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Vertical variations of larval release and settlement of the intertidal barnacle, *Chthamalus challengeri* Hoek*

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Abstract: The intertidal barnacle, *Chthamalus challengeri* Hoek, is common in the high tide zone of rocky shores in Japan. The total number of settlers and total reproductive output of the species were estimated different tidal levels at Amakusa, Kyushu, Japan. The larvae of this species settled throughout the intertidal zone. However, most of the settlement was occurred near the *Chthamalus* zone, which is actual high tide zone. In the lower half of the *Chthamalus* zone (high density zone), larval settlement and total reproductive output were high because of high density. In contrast, in the upper half of the *Chthamalus* zone (upper zone), larval settlement was only moderate but total reproductive output was high because of existing largest barnacles. In the middle and lower intertidal zones (*Tetraclita* zone and limpet zone), most barnacles died before reproduction.

Contribution to the next generation (total reproductive output per unit area) from the upper zone was as much as that from the high density zone, even though the adult density and coverage at the reproductive season were lower. The ratio of total number of settlement to total number of the reproductive output was estimated as 0.107% of the total population of entire intertidal zone which differed greatly for various tide levels (0.02–64%). The ratio at the upper zone was 0.02%, which was the lowest value, and that of the high density zone was 0.079%. The highest value of this ratio was observed at upper *Tetraclita* zone.

1. Introduction

Many marine invertebrates have a planktonic larval stage (THORSON, 1950; CHIA, 1974). When studying the life history or population dynamics of benthic species with a pelagic larval stage, usually only the life cycle after settlement has been investigated, because planktonic stages make larval survivorship impossible to measurve. Also, mortality after settlement is more important than mass mortality in the planktonic stage in determining the total level of the population (THORSON, 1966). Ecological distribution of a benthic species is generally limited or determined by the settlement patterns with time and space. Therefore, detailed investigation of settlement pattern (spatial distribution and temporal variation in the amount of settlement) is needed to understand the population dynamics of a species.

ROUGHGARDEN and his colleagues proposed a demographic theory, which is basically constructed by two components (adults population and larval pool), for an open marine population with space-limited recruitment (ROUGHGARDEN *et al*., 1984, 1985; ROUGHGARDEN, 1986). However, they did not consider the vertical variation of population characteristics and life history traits, that varies greatly with tidal level (CONNELL, 1961a, 1961b; LEWIS and BOWMAN, 1975, and many others).

The acorn barnacle, *Chthamalus challengeri* Hoek, is common in the high tide zone on both exposed and sheltered rocky shores in Japan, and juveniles settle throughout the intertidal zone (MORI *et al*., 1985a, 1985b; MORI and TANAKA, 1989). An exposed natural rocky shore covering the whole intertidal zone was selected for the study. In this paper, vertical variation of total number of settlers and total reproductive output of *C. challengeri* subpopulation at several tidal levels are reported. Then, the population system model for an open population is proposed, and mechanisms for the persistence

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of this population are discussed.

2. Study sites, materials and methods

The main study station, E13, is located in the west coast of Tsuji-shima Island, Amakusa, Kyushu, Japan. Topography and the community structure at Tsuji-shima Island has been reported in previous papers (Mori *et al*., 1985a, 1985b; Mori and Tanaka, 1989; Tanaka *et al*., 1985). Full details of environmental conditions and community structures of E13 station were given in Mori and Tanaka (1989).

The lower part of Fig. 1 shows the profile of the E13 station and the arrangement of the sampling quadrats. A belt transect method was adopted for sampling, and 22 quadrats (50 cm × 50 cm) were set up from the 290 cm tide level to the 0 cm tide level. Field population dynamics were investigated by photo-sampling the permanent quadrats. Permanent quadrats were set up on the shore with no conspicuous marks to eliminate artificial disturbances. However, I could find the position of every quadrat at every sampling time by using the photographs in which the crevices, bumps and small grooves of the rock surfaces have been taken. From April 1981 to August 1987, routine photo-sampling was carried out biweekly (every ebb tide of spring tide) in the warm seasons and monthly in the cole seasons. At a sampling time (one spring tide), about seven days continuous photo-sampling was carried out.

The field population of the barnacle *C. challengeri*, at various stations were estimated by photo-sampling. As described before, 50 cm × 50 cm permanent quadrats were set up at Stn. E13 and each quadrat was divided into twenty-five 10 cm × 10 cm sub-quadrats. Five to fifteen sub-quadrats were randomly selected, and monochrome photographs were taken from an overlooking position. In order to investigate the juveniles just after settlement, a close-up photograph at the center of each sub-quadrat was taken with a 35 mm camera using a 50 mm macrolens with a focal framer. By this method, half of the real size picture was documented on film, and clear printed copies could be obtained after high magnification enlargement. We could recognize cyprid larvae just after settlement in those photographs.

Reproductive output of the subpopulations at different tide levels was estimated as the number of eggs produced during the reproductive season from April to August in 1982. This gave a precise assessment of their respective contributions to the next generation. Possible number of eggs per unit area (10 cm^2) was estimated using the data of the population characteristics and reproductive characteristics of the barnacle. Reproductive characteristics of the barnacle, such as size-egg number relation, size-maturity relation, brooding percentage and number of broods were investigated in two tide levels, E13-2 and E13-4. Reproductive characteristics at E13-2 were applied to E13-1 and E13-3, while those at E13-4 were applied to the rest of the quadrats. Thus, the total reproductive output for E13 station was estimated from the data of reproductive output of each quadrat.

3. Results

Vertical distribution

The vertical distribution of coverage and density of *C. challengeri* in July 2, 1982 is shown in the middle part of the Fig. 1. High values of percentage cover (more than 50%) were recorded in the upper intertidal zone and this zone was recognized as the *Chthamalus* zone. No barnacle was found in zones higher than E13-1. Below E13-20, there was a calcareous algae zone with about 100% calcareous algae cover. *C. challengeri* has never been seen in this zone. The highest coverage (80%) was recorded in the quadrat E13-3, and henceforth decreased continuously to 10% at E13-7. The coverage never exceeded 10% in the middle and lower intertidal zones. The highest value of density was recorded at E13-5. Even though the peak of density was observed at a lower tide level than that of the coverage, the pattern of distribution remained same. In quadrats E13-19 and 20, variance was larger than the other quadrats because the barnacles showed patchy distribution within the quadrat (50 cm × 50 cm). Almost

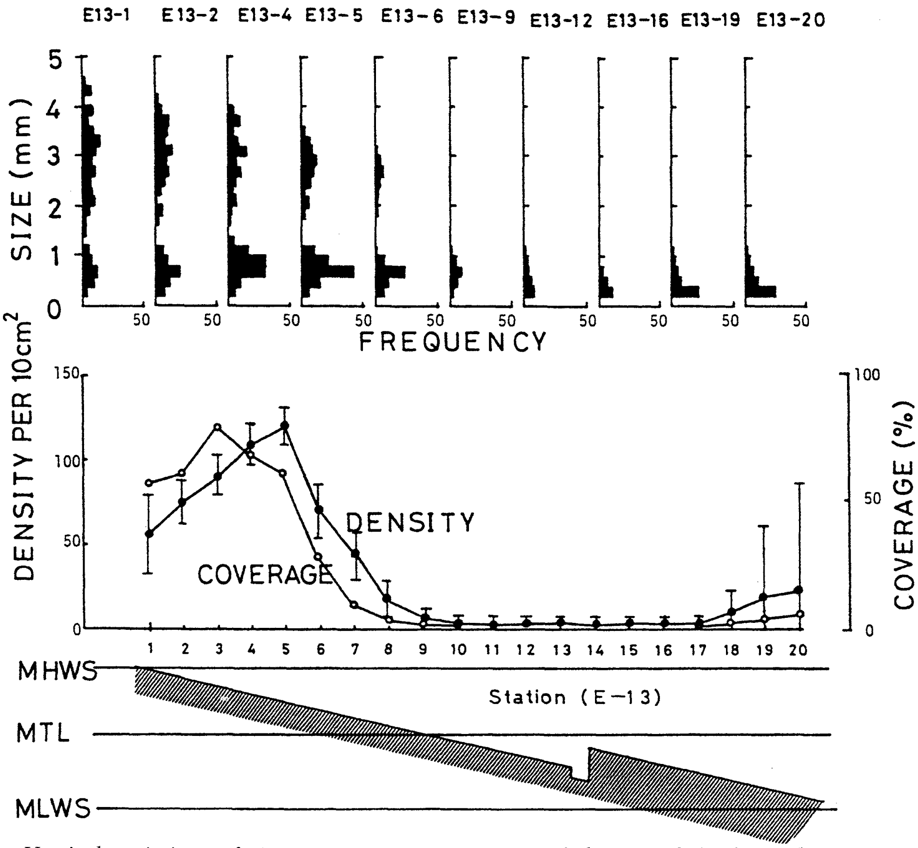

Fig. 1. Vertical variations of size composition, coverage and density of the barnacle at E13 station, in July, 1982, and profile of the E13 station. The size of barnacle is represented by length of the opercular portion. Vertical bar of density shows standard deviation.

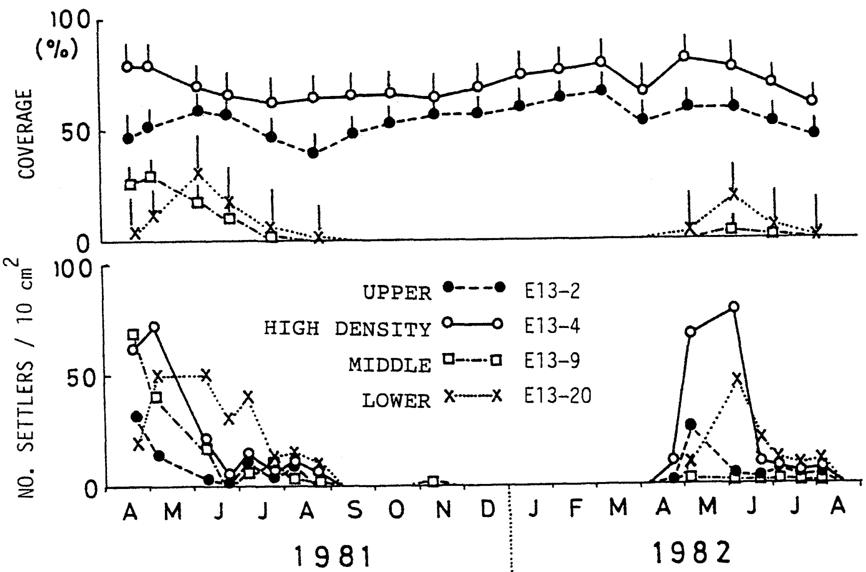

Fig. 2. Seasonal fluctuations of percentage coverage and settlement of *C. challengeri* at four tidal levels of E13 station, Tsuji-shima in 1981 and 1982. Each value for coverage shows the mean ±standard deviation.

the same density as the upper tide zone was recorded in some small quadrats (25 ㎠, 10 ㎠) but no barnacles were recorded in other small quadrats.

The size frequency distribution of the barnacle at each quadrat is shown in the upper part of Fig. 1. Individuals with an opercular length greater than 1.4 mm (indicating the 1 +and older year classes were collected from E13-6 and upward. Larger individuals (based on the mean and maximum size) appeared at the higher tide levels. Small barnacles with an opercular length less than 1.2 mm (indicating the 0+ year class) occurred in all zones. In the upper zone, the larger size (0.6-0.8 mm) barnacles were the dominant size within the 0+ year class. Individuals of 0.2 mm to 0.4 mm occurred densely in the lower quadrats. The size range suggested that they settled within two weeks and the absence of large size classes suggest quick elimination of barnacles after settlement.

Seasonal changes of settlement and percent coverage

Fig.2 shows the seasonal changes of settle ment and percentage cover of *C. challengeri* at four tide levels, E13-2, 4, 9 and 20. Few barnacles settled even in mid-winter, and more than 99% of the barnacles settled from April to August. Generally, the settlement season is from April to August, and most settlement occurs between April and May. The beginning and peak of settlement at E13-20 were later than the rest of the tidal levels. Furthermore, the spatial distribution of settling at E13-20 was patchy.

At middle and lower tidal zones, almost all the barnacles died off by September, although in April 30% coverage was observed in the lower zone (E13-20). At E13-9, settlement was dense in 1981, but sparse in 1982. At the upper two tidal zones, coverage was observed to be high in all the years. Available space for settlement was 40% to 60% at E13-2 and 20% to 35% at E13-4. Number of recruits per available space at E13-4 was five to ten times more than that of E13-2 and E13-20.

Vertical variation of total number of settlements

Table 1. Total number of settlements at each subpopulation and that of E13 station during the settling season in 1982.

Sub-population	Total number of settle. /10 ㎠	%
E13-1	22.4	2.5
E13-2	51.4	5.8
E13-3	93.3	10.5
E13-4	178.7	20.2
E13-5	196.5	22.2
E13-6	113.2	12.8
E13-7	79.3	8.9
E13-8	18.1	2.0
E13-9	9.3	1.1
E13-10	5.1	0.6
E13-11,14	2.2	0.2
E13-12,15	4.1	0.5
E13-13,16	2.7	0.3
E13-17	4.4	0.5
E13-18	27.1	3.1
E13-19	30.1	3.4
E13-20	47.3	5.3
Total	885.2	99.9
Mean settlements /10 ㎠		52
Total settlements in St. E13 (0.5m × 8.5m =4.25 ㎡)		221,300

Total number of settlements of each sub population (E13-1 to E13-20) and that of Stn. E13 based on the data from 1982 are shown in Table 1. High values of total number of settlements were recorded in upper zone, and the highest settlings occurred at E13-4 and E13-5, which was located at the lower part of *Chthamalus* zone and below. No barnacles settled in higher tide levels than E13-1.

Reproductive output of each subpopulation

Table 2 shows the estimated reproductive output as the number of eggs per unit area during the reproductive seasons, based on the data from 1982. Details of reproductive traits and population characteristics of each subpopulation are under preparation. The total reproductive output of the subpopulation at 5 quadrats in the high tide zone (E13-1 to E13-5) reached 96% of that of whole population of Stn. E13. It is clear that the low and mid intertidal zone subpopulations hardly contribute to the next generation of

Table 2. Possible reproductive output per unit area during the reproductive season in 1982 and total reproductive output of E13 station.

Sub-population	No. of eggs per 10 ㎠	%
E13-1	99,742.0	12.1
E13-2	176,252.8	21.4
E13-3	188,756.9	23.0
E13-4	225,937.0	27.5
E13-5	96.741.5	11.8
E13-6	30,381.0	3.7
E13-7	123.6	0.02
E13-8	103.8	0.01
E13-9	201.5	0.02
E13-10	210.0	0.02
E13-11,14	317.2	0.04
E13-12,15	105.6	0.01
E13-13,16	97.7	0.01
E13-17	321.0	0.04
E13-18	274.1	0.03
E13-19	1,006.0	0.12
E13-20	1,247.3	0.15
Total	821,819.0	99.97
Mean output per 10 ㎠ in St. E13		48,342
Total output in St. E13 (0.5m x 8.5m =4.25㎡)		205,454,775

the population. In the *Chthamalus* zone, subpopulations in the upper quadrats (E13-1 to 3) characterized by low density, moderate coverage and large size of the barnacles by low density, moderate coverage and large size of the barnacles played an important role in the reproductive output compared to the lower quadrats (E13-4, 5) characterized by high density and high coverage.

Maximum total reproductive output (number of released nauplii) in 1982 of a subpopulation (10 ㎠) was estimated at about 200,000 and that in E13 station (4.25 ㎡) reached 220,000,000. Total number of settlements in 1982 at Stn. E13 (4.25 ㎡) was reached about 220,000 and maximum number of settlement of a subpopulation (10 ㎠) was estimated to about 200 (Table 1). At Stn. E13, about 0.1% of the total nauplii released were estimated to settle back. Regarding each subpopulation, 0.02% to 64% of nauplii did come back. Upper subpopulations from E13-1 to E13-3 show a low recruitment rate but high reproductive output. While middle and lower subpopulations below E13-5 show high recruit ment rate but low reproductive output.

4. Discussion

Estimation of reproductive output with respect to tidal level is important to understand persistence of a population. A few studies have estimated the reproductive output of integrated barnacle population (Connell, 1970; Hines, 1979), but, unfortunately, none of them considered the significance of tide level difference.

In the present study, the contribution of subpopulations from upper to lower tide levels were represented by means of reproductive output of each subpopulations (Table 2). The contribution of subpopulations in the upper zone is disproportionately high. This is the result of the occasional and sparse settlement and low rate survival of barnacles in the middle and lower intertidal zones. In regard to the difference of total reproductive output per year within the *Chthamalus* zone, the subpopulation in the upper part of the *Chthamalus* zone had a larger reproductive output. At the upper *Chthamalus* zone (E13-1 to E13-3), subpopulations included a considerable number of large sized overwinter generations resulting from higher survival rates. These larger individuals produce more eggs and hence the total reproductive output per unit area was high. Based on the distribution of adults, *C. challengeri* can be regarded as an organism of the high intertidal zone. In the present study, population processes of the barnacle from the settlement of larvae, reproduction and mortality at different tide levels were investigated. Large variation of those population characteristics was observed among the subpopulations at different tide levels. Then, the predominance of the subpopulation in the *Chthamalus* zone was establ ished by estimating its contribution to the total reproductive output.

The existence of a planktonic larval stages is an important feature in the benthic marine invertebrate life history, and it forms an open system (Roughgarden *et al*., 1985, Roughgarden, 1986). The open system means

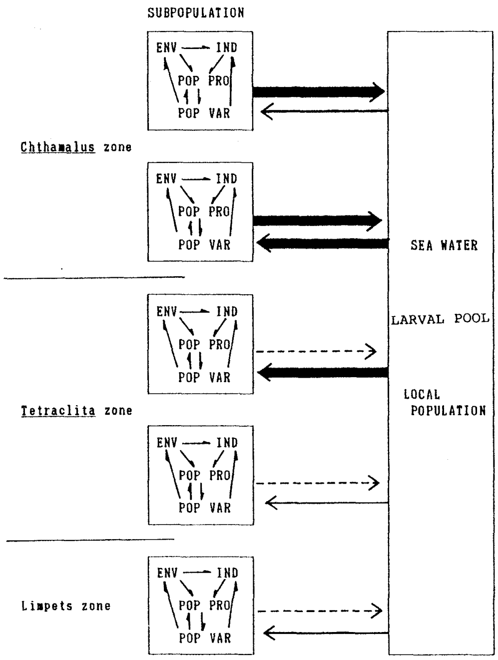

Fig. 3. The population system of *C. challengeri*. Arrows from the subpopulation to the larval pool indicate the relative amount of reproductive output (larval release), and reverse arrows indicate the relative amount of recruitment (settlement).ENV: Environmental properties, IND: Individual properties, POP PRO: Population processes, POP VAR: Population state variables Terminology was used following BERRYMAN (1981).

that planktonic larvae disperse widely (near and away) from the system where they were released. This can also enter into an another system of similar kind. The settlement rate on a particular substrate reflects the number of larvae in the water column and the time of exposure of the substrate to the water column (de WOLF, 1973; HAWKINS and HARTNOLL, 1982; GERACI and ROMAIRONE, 1982). A demographic theory for an open marine population with space-limited recruitment was proposed by ROUGHGARDEN and his colleagues, and is composed basically of two components, one, the subpopulation of adults, and two, their larval pool in water column (ROUGHGARDEN *et al*., 1984, 1985; ROUGHGARDEN, 1986). The main premise of the model, however, is that the total settlement rate into the system is proportional to the amount of unoccupied space (free space) in it. Although this assumption can not apply directly to the *C. challengeri* population because of wide variation of population characteristics according to tidal levels. However, the subpopulation-larval pool system for open populations is useful for population system of *C. challengeri* as a basic concept.

The structure and persistence mechanism of an open population (in the meaning of ROUGHGARDEN, 1986), is discussed using a new system model (Fig. 3). According to BERRYMAN (1981), the open population system is organized as a system of subpopulation systems. From this model, importance of the upper half of *Chthamalus* zone of this study area was demonstrated. Larval release is necessary for the persistence of a population. Release from the upper half of the *Chthamlus* zone was as high as from the lower half of the *Chthamalus* zone (high density zone). In the upper half of the *Chthamalus* zone, larval settlement was only moderate and initial mortality was high, but subsequent survivorship was very high and individuals showed high longevity. Since the growth was continuous, some barnacles reached large size, and they could produce a large number of eggs. This system model analysis indicated that although the abundance of the upper half of the *Chthamalus* zone was only moderate this zone was important in maintaining the population.

As shown in Fig. 3, The values of population parameters varied greatly with tide level, and therefore, the population parameters from only one point (main habitat, or distribution center) may differ from the whole population system. Moreover, since the population traits are functioned by biotic and abiotic environmental factors, it is suggested that the local population should be divided into representative subpopulation. And also, structure of subpopulation has to be measured quantitatively at each tide level that based on population characteristics and environmental conditions.

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イワフジツボの幼生放出と定着の垂直変異

森　　敬介

潮間帯性小型橈脚類イワフジツボ（*Chthamalus challengeri* Hoek）は高潮帯を代表する種であるが、幼生は潮間帯全域に定着している。九州西岸、天草（潮位差3.5m）の緩傾斜の岩を17の潮位に細かく分割し、イワフジツボの個体群動態を調査した。潮位ごとの総定着量と総繁殖量を推定し、個体群維持における生息潮位の重要性を論議した。本調査地においては繁殖期は３月から８月であった。幼生定着の垂直分布中心はイワフジツボ成体の高密度域およびその下部であった。一方、総繁殖量の垂直分布中心は、イワフジツボの高密度域およびその上部（最上部）であった。最上部は成体密度は低いが大型個体が出現した。中・低潮部では定着が少なく、空間的ばらつきや年変動が大きかった。また翌年の繁殖まで生存できる個体は稀であった。潮間帯全域での幼生放出に対する定着の割合は0.1%であったが、各潮位ごとでは0.02-64%と非常にばらつきが大きかった。次世代への貢献に関しては、多数の定着と多数の幼生放出がみられた高密度域とならんで、少数の定着ながら多数の幼生放出がみられた最上部が重要な役割を果たしていた。