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First Maturity and Initial Growth of Some Common Species of Barnacles in Japan.

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The biological minimum sizes and growth rates of six species of barnacles have been determined by examination of specimens taken from rafts or intertidal piles and by measuring the rostro-carinal diameter of animals growing on glass panels suspended from a raft.

The size and age at first maturity were determined as follows ; *B. improvisus* 4.5mm basal diameter (17 days), *B. albicostatus* 5.2mm (17 days), *B. reticulatus* 7.5mm (?), *B. amphitrite* 7.3mm (22days), *B. eburneus* 12.0mm (50days) and *B. kondakovi* 10.0mm (?). From comparison of these results with other barnacles, it follows that all of the barnacles studied here show early age and smaller size at first maturity. Initial growth in rostro-carinal direction is slow until 6 days or so after settlement, barnacles reaching approximately 1 mm in basal diameter. From 6 to 18 days the rate of growth of any species accelerates and barnacles become 3.5 to 5.0mm large at the end of this period. Subsequent decline of the growth rate is expected to be due to the sexual maturity. Until 10 days after metamorphosis barnacles tend to expand the basal margin rather than the opercular portion.

Key word : Breeding, Growth, Barnacles

In previous papers (IWAKI, 1975 ; 1981), it has already been clarified that the adult barnacles, *Chthamalus challengeri* HOEK, *Balanus amphitrite* DARWIN, *Balanus eburneus* GOULD, *Balanus improvisus* DARWIN, *Balanus albicostatus* PILSBRY, *Balanus kondakovi* TARASOV & ZEVINA and *Balanus reticulatus* UTINOMI, showed the different reproductive activities, compared with those of northern species ; any individual of the above-mentioned species could breed several times during the breeding season.

Several papers have been published on the breeding and the growth of other barnacles (CRISP and PATEL, 1961 ; BARNES and STONE, 1973 ; HINES, 1979) and recently the literatures has been reviewed by CRISP and BOURGET (1986). AYLING (1976) and HURLEY (1973) attempted to rationalize their data on life histories of *Balanus trigonus* and *Balanus pacificus* using MACARTHER and WILSON'S concept and reached the same conclusion that the rapid growth, early sexual maturity, high fecundity and great dispersal abilities were advantageous for adaptive strategies of these 'opportunistic' or 'fugitive' (r-selected) species.

First maturity and initial growth are important items of basic information for understanding the life history and reproductive biology of barnacles. To make careful conclusions on the biological minimum size and the breeding activity in relation to size or age, observations on a great deal of materials covering the whole size range and frequent measurements of growing individuals were made.

Materials and methods

During May-October 1986 specimens of *B. amphitrite* and *B. kondakovi* at Izo-ura in the recess of Matoya Bay and those of *B. improvisus* at Matiya-ura due east of the campus of Mie University were removed from bamboo poles, which had been stuck into the sea bed in the littoral zone by farmers for culturing edible red and green algae. During August-September, *B. eburneus*, *B. albicostatus* and *B. reticulatus* were obtained from styrofoam floats and other artificial structures under the rafts, which were also moored in the marginal plots of Matoya Bay and Ago Bay for culturing oyster and pearl oyster respectively. So, the barnacle population on the bamboo poles and under the rafts were influenced by the different hydrographic conditions.

Barnacles from the entire size range of each species were selected at random for processing in the laboratory. Each barnacles was measured along the apical and basal diameter of rostro-carinal axis, and examined for the presence of egg masses.

Six rectangular panels of transparent glass measuring 18×14cm were prepared for periodical inspection of growth rate. In order for the larva to attach themselves well, each panel was processed by drilling a number of small pits onto the surface. The pattern of settlement can be predetermined by this methods, because the cyprids settle preferentially into hemispherical small pits (CRISP, 1960). Each two panels holding a black panel between themselves were fixed together into a wooden frame and then three sets of panels were suspended at 0.5, 2 and 4 m below the surface of the sea from a raft moored in Matoya Bay. The panels were examined every three days from August to September and thereafter at some more longer intervals. At each examination the position of each settled barnacle was traced onto another clear plate, placed on the back of a surface of the panel with growing barnacles, all additional fouling growth was removed and then apical and basal diameter of rostro-carinal axis were measured under a binocular microscope with ocular micrometer.

Results

1) Reproductive condition.

In studying the area on the Pacific coast of central Japan, it has been found that successional broods apparently occur during April-December in *B. improvisus, B. amphitrite* and *B. eburneus* and during May-October in *B. kondakovi, B. reticulatus* and *B. albicostatus.* They show no distinct seasonal cycle with synchronous release of young as observed in northern species (BARNES and BARNES, 1954 ; CRISP, 1954 ; BARNES, 1959). All of the samples examined here which were collected during May-October were therefore in reproductive condition.

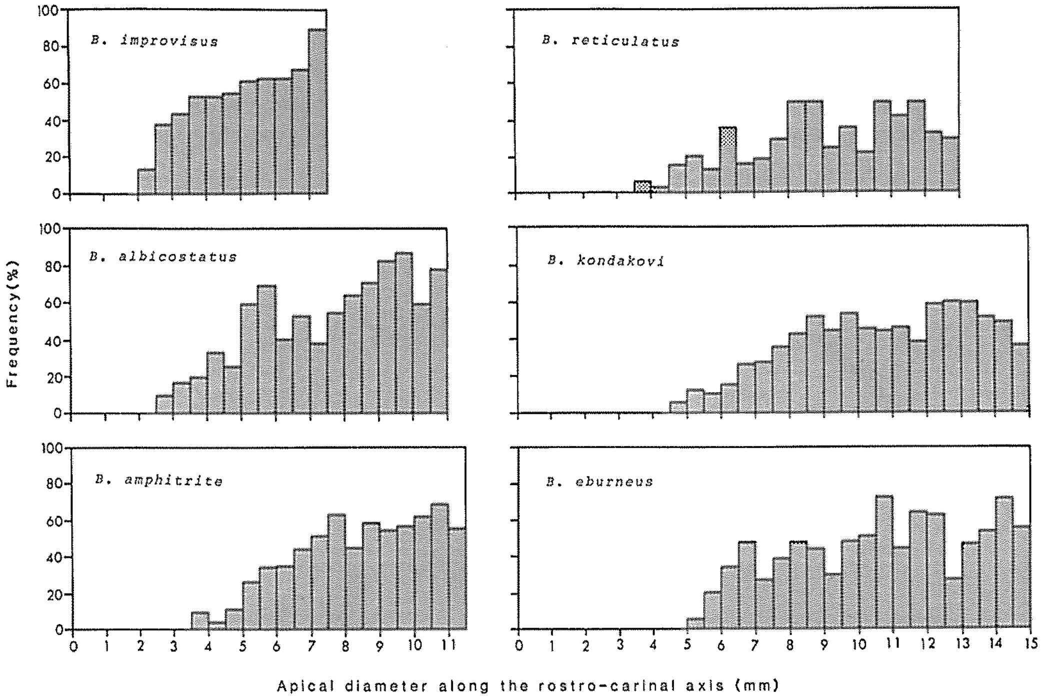

Fig. 1. Percentage occurence of barnacles bearing egg masses.

In **Fig. 1** the percentages of animals with egg masses in the samples are shown as a function of the apical diameter. The size ranges and frequencies pertaining to the smallest individuals carrying egg masses varied with species. Precise dimensions of the smallest ones were 2.15mm for *B. improvisus* (N=474), 2.54mm for *B. albicostatus* (N=509), 3.56mm for *B. reticulatus* (N=510), 3.65mm for *B. amphitrite* (N=842), 4.85mm for *B. kondakovi* (N=999) and 5.08mm for *B. eburneus* (N=660). In an adult, especially southern species of barnacle which is producing broods rapidly and repeatedly during the breeding season, the fertilization occurs immediately after maturation of gonads (CRISP and DAVIES, 1955). If it did so in animals which had just reached maturity for the first time in their life, the values given above for each species can be regarded as the biological minimum size. Thereafter the proportions of animals bearing fertilized eggs increased with increase in size, and on reaching certain size became almost a steady state indistinguishable from those of larger individuals. The size at which the frequencies ceased to increase could be roughly decided as follows ; 4.0 mm for *B. improvisus*, 5.0 mm for *B. albicostatus*, 5.5 mm for *B. reticulatus*, 6.0 mm for *B. amphitrite*, 6.5 mm for *B. eburneus* and 8.0 mm for *B. kondakovi*. These values likewise suggested to be parallel with maximum sizes of barnacles observed in natural populations, as shown by marginal sizes ranges in **Fig. 1**.

2) Growth

Before drawing growth curves the relations between apical and basal diameter were first established. **Fig. 2** is based on a number of measurements of animals which were able to expand the base freely under experimental conditions. The relationship found to give the best correlation was two allometric equations that were obtained separately, for the smaller

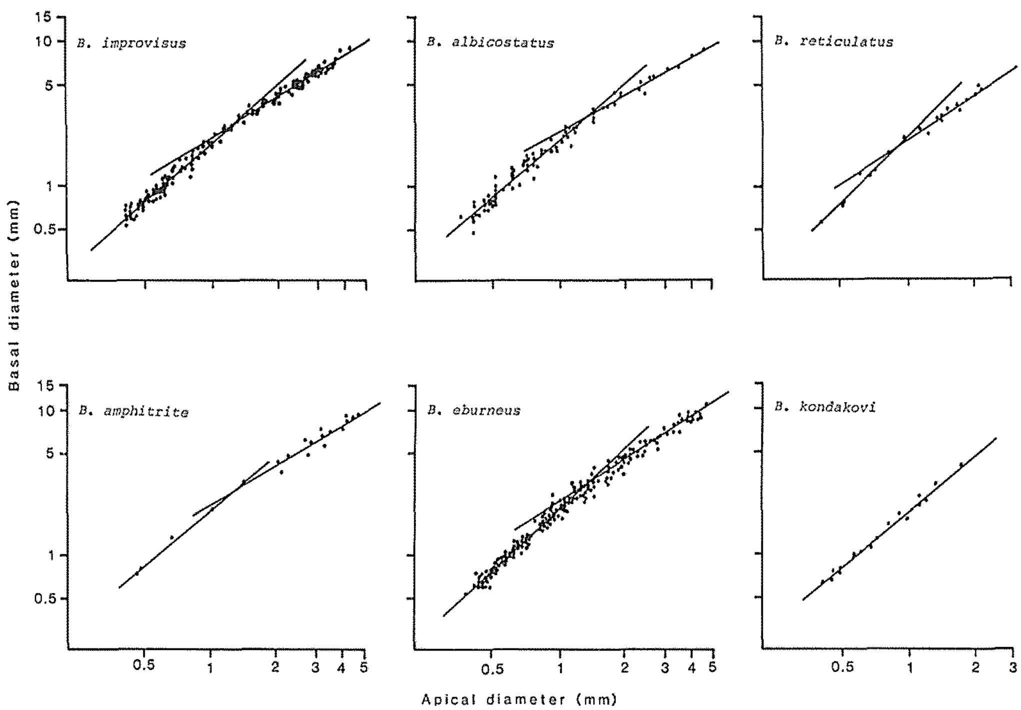

Fig. 2. Relations between apical and basal diameters measured along the rostro-carinal axes of shell.

Table 1. Regression formula showing the allometric growth of apical diameter (X in mm) relative to basal diameter (Y in mm) of barnacles.

Species	Smaller group	Larger groups
B. improvisus	Ln Y=0.692+1.362×Ln X	Ln Y=0.770+0.948×Ln X
B. albicostatus	Ln Y=0.718+1.318×Ln X	Ln Y=0.827+0.870×Ln X
B. reticulatus	Ln Y=0.744+1.538×Ln X	Ln Y=0.699+1.035×Ln X
B. amphitrite	Ln Y=0.698+1.298×Ln X	Ln Y=0.743+0.964×Ln Y
B. eburneus	Ln Y=0.728+1.384×Ln X	Ln Y=0.833+1.016×Ln X
B. kondakovi	Ln Y=0.636+1.248×Ln X	—

groups less than 2mm and for larger groups exceeding 1mm in apical diameter. The intersections of the two regression lines for each species were not largely different from each other, the co-ordinates showing the values of 1.14 to 1.33 mm in apical diameter and 2.40 to 3.07 mm in basal diameter, except that *B. reticulatus* had rather smaller sized point and *B. reticulatus* only gave a single line as the result of insufficient data. Above these results were summarized in **Table 1**. Whereas in any smaller groups the relative growth coefficients, or exponents, were larger than one, those values in larger groups were equal to, or somewhat smaller than one. Animals composing smaller groups therefore had their shell bases which had achieved at higher specific growth rate (dy/ dt/ y) than that rate (dx/ dt/ x) of the orifice of shell, but in larger groups both these compartments of shells developed isometrically (dy / dt / y = dx/ dt/ x). This fact can be understood from the allometric equation in its differential form.

In any species of barnacles the heavy settlement is observed from June to October in Matoya Bay (IWAKI, HIBINO and KAWAHARA, 1977). *B. reticulatus* and *B. improvisus* mainly settled on panels at depth of 2 and 4 m respectively and other four species preferred to settle on uppermost one. **Fig. 3** gives the growth curves of barnacles based on average size of five to twelve individuals for each species at every measurement, but the measurements of *B. kondakovi* and *B. reticulatus* were limited to a few number of individuals as well as to short periods owing to a large number of mortalities. It seemed that there was a short lag phase very early in any growth course, showing the growth rate of ca. 0.1mm/day in the first 6 days. From 6 to 18 days the growth of any species accelerated, barnacles reaching a length of 3.5 to 5.0mm at the end of this period. Thereafter it slowed down, except that *B. eburneus* continued to grow in the same manner as before for 30 days or more. The growth rates of *B. improvisus, B. albicostatus* and *B. amphitrite* during the interval from 15 to 18 days were 0.28 mm/day, 0.44mm/day and 0.55mm/day respectively and during the next interval the rates reduced by half. Coefficients of variation associated with average sizes of basal diameter were 13 to 18% at the first and 21 to 40% at the end of growth course of each species.

Fig. 3 can be used in conjunction with both **Fig. 1** and **Fig. 2** given above to determine approximate size and age at which the barnacle first reaches maturity and those corresponding with the intersection of two regression lines correlating apical diameters with basal diameters.

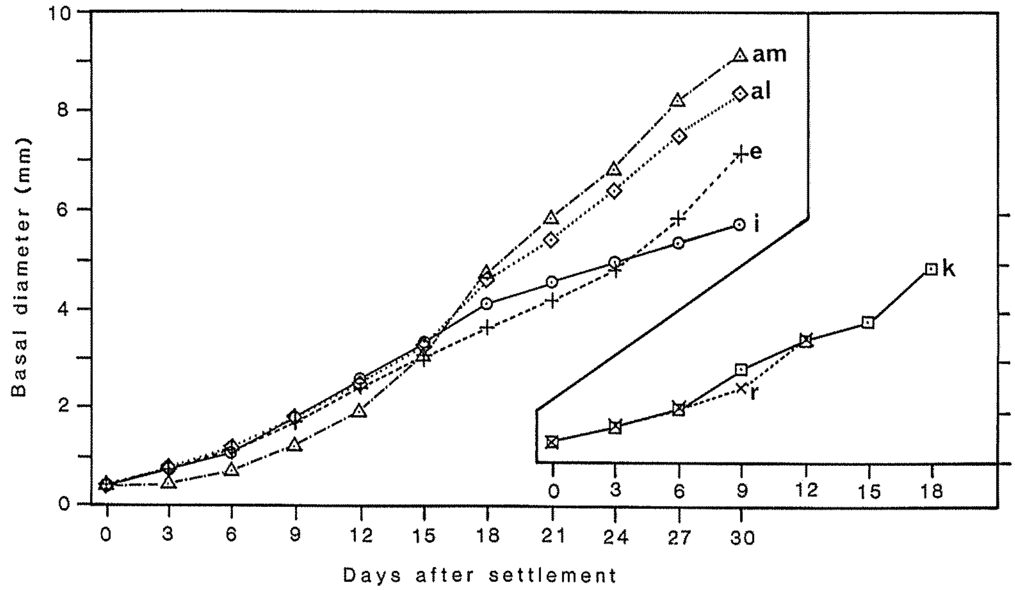

Fig. 3. Growth of barnacles allowed to settle on glass panels in Matoya Bay from mid August to mid September.
i : *B. improvisus*, e : *B. eburneus*, al : *B. albicostatus*, am : *B. amphitrite*, k : *B. kondakovi*, r : *B. reticulatus*.

Table 2. Sizes and ages corresponding to inflection point of allometric growth of the shell and onset of first maturity.

Species	Inflection point			First Maturity		
	Apical dia.	Basal dia.	Age	Apical dia.	Basal dia.	Age
B. improvisus	1.21mm	2.58mm	9days	2.15mm	4.46mm	17days
B. albicostatus	1.28	2.83	10-11	2.54	5.15	17
B. reticulatus	0.91	1.83	7	3.56	7.48	—
B. amphitrite	1.14	2.40	10	3.65	7.32	22
B. eburneus	1.33	3.07	12-13	5.08	11.99	ca.50
B. kondakovi	—	—	10	4.85	9.98	—

The results are given in **Table 2.** It can be seen that the changes of positive allometry to isometry in the relative growth of barnacle shells occur first of all before first maturity, and that as regards *B. improvisus*, *B. albicostatus* and *B. amphitrite* the age and size of the smallest barnacles bearing eggs nearly coincide with those at which the growth fell off (viz. 3.5-5.0mm in basal diameter ; 18 days after settlement), but there is a slight discrepancy of sizes only in *B. amphitrite*.

Discussion

All individual barnacles examined here were from the natural population under crowded conditions, so they would be capable of cross-fertilization in natural conditions. Barnacles separated from others by a distance greater than that of the extended penis probably do not fertilize (CRISP, 1950). This feature is quite general in cirripeds, except in the case of *Chthamalus stellatus, Verruca stroemia* and *Balanus perforatus* (BARNES and CRISP, 1956).

In his study of breeding in *Balanus balanoides* MOORE (1935) suggested that the sterility was found in the larger or older individuals, becoming more frequent with increasing size, and was common in members of crowded communities. As regards species studied here, the barnacles more than two years old were rarely found in their habitats where sampling was made, because intense settlement occurs annually over the greatly extended period and is largely responsible for death of animals settled in preceding year. The majority of specimens brought out in **Fig. 1** are therefore considered to be relatively young and normal condition without sterility.

The important factors determining the size attained by individuals are the intra- and inter-specific competition, the time of submergence and the water movement carrying food within range of the animals. Crowding may slow down growth and delay the maturation of the ovary considerably (CRISP, 1961) and the raft conditions are far better from the point of view of growth than those which are obtained on intertidal substrata (CRISP, 1964). Using the results recorded here for the rate of growth under the raft condition, these would therefore give the minimum ages of first maturity for *B. amphitrite, B. kondakovi* and *B. improvisus*, which were sampled from crowded populations on intertidal piles.

By comparing many results of this and other studies for breeding of barnacles, it can be seen that there are considerable differences in age and size of the first maturity of the same kind of barnacles from different regions. New generations of *B. eburneus* in Trinidad Mangrove Swamp can reach maturity in less than two weeks, during which the barnacles grow from about 3 to 5mm in basal diameter (BACON, 1971), compared with the two months required at Woods Hole (GRAVE, 1933) and the 50 days (12mm) in Matoya Bay. HIRANO and OKUSHI (1952) found that in late spring and summer *B. amphitrite* released its first nauplii about 40 days after settlement in Aburasubo Bay. In this area the temperature of the sea during the same season was about 22 to 27 ℃, so the brood period of *B. amphitrite* is considered to be 4 to 6 days which is estimated from the relationship between the brood period and temperature previously published for the same varieties, *B. amphitrite* var. *denticulata* (PATEL and CRISP, 1960) and *B. amphitrite amphitrite* (CRISP and COSTLOW, 1963). In this case a reasonable estimate of the age for the first maturity of *B. amphitrite* is therefore about 34 to 36 days, and the size at that time quoted from HIRANO and OKUSHI's growth data is 8 to 10mm. Also it can be found in size-frequency histograms of *B. amphitrite* in Shimizu Harbor given by KOSAKA and ISHIBASHI (1980) that the smallest animals having egg masses are from 3 to 3.5mm in apical diameter. These values correspond with the 6 to 7mm basal diameter obtained by calculation using the equation shown in **Table 1**. In Amsterdam a few individuals of *B. improvisus* observed to contain egg masses are 5 mm in basal diameter (BREEMEN, 1934). It is approximately similar to the values obtained here for the same dimension, though the growth rate is slower than that in Matoya Bay. Comparisons of the ages of first maturity within a wide diversity of barnacles show that the values quoted for southern species are generally lower than those for northern species, such as *B. balanoides*, *B. porcatus* and *B. hameri* that do not release nauplii until nearly the end of their first year (CRISP, 1954 ; MOOR, 1935). The values of size at first maturity, even if limited to southern species, vary markedly with species from about 2 mm for *Balanus trigonus* and *Chthamalus fissus* to 18 mm basal diameter for *Tetraclia squamosa* (AYLING, 1976 ; HINES, 1979). We may conclude that all of the barnacles studied here reach their maturities at relatively earier age and smaller size.

Early growth just after settlement was observed to be slower in the present study. Similar results were obtained by CRISP (1960) for *Elminius modestus, Balanus crenatus* and *Balanus balanoides* and he ascribed this fact to reduction of the rate of flow in the immediate vicinity of the solid substratum. Another possible explanation of the delay was that after settlement endogenous control of the growth was for a while limited to low degree in consequence of the metamorphosis. The slowing down in growth rate after maturity is obviously caused by metabolic changes associated with reproduction. The most critical phase for survival occurs during or just after metamorphosis, while the shell plates are not fully formed, hardened, and cemented to the substratum (CRISP, 1961). The faster expansion of the basis rather than aperture of shell is therefore advantageous for such individuals as have aged less than 10 days or so after settlement and in crowding condition small specimen must complete as fast as possible to fix itself firmly to the substratum.

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