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LARVAL INVERTEBRATE WORKSHOP

LARVAE WHICH FALL FAR SHORT OF THEIR POTENTIAL: HIGHLY LOCALIZED RECRUITMENT IN AN ALPHEID SHRIMP WITH EXTENDED LARVAL DEVELOPMENT

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ABSTRACT

Many marine invertebrates which are sessile or sedentary as adults have larvae which swim actively for days or weeks in the laboratory. In such species it is generally assumed that the larvae disperse widely, and that settlement in the immediate vicinity of parents is a rare event. Here we present the results of a series of experiments whose purpose was to test this assumption. The subjects were three sibling species of alpheid shrimp which live symbiotically with the Caribbean sea anemone, *Bartholomea annulata.* The shrimp have larvae which in the laboratory are phototactic and swim actively for up to one week. On an isolated patch reef we placed anemones and either no adult shrimp, fertile pairs of *Alpheus immaculatus,* or pairs of *A. immaculatus* which were rendered infertile surgically. We monitored recruitment by all three alpheid species into anemones placed from 0–70 m from the reef. The three treatments allowed us to distinguish the effect of adult conspecifics in general (gregarious settlement) from the effect of conspecifics releasing young. Recruitment patterns of the three species were similar except in the presence of fertile pairs of *A. immaculatus.* During this treatment, there was a significant difference between *A. immaculatus* and the other two species, with the former showing enhanced recruitment into anemones placed within 6 m of the reef. This suggests that a detectable proportion of the successful recruits settled extraordinarily close to their parents.

Knowing how far organisms disperse is central to understanding behavioral interactions, ecological relationships and evolutionary potential. For this reason the dispersal of seeds and pollen in terrestrial plants (Harper, 1977; Handel, 1983), and the migrations of vertebrates and insects (Baker, 1978) have been well studied. Many marine invertebrates which are sessile or sedentary as adults have motile larvae which may account for much or all of the movement that occurs during the life cycle. Because it is difficult to study the behavior of these larvae, however, we still know relatively little about the distances successfully travelled for this important group of organisms, despite a long tradition of interest (Strathmann, 1974).

Our best information concerns the two extremes of dispersal potential. At one end of the spectrum, many marine invertebrates with direct development release larvae which typically travel very short distances and are incapable of extended swimming (reviewed by Jackson, 1985, 1986). These data come from direct monitoring of larvae in the field after their release (Olson, 1985) and from observations of settlement in the immediate vicinity of known or probable parents (Gerrodette, 1981; Neudecker, 1982), as well as from many laboratory studies of maximum larval longevity.

At the other end of the spectrum, for species whose young have at least the potential for moderate to wide dispersal, there are some data related to maximum dispersal distance. For example, range increases of 20–30 km/yr have been recorded for the introduced barnacle *Elminius,* whose larvae spend 10–15 days in the plankton (Crisp, 1958), and viable larvae of some species have been collected very far from potential sources (Scheltema, 1971). However, while maximum dispersal distance of larvae can be interesting, particularly in terms of biogeo-

graphic range (Jackson, 1986; Scheltema, 1986) and its evolutionary consequences (Vermeij, 1978), it does not tell us how far the majority of the successfully settling larvae travel. The possibility that many larvae in such taxa might settle close to their parents is rarely considered seriously, with the exception of some studies of larval retention in estuaries (Levin, 1983; Cronin and Forward, 1986). Yet information of this type is essential for evaluating, for example, the potential for kin selection, speciation, or the evolution of local adaptation (Crisp, 1978; Strathmann, 1982).

Here we present the results of a series of experiments whose purpose was to determine whether detectable levels of recruitment occur close to parental populations in a species with actively swimming larvae which are not initially competent to settle. We monitored recruitment both near and far from a central manipulated area where reproductive adults were either present or absent. We were able to distinguish between the effect of adult conspecifics in general [i.e., their role in promoting gregarious settlement, *sensu* Scheltema (1974)] and the effect of conspecifics releasing young, by comparing recruitment patterns in the presence of fertile vs. infertile adult conspecifics. The experiments were done in Discovery Bay, Jamaica, during 1983 and 1984.

The organisms we studied were three sibling species of alpheid shrimp which are obligate symbionts of the Caribbean sea anemone *Bartholomea annulata*: *Alpheus armatus* Rathbun and the newly described *A. immaculatus* Knowlton and Keller (1983) and *A. polystictus* Knowlton and Keller (1985). The first two species are abundant in Discovery Bay, while the third is comparatively rare. The three species can be distinguished reliably by subtle but consistent color differences at all post-settlement stages. Their association with anemones makes it relatively easy to collect recent recruits and manipulate the number and location of settlement sites, as the anemones act much like fouling panels do for sessile organisms inhabiting hard substrata.

In all three species reproductive adults live in male-female pairs (Knowlton, 1980). Mating occurs during every reproductive cycle because females do not store sperm; in the laboratory the eggs of females without mates never develop and are shed within 1 week. Females produce a new clutch of eggs every 3 weeks throughout the year, and these are brooded under the abdomen for a little over 2 weeks (Knowlton, 1980). Hatching typically occurs after dark but before midnight (pers. obs.).

Upon release, the first zoeal stage larvae (4.5 mm total length) lack chelae on the thoracic appendages and pleopods; thus they do not possess the morphological characteristics typically associated with abbreviated development (R. Knowlton, 1973). In the laboratory (unpubl. obs.) they swim actively towards the light, and are stung and usually killed if they touch the tentacles of their potential host. We have been unable to rear the larvae to metamorphosis in the laboratory, and all die within 8 days. The smallest juveniles found with anemones (5.5 mm total length) resemble the larvae in that they lack strong pigmentation and still have iridescent blue eyes, but the pleopods and the large, unequal first chelae characteristic of the family are by then well developed.

The minimum time required before the onset of metamorphosis is not known. R. E. Knowlton (1973) reported 4 days for an alpheid species with abbreviated development raised at 25°C [Discovery Bay water temperatures range from 26 to 29°C (Keller, 1983)], and suggested 2 to 3 weeks for species with "extended" development. Since the three species discussed here share the morphological characteristics of alpheids with extended development and are initially incapable

of living with anemones, they probably develop for at least 1 week prior to metamorphosis.

METHODS

The basic experimental procedure was to manipulate an isolated population of adult shrimp of one species and monitor recruitment by all three species at various distances from the manipulated area. The three experimental treatments in this area were: 1) no adults present, 2) fertile adult pairs of *A. immaculatus* present, and 3) infertile adult pairs of *A. immaculatus* present (see below for surgical technique). An increase in the proportion of *A. immaculatus* among all recruits collected near the manipulated area during treatment 2 (fertile conspecifics) would be consistent with the hypothesis of localized recruitment. Failure to obtain a comparable increase during treatment 3 (infertile conspecifics) would indicate that the shift in recruitment could not be attributed to gregarious settlement, that is a tendency for larvae from a variety of sources to settle near conspecifics (unless larvae distinguish between fertile and infertile conspecifics; see discussion).

All experiments were done on the east side of Discovery Bay, in and around an area called SAII (Knowlton, 1980). This site consists of a small patch reef with *B. annulata* (including large clusters capable of sheltering pairs of shrimp) surrounded by a sand plain largely lacking anemones. This site was chosen to minimize the problem of immigration by shrimp from other areas [previous mark-recapture studies of adults at SAII detected no movements greater than 4 m (Knowlton, 1978)]. Both of the abundant alpheid species are regularly found here (e.g., light and dark spined morphs of Knowlton, 1980).

On and immediately surrounding the patch reef we placed additional clusters of *B. annulata*, generally maintaining 40 in total. Each cluster consisted of from four to six anemones partially covered by coral rubble or a longitudinally split cement block to provide the anemones with an attachment surface. All shrimp were initially removed from the patch reef. Then, depending on the experimental treatment, the clusters were either left unoccupied or occupied by experimentally introduced pairs of shrimp. Numbers of adult shrimp on the reef during the experiments generally varied from 55 to 65 for fertile adult and infertile adult treatments, in comparison to 26 recorded during a 1976 census (Knowlton, 1978).

On the surrounding sand plain were 13 lines, each with 8 recruitment sites (Fig. 1). A recruitment site consisted of a single anemone (or sometimes two small anemones with overlapping tentacles), as juveniles typically live with and are easier to collect from single anemones or small clusters. Along a line the eight anemones were spaced 1 m apart. Ten of the lines were arrayed at 0, 2, 6, 14, and 30 m to the north and south of the patch reef; three were positioned 60 m to the northwest, 70 m to the east and 65 m to the southeast of the patch reef (directions and distances chosen because they led to areas −12 m or less in depth within the sand plain). The depth of the patch reef was −9.5 m, while the lines ranged from −7.5 to −12 m.

All shrimp were collected from the anemones at the recruitment sites during a 2-day period about once every 2 weeks. The shrimp were measured to the nearest 0.5 mm in total length and examined under a microscope to confirm species identifications. Occasionally an introduced adult from the reef would move to an anemone at a nearby recruitment site; these shrimp were returned to an available cluster. Otherwise, all collected shrimp were preserved. Anemones which had disappeared from recruitment sites during the preceding 2 weeks were replaced following the collection. All anemones on the reef were checked periodically to insure that no shrimp or only adult *A. immaculatus* were present (depending on the treatment). Additional *A. immaculatus* were added as needed to maintain the fertile adult and infertile adult treatments.

Changes in treatment were always preceded by a collection and followed by a 2-week interval before the first collection for the new treatment. The order of manipulations was no adults #1 (3 collections; 30 May–21 June 1983), fertile adults #1 (6 collections; 9 August–18 October 1983), infertile adults (6 collections; 3 November 1983–18 January 1984), no adults #2 (4 collections; 2 February–13 March 1984), and fertile adults #2 (6 collections; 26 March–4 June 1984).

At the beginning of the experimental treatment using infertile pairs, the adult shrimp were brought to the laboratory. All brooded eggs were removed from females with suction from an eyedropper. The second pleopods of males, which bear the structure used to transfer sperm (the appendix masculina), were cut off near the base with small scissors. Animals were restrained in a mesh bag to minimize injury during these procedures, and were returned to the field within 24 h. The process was repeated after 1 month because by then some males had regenerated functional second pleopods. During this treatment we saw no evidence of mortality, and pairs remained together as before, but as previously observed for females in the laboratory without mates, the eggs were a slightly paler color, failed to develop, and were shed prematurely.

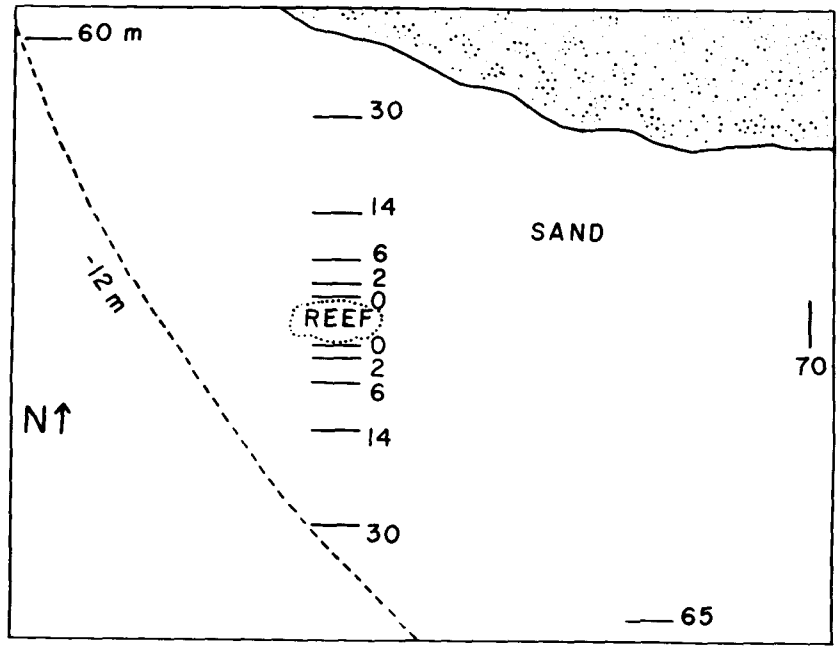

Figure 1. Diagram of study area. Bars (=8 m) represent lines of recruitment sites, each with eight anemones, on sand plain surrounding patch reef. Patch reef contained large clusters of anemones with no adults, fertile adults, or infertile adults, depending on treatment. Distance in meters from reef to each line of recruitment sites is indicated. Dotted line shows position of −12 m depth contour, and stippled area represents region nearest to patch reef with scattered rubble and naturally abundant *Bartholomea annulata.*

Results

Collections from anemones at recruitment sites yielded shrimp ranging from 5.5 to 40 mm in total length, i.e., a mixture of new recruits and individuals which moved to these anemones after settlement. Since only smaller individuals could reasonably be included in an analysis of recruitment, an upper size limit for recruits was set at 9.5 mm. This figure was based on earlier observations of growth rates of juvenile *A. armatus* at another site in Discovery Bay (Knowlton, 1978). These yielded the growth rate equation:

$$\text{mm/day} = 1.338(0.993)^{TL} - 1$$

where TL is total length in mm ($r^2 = 0.71$, $P < 0.001$). This equation was used to estimate an age of 14.8 days for 9.5-mm shrimp, assuming a starting point of 5.5 mm at time of settlement (days to grow 1 mm summed for the four 1-mm intervals between 5.5 and 9.5 mm). The size distribution of juveniles collected during this study supports the assignment of this cutoff point (Table 1). Most small shrimp were 6–7.5 mm long, with a small proportion of very recent recruits and a small proportion of individuals settling immediately after the previous census. Although the size classes bordering this cutoff point may have comprised a mixture of immigrants and recruits, their inclusion does not change the results of the analyses in any case. For the remainder of this paper, the term recruit will thus be used to refer to any individual 9.5 mm or less in total length.

Table 1. Size distribution of all shrimp 10.5 mm or less collected from anemones at recruitment sites during all treatments (each size class includes shrimp ranging from indicated size to indicated size plus 0.5 mm)

	Size classes						
	5 mm	6 mm	7 mm	8 mm	9 mm	10 mm	Total
A. armatus	21	257	126	66	41	26	537
A. immaculatus	17	96	39	18	9	6	185
A. polystictus	1	22	7	1	1	0	32
Total	39	375	172	85	51	32	754
% Grand total	5	50	23	11	7	4	

Several aspects of recruitment varied through time (Table 2). This can be seen in several measures, e.g., the overall recruitment rate and the proportion of recruits among all shrimp collected. Although the cause of this variation is not known, the higher incidence of storms between December and March was probably a contributing factor. This is reflected in the higher percentage of anemones missing per census and the greater movement of previously settled individuals into anemones at recruitment sites. Because of this temporal variation, all statistical analyses are made within treatments, rather than comparing recruitment patterns for particular species or distance classes across time intervals.

Alpheus immaculatus differed significantly from the other two species in settlement pattern only when fertile pairs of *A. immaculatus* were present (Table 3). Inspection of the percentages shows that during this treatment, recruitment by *A. immaculatus* increased markedly for the 0–6-m distance class, while the other two species showed no such trend. Thus if one compares the proportion of all recruits made up by *A. immaculatus* for the 0–6- vs. 14–70-m distance classes (Table 4), one again finds that differences are significant only when fertile pairs of *A. immaculatus* were present.

To further examine this pattern, we calculated for *A. immaculatus* and for the other two species the proportion of recruits observed to settle in the 0–6-m anemones vs. the number expected, considering only the distribution of available anemones in the three distance classes (that is, excluding all anemones except those

Table 2. Temporal variation in collections of shrimp (all species) from anemones at recruitment sites. Percent missing anemones indicates percentage of recruitment sites totaled over all censuses which had lost their anemones since the previous census. Percent recruits indicates the percentage of all collected shrimp which were 9.5 mm or less in total length

Treatment	Censuses (Nos.)	Missing anemones (%)	Recruits per anemone per census	Recruits (%)
No adults 1 5/30/83–6/21/83	3	11	0.47	92
Fertile adults 1 8/9/83–10/18/83	6	9	0.29	88
Infertile adults 11/3/83–1/18/84	6	17	0.27	69
No adults 2 2/2/84–3/13/84	4	44	0.37	63
Fertile adults 2 3/26/84–6/4/84	6	29	0.46	87

Table 3. Number of recruits of *A. immaculatus* vs. the other two species as a function of distance from manipulated area and treatment type. Anemones at recruitment sites were lumped into distance classes to achieve adequate sample sizes. Total number of anemones present for each treatment and distance class is given in parentheses next to distance; numbers vary depending on number of anemones present at each census and number of censuses. Total number of recruits slightly exceeds that indicated in Table 1 as several very small shrimp were not measured to nearest 0.5 mm. *Alpheus polystictus* is rare in Discovery Bay and made up less than 5% of all recruits collected (Table 1). Note that the distribution of recruits for *A. immaculatus* vs. the other two species across the three distance classes was similar except when fertile adults of *A. immaculatus* were present

Treatment	Distance (N)	No. recruits (%) *A. imm.*	No. recruits (%) *A. arm.* *A. pol.*	χ^2 P (2 df)
No adults	0–6 (232)	20 (43%)	64 (38%)	0.42
	14–30 (174)	16 (34%)	65 (38%)	$P > 0.75$
	60–70 (105)	11 (23%)	41 (24%)	
Fertile *A. imm.*	0–6 (458)	48 (52%)	100 (36%)	7.58
	14–30 (324)	26 (28%)	103 (37%)	$P < 0.025$
	60–70 (230)	18 (20%)	75 (27%)	
Infertile *A. imm.*	0–6 (249)	17 (40%)	42 (42%)	0.15
	14–30 (164)	18 (42%)	38 (38%)	$P > 0.90$
	60–70 (108)	8 (19%)	19 (19%)	

empty or occupied by recruits of the species in question) (Table 5). For *A. immaculatus* this ratio of observed to expected increased when fertile pairs of *A. immaculatus* were present, while for the other two species there was no strong pattern. This suggests that the increased relative importance of *A. immaculatus* recruitment within 6 m of the reef during the fertile adult treatment was not due to any change in recruitment pattern by the other two species, but rather simply to an increase in the number of *A. immaculatus* settling near conspecific, fertile adults.

Discussion

The patterns described above imply that even in a species whose larvae take from 1 to 2 weeks to reach readiness to settle, a detectable proportion of the successful larvae settled extraordinarily close to their parents. Note that the localized nature of recruitment is not simply within the same bay or estuary, as has

Table 4. Proportion of all recruits which were *A. immaculatus*. These proportions differed significantly between the 0–6 m anemones and the 14–70 m anemones only during the fertile adult treatment (test in Sokal and Rohlf, 1969, p. 607). Failure to achieve significance for the no adults treatment cannot be attributed to the smaller sample size, as the required sample size for each distance class to have an 80% chance of detecting a difference between 0.24 and 0.20 at a significance level of 0.05 is an order of magnitude larger than that realized for the fertile adults treatment (test in Sokal and Rohlf, 1981, p. 765). Required sample size was not calculated for the infertile adults treatment since the trend was in the wrong direction

Treatment	Proportion *A. imm.* (N) 0–6 m	Proportion *A. imm.* (N) 14–70 m	t	P (2 tailed)	Req. N
No adults	0.24 (84)	0.20 (133)	0.61	>0.50	2,259
Fertile *A. imm.*	0.32 (148)	0.20 (222)	2.72	<0.01	205
Infertile *A. imm.*	0.29 (59)	0.31 (83)	−0.32	>0.50	–

Table 5. Ratio of observed recruitment in the 0–6 m distance class to that expected. Calculation of expectation was based on the proportion of all available anemones found within 6 m of the reef. Calculations for *A. immaculatus* and the other two species were made separately, as available anemones were defined as those which were empty or contained a recruit of the species in question. Note that in general, recruitment within 6 m of the reef was lower than expected based on chance alone, but that it increased for *A. immaculatus* when fertile adults of that species were present

Treatment	Observed/Expected, 0–6 m	
	A. imm.	*A. arm.* *A. pol.*
No adults	0.79	0.78
Fertile *A. imm.*	1.04	0.80
Infertile *A. imm.*	0.76	0.83

been previously proposed for some species with larvae which can swim actively for days to weeks (Levin, 1983; Cronin and Forward, 1986), but on the scale of meters. This degree of localization has only been observed previously for those species known to have demersal, very short-lived larvae [e.g., the solitary coral, *Balanophyllia* (Gerrodette, 1981)].

Limitations.—Given the controversial nature of the results, one must carefully consider the limitations of these experiments. Two general categories of problems exist. First, the distinctiveness of the recruitment patterns observed during the presence of fertile adults could have been the result of chance, or of some specific environmental conditions affecting *A. immaculatus* differentially which happened to coincide with the time during which fertile adults of this species were present. Second, even if the distinctiveness were real, the interpretation of localized recruitment rather than gregarious settlement would be incorrect if widely dispersing larvae were attracted to settle in the presence of fertile conspecifics but were not attracted to settle in the presence of infertile, adult conspecifics. Although only further replications and modifications of these experiments can fully address these criticisms, several points which strengthen the proposed interpretation can be made at this time.

CONFOUNDING OF TREATMENT AND TIME. First, while the data for collections under identical treatments separated in time were pooled to achieve larger sample sizes, the trends were the same for both time periods for the two treatment types which were repeated, despite the fact that for both treatments the two time periods were at different times of the year and were characterized by different overall recruitment patterns (Table 2). For example, the within species percentages of recruits collected within 0–6 m for *A. immaculatus* vs. the other two species (Table 3) were 38% vs. 35% and 48% vs. 42% for the two no adult treatments, and 53% vs. 30% and 52% vs. 41% for the two fertile adult treatments. That is, the differences between *A. immaculatus* and the other two species in proportional recruitment close to the reef were consistently greater in the presence of fertile *A. immaculatus*. Second, a preliminary experiment (unpubl.) at the same site in 1981 produced similar although statistically insignificant results. In the absence of any adults on the patch reef, 83% of the 24 recruits collected within 5 m of the reef were *A. immaculatus,* while after the introduction of nine pairs of *A. armatus,* 66% of the 32 recruits collected were *A. immaculatus*. Finally, the pattern of recruitment by the rare *A. polystictus* during three censuses following the only observation of a pair of this species on the reef (Table 6) is also consistent with an interpretation of partially localized recruitment. These censuses had signifi-

Table 6. Recruitment patterns during the three censuses following the single observation (2/16/84) of a pair of *A. polystictus* on the reef, compared to recruitment patterns during the other censuses. Recruitment by *A. polystictus* was significantly higher during the three censuses in both the 0–6 m anemones and the 14–70 m anemones, but the effect was stronger near the reef (note the higher G value despite the smaller sample size for the 0–6 m anemones)

Distance Species	No. recruits 3/2/84–3/26/84	No. recruits Other censuses	G P (1 df)
0–6 m			
A. pol.	6	7	
A. imm.			7.74
A. arm.	37	241	$P < 0.01$
14–70 m			
A. pol.	5	14	
A. imm.			4.16
A. arm.	40	379	$P < 0.05$

cantly higher recruitment by *A. polystictus,* and the effect was much stronger within 6 m of the reef.

SUITABILITY OF CONTROLS. Selection for the ability of larvae to detect areas which are suitable for growth and reproduction is presumably one of the most important reasons for the widespread occurrence of gregarious settlement (Levinton, 1982, p. 154). In these symbiotic species effective habitat choice could be most easily accomplished by larval preferences for settlement in areas with the host anemone, or in areas with the host anemone and pairs of adult conspecifics. Since we know of no areas in which most pairs of adult shrimp living with anemones are unable to reproduce, selection for the more refined ability to detect the presence of fertilized eggs or recently hatched eggs or larvae seems unlikely. Moreover, in the one natural situation where this ability should be favored, it does not seem to occur: neither males nor females are apparently able to detect infertility caused by parasites in their mates, since pairs involving such individuals are stable (pers. obs.). Neither, to our knowledge, have settlement cues involving fertilized eggs or recently hatched eggs or larvae of conspecifics been reported for any gregariously settling species.

Possible Mechanisms and Adaptive Significance.—Although we have emphasized the localized portion of recruitment detected by these experiments, it must be remembered that a considerable proportion of the recent recruits came from more distant areas, since many recruits were also collected during the no adult and infertile adult treatments (Table 2). Although these other sources are unknown, they were at least 40–50 m distant, and it seems likely that populations throughout Discovery Bay and perhaps other areas as well were involved. Thus any discussion of mechanism or adaptive significance must address this variability in dispersal distance.

One way of achieving variable dispersal distance is through certain types of morphological variability in the larvae (Hadfield, 1972). However, these alpheid larvae show no obvious morphological variability either between or within clutches. Behavioral variability could be genetically programmed or dependent on variable experiences immediately following hatching (e.g., success or failure in encountering some threshold number of available host anemones). Models for the

evolution of both these types of mechanisms have been proposed. Hamilton and May (1977), for example, presented a model for the evolutionarily stable percentage of offspring which should leave the parental environment, and predicted that the percent of larvae leaving the parental environment should increase from 0% to 100% as the relative survival prior to settlement of dispersing vs. non-dispersing larvae increases from 0.5 to 1.0. Unlike many dispersal models (Strathmann, 1982), theirs does not require spatial or temporal variability, but rather assumes uniform, predictable environments with both local and distant sites occasionally vacant and available for recruitment. Optimal foraging models concerned with the problem of patch desertion (Krebs, 1978), on the other hand, would be most appropriate for the situation of disperal depending on the post-hatching experiences of individual larvae. Alternatively, one could assume that all larvae simply settle into the first available anemone they encounter, although some mechanism for maintaining position must be assumed when anemones are encountered soon after release, since larvae are initially stung and killed by anemones.

Implications.—Regardless of mechanism or any immediate adaptive significance, a mixture of local and longer-distance dispersal would have several interesting ecological and evolutionary implications. First, the larger the proportion of locally derived young, the greater is the likelihood of geographic variation in morphological, behavioral or electrophoretic characters (Crisp, 1978; Grassle and Grassle, 1978; Hedgecock et al., 1982; Burton and Feldman, 1982). Second, partially localized dispersal would increase the probability of interactions with relatives, with possible effects on patterns of aggressive behavior (Holmes and Sherman, 1982) and inbreeding (Shields, 1982). Third, interspecific competition in this context could make the establishment of a stable equilibrium mixture of species in a particular area less likely, as the species which finally became established in an area suitable for several species could largely depend on initial densities. If rarer species produced fewer offspring per female (as is likely for these alpheid symbionts, since individuals of locally rare species have more difficulty finding mates), then initial local inequalities in the relative abundance of species would be subsequently amplified through the proportional reduction in locally derived offspring produced by rarer species. Fourth, speciation through abrupt changes in host preference or mate preference would be more likely if relatives sharing the same characteristics were locally available as mates.

The potential importance of these factors depends on the average proportion of a female's successfully recruiting offspring which settle locally, as well as on the local density of adults and their degree of isolation from other populations. Since *B. annulata* is, in fact, quite patchily distributed (pers. obs.), at least some of these ecological and evolutionary effects would be expected in the alpheid symbionts of this anemone. In the absence of genetic markers it is not possible to estimate the proportion of young which were locally derived during this study. But measurable changes in recruitment patterns were obtained by manipulating a population of adults which represented a small fraction of the total populations of the three alpheid species in Discovery Bay (at most 1/20, and probably considerably less).

Finally, we do not claim that the pattern we have found must be typical of all groups with the potential for moderate to long-distance dispersal. But given these results and previously reported discrepancies between potential dispersal ability and patterns of genetic subdivision of populations (Burton and Feldman, 1982), one cannot assume that a capability for long-distance dispersal eliminates the

possibility of measurable recruitment in the immediate vicinity of parents. This view represents a marked departure from the traditional marine biological perspective.

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