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Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus*. IV. Larval settlement

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ABSTRACT: Settlement patterns of juveniles of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao were examined in 1982 and 1983. Newly settled crabs were found from mid-August to the beginning of December, and peak settlement occurred in September. Crabs settled near the water level of extreme low water spring tide (ELWS) in the study area, where small, vacant shells were abundant. The density of settled crabs and that of small vacant shells were positively correlated in August, November and December. The recently settled crabs were not found on the upper flat (about 1 m above ELWS) or in the subtidal zone 5 m below the ELWS, in spite of the abundance of small shells at those locations. Small, vacant shells were introduced into the lower intertidal zone of the study area, and their presence may have resulted in an increase in the number of settled juveniles. This possibility suggests that shortage of small shells limits the settlement of hermit crabs.

INTRODUCTION

Settlement and metamorphosis of planktonic larvae of marine invertebrates have been reviewed extensively in recent years (Thorson 1950, 1961, 1966, Mileikovsky 1971, 1976, Meadows & Campbell 1972, Crisp 1974, 1976, Gray 1974, Scheltema 1976, Chia & Rice 1978, Sastry 1983) in study which generally have been designed to increase our understanding of the spatial distribution and density of animals in nature.

In common with other decapod crustaceans, hermit crabs undergo a planktonic larval (zoea) stage, which becomes a megalopa (= glaucothöe) after several molts, settles, and metamorphoses into the benthic first crab. It is essential for the survival of hermit crabs and, therefore, for the establishment and maintenance of the crab population that glaucothöes find empty shells, because gastropod shells are an indispensable resource for hermit crabs. The shells provide protection against predators (Reese 1969, Vance 1972b) and physical stress (Reese 1969, Hazlett 1981). However, empty shells are scarce in nature (Hazlett 1970, Childress 1972, Fotheringham 1976b, Kellogg 1976, Scully 1979, Abrams 1980, 1981, Bertness 1980), and their availability may limit the size of individuals (Drapkin 1963, Markham 1968, Fotheringham 1976a, Bertness 1981a, d), the size of each clutch (Fotheringham 1980, Bertness 1981d), and the size of the population (Vance 1972a, Spight 1977).

I have studied the population ecology of and utilization of shells by the sand-dwelling hermit crab *Diogenes nitidimanus* on the sand flats of Amakusa, Kyushu, Japan. This species is by far the dominant species in the hermit crab assemblage of the flat, and most of the individuals use the shells of the sand snail *Umbonium moniliferum*, a dominant gastropod (Asakura & Kikuchi 1984a). Ovigerous females can be found from April to November with a peak in August, and they migrate to live in the subtidal water in summer (Asakura & Kikuchi 1984b, Asakura 1987a, b, c, d). The duration of the egg incubation is about 2 wk in water at 24 to 28 °C (Asakura 1987a), and the pelagic stage lasts 20 d at 26 to 29 °C (Baba & Fukuda 1986).

This report describes the pattern of crab larval settlement in relation to the abundance of vacant gastropod shells in the substratum and to the density of the adult crab population.

STUDY SITE AND METHODS

Study site and sampling methods. A sand flat (32° 3'N, 130° 1'E) at the northwestern corner of Amakusa Shimoshima Island, Kyushu, Japan, was selected for the study (Fig. 1; see also map in Asakura & Kikuchi 1984a). The flat extends about 2.5 km along the coast, and a strip 330 m wide is exposed to air at the low level of the extreme spring tide. In the subtidal zone, a

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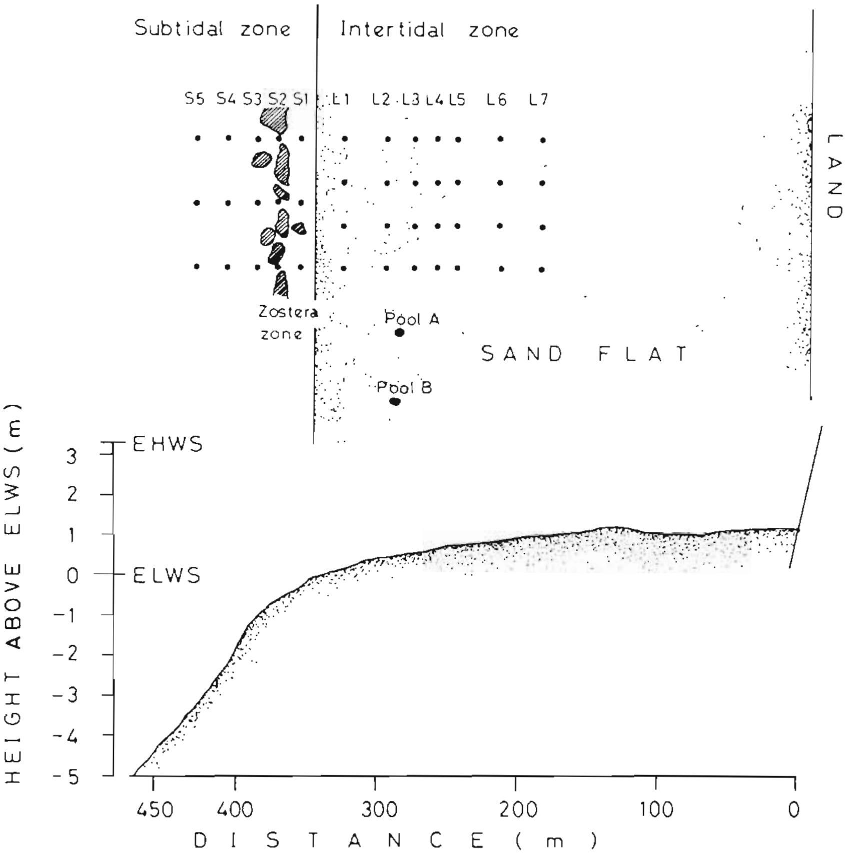

Fig. 1 Topographical profile of the sand flat and arrangement of the sampling points, with station codes. Pools A and B were used as experimental and control pools, respectively, when shells were introduced artificially. ELWS: extreme low water spring tide; EHWS: extreme high water spring tide

gentle slope continues for a distance of 10 to 12 m into the water, and then becomes much steeper. The sediment changes from sand to sandy mud at the lower edge of the gentle slope. There are several patches of eelgrass (*Zostera marina* L.), submerged at a depth of less than 5 m at low tide (Fig. 1).

Permanent sampling points were fixed on the lower shore (28 points) and subtidal zone (15 points) of the central part of the flat (Fig. 1). I took a quadrat sample (25 × 25 × 5 cm) at each intertidal point, and a grab sample (Ekman-Birge grab sampler; 20 × 20 cm; mean depth 5 cm, range 4 to 8 cm depending on type of sediment) at each subtidal point at the low level of spring tide, monthly, from June 1982 to June 1983.

The sampling depth (5 cm) was determined by the following considerations. (1) Crabs bury their bodies no more than 1.0 cm deep in the sand (Asakura 1984). (2) A preliminary field experiment was conducted with 3 replicates of 50 marked, small (< 5.0 mm in diameter), vacant shells of *Umbonium moniliferum* (in an area of 625 cm^2), in the layer from 2.5 to 5.0 cm below the surface. After 2 wk, 16.0 % (± 5.7 %, SD) of shells had been washed out from the substratum, and, after 4 wk, an additional 22.0 % (± 8.5 %, SD) had been washed away. By way of contrast, 3 sets of marked shells in the layer from 5.0 to 7.5 cm below the surface were not dispersed over a period of 4 wk (Asakura 1984). Based on these results, although shells buried at a depth of more than 2 cm were obviously too deep for crabs to use immediately, such shells were considered to be potentially available for crabs during the considerable time span of this experiment.

The sediment samples were sieved through 0.5 mm mesh, and hermit crabs, gastropods, and vacant shells were sorted from the residue in the sieve, fixed in a 10 % formalin solution, and identified to species. The shield length (SL, hard portion of the carapace; McLaughlin 1980) of each crab and the diameter of each shell were measured with an ocular micrometer.

Crabs less than 1.0 mm in SL were regarded as recently settled and are defined here as juveniles, because just-settled crabs (SL = 0.5 ± 0.05 mm) grew to 1.0 mm in SL within 7 d during culture in the laboratory with sufficient food and a supply of shells (Asakura 1987a).

Factors influencing distribution of juveniles. The relationship between the distribution of juveniles and that of crabs more than 1.0 mm in SL was examined and assessed in terms of the correlation coefficient, r.

To investigate the spatial distribution of small shells acceptable to the recently settled crabs, the sizes of such shells were assessed by measuring shells already

Table 1. *Diogenes nitidimanus*. Sizes of shells utilized by newly settled hermit crabs (<1.0 mm SL). Shells were collected from the sampling points in the study area shown in Fig. 1; 377 juveniles were examined

Species	Shell diameter (mm)	No. of crabs examined
Cantharidus japonicus	1.80–4.50	23
Iwakawatrochus eucosmius	2.50–4.65	6
Umbonium moniliferum	1.90–4.80	140
Batillaria multiformis	1.35–4.00	25
Australaba picta	1.30–4.00	28
Proclava kochi	1.60–3.90	7
Bedevina birileffi	2.20–3.35	27
Mitrella lischkei	1.30–3.35	16
Reticunassa japonica	1.35–3.25	40
Hinia festiva	1.70–3.80	19
Niotha livescens	1.50–3.55	8
Nassariidae g. sp.	1.70–3.20	15
Paradrillia consimilis	1.80–3.25	8
Terebridae g. sp.	2.05–3.20	15

occupied by 377 crabs of less than 1.0 mm SL. They were collected from the study area shown in Fig. 1 during the period from June 1982 to June 1983. Table 1 shows the sizes of these shells, which are defined here, as 'suitable' for recently settled crabs.

The relationship between the distribution of juveniles and that of the small vacant shells was examined and assessed in terms of the correlation coefficient, r, for all sampling stations (rows of sampling points) and for all stations excluding peripheral ones (L6, L7 and S5; see Fig. 1), where both adults and juveniles were very rare (see 'Results').

Introduction of small shells. To examine the influence of a high density of small vacant shells on crab settlement, a large number of small shells acceptable to juveniles was introduced onto the flat.

In March 1984, a considerable quantity (ca 120 m^3) of dredged sediment, including pebbles, was dumped onto the lower part of the sand flat, forming a mound about 18 m in diameter and 75 cm in height at its thickest point. Two shallow pools, situated 15 m from each other, formed naturally, landward of the mound (Pools A and B in Fig. 1), as a result of alterations in the discharge route of seawater at low tide.

About 10000 vacant shells of young *Batillaria multiformis* (< 4.0 mm in diameter, suitable size for use by juveniles; see Table 1) were introduced on 2 August 1984 into Pool A (72 m^2). [Ovigerous females are present at the highest density during August (Asakura & Kikuchi 1984b).] The vacant shells were those of snails which had been collected at a separate site and boiled and cleaned to remove the flesh. Pool B (80 m^2) remained in its natural state, as a control. The environmental conditions of both pools were very similar, i.e. they were situated at the same tidal level, mean water depths at low tide were ca 10 cm, bottoms were very smooth, and the bottom sediment was sand. At low water of spring tide (the period from 8 to 12 August and from 24 to 30 August), juvenile crabs were collected by sieving sediment from the upper 1 cm layer at the bottom of the pools through 0.5 mm mesh. Juveniles bury their bodies within 0.5 mm of the surface at the time of low water (Asakura unpubl.), so the sampling depth was adequate for such collection.

The sampling was completed on 30 August (1 mo after shell introduction) for the following reason. In a preliminary field experiment, in which 3 replicates of 50 marked, small (< 5.0 mm in diameter), vacant shells (in an area of 625 cm^2) were placed on the surface of the sand flat, the shells disappeared from the surface within 3 d, some being lost by wave action, others being buried in the sand. After 2 wk, no shells remained in the upper 2.5 cm layer, and 74.0 % (± 2.8 %, SD) of the marked shells were found at a depth of more than 2.5 cm (Asakura 1984). Thus, 1 mo was considered sufficient time to allow for most of the introduced shells to be buried deeper than 2.5 cm depth or to be washed away, with no available introduced shells remaining in the upper 2.5 cm layer

RESULTS

Seasonal variations in the numbers of juveniles collected are shown in Fig. 2. Juveniles appeared from 19 August to 1 December 1982. No juveniles were collected on 3 and 21 July 1982 or during the sampling period from 16 December 1982 to 11 June 1983.

Fig. 3 shows the spatial distribution pattern of the juveniles. The higher densities of juveniles were observed near the water level of ELWS (extreme low water spring tide), i.e. at the sampling points on the lower half of the flat in August (L1), September (L1), October (L2) and November (L2), and at the sampling points in the upper subtidal zone in December (S2). Thus, the main settlement area was between Stns S3 and L4. The juveniles seldom settled in the upper flat (above Stn L4) or in the lower subtidal zone (below Stn S3).

Fig. 2. *Diogenes nitidimanus*. Seasonal changes in the density (no. per 7500 cm^2; means ± SD) of newly settled juveniles (< 1.0 mm SL) in the study area, 1982 and 1983

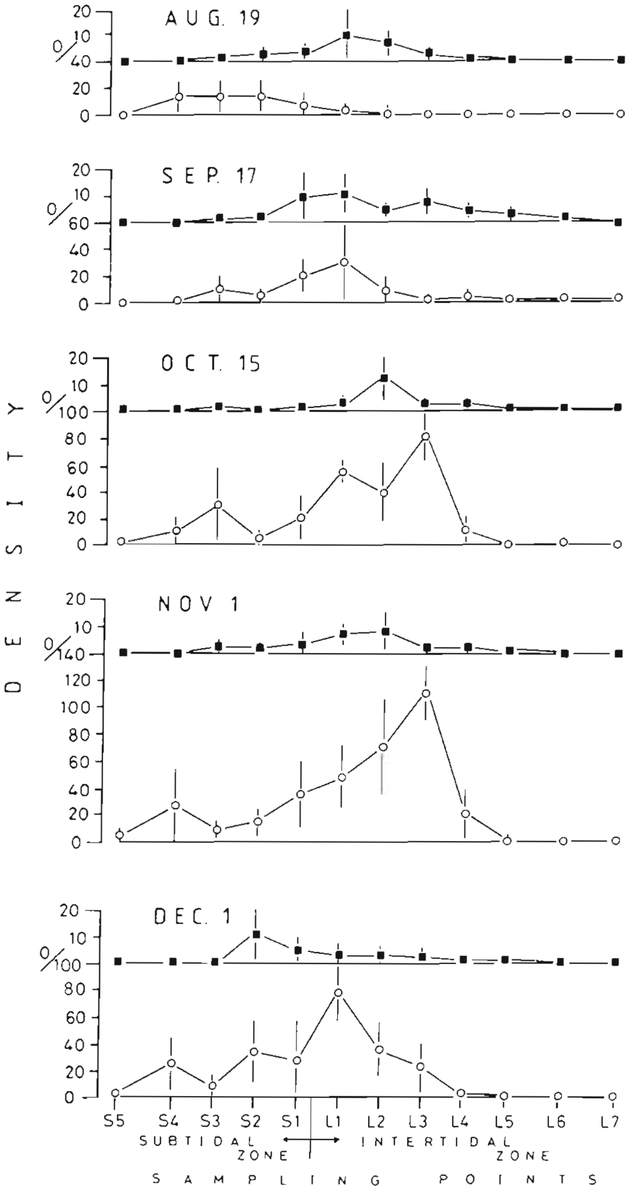

Fig. 3. *Diogenes nitidimanus*. Changes in distribution patterns of newly settled juveniles (< 1.0 mm SL; ■—■) and larger crabs (≥ 1.0 mm SL; ○—○) from August to December 1982. Density: no. per 625 cm^2; means ± SD. No juveniles were collected in June and July 1982 or from January to June 1983 (see Fig. 2)

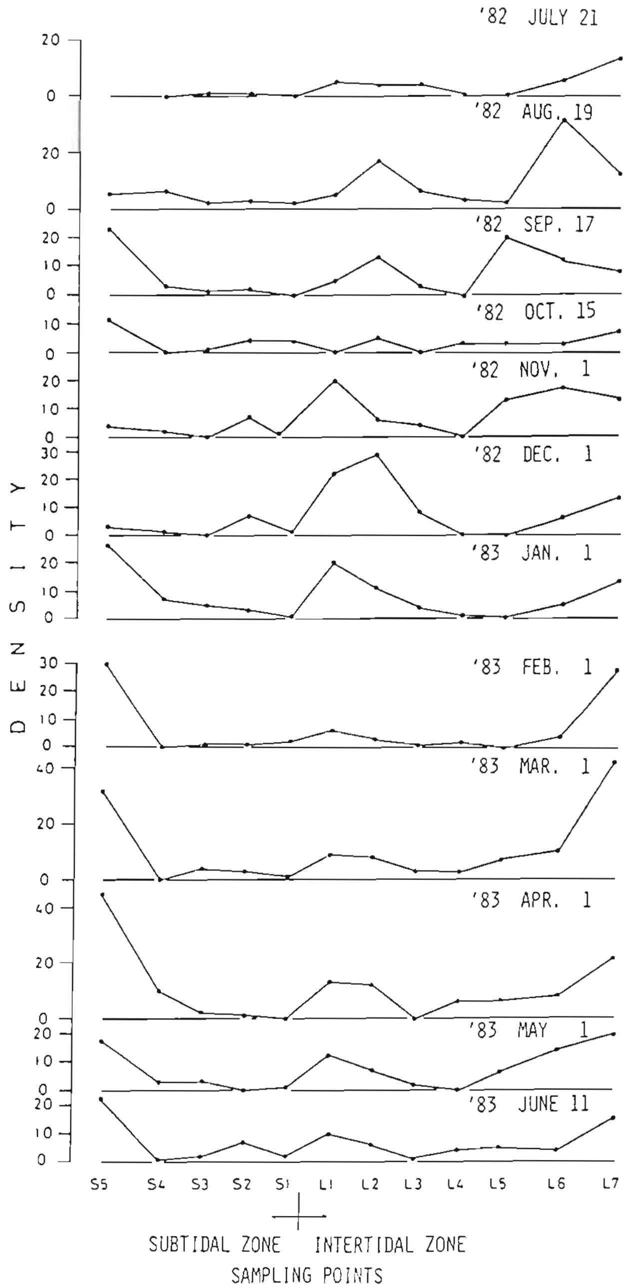

Fig. 4. Distribution pattern of the small vacant shells suitable for newly settled hermit crabs *Diogenes nitidimanus* (< 1 mm SL) along the sampling transects in 1982 and 1983. Density: no. per 625 cm^2

Significant positive correlations were detected between the distribution of the juveniles and that of crabs larger than 1.0 mm SL for the period from September to December (Table 2).

The temporal patterns of distribution of vacant shells suitable for the settled juveniles (see Table 1) are shown in Fig. 4. Three obvious regions of increased density of shells were observed in most months: around the stations on the upper flat (L6 and L7), near the ELWS stations (L1 and L2), and around the lower subtidal stations (S5).

Each region corresponds to the presence of different kinds of shell. The upper intertidal zone is inhabited by small individuals of *Umbonium moniliferum* (< 5.0 mm in diameter), which migrate into the lower intertidal zone as they grow and die, in particular from March to May (Tamaki 1984a, Asakura 1987a). The large number of shells of *Cantharidus japonicus* in the subtidal zone was derived from the patches of *Zostera marina* (Asakura & Kikuchi 1984a). The shells collected

Table 2. *Diogenes nitidimanus.* Correlation between the density of newly settled crabs (< 1.0 mm SL) and that of crabs > 1.0 mm SL (sample size = 43 for each month and 215 for all data from 5 mo). r: correlation coefficient

Date (1982)	r
19 Aug	−0.17
17 Sep	0.57***
15 Oct	0.35*
1 Nov	0.47**
1 Dec	0.63***
All 5 months	0.27**

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

Table 3. *Diogenes nitidimanus.* Correlation between the density of newly settled crabs (< 1.0 mm SL) and that of small vacant shells (see Table 1). Sampling Group 1. calculations for all of the sampling stations (sample size = 43 for each month and 215 for all data from 5 mo); Sampling Group 2: calculations for all of the stations except for those on the periphery of the study area (L6, L7, and S5) (sample size = 32 for each month and 160 for all data from 5 mo). r: correlation coefficient

Date (1982)	Sampling group	r
19 Aug	1	0.16
	2	0.81***
17 Sep	1	−0.43**
	2	0.20
15 Oct	1	−0.20
	2	0.09
1 Nov	1	−0.21
	2	0.35*
1 Dec	1	−0.04
	2	0.35*
All 5 months	1	−0.08
	2	0.25**

* $p<0.05$, ** $p<0.01$, *** $p<0.005$

near ELWS were of many different types, coming from both the intertidal and subtidal areas and from both soft and hard bottoms (Asakura & Kikuchi 1984a).

In the main settlement area (Stns S4 to L5), positive correlations were detected between the distribution of the juveniles and that of the small shells during the entire period from August to December; these correlations were significant in August, November and December (Table 3). In contrast, in the entire sampling area, no significant correlation was detected in August, October, November and December, and even a negative correlation was found in September.

The introduction of small shells (Pool A) resulted in an increase in the number of juveniles, as compared with the control area (Table 4). No small vacant shells remained in the upper 1 cm layer of bottom sand in the control pool at the end of the observation. At no time during the study period did juveniles under natural conditions attain the high densities found in Pool A.

DISCUSSION

Factors influencing spatial distribution of juveniles

There was a general tendency for juveniles to appear near the water level of ELWS, between Stns L5 and S4. Adult crabs also predominantly inhabited this area, and a positive correlation between the distribution of juveniles and that of adults was seen from September to December. However, no such correlation was seen in August, so the seasonal migration of adults (Asakura & Kikuchi 1984a) seems to have no major effect on the distribution of juveniles. However, since the influence of adults on larval settlement has frequently been reported for many marine invertebrates (Allen 1963, Crisp 1964, 1974, 1976, Thorson 1966, Woodin 1974, Brock 1980, Peterson 1982), further detailed investigation of this issue is necessary.

The area near ELWS also contained many shells, and there was a significant positive correlation between the distribution of the juveniles and that of the small shells in most months. In some cases, values of the correlations were rather low or not significant. This is probably because I collected crabs within 1 wk after settlement (see 'Methods'), so that they had time to become slightly dispersed from the settlement points.

Table 4. *Diogenes nitidimanus.* Numbers of newly settled crabs (< 1.0 mm SL) in pool A, into which ca 10 000 vacant, small shells of *Batillaria multiformis* were introduced on 2 August and in the control pool (Pool B)

Date (1984)	No. of juveniles	
	Pool A	Pool B
8 Aug	80	6
9 Aug	76	7
10 Aug	15	3
11 Aug	0	0
12 Aug	2	0
24 Aug	45	1
25 Aug	104	3
26 Aug	44	2
27 Aug	7	0
28 Aug	0	0
29 Aug	32	2
30 Aug	21	0
Total	426	24

Although there appeared to be more shells available in this area, those which were immediately available for juveniles were completely utilized, probably for the following reason. The vertical distribution of vacant shells in the sand on the flat was studied previously by analysis of core samples (cross-sectional area = 100 cm^2; 5 cm depth) taken from each sampling point (Asakura 1984). The small shells in the upper 1 cm layer accounted for only 11.42 % (± 10.06 %, SD; n = 55) of the total number of shells in the upper 5 cm layer. The rest were buried at depths greater than 2 cm, so that crabs could not immediately utilize them, although they were potentially available over the long term (as mentioned in the 'Methods'). Thus, most of the shells in the area near ELWS were believed to be buried at a depth of more than 2 cm.

In the lower subtidal zone, juveniles were scarce despite the abundance of shells. Since very few adults were found there (Fig. 3), the depth of seawater (ca 5 m at low tide) may limit the distribution of crabs. This species generally inhabits intertidal and very shallow subtidal areas less than 3 m in depth, and their seasonal migration occurs in these areas (Miyake & Imafuku 1980, Nojima et al. 1980, Asakura & Kikuchi 1984a, b, Asakura 1987a).

Juveniles were also scarce in the upper flat in spite of the abundance of small shells. This scarcity was probably due to the presence of ghost shrimp *Callianassa japonica*. The fauna of this same flat has been intensively investigated by Tamaki (Tamaki & Kikuchi 1983, Tamaki 1984a, b, 1985a, b, c, 1986, 1987, 1988), who found that *C. japonica* had recently invaded the upper flat, attained a high density (mean 330 ind. cm^{-2} in 1982, above Stn L5), and inhibited the habitation and settlement of many animals, including *Diogenes nitidimanus* (Tamaki 1984a). Such negative effects of ghost shrimp on other organisms have also been reported by others recently (Aller & Dodge 1974, Peterson 1977, Posey 1986, Suchanek & Colin 1986, Suchanek et al. 1986).

However, if we are to define completely those factors that limit the upper distribution of juveniles, we must also investigate other possibilities, such as physical effects that influence conditions on the upper flat (desiccation, extreme temperature upon emersion, etc.) and may affect settlement.

Population process and small-shell limitation

The results of the shell introduction experiment suggest that high numbers of small shells may increase the number of settled crabs on the flat. In general, there is much inferential and little direct evidence to indicate that the number of shells limits the population size of hermit crabs (Vance 1972a, Spight 1977, Wilber & Herrinkind 1984; see Hazlett 1981 for review). Earlier studies have not, however, included any emphasis on the size of shells.

Nevertheless, the presence of many small shells in the field has been observed by Vance (1972a), Fotheringham (1976b), Conover (1979), and Hazlett (1981). It has also been reported that small crabs have used shells of a preferred size in several populations (Vance 1972a, Bertness 1980, 1981b, c). Fotheringham (1976b) and Hazlett (1981) concluded that, in the field, there is a surplus of appropriate-sized shells for recently settled crabs. The results of the present study are not in agreement with their conclusion; this discrepancy may arise from a failure to consider the population processes of both hermit crabs and gastropods.

The stages at which shells are scarce should be related to the size of crabs, particularly the size during settlement by larvae and during the growth period, and when the crabs are mature adults. In temperate regions, these stages cycle seasonally, because reproduction of most species of hermit crabs is seasonal (see discussion in Asakura & Kikuchi 1984b). Temperate gastropods also exhibit seasonality in their growth and survival (Underwood 1979). Therefore, an appropriate determination of whether shells are scarce or abundant is complex, since relative scarcity or abundance depends on timing and on the balance between the number and size of shells produced by snail populations and the number and size of shells required by hermit crab populations.

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