

Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*

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ABSTRACT: Dispersal polymorphisms are known from many terrestrial organisms that inhabit fluctuating environments, but they are not well-recognized among marine invertebrates. An unusual form of variation was found in the settlement behavior of lecithotrophic larvae of the mollusc *Alderia modesta* (Lovén, 1844) that markedly altered the dispersal potential of sibling larvae. Most clutches contained, in variable proportions, larvae that spontaneously metamorphosed in the egg mass or within 2 d of hatching, and larvae that delayed metamorphosis until encountering the obligate adult food, the yellow-green alga *Vaucheria longicaulis*. The proportion of larvae undergoing spontaneous metamorphosis within a clutch was highly variable, ranging from 0 to 90%, and was unrelated to adult size. The proportion of intracapsular metamorphosis was also variable, ranging from 0 to 32%. The percentage of spontaneous metamorphosis per clutch was phenotypically plastic: when adults were starved, there was a significant tendency for each successive clutch to have a lower percentage of spontaneous metamorphosis, thus increasing the dispersal potential of the offspring. The decrease in spontaneous metamorphosis was significant after only 24 h of starvation. There was no significant increase in the cumulative level of spontaneous metamorphosis after the 2nd day post-hatching, but larval mortality increased as a linear function after the 5th day. Most larvae that did not spontaneously settle in the first 2 d delayed metamorphosis until they were exposed to the adult host alga, *V. longicaulis*. When 2 d old larvae were exposed to 17 species of macroalgae and sediment from the adult habitat, only *V. longicaulis* induced significant metamorphosis ($93.3 \pm 6.7\%$); all other species of algae and field sediment induced no metamorphosis or low levels (0–9%) that were not significantly higher than sea water controls. There was no difference in the settlement specificity of 2 and 9 d old larvae when tested against 2 different algae, nor in their ability to complete metamorphosis. The high initial percentage of spontaneous metamorphosis reduces the dispersal potential of some larvae in each clutch relative to their siblings that delay metamorphosis until stimulated by *V. longicaulis*; this settlement dimorphism represents a novel bet-hedging strategy among marine invertebrates.

KEY WORDS: Bet-hedging · Dispersal · Phenotypic plasticity · Larval settlement · Metamorphosis · Opisthobranch · *Alderia modesta* · *Vaucheria longicaulis*

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INTRODUCTION

Environments prone to spatial and temporal variation exert strong selective pressure on organisms to maintain variability in life-history traits associated with

reproduction and dispersal (Levins 1968, Giesel 1976, Stearns 1977, Johnson & Gaines 1990, McPeck & Holt 1992, Kawecki & Stearns 1993). Pronounced variation in the dispersal potential of offspring is well-documented for terrestrial animals and plants from variable habitats (Bradshaw 1965, Gaines & McClenaghan 1980, Harrison 1980, McPeck & Holt 1992,

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Dingle 1996). Although many marine invertebrates inhabit environments that fluctuate over space and time, few species are known to exhibit adaptive variation in modes of larval development, dispersal, and settlement (Raimondi & Keough 1990, Chia et al. 1996, Hadfield & Strathmann 1996).

A common feature of marine invertebrate life histories is a larval stage which completes development either encased on the bottom (benthic development) or swimming freely in the plankton (Strathmann 1985, 1990, Levin & Bridges 1995). Planktonic development achieves the dispersal of offspring, resulting in gene flow and the colonization of new habitats (Scheltema 1971, Todd 1998, Pechenik 1999). However, dispersal incurs biotic risks, such as larval mortality due to predation (Gaines & Roughgarden 1987, Rumrill 1990) and scarcity of planktonic food (Olson & Olson 1989), and abiotic risks, such as physical transport away from appropriate settlement sites by ocean currents (Roughgarden et al. 1988, Gaines & Bertness 1993). These risk factors may result in great inter-generational variance in recruitment success (Gaines et al. 1985, Raimondi 1990, Gaines & Bertness 1993). Benthic development avoids the hazards of a planktonic phase but carries the risk of population extinction due to local disasters or exhaustion of adult food supplies and predation on the bottom (Strathmann 1985, Jablonski 1986, Todd 1998, Pechenik 1999). The costs, benefits, and consequences of different dispersal strategies are fundamental factors that structure marine life histories (Grahame & Branch 1985, Strathmann 1990, Todd 1998, Pechenik 1999).

Larval dispersal and recruitment are crucial factors affecting population dynamics, biogeography, gene flow, and macroevolution of marine invertebrates (Scheltema 1971, Hansen 1978, Vermeij 1982, Jablonski 1986, Roughgarden et al. 1988, Underwood & Fairweather 1989). Fluctuating marine environments might therefore select for increased flexibility in life-history traits associated with these processes. Examples of variable reproductive and dispersal strategies are found in species exhibiting poecilogony, the presence of multiple larval development modes within a single species (Giard 1905). Poecilogony is a rare phenomenon, occurring mainly among polychaetes and opisthobranchs (Levin 1984a, Hoagland & Robertson 1988, Bouchet 1989, Gibson & Chia 1989, Chia et al. 1996, Gibson 1997, Krug 1998). Most of these species inhabit estuaries, suggesting that the estuarine environment may be prone to greater fluctuation than other marine habitats, selecting for variable reproductive patterns (Chia et al. 1996).

Two mechanisms by which individual genotypes maximize fitness in fluctuating environments are bet-

hedging and phenotypic plasticity. The term 'bet-hedging' describes a strategy which increases the geometric mean fitness of a genotype, the measure of its relative growth rate, by decreasing fitness variance between generations (Segger & Brockmann 1987, Philippi & Segger 1989). A bet-hedging genotype trades off a reduction in mean fitness during good seasons for an advantage in bad seasons (Philippi & Segger 1989). An individual can also regulate its phenotypic expression in response to environmental cues which may indicate impending changes in habitat quality (Giesel 1976, Caswell 1983). This is termed phenotypic plasticity, the condition-sensitive expression of alternative phenotypes (Stearns 1989, West-Eberhard 1989, Gotthard & Nylin 1995). A phenotype may show continuous variation in response to an environmental factor, a function termed a 'reaction norm' (Stearns 1989). Phenotypic plasticity is itself a genetically variable trait, and can evolve in response to natural selection (Shapiro 1976, Schlichting 1989).

The opisthobranch mollusc *Alderia modesta* (Lovén, 1844) is found in temperate estuaries in both the Atlantic and Pacific, always in association with its obligate food source, yellow-green algae of the genus *Vaucheria* (Xanthophyta: Xanthophyceae) (Engel et al. 1940, den Hartog & Swennen 1952, den Hartog 1959, Bleakney & Bailey 1967, Trowbridge 1993). In most places, *A. modesta* produces planktotrophic larvae which must feed for several weeks before becoming competent to metamorphose (Seelemann 1967, Gibson & Chia 1989). However, in southern California *A. modesta* exhibits a rare reproductive polymorphism: individuals produce either planktotrophic (feeding) or lecithotrophic (nonfeeding) veliger larvae (Krug 1998). Further study of the lecithotrophic larvae from this population has revealed pronounced variation in the settlement requirements of sibling larvae, which functions as part of a complex bet-hedging dispersal strategy. Two sub-types of larvae occurred in almost every lecithotrophic clutch: larvae that spontaneously metamorphosed in clean culture dishes within 2 d of hatching, and larvae that delayed metamorphosis until encountering a chemical cue from the adult host alga *V. longicaulis*. Adults were surveyed to determine how variable this trait was in the population, and starvation experiments were conducted to test whether individual specimens exhibited phenotypic plasticity of this trait. Larvae that did not metamorphose spontaneously were exposed to a variety of potential habitat cues to determine the specificity of the settlement response to *V. longicaulis*. The results support the conclusion that, in addition to variable larval development modes, variation in sibling settlement-cue requirements further contributes to the bet-hedging, life-history strategy of *A. modesta*.

MATERIALS AND METHODS

Study site. The present study was conducted in Mission Bay, a shallow estuary located in San Diego, California, USA, 21 km north of the border between the USA and Mexico. The remaining natural wetlands are confined to the Kendall-Frost Marine Reserve and Northern Wildlife Preserve in the northeastern corner of the back bay. For a full description and photographs of the study site, see Levin (1982, 1984b). The mudflat extends out into the bay, and is bisected by a main channel into eastern and western halves. The mudflat is divided into a network of flat-topped surfaces by many small channels (approximately 0.5 m deep, 1 m wide). The surface of the mud is exposed to the air for at least 5 h during daily low tides. The exposed surfaces are colonized year-round by mats of the yellow-green alga *Vaucheria longicaulis* (Abbott & Hollenberg 1976). The alga *V. longicaulis* has a moss-like appearance, forming thick mats which can grow as discrete patches or continuous sheets covering the mud.

Collection and maintenance of experimental organisms. Adult *Alderia modesta* and patches of *Vaucheria longicaulis* were collected from the Kendall-Frost mudflat. Specimens were individually isolated overnight in covered plastic culture dishes. Egg masses were collected the following morning, typed according to development mode (Krug 1998), and maintained in 4 ml of 0.45 μm -filtered sea water (FSW), which was changed every other day until hatching. Patches of *V. longicaulis* were grown under continuous lighting in the laboratory. Blades of algae were pulled free of the sediment base and rinsed in FSW before use in assays.

Spontaneous versus *Vaucheria longicaulis*-induced metamorphosis. In March 1996, 30 lecithotrophic egg masses were individually isolated and allowed to develop in FSW. After 4 d of development, each egg mass was inspected twice daily under a dissecting microscope for signs of imminent hatching, characterized by larval escape from individual egg capsules and rapid ciliary beating to break down the egg case matrix. Once hatching had commenced, a piece of live *Vaucheria longicaulis* was introduced to the culture dish, and veligers were scored daily for metamorphosis in response to the algae for 3 d after hatching.

An additional 30 lecithotrophic egg masses were isolated and allowed to develop as above, but hatched in dishes containing FSW only. Larvae from each clutch were scored daily for spontaneous metamorphosis (metamorphosis occurring in FSW in clean culture dishes) for 3 d after hatching. The number of veligers, if any, which had metamorphosed intracapsularly was recorded for each egg mass when hatching began. After 3 d, the remaining unmetamorphosed veligers from each clutch were transferred to a dish containing

a piece of live *Vaucheria longicaulis* and were scored for metamorphosis in response to the algae daily for a further 3 d (total duration of trial = 6 d). Ten egg masses hatched and were maintained in FSW for 6 d as a control for delayed spontaneous metamorphosis.

The cumulative daily percentage of metamorphosis was determined for each egg mass hatched in the presence or absence of *Vaucheria longicaulis*. Mean daily metamorphosis as a cumulative percentage was arcsine-transformed to normalize data for both experimental groups, and metamorphosis in the presence and absence of *V. longicaulis* over the first 3 d was compared using a 2-tailed unpaired *t*-test. The cumulative percentages of metamorphosis after 3 d (hatched with *V. longicaulis*) and after 6 d (hatched in FSW and subsequently exposed to *V. longicaulis*) were also calculated, transformed, and compared with a 2-tailed unpaired *t*-test. Values are given as means \pm 1 SD.

Inter-annual variation in percentage of spontaneous metamorphosis per clutch. The mean percentage of spontaneous metamorphosis per clutch was determined for the Kendall-Frost population during February of each year from 1996 to 2000, and also in August 1999. Adults were collected and lecithotrophic egg masses deposited overnight were harvested and isolated as described above. The percentage of spontaneous metamorphosis was scored for each clutch 2 d after hatching. Individual percentages were arcsine-transformed to normalize the data, and means for each year were compared with a 1-way ANOVA with a post-hoc Scheffé test for unplanned comparisons of means (Day & Quinn 1989). Values are stated as means \pm 1 SD.

Reproductive traits and spontaneous metamorphosis. Adults ($n = 29$) randomly collected from the field in July 1997 were blotted dry, weighed to the nearest 0.01 mg, and individually maintained in isolation for 7 d without food. The first 4 egg masses deposited by each adult during the starvation period were transferred to a culture dish containing 4 ml FSW and scored for egg number per clutch. The percentage of spontaneous metamorphosis was determined for each clutch by scoring the number of larvae which had completed metamorphosis 2 d after hatching in FSW. The relationship between adult body weight and (1) egg number per clutch and (2) the percentage of spontaneous metamorphosis (arcsine-transformed before analysis) per clutch was estimated for the first 2 egg masses deposited by isolated adults using a Model 1 Regression (Sokal & Rohlf 1981, La Barbera 1989).

The effect of adult starvation on egg number per clutch and the percentage of spontaneous metamorphosis per clutch were estimated for the first 4 egg masses deposited during the 1 wk period during which adults were held without food. Percentages were arc-

sine-transformed and relationships between traits were estimated with a Model 1 regression. The regression suggested that the decrease in the percentage of spontaneous metamorphosis between the first and second clutches of starved adults might be significant given a larger sample size. Spontaneous metamorphosis was thus measured in the first 2 clutches deposited by each of an additional 18 individuals held without food for 2 d after collection. No between-group variation was found between percentages from these 18 adults and the original 29 adults (2-tailed unpaired *t*-test on arcsine-transformed percentages of spontaneous metamorphosis: $p = 0.36$ for the first clutch, $p = 0.75$ for the second clutch). Data were therefore pooled for both groups of starved adults ($n = 47$ total); the combined data set was arcsine-transformed, and the percentages of spontaneous metamorphosis in the first and second egg masses were compared with a 1-tailed paired *t*-test.

Larval bioassay and specificity of *Vaucheria longicaulis*-dependent response. Adults were collected from the field and lecithotrophic egg masses deposited overnight were pooled and maintained in FSW until hatching. Larvae (~1000) were maintained in 100 ml FSW for 2 d, during which time most of the spontaneous metamorphosis occurred. Larvae were subsampled from the pool of remaining veligers for use in metamorphosis bioassays. For each experimental treatment, 15 larvae were added to each of 3 replicate dishes containing 4 ml FSW. After 2 d larvae were scored for metamorphosis. Each experiment included a FSW-only treatment as a negative control for residual spontaneous metamorphosis. The percentage of metamorphosis for each replicate was arcsine-transformed and treatments were compared with a 1-way ANOVA with a post-hoc Scheffé comparison. Values are given as means ± 1 SD.

Larval metamorphosis was initially measured in response to *Vaucheria longicaulis* and 4 other macroalgal species in a preliminary experiment in June 1996. *Enteromorpha clathrata* and *Ulva expansa* are the only 2 macroalgae found co-occurring with *V. longicaulis* at the San Diego study site. The macroalgae *Chaetomorpha linum* and *Codium fragile* are siphonaceous green algae eaten by other local ascoglossan species (*Aplysiopsis enteromorphae* for *Chaetomorpha linum*, *Elysia hedgpethi* and *Placida dendritica* for *Codium fragile*); these 2 algal species have not been observed to co-occur with *V. longicaulis* at the study site over a 5 yr period.

An expanded experiment was conducted in January 2000. Larvae were exposed to 17 different species of macroalgae collected from the Kendall-Frost study site (*Vaucheria longicaulis*) or from the rocky intertidal zone at Bird Rock (all other species) in La Jolla, Cali-

fornia, USA. Surface sediment was collected from around mats of *V. longicaulis* and was assayed as a control for the general microbial film from the adult habitat. Branchlets of algae were cleaned of epiphytes and fully immersed in assay dishes. Identifications were based on Abbott & Hollenberg (1976). Algae used were: *V. longicaulis* (Xanthophyta); *Chaetomorpha linum*, *Codium fragile*, *Enteromorpha clathrata*, and *Ulva expansa* (Chlorophyta); *Cytoseira osmundacea*, *Egregia menziesii*, *Laminaria* sp., *Macrocystis pyrifera*, *Colpomenia sinuosa* (Phaeophyta); *Gigartina canaliculata*, *Gymnogongrus platyphyllus*, *Lithothamnium californicum*, *Microcladia coulteri*, *Plocamium cartilaginum*, *Pterocladia capillacea*, *Rhodymenia californica* (Rhodophyta). Filtered sea water served as a negative control.

Larval mortality and spontaneous metamorphosis over a 2 wk interval. To determine how long lecithotrophic larvae of *Alderia modesta* would delay metamorphosis in the absence of the *Vaucheria longicaulis*-associated cue, larvae were maintained in FSW for 14 d after hatching. Lecithotrophic egg masses ($n = 14$) were collected from freshly collected adults held in glass dishes in the laboratory in January 2000; each egg mass was kept in FSW in a separate, sterile plastic culture dish until hatching. Larvae from each clutch were scored daily for spontaneous metamorphosis and mortality for 14 d post-hatching. Every other day, surviving larvae were transferred to clean FSW in a sterile culture dish. Larvae that appeared to undergo spontaneous metamorphosis were transferred as juveniles to separate dishes containing a piece of *V. longicaulis*. Juveniles were monitored for 2 d to determine whether they commenced feeding on the algae (observed for all juveniles metamorphosing in the first 3 d) or were unable to begin feeding (indicating that an aberrant or incomplete metamorphosis had occurred). Data are plotted as daily cumulative mean percentages of spontaneous metamorphosis, mortality, and swimming larvae. Daily percentages of mortality from the 6th to the 14th day of the experiment were arcsine-transformed, and the relationship between mortality and time was estimated with a linear regression.

Effect of larval age on specificity of metamorphic response. Two series of bioassays were set up in parallel, each using 3 replicate dishes of 15 larvae each. The first series of treatments used 2 d old larvae (i.e., 2 d post-hatching), and the second used 9 d old larvae. In both series, 1 set of replicate dishes contained a piece of live *Vaucheria longicaulis* as a positive control, a second set contained a piece of *Enteromorpha clathrata*, and a third set contained only FSW as a negative control. The larvae in each dish were scored for metamorphosis after 2 d. Percentages of metamorphosis were arcsine-transformed and analyzed by a 1-way ANOVA.

RESULTS

Spontaneous versus *Vaucheria longicaulis*-dependent metamorphosis in sibling larvae

When lecithotrophic egg masses ($n = 30$) of *Alderia modesta* hatched in the presence of *Vaucheria longicaulis*, $90 \pm 12\%$ SD of larvae completed metamorphosis by the 3rd day (Fig. 1: black bars). Most larvae were observed to settle and metamorphose directly on blades of the algae within the first 48 h after hatching. When egg masses ($n = 30$) hatched in filtered sea water (FSW) in clean, previously sterile culture dishes, an unexpectedly high percentage of larvae metamorphosed without the addition of any algae (Fig. 1: shaded bars). Over the first 3 d post-hatching, $34 \pm 26\%$ SD of the veligers in FSW completed metamorphosis, significantly less than in *V. longicaulis* treatments (2-tailed unpaired t -test: $t_{58} = -10.77$, $p < 0.0001$), but far higher than was expected in sea water alone. About a third of all lecithotrophic larvae thus completed what is termed 'spontaneous' metamorphosis, which denotes metamorphosis in the absence of any specific substrate or cue other than a hard surface. Larvae that were trapped by surface tension at the air/water interface completed spontaneous metamorphosis as well as larvae settled on the bottom of the dish, indicating that a hard surface was not necessary for metamorphosis. A low percentage of larvae ($6 \pm 9\%$ per clutch) metamorphosed spontaneously within the egg capsule prior to hatching (intracapsular metamorphosis), emerging as crawling juveniles (47 out of 972 larvae; $n = 30$ clutches). Almost half of all egg masses (14 out of 30) exhibited some benthic development as well as planktonic lecithotrophy, releasing both crawl-away slugs and swimming veliger larvae.

Two-thirds of the lecithotrophic larvae that hatched in FSW remained unmetamorphosed after 3 d (Fig. 1: shaded bar, Day 3). To test whether these larvae were dependent upon *Vaucheria longicaulis* to trigger metamorphosis, they were exposed to a piece of the algae for a further 3 d and were scored daily for metamorphosis (Fig. 1: shaded bars, Days 4 to 6). By Day 6, $75 \pm 16\%$ of the transferred larvae had completed metamorphosis in response to the algae. This was termed '*Vaucheria*-dependent' metamorphosis, since these larvae did not undergo spontaneous metamorphosis when hatched and maintained in the absence of the algae. The cumulative percentage of metamorphosis was $84 \pm 12\%$ by Day 6 of this treatment (Fig. 1: shaded bar). This percentage is the sum of the spontaneous metamorphosis that occurred over Days 1 to 3 plus the metamorphosis induced in the remaining larvae by exposure to *V. longicaulis* over Days 4 to 6. The final percentage in this treatment was not statistically dif-

ferent from the $90 \pm 12\%$ metamorphosis measured for larvae hatched and maintained in the presence of *V. longicaulis* for the first 3 d of the experiment (Fig. 1; black bars). Taken together, these 2 treatments demonstrated that although 90% of larvae were competent within 2 d of hatching, the majority of larvae delayed settlement in the absence of *V. longicaulis*.

A control group of egg masses hatched and was maintained in FSW for the entire duration of the experiment (Fig. 1: hatched bars). The cumulative percentage of spontaneous metamorphosis in these larvae did not increase significantly from Day 1 ($19 \pm 13\%$) to Day 6 ($21 \pm 17\%$). This confirmed that the metamorphosis induced in larvae hatched in FSW and then exposed to *Vaucheria longicaulis* during Days 4 to 6 (Fig. 1: shaded bars) truly represented a response to the algae and did not result from delayed spontaneous settlement. No spontaneous metamorphosis occurred after the 3rd day in the 6 d FSW treatment (Fig. 1: hatched bars, Days 3 to 6). Larvae which had not settled by the 6th day after hatching began to die off in significant numbers, at which point the experiment was terminated.

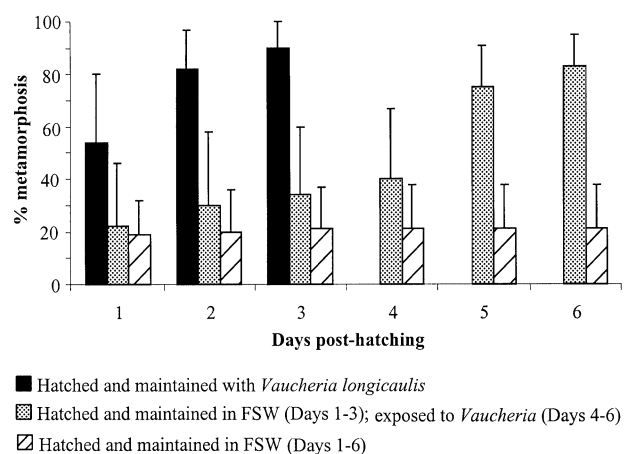


Fig. 1. *Alderia modesta*. Cumulative levels of metamorphosis over a 3 d or 6 d period post-hatching for lecithotrophic larvae. Data are daily cumulative mean (± 1 SD) percentages for each of 3 treatments. In the first treatment, larvae hatched from egg masses ($n = 30$) and were maintained for 3 d in the presence of the adult host algae, *Vaucheria longicaulis* (black bars). In the second treatment, larvae hatched from egg masses ($n = 30$) and were maintained in filtered sea water (FSW) for 3 d (shaded bars, Days 1 to 3); larvae that had not undergone spontaneous metamorphosis by Day 3 were subsequently exposed to *V. longicaulis* for a further 3 d (shaded bars, Days 4 to 6). The final cumulative mean percent metamorphosis for this group (shaded bar, Day 6) represents the sum of the spontaneous metamorphosis in FSW (Days 1 to 3) plus the metamorphosis induced by exposure to the algae (Days 4 to 6). In the third treatment, larvae hatched from egg masses ($n = 10$) in FSW, and were maintained in FSW for the 6 d duration of the experiment (hatched bars)

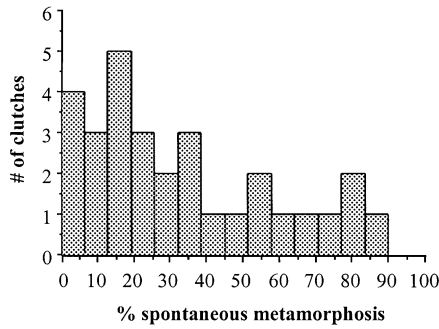


Fig. 2. *Alderia modesta*. Distribution of the percentage of spontaneous metamorphosis per lecithotrophic clutch in a field population. Histogram shows the range of the percentage of spontaneous metamorphosis over the first 2 d post-hatching for egg masses (n = 30) deposited in February 1996

Variation in spontaneous metamorphosis per lecithotrophic clutch

The proportion of spontaneous metamorphosis per clutch was highly variable among adults collected from the field population. Over the first 2 d post-hatching, the percentage of spontaneous metamorphosis varied from 0 to 90% (n = 30) among egg masses, as shown for 1996 (Fig. 2). Similarly, the percentage of intracapsular metamorphosis was also variable, ranging from 0 to 32%.

The mean percentage of spontaneous metamorphosis in the field population showed significant variation both within and between years (Fig. 3, and results of a 1-way ANOVA, $F_{4,143} = 9.29, p < 0.0001$). The mean percentage in February 1996 was not significantly different from the means in February 1997 and February 1998, but was significantly higher than the means for February 1999 and February 2000 (Scheffé test, $p < 0.05$). There was no significant difference in the mean number of eggs per clutch between February 1996 (32.4 ± 12.7) and February 1999 (30.2 ± 16.4) (unpaired *t*-test: $p = 0.56$). However, there was an order of magnitude difference in the mean percentage of spontaneous metamorphosis over that time period, ranging from 33.5% in February 1996 to 3.5% in February 1999. A similarly low percentage (6.5%) was found for a separate population (La Costa estuary) 25 km to the north of the Kendall-Frost field site in February 1999, indicating that the low percentage found in the Kendall-Frost population was not a strictly local phenomenon.

There was significant intra-annual variation in 1999; the mean percentage of spontaneous metamorphosis in February 1999 was significantly lower than the mean in August 1999

(Scheffé test, $p < 0.005$). Qualitative observations indicated that a period of sparse algal growth had preceded the sampling in February 1999, whereas field densities of *Vaucheria longicaulis* were high in August 1999, when the mean percentage of spontaneous metamorphosis rebounded to 33.7%. Algal densities had decreased by February 2000, due to overgrowth by mats of the filamentous green alga *Enteromorpha clathrata* (Krug pers. obs.). A significantly lower mean level of spontaneous metamorphosis, 8.8%, was measured in February 2000, compared with August 1999 (Scheffé test, $p < 0.05$). However, even though conditions were poor in February 2000 and most specimens of *Alderia modesta* (12 out of 14 adults) produced clutches with less than 15% spontaneous metamorphosis, a few individuals still had high levels of spontaneous metamorphosis among their offspring (31 and 45% spontaneous metamorphosis for 2 out of 14 adults).

Effects of adult body weight and starvation

The relationship between adult body weight and the number of eggs per clutch was estimated for the first 2 egg masses deposited by each of 29 adults, to determine whether larger adults produced more offspring per clutch (Fig. 4). Adult wet weight accounted for a significant but small percentage of the variance in egg number for the first deposited egg mass (Model 1 regression of effects of adult body weight, *x*, on clutch

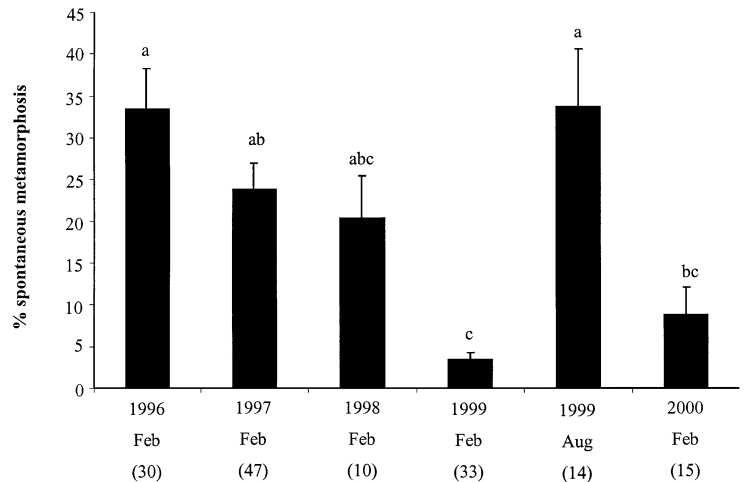


Fig. 3. *Alderia modesta*. Inter-annual variation in the mean percentage of spontaneous metamorphosis per clutch in the field population. Data are mean (+1 SD) percentages determined by sampling in February of a given year, as well as in August 1999. Percentages were arcsine-transformed and compared with a 1-way ANOVA; means marked with the same letter did not differ significantly ($\alpha = 0.05$, post-hoc Scheffé comparison). Month of sampling and number of clutches is given under each bar

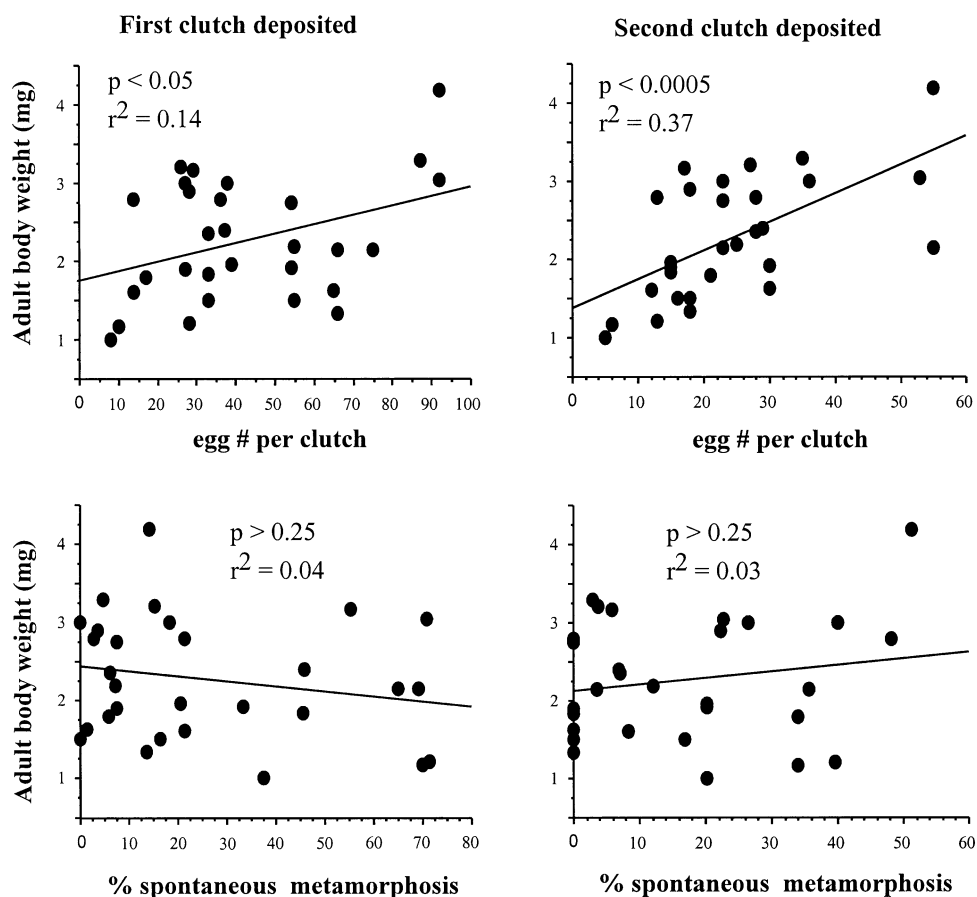


Fig. 4. *Alderia modesta*. Relationship between maternal body weight and egg number per clutch, and between body weight and the percentage of spontaneous metamorphosis per clutch, for lecitotrophic specimens. Data are given for the first 2 clutches deposited after collection of adults ($n = 29$) from the field. Lines are the results of a linear regression (of arcsine-transformed data for percentages)

size, $y = 0.01x + 1.74$; $p < 0.05$, $r^2 = 0.14$) and a higher percentage for the second egg mass (Model 1 regression: $y = 0.04x + 1.38$; $p < 0.0005$, $r^2 = 0.37$). No relationship was found between adult weight and the percentage of spontaneous metamorphosis in either the first or second egg mass (Fig. 4).

The effects of starvation on the number of eggs per clutch and the percentage of spontaneous metamorphosis per clutch were estimated for the first 4 egg masses produced by isolated adults ($n = 29$) during 7 d without food (Fig. 5). The number of eggs tended to decrease with each successive clutch (Fig. 5A, and results of a Model 1 regression where $x =$ clutch size, $y =$ order of clutch deposition: $y = -10.22x + 49.46$; $p < 0.0001$, $r^2 = 0.31$). Starvation also had a significant effect on the percentage of spontaneous metamorphosis per clutch; during the period of adult starvation, a lower percentage of larvae tended to spontaneously metamorphose from each successively deposited egg mass (Fig. 5B, and results of a Model 1 regression where $x =$ arcsine-transformed % spontaneous meta-

morphosis per egg mass, $y =$ order of clutch deposition: $y = -0.06x + 0.32$; $p < 0.005$, $r^2 = 0.09$). Mean percentages of spontaneous metamorphosis and sample sizes for the 4 clutches were as follows: 1st clutch, $27.5 \pm 27.3\%$ ($n = 29$ clutches); 2nd clutch, $16.6 \pm 16.1\%$ ($n = 29$); 3rd clutch, $14.1 \pm 19.7\%$ ($n = 25$); 4th clutch, $8.2 \pm 16.9\%$ ($n = 15$). The low r^2 value for the effect of starvation on percentage of spontaneous metamorphosis was probably due to the high initial variation in this trait in the population.

Sample size was increased to determine whether the proportion of spontaneous metamorphosis decreased significantly between the first and second egg masses deposited during an initial period of starvation. Adults ($n = 47$) were collected from the field and maintained without food, and the first and second egg masses deposited during the first 2 d of starvation were removed and hatched in FSW. The mean percentage of spontaneous metamorphosis in the second clutch was significantly lower than in the first clutch (1-tailed paired t -test: $t_{46} = 2.43$, $p < 0.01$).

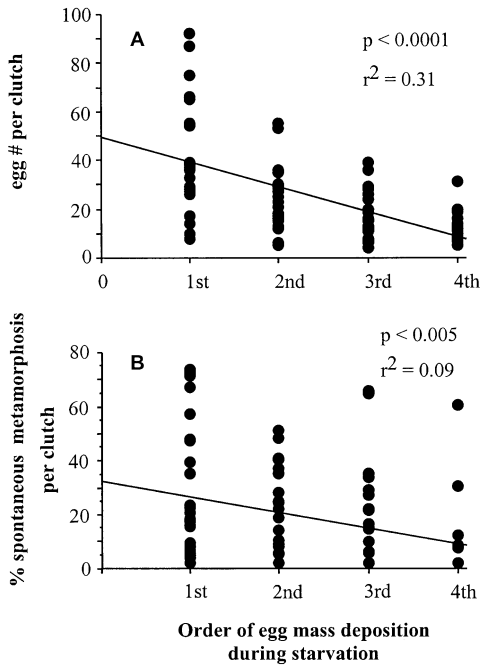


Fig. 5. *Alderia modesta*. Effect of adult starvation on clutch characteristics for lecithotrophic egg masses. Data are given for the first 4 egg masses deposited by adults ($n = 29$) during a week in which specimens were maintained without food; data are plotted with the results of a linear regression (of arcsine-transformed data for percentages). Results of a linear regression of order of clutch deposition during starvation (A) on egg number per clutch and (B) on the percentage of spontaneous metamorphosis per clutch

Specificity of *Vaucheria longicaulis*-induced metamorphic response

Lecithotrophic larvae which did not undergo spontaneous metamorphosis during the first 2 d after hatching were exposed to a variety of substrata to determine whether other macroalgae or sediment from the adult habitat would induce metamorphosis. There was highly significant variation in larval response to different substrata (Fig. 6, and results of a 1-way ANOVA: $F_{18,38} = 45.40$, $p < 0.0001$). Out of 17 species of macroalgae tested, *Vaucheria longicaulis* treatments elicited significantly higher levels of metamorphosis than all other substrata (Scheffé test, $p < 0.0001$), none of which differed significantly from FSW controls. In a preliminary experiment in 1996, *Codium fragile* induced an intermediate level of metamorphosis if larvae were exposed for a prolonged time period, but in subsequent assays, *C. fragile* did not induce significant metamorphosis. Larvae did not metamorphose in response to sediment collected from around *V. longicaulis* mats in the field, indicating that the general microbial film of the natural habitat was not a sufficient cue.

Effects of prolonged larval life: mortality versus metamorphosis

When larvae were maintained in FSW for 14 d post-hatching, there was no significant increase in the percentage of spontaneous metamorphosis from the 1st d ($9.2 \pm 13.1\%$) to the 14th d ($13.8 \pm 16.8\%$) of the experiment (Fig. 7, and results of a 1-tailed unpaired *t*-test: $p = 0.21$). Although some larvae appeared to undergo spontaneous metamorphosis during the second week of the experiment, fewer than 10% of those juveniles were able to begin feeding when transferred onto a piece of *Vaucheria longicaulis*. Upon closer examination, many of these non-feeding, putative juveniles were observed to have remnants of larval cilia still attached to the head, indicating that they had undergone a partial or incomplete metamorphosis. The mean percent mortality increased dramatically during the 2 wk time period, rising from $5.3 \pm 7.6\%$ on Day 6 to $71.8 \pm 22.4\%$ by Day 14. The increase in mortality over time was linear and highly significant after the 5th day (Fig. 7, and results of a regression where $x = \text{arcsine-transformed } \% \text{ mortality per clutch}$, $y = \text{days of the}$

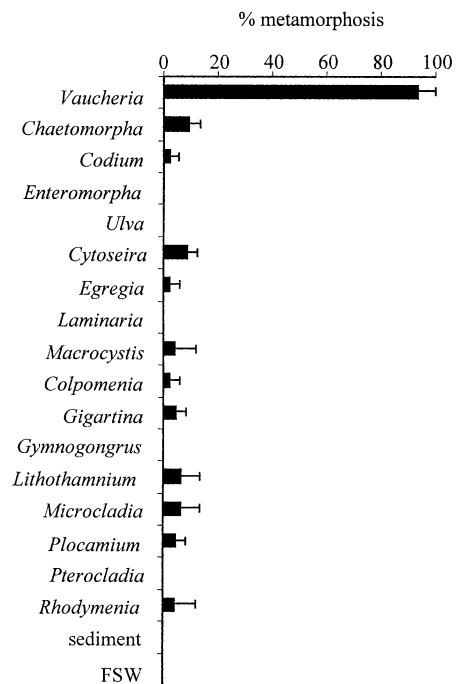


Fig. 6. *Alderia modesta*. Specificity of the metamorphic response of 2 d old lecithotrophic larvae. Larvae which did not undergo spontaneous metamorphosis in the first 2 d after hatching were exposed to assorted macroalgae and sediment. Data are mean (+1 SD) percentages of metamorphosis in response to a 2 d exposure to the assayed substrata ($n = 3$ replicates). Fifteen larvae were used in each replicate; percentages were arcsine-transformed and compared with a 1-way ANOVA

experiment: $y = 0.93x - 0.52$; $p < 0.0001$, $r^2 = 0.99$). The majority of larvae (85%) had either spontaneously metamorphosed or died by the 14th day post-hatching.

Effect of larval age on metamorphic response

A larval bioassay was used to probe the effect of larval age on metamorphic success. Nine day old larvae represented larvae near the end of their potential life-span under laboratory conditions, yet still able to complete metamorphosis. Larvae were assayed either 2 d or 9 d after hatching, and were exposed to *Vaucheria longicaulis*, *Enteromorpha clathrata*, or FSW only. There was significant variation in the percentage of metamorphosis induced by different treatments (Fig. 8, and results of a 1-way ANOVA: $F_{5,12} = 43.83$; $p < 0.0001$). *A posteriori* comparisons revealed no difference between the response of 2 d larvae ($89 \pm 10\%$) and 9 d larvae ($87 \pm 1\%$) to *V. longicaulis*. For larvae of both age groups, *V. longicaulis* elicited significantly higher metamorphosis than *E. clathrata* and FSW controls (Scheffé test, $p < 0.001$), indicating that larval ability to discriminate among potential substrata did not diminish with age. There was no difference between 2 d and 9 d larval response to either *E. clathrata* or FSW.

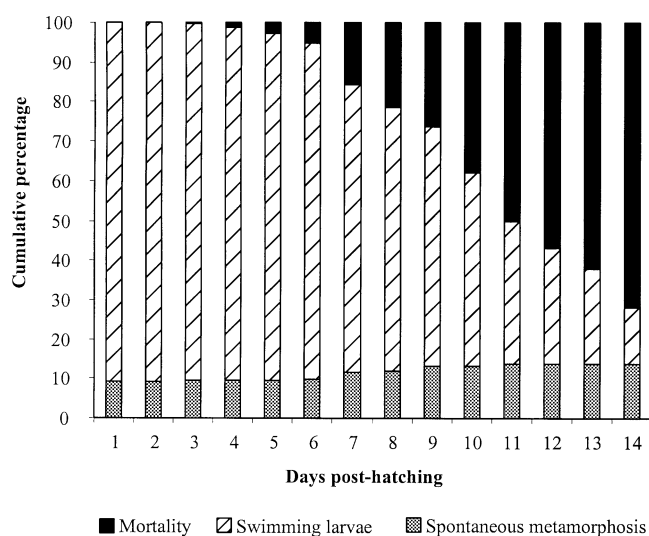


Fig. 7. *Alderia modesta*. Cumulative levels of larval mortality and spontaneous metamorphosis during 14 d after hatching. After lecithotrophic egg masses ($n = 14$) hatched, larvae were maintained in filtered sea water (FSW) and scored daily for spontaneous metamorphosis and mortality. Data are plotted as daily mean percentages of larvae that completed spontaneous metamorphosis (shaded bar), larvae that remained as swimming veligers (hatched bar), and larvae that died (solid bar). Mean percentages of metamorphosis and mortality are cumulative over the 14 d period

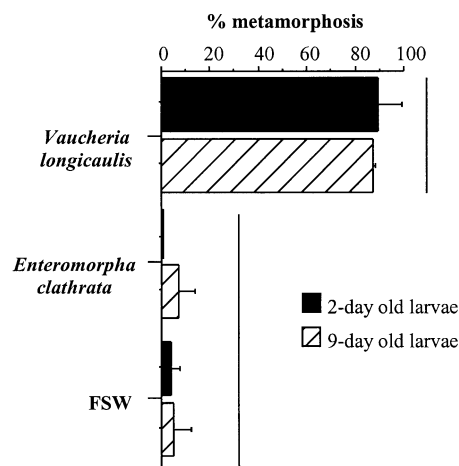


Fig. 8. *Alderia modesta*. Effect of larval age on specificity of the metamorphic response. Data are mean (± 1 SD) percentages of metamorphosis in response to the assayed substrata for 2 d and 9 d old larvae ($n = 3$ replicates). Percentages were arcsine-transformed and compared with a 1-way ANOVA; groups joined by vertical bars did not differ significantly ($\alpha = 0.05$, post-hoc Scheffé comparison)

DISCUSSION

Variation in dispersal potential among sibling larvae

Alderia modesta was previously found to exhibit extreme developmental variability in southern California, producing both planktotrophic and lecithotrophic larvae (Krug 1998). A second level of life-history variability has now been identified in specimens of *A. modesta* that produce lecithotrophic larvae. Some larvae from each clutch hatched as swimming veligers that settled spontaneously, mostly within 2 d of hatching, while sibling larvae delayed metamorphosis until encountering *Vaucheria longicaulis*. Intracapsular metamorphosis resulted in direct benthic development for a small percentage of larvae, resulting from pre-hatching spontaneous metamorphosis. Three aspects of the settlement dimorphism in lecithotrophic specimens of *A. modesta* are unusual and appear to be unprecedented in the marine literature: (1) the high mean percentage of spontaneous metamorphosis in a species which otherwise has a specific settlement cue requirement; (2) the occurrence of almost all the spontaneous metamorphosis in the first 2 d after hatching; and (3) the extreme variability in the percentage of spontaneous metamorphosis between clutches.

The larval settlement requirements of a given species generally fall into 1 of 3 categories. Larvae of some species settle on nothing more than a hard surface, which even in filtered sea water probably always supports a microbial film; this is often termed 'sponta-

neous metamorphosis', as no added substrate is necessary to induce metamorphosis (Franz 1971, Bickell & Kempf 1983, Woollacott et al. 1989, Pechenik 1990, Maldonado & Young 1999). Other species produce larvae that metamorphose in response to general features of the adult habitat, which may be coated with a microbial film particular to that environment (Harrigan & Alkon 1978, Brancato & Woollacott 1982, Leitz & Wagner 1993, Johnson & Sutton 1994, Gibson 1995). In the most extreme case, larval metamorphosis is induced exclusively by a specific substrate of relevance to the ecology of the adult stage (Hadfield & Miller 1987, Pawlik 1992). In some species with a specific requirement, larvae settle gregariously in response to adult conspecifics, while in others metamorphosis is induced by the adult prey or host organism.

Many species with an identified settlement requirement exhibit a low level of spontaneous metamorphosis during the first few days after larvae attain competence. A survey of the literature indicates that levels of spontaneous metamorphosis range from 0 to 10% for diverse taxa including aplysiids (Switzer-Dunlap & Hadfield 1977, Pawlik 1989, Plaut et al. 1995), other opisthobranchs (Chia & Koss 1978, 1988, Hubbard 1988, Lambert et al. 1997, Avila 1998), abalone (Morse & Morse 1984), echinoderms (Burke 1984, Pearce & Scheibling 1990, Kitamura et al. 1993, Johnson & Sutton 1994), polychaetes (Williams 1964, Pawlik 1986, Toonen & Pawlik 1996), hydroids (Leitz & Wagner 1993), and barnacles (Matsumura et al. 1998). The mean 34% spontaneous metamorphosis reported here for lecithotrophic larvae of *Alderia modesta* is at least 3 times greater than the percentage of metamorphosis in sea water controls reported for any other species with a specific settlement-cue requirement. The 50 to 90% spontaneous metamorphosis in some clutches of *A. modesta* is an order of magnitude higher than levels of background metamorphosis that have been reported for species which otherwise respond only to a specific substrate.

In several species, levels of spontaneous metamorphosis increase with increasing larval age. Larvae of *Capitella* sp.1 delayed metamorphosis in the absence of mud for 6 d in 1 experiment and 12 d in a second experiment, but thereafter some larvae were observed to metamorphose spontaneously (Pechenik & Cerulli 1991). Lecithotrophic larvae of *Haminaea calledigenita* initially delayed metamorphosis after attaining competence if not exposed to settlement cues, but after 4 d, larvae metamorphosed spontaneously in sea water (Gibson 1995). Planktotrophic larvae of the nudibranch *Hermisenda crassicornis* showed significantly higher levels of spontaneous metamorphosis with increasing larval age (Avila 1998). In contrast, the majority of spontaneous metamorphosis in *Alderia modesta* oc-

curred within the first 2 d of hatching. Of the larvae that did not metamorphose spontaneously in the first 2 d, more than 80% died over the next 2 wk when kept in FSW, rather than initiating a delayed spontaneous metamorphosis in the absence of *Vaucheria longicaulis*.

Larval selectivity among potential substrata has also been shown to decrease with increasing age in some species. Planktotrophic larvae of the nudibranch *Hypselodoris infucata* metamorphosed preferentially on sponges compared with a primary biofilm after initially attaining competence, but showed no preference after a further 3 d (Hubbard 1988). Larvae of *Haminaea calledigenita* responded to the sea grass *Zostera marina* but not to the alga *Chaetomorpha linum* prior to hatching, but there was no difference in response by the 4th day after hatching (Gibson 1995). Older lecithotrophic larvae of *Alderia modesta*, however, responded specifically to *Vaucheria longicaulis* even after an extended larval period.

In some species, the increase in nonspecific or spontaneous metamorphosis over time may represent an attempt by older larvae to avoid the risks of a prolonged planktonic period. For example, starvation induced competent larvae of *Crepidula fornicata* to metamorphose roughly 10 d before fed larvae (Pechenik et al. 1996). Such 'desperate measures' by older larvae are not exhibited by lecithotrophic larvae of *Alderia modesta*. The occurrence of most spontaneous metamorphosis on the day of hatching suggests that, in *A. modesta*, spontaneous metamorphosis is a component of a bet-hedging dispersal strategy, rather than a consequence of larval age. As 90% of larvae that hatched in the presence of *Vaucheria longicaulis* had initiated metamorphosis within 2 d, the vast majority of larvae are competent within 2 d of hatching. Since only a subset of these larvae spontaneously metamorphosed when hatched in FSW, the observed delay in metamorphosis in the remaining larvae reflected the absence of *V. longicaulis*, and did not represent the delayed attainment of competence by some larvae relative to their siblings, as in other species (Pechenik 1990, Maldonado & Young 1999).

The extreme between-clutch variability in the percentage of spontaneous metamorphosis represents yet another level of variation in lecithotrophic *Alderia modesta*. A range of 0 to 90% spontaneous metamorphosis was spanned by a sample of only 30 clutches. No previous study has documented such high variation in spontaneous metamorphosis between clutches for a marine species. Adult body weight, although positively related to fecundity, was not related to the percentage of spontaneous metamorphosis per clutch, indicating that the percentage is not simply a factor of adult size. It remains to be determined whether the observed

variation represents a phenotypic reaction norm to some environmental parameter (i.e., recent food availability), or varies genetically or randomly between individuals in the population (Schlichting 1989). Current experiments are investigating the heritability of spontaneous metamorphosis as an adult phenotype.

Variation in the settlement requirements of sibling larvae may be a more widespread phenomenon than is presently appreciated (Raimondi & Keough 1990, Hadfield & Strathmann 1996). Genetic differences may exist among conspecific larvae that generate behavioral variation during settlement, which in turn would be subject to selection (Raimondi & Keough 1990). For example, larvae from a sheltered population of the polychaete *Spirorbis borealis* settled preferentially on the algae *Ascophyllum* spp. and gregariously in response to conspecific juveniles, while larvae from an exposed population settled on *Fucus* spp. and were not gregarious (Mackay & Doyle 1978). Cyprid larvae of a specialist barnacle settled either on the exposed axial skeleton of gorgonian corals or on adult conspecifics, ensuring proximity to mates for some larvae (Gomez 1973). However, variation as an adaptive mechanism has rarely been demonstrated. Most larvae of the tube-dwelling polychaete *Hydroides dianthus* settled gregariously only in response to adult conspecifics, but a distinct subset of larvae termed 'founders' settled on a primary biofilm (Toonen & Pawlik 1994). Founder larvae are presumably necessary in a gregariously settling sessile species if new habitats are ever to be colonized. In a similar manner, spontaneous metamorphosis in lecithotrophic species could function as an adaptation to vary the dispersal of offspring, rather than merely resulting from the accidental or premature metamorphosis of a few larvae as is sometimes presumed.

Herbivorous opisthobranchs are often highly stenophagous as adults, but the larval settlement requirements for these specialist herbivores are not well understood. Larvae of aplysiid opisthobranchs generally exhibit a graded settlement response, metamorphosing in varying percentages on different algae. When competent larvae of the sea hare *Aplysia californica* were exposed to 18 species of macroalgae, 30% or more metamorphosed on 10 of the algae, and 15% or more settled on 15 of the algal species (Pawlik 1989). Larvae of *A. oculifera* gave a mean 25% or more metamorphosis in response to 4 of 12 macroalgae, but no metamorphosis was induced by 6 of 12 algae (Plaut et al. 1995). Aplysiid larvae may respond to a variety of algae due to the less restricted diet of juveniles (Switzer-Dunlap & Hadfield 1977, Pawlik 1989). In contrast, more than 50% of cultured larvae of the ascoglossan *Elysia chlorotica* metamorphosed on the adult food, *Vaucheria* spp., but only 0 to 2% settled in

response to the algae *Bryopsis plumosa*, *Enteromorpha* sp., and *Cladophora* sp. (Harrigan & Alkon 1978, West et al. 1984). As juvenile ascoglossans generally feed on the same alga as the adult, ascoglossan larvae may have highly specific settlement requirements, but few studies have tested a range of algal species to demonstrate such specificity (Havenhand 1991).

The present study on lecithotrophic larvae of *Alderia modesta* is the most extensive analysis of larval settlement specificity for an ascoglossan. Lecithotrophic larvae that did not undergo spontaneous metamorphosis in the first 2 d post-hatching were extremely specific in their settlement requirements. A mean 93% of larvae metamorphosed on the obligate adult host alga *Vaucheria longicaulis* compared with 0 to 9% metamorphosis in response to 17 other species of algae and a natural biofilm. Larval metamorphosis is induced by both high- and low-molecular weight carbohydrates produced by *V. longicaulis* (Krug & Manzi 1999). Algal polysaccharides often have species-specific structural characteristics, which may account for the specificity of the settlement response in *A. modesta*. Cultured planktotrophic larvae of *A. modesta* from Europe settled on *Vaucheria* sp. after initially attaining competence, but were reported to metamorphose non-specifically after a prolonged but unspecified planktonic period (Seeleman 1967). Cultured planktotrophic larvae of *A. modesta* from the San Diego study population did not settle non-specifically, and exhibited the same level of specificity for the *V. longicaulis*-associated settlement cue as lecithotrophic larvae (Krug & Zimmer 2000, and unpubl. data).

Bet-hedging life-history strategy of *Alderia modesta*

Organisms from fluctuating environments frequently exhibit pronounced variation in reproductive traits at the population or individual level, and have often evolved bet-hedging life-history strategies (Levins 1968, Giesel 1976, Seger & Brockmann 1987, Philippi & Seger 1989). When environmental conditions are variable and unpredictable, the optimal strategy for a genotype is to ensure that some offspring survive bad seasons even at the cost of reduced fitness during good seasons (Philippi & Seger 1989). For example, insects that inhabit climates where the onset of winter is unpredictable may produce mixtures of direct-developing and diapausing eggs (Bradford & Roff 1993, Hopper 1999). Some terrestrial plants produce seeds which develop after 1 yr along with other seeds that develop after 2 or more years, while other plants produce both dispersing and non-dispersing seeds (Payne & Maun 1981, Schmitt et al. 1985, Philippi & Seger 1989).

Planktonic larvae of marine invertebrates face high mortality rates from biotic and abiotic factors, but are able to colonize rare or ephemeral adult food patches. Direct development avoids the risk of planktonic mortality, but leaves populations vulnerable to local extinction from predation, desiccation, or the disappearance of adult food resources. The settlement dimorphism among sibling larvae of *Alderia modesta* serves as a bet-hedging strategy by decreasing variation in recruitment success of planktonic larvae between generations. Offspring that settle directly into the parental population, through intracapsular and post-hatching spontaneous metamorphosis, can take immediate advantage of an adult food patch, while larvae that delay settlement can colonize distant patches through *Vaucheria*-dependent metamorphosis. Regardless of whether conditions in the adult environment are good or bad, some offspring from each clutch will have a good chance of locating a *V. longicaulis* patch and metamorphosing into juveniles.

The 2 biotic factors that most impact larval dispersal potential are (1) the length of time competent larvae delay settlement, and (2) the duration of the larval pre-competent period (Pechenik 1990). Selection for increased variation in either of these factors may result in the evolution of bet-hedging life-history strategies. The settlement dimorphism of *Alderia modesta* represents the first case where some larvae metamorphose immediately upon hatching while competent siblings delay settlement until encountering *Vaucheria longicaulis*. An example of the second case is the cephalaspidean opisthobranch *Haminaea calledigenita*, which hatched both swimming lecithotrophic larvae and juvenile slugs from most egg masses (Gibson & Chia 1989). In contrast to *A. modesta*, however, *H. calledigenita* achieved this result by varying the rate at which sibling offspring attained competence. Some larvae became competent prior to hatching, and metamorphosed intracapsularly in response to the egg mass jelly, while their siblings hatched as swimming veligers that settled after a planktonic period in response to general environmental cues (Gibson 1995, Gibson & Chia 1995). The high percentage of spontaneous metamorphosis in *A. modesta* and the variable attainment of competence in *H. calledigenita* represent different settlement dimorphisms that function similarly in bet-hedging dispersal strategies.

It is striking that *Alderia modesta* and *Haminaea calledigenita*, both small estuarine opisthobranchs, have comparable strategies for varying larval dispersal patterns. It has been suggested that estuaries are particularly prone to environmental fluctuations, which may select for increased variability and plasticity of traits linked with reproduction and dispersal (McPeck & Holt 1992, Kawecki & Stearns 1993, Gotthard &

Nylin 1995, Chia et al. 1996). The mudflats at the Kendall-Frost study site are a dynamic and stressful environment. Bay water salinities range seasonally from 2 to 32‰ due to freshwater input (Levin 1982). Low tides expose *Vaucheria longicaulis* to the air for roughly 5 h a day, and water trapped in algal mats can exceed 44‰ salinity after drying in the sun (Krug & Zimmer 2000). Mats of *V. longicaulis* are patchily distributed, and have been periodically observed to senesce or die off from several field sites (P. J. Krug pers. obs.). The uncertainty of the adult environment may have selected for a strategy to minimize variance in recruitment success across generations in *A. modesta*.

The presence of variable larval development modes within a single species (poecilogony) is extremely rare, occurring mainly among polychaetes and opisthobranchs (Hoagland & Robertson 1988, Bouchet 1989, Chia et al. 1996). The only 2 invertebrate species known to exhibit planktonic lecithotrophy, planktotrophy, and natural hybrid intermediates are *Alderia modesta* and the infaunal polychaete *Streblospio benedicti*, which co-occur at the Kendall-Frost study site (although only the lecithotrophic morph of *S. benedicti* occurs in California) (Levin 1984a, Krug 1998). The east-coast ascoglossan *Elysia chlorotica*, which also feeds on *Vaucheria* spp., exhibits either planktotrophy or direct development in different populations (West et al. 1984). Either the general mudflat environment or some feature of an association with *Vaucheria* spp. may select for variation in reproductive mode, which is generally a canalized species-specific trait in marine invertebrates (Hoagland & Robertson 1988, Levin & Bridges 1995). However, other factors such as small body size may also contribute to the evolution of dispersal polymorphisms, particularly in opisthobranch molluscs (Eyster 1979, Chester 1996, P. J. Krug unpubl. data).

Lecithotrophic larvae of *Alderia modesta* that delayed metamorphosis for 1 to 2 wk were still able to selectively metamorphose on *Vaucheria longicaulis*. The impact of a potential 2 wk planktonic period on the realized dispersal of larvae of *A. modesta* has not been directly determined. However, studies of the dispersal patterns of larvae from an infaunal polychaete assemblage at the same field site demonstrated that larval planktonic period greatly affected dispersal potential (Levin 1982, 1983, 1984b). Moreover, Levin (1982) concluded that for polychaetes: 'Successful species in an isolated back bay habitat are those which exhibit life-history characteristics conferring reduced dispersal ability: small size, brood protection, reduced or flexible planktonic larval stages'. *A. modesta* conforms to this observation in 2 respects. Lecithotrophy, first described for *A. modesta* from this site, generally confers more limited dispersal capabilities than planktotrophy (Todd

1998, Pechenik 1999). The settlement polymorphism in *A. modesta* further reduces the dispersal potential of spontaneously metamorphosing larvae relative to their siblings, maintaining direct recruitment of some offspring into the parental habitat while allowing for dispersal of other larvae to colonize new food patches.

Phenotypic plasticity: effect of adult starvation on larval dispersal potential

The ability to alter a trait in response to environmental fluctuations is termed phenotypic plasticity, and is often an adaptive part of the life-history strategy of organisms from habitats prone to spatial or temporal variation (Schlichting 1989, Stearns 1989, West-Eberhard 1989, McPeck & Holt 1992, Gotthard & Nylin 1995). A bet-hedging genotype spreads risk in advance, given that a bad season will eventually occur; phenotypic plasticity allows an individual to respond once conditions actually become unfavorable. The proportion of spontaneous metamorphosis per clutch is a phenotypically plastic trait in *Alderia modesta*, adding another element of flexibility to the life history of this mollusc. Starved adults rapidly lowered the proportion of spontaneous metamorphosis in their clutches, producing more larvae that settle only in response to *Vaucheria longicaulis*. Even during the first 24 h after collection, the percentage of spontaneous metamorphosis decreased significantly from the first to the second egg mass of adults held without food. By depositing clutches with lower levels of spontaneous metamorphosis, starved adults produce a higher percentage of larvae that will disperse until encountering a new patch of the adult food source.

Plasticity of the proportion of spontaneous metamorphosis per clutch may be highly adaptive in the natural habitat, given the ephemeral nature of *Vaucheria longicaulis* patches. The abrupt disappearance of *V. longicaulis* has been connected to starvation of adult *Alderia modesta* in the field, and starvation was previously shown to cause some lecithotrophic specimens to begin producing planktotrophic clutches after 3 d (Krug 1998). The mean percentage of spontaneous metamorphosis in the study population appeared to correlate with the abundance of *V. longicaulis*, such that when algal densities were noticeably low, mean levels of spontaneous metamorphosis were <10% in clutches of newly collected adults. Phenotypic plasticity may allow adults to adaptively lower the percentage of spontaneous settlement among their offspring during bad seasons, to produce more dispersing larvae able to locate new food patches. However, even when conditions were poor, a few adults still produced clutches with >30% spontaneous metamorphosis.

These individuals may be at a competitive advantage when conditions again favor algal growth in the parental habitat.

A plastic starvation response has been reported for 2 other estuarine opisthobranchs, in which the proportion of larvae undergoing intracapsular metamorphosis decreased following adult starvation. Starved specimens of the aeolid nudibranch *Tenellia adspersa* produced egg masses with entirely planktonic lecithotrophic development, whereas 10 to 15% of the larvae produced by fed adults metamorphosed intracapsularly (Chester 1996). Adult *Haminaea calledigenita* fed half-rations produced egg masses hatching significantly more veligers and fewer juveniles than fully fed individuals (Gibson & Chia 1995). Environmental instability in estuaries may lead to fluctuating adult food supplies and unpredictable conditions, selecting for plastic responses that increase larval dispersal when conditions become unfavorable for adults (Chia et al. 1996).

Spontaneous metamorphosis may be a threshold trait in the lecithotrophic larvae of *Alderia modesta*, resulting from an underlying, continuously distributed trait such as larval size or energy content of stored nutrients. According to this model, when a developing larva is above a certain size or energy threshold, metamorphosis will occur spontaneously 1 to 2 d after hatching; larvae below the threshold will delay metamorphosis until triggered by the *Vaucheria longicaulis*-associated cue. Starved adults may produce slightly smaller or less energetically rich eggs, resulting in lower levels of spontaneous metamorphosis in their clutches. The high variation in the percentage of spontaneous metamorphosis between individuals could result from variation in egg size or energetic investment per offspring (Krug 1998), or from variation between adults in the level at which the threshold itself is set (Roff 1996).

Conclusions

The patterns exhibited by *Alderia modesta* represent an extreme case of reproductive bet-hedging for a marine species, encompassing a wide range of larval development, dispersal, and settlement strategies (Grahame & Branch 1985, Levin & Bridges 1995, Todd 1998, Pechenik 1999). In southern California, individuals produce either planktotrophic or lecithotrophic larvae, and rare adults produce larvae of both types and intermediate sizes in every egg mass (Krug 1998). Lecithotrophic clutches usually contain a mixture of sibling larvae, some of which settle spontaneously soon after hatching, while the remainder depend specifically upon *Vaucheria longicaulis* to induce meta-

morphosis. Intracapsular metamorphosis leads to direct benthic development for a small proportion of larvae in some lecithotrophic egg masses. The variation in the proportion of spontaneous metamorphosis per clutch, and the plasticity of this trait under changing adult conditions, add new levels of variability to the life history of *A. modesta*.

Although dispersal polymorphisms are well-known in many terrestrial taxa (Gaines & McClenaghan 1980, Harrison 1980, McPeck & Holt 1992, Dingle 1996), their potential importance in marine life histories is unknown. Variation in settlement requirements of conspecific larvae, if more widespread among marine species than is currently recognized, could significantly affect recruitment and thus population dynamics of benthic ecosystems (Roughgarden et al. 1988, Underwood & Fairweather 1989, Raimondi & Keough 1990, Hadfield & Strathmann 1996). Extinction and speciation rates of molluscs are directly tied to larval dispersal capabilities, as inferred from development mode (Hansen 1978, Jablonski 1986); it thus remains intriguing that so few species hedge their macroevolutionary bets by exploiting variable dispersal strategies. More detailed studies of other taxa will be necessary to determine whether this is a more common but unrecognized phenomenon among marine invertebrates, or if it exists primarily as a specialized adaptation to highly variable and stressful environments.

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