

LIFE HISTORY AND ENVIRONMENT IN TWO SPECIES OF INTERTIDAL BARNACLES

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ABSTRACT

The reproductive ecology of *Chthamalus anisopoma* and *Tetraclita stalactifera* is compared in order to understand how their life histories function in the context of their present environment, and what selective forces might have shaped their life histories. *C. anisopoma* is common in the lower intertidal of the Gulf of California. It initiates breeding six weeks after settlement; brooding and recruitment is year-round. Growth after settlement is rapid for two months, then slows markedly. Survivorship is fairly constant at all ages. Observations indicate that most mortality results from predatory gastropods, and from intraspecific crowding. *T. stalactifera* is generally confined to the upper intertidal. It failed to brood during the study period. The ovarian cycle indicates that brooding would otherwise take place during the summer. The age of first reproduction is estimated at two years. Recruitment of cyprids is strongly seasonal, peaking during August. The growth rate is relatively constant. Survivorship is initially very poor, apparently due to desiccation stress, but improves substantially after four months.

An examination of the intertidal positions and life histories of *Tetraclita* and *Chthamalus* congeners from different coastlines of the world reveals a relative conservatism of life histories, regardless of position in the intertidal. This conservatism is discussed as a general phenomena in *Chthamalus* and *Tetraclita*, and is contrasted with the relative diversity exhibited in another genus of barnacles, *Balanus*.

INTRODUCTION

In this paper I compare the reproductive ecology of *Chthamalus anisopoma* Pillsbry and *Tetraclita stalactifera* Lamarck, two species of rocky intertidal barnacles which occur at different intertidal elevations. The effect of exposure in the rocky intertidal zone is often reflected in the patterns of mortality at different intertidal levels. Abiotic factors such as desiccation stress are often a primary source of mortality at higher shore levels, while the relatively favorable conditions in the lower intertidal are associated with a predominance of biotic interactions such as competition for space, and predation (Connell, 1972, 1975; Wethey, 1983; but see Underwood and Denley, 1984, for critique). Given that organisms differ in age-specific reproductive effort, growth, and mortality, it is reasonable to assume that the differences between the low and high intertidal zones might be manifested in contrasting life history traits between ecologically similar high and low intertidal species.

The bulk of this paper is the presentation of reproductive, growth, and survivorship data gathered during a 13 month field study. The remainder of the work emphasizes how the barnacle's life histories function to allow persistence in their present envi-

Received 12 August 1985; accepted 26 February 1986.

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ronment, and asks if we can explain the selective forces that have shaped their life histories. With regard to the latter, I argue that the life histories of *C. anisopoma* and *T. stalactifera* are relatively constrained, and better understood as products of their phylogenetic histories than as adaptations to contemporary local environments (Gould and Lewontin, 1979; Stearns, 1982, 1984).

Some key life history parameters include the timing and duration of the reproductive effort, patterns of recruitment, and age-specific survivorship and growth (Stearns, 1976, 1977). These parameters are relatively easy to measure in acorn barnacles (*e.g.*, Connell, 1970; Hines, 1978). Acorn barnacles are sessile, simultaneous hermaphrodites that brood their eggs. The timing and duration of reproduction can be ascertained from sequential samples; recruitment can be quantified, and the new individuals can be mapped and followed through time to measure age-specific growth and mortality. Combining information from growth rates and dissections of small individuals, the age of first reproduction can be approximated. At present the planktonic larval stage of barnacles precludes the direct measurement of mortality before settlement and metamorphosis. The fate of larvae released from a particular local population and the geographic origin of new recruits cannot yet be determined with certainty.

MATERIALS AND METHODS

C. anisopoma is a small barnacle, with a maximum basal diameter of 6 to 7 mm. *T. stalactifera* is relatively large, reaching a basal diameter of 30 to 40 mm, and generally occurs higher on the shore (Dungan, 1985). Both species are endemic to the Gulf of California, which extends approximately 1200 km latitudinally from 23°N to about 32°N. The study site is located on open coast approximately 10 km northwest of the town of Puerto Penasco, Sonora, Mexico, (31°18'N, 113°35'W) on the mainland side of the northern Gulf of California (Fig. 1). The northern Gulf has a great tidal range (7 m spring tides at the study site), and large seasonal fluctuations in sea temperature owing to the influence of the adjacent Sonoran desert (Maluf, 1983). The study site is a granitic promontory facing west, exposed to wave action, with a broken topography composed of numerous angular boulders and sloping benches. It was visited at monthly intervals from January 1982 to February 1983. Each time samples were collected, and permanent quadrats were either photographed or censused.

Because it is not known if *C. anisopoma* and *T. stalactifera* are obligatory cross-fertilizers, specimens were collected where individuals were common and close enough together to ensure the availability of a potential mate. Samples were preserved in 70% isopropanol and brought to the laboratory, where 50 individuals of each species were selected for dissection. All size classes were represented. During each dissection I recorded the rostral-carinal axis of the opercular opening to the nearest 0.05 mm, the condition of the ovary, the presence or absence of eggs brooding in the mantle cavity, and the developmental stage of the brooding eggs. Ovaries were classified as either ripe or unripe. Ripe ovaries contained unfertilized eggs in sufficient quantity as to be visible to the unaided eye, and a considerable amount of yellow ovarian tissue bulging out into the mantle cavity; unripe ovaries lacked these qualities. Under this scheme an unripe ovary may be partially undeveloped or entirely undeveloped. Oviposition of the eggs to the mantle cavity for brooding takes place immediately after copulation (Crisp and Davies, 1955). Brooding eggs were classified as either late stage, with the nauplius eyespot visible under 10× magnification, or as early stage, lacking a visible eyespot.

To assess recruitment, growth, and survivorship, 33 permanently marked 100 cm² quadrats were placed at intertidal levels over nearly the entire vertical range of *C.*

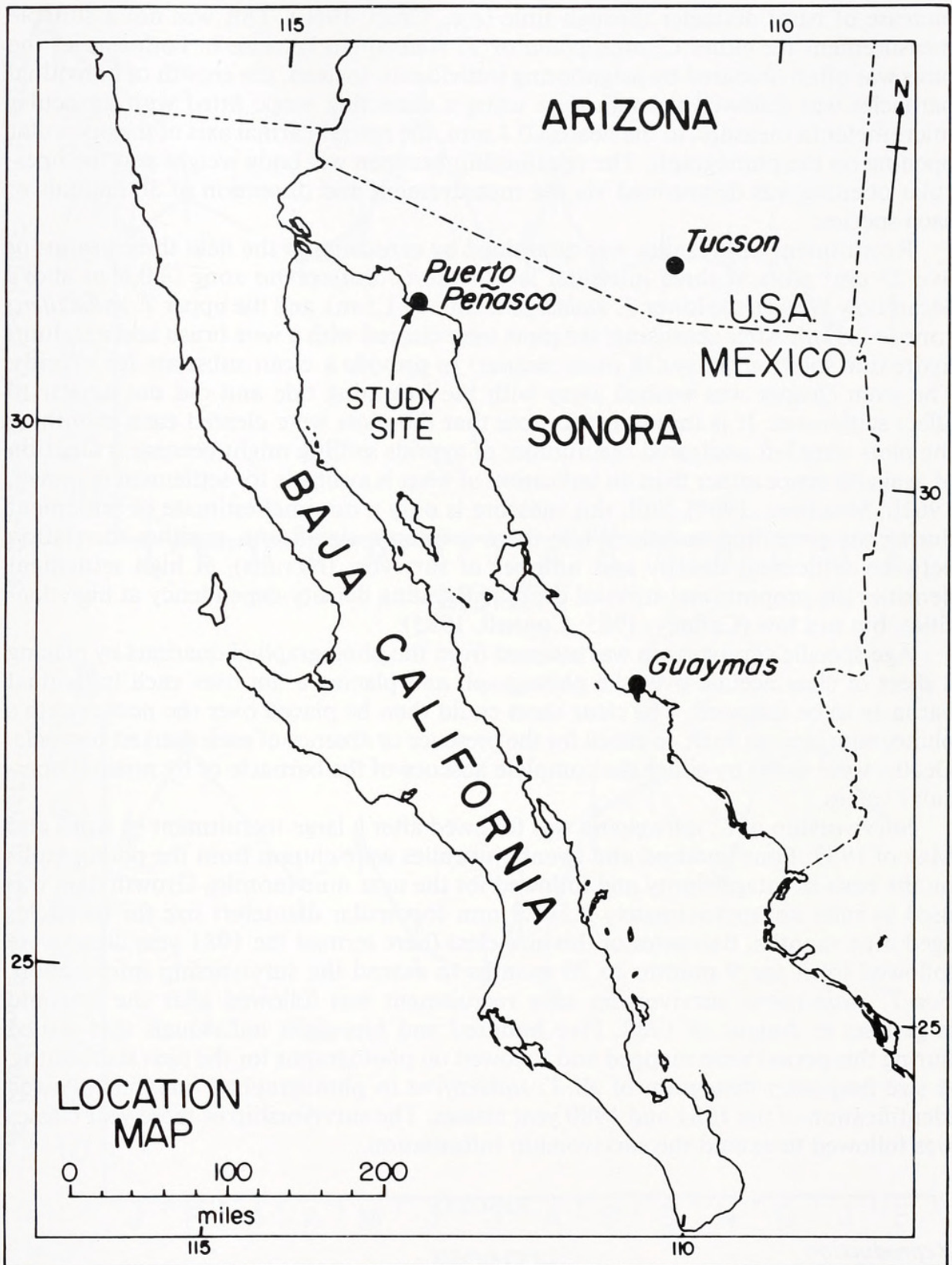


FIGURE 1. The study site, 10 km NW of Puerto Peñasco.

anisopoma and *T. stalactifera*. These quadrats were photographed monthly, using a fixed focal length and focus to ensure the same perspective. Accuracy was checked against an included scale. The most common measure of growth in barnacles is the

increase of basal diameter through time (e.g., Crisp, 1960). This was not a suitable measurement for either *C. anisopoma* or *T. stalactifera* because in both species the basis was often obscured by neighboring individuals. Instead, the growth of individual barnacles was followed through time using a dissecting scope fitted with an ocular micrometer to measure, to the nearest 0.1 mm, the rostral-carinal axis of the opercular opening on the photograph. The relationship between wet body weight and the opercular opening was determined via the measurement and dissection of 30 animals of each species.

Recruitment of juveniles was quantified by censusing in the field three groups of five 25 cm² plots at three intertidal levels: the *C. anisopoma* zone (+0.6 m above Mean Low Water), the lower *T. stalactifera* zone (+1.5 m), and the upper *T. stalactifera* zone (+2.3 m). After censusing, the plots were cleared with a wire brush and a sodium hydroxide solution (Easy-Off oven cleaner) to provide a clean substrate for cyprids. The oven cleaner was washed away with the incoming tide and did not appear to affect settlement. It is important to note that the plots were cleared each month. If the plots were left uncleared the number of cyprids settling might become a function of available space rather than an indication of what is available for settlement (Connell, 1961b; Meadows, 1969). Still, this measure is only a minimal estimate of settlement during the preceding month. While there is often a significant, positive correlation between settlement density and number of survivors (recruits), at high settlement densities the proportional survival drops, suggesting density-dependency at high densities, but not low (Caffney, 1985; Connell, 1985).

Age-specific survivorship was assessed from the photographed quadrats by placing a sheet of clear acetate over the photograph and placing a dot over each individual barnacle to be followed. The clear sheet could then be placed over the next month's photograph, and so forth, to check for the presence or absence of each marked barnacle. Deaths were noted by either the complete absence of the barnacle or by missing opercular valves.

Survivorship of *C. anisopoma* was followed after a large recruitment in April and May of 1982. Four hundred and twenty juveniles were chosen from the photographs on the basis of image clarity and followed for the next nine months. Growth data was used to infer an approximately 2.5–2.8 mm (opercular diameter) size for barnacles aged nine months. Barnacles of this size class (here termed the 1981 year class) were followed from age 9 months to 20 months to extend the survivorship information. For *T. stalactifera*, survivorship after recruitment was followed after the first and largest set in August of 1982. Five hundred and fifty-eight individuals that settled during this period were mapped and followed on photographs for the next six months. A size frequency histogram of all *T. stalactifera* in photographed quadrats allowed identification of the 1981 and 1980 year classes. The survivorship of these year classes was followed to extend the survivorship information.

RESULTS

Reproduction

Ovarian cycles and brooding frequencies of *C. anisopoma* are shown in Figure 2. Ripe ovaries were found throughout the year. With the exception of a peak of 90% in July, there was no clear seasonal pattern of ovarian development. Brooding also occurred year-round, but with a significant drop during the summer. In June and July, 44% to 52% of the sample contained developing embryos; in January, February, and December of 1982, and January and February of 1983, the percentage brooding fluctuated between 76% and 94%.

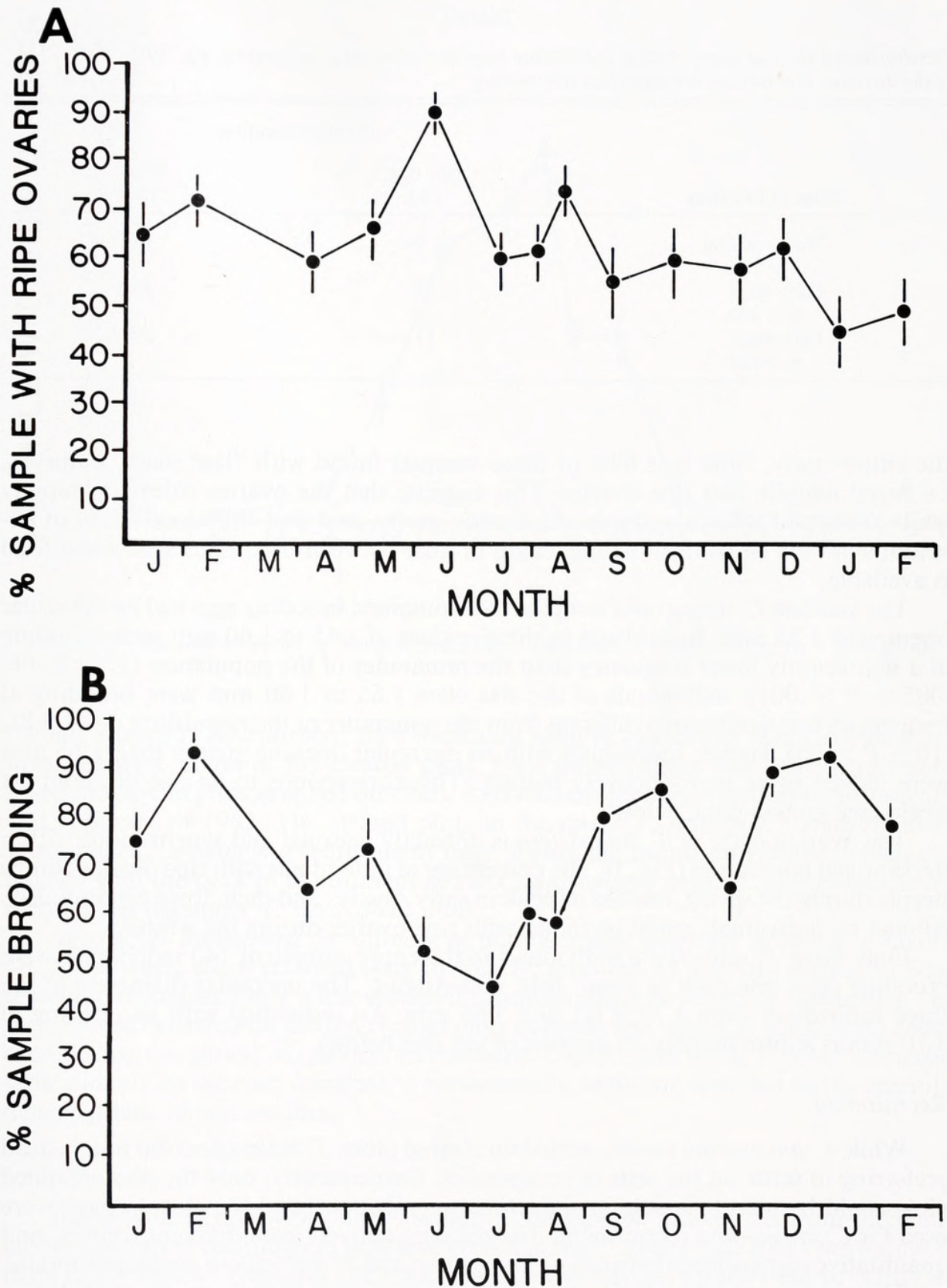


FIGURE 2. (A) The ovarian cycles and the (B) brooding frequencies in *Chthamalus anisopoma*. Bars indicate standard error ($n = 50/\text{month}$).

During each dissection of *C. anisopoma* the condition of the ovary relative to the developmental stage of the brooding embryos was recorded; this information is compiled in Table I, which sums the information for all samples of *C. anisopoma* over

TABLE I

Developmental stage of ovary relative to brooding stage in Chthamalus anisopoma; e.g., 91% of the dissected animals not brooding had ripe ovaries

Stage of brooding	Ovary condition	
	Not ripe (%)	Ripe (%)
Not brooding n = 193	9	91
Early stage n = 370	61	39
Late stage n = 137	11	89

the entire study. Note that 89% of those samples found with "late stage" embryos, *i.e.*, eyed nauplii, had ripe ovaries. This suggests that the ovaries redevelop rapidly while the brood is developing in the mantle cavity, and that the brood's rate of development may be controlling the length of time between broods, at least when food is available.

The smallest *C. anisopoma* sampled that contained brooding eggs had an opercular opening of 1.25 mm. Individuals in the size class of 1.45 to 1.60 mm were brooding at a significantly lower frequency than the remainder of the population ($\chi^2 = 10.06$, $.005 > P > .001$); individuals of the size class 1.65 to 1.80 mm were brooding at frequencies not significantly different from the remainder of the population ($\chi^2 = 3.81$, $.10 > P > .05$). Hence, individuals with an opercular opening greater than 1.65 mm were judged to be reproductively mature. This corresponds to an age of about six weeks (see growth data, below).

The ovarian cycle of *T. stalactifera* is distinctly seasonal and synchronous within the sampled population (Fig. 3). The percentage of individuals with ripe ovaries climbs steeply during the spring, reaches its peak in early August, and then drops precipitously. Almost no individuals could be found with ripe ovaries during the winter.

Only three *T. stalactifera* individuals in the entire sample of 740 individuals were brooding eggs, one each in June, July, and August. The opercular diameters of the three individuals were 3.70, 4.80, and 5.65 mm. An individual with an opening of 3.70 mm is approximately 20 months of age (see below).

Recruitment

While *C. anisopoma* readily settled on cleared plots, *T. stalactifera* did not, instead preferring to settle on the tests of conspecifics. Consequently, only the photographed plots could be used to assess *T. stalactifera* recruitment, and the cleared plots were used for *C. anisopoma* recruitment. The data are derived from different sources, and quantitative comparisons between *C. anisopoma* and *T. stalactifera* are inappropriate.

The average number of *C. anisopoma* recruits each month on cleared plots is shown in Figure 4a. Because the plots were not cleared until April, recruitment for February through April was estimated by examination of photographed quadrats. There was light recruitment during this period, averaging about 50 individuals per 25 cm². Recruitment appeared to increase gradually from February to April.

Recruitment was very heavy from April to September on cleared plots in the *C. anisopoma* zone, with a maximum of nearly 600 individuals per 25 cm² during

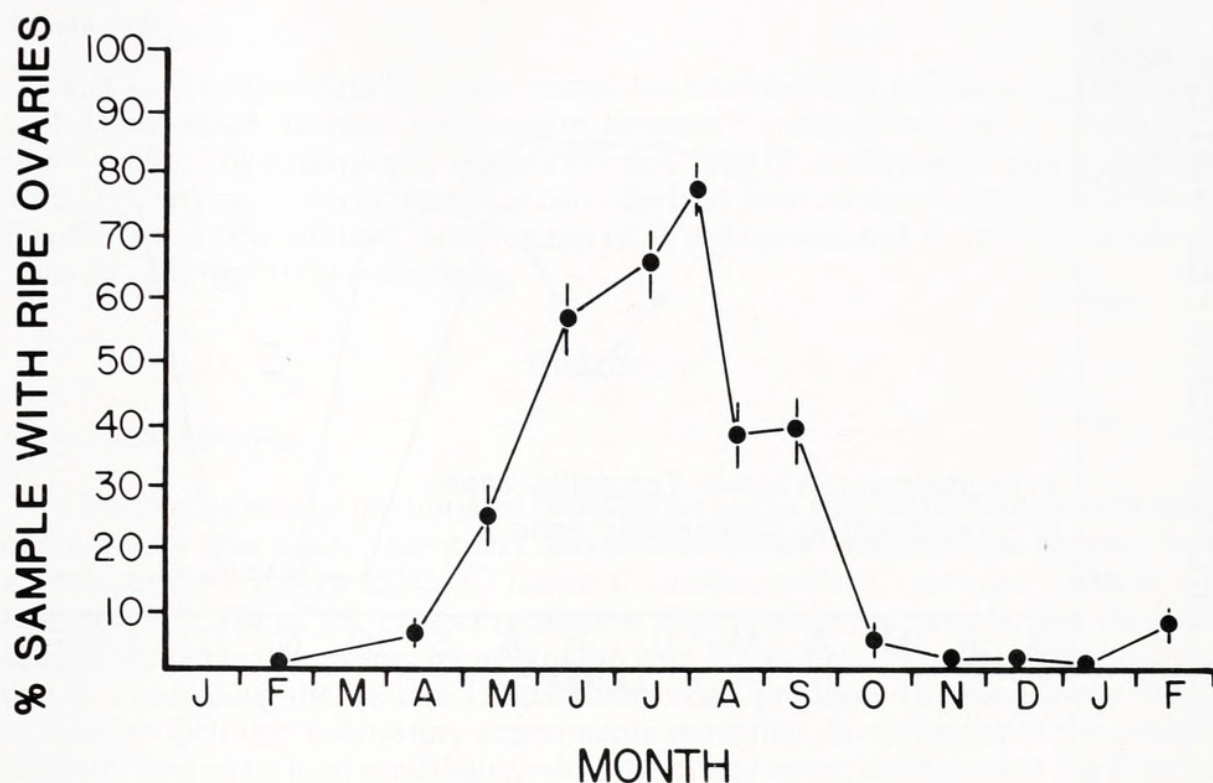


FIGURE 3. The ovarian cycles in *Tetraclita stalactifera*. Bars indicate standard error ($n = 50/\text{month}$).

the late summer. Recruitment then decreased until in November and December no juveniles were noted in the cleared plots, even though there was light recruitment noted in some of photographed quadrats. Recruitment then increased again in January and February of 1983. The cleared plots in the lower *T. stalactifera* zone received substantial *C. anisopoma* recruitment only during the month of August, which coincided with the peak of recruitment in the *C. anisopoma* zone. *C. anisopoma* never recruited in the upper *T. stalactifera* plots.

Average *T. stalactifera* recruitment in photographed quadrats is shown in Figure 4b. There was a sharp seasonal peak in August, followed by a steady decline in September and August. Only a few scattered juveniles could be found in November. No recruitment occurred on the ten cleared plots in lower and upper *T. stalactifera* zone, even during the period of heaviest recruitment. I noted that when *T. stalactifera* did settle directly on the rock substrate, it preferentially settled on scars left by the recently detached tests of conspecifics.

Growth

The growth of thirty-four newly settled *C. anisopoma* individuals from three adjacent quadrats at two different tidal levels (both in the *C. anisopoma* zone) was followed from April 1982 to February 1983. Individuals were chosen on the basis of clarity of image in photographs. Data from individuals in the higher quadrats are shown in Figure 5a. After eight to nine months many *C. anisopoma* had died, resulting in the smaller sample sizes and larger confidence intervals. A summary of growth data for *C. anisopoma* is shown in Figure 5b. Visual inspection of growth curves suggests no consistent differences between individuals at the two different tidal levels. All individuals grew quickly for the first two months before sharply leveling off.

Data for the growth of newly settled *T. stalactifera* was obtained in a manner

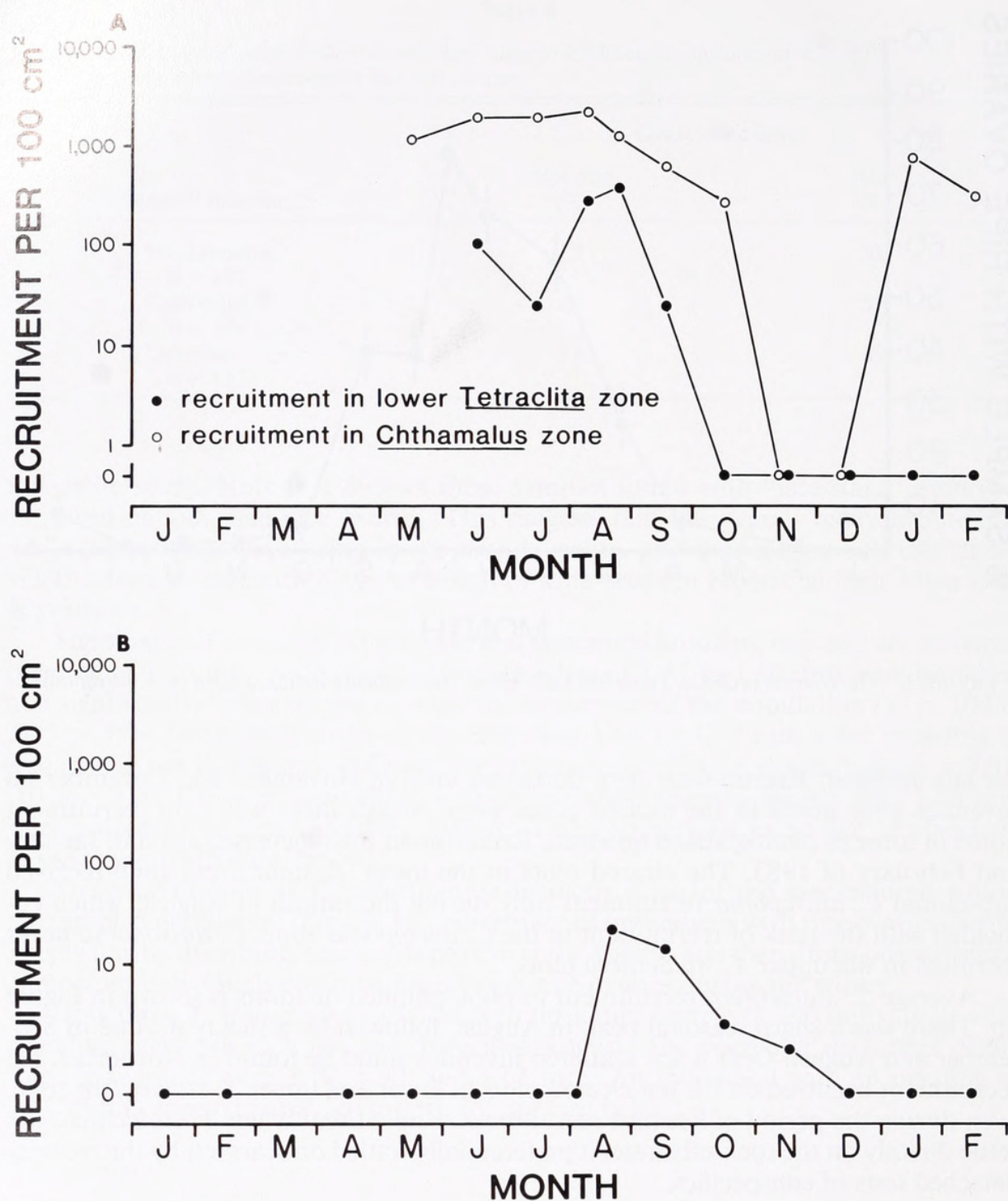


FIGURE 4. (A) The recruitment of *Chthamalus anisopoma* in cleared 25 cm² plots and the (B) recruitment of *Tetraclita stalactifera* in photographed 100 cm² quadrats.

similar to that described for *C. anisopoma*. An example of growth rates is shown in Figure 6a. Growth rate information was extended by measuring the growth of the 1981 year class individuals, as identified from a size frequency histogram of all measurable *T. stalactifera* in photographed quadrats. An example of the growth rates of 1981 year class individuals is shown in Figure 6b. Data from both newly settled and 1981 year class individuals are compiled in Figure 6c, which summarizes approximately 19 months of growth. All data were from areas of similar exposure and elevation. For further growth data see Malusa (1983).

Survivorship

The survivorship data for each species was summed and adjusted to 1000 newly settled individuals to allow comparison between *C. anisopoma* and *T. stalactifera* survivorship. The survivorship of the 1981 and 1980 (*T. stalactifera* only) year classes are treated as extensions of the initial curve derived from the newly settled individuals. Figure 7 shows the adjusted survivorship of *C. anisopoma* and *T. stalactifera* plotted from an arbitrary 1000 individuals.

DISCUSSION

Reproductive ecology

Chthamalus anisopoma initiated breeding six weeks after settlement, and brooded continuously thereafter, year-round and in sea surface temperatures ranging from approximately 13°C to 33°C. *C. fissus*, *C. stellatus*, and *C. dentatus* (Klepal and Barnes, 1975; Hines, 1978) also produce a large number of broods, but these are usually limited to the warmer months of the year. For example, Hines (1978) estimates that *C. fissus* along the western United States coast produces 16 broods from March or April to October. Laboratory experiments show that development of the ovary is generally limited by food availability, while the rate of brood development is a function of temperature (Crisp, 1950; Patel and Crisp, 1960a, b). When food is available, reproduction is virtually continuous, with the hatching and release of one brood followed by the deposition of another (Hines, 1976). That 91% of those *C. anisopoma* not brooding had ripe ovaries apparently ready for deposition (Table I) provides strong circumstantial evidence for similar continuous reproduction.

C. anisopoma recruited throughout most of the year, with a maximum in August and a minimum in November and December. *C. fissus* also recruits throughout the year, and at all intertidal levels (Hines, 1979). *C. anisopoma* recruitment was largely limited to the *Chthamalus* zone, recruiting higher only during August, when most space in the *Chthamalus* zone had already been pre-empted by other *C. anisopoma*.

C. anisopoma grew quickly for the first two months, after which growth dropped off dramatically. The sharp decline in the growth rate occurs shortly after the estimated age of first reproduction of six weeks. Crowding may also play a role in the change in growth rate, but there were no controls for comparison to substantiate this. *Elminius modestus* in the northeastern Atlantic has a similar pattern of growth. It begins reproducing at about two months of age, after which growth is sharply curtailed (Crisp, 1960). The early age of reproduction is indicative of the relatively short life span of *C. anisopoma*. The largest individual in photographed quadrats had an opercular diameter of 3.85 mm. Extrapolating from the growth rate in Figure 6, this corresponds to an age of approximately three years.

The mortality rate of *C. anisopoma* in photographed quadrats was fairly constant at all ages. Eighty percent of the newly recruited individuals survived at least six weeks, when reproduction begins. Adults were frequently consumed by the gastropods *Acanthina angelica* and *Morula ferruginosa*, barnacle predators common in the lower intertidal (Paine, 1966; Dungan, 1984; Malusa, 1985). Also, sequences of photographs revealed that *C. anisopoma* was often a victim of its own growth. Intraspecific competition for space resulted in the formation of hummocks, raised mats of barnacles, which eventually were dislodged by wave action. Connell (1961b) documents a similar source of mortality for *Semibalanus* (= *Balanus*) *balanoides* off the coast of Scotland.

The ovaries of *T. stalactifera* showed distinct seasonal variation, developing as the

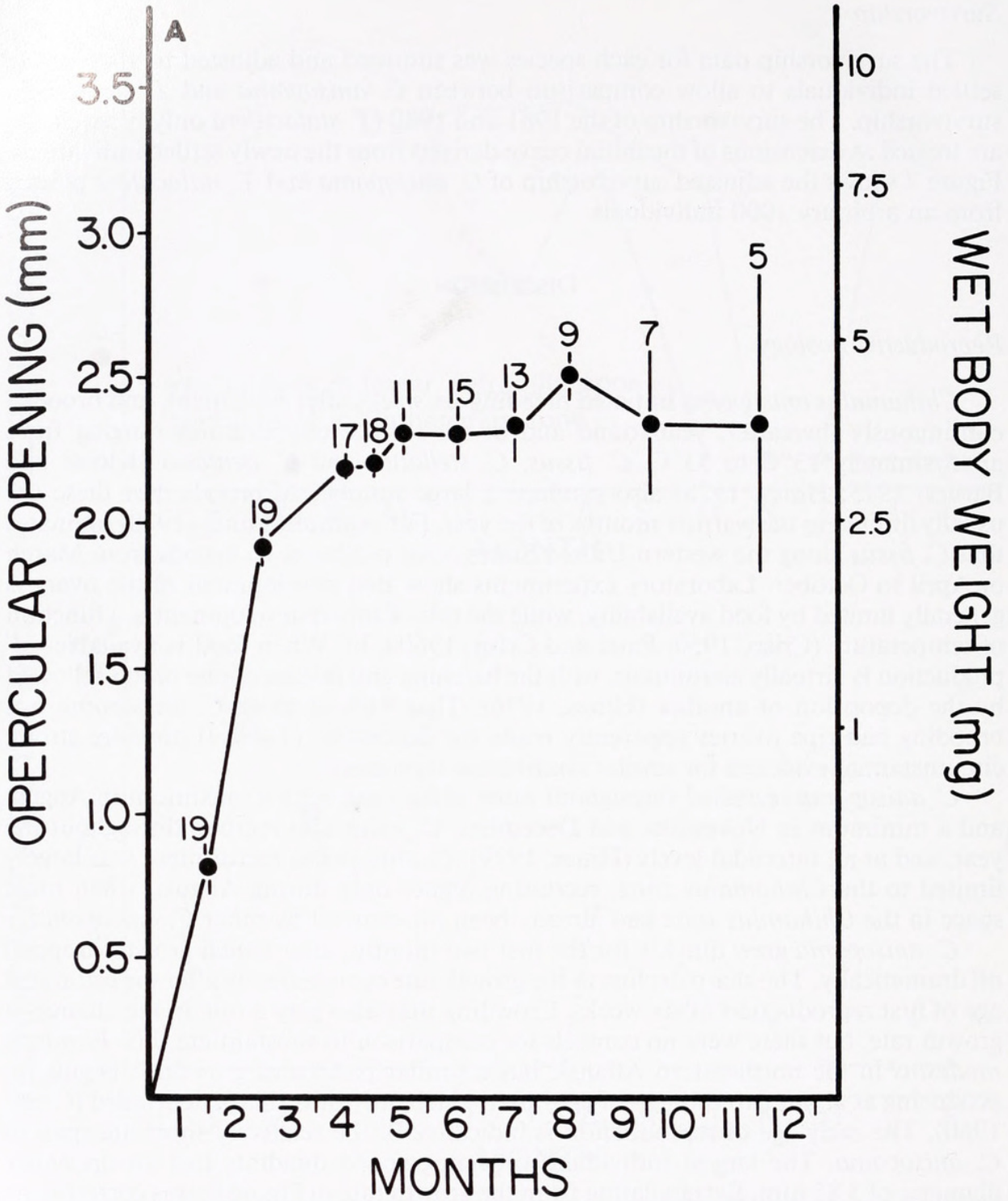


FIGURE 5. (A) The growth from settlement of *Chthamalus anisopoma* from three photographed quadrats in the upper *Chthamalus* zone. Means, sample sizes, and 95% confidence intervals are indicated. (B) Growth summary for *Chthamalus anisopoma*, plotting the means at all ages from two groups of three quadrats each. Wet body weight is inferred from the regression equation: Weight (mg) = 0.49 (length [mm])^{2.34}. $r^2 = 0.88$.

sea temperatures rise in the spring and summer. Hines (1978) found a similar pattern in *Tetraclitra rubescens* (= *T. squamosa*) along the western U. S. coast. Although *T. stalactifera* apparently failed to brood during this summer, the ovarian cycles indicate that brooding would otherwise take place during the summer, as it did in *T. rubescens*.

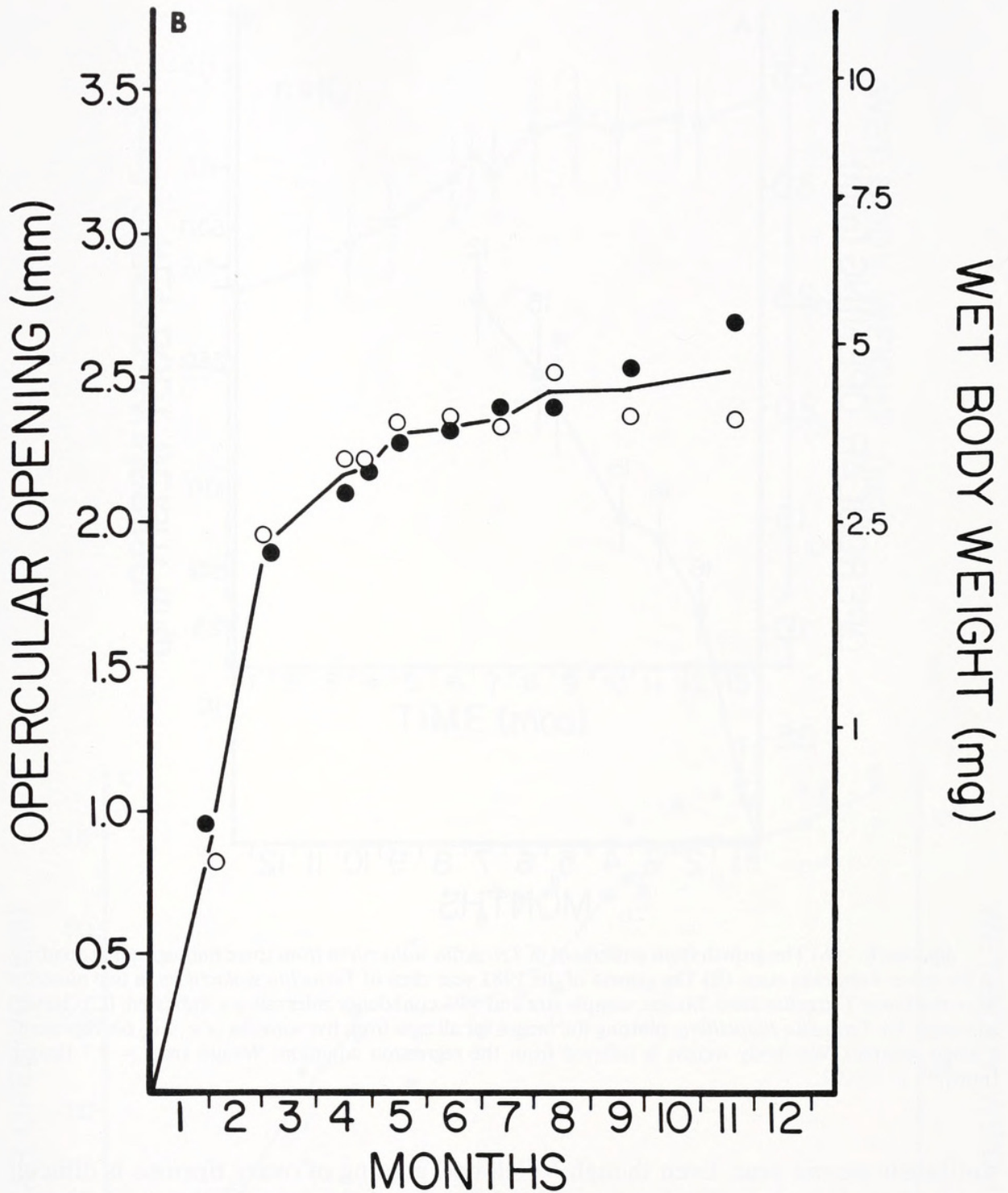


FIGURE 5. (Continued)

Only 3 *T. stalactifera* out of 740 dissected contained brooding eggs. Related incidents observed in other species of *Tetracrita* suggest that reproduction in *Tetracrita* is highly variable and supports the hypothesis that reproduction failed to occur in the population under study. Hines (1978) attempted to elicit brooding in laboratory of *T. squamosa* (= *rubescens*). Though similar lab populations of *Chthamalus fissus* and *Balanus glandula* brooded, the *Tetracrita* did not, developing only ripe ovaries. Vilalobos (1980) sampled monthly a population of *T. panamensis* in Costa Rica and found that the first year individuals all had "mature ovaries," but did not reproduce

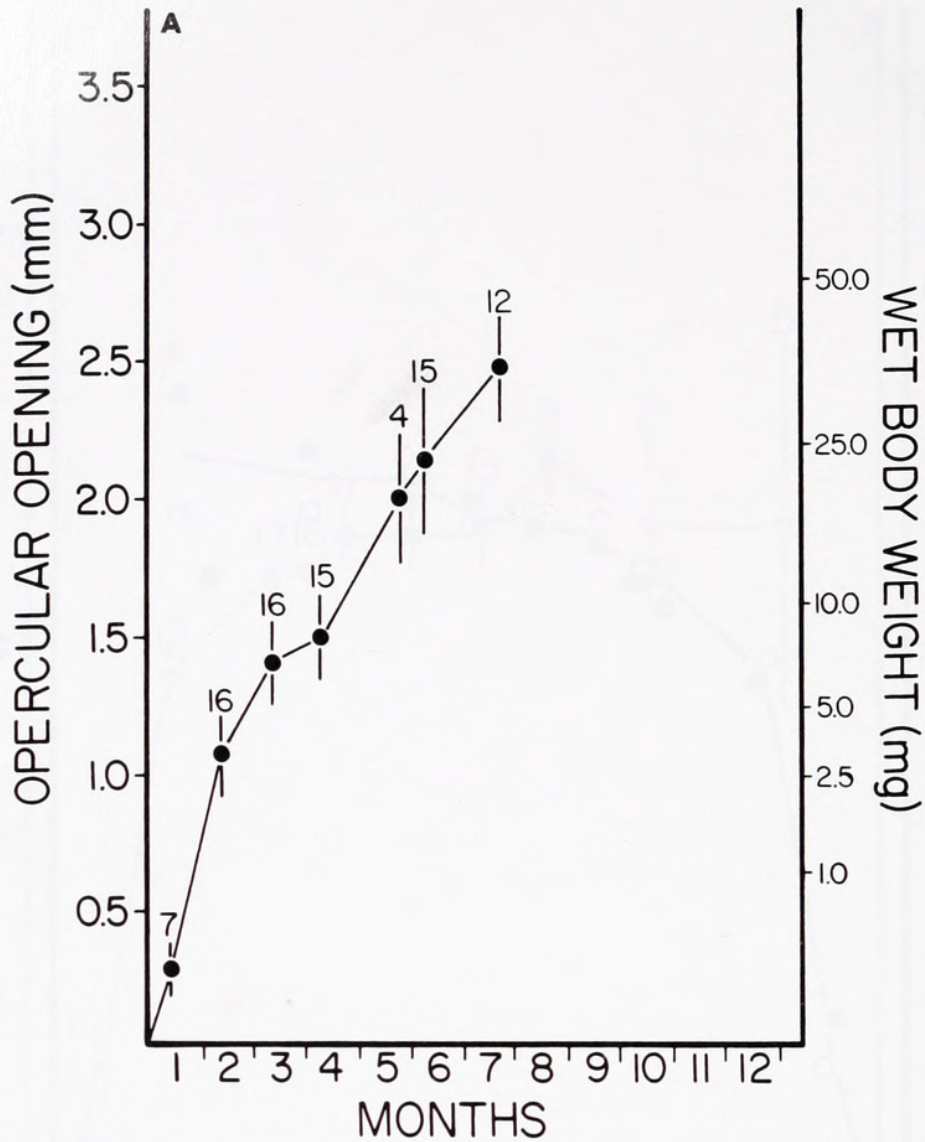


FIGURE 6. (A) The growth from settlement of *Tetracita stalactifera* from three photographed quadrats in the lower *Tetracita* zone. (B) The growth of the 1981 year class of *Tetracita stalactifera* in two quadrats from the lower *Tetracita* zone. Means, sample size and 95% confidence intervals are indicated. (C) Growth summary for *Tetracita stalactifera*, plotting the means for all ages from five samples (e.g., Fig. 6A represents a single sample). Wet body weight is inferred from the regression equation: Weight (mg) = 2.7 (length [mm])^{2.8}. $r^2 = 0.92$.

until their second year. Even though Villalobos' grading of ovary ripeness is difficult to interpret, it is clear that there was development of the ovary without subsequent brooding. Achituv and Barnes (1978) maintained laboratory populations of *T. stalactifera rufotincta*. In July the samples had ripe ovaries with visible unfertilized eggs. In August, the condition of the ovaries regressed, yet none of the animals were brooding embryos. This is the closest parallel to the data in this study.

Recruitment of *T. stalactifera* cyprids was predominantly on the tests of conspecifics, a gregarious behavior also noted in *Tetracita squamosa* of the Caribbean Sea (Bierbaum and Zischke, 1979). Settlement was heaviest in August and September, and had ended by November. A minority of individuals settled on bare substrate at all intertidal levels, albeit in reduced numbers.

The recruitment of barnacle cyprids in a given population may be interpreted as an indication that brooding has taken place in the same or nearby population. However,

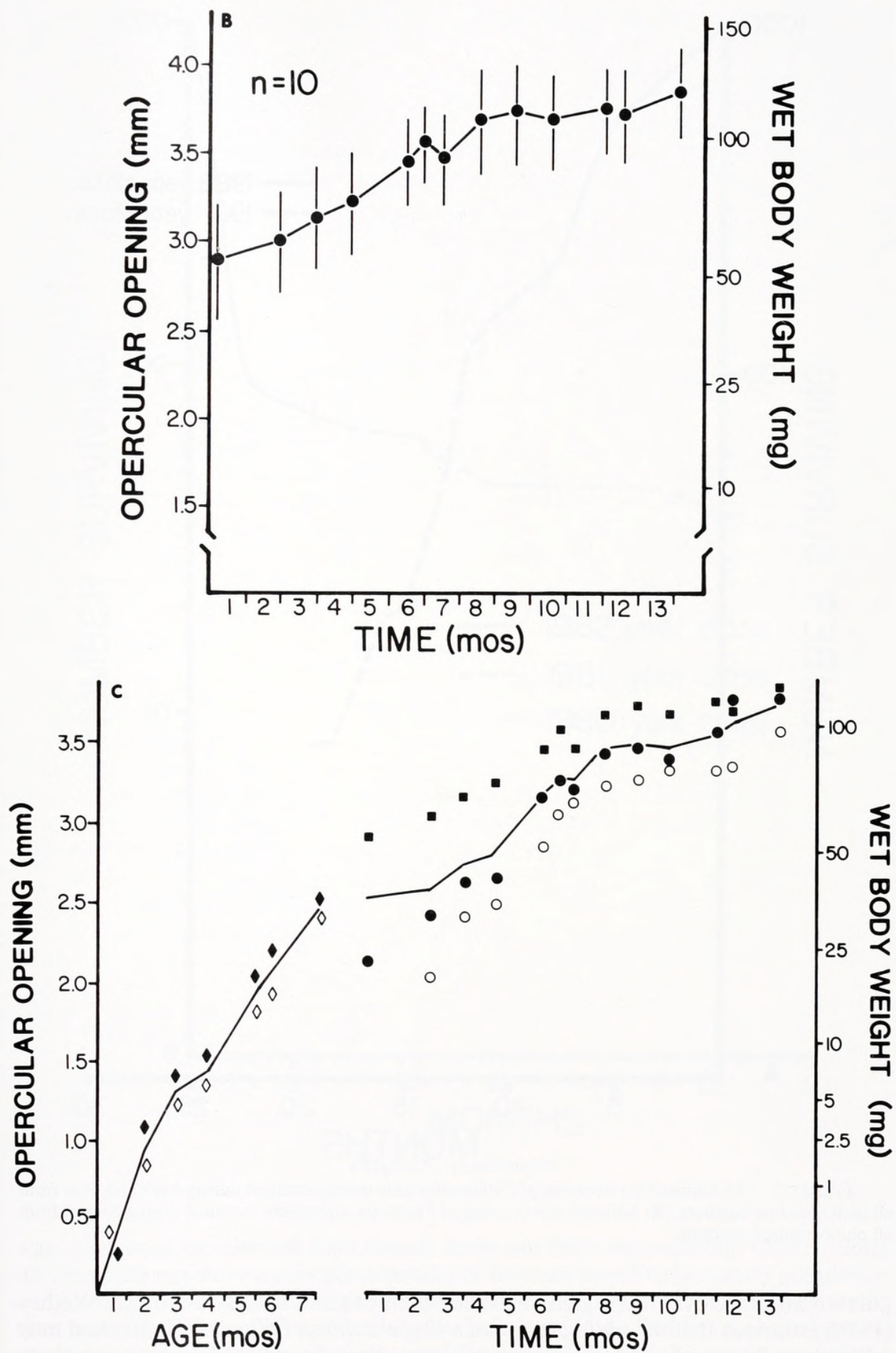


FIGURE 6. (Continued)

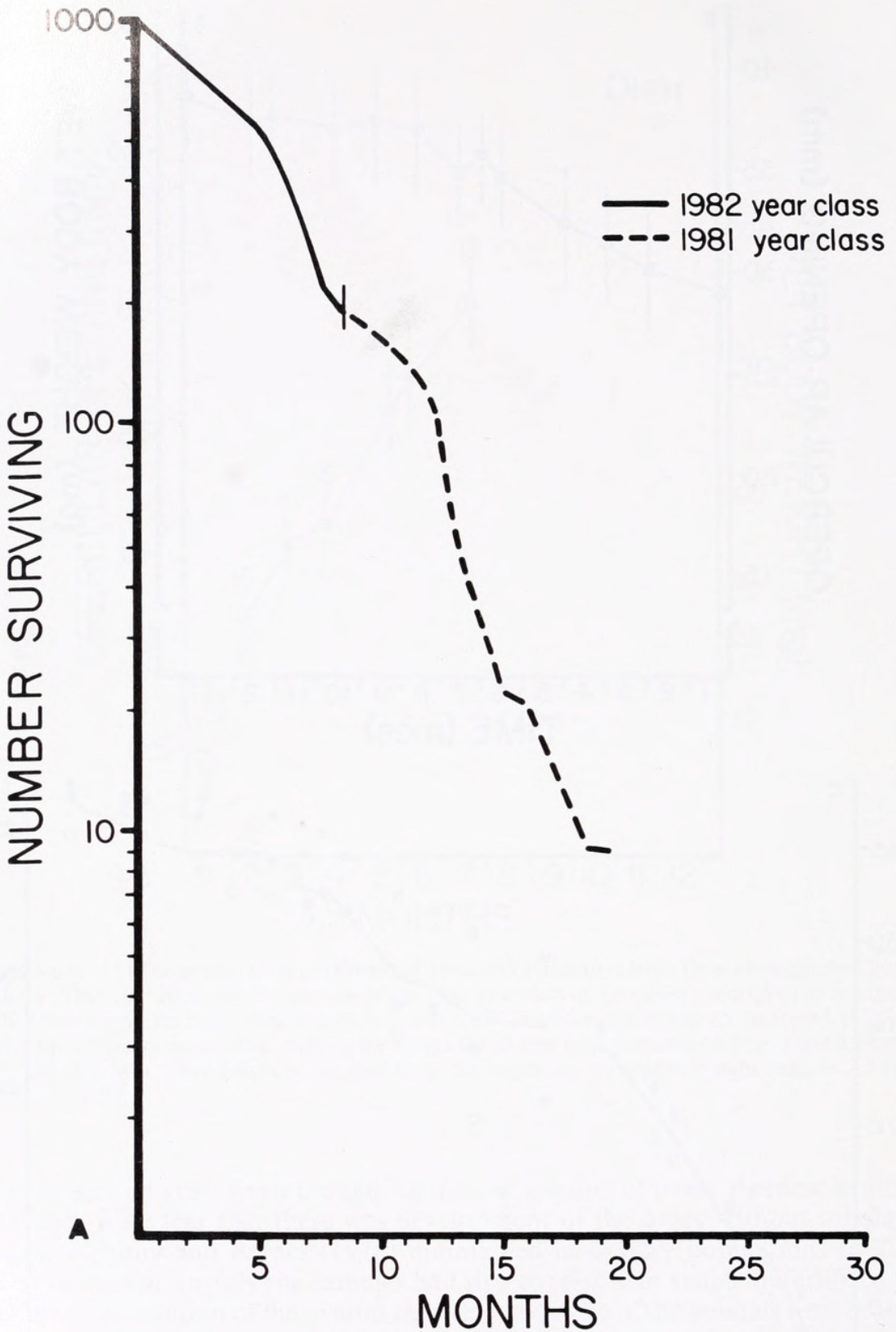


FIGURE 7. (A) Adjusted survivorship of *Chthamalus anisopoma* recruited during April and May from all photographed quadrats. (B) Adjusted survivorship of *Tetraclita stalactifera* recruited during August from all photographed quadrats.

planktonic larvae may travel great distances; their origin is usually unknown. Wetthey (1980) estimated that the sibling larvae of a single *Balanus balanoides* individual may settle along 50 km of coast in a period of several days. In my study population there

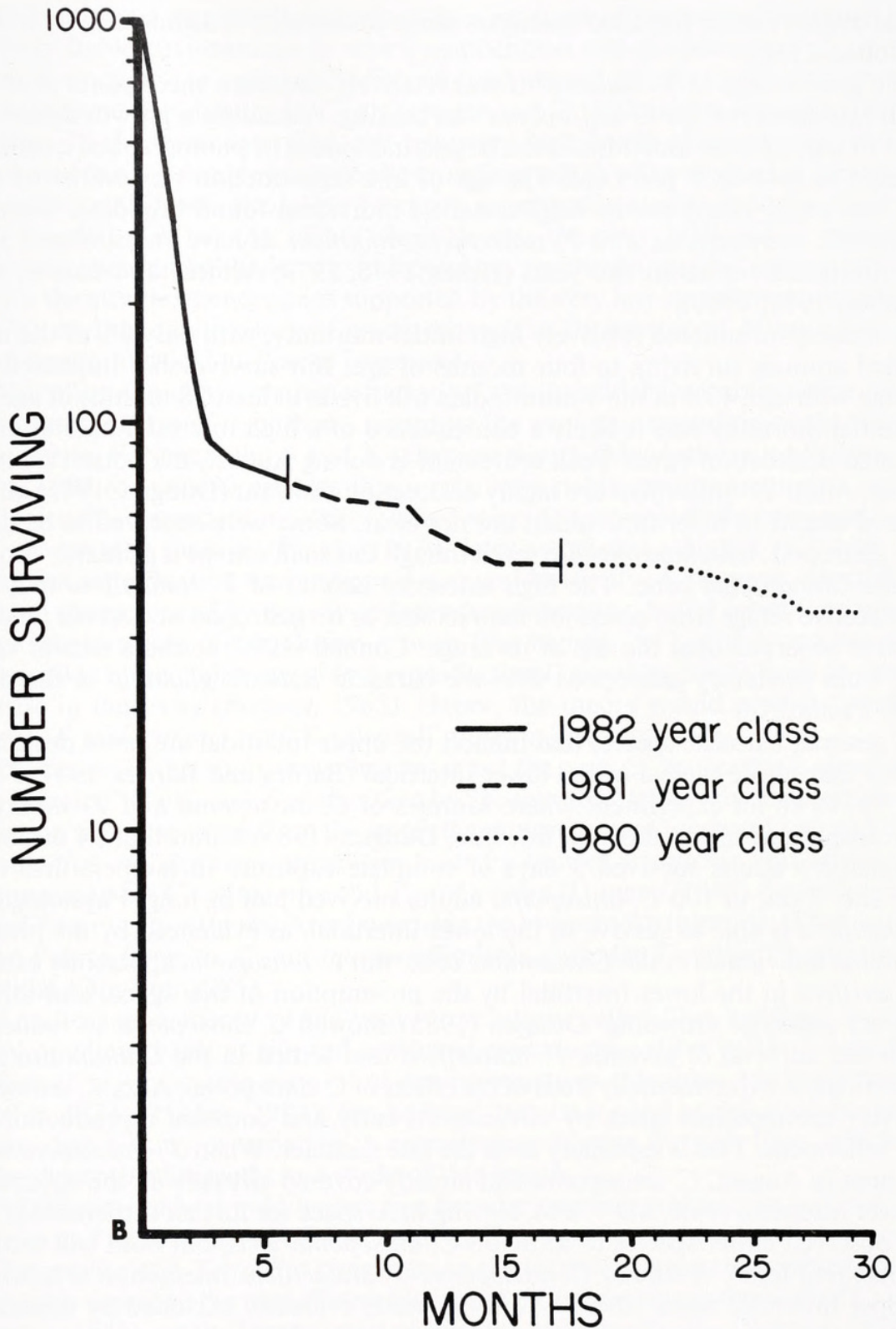


FIGURE 7. (Continued)

was substantial recruitment even though there was little reproduction. Other studies on *Tetraclita* spp. show a poor correspondance between brooding in a study population and recruitment in the same. *Tetraclita rubescens* recruited approximately three months after brooding (Hines, 1979), *T. stalactifera rufotincta* of the Red Sea recruited during the last month of brooding (Achituv and Barnes, 1978), and *T. panamensis* of the

tropical eastern Pacific recruited during the same month that brooding activity initiated (Villalobos, 1980).

The growth rate of *T. stalactifera* was relatively constant; the distinct change in growth rate observed for *C. anisopoma* was lacking. Assuming a growth rate similar to that of second-year individuals, the largest individual in photographed quadrats is estimated to be 8 to 9 years old. The age of first reproduction was estimated to be about two years, based on the single smallest individual found brooding. *Tetraclita panamensis*, *T. rubescens*, and *T. stalactifera rufotincta* all have an estimated age of first reproduction of about two years (Hines, 1976, 1979; Achituv and Barnes, 1978; Villalobos, 1979, 1980).

T. stalactifera suffered relatively high initial mortality, with only 8% of the newly recruited animals surviving to four months of age. But survivorship improved considerably with age: 43% of the 4-month-olds will live to at least 28 months of age. The high initial mortality rate is likely a consequence of a high intertidal habitat and its associated desiccation stress. Peak settlement is during August, the hottest month of the year. Adult *T. stalactifera* are highly desiccation resistant (Dungan, 1985) and the causes of deaths in older individuals are not clear. Some were observed to be drilled by the gastropod *Acanthina angelica*, even though this snail's range is primarily centered over the *Chthamalus* zone. The high intertidal habitat of *T. stalactifera* may be a more effective refuge from predation than its size, as no gastropod or asteroid predators were ever observed near the top of its range. Connell (1970) found a similar spatial refuge from predatory gastropods with the barnacle *Balanus glandula* in the north-eastern Pacific.

In general, barnacle species that inhabit the upper intertidal are more desiccation resistant than those typical of the lower intertidal (Barnes and Barnes, 1957; Foster, 1971, 1974). In an experiment where samples of *C. anisopoma* and *T. stalactifera* were transplanted above the high tide line, Dungan (1985) found that 54 out of 100 *T. stalactifera* adults survived 3 days of complete exposure in temperatures up to 35°C; only 3 out of 100 *C. anisopoma* adults survived half as long. Physiologically, *T. stalactifera* is able to survive in the lower intertidal, as evidenced by the presence of scattered individuals in the *Chthamalus* zone. But *C. anisopoma* apparently excludes *T. stalactifera* in the lower intertidal by the pre-emption of free space, and through the direct effects of crowding. Dungan (1985) showed *C. anisopoma* to reduce the growth and survival of juvenile *T. stalactifera* that settled in the *Chthamalus* zone, relative to those experimentally freed of the effects of *C. anisopoma*. Also, *C. anisopoma* effectively monopolizes space by virtue of its early and constant reproduction and heavy settlement. This is especially so in the late summer. When *T. stalactifera* began settlement in August, *C. anisopoma* had already covered virtually all the substrate in the lower intertidal (94%, SD = 3%), leaving little space for further settlement (I have never observed either species to settle on *C. anisopoma* tests, but both will settle on *T. stalactifera* tests). A similar *C. anisopoma*-*T. stalactifera* interaction is lacking in the upper intertidal zone, where *C. anisopoma* is evidently excluded by desiccation stress.

Life histories as adaptations: cause and effect

Assuming that natural selection acts upon variation in age-specific reproductive effort, growth, and mortality, life history theory attempts to predict what suite of traits should be selected for in a given environment (Stearns, 1976, 1977). Within this framework, a species' schedule of reproduction and growth is often interpreted as an adaptation to the biotic and abiotic components of the environment (e.g., Hines, 1979).

The intertidal can be characterized as a gradient of increasing exposure from a relatively stable environment in which competition and predation are an important source of mortality, to a physically rigorous and physiologically limiting environment. A comparison of mortality in *C. anisopoma* and *T. stalactifera* supports this generalization. In the lower intertidal, the relatively high levels of recruitment in *C. anisopoma* led to considerable intraspecific crowding, which often resulted in hummocking and subsequent death. Predation intensity is generally greater at lower shore levels (e.g., Connell, 1961a). At higher shore levels, the very high initial mortality of *T. stalactifera* is probably density-independent, resulting from desiccation stress. The case for density-independence is supported by the very low recruitment densities (see Fig. 7b), and the relative lack of predators such as the gastropod *Morula ferruginosa* in the upper intertidal at Puerto Penasco.

Accepting the above characterization of the intertidal for comparative purposes allows examination of hypotheses regarding the evolutionary origin of the barnacles' life histories. For example, r- and K-selection theory (MacArthur and Wilson, 1967; Boyce, 1984 for review) predicts that a relatively stable environment with predominantly density-dependent mortality should select for increased efficiency and a higher "K", or carrying capacity. Pianka (1970) later associated a higher "K" with a later age of first reproduction and increased size and longevity. A rigorous, unstable environment characterized by density-independent mortality should select for an increase in the intrinsic rate of population growth (the logistic "r"), which can be attained most quickly by an earlier age of first reproduction (Lewontin, 1965), with an attendant decrease in longevity (Bonner, 1965). Hence, the theory would predict "r-selected" traits in *T. stalactifera*, and "K-selected" traits in *C. anisopoma*.

The results of this study show that this is not the case. *C. anisopoma* is characterized by "r-selected" traits, and *T. stalactifera* by "K-selected" traits. This disparity between prediction and data stems from the implicit assumption that increased size and delayed reproduction are superior competitive traits for limited resources. This assumption is not supported for *C. anisopoma* and *T. stalactifera* (Dungan, 1985). Space is generally the limiting resource for sessile organisms in the lower rocky intertidal (Dayton, 1971), and at Puerto Penasco, *C. anisopoma* effectively excludes *T. stalactifera* in the lower intertidal (Dungan, 1985).

An alternative theory of life history evolution, called "bet-hedging" by Stearns (1976), predicts that long life and a reduced reproductive effort will be selected for in the face of unpredictable survival of prereproductives (Murphy, 1968; Charnov and Schaffer, 1973; Schaffer, 1974). Bet-hedging may be a good explanation in this case, but requires a study of variation in reproductive success through time, which could not be determined directly in a study of this length.

Additional study should be put in a broader context, taking into account the life histories and environments of close relatives. It is significant that the relative positions of *Chthamalus* and *Tetraclita* congeners in the intertidal zone are reversed from one geographic region to the next. *Tetraclita* is above *Chthamalus* in the Gulf of California (Dungan, 1985), on the Pacific coast of Panama at Punta Paitilla (Reimer, 1976), and the Gulf of Elat, Red Sea (Achituv, 1972). *Chthamalus* is above *Tetraclita* along the California coast (Hines, 1979), and along the Florida Keys (Bierbaum and Zischke, 1979). Yet while their intertidal positions are highly variable, some of the life histories characteristic of *Chthamalus* and *Tetraclita* appear essentially conservative from one region to the next. Body size varies little within the two genera, with all the members of *Chthamalus* being smaller than all the members of *Tetraclita* (Newman and Ross, 1976; Stanely and Newman, 1980; Paine, 1981). The age of first reproduction is approximately two years for the four species of *Tetraclita* on which data are available (Hines, 1976; Achituv and Barnes, 1978; Villalobos, 1979, 1980).

The age of first reproduction in *Chthamalus* is more variable. Based on settlement patterns, *C. stellatus* in Europe and *C. fragilis* of the U. S. Atlantic coast first reproduce at about nine months of age (Connell, 1961a; Wethey, 1983). But the appropriate comparison for this study is between *C. anisopoma* and its closest relative, which biochemical evidence suggests is *C. fissus* of the eastern Pacific (Hedgecock, 1979). The upper intertidal species, *C. fissus*, reproduces first at approximately two months after settlement (Hines 1976); the lower intertidal species, *C. anisopoma*, reproduces first at about six weeks. This and other life history similarities (such as size and life span; see Hines, 1976) between the two species make it difficult to provide a causal explanation for the life history traits of *C. anisopoma* in terms of environmental selection forces along an intertidal gradient.

These examples of apparent conservatism in *Tetraclita* and some members of *Chthamalus* suggest that historic explanations should be considered when drawing inferences from comparative studies (Gould and Lewontin 1979; Felsenstein 1985). On the other hand, such conservatism cannot be considered a general feature of all acorn barnacles. For example, the age of first reproduction in different species of the genus *Balanus* varies from four to eight weeks (Walker, 1961; Werner, 1967; Hurley, 1973), to one to two years (Crisp, 1954; Barnes and Barnes, 1954). If *Balanus* is a monophyletic taxon, it may be a profitable group to focus on if we wish to understand the adaptive significance of a trait such as age of first reproduction. The observation that some genera appear relatively variable, and others conservative, suggests that further hypotheses of life histories as adaptations be firmly grounded in a phylogenetic context.

ACKNOWLEDGMENTS

This work formed part of a thesis submitted to San Diego State University. I am much indebted to Thomas Ebert for sharing his expertise in life histories, and to Michael Donoghue for opening my eyes and mind to the importance of an organism's history. Michael Dungan was the original impetus for this project; his enthusiasm and scientific insight were a driving force. I thank Sherman Suter, Donald Thomson, and an anonymous reviewer for their criticisms of earlier drafts of this paper, and Andy Wyss, Susan Fansler, Lissa Findley, Michael Russell, and Fernando Jara for their assistance in transportation to and work at the field site. This work was supported in part by a Sigma Xi Grant-In-Aid of Research.

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