consistent with a, b, and c, and regression equations are shown in Table 1. Solid lines are least-squares regressions; dotted lines are 95% prediction intervals around a single value of *y* at a given *x* value (Zar 1996). Note that, in each case, the 95% prediction intervals for the largest and smallest hatchlings are nonoverlapping, indicating that shell length can be used to predict at the 95% confidence level that individual large and small hatchlings differ in organic content. Prior to log-transforming, organic content was measured in micrograms (μg).

well (Fig. 1d). Each of ten subsampled clutches (sub-sampled from siblings of snails used in the 12-clutch experimental outplant) also exhibited a significant and positive correlation between organic content and shell length (Table 1, clutches E–N).
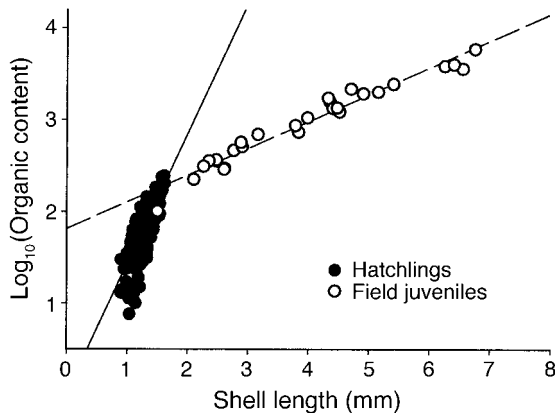

FIG. 2. Log_{10} organic content plotted against shell length for individual, post-hatching juvenile *Nucella ostrina* of a range of sizes (1.5–7 mm) collected in the field (open circles; dashed line), measured as ash-free dry mass. For comparison, all data from individual hatchlings removed from ripe egg capsules are also plotted (closed circles; solid lines). Lines are least-squares regressions. Prior to log-transforming, organic content was measured in micrograms (μg).

Very small field-collected, post-hatching juveniles were predicted to be similar in organic content to pre-hatching juveniles in the same size range (Fig. 2). However larger (and older) juveniles of >2 mm shell length had lower organic content per unit shell than did recently metamorphosed hatchlings from ripe clutches, and the slope of the regression line of organic content on shell length was significantly different from the slopes calculated for hatchlings from ripe clutches (Fig. 2; ANCOVA, slope *F* ratio = 25.71, df = 1, 400, *P* < 0.001).

Size-dependent survivorship and growth in the field

When recovery rates of large and small hatchlings were compared across outplants, large hatchlings exhibited higher overall recovery than small hatchlings in every case (outplants 1A, 1B, 2A, 2B, 3, 4A, and 4B), and this pattern was significant in a two-tailed sign test (*n* = 7, *P* ≤ 0.02). However, when recovery was compared within outplants, large hatchlings exhibited significantly higher recovery in only four: outplant 2A (paired Student's *t* test, *t* = 7.75, *P* < 0.002; Fig. 3), outplant 3 (paired Student's *t* test, *t* = 6.9, *P* < 0.0001; Fig. 3), and outplants 4A and 4B. Size did not significantly affect recovery in outplants 1 A and 1B (paired Student's *t* test, 1A, *t* = 1.32, *P* = 0.26; 1B, *t* = 1.48, *P* = 0.21; see Fig. 4) or outplant 2B (paired Student's *t* test, *t* = 1.7, *P* = 0.16; see Fig. 3).
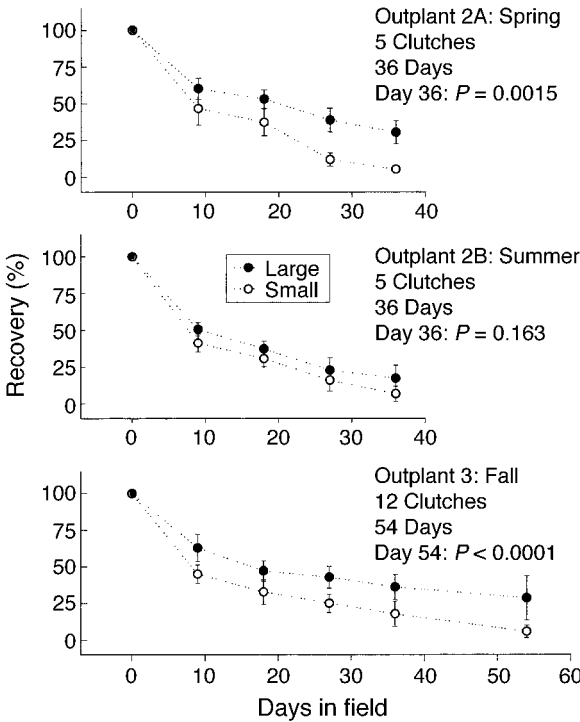
FIG. 3. Mean percentage recovery of large and small hatchlings over time in three field outplants. Error bars represent ± 1 SE.
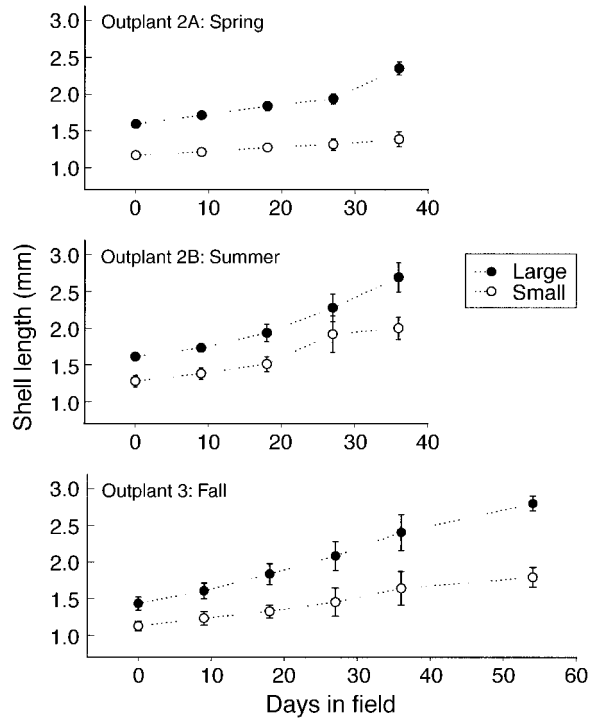

FIG. 5. Grand mean of sizes of large and small *Nucella ostrina* hatchlings over time in three field outplants. Data shown are absolute sizes, not growth measurements (see Table 2 for analyses of growth measurements). Error bars represent ± 1 SE.

Large hatchlings grew significantly more than small hatchlings in all outplants, as tested on day nine of outplants 1A and 1B, day 18 of outplants 2A and 2B, and day 26 of outplant 3. The grand means of large and small hatchling sizes at each sampling day in 2A, 2B, and 3 are shown in Fig. 5; results of model III ANOVAs (fixed factor = size, random factor = clutch) for each outplant (1A, 1B, 2A, 2B, 3) are presented together for convenience in Table 2. Clutch significantly affected growth in 2B and 3, and there was a significant interaction between clutch and size class in outplant 3, indicating that the effect of size class on growth varied among clutches (Table 2). Growth data

in outplant 3 violated the assumption of homogeneity of variances (Cochran C statistic = 0.1539, P = 0.019), and transformations were not successful at removing variance heterogeneity. The P value of the size effect was considerably lower than that of the Cochran C statistic (0.000 and 0.019, respectively) and therefore the effect of size on growth was robust (Underwood 1981). However, because the P value for the interaction term in outplant 3 was >0.029, this result may be subject to Type I error and the significance of the interaction term should be viewed with caution.
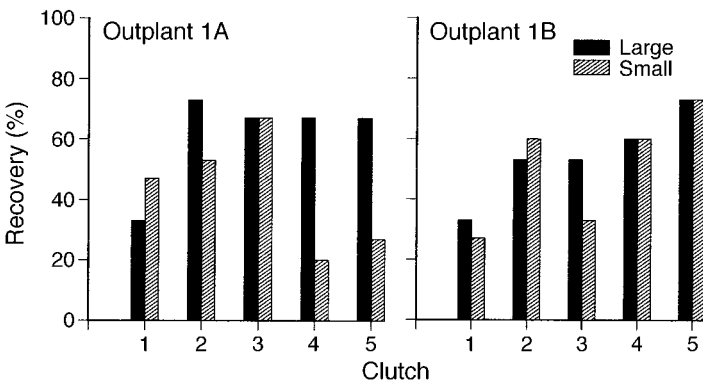

FIG. 4. Percentage recovery of large and small hatchlings over two nine-day outplants (1A and 1B), each comprising five clutches. Recovery of large and small hatchlings was not significantly different in either outplant.

TABLE 2. Results of model III ANOVAs for large and small hatchlings' growth during six experimental field outplants.

Experiment	Source	df	ss	F	P
Outplant 1A (9 d)	Clutch (C)	4	1.57†	0.854	0.496
	Size Class (SC)	1	10.62†	7.967	0.048
	C × SC	4	5.33†	1.030	0.029
	Error	68	30.41†		
Outplant 1B (9 d)	C	4	2.77†	1.159	0.337
	SC	1	4.79†	7.787	0.049
	C × SC	4	2.46†	1.030	0.398
	Error	66	40.61†		
Outplant 2A (on d 18)	C	4	0.826	1.098	0.366
	SC	1	9.242	85.075	0.001
	C × SC	4	0.435	0.578	0.680
	Error	59	11.094		
Outplant 2B (on d 18)	C	4	0.866	14.436	0.000
	SC	1	0.433	51.131	0.002
	C × SC	4	0.034	0.564	0.690
	Error	41	0.615		
Outplant 3 (on d 27)	C	11	0.965	1.906	0.047
	SC	1	2.470	25.808	0.000
	C × SC	11	1.053	2.081	0.029
	Error	98	4.509		
Outplant 4A (on d 9)	Side	1, 12	0.002	0.162	0.695
	C	12, 179	0.184	3.120	<0.001
	SC	1, 12	0.314	29.805	<0.001
	Side × SC	1, 12	<0.001	<0.001	0.988
	C × SC	12, 179	0.126	2.141	0.016

Notes: P values were calculated independently for each experiment.
† Actual values were divided by 1×10^5 for convenience.

Size-dependent survivorship under contrasting field conditions

Temperature data recorded by the Optic StowAways indicated that the east-facing side reached considerably higher temperatures than the west-facing side in outplants 4A and 4B. The greatest differences between sides occurred during morning low tides (Fig. 6) when both sides were exposed to air, the east-facing side was in direct sunlight, and the west-facing side was completely shaded. Temperature measurements taken with a thermocouple probe at three sites on each panel showed that on the west-facing side, temperatures varied by <1°C within panels and by <2°C among panels, and were within 1°C of temperatures recorded by the thermistor dataloggers. On the east-facing side temperatures varied by as much as 5°C within panels and by >6°C between panels. The highest temperature recorded by the probe on or around panels was 3°C lower than the temperature recorded by the thermistor datalogger at the same time, suggesting that dataloggers may have reached slightly higher temperatures than panels or surrounding substrate during periods of greatest sun exposure, but this difference was small.

Large hatchlings grew significantly more than small hatchlings by day nine of outplant 4A, but growth did not differ between the two sides of the surge channel nor was there a significant interaction between side and size (Table 2). Overall per-panel recovery on the final day of outplants 4A and 4B (outplant 4A, day 27; outplant 4B, day 18) was significantly higher on the west-facing side than on the east-facing side (4A: Kruskal-Wallis test, Mann-Whitney U test statistic = 139.00, $P = 0.004$. 4B: Student's two-sample t test, $t = 3.60$, $P = 0.01$). In both outplants, large hatchlings exhibited significantly higher recovery than small hatchlings on the west-facing side (paired Student's t test, 4A, $t = 3.77$, $P = 0.013$; 4B, $t = 2.58$, $P = 0.042$) but not on the east-facing side (paired Student's t test, 4A, $t = 1.00$, $P = 0.36$; 4B, $t = 0.94$, $P = 0.34$; Fig. 7).

PD_L (the proportional deviation of large hatchlings from mean recovery on each panel) was positive in all cases (Fig. 8). When the two sides of the surge channel were compared, PD_L was significantly higher on the west-facing side than on the east-facing side (means and standard errors shown in Fig. 8, ANOVA results in Table 3), suggesting the advantage of large hatching size was greater on the west-facing side. There was no significant effect of outplant and no significant interaction between outplant and side (Table 3).

DISCUSSION

Size and organic content

A primary assumption underlying many life-history models is that offspring size reflects both resource content and maternal investment per offspring (McEdward and Carson 1987). Among hatchling *Nucella ostrina,* there is a strong, significant and predictive relationship between hatching length and organic content both within and among clutches (Fig. 1). This relationship is much stronger in *N. ostrina* than in other marine taxa
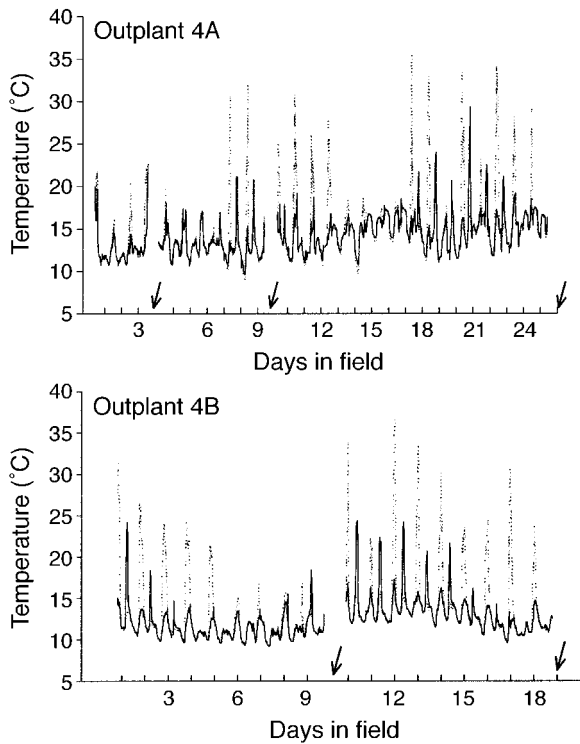
FIG. 6. Temperature as recorded during two outplants to an intertidal surge channel. Each graph shows temperatures measured every 5 min by a StowAway datalogger on the east-facing (dotted lines) and west-facing (solid lines) sides. Tick marks on the *x*-axis are situated at 1200 on each day; note that on the east-facing side, the highest temperatures occurred during morning low tides. Arrows indicate sampling dates.

examined over a similar range of egg sizes and organic content values (echinoderms, McEdward and Carson 1987, McEdward and Coulter 1987; fish, Niciu and McEdward 1994; r^2 between 0.02 and 0.39; ~60–230 μg organic content). Therefore, in *N. ostrina,* offspring size can be used as a nondestructive, indirect index to examine the effects of maternal investment on off-spring performance.

There was considerable variation in the slopes of the regression line of organic content on shell length among clutches (Table 1, Fig. 1). One source of this variation may be natural within-population variation in scaling of size and organic composition among clutches. This situation might arise if nurse eggs varied in quality within some clutches and large embryos in these clutches selectively consumed high-quality nurse eggs, making large offspring more organically dense than small offspring. While somewhat elaborate, this possibility cannot be ruled out because very little information is available on either variation in nurse egg quality or intracapsular feeding behavior in *Nucella* or other gastropods.

A second explanation for interclutch variation is that embryonic shell growth geometry may vary among clutches, thereby altering the scaling of size (=shell
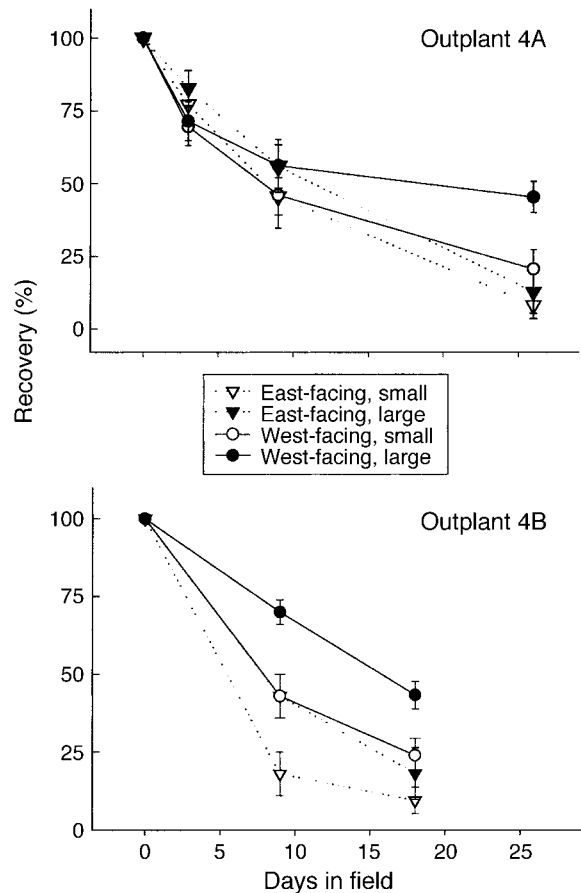

FIG. 7. Percentage recovery of large (closed symbols) and small (open symbols) *Nucella ostrina* hatchlings on two sides of an intertidal surge channel. Hatchlings from the east-facing side are represented by triangles and dotted lines; hatchlings from the west-facing side are represented by circles and solid lines. Error bars represent ± 1 SE.
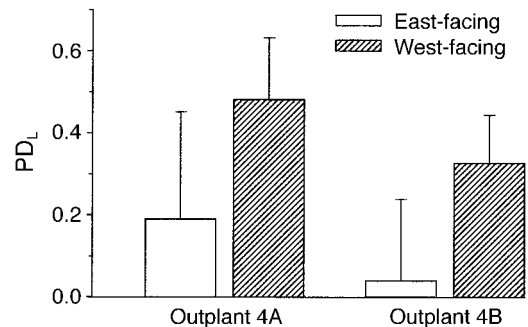

FIG. 8. Percentage deviation of recovery of large hatchlings from mean recovery on each panel (PD$_L$) for the east-facing and west-facing sides in the two surge channel experiments. Positive values in each outplant indicate that more large hatchlings than small were recovered in all cases, but the advantage of large size was greater on the west-facing side (ANOVA results in Table 3). Error bars represent + 1 SE.

TABLE 3. Results of model III ANOVA for side, outplant, and side × outplant effects using PD_L (relative advantage of large hatching size) as the dependent variable.

Source	df	ss	F	P
Side	1, 23	0.559	19,917.49	0.005
Outplant	1, 23	3.611	0.620	0.438
Side × Outplant	1, 23	<0.001	<0.001	0.992
Error	23	5.784		

length) and organic content without a change in organic density. There were qualitatively observed differences in coiling geometry among clutches (A. Moran, *personal observation*) that may have accounted for some of the unexplained variance in the relationship between organic content and length both within and among clutches. The dramatic shift in scaling between organic content and length after hatching and concurrent with the shift from embryonic to adult shell growth patterns (see Fig. 2) demonstrates that changes in shell coiling geometry can affect this relationship.

Under some circumstances, offspring performance may be affected by resource content rather than by the physical correlates of size. For example, in some marine taxa large offspring size is associated with greater survival under conditions of starvation (Emlet and Hoegh-Guldberg 1997, Ito 1997), suggesting the advantage of large size is in part due to greater nutrient reserves rather than to increased resistance to desiccation or predation. If resource content affects performance and the relationship between size and resource content varies among cohorts or populations, then the relationship between offspring size and performance will vary as well; this may affect the extent to which patterns seen in single cohorts or populations can be generalized to apply to entire species. It is unlikely that the experiments described in this study were greatly affected by varying relationships between size and resource content among experiments because (1) shell length was a very good predictor of organic content in all clutches and (2) size-dependent performance was in all cases compared within a clutch. However, the degree of intrapopulation variation among clutches in this study and others (e.g., McEdward and Coulter 1987, George 1994) suggests that if the population or clutch affinity of experimental offspring is not controlled, size may not be a reliable indicator of maternal investment, and any test of size-dependent performance should be interpreted with caution.

Survivorship and growth in the field

Large *Nucella ostrina* hatchlings grew more than small siblings in all experimental outplants. One possible explanation for this pattern is that large hatchlings competitively exclude small hatchlings from food resources; however, because food was abundant on seasoned panels and reports of interference competition (in which individuals actively exclude each other from

a resource [Begon et al. 1996]) are rare in gastropods, this scenario is unlikely. A second and more likely explanation is that large hatchlings feed more efficiently than small hatchlings. For example, Palmer (1990) found that while there was no relationship between the size of a hatchling and the size of prey it would attack, attacks by small hatchlings on large prey items were often unsuccessful. This suggests that small hatchlings assimilate prey less efficiently than large hatchlings (Palmer 1990).

Hatchlings may also share a common von Bertalanffy-type growth curve, with absolute growth dependent on initial position along the curve (=hatching size), as is the case for some oysters (Mason et al. 1998). If so, small *Nucella ostrina* hatchlings would be slowed from reaching reproductive maturity by approximately the amount of time required to grow to the initial hatching size of larger siblings (assuming no variation in size at first reproduction). Overall growth differences between large and small hatchlings suggest that under natural conditions, small hatchlings are set back one month or more relative to large hatchlings (Fig. 5). This is a considerable fraction of the total life span of *Nucella ostrina,* which lives one to two years in the field (Spight 1975). Because the juvenile period is probably more vulnerable to environmental stresses than the adult stage (Gosselin 1997, Vermeij 1987), small hatchlings may suffer higher mortality in part because they take considerably longer to reach the ''safe harbor'' of adult size.

In field experiments, hatchling growth was affected by the ''clutch'' factor in two out of five outplants (2B and 3) and there were also significant clutch by size interactions in outplants 1A and 3. Potential sources of variation in the clutch factor within experiments include effects of clutch, panel quality, and panel location. Panel quality and location are unlikely sources of variation because all panels were seasoned equivalently and there were no obvious differences in biota, orientation or exposure of panel sites. In addition, outplants 1A and 1B used the same panels and panel positions (but different clutches, and at different times) yet exhibited no consistent patterns of panel or position specific mortality or growth between the two experiments. Significant differences in overall growth and size-dependent growth among clutches, such as those seen in outplants 1A, 2B, and 3, might be due to a combination of maternal effects, genetic effects, and different environmental conditions experienced by embryos during encapsulated development.

Recovery rates were used as an estimator of survivorship. Mortality is the most likely source of hatchling nonrecovery; the Tanglefoot barriers were a very effective deterrent to hatchling emigration, as demonstrated by field tests using ''corral'' panels (described in Moran 1997). *Nucella* juveniles do not exhibit the ''ballooning'' behavior that some gastropods employ as a strategy for leaving undesirable microhabitat (Mar-

tel and Chia 1991, Gosselin and Chia 1995*b*), though hatchlings might have been washed off panels by wave action and successfully reattached elsewhere. However, *Nucella* inhabit a relatively narrow band of the intertidal and are unlikely to survive if deprived of appropriate microhabitat (Gosselin and Chia 1995*b*).

A small number of snails were not dislodged by the freshwater spray in the washing process; on two occasions single hatchlings were recovered on a later sampling date that were evidently missed in earlier sampling. Therefore, true survivorship may have been slightly higher than recovery rates seen in field experiments. However, pilot studies determined that the washing process resulted in very high total recovery, and that the recovery process was not biased towards large hatchlings. Mortality is the most likely explanation for failure to recover a hatchling, and there is no evidence to suggest that either crawling, dislodgment and subsequent reattachment elsewhere, or limitations of the panel-washing process acted on recovery in a size-dependent manner.

The field outplants performed in this study strongly suggest that hatching size influences survival of *N. ostrina* hatchlings, a finding consistent with the relationship between offspring size and survivorship found in many other taxa (Stearns 1992) and with the predictions of many models and experiments. However, the magnitude of the advantage of large hatching size in *Nucella* varied in both time and space; the effect of hatching size on recovery was not statistically significant in two short (9 d) outplants (1A and 1B) and one long-term outplant (2B), while a significant effect of hatching size was seen in two out of three longer-term outplants performed at the same site (2A and 3) and on the west-facing side in both two-site outplants (4A and 4B). These data suggest that environmental factors favoring large hatching size, such as desiccation stress or predation, differed in severity between outplants. This in turn suggests that selection for hatching size may vary over small spatial and temporal scales in the natural habitat of *N. ostrina,* likely due at least in part to the variable nature of the intertidal environment.

Survivorship as an index of habitat severity

Small-scale spatial variation (centimeters to meters) in microhabitat quality is well documented in rocky intertidal environments (Underwood and Chapman 1996, Helmuth 1998). Although the two sides of the surge channel in this study were only 2 m apart, the west-facing side was a quantitatively better habitat (based on survivorship) than the east-facing side and probably represented relatively good hatchling *Nucella* habitat. The mean number of snails lost on the west-facing side was 2.6%/d (outplant 4A) and 3.7%/d (outplant 4B), well within the 1.7–30% range of *N. ostrina* hatchling mortality found by Gosselin and Chia (1995*b*) over a single low tide. Rates of mortality on the east-facing side, though higher (3.2%/d and 4.8%/d

for outplants 4A and 4B respectively), were still easily within this range; therefore, even the east-facing side was probably not unnaturally severe.

While the mechanisms of hatchling mortality in this study were not explicitly tested, it is very likely that mortality was greater on the east-facing side because of increased desiccation stress. The east- and west-facing sides were similar in many ways, sharing comparable wave exposure, tidal height, angle of orientation, and the same population of potential predators. However, the east-facing, high-mortality side consistently reached much higher temperatures during low tide, which would increase desiccation stress to which hatchlings are extremely vulnerable (Gosselin 1994, 1997).

Other evidence also supports desiccation as an important source of hatchling mortality in these experiments. When temperature differences between the two sides were small, for example in the first 3-d interval of the first two-site outplant (Figs. 6 and 7), recoveries of hatchlings were similar. Likewise, though temperatures were not measured during outplants 2A, 2B, and 3, overall recovery was lowest in outplant 2B, which was carried out in summer when desiccation stresses might be expected to peak. Desiccation stress is thought to be one of the most important causes of *Nucella* hatchling mortality (Spight 1976*b*, Etter 1989, Gosselin 1994), and probably contributed substantially to higher mortality on the East-facing side. Desiccation, and not temperature stress alone, was likely the main source of mortality: Gosselin (1994) found that *N. ostrina* hatchlings immersed in seawater can easily survive short periods (≤8 h) of temperatures as warm as 30°C.

Because the east-facing side received considerably more sun exposure than the west-facing side, solar ultraviolet radiation (UV) may have been another factor influencing differential mortality between the two sides of the surge channel. While its effects on juvenile stages have not been well established, UV exposure has detrimental effects on many marine organisms (e.g., Damkaer and Dey 1983, Herndl et al. 1993) including encapsulated *N. ostrina* embryos (Rawlings 1996). It has yet to be determined whether UV radiation from solar exposure has detrimental effects on *Nucella* hatchlings, or how effectively UV radiation penetrates into hatchling microhabitat.

Size-dependent survivorship in habitats that vary in severity

Habitats have been categorized based on the relationship between offspring size and fitness as either offspring-size sensitive (OSS) or offspring-size insensitive (OSI; Begon 1985, Begon et al. 1996). In OSS habitats, size affects individual offspring fitness because either (1) the habitat contains sources of mortality to which small offspring are particularly vulnerable, or (2) competitive interactions among offspring favor large size. In OSI habitats, in contrast, fitness of

individual offspring is not related to size because (1) resources are superabundant and all offspring do well, (2) some environmental factors favor small offspring size, or (3) mortality is random with respect to offspring size (Begon 1985, Begon et al. 1996). The return on different maternal investment strategies will vary depending on the type of habitat (OSS or OSI), which may affect many aspects of life-history evolution.

Many models of life-history evolution assume that "harsh" environments will fit the OSS habitat type, in that fitness of parents producing large offspring will be higher under conditions of physiological or competitive stress (e.g., Kaplan and Cooper 1984) or larger offspring will do better in all environments, but this difference will be more pronounced in severe environments (e.g., McGinley et al. 1987; Fig. 3C). Benign conditions at the time of an experiment have been invoked to explain the absence of a survival advantage of large offspring (Smith et al. 1995, Fox and Mousseau 1996), and several studies testing the effects of size under different resource regimes have borne out the prediction that large offspring exhibit a performance advantage under adverse conditions. For example, in the seed beetle *Stator limbatus,* offspring from large eggs perform better on a poor-quality host plant but the effect of egg size is greatly reduced on a high-quality host (Fox and Mousseau 1996, Fox 1997). This hypothesis is also supported by other studies comparing the effect of offspring size under different regimes of resource availability (e.g., Ferguson and Fox 1984, Tessier and Consolatti 1989, Hutchings 1991). Because offspring size affects many other aspects of life history biology (Stearns 1992), such predictions have important implications for understanding how life histories evolve in different environments.

Similar predictions have been made about the relationship between offspring size and habitat type in intertidal gastropods. Spight (1976*b*) predicted that selection should favor large hatching size of *Nucella* under more severe environmental conditions, because large hatchlings exhibit superior feeding abilities and lower susceptibility to environmental stresses (predation, starvation, desiccation). Etter (1989) found that hatching size in *N. lapillus* was greater on wave-protected shores than on wave-exposed shores, and argued that this pattern was consistent with Spight's (1976*b*) hypothesis because hatchlings on wave-sheltered shores suffer greater levels of predation (Menge 1978, 1983) and greater physiological stresses (Etter 1988, 1989). If large hatching size provides protection from a wide range of mortality factors, why was the advantage of large hatching size greater in the "benign" habitat than in the "harsh" habitat in the experiments described in this study?

One explanation may lie in the fact that thermal stress, which was likely a major source of hatchling mortality in these experiments, was spatially variable within and between panels on the east-facing side. Temperatures at different points on east-facing panels varied by as much as 5°C within panels during direct sun exposure, and the higher temperatures would, during emersion, cause sufficient desiccation stress to be lethal to all hatchlings regardless of size (see Gosselin 1997). Therefore, the ability of a given hatchling to survive when panels were in direct sunlight may have depended not on hatchling size, but on hatchling location within the panel.

Although mortality was lower overall on the west-facing side, conditions were not so benign that all hatchlings performed well regardless of size (as in the first OSI environment type described by Begon [1986] and Begon et al. [1995]); in fact, the advantage of large size increased. On the west-facing side hatchlings were constantly cooler and shaded; and, based on within-panel measurements with a thermocouple probe, west-facing hatchlings experienced a more constant thermal environment. However, hatchlings were still exposed to other sources of mortality including predation, disease, and wave action, and large hatching size may confer more protection against these forces than against severe desiccation. Direct field manipulations of the many factors implicated in hatchling mortality would shed light on which of these stresses cause large size to be advantageous.

This study demonstrates that the relationship between habitat quality and the advantage of large offspring size is not always inverse, particularly for motile organisms that inhabit a complex environment. Temporal and spatial variation over both small and large scales is high in intertidal environments (Underwood and Chapman 1996), and it is possible that in nature, *Nucella* hatchlings rarely experience long-term conditions of the benign OSI type in which offspring of all sizes perform equally well. In the seven field outplants in this study, more large hatchlings than small hatchlings were recovered in each case (although the effect was not always statistically significant); this supports the idea that benign-type OSI conditions may be rare.

If an organism's environment varies only in stresses that act in a size-dependent manner, habitats will be OSI when these stresses are absent and all offspring sizes perform well; this is the OSI habitat type that has received the most attention (e.g., Williams 1994, Ferguson and Fox 1996). However, some habitats are OSI because mortality, though high, is random with respect to offspring size (Begon 1986). In *Nucella ostrina* hatching size had the smallest effect on recovery when overall recovery was lowest (e.g., outplant 2B and east-facing side of outplants 4A and 4B), suggesting high-mortality habitats may come close to fitting this second OSI type. The intertidal environment is spatially and temporally variable in a number of factors that may interact in both size-dependent and size-independent manners, and so the relationship between offspring size and performance (and hence selection on offspring

size) is likely to be highly complex; and, contrary to predictions, poor environmental conditions may not necessarily select for large offspring size.

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