FOUNDATIONS OF GREGARIOUSNESS: A DISPERSAL POLYMORPHISM AMONG THE PLANKTONIC LARVAE OF A MARINE INVERTEBRATE

ROBERT J. TOONEN^{1,2} AND JOSEPH R. PAWLIK¹

¹Department of Biological Sciences, Center for Marine Science Research, University of North Carolina at Wilmington, Wilmington, North Carolina 28403-3297

Abstract.—Theory predicts that selection should favor genotypes that can vary their tendency to disperse in habitats that are spatially or temporally variable or those that remain near their carrying capacity. Although many marine habitats appear to fit these criteria, confirmed examples of dispersal polymorphism among marine invertebrates are exceedingly rare. Competent larvae of the gregarious tubeworm, Hydroides dianthus, settle specifically in response to living conspecific worms, but a small proportion of each spawn settle nonspecifically on uninhabited substrata concurrently with their gregarious siblings. Here, using a parental half-sib analysis, we show that the proportion of a spawn settling in response to uninhabited biofilm is highly heritable. When estimated as a continuous trait based on a one-way ANOVA, heritability is estimated to be 0.83 ± 0.31 . When founder production was analyzed as a threshold trait, heritability was estimated to be 0.68 ± 0.10 based on the breeding design experiment and 0.65 ± 0.09 based on the artificial selection experiments. Realized heritability based on the selection experiments was considerably lower, however (0.17 per generation and 0.02 cumulative). Artificial selection was ineffectual at sequentially increasing the proportion of founder larvae among inbred family lines, but after three generations of selection, the proportion of larvae settling in response to biofilm was significantly higher among inbred lines than among the field-collected parents. The obligate planktonic larval stage common among so many marine invertebrates is thought to preclude the evolution of dispersal polymorphisms in these animals. Theoretical expectations of variable dispersal may instead be realized through individual behavioral differences resulting in differential transport or settlement preference, but this possibility remains largely unexplored among marine invertebrates.

Key words.—Bet-hedging, dispersal polymorphism, gregarious settlement, Hydroides dianthus, larval dispersal, polychaete.

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Dispersal polymorphisms are well documented for terrestrial species from such diverse groups as arthropods (reviewed by Harrison 1980; Dingle 1996; Zera and Denno 1997) and plants (reviewed by Venable and Lawlor 1980). Among animal species, the insects are perhaps the most studied, and many species are known to exhibit obvious morphological differences, such as variation in wing length and flight muscle development, that affect flight ability. Insects that fly well are able to disperse over long distances, but as the costs associated with dispersal increase, the selective advantage of the dispersal morph decreases (Harrison 1980). Theoretical work predicts that selection should favor genotypes that can vary their tendency to disperse in habitats that are spatially or temporally variable, or those that remain near their carrying capacity (Harrison 1980; McPeek and Holt 1992).

In contrast to the striking morphological variation among terrestrial arthropods, many other animal species display behavioral polymorphisms that result in dispersal differences among individuals despite morphological similarity (reviewed by Gaines and McClenaghan 1980; Stenseth and Lidicker 1992; Dingle 1996). Among small mammals, for example, some individuals feed heavily to deposit fat and then ignore easily available resources in order to disperse while others remain in the natal patch (Gaines and McClenaghan 1980; Dingle 1996). Because many of these behavioral differences in dispersal have been shown to have a heritable genetic basis (e.g., Howard 1960; Hilborn 1975; Beacham 1979; reviewed by Gaines and McClenaghan 1980; Stenseth and Lidicker 1992) and can have the same ecological outcome as morphologically based dispersal polymorphisms (such as wing development polymorphisms among insects), the two are analogous processes (Dingle 1996).

Surprisingly, dispersal polymorphisms are virtually unknown among marine invertebrates, although many marine habitats are strongly variable in both space and time and/or remain close to carrying capacity (e.g., Connell and Jones 1991; Metaxas et al. 1994; Metaxas and Scheibling 1994; Millet and Guelorget 1994; Pineda 1994; Gleason 1996). The best example of dispersal polymorphisms among marine invertebrates are those cases in which a species (or in some cases even an individual) produces two types of egg capsules or larvae, one type which develops directly or demersally and the other which develops within the plankton. This developmental pattern, known as poecilogony in the marine literature, has been described for a number of species, but most of these examples are based on either laboratory artifacts or species misidentifications (Hoagland and Robertson 1988; Chia et al. 1996) and relatively few true cases of poecilogony exist. Confirmed examples of this developmental dispersal polymorphism among marine invertebrates are limited to a few species of opisthobranch molluscs and polychaete worms (reviewed by Chia et al. 1996). Pechenik (1999, p. 269) reviews the potential advantages and disadvantages of planktonic larvae in the life histories of marine invertebrates and concludes that "the prominence of larval development in modern life cycles may reflect difficulties in losing larvae from life cycles more than selection for their retention."

The obligatory planktonic larval stage common among so many marine invertebrates may also preclude the evolution

² Present address: Center for Population Biology, University of California, Davis, California 95616; E-mail: rjtoonen@ucdavis.edu.

of dispersal polymorphisms in these animals. However, the dispersal polymorphisms predicted by theory may be realized instead from behavioral differences among planktonic larvae: individual behavioral differences resulting in differential transport or settlement preferences could lead to variation in realized dispersal, but this possibility remains largely unexplored among marine invertebrates. In most cases, planktonic larvae are thought to be capable of dispersing far from the natal patch, but the actual movement of microscopic larvae is typically impossible to know in the field and several authors have recently questioned this common assumption (e.g., Todd et al. 1998; Jones et al. 1999; Robertson et al. 1999; Swearer et al. 1999). If individual settlement preferences of larvae vary in a heritable manner, this could result in a dispersal polymorphism analogous to better-known terrestrial examples such as wing polymorphisms of insects or behavioral polymorphisms of small mammals. Unfortunately, such dispersal differences can only be inferred from settlement choice experiments or genetic data because with few exceptions, field observations of planktonic larval dispersal are virtually impossible.

Planktonic larvae spend some variable amount of time in the water column before settling into the benthos, and from an individual perspective it is not clear why larvae should vary in their ability to locate and select an appropriate site for metamorphosis into the adult body form. The usual adaptive explanation for larval response to settlement cues is increased average fitness (Raimondi 1988a), and conventional wisdom suggests we should expect a fixed larval response to discrete settlement cues associated with appropriate post-settlement habitat. Contrary to conventional wisdom, however, larval behavior is not uniform in response to cues for settlement, and variability in larval settlement behavior is the rule rather than the exception (reviewed by Raimondi and Keough 1990). In virtually every study of larval settlement preference to date, there is evidence for variability in larval behavior in response to settlement inducing stimuli, and the capacity for larvae to choose substrata based on their specific properties provides an obvious mechanism for the larvae of sedentary marine invertebrates to vary in their dispersal tendencies. Despite the generality of variable larval response among studies of settlement behavior, this pattern is often overlooked such that "any variation that might have been present in the original study vanishes when the work is later summarized" (Raimondi and Keough 1990, p. 90).

Because specific settlement cues for the larvae of virtually all marine invertebrates remain contested or unknown, the easiest system in which to study individual variation to specific settlement cues among larvae is one in which the larvae settle gregariously in response to cues associated with the presence of conspecific adults. Gregarious settlement is relatively common among benthic marine invertebrates; at least 35 species representing eight phyla have been documented to produce larvae that settle preferentially on or near conspecific adults (reviewed by Burke 1986; Pawlik 1992a, b). However, in order for an aggregation to become established, some individual must have initially selected a habitat devoid of conspecifics in which to settle. Thus, aclonal aggregations of marine invertebrates must logically develop from a twostep process: first, some larvae (founders) colonize a suitable but previously uninhabited substratum, then other larvae (aggregators) settle gregariously in response to the presence of living conspecifics on suitable substrata (Toonen and Pawlik 1994).

Previous research found that most larvae of the gregarious tubeworm Hydroides dianthus (Polychaeta: Serpulidae) settle specifically in response to a water-borne cue associated with live conspecifics (Toonen and Pawlik 1996), but that some larvae also settle concurrently on substrata devoid of conspecifics, even after being previously exposed to substrata inhabited by conspecific adults acceptable to other competent larvae (Toonen 1993; Toonen and Pawlik 2001a,b). We found that cultured larvae differ in their tendency to settle in the presence or absence of living conspecific adults, and that temporally discrete patterns of settlement on experimental substrata are consistent across a variety of experiments (Toonen and Pawlik 1993, 1994, 2001a,b). Based on these data, we concluded that colonization of previously uninhabited substrata was not a result of "larval desperation" (sensu Knight-Jones 1953; Wilson 1953) in this species, and hypothesized that these temporally discrete patterns of settlement may result from different behavioral classes of larvae. Here, we expand on that hypothesis and show that spawns produced by a single female differ in the proportion of larvae willing to settle apart from conspecifics. Using breeding and selection experiments, we also show that the proportion of founding larvae in a spawn is strongly heritable. The variation in settlement behavior among sibling larvae likely results in the colonization of previously uninhabited substrata by some larvae we have dubbed founders, and aggregation on conspecific-inhabited substrata by other larvae we have dubbed aggregators (Toonen and Pawlik 1994). In the field, these behavioral differences could lead to a small proportion of larvae colonizing previously uninhabited substrata and, if successful at attracting subsequent gregarious settlement of conspecifics, founding a new aggregation. Here, we suggest that the variation observed in settlement in response to biofilm and conspecifics among sibling larvae of H. dianthus may effectively provide the dispersal polymorphism predicted by theory but currently thought exceedingly rare among marine invertebrate species.

MATERIALS AND METHODS

Study Species

Hydroides dianthus (Verrill 1873) is a tube-dwelling serpulid polychaete which ranges from New England through the West Indies and is found commonly on the underside of rocks, shell hash and other natural and anthropogenic hard substrata (Hartman 1969). Individuals are gonochoristic (sexes are separate) and reproduce sexually, with gametes broadcast every 2–4 weeks at 23°C (Zuraw and Leone 1968). Spawning can be induced artificially by temperature shock (6–8°C), immersion in the sex products of congeners, or mechanical disruption of the tubes (Zuraw and Leone 1972). Zuraw and Leone (1968) observed that animals maintained in the laboratory could spawn naturally up to four times in a single season, but only three artificial spawns could be induced (using temperature shock), and only if animals were allowed to recover for ≥ 32 d between spawning attempts.

Mature adult females release an average of 30,000 ova, and males an average of 6×10^7 sperm when induced to spawn artificially (Zuraw and Leone 1972).

Fertilized eggs develop into trochophore larvae, which begin feeding 18–24 h after fertilization and become competent to settle after about five days at 23°C (Scheltema et al. 1981; Toonen and Pawlik 1994, 2001a). Larvae of this species are strongly gregarious (Scheltema et al. 1981; Toonen and Pawlik 2001a), and often form monospecific aggregations which typically persist for at least several seasons until disturbance eliminates them. Personal observation during this research suggests that physical disturbance (either in the form of anthropogenic or storm damage) is the primary cause of aggregation death, and mortality is positively correlated with aggregation size (Toonen and Pawlik 2001b).

On anthropogenic substrata, large aggregations may include several thousand individual worms, but such high numbers are rarely seen on natural substrates. Natural substrata, primarily large rocks and shell hash of *Mercenaria* clams in North Carolina, are often inhabited by several to several dozen worm tubes of varying sizes, and appear subject to frequent disturbance by winter storms. Worms reach sexual maturity at approximately 10 mm, which takes as little as 17–31 days at 23°C (Zuraw and Leone 1972). Among aggregations on anthropogenic substrata, worm tubes of 4–5 mm in diameter and up to 150 mm in length were found commonly; in contrast, individuals on natural substrata that exceed ~80 mm in length were uncommon.

Settlement of larvae occurs only on surfaces coated with an organic/bacterial film (biofilm), and most larvae settle gregariously in response to an unidentified, water-soluble chemical cue which can be isolated from the bodies of live conspecifics (Toonen 1993; Toonen and Pawlik 1996). The requirement of a biofilm for settlement has also been documented for the congeneric worm, Hydroides elegans (Hadfield et al. 1994; Bryan et al. 1997), and appears to be the primary cue for settlement of this species in Hawaii (Hadfield et al. 1994; Unabia and Hadfield 1999) but apparently not in Hong Kong (Bryan et al. 1996, 1997, 1998; Harder and Qian 1999; but see Beckmann et al. 1999). Larvae are approximately 300 µm in length at competency and undergo obvious morphological changes during metamorphosis that distinguish settled individuals from attached, premetamorphic larvae (Scheltema et al. 1981). Settled juveniles are easily maintained in the laboratory, and can be raised to sexual maturity within a few months (Toonen and Pawlik 2001a,b).

Culture Techniques

Adult *Hydroides dianthus* were collected from large ($\approx 125,000$ L) seawater settling tanks at the former Wrightsville Beach desalination plant or from Banks Channel under the drawbridge access to Wrightsville Beach, North Carolina (where the seawater intake for the settling tanks is located). Aggregations of *H. dianthus* were kept in running, unfiltered seawater drawn from these same settling tanks until spawned.

Spawning was induced by breaking individual worms from their calcareous tubes. Induction of spawning via tube rupture causes animals to release all their gametes (including immature ones), and almost without exception leads to the demise of the worm; females spawned in this way produced between 20,000 and 348,000 ova, and number of eggs produced was positively correlated with the size of the worm (Toonen and Pawlik 2001b). We chose this method of spawning because it affords the greatest confidence in controlling fertilization from known sources, however it also suffers the drawback of killing the worm such that only a single spawn can be analyzed from each individual. Each female was placed into a 10-cm dish containing 50 ml of 1- μ m-filtered seawater, and each male was placed on a watch glass without seawater until gamete release ended. A small number of eggs were isolated into a separate container prior to fertilization and checked for development after 24 h. Any eggs showing cleavage in these isolated dishes were considered evidence of sperm contamination and suspect cultures were discarded.

Fertilization by a known male involved placing dishes containing freshly spawned eggs on a shaker table rotating at 50 rpm and initially adding five drops of sperm suspension (~1 ml of concentrated sperm diluted in 20 ml of 1- μ m-filtered seawater). Additional sperm suspension was added twice thereafter at 10 min intervals, the volume being doubled with each addition (i.e., first 10 drops, then 20 drops). Each family of trochophore larvae were cultured in 2-L glass jars filled with 1.5 L of 1- μ m-filtered seawater, following techniques described in Toonen and Pawlik (1996).

Larval cultures were initially cleaned every second day, and larvae were resuspended in a clean jar filled with 1- μ mfiltered seawater; used jars were scrubbed in hot fresh water and allowed to air-dry prior to reuse. After six days, cultures were cleaned daily to keep surfaces as clean as possible and minimize larval settlement in response to the organic/microbial film (biofilm) which inevitably develops in culture jars. Larvae were fed monospecific cultures of the diatom *Phaeodactylum tricornutum* at 10⁵ cells/ml each time larval cultures were cleaned. Algal culture methods for *P. tricornutum* were adapted from Guillard (1975).

Larval Settlement Assays

Experimental substrata consisted of biofilmed etched glass microscope slides (75 \times 25 mm) with adult conspecifics attached to half of them; hereafter we shall simply refer to experimental substrata without conspecific adults as *biofilm*, and to those with conspecific adults attached as *conspecifics*. These substrata were constructed and treated as described in Toonen and Pawlik (1996). We performed two different types of settlement assays in this study: sample assays and wholeculture assays. Sample assays gauged the individual responses of a sample of 25 larvae to the experimental substrata while the remainder of the larvae remained in the culture jars and did not encounter any experimental substrata (thereby prolonging the planktonic period). In contrast, whole-culture assays gauged the proportion of a spawn that would respond to a given substratum by allowing all larvae to encounter the experimental substrata, thereby providing the chance for all competent larvae in the culture to settle if they choose to do SO.

Sample assays were performed as described in Toonen and Pawlik (1996), and for each experiment in which this type of assay was used, there were 12 replicate sample assays (run simultaneously) for each substratum. At the end of the experiment, after being rinsed gently with 1-µm-filtered seawater to remove larvae, we examined each slide through a dissecting microscope and counted settled juveniles (identified by rudimentary crown and tube formation; for photographs, see Scheltema et al. 1981) as they were removed individually.

For those experiments in which we used whole-culture assays, the entire culture of larvae was filtered down into a single small volume before being rinsed into a 10-cm glass dish containing a single experimental substratum (either biofilm or conspecifics). Dishes were placed on a shaker table rotating at 50 rpm for one hour, then the slides were removed, rinsed, and scored as previously described. The larvae remaining in the dish were returned to a clean culture jar and fed. We exposed larvae to only a single substratum at a time, and in each experiment, larvae could either settle or reject the lone experimental substratum provided. Although larvae were free to settle on the assay dishes in these experiments, we never found juveniles attached to any surface other than the experimental substrata in our assays. Unless otherwise specified, assays were repeated daily following the onset of larval feeding until no larvae settled in response to biofilm in whole-culture assays for three consecutive days.

Experimental Design

Variation among dams in the proportion of founders spawned

We used whole-culture assays seven days postfertilization to assess the proportion of larvae, spawned by 308 fieldcollected females, that would settle in response to biofilm upon reaching competency. We estimated the total number of eggs spawned by subsampling a known culture volume three times and extrapolating the average counts in these samples to the entire spawn (modified from Pawlik 1986). After larvae had ceased to settle on biofilm in our wholeculture assays (as outlined above), the proportion of larvae settling as founders was estimated assuming that all fertilized eggs had developed into competent larvae without mortality. Although unrealistic to assume absolutely no mortality occurs in culture, such estimates are not terribly inaccurate because in experiments in which we artificially prolonged the planktonic period through 70 days (an order of magnitude longer than that used in this experiment), we still recovered an average of 79.7 \pm 5.6% of the number of larvae estimated in this way (Toonen 1993).

We also used sample assays to examine the differences in the relative proportion of larvae settling in response to biofilm and to conspecifics among unrelated dams. For this experiment, we used 10 maternal full-sibling cultures—all fertilized from the same male to standardize paternal influences—and assayed samples of larvae from each dam daily. To ensure fertilization from a known source within full-sibling cultures, each female was spawned in isolation in a clean finger bowl, and a small subsample of her eggs were removed prior to addition of sperm as described previously. If any of these isolated eggs had undergone division after 24 h, the entire culture was discarded. Previous data (Toonen 1993; Toonen and Pawlik 1994) showed that settlement in response to biofilm occurred primarily within the first seven days of larval competency, so we compared settlement of larvae in response to biofilm and to conspecifics during the first 10 days.

Estimates of heritability

Given that there was individual variation in the proportion of larvae per spawn which settle in response to biofilm, we conducted a breeding experiment to determine whether there was an additive genetic component influencing larval settlement preference. We used an NCM1 (or nested maternal fullsib, paternal half-sib) mating design (Lawrence 1984; Lynch and Walsh 1998) to estimate the heritability of founder production. In this breeding design, a number of females (10 in this case) are each crossed to a single male to form a "family" that simultaneously provides data for both full-sib (within dams) and half-sib (among dams, within sires) progeny (Table 1). A different set of females are then crossed to a second male to form the second family, and so on (Fig. 1). In all, 11 sires were crossed to up to 10 unrelated dams (depending on sperm concentration) in each family for a total of 110 possible maternal full-sib families (see Table 1). Larvae were cultured in 2-L glass jars filled with 1.5 L of 1µm-filtered seawater, and treated as described previously. We started 90 full-sib cultures, but attrition, primarily from accidental loss of cultures, but also due to a couple of cases of low fertilization success (< 75%) or fertilization of unknown origin, resulted in the final number of dams per family ranging from four to 10, and totaling 77. The number of larvae settling as founders was scored in whole-culture assays performed each day following fertilization until there was no settlement in response to biofilm for three consecutive days.

In these analyses, progeny refers to an entire spawn (ranging from approximately 1000 to 143,500 larvae), and the proportion of larvae settling in response to biofilm in each paternal half-sib line is the trait. Thus, the result of the settlement assays from each male-female cross is a single datum. Because we assayed the settlement response of larvae from varying numbers of females per family in these experiments, the breeding experiments yielded unequal sample sizes in an unbalanced design, and we had to use correction coefficients for each of these estimates (Becker 1984; Lynch and Walsh 1998).

Using these data, we estimated the heritability of founder production in two different ways. First, we used a one-way analysis of variance (ANOVA) to examine the effects of sire on the frequency of founder larvae settling among families. Second, we estimated the heritability of founder production as a threshold trait. The first method treats settlement response as a quantitative trait, assumes that there is no epistasis, and that the character is determined by the combined effect of many genes such that the underlying distribution approximates continuous normal (Falconer and MacKay 1996). There may be a threshold of response, such that a binary distribution results from a fundamental underlying continuous distribution (one behavior when below the threshold value and another when above it), without violating these assumptions, but no such phenotypic discontinuity is assumed (Falconer and MacKay 1996). The second method makes the same initial assumptions, but explicitly assumes

	Ŷ1	Ŷ2	¥3	¥4	¥5	₽ <u>6</u>	Ŷ7	£ 8	Ŷ9	Ŷ10
ðА	5.90	0.28		11.38	1.10	17.30	21.21			
	Q11	Ŷ12	Ŷ13	Ŷ14	Ŷ15	Ŷ16	Ŷ17	Ŷ18	Ŷ19	Ŷ20
₫B	3.96	3.22			0.52	14.10				
	Ŷ21	♀22	Ŷ23	₽24	Ŷ25	₽26	Ŷ27	₽28	♀ 2 9	\$ 3 0
ðС	_	1.36	0.10	0.82	1.60	1.31	7.10	1.98		
	\$31	\$32	\$33	\$34	\$35 \$	₽36	\$37	\$38 \$	\$39 \$	₽40
ðD	0.007	0.60	0.62	8.07	0.42	0.47	_	_	0.37	
	Ŷ41	\$42	\$43	\$44	Ŷ45	₽46	Ŷ47	\$48	\$49	\$50
ðЕ		11.06		1.29	7.73	0.50	0.25	1.93	0.18	
	Ŷ51	\$52	\$ 53	\$ 5 4	Ŷ55	₽56	\$ 57	\$ 58	♀59	¢60
ð F	0.64	1.45		51.34	0.51	17.56	0.13	0.32		
	♀61	₽62	\$63	₽64	Ŷ65	\$66	Ŷ67	₽68	♀69	₽70
đG	2.10	3.51	2.50	9.10		9.32	20.51	2.40		
	\$71	₽72	Ŷ73	Ŷ74	Ŷ75	₽76	Ŷ77	₽78	\$79	₽80
δH		14.01	4.77	2.30		17.75	16.95		6.04	
	\$¥81	₽82	\$¥83	₽84	Ŷ85	₽86	\$ 87	\$ 88	\$89 ^{\$}	¢90
3I	0.88	8.12	8.81	0	15.93	27.50	0.75	20.80		
	<u>91</u>	♀ 92	Ŷ93	♀94	Ŷ95	\$96	Ŷ97	♀98	\$99	♀100
ζì	2.56	2.73	0.64	4.60	0.50	0.70	1.32	9.16	0.75	16.03
	Ŷ101	Ŷ102	Q103	♀104	♀105	Ŷ106	Ŷ107	Q108	Ŷ109	Q110
δК	4.82	5.56	36.84	31.25	1.30	43.52	27.30	39.84		

TABLE 1. The percentage of founders per family from the nested maternal full-sib, paternal half-sib crosses used to estimate heritability (see Fig. 1 for experimental design). The high and low values observed for any spawn in these experiments are highlighted in bold text.

that a threshold of some sort imposes a discontinuity on the visible expression of the underlying quantitative trait (Lynch and Walsh 1998).

Using a one-way ANOVA to estimate the heritability of the proportion of founders spawned by females involves partitioning the observed phenotypic variance into components due to differences among paternal-half sib families and differences within maternal full-sib families (for the complete model and statistical formulae, including interpretation of the MS components, see pp. 554–559 in Lynch and Walsh 1998). We were forced to use this design because we artificially spawned worms by breaking them from their tubes, and were therefore unable to collect more than a single spawn from any dam. A cartoon of the experimental design for this experiment is presented in Figure 1.

The second method of estimating the heritability of founder production involves calculating the correlation between trait incidence among siblings relative to the incidence in the population as a whole (see pages 299–310 in Falconer and MacKay 1996 for the complete model and statistical formulae). Both analyses are presented, along with the estimates of the variance components based on the ANOVA, in Table 2.

There are two problems with applying these techniques to estimate trait heritability using our data: (1) we have a zero datum which violates the assumptions of parametric statistics (Table 1), and (2) it is difficult to estimate standard error values for a heritability estimate in an unbalanced design with unequal sample sizes (Becker 1984). We have tried to deal with these issues in a variety of ways. First, the heteroscedasticity of the data appears to be largely alleviated by using the $-\log[1/(x + 1)]$ transformation (Bartlett's test = 9.64, df = 10, P = 0.47, Cochran's Q = 0.19). We also tried to apply an analysis of variance to ranked data as one alternative and artificially coded the zero datum as the lowest nonzero value in Table 1 (0.0001) as another alternative; none of these had any qualitative effect on the significance of the statistical results (P = 0.0052, 0.0032 and 0.0053, respectively). Therefore, we have used the uncoded $-\log[1/(x + 1)]$ data set for all analyses herein.

There are several different methods by which to estimate the standard error for our heritability estimates. We first calculated the variance of the variance terms and substituted these maximum and minimum estimates for the variance components in the heritability equation above to get our upper and lower bounds on the heritability estimate (as recommended by Becker 1984). Alternatively, Falconer and MacKay (1996) provide an analytical approximation for the error term, and Lynch and Walsh (1998) suggest either: (1) a more general method for estimating standard error, which allows for unbalanced designs, but which assumes normality and ignores some potential sources of sampling variance to provide an upwardly biased estimate; or (2) a variety of resampling methods that make no assumptions about the form of the distribution of the data or the structure of the exper-



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Source	df	MS	EMS
Among paternal half-sib families	s - 1	MSs	$\sigma_e^2 + n_0 \sigma_s^2$
Within paternal half-sib families	t - s	MS _e	σ_{e}^{2}

FIG. 1. Decomposition of variance terms in the nested maternal full-sib, paternal half-sib cross-breeding analysis (after Becker 1984; Holm 1990; Falconer and MacKay 1996; Lynch and Walsh 1998). (A) Cartoon of mating design used to generate the paternal half-sib family lines for estimating heritabilities. In this design, each of 11 males (\Im A-K) were crossed with 10 unrelated females (\Im 1-110), from which the entire spawn of larvae (ranging from approximately 1000 to 143,500 offspring) were assayed (see Table 1 for actual crosses and experimental data). (B) The form of the one-way ANOVA of data collected from the breeding experiments and composition of MS components (after Becker 1984; Holm 1990; Falconer and MacKay 1996; Lynch and Walsh 1998), where *t* is the total number of individuals included in the experiment, and *s* is the number of sires.

TABLE 2. Heritability analyses for production of founder larvae by females of *Hydroides dianthus* when treated as a quantitative trait ("progeny" = spawn). Percent of spawn settling on biofilm was $-\log [1/(x + 1)]$ transformed to meet assumptions of normality and heteroscedasticity prior to analysis (A and B). Heritability of founder production was also estimated as a threshold trait (C).

(A) Results of paternal half-sib analysis one-way ANOVA for the production of founders for formulae from which variance components and heritabilities were calculated (*see* pp. 554–559 in Lynch and Walsh 1998).

Source	df	MS	F	Р
Among paternal half-sib families	10	1.07	2.85	< 0.01
Within paternal half-sib families	66	0.35		

(B) estimates of variance components and heritabilities based on the one-way ANOVA.

Component	Estimate	Maximum	Minimum
$\hat{\sigma}^{2_2}$	0.10 ± 0.03	0.12	0.06
$\hat{\sigma}^{e_2}$	0.38 ± 0.03	0.40	0.33
V	0.39 ± 0.15	0.48	0.19
VP	0.47 ± 0.04	0.50	0.43
$h^2 = (V_A/V_P)$	0.83 ± 0.31	1.07	0.45

(C) Estimates of founder heritability when analyzed as a threshold trait.

	Incidence		
	of trait (%)	Normal deviate	h^2
Population	0.36	2.69	
Selection experiment	1.39	2.20	0.65 ± 0.09
Breeding design experiment	4.89	1.67	0.68 ± 0.10

imental design. We have tried all of these methods and decided to use the analytical approximation of Falconer and MacKay (1996) because it gave the most liberal of the standard errors we calculated and should be the most conservative indicator of how closely the estimated heritability corresponds to the population mean.

Response to artificial selection

Given the results of the breeding experiment, the obvious question remained whether that trait could be manipulated by artificial selection. To determine whether or not we could artificially select for an increased proportion of founders per spawn, we conducted a series of artificial selection experiments. We collected 50 presumably unrelated females from a single aggregation in the field, spawned them as described previously, and maintained single family lines from the spawn produced by each female. The settlement patterns of larvae produced from this parental generation were then scored in both whole-culture (to assay the proportion of founders per spawn) and sample assays (to assay individual settlement preferences) seven days postfertilization (data not shown and Fig. 2, respectively). We applied selection over three generations using a within-family selection design, because this is the most powerful design when the environmental variance component common to the members of each family is large (Falconer and Mackay 1989). Given that we saw substantial variation among field-collected animals that



FIG. 2. Mean percentage settlement (n = 4, +1 SE) of larvae of *Hydroides dianthus* in response to biofilm and conspecifics over three generations of within-family selection for founders, compared to that seen in a random sample from the field (Parental generation). Samples of larvae were assayed seven days after fertilization for response to biofilm and conspecifics in sample assays, as previously described (see text) for 20 inbred lineages (family 1–20) and one mixed-lineage culture composed of founders selected from all family lines in each generation (Mix).

included zero values in initial trials, we chose this design for two primary reasons: (1) to minimize any potential non-genetic components from the variation upon which selection was applied, and (2) to economize the space required to maintain the cultures required for the breeding experiment and slow inbreeding. Juveniles that settled as founders were isolated and raised to maturity in the laboratory to continue the family line. Not all cultures produced founders on day 7 (data presented in Fig. 2), but most cultures produced at least a few founders (in sample assays, if not in whole-culture assays). In eight cases, however (Parental Generation, 94 and 5; Generation 1, 94, 95, 96, 97, and 913; Generation 2, 911), no founders were produced; these lines were excluded from all subsequent analyses.

Once mature, up to 25 founding females (depending on availability of founders from the previous generation) were spawned and their eggs were combined prior to fertilization by a single founding male from within the same family line. Settlement patterns of the offspring were assayed seven days after fertilization. Again, founders were isolated and raised to maturity in the laboratory for future assays. This procedure was repeated through three generations to determine whether we could increase the proportion of founders spawned by individual females.

These data also provide us with a second, independent estimate of the heritability of founder production. Similar to the breeding design experiment described above, this experiment involved the formation and maintenance of several family lines. Using these family lines, we again estimated heritability in two different ways: first, we applied the second method described above (the threshold trait analysis) to these data for comparison; second, we used the standard breeders equation $(R = h^2 S)$, see Falconer and MacKay 1996; Lynch and Walsh 1998) to estimate the heritability of founder production based on the response to selection within each family. There are two ways in which the selection differential can be calculated for these data. First, we calculated the selection differential ($\Delta \mu = 1 - \%$ gregarious settlers) across single generations, and estimate the trait heritability from the mean response to selection across each generation to the next. The other method for estimating heritability is by using the cumulative selection differential across all three generations $(\Sigma \delta \mu)$. We will discuss the differences between these methods and our interpretation of the estimates obtained using each below.

RESULTS

Variation among dams in the proportion of founders spawned

A frequency histogram of the proportion of founders produced by each of 308 field-collected females shows that the vast majority of dams produce a very small proportion of larvae that settle in response to biofilm (Fig. 3). An average of 4.3 \pm 9.0% of spawned larvae settled in response to biofilm, and the individual proportions of founders spawned ranged from 0 to 51% in our assays (Table 1). It is important to note that this variation occurs within the offspring of a single dam depending on the male to which she was mated. Overall, 89.9% of females we assayed produced some larvae that settled in response to biofilm at day 7. Because we spawn the animals artificially by breaking their tubes (which is lethal), we were unable to collect subsequent spawns to determine whether multiple spawns from the same female produced similar proportions of founders. Without examining all clutches spawned by a female through her adult lifespan, we cannot say that any worm failed to produce at least some founder larvae, but even with only a single spawn examined,



FIG. 3. Frequency distribution of the number of founding settlers produced by 308 field-collected females of *Hydroides dianthus*. The proportion of founding settlers spawned by individual females ranged from 0 to 50%, and the arithmetic mean proportion of found-er per clutch is $4.3 \pm 9.0\%$ in these experiments.

almost 90% of worms assayed produced some proportion of larvae that settle in response to biofilm.

Sample assays revealed that clutches of larvae differ in the proportion of larvae that respond to each of the experimental substrata (Fig. 4). Some females (e.g., 96) produced spawns in which a relatively high proportion of larvae settled in response to biofilm (38.56%), while others produced relatively few (e.g., 91-1.5%) or none (98) in this single spawn experiment. Differences among the proportion of founders produced by various females were significant (G = 289.35, df = 9, P < 0.0001), and although Scheffé's unplanned contrasts among means test ($F_{Crit} = 2.04$) detected no subdivision among females in the production of aggregators, it did break females into two groups between which the mean number of founders spawned differed significantly (Fig. 4). The mean proportion of larvae spawned by each dam settling in response to biofilm and to conspecifics as well as the total proportion of founders from the total spawn are presented below the individual settlement plots for easy comparison (Fig. 4).

Estimates of heritability

The percentage of larvae settling in response to biofilm from each family line in the paternal half-sib crosses is presented in Table 1. The mean proportion of founders per female was $8.08 \pm 1.27\%$, with a minimum of 0 and a maximum of 51.34% (Table 1).

Treating the proportion of larvae settling as founder as a quantitative trait, and partitioning the observed variance with a one-way analysis of variance, we find that the among sires component of variation has a significant *F*-ratio (Table 2A). Our estimate of the heritability of the proportion of founder larvae spawned by dams is 0.83 ± 0.31 , with a range of 0.45 - 1.07 (see Table 2B). Because the estimated variance components have error associated with them, heritabilities greater than 1.0 may result from that error. Positive assortative mat-



FIG. 4. Mean percentage settlement (n = 12, +1 SE) of 10 maternal full-sib, paternal half- sib cultures (females 1–10) of *Hydroides dianthus* over the first seven days of competency. Larvae were assayed for response to biofilm and conspecifics daily in 24-h sample assays. Letters on graphs (a,b) represent groups among which the mean number of founders do not differ significantly (Scheffé test, $\alpha = 0.05$, $F_{crit} = 2.04$). The upper plots are the data presented individually for each mother, and two summary plots are included at the bottom for ease of comparison: the mean proportions of larvae settling in response to conspecifics and biofilm across the experimental period, and the total proportion of larvae settling as founders within each maternal half-sib family.

ing may also give inflated estimates of heritability, but because we spawned animals without a priori knowledge of their substratum preference at the time of settlement, it is unlikely that we accidentally forced assortative mating in our design. An estimate of heritability bracketing 1.0 in this design means that the effect of sires on the frequency of founding settlers in a spawn may explain almost all of the variation in the proportion of founders per spawn among the half-sib lines.

Analyzing the data as a threshold trait, and estimating the heritability of founder production by calculating the correlation between trait incidence among siblings relative to the incidence in the population as a whole gives an estimate of 0.68 ± 0.10 (see Table 2C). This estimate is lower than that of the ANOVA technique, but is well within the 95% confidence range of the ANOVA estimate.

Applying the breeders equation $(R = h^2)$ to estimate the heritability of founder production based on lineage responses to selection yields lower estimates than any of the other methods outlined above. Calculating the selection differential across single generations ($\Delta \mu = 1 - \%$ gregarious settlers), we estimate realized heritability to be 0.17 ± 0.22. Using the cumulative selection differential across all three generations ($\Sigma \delta \mu$) to calculate trait heritability, we estimate $h^2 =$ 0.02 ± 0.12.

Response to artificial selection

Our experiments were ineffective at either increasing sequentially the proportion of founders produced by subsequent generations or the settlement preference of individual larvae in response to biofilm (Fig. 2). Because there were eight instances (within six inbred lines) in which there were no larvae settling in response to biofilm that could continue the inbred lineages from founders, we have excluded those lines from our data analyses (leaving 15 of 21 within-family lines). We have included all 21 family lines in Figure 2 to display the complete data set, but the six excluded lines (4, 5, 6, 7, 11, and 13) were not used in statistical or genetic analysis calculations. Although there is no obvious sequential increase in the proportion of founders in selected lineages from this experiment, the mean proportion of founders per family line is significantly higher (t = 6.03, df = 41, P < 0.01) in the second and third (0.17 \pm 0.05) than in the first and parental generations (0.02 ± 0.02) .

There was also no consistent increase in the percentage of larvae that settled in response to either biofilm or conspecifics in sample assays within selected lines (Fig. 2). In some cases, settlement of larvae in response to biofilm in sample assays reflected the same pattern as that observed in whole-culture assays, while in other cases, the responses in the different assay methods appeared contradictory (data not shown). Overall, there was little evidence of any consistent pattern, but there was a significant increase in the proportion of larvae settling in response to biofilm across generations (Fig. 2). Differences between the inbred lines, however, were not significant (Table 3).

As explained above, using the single generation selection differentials to estimate the heritability of founder production from the artificial selection lines provides an independent

TABLE 3. Two-way ANOVA examining the significance of lineage and generational effect on the proportion of founders spawned by dams from inbred lines of *Hydroides dianthus*. An asterisk (*) denotes significance at $\alpha = 0.05$.

Source	df	MS	F	P
Family	20	5.71	1.18	>0.05
Generation	3	19.85	4.11	< 0.01*
Error	60	4.83		

estimate of h^2 , and these data yield an estimate of heritability (0.65 \pm 0.09) almost identical to that obtained from the breeding design data (0.68 \pm 0.10—see Table 2C).

DISCUSSION

Previous work shows that individual larvae of the gregarious tube worm *Hydroides dianthus* differ in their individual response to substrata, and that upon reaching competency, some larvae are willing to accept biofilm as suitable habitat, whereas others additionally require the presence of living conspecific adults in order to settle and metamorphose into the adult body form (Toonen 1993; Toonen and Pawlik 1994, 1996). Although both founding and aggregating larvae become competent to settle concurrently about four days postfertilization, settlement of founding larvae rapidly peaks and subsides within 10 days (Toonen and Pawlik 1994, 2001a,b).

Aggregating larvae, on the other hand, continue to settle up to 20 days beyond metamorphosis of the last founding settler, even when exposed to suitable substrata daily (Toonen and Pawlik 1994, 2001a,b). Assuming passive transport of larvae, this suggests that aggregating settlers should be transported further from natal sites on average than are founding settlers. Furthermore, although founding settlers were uniformly culled within 14 days, aggregating larvae delay settlement for up to 70 days until they begin to die in culture rather than settle in response to biofilm (Toonen and Pawlik 1994). In this study, we have shown further that family lines differ in their tendency to produce founding settlers and that production of founders is a strongly heritable trait, although it does not respond to selection as expected.

Given the obvious fitness consequences of larval habitat choice, it seems reasonable to expect that additive genetic variation would play a measurable and important part in the settlement preference of the larvae of marine invertebrates. There are few studies which examine specifically the heritability of, or attempt to estimate the contribution of additive genetic variation to, larval settlement preference. Among those few species studied to date, there appears to be reasonable support of this expectation (Doyle 1974; Mackay and Doyle 1978; Levin et al. 1991; Gibson 1993), other than for the barnacle, *Balanus* (Holm 1990). We show here that the proportion of larvae in a single clutch that will settle in response to biofilm is strongly heritable for the polychaete tubeworm *Hydroides dianthus*.

Despite a significant heritable additive genetic component of settlement, however, we failed to elicit a progressive change among inbred lineages by artificial selection. In a similar experiment to this one, Hadfield (1984) tried to select for both increased sensitivity to a metamorphic inducer (sensitive strain) and for earlier metamorphic competence (early strain) among inbred lines of the mollusc *Phestilla sibogae*. Hadfield was unsuccessful in producing a consistent response in either strain over 29 and 27 generations of selection, respectively, although in the case of the sensitive strain there was a significant difference between responses of the highly inbred line and a sample of wild animals by the end of the experiment (Hadfield 1984). We find a similar, albeit quicker, response to selection in our data, and the proportion of founders in family lines assayed in the third generation is significantly higher than that of the parental generation (Table 3).

The unexpectedly strong influence of sires on the proportion of founding settlers spawned may be responsible for the weak response to selection we observed using within-family selection. The variation in the proportion of founders in a given spawn ranges from 0-51%, but this range occurs among the offspring of a single dam depending on the male used to fertilize her eggs (Table 1). Given that these animals are freespawners, and that the paternity of clutches is likely to be mixed in dense aggregations, it seems likely that the proportion of founders per clutch will vary as a function of multiple sires. However, variation among sires does not of itself explain the variation in founder production. The degree of variation among sires is nearly as great as among dams, and these data suggest a complex interaction between sire and dam that ultimately determines the proportion of founding settlers spawned.

Alternatively, the response to selection observed in our study could be the result of intergenerational effects similar to that documented in such taxonomically diverse organisms as insects, (e.g., Smith et al. 1995; Fox et al. 1999; Wedell and Tregenza 1999), plants (e.g., Lacey 1996; Thiede 1998), and humans (e.g., Foster et al. 1993; Ramakrishman et al. 1999). Direct additive genetic covariances between parental performance and the trait of interest in the offspring are frequently found to be strongly negative (e.g., Baker 1980; Meyer 1992a, b; Robinson 1996; Lee and Pollack 1997), and the general outcome of selection is simply difficult to elucidate in these cases: selection may have no apparent effect or even a counter-intuitive effect on the response of a trait subjected to selection under these circumstances depending on the strength of the covariance between the traits (e.g., Kirkpatrick and Lande 1989, 1992; Lande and Price 1989; Lande and Kirkpatrick 1990).

There are many possible explanations for the discrepancy between trait heritability estimated from resemblance among relatives and artificial selection (Lynch and Walsh 1998). However, in the first study of the genetic basis of a marine developmental dichotomy, Levin et al (1991) found that nonadditive genetic components of variance were important, and that strong negative maternal covariance with offspring traits resulted in an intergenerational effect for the polychaete worm Streblospio benedicti. The authors conclude that the suite of life-history trait correlations that define distinct planktotrophic and lecithotrophic trait complexes in this species, coupled with negative genetic correlations of larval to maternal characters may constrain responses of individual characters to directional selection, and indirectly perpetuate the larval settlement dichotomy (Levin et al. 1991). When maternal covariances with offspring traits are found to be

negative, offspring frequently show a negative response to positive selection in the F_1 generation, a positive response in the F_2 , negative in the F_3 and so on with damped oscillations to an asymptotic response value (e.g., Falconer 1955, 1965; Dingle 1988; Janssen et al. 1988; Schluter and Gustafsson 1993; Thiede 1998). Thiede (1998) demonstrated that response to selection depends not only on the direct (i.e., Mendelian) additive and environmental causal components of variance, but also on the unmeasured maternal attributes that influence phenotypic expression in the subsequent generation. Thiede (1998) conducted a three generation heritability breeding design which generated seven types of relatives, and showed that these infrequently measured maternal inheritance traits were not only important, but persisted for more than a single generation. The negative direct-maternal covariances resulted in a trait response opposite to the direction to selection for some traits, and near zero responses for a variety of others despite high estimates of heritability (Thiede 1998). Our results are of the same magnitude as those reported by Thiede (1998), and appear consistent with such an intergenerational effect; this may explain why estimates of heritability based on the response to selection $(R = h^2 S)$ are so low relative to the other estimates which all indicate the proportion of larvae settling in response to biofilm is a highly heritable trait (Table 2). Additional research with a much more complicated factorial breeding design, incorporating seven different sets of relatives, is required to rigorously test this hypothesis (for necessary breeding design, see table 1 of Thiede 1998).

Regardless of the ultimate mechanism underlying the willingness of individual larvae to settle in response to biofilm or conspecifics, our results suggest that larvae settling on biofilm are not 'lost souls' that simply made a fatal mistake in their choice of substratum. The presence of an obligatory planktonic period of development may preclude the evolution of traditional dispersal polymorphisms typical of terrestrial systems, and in his review of planktonic larval life histories of marine invertebrates, Pechenik (1999) argues that it is difficult for these species to alter their historical developmental patterns. Our work with Hydroides dianthus suggests that the planktonic larvae of this tube-dwelling polychaete worm could instead possess the adaptive dispersal polymorphism predicted by theory expressed as a behavioral settlement choice polymorphism rather than a physical difference. Variable settlement patterns among sibling larvae has also been described for the sea slugs Alderia modesta (Krug 1998; Krug and Zimmer 2000; Krug 2001) and Haminaea callidegenita (Gibson and Chia 1991, 1995; Gibson 1995). Furthermore, research with larvae of species such as Phestilla sibogae (Hadfield and Scheuer 1985) and Haliotis rufesens (Trapido-Rosenthal and Morse 1986) suggests that larvae continuously exposed to metamorphic inducer become habituated leading to decreased settlement of competent larvae, a pattern analogous to dispersal polymorphism patterns described among aphids (reviewed by Dingle 1996). Gibson (1995) and Maldonado and Young (1999) describe intraclutch variability in the onset of larval competence and review possible adaptive significance of individual variability in settlement choice among larvae within a clutch of offspring. If a similar pattern of heritable genetic variation in

habitat choice or the onset of competency proves common among other marine invertebrates with planktonic larvae, this behavioral difference could provide the dispersal polymorphism predicted by theory, but currently thought rare, for organisms inhabiting marine benthic habitats.

Dispersal Polymorphism or Imperfect Larvae?

A behavioral polymorphism such as described herein may actually be common among other benthic marine invertebrates with planktonic larvae, because in most studies of gregarious settlement there is appreciable settlement of larvae in "control" treatments. Variability in settlement preference among sibling larvae of marine species seems to be the norm rather than the exception (reviewed by Raimondi and Keough 1990, Gibson 1995). Raimondi and Keough (1990, p. 433) reviewed the literature on variability of larval settlement behavior and predicted the results of our experiments: "Whatever the mechanisms, variable behaviour exists in the larvae of most species; even under controlled laboratory conditions, most parents produce offspring that exhibit a range of behaviours in response to clear, simple stimuli. . . If both short and long range dispersal occurred there would effectively be a dispersal polymorphism." They go on to summarize three examples: (1) settlement of the bryozoan Bugula neritina on basal versus distal portions of sea grass blades (Keough 1986; Keough and Chernoff 1987); (2) gregarious and non-gregarious settlement of the barnacle Chthamalus anisopoma (Raimondi 1988a, b, 1990a, b); and (3) variation in phototactic behavior exhibited by larvae of ascidians and bryozoans (Raimondi and Keough 1990), to support their contention that variability in larval settlement behavior is likely to be an adaptive response to either fluctuating selection pressures (possibly as a result of the temporally and spatially variable nature of benthic marine habitats), or negative genetic correlations with other traits. The data we present here supports the prediction of Raimondi and Keough (1990), and further indicate that because founding and aggregating individuals differ, theoretical models based on random colonization of patches from a panmictic larval pool should be scrutinized closely for biological realism; all larvae are not created equal.

Experimental analyses of larval settlement rarely discuss those individuals that settle spontaneously on control substrata, and any variation in settlement response recorded in the original study typically "vanishes when the work is later summarized" (Raimondi and Keough 1990). By this general dismissal of vagrants, potential founders are effectively relegated to the realm of experimental slop. We argue that the dismissal of these vagrant larvae is inappropriate because most reported examples, especially from the insect and ornithological literature, demonstrate that rather than being a consequence of experimental error, diversity of population and individual patterns of migration and settlement behavior can be an important outcome of natural selection (Dingle 1996). Empirical evidence from insects (e.g., Davis 1980; Dingle 1980), small mammals (e.g., McShea 1992), migratory birds (e.g., DeSante 1983; Ketterson and Nolan 1983), stickleback fishes (e.g., Quinn and Brodeur 1991), spiny dogfish sharks (e.g., McFarlane and Beamish 1986), american eels (e.g., Helfman et al. 1987), and sockeye salmon (e.g.,

Leggett 1984, 1985; Quinn 1984, 1985; Quinn and Brodeur 1991) all suggest that deviants from typical patterns of migration are important in their own right, and that colonization of new habitats and population range expansion are most likely the result of these vagrants (reviewed by Dingle 1996). Straying of some proportion of offspring is likely adaptive in heterogeneous conditions, because as the possibility of breeding failure increases, so does the advantage of producing young that sample habitats different from the natal patch.

Further, variability in larval settlement preference may actually be a means of increasing individual reproductive success. Founders gain a head start on growth, and this initial growth may provide a significant fitness advantage, because gamete production is positively correlated with body size in Hydroides dianthus (Toonen and Pawlik 2001b). Several recent studies have also demonstrated that differences in size, larval nutrient stores, or larval feeding history can strongly affect the performance (measured as growth and survivorship) of juveniles (reviewed by Moran 1999). For example, Pechenik and colleagues have shown significant effects of nutritional stress on juvenile performance in a variety of species (e.g., Pechenik et al. 1996; Pechenik and Rice 2001). Likewise, Moran and Emlet (2001) demonstrated that increased hatching size in the intertidal gastropod Nucella ostrina resulted in increased growth rates, survivorship and shortened time to maturity. Earlier settlement of founding larvae may provide a direct benefit to juveniles. Examining the growth consequences of aggregation on barnacles, Pullen and LaBarbera (1991) demonstrated that individuals experience differential survival and growth depending on precedence and position in an aggregation. The same may be true for H. dianthus; growth rates of solitary worms is significantly higher than that of aggregated individuals in the field (Toonen, unpubl. data). This early advantage is likely maintained as an aggregation develops, because early settlers start to grow vertically from the substrate when encountering conspecifics, and the peak of an aggregation is the optimal position for growth and survival in bidirectional flow (Pullen and LaBarbera 1991), such as the tidal estuary in which these animals were collected. Finally, mortality rate is correlated with individual density, and larger aggregations suffered a higher per capita mortality rate than smaller aggregations or solitary individuals in field manipulations (Toonen, unpubl.data). All of these factors suggest that the potential fitness pay-off for a successful founder may be great. In this case a mixed strategy that produces many "safe" larvae and a few "risky" opportunistic settlers might reasonably be expected to lower the inter-generational variance in recruitment success and subsequently raise the mean fitness of genotypes that produce at least some founder larvae in each clutch. This mixed strategy, often referred to as bet-hedging, is rarely described among marine invertebrates (reviewed by Krug 2001). As with the finding of Gibson (1993) and Krug (1998), the data presented herein suggest that behavioral differences in metamorphic tendencies among marine invertebrates may be a bet-hedging strategy.

Although the potential for increased gamete production appears great among founders which become the nucleus of an aggregation, these individuals likely have a reduced probability of successfully reproducing relative to a conspecific that settles gregariously. Because fertilization decreases rapidly with distance among marine broadcast spawners (e.g., Levitan 1991, 1993; Levitan et al. 1991, 1992), the probability of successful fertilization drops as a function of sperm dilution when mature worms are not part of an aggregation. Founding settlers also have the additional hazard that they are selecting a habitat without obvious cues of suitability for long-term survival and growth (i.e., the substrate may be unoccupied for a good reason). Therefore, even if a founding settler colonizes a habitat suitable for post-metamorphic survival and growth, unless it is also able to attract gregarious settlement subsequently, the probability of successful reproduction is low. Aggregators, on the other hand, respond specifically to water-soluble cues associated only with the bodies of living conspecific adults (Toonen and Pawlik 1996), which is an obvious indicator that the habitat is suitable for postsettlement survival and growth. Aggregating settlers may lose the advantage of precedence, and therefore suffer increased levels of intraspecific competition, leading to decreased growth and reproductive rates, but the initial risk of settlement is greatly decreased. Furthermore, as aggregations grow, individual survival rates decrease, because mortality rate and aggregation size are positively correlated in the field (Toonen, unpubl. data). Hydroides dianthus may increase individual fitness by producing mostly larvae that respond to an obvious indicator of habitat suitability for post-settlement survival, but by also producing a few higher-risk larvae that could increase fitness disproportionately should they prove successful in becoming the nucleus of a new aggregation.

These differences among larval settlement choice are likely to lead to a parent-offspring conflict: although parents may maximize persistence of their genotype by distributing their offspring among different habitats with varying pay-offs, founding and aggregating offspring are unlikely to experience similar risks of post-metamorphic survival given their settlement preferences. Those larvae destined to settle as founders may be a good risk when considering inclusive fitness from the viewpoint of the parents, because the benefits of both strategies (founding and aggregating) may be realized while the costs associated with either strategy need not be paid in full. As an individual larva, however, the safest bet surely lies with habitats already inhabited by living conspecific adults.

For the larvae of Hydroides dianthus, behavioral differences in habitat choice among sibling larvae effectively leads to a dispersal polymorphism in which some larvae contribute to existing aggregations while others disperse to colonize new habitats. Although this claim is unusual for the planktonic larvae of marine invertebrates (but see Raimondi and Keough 1990), the pattern of larval settlement we describe herein is analogous to the multitude of well-documented dispersal polymorphisms in the diverse systems we mentioned previously. Individuals of H. dianthus may also be increasing individual reproductive success by producing mostly larvae that respond to an obvious indicator of habitat suitability for postsettlement survival (live adult conspecifics), but by also producing a small proportion of risky larvae that could provide a disproportional fitness pay-off if they become the nucleus of a successful aggregation. The ubiquitous nature of settlers on "control" substrata in studies of settlement preference among the planktonic larvae of marine invertebrates may indicate that larval habitat-choice polymorphisms are widespread, and we look forward to additional studies which examine this hypothesis.

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LITERATURE CITED

- Baker, R. L. 1980. The role of maternal effects on the efficiency of selection in beef cattle—A review. Proc. N. Z. Soc. Anim. Prod. 40:285–303.
- Beacham, T. D. 1979. Dispersal tendency and duration of littermates during population fluctuations of the vole *Microtus townsendii*. Oecologia 42:11–22.
- Becker, W. A. 1984. Manual of quantitative genetics. Academic Enterprises, Pullman, WA.
- Beckmann, M., T. Harder, and P.-Y. Qian. 1999. Induction of larval attachment and metamorphosis in the serpulid polychaete *Hydroides elegans* by dissolved free amino acids: Mode of action in laboratory bioassays. Mar. Ecol. Prog. Ser. 190:167–178.
- Bryan, P. J., D. Rittschof, and J. B. McClintock. 1996. Bioactivity of echinoderm ethanolic body-wall extracts: An assessment of marine bacterial attachment and macroinvertebrate larval settlement. J. Exp. Mar. Biol. Ecol. 196:79–96.
- Bryan, P. J., P. Y. Qian, J. L. Kreider, and F. S. Chia. 1997. Induction of larval settlement and metamorphosis by pharmacological and conspecific associated compounds in the serpulid polychaete *Hydroides elegans*. Mar. Ecol. Prog. Ser. 146:81–90.
- Bryan, P. J., J. L. Kreider, and P.-Y. Qian. 1998. Settlement of the serpulid polychaete *Hydroides elegans* (Haswell) on the arborescent bryozoan *Bugula neritina* (L.): evidence of a chemically mediated relationship. J. Exp. Mar. Biol. Ecol. 220:171–190.
- Burke, R. D. 1986. Phermones and the gregarious settlement of marine invertebrate larvae. Bull. Mar. Sci. 39:323-331.
- Chia, F. S., G. Gibson, and P. Y. Qian. 1996. Poecilogony as a reproductive strategy of marine invertebrates. Oceanol. Acta 19: 203–208.
- Connell, S. D., and G. P. Jones. 1991. The influence of habitat

complexity on postrecruitment processes in a temperate reef fish population. J. Exp. Mar. Biol. Ecol. 151:271–294.

- Davis, M. A. 1980. Variation in flight duration among individual *Tetraopes* beetles: implications for studies of insect flight. J. Insect Physiol. 26:403–406.
- DeSante, D. 1983. Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. Auk 100: 826–852.
- Dingle, H. 1980. The ecology and evolution of migration. Pp. 1– 101 *in* J. S. A. Gauthreaux, ed. Animal migration, orientation, and navigation. Academic Press, New York.
- ———. 1988. Quantitative genetics of life history evolution in a migrant insect. Pp. 83–93 in G. DeJong, ed. Population genetics and evolution. Springer, Berlin.
- ——. 1996. Migration: the biology of life on the move. Oxford Univ. Press, New York.
- Doyle, R. W. 1974. Choosing between darkness and light: the ecological genetics of photic behaviour in the planktonic larva of *Spirorbis borealis*. Mar. Biol. 25:311–317.
- Falconer, D. S. 1955. Patterns of response in selection experiments with mice. Cold Spring Harbor Symp. Quant. Biol. 20:178–196.
 ——. 1965. Maternal effects and selection response. Pp. 763–774 in S. J. Geerts, ed. Genetics today. Proceedings of the XI International Congress of Genetics. Pergamon, Oxford, U.K.
- Falconer, D. S., and T. F. C. Mackay. 1989. Introduction to quantitative genetics. Longman Group, Essex, U.K.
- ——. 1996. Introduction to quantitative genetics. Longman, New York, NY.
- Foster, H. W., J. Thomas, K. A. Semenya, and J. Thomas. 1993. Low birthweight in African Americans: does intergenerational well-being improve outcome? J. Nat. Med. Assoc. 85:516–520.
- Fox, C. W., M. E. Czesak, T. A. Mousseau, and D. A. Roff. 1999. The evolutionary genetics of an adaptive maternal effect: egg size plasticity in a seed beetle. Evolution 53:552–560.
- Gaines, M. S., and L. R. J. McClenaghan. 1980. Dispersal in small mammals. Annu. Rev. Ecol. Syst. 11:163–196.
- Gibson, G. D. 1993. Developmental variability and the induction of metamorphosis in *Haminaea callidegenita* (Mollusca: Opisthobranchia). Ph.D. diss., University of Alberta, Edmonton, AB.
 ——. 1995. Why be choosy? Temporal changes in larval sensitivity to several naturally-occurring metamorphic inducers in the opisthobranch *Haminaea callidegenita*. J. Exp. Mar. Biol.
- Ecol. 194:9–24.Gibson, G. D., and F.-S. Chia. 1991. Contrasting reproductive modes in two sympatric species of *Haminaea* (Opisthobranchia: Cephalaspidea). J. Molluscan Stud. 57:49–60.
- . 1995. Developmental variability in the poecilogonous opisthobranch *Haminaea callidegenita*: life-history traits and effects of environmental parameters. Mar. Ecol. Prog. Ser. 1995. 121(1– 3):139–155.
- Gleason, M. 1996. Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. J. Exp. Mar. Biol. Ecol. 207:79–101.
- Guillard, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates. Pp. 29–60 in W. L. Smith and M. H. Chanley, eds. Culture of marine invertebrate animals. Plenum Press, New York.
- Hadfield, M. G. 1984. Settlement requirements of molluscan larvae: new data on chemical and genetic roles. Aquaculture 39: 283–298.
- Hadfield, M. G., and D. Scheuer. 1985. Evidence for a soluble metamorphic inducer in *Phestilla*: ecological, chemical and biological data. Bull. Mar. Sci. 37:556–566.
- Hadfield, M. G., C. C. Unabia, C. M. Smith, and T. M. Michael. 1994. Settlement preferences of the ubiquitous fouler *Hydroides elegans*. Pp. 65–74 *in* M.-F. Thompson, S. R. Nagabushanam, and Fingerman, eds. Recent developments in biofouling control; Indo-United States Conference, Bangalore, India, July 12–16, 1992. A. A. Balkema, Rotterdam, Netherlands; Brookfield, VT.
- Harder, T., and P.-Y. Qian. 1999. Induction of larval attachment and metamorphosis in the serpulid polychaete *Hydroides elegans* by dissolved free amino acids: isolation and identification. Mar. Ecol. Prog. Ser. 179:259–271.

- Harrison, R. G. 1980. Dispersal polymorphisms in insects. Annu. Rev. Ecol. Syst. 11:95-118.
- Hartman, O. 1969. Atlas of the Sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
- Helfman, G. S., D. E. Facey, L. S. Hales, and E. L. Boyeman. 1987. Reproductive ecology of the American eel. Am. Fish. Soc. Symp. 1:42–56.
- Hilborn, R. 1975. Similarities in dispersal tendency among siblings in four species of voles (*Microtus*). Ecology 56:1221–1225.
- Hoagland, K. E., and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? Biol. Bull. 174:109–125.
- Holm, E. R. 1990. Attachment behaviour in the barnacle *Balanus* amphitrite amphitrite (Darwin): genetic and environmental effects. J. Exp. Mar. Biol. Ecol. 135:85–98.
- Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. 63:152-161.
- Janssen, G. M., G. de Jong, E. N. G. Joosse, and W. Scharloo. 1988. A negative maternal effect in springtails. Evolution 42:828–834.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature 402: 802-804.
- Keough, M. J. 1986. The distribution of a bryozoan, *Bugula neritina*, on seagrass *Thalassia testudinus*, blades: settlement growth and mortality. Ecology 67:846–857.
- Keough, M. J., and H. Chernoff. 1987. Dispersal and population variation in the bryozoan *Bugula neritina*. Ecology 68:199–210.
- Ketterson, E. D., and J. V. Nolan. 1983. The evolution of differential bird migration. Pp. 357–402 in R. F. Johnston, ed. Current Ornithology. Plenum Press, New York.
- Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. Evolution 43:485–503.
- ——. 1992. The evolution of maternal characters: errata. Evolution 43:485–503.
- Knight-Jones, E. W. 1953. Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. J. Exp. Biol. 30:584–599.
- Krug, P. J. 1998. Chemical and larval ecology of opisthobranch molluscs: variable development modes and settlement requirements for larvae of *Alderia modesta*. Ph.D. diss., University of California, San Diego, San Diego, CA.
- ——. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. Mar. Ecol. Prog. Ser. 213:177–192.
- Krug, P. J., and R. K. Zimmer. 2000. Developmental dimorphism and expression of chemosensory-mediated behavior: habitat selection by a specialist marine herbivore. J. Exp. Biol. 203: 1741–1754.
- Lacey, E. P. 1996. Parental effects in *Plantago lanceolata* L. I. A growth chamber experiment to examine pre- and postzygotic temperature effects. Evolution 50:865–878.
- Lande, R., and M. Kirkpatrick. 1990. Selection response in traits with maternal inheritance. Genet. Res. 55:189–197.
- Lande, R., and T. Price. 1989. Genetic correlations and maternal effect coefficients obtained from offspring-parent regression. Genetics 122:915–922.
- Lawrence, M. J. 1984. The genetical analysis of ecological traits. Pp. 27–63 *in* B. Shorrocks, ed. Evolutionary ecology: the 23rd symposium of the British Ecological Society Leeds (1982). Blackwell Scientific, Oxford, U.K.
- Lee, C., and E. J. Pollack. 1997. Relationship between sire x year interactions and direct maternal genetic correlations for weaning weight of Simmental cattle. J. Anim. Sci. 75:68–75.
- Leggett, W. C. 1984. Fish migrations in coastal and estuarine environments: a call for new approaches to the study of an old problem. Pp. 159–178 *in* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, eds. Mechanisms of migration in fishes. Plenum Press, New York.
- ———. 1985. The role of migrations in the life history evolution of fish. Pp. 277–295 *in* M. A. Rankin, ed. Migration: mechanisms and adaptive significance. 27 (suppl.). Marine Science Institute, The University of Texas at Austin, Port Aransas, TX.

- Levin, L. A., J. Zhu, and E. Creed. 1991. The genetic basis of lifehistory characters in a polychaete exhibiting planktotrophy and lecithotrophy. Evolution 45:380–397.
- Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. Biol. Bull. 181:261–268.

——. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates. Am. Nat. 141:517–536.

- Levitan, D. R., M. A. Sewell, and F.-S. Chia. 1991. Kinetics of fertilization in the sea urchin *Strongylocentrotus franciscanus*: interaction of gamete dilution, age and contact time. Biol. Bull. 181:371–378.
- ———. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology 73:248–254.
- Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer Associates, Sunderland, MA.
- Mackay, T. F. C., and R. W. Doyle. 1978. An ecological genetic analysis of the settling behaviour of a marine polychaete. I. Probability of settlement and gregarious behaviour. Heredity 40: 1–12.
- Maldonado, M., and C. M. Young. 1999. Effects of the duration of larval life on postlarval stages of the demosponge Sigmadocia caerulea. J. Exp. Mar. Biol. Ecol. 232:9–21.
- McFarlane, G. A., and R. J. Beamish. 1986. A tag suitable for assessing long-term movements of spiny dogfish and preliminary results from the use of this tag. N. Am. J. Fish. Manage. 6: 69–76.
- McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally verying environments. Am. Nat. 140: 1010-1027.
- McShea, W. J. 1992. Alternative approaches to the study of small mammal dispersal: Insights from radiotelemetry. Pp. 319–332 in N. C. Stenseth and J. W.Z. Lidicker, eds. Animal dispersal: small mammals as a model. Chapman and Hall, London.
- Metaxas, A., and R. E. Scheibling. 1994. Spatial and temporal variability of tidepool hyperbenthos on a rocky shore in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 108:175–184.
- Metaxas, A., H. L. Hunt, and R. E. Scheibling. 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 105:89–103.
- Meyer, K. 1992a. Bias and sampling covariances of estimates of variance components due to maternal effects. Genet. Select. Evol. 24:487–509.
- ———. 1992b. Variance components due to direct and maternal effects for growth traits in Australian beef cattle. Livest. Prod. Sci. 31:179–204.
- Millet, B., and O. Guelorget. 1994. Spatial and seasonal variability in the relationships between benthic communities and physical environment in a lagoon ecosystem. Mar. Ecol. Prog. Ser. 108: 161–174.
- Moran, A. L. 1999. Size and performance of juvenile marine invertebrates: potential contrasts between intertidal and subtidal benthic habitats. Am. Zool. 39:304–312.
- Moran, A. L., and R. B. Emlet. 2001. Offspring size and performance in variable environments: field studies on a marine snail. Ecology 82:1597–1612.
- Pawlik, J. R. 1986. Chemical induction of larval settlement and metamorphosis in the reef-building tube worm *Phragmatopoma* californica (Sabellariidae: Polychaeta). Mar. Biol. 91:59-68.
- ——. 1992a. Induction of marine invertebrate larval settlement: evidence for chemical cues. Pp. 189–236 in V. J. Paul, ed. Explorations in chemical ecology: ecological roles of marine natural products. Cornell Univ. Press, Ithaca, NY.
- ——. 1992b. Chemical ecology of the settlement of benthic marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. 30:273–335.
- Pechenik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Mar. Ecol. Prog. Ser. 177:269–297.
- Pechenik, J. A., and M. E. Rice. 2001. Influence of delayed metamorphosis on postsettlement survival and growth in the sipunculan *Apionsoma misakianum*. Invert. Biol. 120:50–57.

- Pechenik, J. A., M. S. Estrella, and K. Hammer. 1996. Food limitation stimulates metamorphosis of competent larvae and alters postmetamorphic growth rate in the marine prosobranch gastropod *Crepidula fornicata*. Mar. Biol. 127:267–275.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern california rocky shore. Mar. Ecol. Prog. Ser. 107:125–138.
- Pullen, J., and M. LaBarbera. 1991. Modes of feeding in aggregations of barnacles and the shape of aggregations. Biol. Bull. 181:442–452.
- Quinn, T. P. 1984. Homing and straying in Pacific salmon. Pp. 357– 362 in J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, eds. Mechanisms of migration in fishes. Plenum Press, New York.
- ———. 1985. Homing and evolution of sockeye salmon (*Oncorhychus nerka*). Pp. 351–366 *in* M. A. Rankin, ed. Migration: mechanisms and adaptive significance. 27 (Suppl.). Marine Science Institute, The University of Texas at Austin, Port Aransas, TX.
- Quinn, T. P., and R. D. Brodeur. 1991. Intra-specific variations in the movement patterns of marine animals. Am. Zool. 31: 231–242.
- Raimondi, P. T. 1988a. Settlement cues and determination of the vertical limit of an intertidal barnacle. Ecology 69:400–407.
- ———. 1988b. Rock type affects settlement, recruitment, and zonation of the barnacle Chthamalus anisopoma Pilsbry. J. Exp. Mar. Biol. Ecol. 123:253–268.
- . 1990a. Patterns, mechanisms, consequences of variability in settlement, and recruitment of an intertidal barnacle. Ecol. Monogr. 60:283–310.
- ———. 1990b. Settlement behavior of *Chthamalus anisopoma* larvae largely determines the adult distribution. Oecologia 85: 349–360.
- Raimondi, P. T., and M. J. Keough. 1990. Behavioral variability in marine larvae. Aust. J. Ecol. 15:427–438.
- Ramakrishman, U., R. Martorell, D. G. Schroeder, and R. Flores. 1999. Role of intergenerational effects on linear growth. J. Nutr. 129:544S-549S.
- Robertson, D. R., S. E. Swearer, K. Kaufmann, and E. B. Brothers. 1999. Settlement vs. environmental dynamics in a pelagicspawning reef fish at Caribbean Panama. Ecol. Monogr. 69: 195–218.
- Robinson, D. L. 1996. Models which might explain negative genetic correlations between direct and maternal genetic effects. Livest. Prod. Sci. 45:111–122.
- Scheltema, R. S., I. P. Williams, M. A. Shaw, and C. Loudon. 1981. Gregarious settlement by the larvae of *Hydroides dianthus* (Polychaeta:Serpulidae). Mar. Ecol. Prog. Ser. 5:69–74.
- Schluter, D., and L. Gustafsson. 1993. Maternal inheritance of condition and clutch size in the collared fly catcher. Evolution 47: 658–667.
- Smith, L., D. K. Weaver, and R. T. Arbogast. 1995. Suitability of the maize weevil and angoumois grain moth as hosts for the parasitoids Anisopteromalus calandrae and Pteromalus cerealellae. Entomol. Exp. Appl. 76:171–177.
- Stenseth, N. C., and W. Z. J. Lidicker. 1992. Animal dispersal: small mammals as a model. Chapman and Hall, London.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799–802.
- Thiede, D. A. 1998. Maternal inheritance and its effect on adaptive evolution: a quantitative genetic analysis of maternal effects in a natural plant population. Evolution 52:998–1015.
- Todd, C. D., W. J. Lambert, and J. P. Thorpe. 1998. The genetic structure of intertidal populations of two species of nudibranch molluscs with planktrophic and pelagic lecithotropic larval stages: are pelagic larvae "for" dispersal? J. Exp. Mar. Biol. Ecol. 228:1–28.
- Toonen, R. J. 1993. Environmental and heritable components of settlement behavior of *Hydroides dianthus* (Serpulidae: Polychaeta). M.Sc. thesis, University of North Carolina at Wilmington, Wilmington, NC.

- Toonen, R. J., and J. R. Pawlik. 1993. For a marine tube worm, all larvae are not created equal. Am. Zool. 33:118A.
- ——. 1994. Foundations of gregariousness. Nature 370:511–512.
- ——. 1996. Settlement of the tube worm *Hydroides dianthus* (Polychaeta: Serpulidae): cues for gregarious settlement. Mar. Biol. 126:725–733.
- ------. 2001a. Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta: Serpulidae). I. Gregarious and nongregarious settlement. Mar. Ecol. Prog. Ser. *In press.*
- ———. 2001b. Settlement of the gregarious tube worm *Hydroides dianthus* (Polychaeta: Serpulidae). II. Testing the "desperate larva" hypothesis. Mar. Ecol. Prog. Ser. *In press*.
- Trapido-Rosenthal, H. G., and D. E. Morse. 1986. Availability of chemosensory receptors is down-regulated by habituation of larvae to a morphogenetic signal. Proc. Natl. Acad. Sci. USA 83: 7658–7662.
- Unabia, C. R. C., and M. G. Hadfield. 1999. Role of bacteria in larval settlement and metamorphosis of the polychaete *Hydroides elegans*. Mar. Biol. 133:55–64.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272–282.

- Verrill, A. E. 1873. Report upon the invertebrate animals of Vineyard Sound and adjacent waters, with an account of the physical characters of the region. Pp. 295–778 in C. S. F. Baird, ed. Report on the condition of the sea fisheries of the South Coast of New England in 1871 and 1872. Part I. Commission of fish and fisheries USA., Washington, DC.
- Wedell, N., and T. Tregenza. 1999. Successful fathers sire successful sons. Evolution 53:620-625.
- Wilson, D. P. 1953. The settlement of *Ophelia bicornis* Savigny larvae. J. Mar. Biol. Assoc. U.K. 32:209-233.
- Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphisms in insects. Annu. Rev. Ent. 42: 207-230.
- Zuraw, E. A., and D. E. Leone. 1968. Laboratory culture of the tubeworm *Hydroides (Eupomatus) dianthus* Verril [sic] 1873. General Dynamics, Electric Boat Division, Groton, CT.
- ———. 1972. Development of a tubeworm bioassay to evaluate antifouling coatings. General Dynamics, Electric Boat Division, Groton, CT.

Corresponding Editor: R. Burton