

The Comparative Reproduction Ecology of Three Species of Intertidal Barnacles

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The life histories of *Chthamalus fissus*, *Balanus glandula* and *Tetraclita squamosa* are compared. *C. fissus* occurs mainly at high tidal levels, *B. glandula* at middle, and *T. squamosa* at low levels, but there is considerable overlap in their distribution. Monthly trips were made for 2 years to Morro Bay, California, to collect barnacles for estimates of reproductive parameters and to photograph marked intertidal quadrats for measurements of recruitment, growth and survivorship. *C. fissus* produces up to 16 small broods during a long summer season, resulting in a high reproductive effort. Brooding is limited by food availability. Settlement of *C. fissus* occurs erratically year-round at all tidal levels, and it grows slowly to about 8 mm in diameter. It survives best at higher tidal levels, but its overall survivorship is the poorest of the species. Early age of first reproduction in *C. fissus* results in short generation time and the highest intrinsic rate of population growth. *B. glandula* stores nutrients in summer and fall until cold temperatures induce production of up to 6 large broods during winter and spring, resulting in a high but intermediate reproductive effort. It has a sharp peak of settlement in May or June, with many more individuals settling at low levels than high. Initial growth is rapid but slows to an intermediate rate, with an asymptotic size of about 22 mm. Survivorship is best at uncrowded high levels, but overall survivorship is intermediate of the three species. *B. glandula* also has an intermediate age of first reproduction, generation time and intrinsic rate of population growth. *T. squamosa* produces up to 3 broods during a shorter summer season and has a low reproductive effort. Settlement occurs in fall only at low tidal levels, is patchy in distribution and annually variable in density. *T. squamosa* grows rapidly, reaching an asymptotic size of 60 mm. It has the best survivorship of the species. Onset of reproduction is delayed until 22 months of age, and maximum survivorship-weighted fecundity is not reached until the third year. This delay results in a long generation time and low intrinsic rate of population growth, but high fecundity and survivorship result in high reproductive value over a long lifespan. The adaptive significance of these three species' life history traits for exploiting different tidal levels is discussed.

Key Words: *Balanus*, barnacles, *Chthamalus*, life histories, life tables, reproductive ecology, *Tetraclita*.

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Introduction

This paper compares the reproductive ecology of three species of intertidal barnacles in the context of their life histories. *Chthamalus fissus* Darwin, 1854, *Balanus glandula* Darwin, 1854, and *Tetraclita squamosa rubescens* Darwin, 1854, exploit different but overlapping intertidal ranges in central California. Selection for different modes of reproduction, settlement, growth, and survivorship may be expected along gradients of greater physical stress in the high tidal range and increasing biological complexity at the low tidal range. The purpose of this paper is first to measure how particular aspects of these modes differ between species facing varying degrees of environmental stress, competition and predation. Secondly, it is to examine how components of the reproductive ecology of the species interact with growth and demography as co-adapted traits selected to solve complex ecological problems.

The important parameters for investigating patterns of reproductive ecology and life histories reviewed by Giesel (1976) and Stearns (1976) are: 1) reproductive effort in terms of the timing of the reproductive season and the size and number of broods during the season; 2) size of the young; 3) age distribution of reproduction; 4) juvenile and adult survivorship rates; and 5) the interaction of reproductive rate with survivorship. Barnacles are excellent organisms for studies of reproductive ecology and life histories because as sessile, brooding animals, nearly all of these parameters can be measured in the field. However, barnacles present two difficulties. First, their planktonic stages make it impossible to measure larval survivorship. Second, the internal brooding of barnacles requires that individuals be killed to determine their reproductive condition, which prevents measuring the succession of broods in an individual through time. Larval mortality can be estimated by calculating the number of nauplii released into the plankton from the known density and sizes of the parents and then subtracting the observed number of barnacles settling in the same area. The only other choice is to ignore the larval period and proceed with analysis from the post-settlement part of the life cycle; this approach also has merits, but will not be presented here. The second problem can be circumvented by estimating the sequence of broods from frequent subsamples of the population combined with laboratory observations. I hope to show that these disadvantages are far outweighed by the advantages of barnacles as a study system of ecological importance in temperate intertidal regions.

The physiological ecology of barnacle reproduction and growth has been extensively studied, particularly in the north Atlantic species *Chthamalus stellatus*, *Balanus balanoides* and *B. balanus*, as well as several other species (see Barnes, 1963; Barnes and Barnes, 1959, 1968; Crisp, 1950, 1954; and many others). Population and community ecology of barnacles have also received much attention in the north Atlantic (see Connell, 1961a,b; Lewis, 1964; Menge, 1976)

and west coast of North America (see Connell, 1970; Dayton, 1971; and many others). Except for Connell's (1970) exemplary demographic study of *Balanus glandula*, life history studies investigating both the reproductive biology and population dynamics of barnacles as integrated adaptations to intertidal communities are lacking.

This paper summarizes patterns of reproductive effort, settlement, growth, and demography in *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa rubescens* (hereafter called *T. squamosa*) from central California. *C. fissus* is small (usually < 8 mm basal diameter) and common in the high intertidal Zone 1 of Ricketts and Calvin (1962). *B. glandula* grows to a maximum of about 20-22 mm in diameter and is most common in the upper midintertidal Zone 2. *T. squamosa* is considerably larger, attaining a maximum diameter of about 60 mm and is found in the low mid-intertidal Zone 3. Although these zonal distributions are characteristic of the three species, they are often found coexisting in Zone 3 (see Fig. 1). The range of *C. fissus* overlaps that of *C. dalli*, its northern congener in central California. However, while *C. dalli* was found in nearby exposed areas, it was not found in the more protected area of my study site. Additional details of the methods and results of this study may be found in Hines (1976).

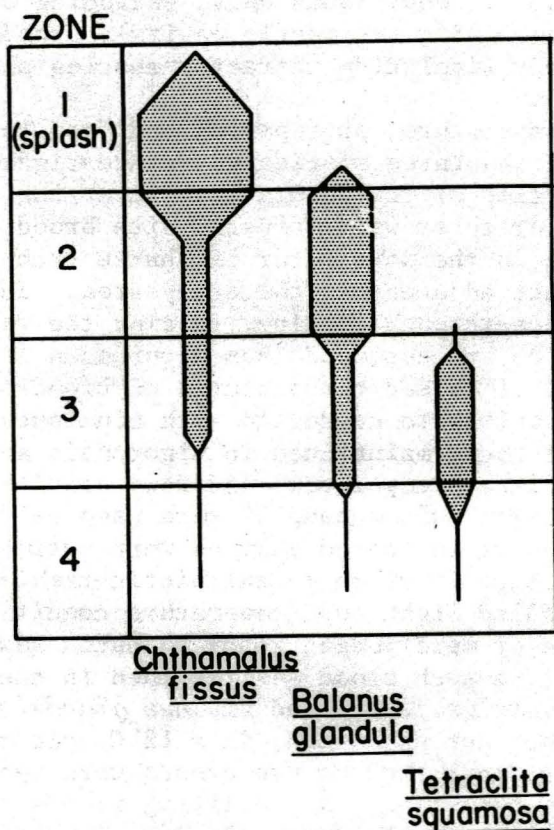


Fig. 1. Schematic diagram of the intertidal distributions and relative densities of the three species of barnacles. The intertidal zones of Ricketts and Calvin (1962) are indicated.

Methods

Approximately monthly trips were made to Morro Bay, California (lat. $35^{\circ}22'30''\text{N}$, long. $120^{\circ}52'30''\text{W}$) from November, 1972, to January, 1975, to collect barnacles and photograph permanent quadrats on the rocks in the protected harbor entrance. All three species were collected from about 0 to 0.3 m above mean lower low water to control for differences in exposure and feeding time. *Chthamalus fissus* and *Balanus glandula* were collected intact on small rocks and brought back to the laboratory; *Tetraclita squamosa* was chiseled off the substrate. Barnacles over the entire size range of each species were selected haphazardly for processing. Brooding frequencies were calculated for barnacles known to be reproductively mature. In addition, several smaller *T. squamosa* in each sample were evaluated for brooding. Each barnacle was measured along the basal diameter of the rostral-carinal axis and examined for the presence of brooded embryos and ripeness of the ovary. Ovaries were staged "ripe" or "not ripe" by the presence or absence of large quantities of yellow, yolky material bulging into the mantle chamber. The following body component weights for each barnacle were determined after drying in a vacuum oven at 60°C : body (soma only, excluding ovary, retractor muscles, and tissue lining the mantle cavity); brooded egg mass; and, in some cases, ovary (including retractor muscles and tissue lining the mantle cavity).

Effects of temperature, photoperiod and food in regulating brooding cycles of the three species were investigated in two ways. First, brooding cycles of the populations occurring at ambient environmental temperatures were compared with brooding cycles of populations living in the warm-water discharge from a large steam-electric power plant adjacent to the study area. The power plant uses ocean water for once-through cooling, raising the temperature $4\text{--}14^{\circ}\text{C}$ above ambient in the process, and thus provided a large field experiment on the effect of raised temperatures on brooding. Second, laboratory experiments were conducted with continuously submerged barnacles on small rocks maintained in vigorously aerated seawater under controlled light, temperature and food conditions. Dense suspensions of *Artemia salina* nauplii were used as food.

Brooding times of incubated embryos were estimated by maintaining freshly deposited eggs in vitro in antibiotic-treated, aerated seawater under controlled light and temperature conditions. The time until they hatched or were judged ready to hatch was noted. Additional estimates of the time each brood was retained in the mantle chamber were made for *Chthamalus fissus* and *Balanus glandula* by keeping barnacles moist, but not submerged, in a 12°C cold room. Since copulation did not occur, and no new broods were deposited unless the barnacles were submerged, only existing broods continued to develop without hatching. Frequent samples of barnacles were sacrificed, and the time at which 100% of the broods were ready to hatch was noted. *Tetraclita squamosa* could not be maintained unsubmerged

for any extended period.

During spring, 1973, several permanently marked, 10 x 15 cm quadrats were established at high (+1.5 to 1.8 m above mean lower low water), middle (+0.7 to 2.9 m), and low (0.0 to 0.3 m) intertidal positions in the collecting area. Settlement, growth and mortality of barnacles in these quadrats were followed. Initially, only field notes and counts were taken for a few quadrats at each level, but beginning in late summer, 1973, several replicates at each intertidal level (for a total of 35 quadrats) were photographed monthly. All quadrats were examined qualitatively to ascertain any obvious differences between adjacent replicates; however, only quadrats for which the longest continuous data were available (including field counts and photographs) were analyzed quantitatively. For *Chthamalus fissus* and *Balanus glandula* two high, one middle, and two low quadrats were analyzed in detail. *Tetraclita squamosa* was present only in low level quadrats, and all quadrats which contained this species (6 adjacent quadrats in one area and 4 adjacent quadrats nearby) were analyzed. Settlement and mortality of *B. glandula* and *T. squamosa* were followed in the standard 150 cm² quadrats. Settlement and survivorship of *C. fissus* was followed in smaller 30 cm² sub-quadrats in the center of each larger quadrat. Barnacles as small as 1-2 mm in basal diameter (about 1-3 weeks old) could readily be identified in the photographs. In periods of very dense settlement, especially of *B. glandula*, it was difficult to distinguish each individual. However, by observations of the quadrats during monthly samples and by working back and forth between successive monthly photographs, each individual was given an identifying number. Growth of the basal diameter on the rostral-carinal axis was measured from the photographs, and deaths were noted when the opercular valves or the whole barnacle disappeared.

To determine egg numbers per brood of each species, the eggs of each brood were dissociated in a weak solution of protease in seawater, fixed in formalin, and run through a Model A Coulter Counter. The counter was modified so that all eggs in each brood were counted. The basal diameter of the parent of each brood was also determined.

Demographic and life table analysis follows Mertz (1970) and Krebs (1972). Estimations of larval survivorship were computed in the following way: the number of nauplii released into the plankton is calculated from the eggs produced by the known sizes, densities, and fecundities of the parents. From this value, the number of barnacles settling in the same area is subtracted, and the difference is larval mortality. This estimation makes the obviously false assumption that the populations recruit only from themselves; neither the fate of the Morro Bay larvae nor the source of those settling there is known. Life table analysis also assumes that the population is in a stable age distribution, with constant survivorship and fecundity rates. There is not space here to evaluate these assumptions for this study, but the reader should be aware of them.

Results

Brooding cycles for the three species are shown in Figure 2. *Chthamalus fissus* brooded during a long summer season from about March or April to October, but low levels of about 10% brooding frequently occurred in the "off" season. *Balanus glandula* brooded embryos in winter and spring from about December or January to May. *Tetraclita squamosa* brooded during summer from about June through September.

Results of studies on the effects of temperature, photoperiod and food availability in regulating the brooding cycles of three species are summarized here. Further details and complete data may be found in Hines (1976, 1978). Brooding in *Chthamalus fissus* is regulated directly by food availability, and laboratory feeding elicited high brooding frequencies during periods when brooding activity and food levels in the field were low. The increased brooding response to food in the laboratory was rapid - within about two weeks -

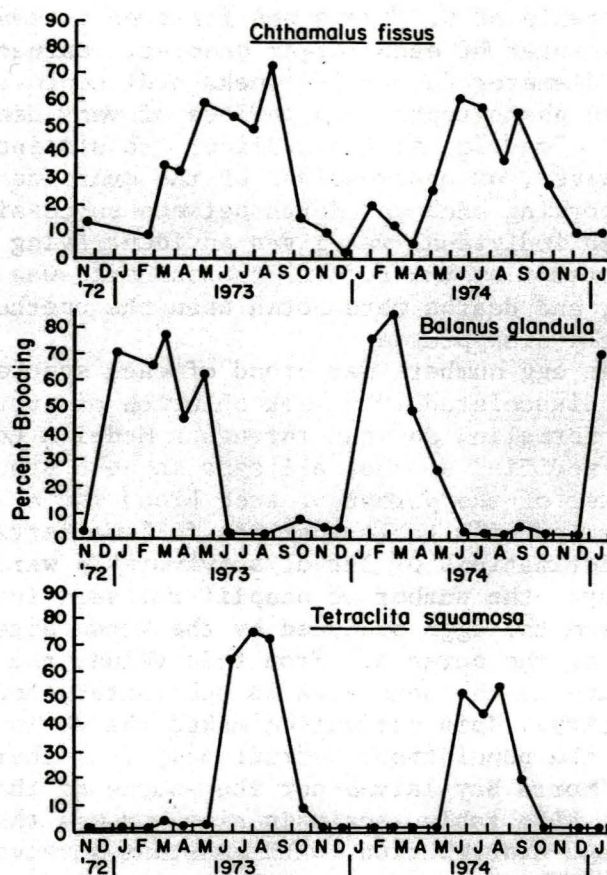


Fig. 2. Brooding cycles of the three species of barnacles. Monthly sample sizes of each species are: 50 *Chthamalus fissus* > 2 mm basal diameter; 60 *Balanus glandula* > 5 mm basal diameter; 60 *Tetraclita squamosa* > 18 mm basal diameter.

and the frequency of brooding was directly proportional to the size of the food dosage, from 15% brooding with no additional food in the lab to 74% brooding at the highest food dosage. Temperature (11.5° or 20°C) and photoperiod (10 hr Light, 14 hr Dark, 12L/12D, or 14L/10D) did not affect brooding in *C. fissus* in the laboratory, nor did the population in the warm-water outfall show a significantly different brooding cycle than the ambient field population. For *Balanus glandula* cold temperatures (11.5°C) induced early brooding in the laboratory during late fall and early winter, and warm temperatures (20°) tended to inhibit it. Further, *B. glandula* in the warm-water outfall showed consistently lower brooding frequencies than the ambient population, and onset of brooding was delayed 1-2 months in two of the three years studied. However, cold temperature did not induce brooding in late summer to early fall even though *B. glandula* appeared ripe then; nor did cold temperature in the laboratory extend the brooding period into summer. Photoperiod (10L/14D, 12L/12D, 14L/10D) did not affect brooding activity in *B. glandula*. *Tetraclita squamosa* in the warm-water outfall began brooding in winter, continued at erratically variable levels throughout spring into early summer, and appeared to be spawned out by the time the ambient temperature population reached peak brooding activity. Although this 6 month shift in the brooding cycle strongly suggests that warm temperatures are required for brooding, *T. squamosa* did not brood in the laboratory under any of the conditions tested (combinations of 11.5° or 20°C with 10L/14D, 12L/12D, 14L/10D and several food regimes), even during the time the field populations were brooding. Individuals appeared ripe with yolk in the laboratory, but the stimulus for brooding seemed missing.

Dimensions of newly deposited eggs are 85 x 110 μ for *Chthamalus fissus*, 160 x 220 μ for *Balanus glandula*, and 180 x 310 μ for *Tetraclita squamosa*.

Regressions of dry brood weight vs. dry body weight for each species with the 95% confidence intervals for the slopes and intercepts are:

$$C. fissus: Y = (0.718 \pm 0.039)X + (0.035 \pm 0.030); N = 391; \\ r = + 0.855.$$

$$B. glandula: Y = (1.58 \pm 0.093)X - (0.962 \pm 0.526); N = 363; \\ r = + 0.868.$$

$$T. squamosa: Y = (1.21 \pm 0.066)X - (8.86 \pm 1.82); N = 248; \\ r = + 0.908.$$

There was no significant difference in size of broods occurring early or late in the respective seasons of any of the three species (intercepts and slopes were not different at the 0.20 level). Because brood weight is positively correlated with body size and because there is a large size range of barnacles both within and between species, the slope of the regressions were taken as a comparative measure of the size-compensated energy partitioned for each brood. By this measure *Balanus glandula* had the largest relative brood size (1.58), *Tetraclita squamosa* an intermediate but still large brood (1.21), and *Chthamalus fissus* a comparatively small brood (0.718).

Estimated times of incubation of broods at 12°C are about 0.5 months for *Chthamalus fissus*, 1.0 month for *Balanus glandula*, and 1.5 months for *Tetraclita squamosa*. Development of all three species was faster at warmer temperatures (Q_{10} ranged from 1.25 to 1.51). Estimates of the maximum number of broods produced per year for each species were calculated by dividing the length of the brooding seasons by the time for each brood, assuming no delay between broods. For *C. fissus* (8 month season) this yields 16 broods per season; for *B. glandula* (6 months), 6 broods per season; and for *T. squamosa* (4.5 months), 3 broods per season. A short period between broods probably occurred, because less than 100% of the populations were brooding at any given time. However, there is no doubt that each species produces several broods in rapid succession.

A schematic model of the patterns of nutrient storage (Fig. 3) shows proportional changes in ovary weight relative to brood weight during the year for each species. In addition to estimates of the length of brooding season, number of broods per season, and the time each brood is held, this model is derived from cycles of ovarian ripeness and comparison of the ovarian weights at maximal and minimal ripeness with brood weights for each species (Hines, 1978). Brooding in *Chthamalus*

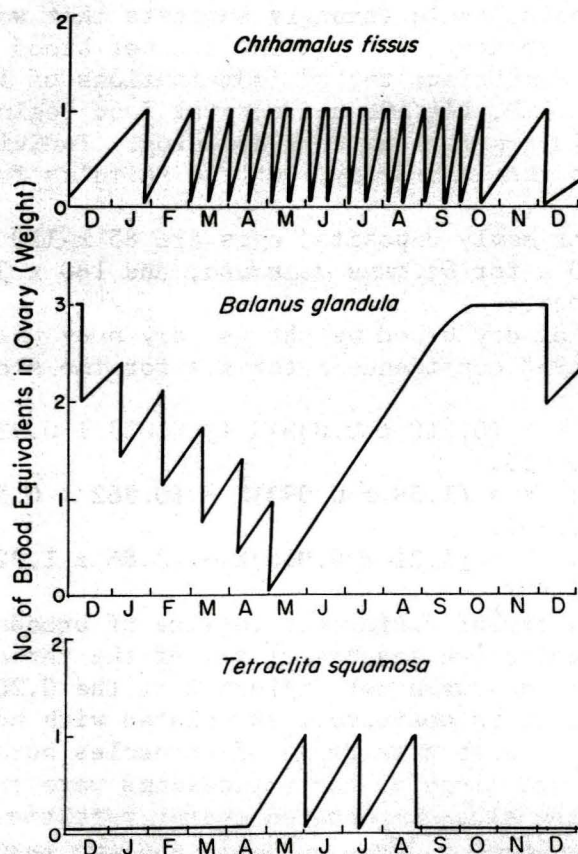


Fig. 3. Schematic model of the patterns of nutrient storage showing proportional changes in ovary weight relative to brood weight during the year for the three species.

fissus is limited by food availability and yolk, for no more than one brood is stored at a time. As soon as enough nutrients for a brood are stored, the eggs are deposited. As food availability increases during spring and summer, the rate of yolk accumulation increases and broods are produced more frequently, until the rate of brood production is probably limited only by the time required for brood incubation. In contrast, *Balanus glandula* rapidly stores nutrients in the ovary during the summer and remains full of yolk during the fall, until the proper cold temperature conditions are met and brooding begins. Yolk for at least three broods is stored initially, and as broods are released during winter and spring more nutrients are probably added as the barnacles feed, until the ovary is spawned out in May. *Tetraclita squamosa* apparently produces only enough yolk for one brood at a time before egg-laying.

Comparisons of reproductive effort, estimated as brood weight relative to body weight per year, are shown in Figure 4. For each species the measured length of the brooding season of the control population has been divided by the laboratory brood incubation time at 12°C to calculate the number of broods produced per year. Brood number was then multiplied by the slope of the regression of brood weight on body weight to calculate the total size-specific brood weight expended during the year. *Chthamalus fissus* had the highest proportional energy allocation to brood production - 11.49 times the body weight; *Balanus glandula* expended an intermediate but large amount - 9.48 times the body weight; and *Tetraclita squamosa* allocated the least amount of energy to brood production - 3.63 times the body weight.

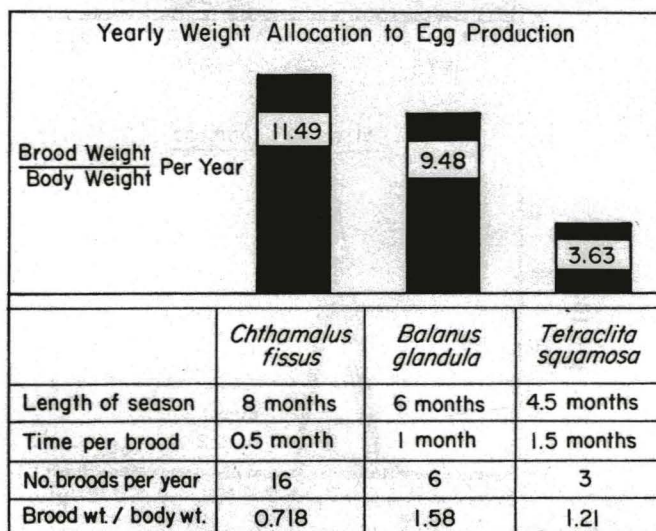


Fig. 4. Comparative yearly weight allocation to egg production. The ratio of brood weight to body weight per year is obtained by multiplying the maximum number of broods per year times the slope of the brood weight on body weight regression. *Chthamalus fissus*, for example, allocates up to 11.49 times its body weight to egg production.

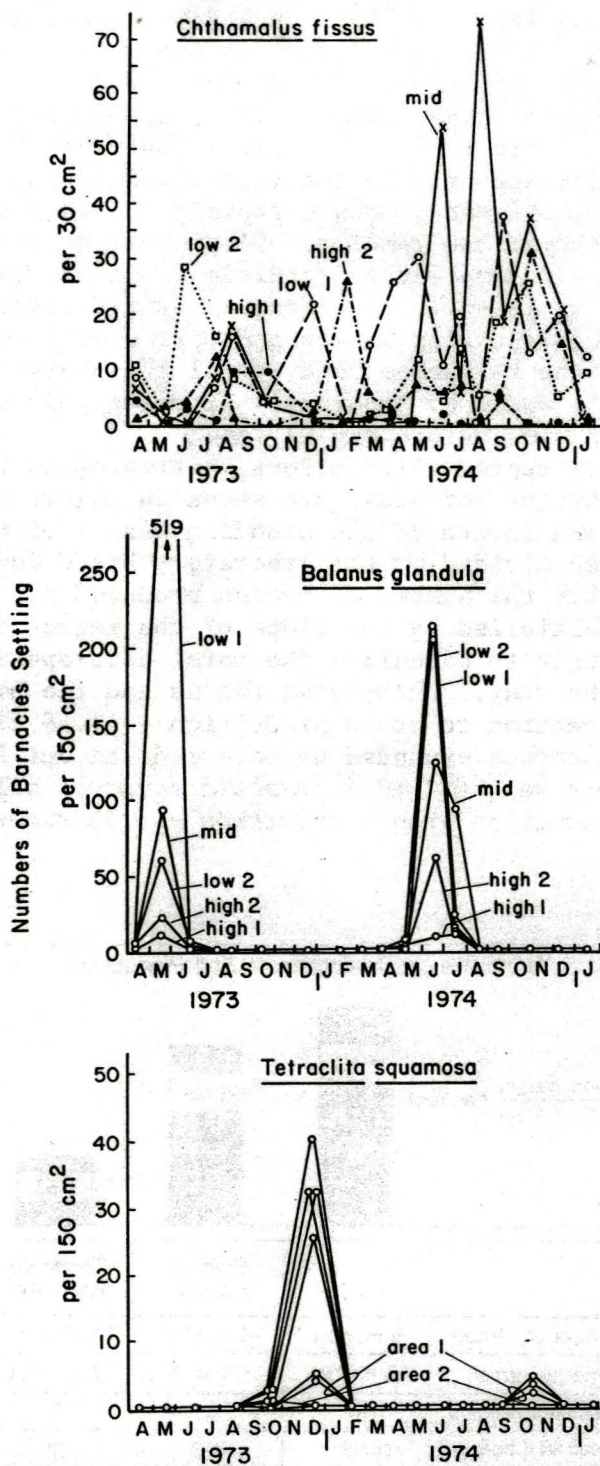


Fig. 5. Settlement patterns of the three species of barnacles in permanently marked quadrats. Settlement of *Chthamalus fissus* and *Balanus glandula* in 2 high, 1 middle, and 2 low quadrats are shown. *Tetraclita squamosa* only settled at low intertidal levels, and recruitment densities in 6 adjacent quadrats in one area and 4 adjacent quadrats in another area are shown.

Settlement patterns of the three species are shown in Figure 5. *Chthamalus fissus* settled erratically at all times of the year and at all tidal heights. *Balanus glandula* shows a markedly seasonal peak of settlement in May or June, and large numbers settled at low intertidal levels, intermediate numbers at the middle level, and fewest at the high level quadrats. The timing and high densities of settlement of *B. glandula* were repeated in 1973 and 1974. *Tetraclita squamosa* also has a markedly seasonal period of recruitment, with a fall peak during October or November. *T. squamosa* settled only at low intertidal levels. The distribution of *T. squamosa* settlement was extremely patchy in space, and the density of settlement was annually variable.

Length of the larval period is not known for these species. For *Chthamalus fissus*, I assume the larval period to be less than 1 month. For *Balanus glandula* and *Tetraclita squamosa*, the larval period can only be estimated from the time of the mid-point of the brooding season to the time of settlement: 3 months for both species.

Since *Chthamalus fissus* does not have a sharp seasonal peak of settlement, growth of some individuals settling in each season was followed. In addition, growth of larger *C. fissus* present in the quadrats at the start of the study, but which could not be aged, was followed in two size-groups of about 5 mm and 6 mm basal diameter. *C. fissus* in all quadrats showed a similar pattern of rapid growth to about 4 mm in the first 6 months, after which growth diminished to a more gradual, constant rate (i.e., see Fig. 6a). There was no

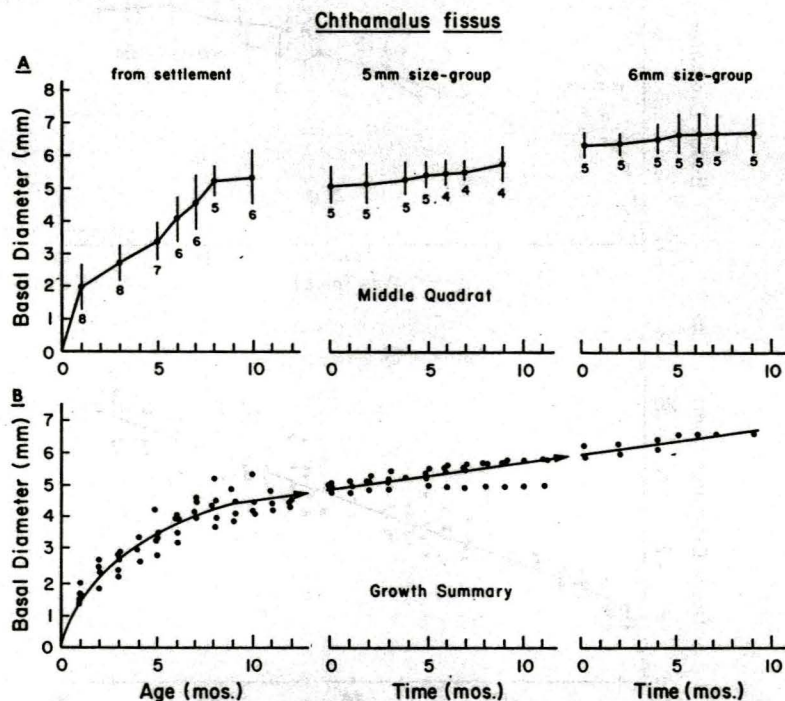


Fig. 6. Top (A): Growth of *Chthamalus fissus* in the middle level quadrat. Means, 95% confidence intervals, and sample sizes are indicated for barnacles growing from settlement, 5 mm and 6 mm in diameter. Bottom (B): Growth summary of *C. fissus*. Mean sizes at each age are plotted for all quadrats.

consistent difference between growth at any tidal level. A single growth curve for *C. fissus* (Fig. 6b) was derived in the following way: a curve was fitted by eye to the mean sizes of barnacles younger than 7 months in all quadrats. The straight line was fitted to the mean sizes of barnacles older than 7 months by the regression equation $Y = 0.09X + 3.55$, assuming a continuum of growth to the two groups of larger barnacles. The largest *C. fissus* I have observed was about 8.5 mm in diameter.

The sharp seasonal peak of settlement in *Balanus glandula* made it possible to identify distinct year-classes of this species, so that growth of barnacles of known age could be followed to about 4 years old (i.e., see Fig. 7a). *B. glandula* in all quadrats showed a similar pattern of extremely rapid growth to about 7 mm in the first 5 months after settlement. Although quite variable, growth rate then becomes more gradual, and there was no consistent difference in growth between any of the tidal levels. A single growth curve for *B. glandula* (Fig. 7b) was derived. A curve was fitted by eye to the mean sizes of barnacles younger than 5 months in all quadrats, and the regression

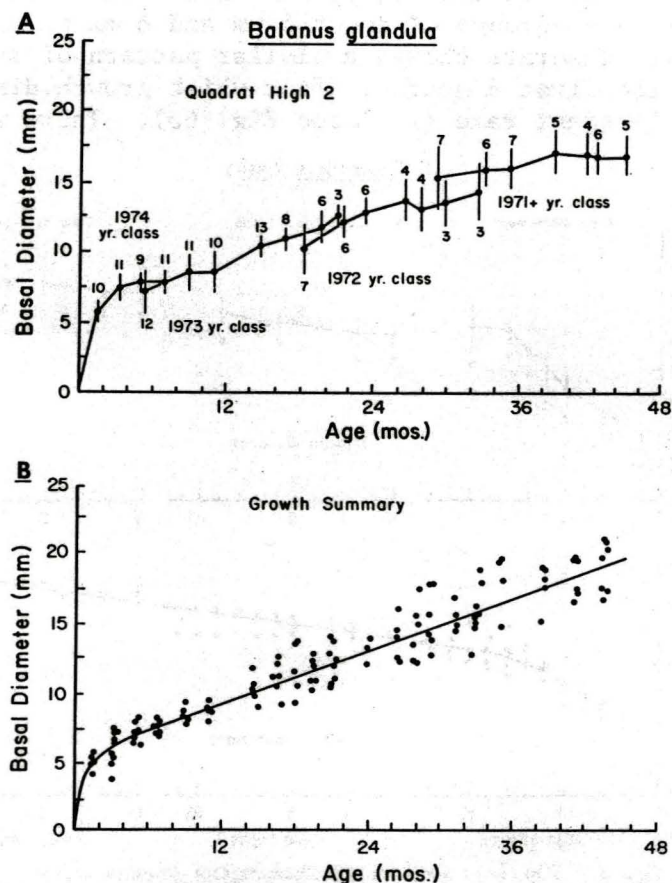


Fig. 7. Top (A): Growth of *Balanus glandula* in high level quadrat. Means, 95% confidence intervals and sample sizes are indicated. Bottom (B): Growth summary of *B. glandula*. Mean sizes at each age are plotted for all quadrats.

line $Y = 0.32X + 5.53$ was fitted to the mean size of barnacles older than 5 months in all quadrats. Because the "1971+ year-class" included some *B. glandula* older than 4 years, and the largest *B. glandula* I have observed was about 23 mm in diameter, I am certain that the growth of barnacles older than about 4 years slows to an asymptote of about 22 mm.

Seasonal settlement of *Tetraclita squamosa* indicated that year-classes could be followed, and members of four year-classes from settlement in 1973 back to 1970 were identified by constructing a size-frequency histogram of all *T. squamosa* in the February, 1974 photographs of quadrats (Fig. 8a). *T. squamosa* in these year-classes were followed for one year, and a growth curve was fitted by eye (Fig. 8b). Since this species lives many years, and individuals as large as 60 mm were occasionally seen outside the quadrat, it is assumed that growth of *T. Squamosa* older than 4 years approaches an asymptote of about 60 mm.

A summary comparison of the derived growth curves of the three species is shown in Figure 9. These curves are extended to the

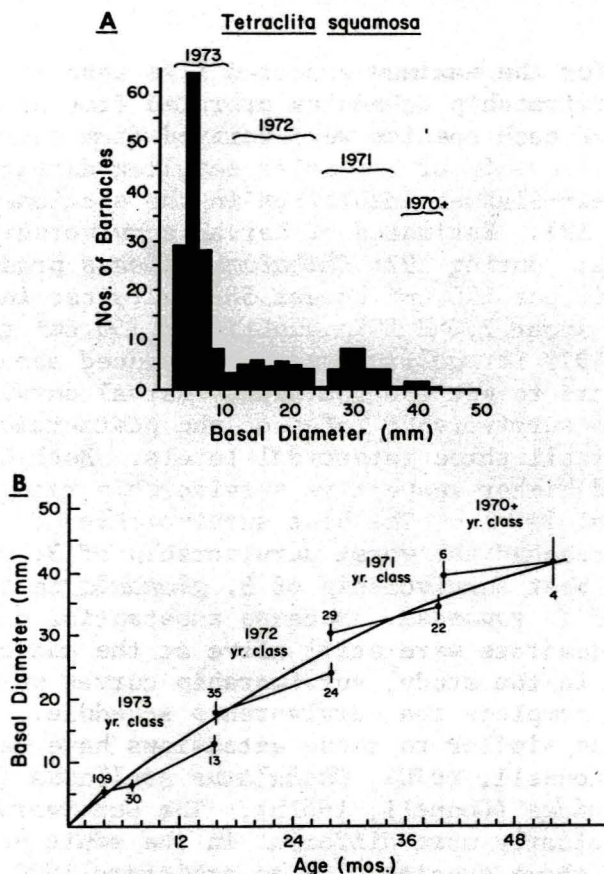


Fig. 8. Top (A): Size-frequency histogram of *Tetraclita squamosa* in all quadrats, February, 1974. Year-classes are indicated. Bottom (B): Growth summary of *T. squamosa*. Means, 95% confidence intervals, and sample sizes of the barnacles belonging to each year-class identified in histogram above as well as growth of the 1973 year-class from settlement are indicated.

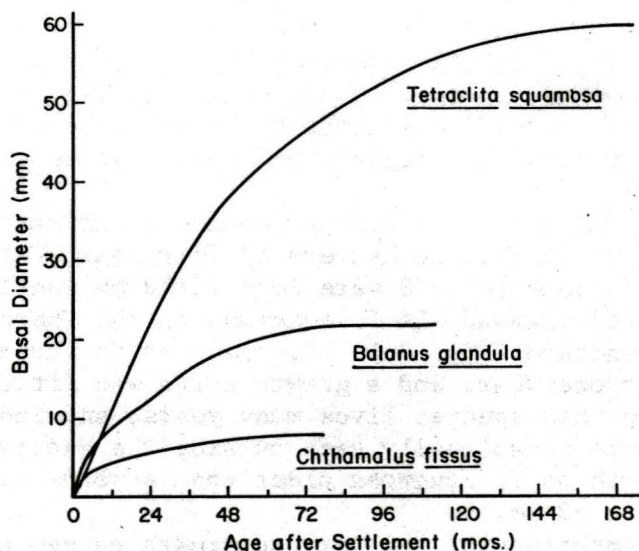


Fig. 9. Summary comparison of the derived growth curve of the three species.

asymptotic sizes for the maximum expected life span for each species.

Composite survivorship schedules prorated from an arbitrary 1000 individuals of each species were derived from estimates of larval survivorship, survivorship of barnacles settling during the study, and size-groups and year-classes identified in the settlement and growth studies (see Fig. 10). Estimates of larval survivorship were computed from the following: during 1974 *Chthamalus fissus* produced about 1.196×10^6 nauplii per 150 cm^2 to get 582 recruits; in 1974 *Balanus glandula* produced about 7.0×10^6 nauplii per 750 cm^2 to get 814 recruits; and in 1973 *Tetraclita squamosa* produced about 3.16×10^6 nauplii per 1500 cm^2 to get 150 recruits. Larval survivorship rates were then added to survivorship rates of the postmetamorphic barnacles in all quadrats at all three intertidal levels. Both *C. fissus* and *B. glandula* showed higher respective survivorship rates at upper than at lower tidal levels. The best survivorship of *C. fissus* in high quadrats approached the worst survivorship of *B. glandula* in low quadrats, and the best survivorship of *B. glandula* in the high quadrats approached that of *T. squamosa*. Because substantial numbers of barnacles in the quadrats were still alive at the end of the age intervals covered in the study, survivorship curves were extended by straight lines to complete the survivorship schedule. Straight-line survivorship curves similar to these extensions have been reported for *B. glandula* (Connell, 1970), *Chthamalus stellatus* (Connell, 1961a), and *Balanus balanoides* (Connell, 1961b). The survivorship curves thus derived are clearly most different in the adult portions of the life spans of the three species. Of an arbitrary 1000 individuals settling, the last *C. fissus* would survive to about 3 years; *B. glandula*, 8 years; and *T. squamosa*, 15 years. Further details and complete survivorship data from Hines (1976) are available on request.

Analysis of brooding frequencies as a function of basal diameter showed that *Chthamalus fissus* begins brooding at about 2 mm, and

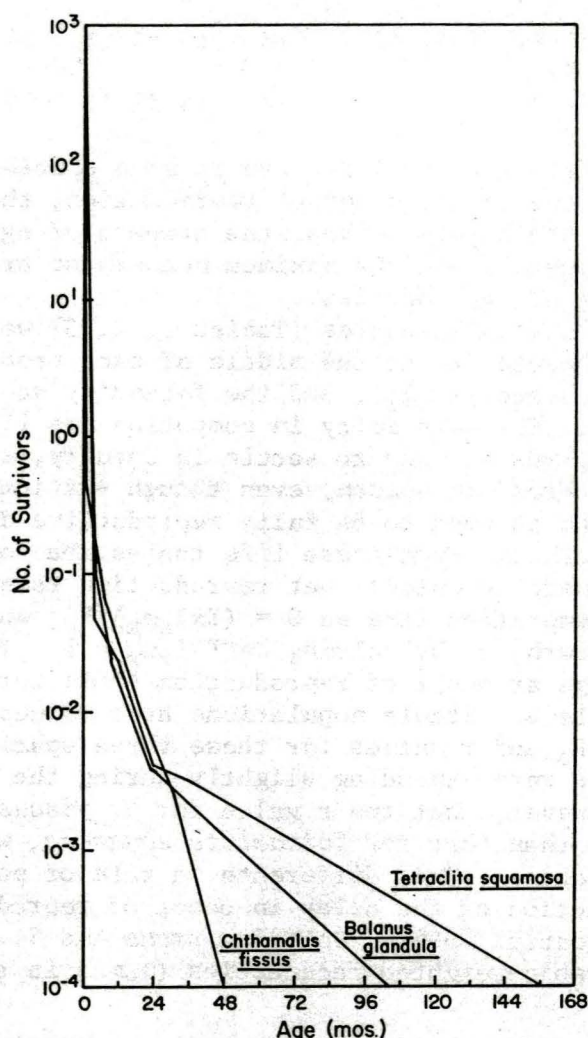


Fig. 10. Derived survivorship curves of each species from hatching of an arbitrary 1000 nauplii into the plankton.

larger *C. fissus* brooded at about equal frequencies. From the growth curve of *C. fissus* this corresponds to an age of onset of reproduction of about 2 months from settlement or 3 months from hatching. All *Balanus glandula* brooded at about equal frequencies by their first brooding season, at which time they were 6 months from settlement or 9 months from hatching and larger than 5 mm. *Tetralita squamosa*, however, did not begin to brood until 19 months from settlement or 22 months from hatching and 18 mm in diameter. *T. squamosa* from 12-18 mm in diameter showed low brooding frequencies, and barnacles larger than 18 mm showed about equal brooding activity.

Egg numbers per brood as a function of basal diameter are given by the following regressions showing the standard errors of the slopes and intercepts:

$$C. fissus: Y = 0.47(\pm 0.06)X - 1.12 (\pm 0.43); N = 24; \\ r^2 = 0.72.$$

B. glandula: $Y = 2.01 (\pm 0.76)X - 14.13 (\pm 9.54)$; $N = 33$;
 $r^2 = 0.82$.

T. squamosa: $Y = 1.14 (\pm 0.11)X - 14.31 (\pm 2.59)$; $N = 33$;
 $r^2 = 0.79$.

Fecundity schedules over the life span of each species can thus be calculated using the age of onset of reproduction, the basal diameter at each age from the growth curves, the numbers of eggs per brood for the basal diameter, and the maximum numbers of broods produced during the season of each species.

Life tables for each species (Tables 1, 2, 3) were computed using the age schedule (x) at the middle of each brooding season, the survivorship schedule (l_x), and the fecundity schedule (m_x) for each species. For simplicity in computing its life table, *Chthamalus fissus* was assumed to settle in January, 2 months before the start of the brooding season, even though settlement occurs year-round. It is thus assumed to be fully reproductive during the entire first brooding season. From these life tables the following population parameters were computed: net reproductive rate per generation as $R_0 = \sum l_x m_x$; generation time as $G = (\sum x l_x m_x) / R_0$; and intrinsic rate of population growth, r , by solving $\sum e^{-rx} l_x m_x = 1$. These values, along with the age at onset of reproduction (AOR) for each species, are shown in Table 4. Stable populations have values of $R_0 = 1.0$ and $r = 0$. The R_0 and r values for these three species indicate that these populations were expanding slightly during the period of the study. Note, however, that the r value for *C. fissus* is an order of magnitude larger than that for *Tetraclita squamosa*, with *Balanus glandula* intermediate. This difference in rate of population increase is largely a function of the delay in onset of reproduction in *T. squamosa* (Lewontin, 1965). Both *C. fissus* and *B. glandula* have maximum survivorship-weighted fecundities ($l_x m_x$) in the first year,

Table 1. Life table of *Chthamalus fissus*. Age schedule (X) is the age at the middle of each brooding season. l_x = survivorship schedule. m_x = fecundity schedule. V_x = schedule of reproductive value.

	Age (x) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood	No. broods per yr.	m_x	$l_x m_x$	$x l_x m_x$	$e^{-rx} l_x m_x$	V_x
hatch	0	1.000	-	0	0	0	0	0	0	1.0
settle?	1	4.865×10^{-4}	-	0	0	0	0	0	0	2,097
	7	6.709×10^{-5}	4.09	802	16	13,837	0.92832	6.4982	0.80987	17,093
	19	1.021×10^{-5}	5.17	1,310	16	20,958	0.21398	4.0658	0.14773	27,037
	31	2.428×10^{-6}	6.25	1,818	16	29,080	0.07061	2.1889	0.03858	32,276
	43	2.428×10^{-7}	7.33	2,325	16	37,202	0.00903	0.3883	0.00390	40,476
	55	2.428×10^{-8}	7.70	2,499	16	39,984	0.00097	0.0534	0.00033	42,130
	67	2.428×10^{-9}	8.00	2,640	16	44,240	0.00011	0.0074	0.00002	30,400

$$\sum l_x m_x = 1.22302$$

$$\sum x l_x m_x = 13.2018$$

$$\sum e^{-rx} l_x m_x = 1.00043$$

Table 2. Life table of *Balanus glandula*. Age schedule (X) is the age at the middle of each brooding season. l_x = survivorship schedule. m_x = fecundity schedule. V_x = schedule of reproductive value.

	Age (x) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood	No. broods per yr.	m_x	$l_x m_x$	$x l_x m_x$	$e^{-rx} l_x m_x$	V_x
hatch	0	1.000	-	0	0	0	0	0	0	1.0
settle?	3	1.1629×10^{-4}	-	0	0	0	0	0	0	8,838
	12	2.0385×10^{-5}	8.7	3,417	6	20,504	0.41797	5.0156	0.37460	54,736
	24	3.8374×10^{-6}	12.6	11,136	6	66,814	0.25639	6.1534	0.20594	203,144
	36	2.0466×10^{-6}	16.4	18,854	6	113,125	0.23152	8.3347	0.16667	285,218
	48	1.2791×10^{-6}	18.7	23,456	6	140,742	0.18002	8.6411	0.11615	307,233
	60	7.3260×10^{-7}	20.3	26,573	6	159,435	0.11680	7.0081	0.06754	324,336
	72	4.1863×10^{-7}	21.2	28,482	6	170,892	0.07541	5.1509	0.03908	331,976
	84	2.4420×10^{-7}	21.7	29,487	6	176,922	0.04320	3.6291	0.02007	271,301
	96	1.4245×10^{-7}	22.0	30,090	6	180,540	0.02571	2.4689	0.01070	180,456

$$\sum l_x m_x = 1.34703$$

$$\sum x l_x m_x = 46.4024$$

$$\sum e^{-rx} l_x m_x = 1.00075$$

Table 3. Life table of *Tetraclita squamosa*. Age schedule (X) is the age at the middle of each brooding season. l_x = survivorship schedule. m_x = fecundity schedule. V_x = schedule of reproductive value.

	Age (x) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood	No. broods per yr.	m_x	$l_x m_x$	$x l_x m_x$	$e^{-rx} l_x m_x$	V_x
hatch	0	1.000	-	0	0	0	0	0	0	1.0
settle?	3	4.75×10^{-5}	-	0	0	0	0	0	0	21,232
	12	2.323×10^{-5}	10	0	0	0	0	0	0	44,457
	24	4.0660×10^{-6}	22	10,770	3	32,310	0.1314	3.1529	0.12333	262,172
	36	3.2300×10^{-6}	31	21,030	3	63,090	0.2038	7.3361	0.18532	298,659
	48	2.285×10^{-6}	38	29,010	3	87,030	0.1989	9.5453	0.17522	343,714
	60	1.5676×10^{-6}	42.5	34,140	3	102,420	0.1605	9.6330	0.13698	386,151
	72	1.09×10^{-6}	47	39,270	3	117,810	0.1284	9.2455	0.10617	421,255
	84	7.84×10^{-7}	50	42,690	3	128,070	0.1004	8.4342	0.08043	435,475
	96	5.70×10^{-7}	52.5	45,540	3	136,620	0.0779	7.4784	0.06046	436,442
	108	3.990×10^{-7}	55	48,390	3	145,170	0.0592	6.2556	0.04451	442,030
	120	2.85×10^{-7}	57	50,670	3	152,010	0.0433	5.1986	0.03154	424,352
	132	2.042×10^{-7}	58	51,810	3	155,430	0.0317	4.1844	0.02237	392,457
	144	1.425×10^{-7}	59	52,950	3	158,850	0.0226	3.2544	0.01545	350,880
	156	1.0447×10^{-7}	59.5	53,520	3	160,560	0.0168	2.6208	0.01112	270,720
	168	7.12×10^{-8}	60	54,090	3	162,270	0.0116	1.9488	0.00744	162,930

$$\sum l_x m_x = 1.1870$$

$$\sum x l_x m_x = 78.2881$$

$$\sum e^{-rx} l_x m_x = 1.00055$$

Table 4. Age at onset of reproduction (AOR), net reproductive rate per generation (R_0), generation time (G), and intrinsic rate of population growth (r) for each species.

	<i>Chthamalus fissus</i>	<i>Balanus glandula</i>	<i>Tetraclita squamosa</i>
A.O.R.	3 mos.	9 mos.	22 mos.
R_0	1.223	1.347	1.187
G	10.8 mos.	34.5 mos.	66.0 mos.
r	0.0195	0.0091	0.0026

although *B. glandula* does not reach its peak until five months after *C. fissus* (see l_{xm} schedule in the life tables). *T. squamosa* does not begin reproducing until the second year and does not reach its peak l_{xm} value until the third year. *C. fissus* has a generation time of less than a year, while that of *B. glandula* is nearly 3.5 years and *T. squamosa* is about 5.5 years. The expected number of offspring that remain to be born to each barnacle of age (x) were computed as the V_x schedule in each life table and plotted in Figure 11. $V_x =$

$$\left(\sum_{y=x}^{\infty} e^{-ry} l_{my} \right) / e^{-rx} l_{mx}$$

and reflects the "reproductive value" of each

barnacle over its expected life span. Because of its long life span and high fecundity, *T. squamosa* maintains high reproductive values for a long time. The low reproductive value of *C. fissus* reflects its poor survivorship and low fecundity. Again, *B. glandula* is intermediate.

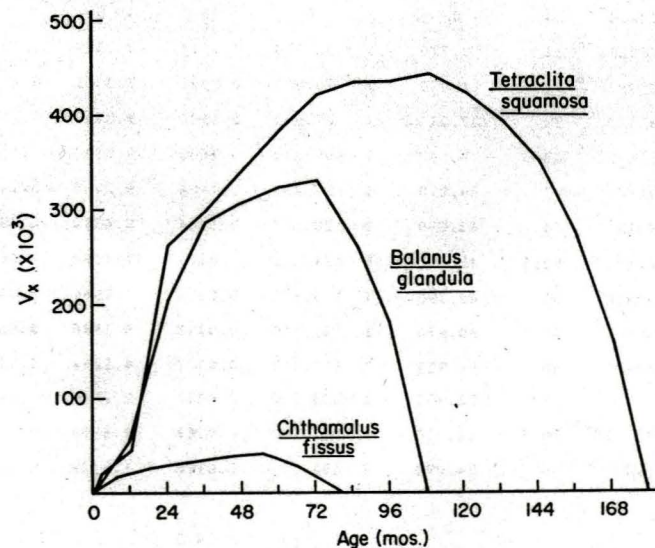


Fig. 11. "Reproductive value" over the life span of each species. V_x is the expected number of nauplii that remain to be released by each barnacle of age (X).

Discussion

Studies on the factors determining the intertidal distribution of barnacles have provided much of the basis for our understanding of the regulation of intertidal zonation and community structure. Thus, barnacles living in high zones are generally more tolerant of high temperatures and desiccation stress (Barnes and Barnes, 1957; Foster, 1971), and desiccation in upper intertidal zones can be an important cause of mortality of cyprids and juvenile barnacles (Connell, 1961a,b; Strathmann and Branscomb, this volume). Connell (1961a) showed experimentally that the zonation pattern of *Chthamalus stellatus* living predominantly in high areas in Scotland was largely caused by competition for space with *Balanus balanoides*. *B. balanoides* exhibited much intraspecific competition for space as well, with crowding in the lower zone killing many of its own kind. Predation by *Thais lapillus* in the summer was a second major source of mortality in the lower range of *B. balanoides*. In a similar system at San Juan Island, Washington, Connell (1970) showed that *Balanus glandula* settles in all but the uppermost zone, but predation by *Thais* spp. limits their survivorship in lower zones. *B. glandula* has a spatial refuge from predators in the upper midintertidal zone, however, where it has much higher survivorship. In the lower zones *Balanus cariosus* may escape predation when it grows to a size larger than most predators can attack. It is a good competitor for space and has a refuge in size which, once attained, allows a year-class to live and dominate an area for many years (Dayton, 1971).

A variety of predators occur at Morro Bay which have been documented to prey extensively on barnacles in lower intertidal zones of western North America. The most important of these are two species of sea stars - *Pisaster ochraceus* and *Leptasterias hexactis* (Feder, 1970; Menge, B., 1972a,b; Paine, 1966), and two species of gastropods - *Thais emarginata* and *Acanthina spirata* (Connell, 1970; Dayton, 1971; Menge, J., 1974). Deaths of young barnacles caused by grazing limpets and abrasion from algae have also been documented, and competition for space with *Mytilus californianus* and *Anthopleura elegantissima* has also been shown to limit the distribution of barnacles in the Pacific Northwest (e.g., Dayton, 1971). Acmaeid limpets and *A. elegantissima* are abundant in my study area at Morro Bay.

My field observations at Morro Bay indicate that the physical and biological factors regulating zonation patterns and community structure in other intertidal areas probably apply to the community interactions in my study areas as well. Thus, *Chthamalus fissus*, like *C. stellatus*, settles initially at all intertidal levels, but has poor survivorship in the lower zones where competition (particularly from *Balanus glandula*) and predation are high. Although it survives best at high levels, the environment there is rigorous for a small animal with a large surface area, and its survival is still less than either of the other two species. *Balanus glandula*, like *B. balanoides*, survives best at the higher zone, where it settles only in low numbers.

Intra-specific crowding following heavy settlement in the low levels seems to be the major cause of mortality of *B. glandula*, although predation by snails and sea stars and competition for space with *Anthopleura elegantissima* and *Tetraclita squamosa* are also important. *T. squamosa*, like *Balanus cariosus*, grows to a large size which exempts it from much of the predation and competition in the lower zone, and it has better survival than the other two species.

The life history characteristics of *Chthamalus fissus* allow it opportunistically to exploit changing conditions in a rigorous unpredictable environment, and quickly to colonize ephemeral open space in the lower intertidal zones. During periods of high food availability from spring through fall (Icanberry and Adams, 1974), it rapidly produces many small broods, resulting in a high yearly allocation of energy to egg production while minimizing the energetic cost of any single brood if conditions turn bad. It also effectively disperses sibling larvae and, combined with its year-round settlement at all tidal levels, improves chances of colonization (see Strathmann, 1974). However, *C. fissus* grows slowly to a small size, resulting in poor competitive ability and little chance of avoiding predation in the lower zones. Its low fecundity, combined with poor survivorship, results in low reproductive values, but its early age of onset of reproduction results in a short generation time and the higher potential for rapid population increase, which is advantageous in exploiting labile conditions.

The life history pattern of *Balanus glandula* allows it to spatially dominate large portions of the lower intertidal zone for parts of the year. Settlement of many larvae at the start of the summer period, when warming temperatures and high food availability are optimal for rapid growth, results in *B. glandula* crowding and smothering other organisms. This dominance may also effectively saturate the predator populations during the summer, when many of the snails and sea stars are most active. The resulting intense intra-specific competition for space, combined with predation, causes high mortality in the lower zones during summer and fall. Storage of large amounts of nutrients in the summer allows *B. glandula* to reproduce in the nutrient-poor winter, and those individuals that survive to reproduce may face reduced predation pressure in winter when many of the snails and sea stars tend to be quiescent. However, information on the annual feeding cycles of predators was gathered in Washington where winter temperatures are very cold, and similar data needs to be gathered for central California communities (Paine, 1963; Connell, 1970; Menge, B., 1972a,b; Menge and Menge, 1974). The few *B. glandula* settling in higher zones have a refuge from competition and predation and show better survivorship. Production of a series of broods improves dispersal, and large brood size results in an intermediate but high reproductive effort. The slight delay in onset of brooding until the first winter results in an intermediate generation time and intrinsic rate of population growth. Intermediate longevity and fecundity results in intermediate reproductive values for *B. glandula*.

In *Tetraclita squamosa*, the long delay in the onset of

reproduction, the timing of reproduction when food availability is high in the summer, and low yearly allocation of energy to egg production all facilitate the advantageous allotment of maximum energy for rapid growth to a size large enough to compete effectively for space and avoid many predators. A fall settlement time is advantageous in that much of the initial smothering by *Balanus glandula* is over by then, and many *B. glandula* have begun to crowd themselves off the substrate, resulting in new open spaces. Further, settlement in the fall means that the smallest individuals, and therefore the individuals most susceptible to predation, will be available only when the predatory snails and sea stars tend to be less active. These barnacles will then have winter and early spring to grow before the major predators are active again and before the next settlement of *B. glandula* occurs. In addition, the patchy nature of settlement makes the availability of this species to predators unpredictable, while still assuring the presence of other *T. squamosa* for cross-fertilization. The long delay in the onset of reproduction results in a long generation time and a relatively low intrinsic rate of population growth, although the long survivorship and high fecundity result in a high reproductive value over many years for this species.

The values for net reproductive rates per generation and intrinsic rates of population increase of the three species presented in this paper need cautious interpretation. More weight should be given to the relative, rather than the absolute values of these parameters in comparing one species to another, because the accuracy of their absolute values depends heavily on the accuracy of the estimates of larval mortality. These estimates are suspect, because they falsely assume that the barnacle populations recruit only from themselves. In any case, the values of (R_0) and (r) presented here apply only to the particular time and conditions of this study. Since populations fluctuate around some average size during "good" and "bad" times, the values of (R_0) and (r) will be expected to oscillate around 1.0 and 0.0 respectively. Long-term studies such as Cornell (1970) and studies over a wide geographic area are necessary to measure these important fluctuations.

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