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Comparative Reproductive Ecology of Three Species of Intertidal Barnacles

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University of California, Berkeley,
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Comparative Reproductive Ecology of Three Species of Intertidal Barnacles

By

Anson Hemingway Hines, Jr.

A.B. (Pomona College) 1969

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Zoology

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA, BERKELEY

Approved: John Pearse

Cadet H. Hand Jr.

Ralph I. Smith

May 14, 1976.

Committee in Charge

DEGREE CONFERRED JUNE 19, 1976

For Linda,

who was loving and generous all the times I was off to the lab or to Morro Bay, and who was patient and understanding all the times I was as crusty as the barnacles I work on.

ACKNOWLEDGEMENTS

Dr. Ralph I. Smith, my major professor, provided enduring support and friendship during the course of this study. Drs. Cadet Hand and John S. Pearse provided much constructive criticism during the preparation of the manuscript, and Dr. Hand, Jon Standing, and Jim Rutherford were instrumental in attaining initial funding for my work. John Cornell, Bruce Hargreaves, and Dr. John E. Simmons gave many hours of valuable advice, critical discussion, friendship, moral support, and technical assistance throughout the work. Brian Jennison accompanied me on many of the long trips to Morro Bay. Pacific Gas and Electric Company's Department of Engineering Research, particularly John Warrick, and the crew at Morro Bay power plant gave generously of their time and their facilities. Dr. George Trezek gave me a friendly introduction to the worlds of engineering and the power industry. Chris Tarp and Marg Race processed the continuous temperature data. Rose Thorvaldson prepared the final manuscript. These studies were funded by National Science Foundation Grant GI-34932 to Drs. George Trezek and Virgil Schrock of the Department of Engineering, Sea Grant NOAA 04-5-158-20 to Drs. Ralph Smith and Cadet Hand of the Department of Zoology, and a small grant from the Pacific Gas and Electric Company. I am most grateful to my family, Linda and Nathan, for helping me in thousands of ways.

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Chapter

CHAPTER I. INTRODUCTION

This dissertation compares the reproductive ecology of three species of intertidal barnacles in the context of their life histories. Emphasis is placed on the patterns of reproduction shown by similar species exploiting different but overlapping ranges of the intertidal zone. The intertidal environment imposes stringent gradients of greater physical stress in the high range of tidal exposure and increasing biological complexity at the low range of tidal exposure. Selection for differing adaptive modes of reproduction, recruitment, growth, and survivorship may be expected in species occupying different positions along these environmental gradients. Ideally, the problem is not just to measure how particular aspects of these modes differ between species facing varying degrees of environmental stress, competition, and predation; but it is also to examine how components of the reproductive ecology of the species interact with important parameters of growth and demography throughout their life histories.

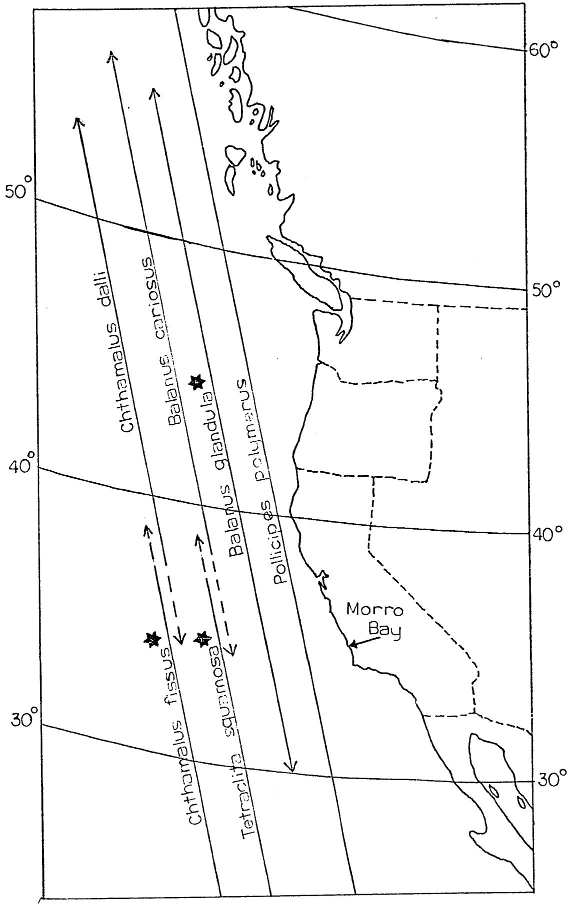
Barnacles are excellent organisms for the study of reproductive ecology and life history for many reasons. First, a considerable amount of work on the biology of barnacles has been done for more than 100 years by many workers, principally in Great Britain but also over much of the world, so that a substantial body of knowledge has accumulated about the systematics, natural history, physiology, and ecology of cirripedes. Barnacles are important components of the fauna of temperate and cold waters. They are a predominantly marine group characteristic of wave-swept rocky shores, but they occupy a variety of habitats from the highest intertidal zones to moderate depths and to floating substrates in the open ocean. Species also invade bays and estuaries and are major components of fouling communities. Almost all are simultaneous hermaphrodites, which simplifies problems involving sex ratios and sexual dimorphism and behavior. They brood their eggs for a period of time, making quantification of their reproductive condition and output easy. Their sessile, intertidal habit makes their populations readily accessible and easy to census. And finally, their calcareous shell makes their growth rates easy to measure.

However, two important aspects of the biology of barnacles present serious problems for the researcher. First, after an embryonic brooding period, nauplius larvae are released by the parent into the water for a planktonic period of feeding and dispersal. After further development in the plankton, a cypris larva is formed, which then selects a suitable substrate for attachment and undergoes metamorphosis into a young barnacle. The pelagic habitat of the larva makes it virtually impossible to quantify much of this important period of the life cycle of barnacles. For this reason this study--as well as most other studies of organisms with such life cycles--is unfortunately limited to measuring the sessile part of the life cycle, while information about the larval period remains largely speculative. The second aspect of the biology of barnacles which presents serious problems is that little can be determined about the reproductive condition of an individual under natural conditions without opening it and killing it. Therefore, the complete reproductive history of an individual cannot be established, and reproductive output over time must be estimated from sequential samples of the population. In spite of these problems, the comparative nature of this study will show that barnacles provide many interesting insights into the adaptive advantages of variations in a basic life history patttern.

The three species of barnacles studied in this work are identified according to Newman (1975) as: Chthamalus fissus Darwin, 1854; Balanus glandula Darwin, 1854; and Tetraclita squamosa rubescens Darwin, 1854 (hereafter referred to as Tetraclita squamosa). See Plate I-1 showing typical examples of the three species. These species are distributed along the intertidal zone of the west coast of North America (see Figure I-1 based on Pilsbry, 1916; Henry, 1942; Cornwall, 1951; and personal observations). C. fissus is a small barnacle found on the open and semi-protected coast from about San Francisco south to Baja California, and it is replaced to the north by Chthamalus dalli Pilsbry, 1916, with some overlap in the distributions of the two species in central California. B. glandula is a medium-sized species widely distributed from British Columbia to Baja California; it is very common on the open coast, but also invades bays and estuaries. T. squamosa is a relatively large barnacle commonly found on the open and semi-protected coast from about San Francisco south to Baja

Plate I-1. Photograph of typical individuals of *Chthamalus fissus* Darwin, 1854 (small barnacles); *Balanus glandula* Darwin, 1854 (medium-size barnacle); and *Tetraclita squamosa rubescens* Darwin, 1854 (large barnacles). Top, side, and bottom views of barnacles which have been removed from the substrate are shown. Magnification = 2X.

Figure I-1. Distributions of *Chthamalus fissus*, *C. dalli*, *Tetraclita squamosa rubescens*, *Balanus cariosus*, *B. glandula*, and *Pollicipes polymerus* along the west coast of North America. (From Pilsbry, 1916; Henry, 1942; Cornwall, 1951; and personal observations.)


60°
50°
50°
40°
40°
30°
30°
Chthamalus dalli
Balanus cariosus
Balanus glandula
Pollicipes polymerus
Balanus nubilus
Chthamalus fissus
Tetraclita squamosa
Morro Bay

California, and it is replaced to the north by *Balanus cariosus* Pallas, 1788. Although considerable overlap in the vertical distributions of these species may occur in places, their intertidal ranges generally display a distinct zonation which corresponds well with the zonation pattern described by Ricketts and Calvin (1962), resulting from a mixed semi-diurnal tidal cycle (see Figure I-2). *C. fissus* occurs at all intertidal levels from the splash zone to below mean lower low water, but it is common only in the splash and high intertidal zones. *B. glandula* is found in all but the splash zone, but it is most common in the upper mid-intertidal zone. *T. squamosa* is limited from the lower mid-intertidal zone to a few feet below mean lower low water. Some of the major features of the morphology of these balanid cirripedes are schematically shown in Figure I-3 for the readers reference.

This study was conducted at the Pacific Gas and Electric Company fossil-fuel power plant at Morro Bay, California (lat. 35°22'30"N, long. 120°52'30"W; see Figure I-1). This 1030 megawatt plant is located on the central California coast and uses ocean water from an intake just inside the Estero Bay harbor entrance for once-through cooling, discharging warmed water on the north side of Morro Rock (see Figure II-3). The discharge canal, or outfall, is about 90 meters long and releases the warmed water into the surf, forming a plume with an isotherm 10°F above ambient of approximately 0.6 to 3.0 acres surface area depending on the plant load, tide, surf, current, wind, etc. (Pacific Gas & Electric Company, 1973).

Figure I-2. Vertical intertidal distributions of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* shown schematically in correspondence to a mixed semi-diurnal tidal cycle and the zones described by Ricketts and Calvin (1962). Width of bars approximates relative densities.

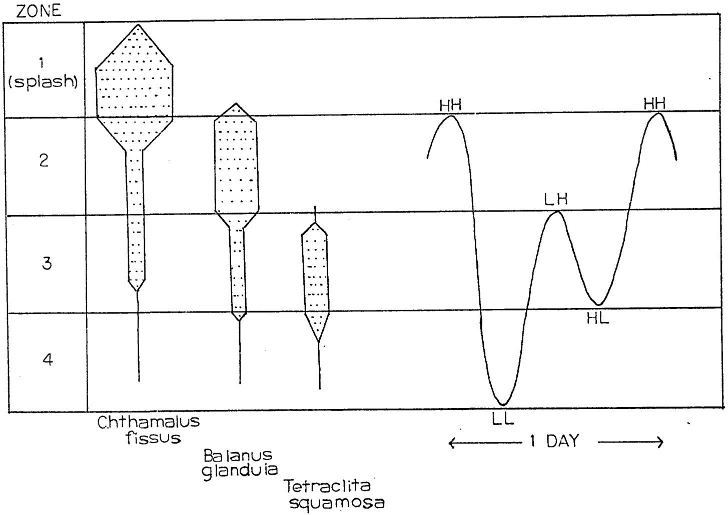
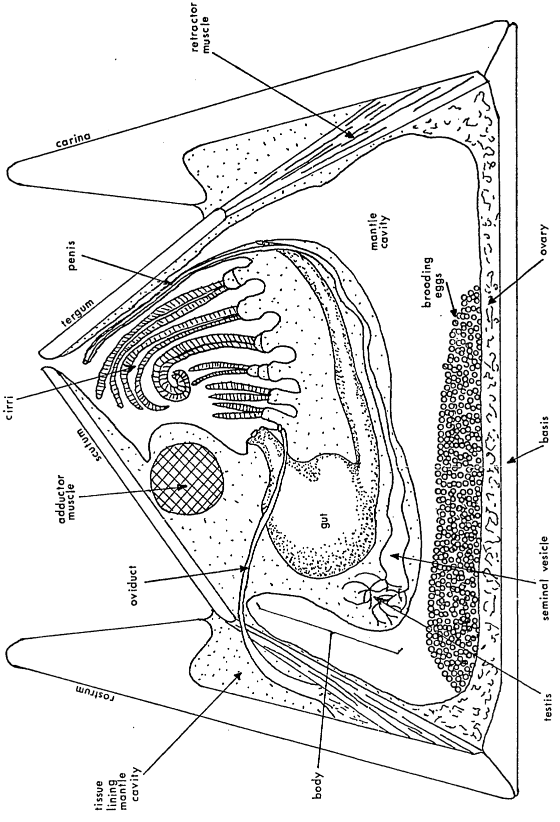

ZONE
1
(splash)
2
3
4
Chthamalus fissus
Balanus glandula
Tetraclita squamosa
HH
LH
HL
LL
HH
1 DAY

Figure I-3. Schematic balanid cirripede shown in mid-sagittal section. The major anatomical structures referred to in this work are indicated.


retractor muscle
carina
penis
tergum
mantle cavity
brooding eggs
ovary
cirri
scutum
adductor muscle
gut
basis
oviduct
seminal vesicle
rostrum
testis
tissue lining mantle cavity
body

Barnacles, mussels, and sea anemones are the dominant invertebrate organisms found on hard substrates in the outfall. Salinities in the region of the intake and outfall do not differ from those of the open coast. Further details about the temperature regimes found at the intake and outfall are presented in Chapter II.

The body of this work is presented in four chapters. Chapter II discusses the patterns of reproductive effort of the three species: their reproductive cycles, environmental controlling factors, size and number of broods produced per season, nutrient storage, and yearly allocation of energy to eggs. Chapter II presents the patterns of settlement of the barnacles, and their variations in space and time. Chapter IV analyzes the patterns of growth of the three species, and Chapter V compares their demographic patterns of survivorship, fecundity, life tables, and aspects of their population dynamics. The reproductive patterns of Chthamalus fissus, Balanus glandula, and Tetraclita squamosa are finally summarized and compared in the context of their life histories in Chapter VI.

CHAPTER II. REPRODUCTIVE EFFORT

A. INTRODUCTION

Barnacles show several patterns of reproductive effort, timing, and reproductive energy partitioning. The boreo-arctic species *Balanus balanus* (=*B. porcatus*), *B. hameri*, and *B. balanoides* (see Crisp, 1954; Barnes, 1963; and others) incubate one large brood during the winter and release nauplii into the plankton in synchrony with the spring diatom bloom (Barnes, 1957). This pattern of reproduction is closely related to that of other annual cyclical factors in boreo-arctic regions, particularly food and temperature (Barnes, 1963). Development of the gonads in summer and fall is preceded by storage of nutrients when food is abundant in spring and early summer (Barnes, Barnes, and Finlayson, 1963), and copulation occurs in late fall or early winter. *Verruca stroemia* in temperate waters is similar to the boreo-arctic species in that it produces a major brood in the winter which is virtually synchronous throughout the whole population, and which is released about the time of the spring diatom increase (Barnes and Stone, 1973). However, unlike boreo-arctic species, several smaller broods are produced during the summer, and the timing of these broods is very asynchronous throughout the population. The temperate and subtropical species *Pollicipes polymerus* (see Hilgard, 1960), *Chthamalus stellatus*, *C. depressus* (see Klepal and Barnes, 1975), *Balanus perforatus*, *B. amphitrite* var. *denticulata* (see Patel and Crisp, 1960), and *B. glandula* (see Barnes and Barnes, 1956) breed over a limited range of temperature which is in accord with both their natural breeding season and their geographical distribution, and broods follow each other in rapid succession at the height of the breeding season. At the other extreme, Elminius modestus is very eurythermal, producing numerous broods at variable rates over a wide range of temperature (Crisp and Davies, 1955).

There are no good studies on allocation of energy to reproduction in barnacles; published studies on reproductive effort in barnacles have largely focused on fecundities in terms of numbers of eggs per brood and of egg size (Crisp, 1954; Barnes and Barnes, 1965, 1968; Klepal and Barnes, 1975). These studies suggest that species such as Elminius modestus or Chthamalus stellatus which produce numerous successive broods of many small eggs have a much higher "reproductive metabolic efficiency" (Barnes and Barnes, 1968) and fecundity than a species such as Balanus balanoides which produces a single large brood of larger eggs. This approach confuses the issue of how much energy is allocated to reproduction with how the reproductive energy is partitioned and packaged.

This chapter examines patterns of reproductive effort in Chthamalus fissus, Balanus glandula, and Tetraclita squamosa. Ideally, the data which form the bases of the reproductive patterns would have been gathered by following individuals sequentially over an entire year. However, it was not possible to tell anything about the reproductive condition of the barnacles without cracking them open and killing them, or without impractical protracted maintenance of isolated individuals in the laboratory so that the release of successive broods could be measured over a reproductive season. Alternatively, the following aspects of the reproductive biology of the barnacles were studied and then combined to formulate a deductive picture of the reproductive effort of each species. Reproductive cycles and aspects of regulation of the cycles by several environmental factors are presented. Field data gathered from populations of the three species occurring in a warm-water outfall and in control areas unaffected by the discharge of a power plant are shown, and a series of laboratory experiments investigating the effects of temperature, photoperiod, and food availability on brooding was conducted. The effect of parental size on brooding frequency is analyzed, but the details of age-specific reproduction are presented later in Chapter V on demography. Brood size (i.e., brood weight) for each species is shown. The time per brood was measured in the laboratory and used to estimate the number of broods produced per season. "Packaging" of the reproductive energy--i.e., egg number and size--is discussed in Chapter V. Cycles of the male and female reproductive systems and weight changes in the body components are used as estimates of seasonal nutrient storage. Finally, these factors are used to formulate a model of the patterns of seasonal nutrient storage and to compute the yearly allocation of energy to reproduction for each species.

B. MATERIALS AND METHODS

This study was conducted at the Pacific Gas and Electric Company power plant at Morro Bay, California. Field data were gathered from populations of Chthamalus fissus, Balanus glandula, and Tetraclita squamosa occurring in the warm-water outfall of the power plant and control areas of ambient temperatures. Collecting trips were made to the power plant at about monthly intervals from November 1972 to January 1975. Surface water temperatures near the intake and at the middle of the north side of the outfall were recorded during these visits and are shown in Figure II-1. More extensive, continuous temperature records were taken from August 1973 through January 1975 (see Figure II-2). The continuous temperature data were obtained from "Ryan" temperature recorders provided by Pacific Gas and Electric Company. A recorder was positioned next to the intake screens and in the outfall next to the discharge tubes of units one and two. Both recorders were at about mean lower low water--corresponding to the approximate intertidal level and subject to similar periods of exposure and submergence as the sampled barnacles. The recorders were calibrated and the 40-day recording strips were replaced on the collecting trips. A period of one day corresponds to 1.5 cm on the recording strips, and the high, mean and low temperatures for every 6-hour period were integrated by eye and noted. From these noted 6-hour temperatures weekly high, mean, and low temperatures were averaged and plotted in Figure II-2.

Figure II-1. Surface water temperatures in outfall and control areas during monthly collecting trips. Outfall = closed symbols; Intake = open symbols.

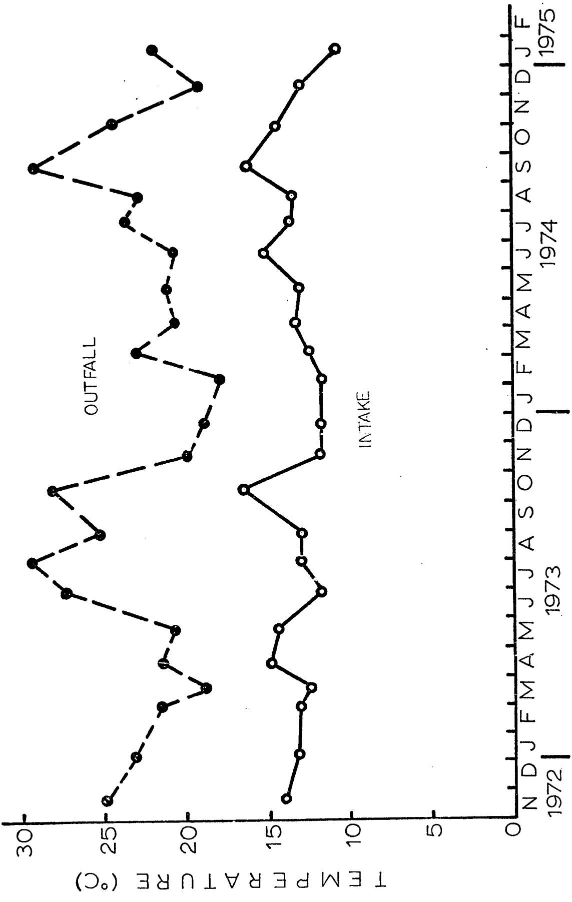
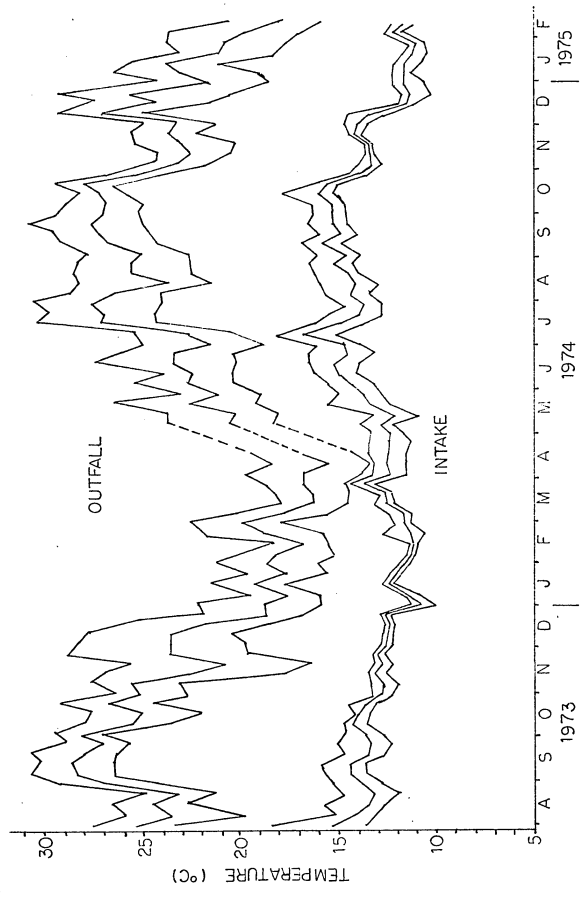

TEMPERATURE (°C)
0
5
10
15
20
25
30
OUTFALL
INTAKE
N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1972
1973
1974
1975

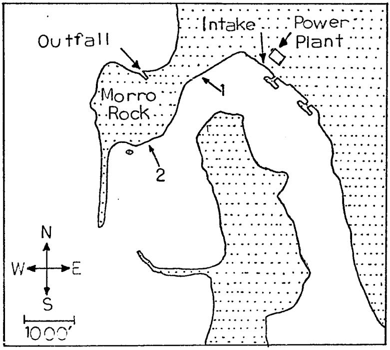
Figure II-2. Continuous temperature data for Morro Bay outfall and intake. Weekly averages of high, mean, and low temperatures from six hour intervals are plotted for the warm-water outfall and for the cool intake water are shown. Temperature recorders were placed at about mean lower low water. See text for further details.


OUTFALL
INTAKE
TEMPERATURE (°C)
30
25
20
15
10
5
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
1973
1974
1975

The temperature differential between the outfall and intake means ranged from about 3°C in March 1974 to about 15°C in September 1973. The intake showed a seasonal cycle of low temperatures around 11-12°C in winter and high temperatures around 14°C during summer and fall. The seasonal variations in the outfall temperatures partly reflect seasonal changes in ambient temperatures and partly seasonal changes in plant load. For example, Morro Bay outfall temperatures tend to peak in late summer and fall because intake temperatures are highest and plant loads are high while generating power for agricultural irrigation pumps. Intake temperatures can fluctuate as much as 2-3°C within a 24-hour period as a result of tidal currents and local solar heating. However, diurnal outfall temperature fluctuations (as much as 7°C) are always considerably greater than those of the intake because of plant load variations compounding intake temperature fluctuations. The Morro Bay outfall canal is large and shows considerable temperature variation (as much as 6°C) from place to place at any given time as a result of uneven mixing of the warm-water discharge with the surge of the cool receiving water. Also, heat treatment every few weeks to kill mussels fouling the cooling tubes periodically raised outfall temperatures in some places to as high as 39°C for a few hours at a time. Because the temperature recorders were positioned in the intertidal zone, periodic exposure to air contributed to the temperature fluctuations.

Collecting sites for the three species are shown in Figure II-3. Populations of all three species were sampled midway along the north side of the warm-water outfall at about mean lower low water. Control populations of *Chthamalus fissus* and *Balanus glandula* were sampled from the southeast, and *Tetraclita squamosa* from the southwest side of Morro Rock in the Estero Bay harbor channel at about mean lower low water. Every effort was made to collect outfall and control samples from equivalent tidal levels to minimize effects of differences in exposure and feeding time. Rocks of manageable size (10-50 cm in diameter) bearing *C. fissus* and *B. glandula* were brought back to the laboratory at Berkeley. *T. squamosa* could not be found in high enough densities on suitably sized rocks to make collecting them alive practical and, except when this species was collected for laboratory experiments, these barnacles were chiseled off the substrate, taking care to damage tissues as little as possible. *C. fissus* and *B. glandula* on rocks were kept moist but not submerged in a 12°C coldroom for no longer than five days before they were processed. Maintained in this way, these species could remain alive and healthy for two weeks or more, but they could not feed, copulate or release nauplii, although brooded embryos continued to mature. Preliminary studies showed that tissue weights did not change significantly (less than 1%) during the five-day holding period. *T. squamosa* were sealed in plastic bags and deep frozen for processing at another time, sometimes months later.

Figure II-3. Collecting sites at Morro Bay, California. 1 = control collecting site for *Chthamalus fissus* and *Balanus glandula*. 2 = control collecting site for *Tetraclita squamosa*.


Outfall
Intake
Power Plant
Morro Rock
1
2
N
W
E
S
1000'

For each species, barnacles of haphazard sizes over the entire range of sizes available were selected for processing. Brooding frequencies were calculated for sample sizes of: 50 *Chthamalus fissus* $\geq$ 1 mm basal diameter; 60 *Balanus glandula* $\geq$ 6 mm basal diameter; and 60 *Tetraclita squamosa* $\geq$ 18 mm basal diameter. In addition, several smaller *T. squamosa* in each sample were evaluated for brooding. Each barnacle was cracked open and examined for the presence of brooded embryos, ripeness of ovary, and ripeness of the male reproductive system. Brooded embryos of light color were judged to be in "early" developmental stages, while those with dark brown pigment and eye spots were judged as "late" developmental stages. Ovaries were staged "ripe" when they had large quantities of yellow, yolky material bulging into the mantle chamber, or "not ripe" when little or no yellow, yolky material was present. The male reproductive system was staged as "ripe" or "not ripe" according to the presence or absence of seminal vesicles discernibly filled with white seminal fluid. It is emphasized that no attempt was made to stage gametogenesis beyond these crude evaluations.

In addition to the basal diameter along the rostral-carinal axis, dry weights of the following body components were determined for each barnacle: the opercular valves (scuta and terga were soaked in 20% KOH at 90^{o}C overnight and rinsed clean in distilled water before drying); the body (soma only, excluding ovary, retractor muscles, and tissue lining mantle cavity); brooded egg mass (both lamellae together when present);

and, in some cases, the ovary (including retractor muscles and tissue lining the mantle cavity). The body component weights were determined by drying in a vacuum oven at 60°C for 24-36 hours and weighing on a Cahn electronic microbalance.

For laboratory experiments barnacles were collected alive on small (10-50 cm) rocks and maintained continuously submerged in seawater in plastic containers under constant light and temperature conditions. Seawater used in these experiments was changed about twice a week or as needed. The water was vigorously aerated and the containers were covered to minimize evaporation from the aeration. Barnacles in the laboratory were fed *ad lib* with dense suspensions of live *Artemia* nauplii hatched in the laboratory, augmented in some cases with cultures of *Duneliella sp*. generously provided by Mr. Bruce Hargreaves. Barnacles of all three species were maintained in the laboratory for many months using these techniques. The only major problems arose from dead *Artemia* nauplii and eggs accumulating in areas of poor aeration and circulation (especially under rocks) and creating stagnant anaerobic conditions fatal to the barnacles.

To estimate the length of time embryos were brooded, embryos of very early developmental stages--judged to be freshly deposited--were removed from mantle chambers and held in the laboratory under conditions of constant temperature and photoperiod until they hatched or reached late developmental stages judged to be ready to hatch. Seawater for these *in vitro* brooding-time experiments was autoclaved and treated with a combination of penicillin (200 units/l), streptomycin (100/μg/l), and neomycin (100 μg/l) to prevent bacterial or fungal damage to the embryos. Embryos were maintained in two ways: (1) individed plastic boxes aerated by small diameter polyethylene tubing, and (2) in 60 ml glass vials supplied with aerated seawater flowing at a constant rate from a manifold regulated to deliver about 2 liters per day to 12 vials. The first method had the advantage of preventing hatched nauplii from escaping, but had the disadvantage of requiring that the seawater be changed every other day to prevent build-up of waste products and fluctuating salinity from evaporation. The second method had the advantage of little maintenance time since enough seawater for 5-6 days could be provided at one time, but had the disadvantage of losing hatched nauplii in the out-flow. Both methods were successful in maintaining embryos for long periods of time. When large clumps of eggs were maintained in vitro, the outer embryos of the clump developed faster than those in the middle, apparently because of a gradient of O_2 levels and waste removal. To ensure that all embryos developed at even rates, egg lamellae were broken up into small clumps of embryos.

Other details of methods, sample sizes, and statistical treatments are presented in the appropriate section of the results.

C. RESULTS

1. Brooding Cycles and Environmental Cues

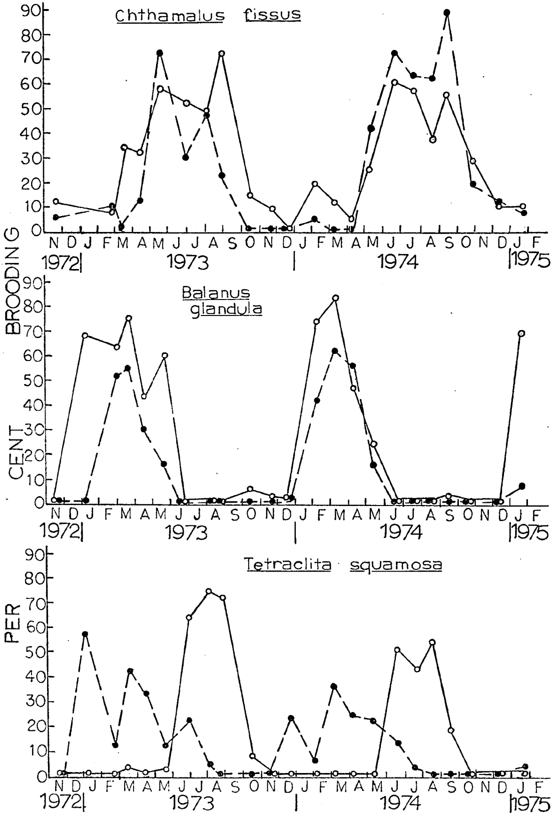
a. Field Data on Brooding Frequency.

Brooding frequencies for outfall and control populations of the three species are shown in Figure II-4.

The control populations of Chthamalus fissus brooded during a long summer season from about March or April to October. In peak periods from June to September 50 to 75% of the sample were brooding, but low levels of about 10% brooding often occurred during the "off" season. Although the brooding frequencies of outfall and control samples of C. fissus were often quite different at any given month, there was no consistent difference in the overall brooding cycle timing or amplitude from the two areas. This suggested that temperature was not an important factor regulating reproduction in this species, and that some other factor, or factors, perhaps light or food availability, acted as the proximate cue for synchronizing the annual cycle.

The control population of Balanus glandula brooded embryos in winter and spring from about December or January to May, with about 60-80% of the control population brooding during peak months. Occasional low levels (about 5%) of brooding occurred in fall months but the onset of the brooding cycle was abrupt. The samples from the warm-water outfall consistently had a lower percent brooding, and the onset of brooding was delayed one or more months in both 1972-73 and 1974-75, but not in 1973-74. These differences between outfall

Figure II-4. Cycles of brooding frequencies. Outfall = closed symbols; Control = open symbols. Sample sizes: *Chthamalus fissus* = 50; *Balanus glandula* = 60; *Tetraclita squamosa* = 60 $\geq$ 18 mm basal diameter.


Chthamalus fissus
Balanus glandula
Tetraclita squamosa
PERCENT BROODING
0
10
20
30
40
50
60
70
80
90
N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1972
1973
1974
1975

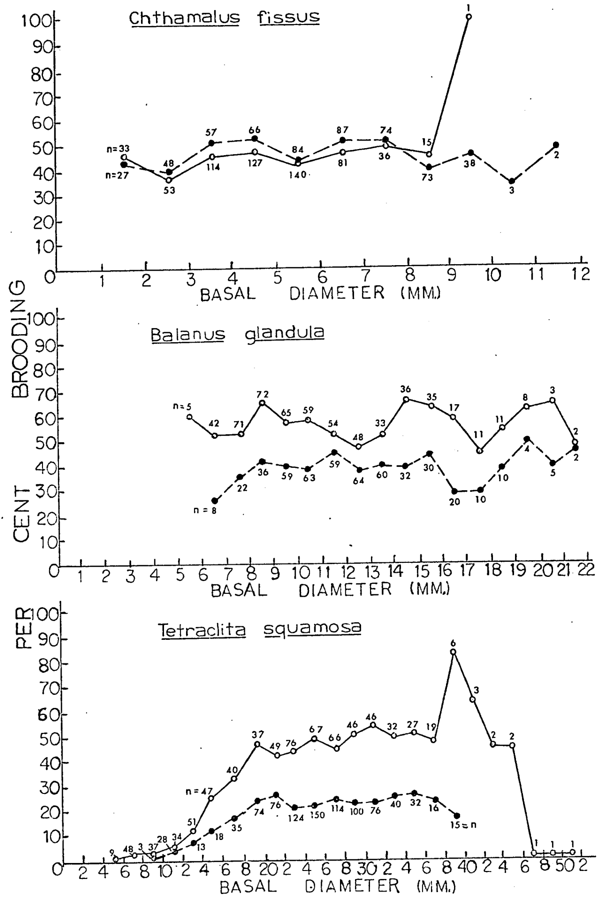
and control populations suggested that temperature was an important factor regulating reproduction in this species, that cold temperatures were required for brooding and warm temperatures inhibited it.

The control population of Tetraclita squamosa brooded during summer from about June through September. The onset of brooding was sharp, and 40-75% of the population brooded embryos during peak months. The population in the warm-water outfall began brooding in or near December and continued at erratically variable levels through spring into early summer, diminishing in June or July when the control population was reaching peak activity. The brooding cycle of the outfall population was thus about 6 months out of phase with the control and more variable in activity, of longer duration but with lower peak brooding frequencies than the control population. This altered brooding cycle suggested that temperature was also important in regulating reproduction in this species, but that warm temperatures were required for brooding and cold temperatures inhibited it.

b. Effect of Size on Brooding Frequency.

Brooding frequencies as a function of basal diameter were calculated for each species (Figure II-5). These percentages were computed from data pooled from all the months of major brooding activity during the study for each species respectively. Because these data were pooled from different numbers of months for outfall and control samples, differences in brooding levels between these groups are meaningless. For

Figure II-5. Brooding frequencies versus basal diameter. Data is cumulative for all months for which there was substantial brooding. Sample sizes for each basal diameter are indicated. Outfall = closed symbols; Control = open symbols.


Chthamalus fissus
PER CENT BROODING
100
90
80
70
60
50
40
30
20
10
0
n=33
n=27
48
53
57
114
66
127
84
140
87
81
74
36
15
73
1
38
3
2
1 2 3 4 5 6 7 8 9 10 11 12
BASAL DIAMETER (MM.)
Balanus glandula
n=5
42
71
72
65
59
54
48
33
36
35
17
11
11
8
3
2
n = 8
22
36
59
63
59
64
60
32
30
20
10
10
4
5
2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
BASAL DIAMETER (MM.)
Tetraclita squamosa
9
48
3
37
28
34
51
n=47
40
37
49
76
67
66
46
46
32
27
19
6
3
2
2
1
1
1
13
18
35
74
76
124
150
114
100
76
40
32
16
15=n
2 4 6 8 10 2 4 6 8 20 2 4 6 8 30 2 4 6 8 40 2 4 6 8 50 2
BASAL DIAMETER (MM.)

example, the data for control *T. squamosa* were taken from summer collections while those for the outfall came from winter and spring. There was no significant change in brooding activity with size in *C. fissus*; any individual above 1 mm basal diameter was judged to be mature. No individual of *B. glandula* less than 5 mm basal diameter was available for sampling during months of brooding activity, since they had all grown to at least that size by December. Above 5 mm there was no significant change in brooding activity with size, so all individuals were considered mature by the time the populations began to brood in the winter. In *T. squamosa*, however, barnacles less than 6 mm basal diameter were not found to brood, and it appeared that they began to mature at about 12 mm and became fully mature at about 18 mm in diameter. Above 18 mm in size there was no significant change in brooding activity, and there were too few data above 38 mm to permit conclusions. None of the three species appeared to have reduced reproductive activity at older ages (larger sizes), although sample sizes are small.

c. Laboratory Experiments on Brooding.

Brooding cycle differences between warm-water outfall and control populations suggested the following hypotheses about environmental control of reproduction in each of the three species. For *C. fissus* temperature is not an important factor regulating brooding, but perhaps photoperiod or food availability is important in timing brooding in this species. In *B. glandula*, the delayed and lower percentages of brooding in the outfall population suggested that temperature is important in regulating both the timing and intensity of brooding, and that cold temperature is necessary for reproduction to proceed normally. In T. squamosa, the outfall population showed a pronounced shift of the brooding cycle, placing it 6 months out of phase with the control population. This shift suggested that temperature is important in regulating reproduction in this species also, but that warm temperatures are required for reproduction and cold temperatures inhibit it.

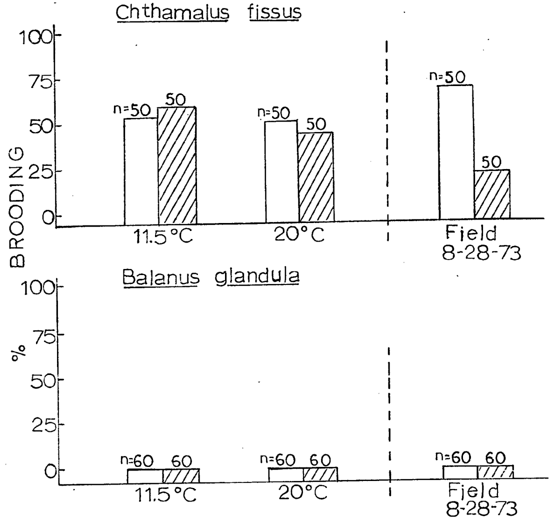
Although temperature was the major difference in the environments of the outfall and control populations, it was obvious that these field data did not reflect a well-controlled experimental situation. Differences in food availability, O_2 saturation, current, turbidity, the presence of chlorine and heavy metals in the discharge water, etc., could also have been partly or wholly responsible for the differences in the reproductive cycles. Moreover, while photoperiod changes could be important for timing reproduction of C. fissus, they do not seem important for timing reproduction in either B. glandula or T. squamosa. To test the hypotheses generated by the field data and to investigate more fully the roles of temperature, food availability, and photoperiod in regulating reproduction, a series of 5 laboratory experiments was conducted. Barnacles from outfall and control populations were used. Temperature experiments were conducted at two temperatures--cold (11.5°± 0.5°C) and warm (20°± 1°C)--which were selected to represent ambient and outfall water temperatures during the winter. Nauplii of *Artemia salina* were fed to the barnacles in the form of a dense suspension added to the water every 2-3 days, in doses judged to be in excess of the barnacles' food requirements. Three photoperiods used in the experiments were selected to represent the long (14L/10D), intermediate (12L/12D), and short (10L/14D) day-lengths the barnacles experienced in nature at Morro Bay. Only barnacles of sexually mature sizes as previously determined for each species were used. Details of the conditions and results of each experiment are outlined below in the order they were conducted, and a summary of the experimental series as a whole is presented.

Laboratory Brooding Experiment No. 1

Chthamalus fissus and *Balanus glandula* collected from both the outfall and control populations were maintained in lab from August 1-30, 1973. Photoperiod = 12L/12D. Food = *Artemia* nauplii fed *ad lib*. Temperatures = 11.5°C or 20°C. To test the effect of temperature and laboratory conditions on brooding in these 2 species, they were maintained in the laboratory for one month during a period when *C. fissus* was actively brooding in the field and when *B. glandula* was apparently ripe with yolky material but not brooding. Results, along with field data at the termination of the experiment, are shown in Figure II-6. Both outfall and control samples of *C. fissus* showed continued high levels of brooding at both temperatures, supporting the hypothesis that temperature was not important in regulating brooding in this species. *B.*

Figure II-6. Laboratory brooding experiment no. 1. *Chthamalus fissus* and *Balanus glandula* collected from both the outfall (hatched bars) and control (open bars) populations were maintained in lab from August 1-30, 1973. Photoperiod = 12L/12D. Food = *Artemia* nauplii fed *ad lib*. Temperatures = 11.5° or 20°C.

BROODING EXPERIMENT NO. 1



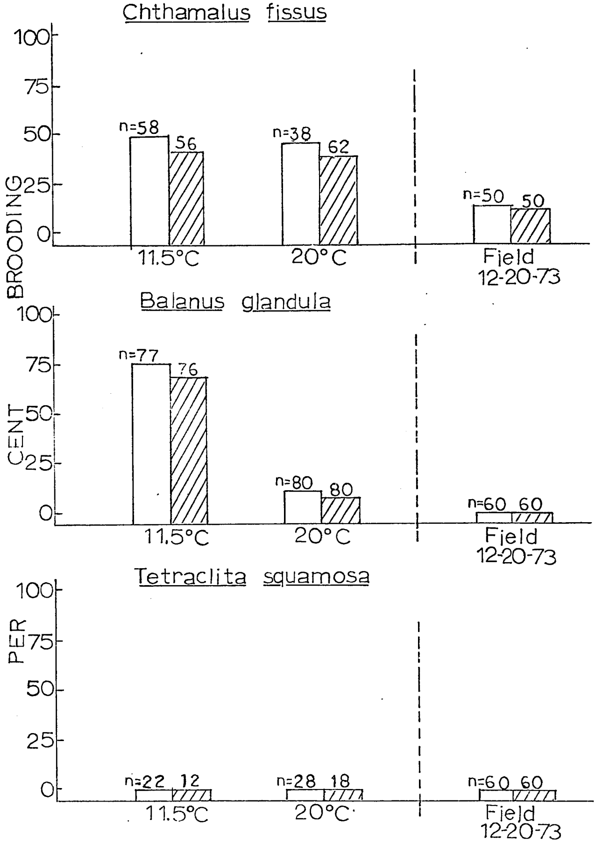
glandula did not show any brooding in the laboratory or the field even though it was ripe with yolky material in the ovary. It was thought that either B. glandula was not maintained for a long enough period at the cold temperature in the laboratory to induce brooding or that laboratory conditions in general were not favorable for this species at this time.

Laboratory Brooding Experiment No. 2

C. fissus, B. glandula, and T. squamosa collected from both the outfall and control populations were maintained in lab from October 12--December 30, 1973. Photoperiod = 12L/12D. Food = Artemia nauplii fed ad lib. Temperatures = 11.5°C or 20°C. To test the effect of warm and cold temperatures on brooding in each species, a longer experiment was run during a period when all three were at minimal brooding levels in the field. Results are shown in Figure II-7. C. fissus showed equivalent high levels of brooding at both temperatures, with no difference between outfall and control samples, again supporting the hypothesis that temperature was not important in regulating brooding in this species. B. glandula showed high levels of brooding at the cold temperature and low levels at the warm temperature, with no signficant difference between outfall and control samples. These results definitely show that temperature is important in regulating reproduction in this species, and that cold temperature brings on early high levels of brooding. T. squamosa did not show any brooding in the laboratory although barnacles at the warm temperature from

Figure II-7. Laboratory brooding experiment no. 2. *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* collected from both the outfall (hatched bars) and control (open bars) populations were maintained in lab from October 12--December 30, 1973. Photoperiod = 12L/12D. Food = *Artemia* nauplii fed ad lib. Temperatures = 11.5° or 20°C.

BROODING EXPERIMENT NO. 2



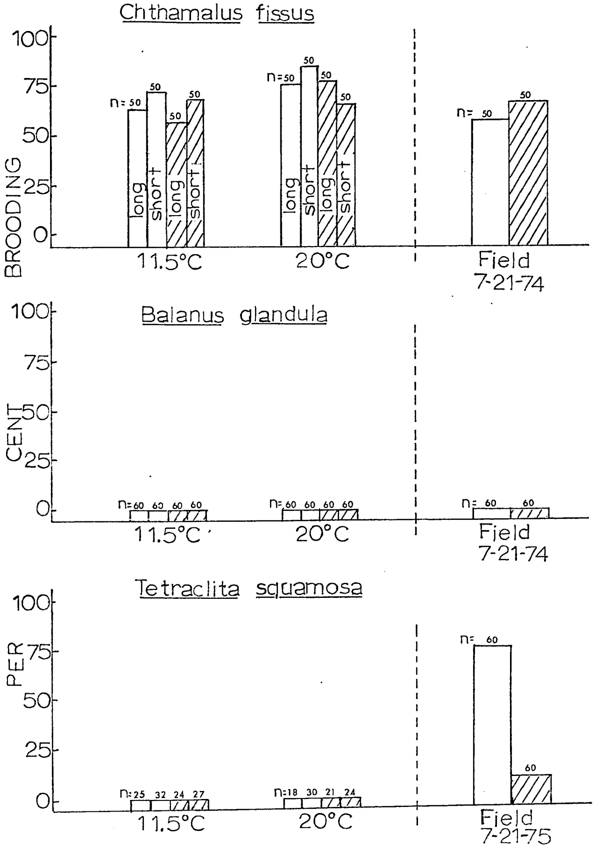
both the control and outfall samples were apparently ripe with yolky material in the ovary. This ambiguous result suggested that the experiment should have been continued into February when the outfall population began to brood in the field or that laboratory conditions in general were not adequate for brooding in this species.

Laboratory Brooding Experiment No. 3

C. fissus, *B. glandula*, and *T. squamosa* collected from both the outfall and control populations were maintained in lab from May 5--July 26, 1974. Photoperiod = 14L/10D (long) or 10L/14D (short). Food = *Artemia* nauplii fed *ad lib*. Temperature = 11.5°C or 20°C. The main purpose of this experiment was to investigate the effect on brooding activity of long and short photoperiods in combination with warm and cold temperatures. The timing of the experiment allowed two additional questions to be asked: First, although brooding in *B. glandula* terminated in May in the field, would continued cold temperature and/or short photoperiod allow continued brooding in the laboratory? Secondly, I wanted to test whether general laboratory conditions were adequate for *T. squamosa* to brood by testing them during a period when both outfall and control populations were brooding in the field. The results are shown in Figure II-8. *C. fissus* showed high levels of brooding at all combinations of day-length and temperature indicating that neither temperature nor photoperiod were not important in regulating brooding. *B. glandula* showed no brooding, suggesting that some endogenous aspect of the

Figure II-8. Laboratory brooding experiment no. 3. *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* collected from both the outfall (hatched bars) and control (open bars) populations were maintained in lab from May 5--July 26, 1974. Photoperiod = 14L/10D (long) or 10L/14D (short). Food = *Artemia* nauplii fed *ad lib*. Temperatures = 11.5°C or 20°C.

BROODING EXPERIMENT NO. 3

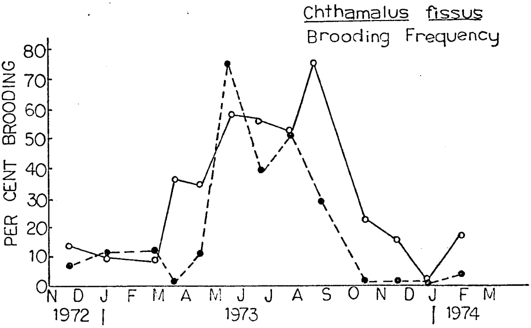


barnacles was responsible for terminating brooding activity in this species. *T. squamosa* did not brood in the laboratory even though outfall animals showed low levels and control animals showed high levels of brooding in the field. Many barnacles in every group of *T. squamosa* contained yolky material in the ovary, and it appeared that conditions adequate for brooding in this species were not provided in the laboratory.

Laboratory Brooding Experiment No. 4.

C. fissus were maintained in lab from September 17, 1974--October 28, 1974. Photoperiod = 12L/12D. Temperature = 12°C. Food = *Artemia* nauplii. The previous three experiments showed that brooding in *C. fissus* is not regulated by temperature or light. The correlation of brooding frequency with the increase in plankton (based on plankton counts from Icanberry and Adams, 1974) in the field (see Figure II-9) suggested that food availability might be limiting environmental factor controlling reproduction. The hypothesis was consistent with results of the previous experiments, especially experiment no. 2, where high or unlimited food availability in the lab induced high levels of brooding compared to the field when food availability was low in winter. To test the relationship between brooding and food availability 5 groups of *C. fissus* from the outfall area were fed increasing doses of *Artemia* nauplii for a 5-week period in the laboratory. The food doses were made by dilutions of thick suspensions of nauplii added to a standard volume of seawater in the plastic boxes containing the barnacles. Because it was

Figure II-9. Brooding frequencies for *Chthamalus fissus* (top) and annual cycle of zooplankton numbers at Morro Bay (bottom) redrawn from Icanberry and Adams (1974).


Chthamalus fissus
Brooding Frequency
PER CENT BROODING
80
70
60
50
40
30
20
10
0
N D J F M A M J J A S O N D J F M
1972
1973
1974

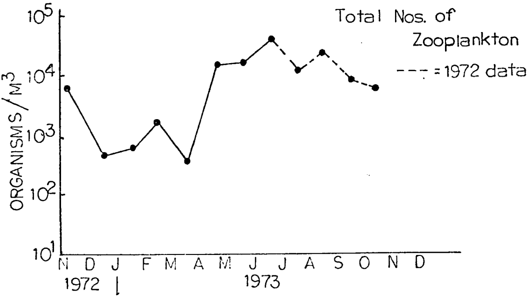
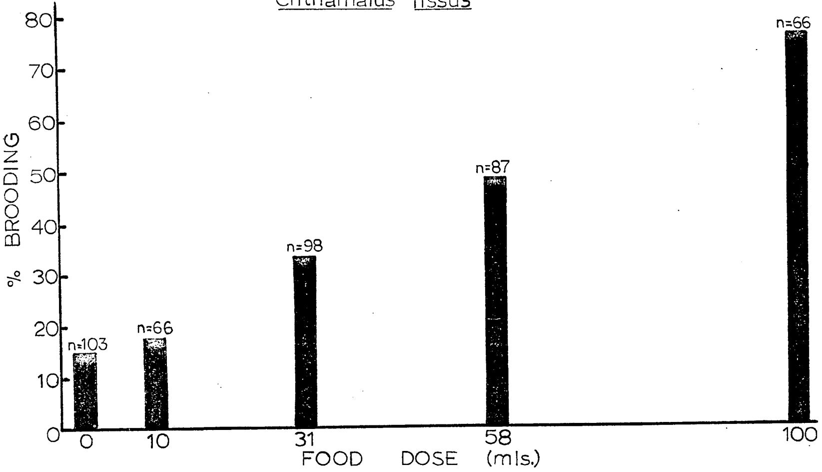

Total Nos. of Zooplankton
--- = 1972 data
ORGANISMS/M^3
10^5
10^4
10^3
10^2
10^1
N D J F M A M J J A S O N D
1972
1973

Figure II-10. Laboratory brooding experiment no. 4. *Chthamalus fissus* maintained in lab from September 17--October 28, 1974. Photoperiod = 12L/12D. Temperature = 12°C. Food = increasing doses of *Artemia* nauplii.

BROODING EXPERIMENT NO. 4
Chthamalus fissus



not possible to know how much food each barnacle was eating, it was only important to control the relative amounts and concentrations of food available to each group. The results are shown in Figure II-10. *C. fissus* showed a brooding response directly proportional to food availability, confirming the hypothesis that food availability is a major environmental factor regulating reproduction in this species.

Laboratory Brooding Experiment No. 5

C. fissus, *B. glandula*, and *T. squamosa* were collected from both the outfall and control areas and maintained in lab from October 30, 1974--February 15, 1975. Photoperiod = 14L/10D or 10L/14D. Temperature = 11.5°C or 20°C. Food = *Artemia* nauplii fed *ad lib* about every three days and fed *Dunaliella sp.* about every 8-10 days. This experiment was similar to experiment no. 2, which was also conducted during late fall and early winter. The purposes of this final experiment were several-fold. First, I wanted to test the effect of photoperiod on the initiation of brooding in *B. glandula*: did short photoperiod (in combination with cold temperature) bring on earlier brooding compared to long photoperiod? Second, in *T. squamosa* would adding algae to the food in the laboratory and extending the experimental period into February provide the necessary stimulus to brood? Third, how rapidly would the barnacles of all three species respond to laboratory conditions favorable for brooding? To answer the last question, 30 *C. fissus* and 15 *B. glandula* were subsampled at two-week intervals. *T. squamosa* were not subsampled during the experimental period because it was not feasible to maintain sufficient numbers of this large barnacle in the laboratory. The results of this experiment are presented in Table II-1. C. *fissus* showed rapid brooding responses to the laboratory feeding regime; within the first two-week subsampling period brooding frequencies had increased markedly from the starting levels. No significant differences were found between groups under the various photoperiod temperature regimes. The experiment was terminated for this species after the sixth week in the laboratory. B. *glandula* did not show a markedly different response to long or short day-length; cold temperature induced early brooding at both photoperiods by the tenth week and in one group as early as the fourth week. B. *glandula* at the warm temperature only began brooding at low frequencies by the 12th week. T. *squamosa* did not brood in the laboratory under any of the food, temperature, and photoperiod regimes. Some T. *squamosa* in all groups appeared ripe, but the trigger for brooding in this species seemed to be missing.

Summary of Results of Laboratory Brooding Experiments

Brooding in C. *fissus* was regulated directly by food availability (experiment no. 4) and feeding in the laboratory elicited high frequencies of brooding during periods when brooding activity and food levels in the field were low (experiments no. 2 and no. 5). The brooding response to food in the laboratory was extremely rapid compared to the other species--on the order of two weeks. The temperature and photo-

Table II-1. Laboratory brooding experiment no. 5. *Chthamalus fissus*, *Balanus glandula*, *Tetraclita squamosa* collected from both outfall and control populations and maintained in lab from October 30, 1974--February 15, 1975. Photoperiod = 14L/10D (long) or 10L/14D (short). Temperature = 11.5° or 20°C. Food = *Artemia* nauplii fed *ad lib* about every three days and doses of *Dunaliella* about every 8-10 days. Laboratory sample sizes: *C. fissus* = 30; *B. glandula* = 15; *T. squamosa* = 15.

BROODING EXPERIMENT NO. 5				CHTHAMALUS FISSUS					BALANUS GLANDULA										TETRACLITA SQUAMOSA			
			date week	10/30/74 0	2	4	12/11/74	6	10/30/74 0	2	4	12/11/74	6	8	10	12	1/27/75	13	10/30/74 0	12/11/74	1/27/75	13
FIELD			control	30			10		0			0					70		0	0	0	0
			outfall	18			12		0			0					8		0	0	5	0
LABORATORY	COLD	short	control		37	73		50		0	7		13	7	60	53		40				0
			outfall		43	57		67		0	7		13	7	47	67		33				0
			$\bar{X}$		40	65		58		0	7		13	7	53	60		36				0
		long	control		37	63		67		0	0		20	13	40	53		40				0
			outfall		40	77		70		0	0		13	13	53	47		53				0
			$\bar{X}$		38	70		68		0	0		16	13	46	50		46				0
		$\bar{X}$			39	67		63		0	3		15	10	50	55		41				0
	WARM	short	control		57	73		67		0	0		0	0	0	7		20				0
			outfall		43	63		70		0	0		0	7	0	7		13				0
			$\bar{X}$		50	68		68		0	0		0	3	0	7		16				0
		long	control		63	77		47		0	0		0	0	0	13		7				0
			outfall		47	80		73		0	0		0	0	0	7		20				0
			$\bar{X}$		55	78		60		0	0		0	0	0	10		13				0
		$\bar{X}$			52	73		64		0	0		0	2	0	8		15				0

period conditions in these experiments did not appear to affect the brooding activities of C. fissus. For B. glandula the situation was more complex. Cold temperature induced early brooding in the laboratory during late fall and early winter, and warm temperature inhibited it (experiments no. 2 and no. 5). However, cold temperature did not induce brooding in late summer to early fall even though B. glandula appeared to be ripe then (experiment no. 1); nor did cold temperature in the laboratory extend the brooding period into the summer after the field populations had stopped. Some endogenous recuperative factor--perhaps a gonad development period--is apparently required during summer and early fall before cold temperatures will induce brooding. Photoperiod did not appear to affect brooding activity in B. glandula in any of the experiments. T. squamosa did not brood in the laboratory under any of the conditions tested, in spite of the strong evidence from field data that warm temperatures affected brooding activity. Although individuals appeared ripe with yellow, yolky material in the ovaries under laboratory conditions, the stimulus for brooding seemed to be missing.

2. Brood Size.

Regressions of dry brood weight versus dry body weight are plotted for each species in Figures II-11 to II-13. The equations with the 95% confidence intervals for slopes and intercepts for these regressions are:

C. fissus - $n = 391$; $r = +0.855$: $y = (0.718 \pm 0.039) x + (0.035 \pm 0.030)$.

Figure II-11. *Chthamalus* *fissus* brood weight versus body weight. Regression total for all samples.

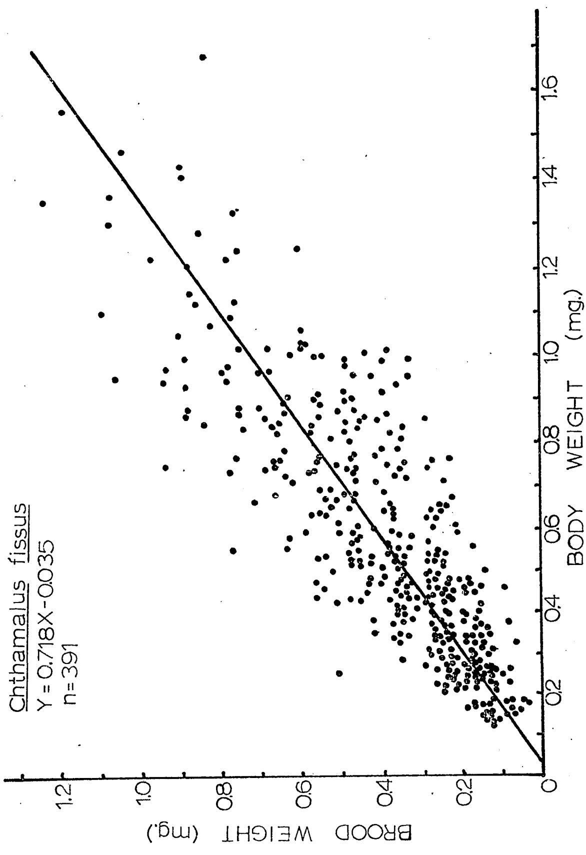

Chthamalus fissus
Y = 0.718X-0.035
n= 391
BROOD WEIGHT (mg.)
0
0.2
0.4
0.6
0.8
1.0
1.2
BODY WEIGHT (mg.)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6

Figure II-12. Balanus glandula brood weight versus body weight. Regression total for all samples.

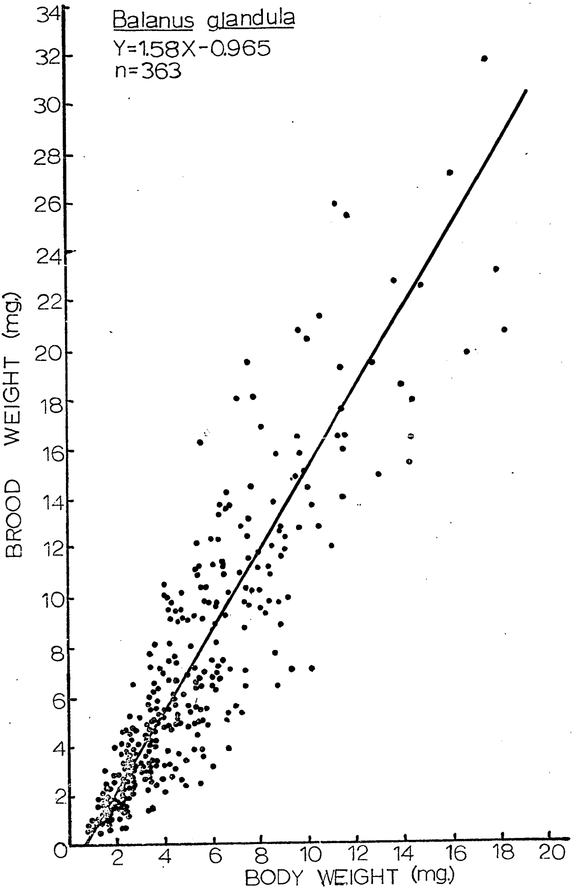
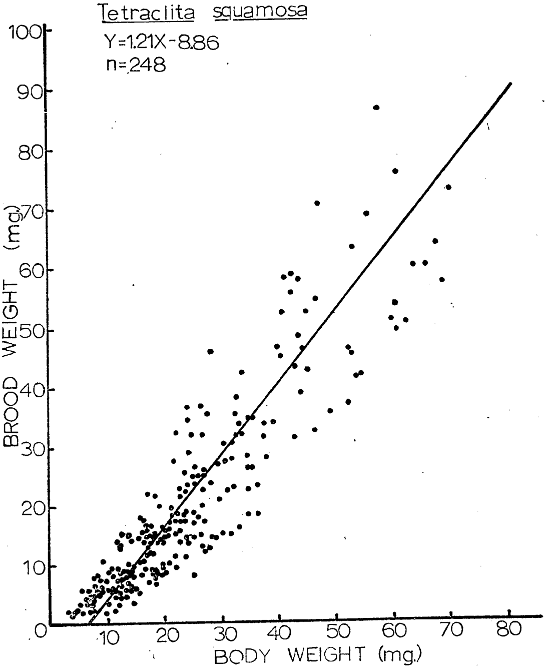

Balanus glandula
Y=1.58X-0.965
n=363
BROOD WEIGHT (mg.)
BODY WEIGHT (mg.)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34

Figure II-13. *Tetraclita squamosa* brood weight versus body weight. Regression total for all samples.


Tetraclita squamosa
Y=1.21X-8.86
n=248
BROOD WEIGHT (mg.)
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
BODY WEIGHT (mg.)

B. glandula - $n = 363$; $r = +0.868 : y = (1.58 \pm 0.093) x - (0.962 \pm 0.526)$.

T. squamosa - $n = 248$; $r = +0.908 : y = (1.21 \pm 0.066) x - (8.86 \pm 1.82)$.

Brood weight is quite variable in all three species, however, there was no significant difference in brood weight/body weight regressions between outfall and control population or between broods occurring early or late in the respective brooding season of any of the three species (p _ 0.20). Because brood weight is positively correlated with body size and because there is a large size range of barnacles both within each species and between species, the slope of these linear regressions of brood weight on body weight was taken as a comparative measure of the weight-specific (i.e., size-compensated) energy partitioned for each brood. By this measure *B. glandula* had the largest relative brood size (1.58); *T. squamosa* puts out an intermediate but still large brood (1.21); and *C. fissus* had a comparatively small brood (0.718).

3. Seasonal Patterns of Nutrient Storage and Reproductive Energy Expenditure:

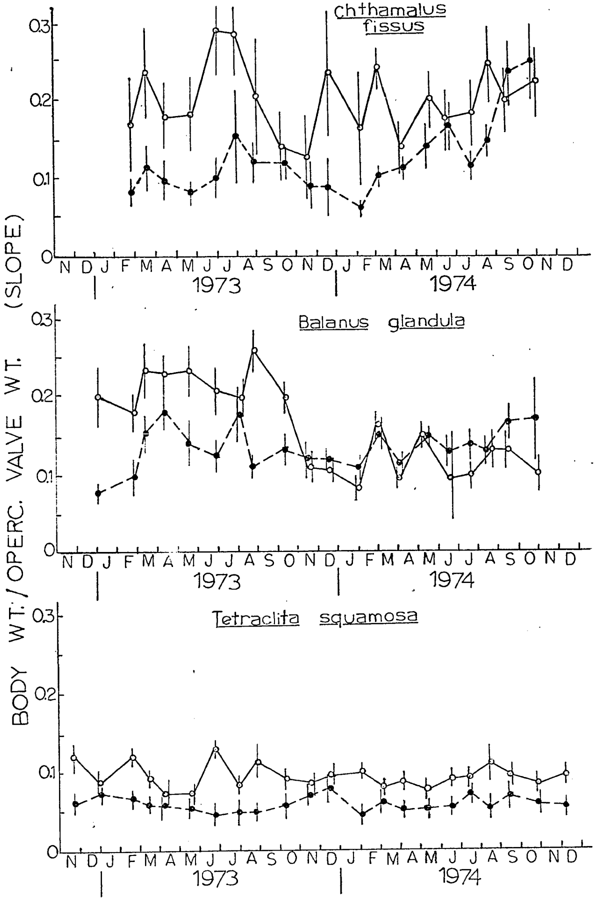
Nutrients can be stored in two body components of acorn barnacles: the body and/or the ovary (including the tissue lining the mantle cavity and adductor muscles). *Balanus balanus*, *B. balanoides*, and *Chthamalus stellatus* apparently store nutrients in the body during spring and early summer periods of high food availability and later transfer the stores to the ovary during gametogenesis (Barnes, Barnes, and

Finlayson, 1963; Barnes, 1972). However, Gardner and Riley (1972) examined types of fatty acids stored in B. balanoides and raised the question whether the nutrients stored in the body were primarily those associated with the male reproductive system rather than those likely to be stored for oogenesis. Nutrient storage in the three species in the present study was examined by following the cycles of body weight, ripeness of the male reproductive system, and ovary ripeness, and by comparing ovary weights with brood weights for each species. The maximum number of broods produced by each species during a season was estimated from the length of time required for one brood to hatch in the laboratory. Finally, all these parameters were combined to present a picture of the patterns of nutrient storage and reproductive energy expended during a season for each species.

a. Body Weight Relative to Opercular Weight.

The regressions of body weight relative to opercular valve weight for each outfall and control sample were computed, and the slopes and 95% confidence limits of these regressions were plotted in Figure II-14 to show the cycles of body weight for each species. (The intercepts of these regressions were all near zero.) There was no discernible seasonal cycle of body weight for any of the three species. The control samples had consistently higher body weights to opercular valve weight ratios than outfall samples of all three species, except for the second year of data for B. glandula where there was no difference between the two populations. It was difficult to

Figure II-14. Body weight "cycles." Slopes and 95% confidence limits for regressions of body weight versus opercular valve weight are plotted. Outfall population = closed symbols; Control population = open symbols.

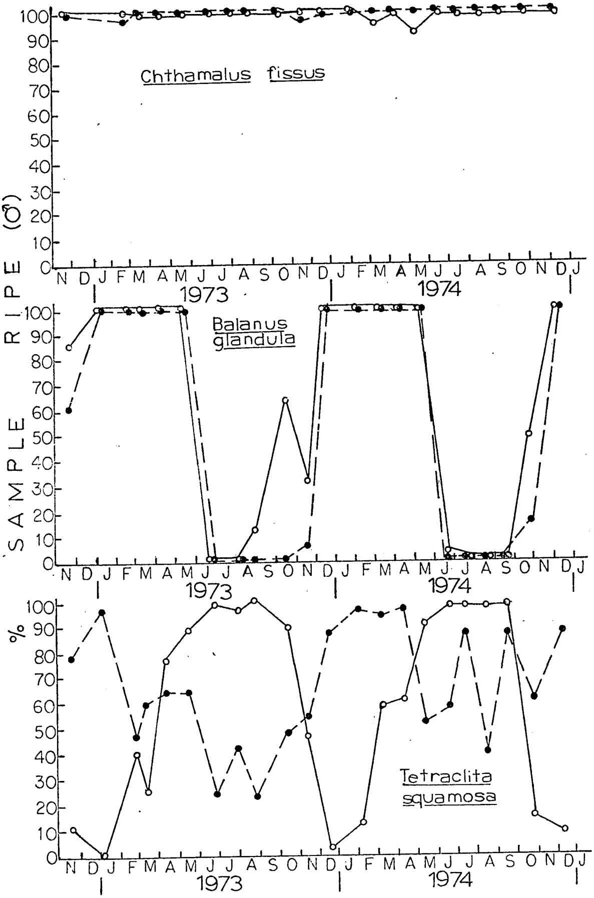

BODY WT./OPERC. VALVE WT. (SLOPE)
Chthamalus fissus
Balanus glandula
Tetraclita squamosa
0
0.1
0.2
0.3
N D J F M A M J J A S O N D J F M A M J J A S O N D
1973
1974

understand the significance of these erratic and variable data. As shown in the previous section, the body weights were not large compared to brood weight in all species, and it was hard to see how any sizeable quantity of nutrients could have been stored there. Variability of body weights in monthly samples could have reflected differences other than stored nutrients, e.g., gut contents. Furthermore, differences between outfall and control samples could have been due to differences in opercular valve weights, since these would have affected slopes as well as body weights. Small increases in calcium deposition at the higher temperature regime of the outfall could have accounted for the smaller body weight to opercular valve weight ratios, because the opercular valves were much heavier than the bodies. The body weight cycles did not correlate with cycles of male reproductive systems of any of the species shown in Figures II-15. It was therefore decided that body weights did not provide good reflections of nutrient storage patterns for these three species.

b. Ripeness of Male Reproductive System.

Cycles of the male reproductive systems of the three species are shown in Figure II-15. Nearly all _C_. _fissus_ appeared to have ripe male reproductive tracts year-round, with no significant difference between outfall and control populations. _B_. _glandula_ had a definite cycle of the male system, developing in the fall from September to November, remaining ripe during the brooding season from December to May, and

Figure II-15. Cycles of male reproductive systems. Outfall = closed symbols; Control = open symbols. Monthly sample sizes: *C*. *fissus* = 50; *B*. *glandula* = 60; *T*. *squamosa* = 60.

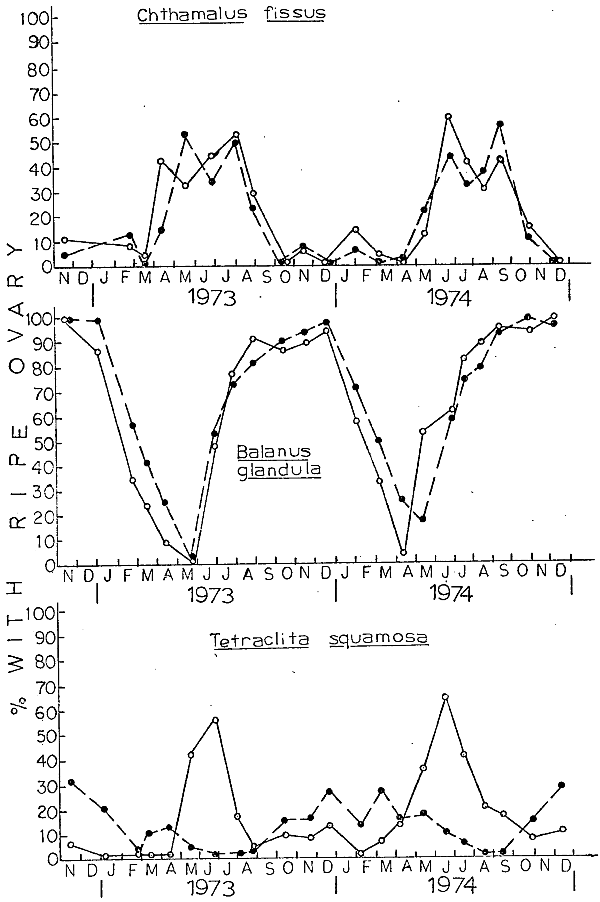

Chthamalus fissus
Balanus glandula
Tetraclita squamosa
% SAMPLE RIPE (♂)
0
10
20
30
40
50
60
70
80
90
100
N D J F M A M J J A S O N D J F M A M J J A S O N D J
1973
1974

rapidly becoming quiescent in summer from June to August. Both populations were very synchronous and similar each year although the control population became ripe slightly in advance of the outfall population. In _T_. _squamosa_ the control population showed a distinct cycle of the male system with peak activity occurring from about April to October and low frequencies of ripe individuals from November to February, when development of the male tracts began again. In contrast, the outfall population tended to be at peak frequencies of ripeness during winter, with erratic intermediate levels of activity during the rest of the year. The warm-water outfall obviously had a major disruptive effect on the cycle of development of the male system in this species.

c. Ovarian Cycles and Ovary Weight-Body Weight Regressions.

Ovarian development cycles are shown in Figure II-16, which are plots of the percentages of each sample which were ripe. Ovarian development in _C_. _fissus_ showed the same cycle as that of brooding frequency except that the summer peaks in ovary development did not reach as high frequencies as those for brooding frequencies. As in brooding frequencies, there were no consistent differences between outfall and control cycles of ovary ripeness. The ovaries of _B_. _glandula_ ripened rapidly in the summer from June to August. Nearly the whole population was ripe from August through December or January when brooding began. The frequencies of ripe individuals dropped during the brooding period to a low in April and May. The cycles for outfall and control populations were nearly

Figure II-16. Ovarian cycles. Outfall = closed symbols; Control = open symbols. Monthly sample sizes: *C. fissus* = 50; *B. glandula* = 60; *T. squamosa* = 60.

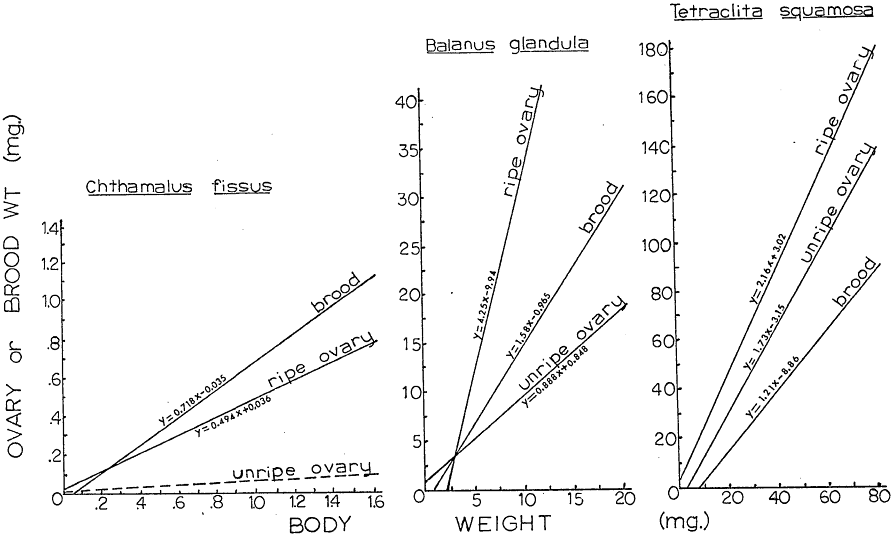

% WITH RIPE OVARY
Chthamalus fissus
Balanus glandula
Tetraclita squamosa
0
10
20
30
40
50
60
70
80
90
100
N D J F M A M J J A S O N D J F M A M J J A S O N D
1973
1974

identical, except that the control population appeared to have spent its ovaries somewhat in advance of the outfall population, which might be expected since it began brooding sooner. The ovarian cycle of the control population of T. squamosa showed that these barnacles became ripe in the late spring from April to May slightly in advance of the brooding period, and percentages of ripe individuals dropped precipitously in July and August when the summer brooding peak was reached. Peak frequencies of ripe individuals roughly corresponded to the peak brooding frequencies attained. However, the outfall population had only low frequencies of ripe ovaries during a long period from October to May or June, encompassing the same time as the brooding period. This population had virtually no ripe individuals in the summer months.

Ovary weight data were taken so that ovary size could be compared to brood size to estimate the number of broods for which the ovary stored nutrients. Initial attempts to measure seasonal cycles in ovary weights as a computed gonad index failed because of difficulties in isolating the ovaries for weighing. The ovary is extremely diffuse and ramifies throughout the compartment walls, and some ovarian tissue always remained uncollected when scraped out for weighing. The percent of the tissue remaining increased with decreasing size of the barnacle and created so much artificial variability that the data were rendered useless. This problem was compounded in T. squamosa which has no calcareous base so that the ovary lies directly on the substrate where it is subject to much damage during collection. Not enough individuals in any class of large barnacles were collected, so analyzing the data for single size-classes was not feasible. To estimate changes in ovary size, ovary weights were analyzed during months when each species was maximally ripe with yellow, yolky material (June, 1973 for C. fissus; December, 1973 for B. glandula; and June, 1974 for the T. squamosa control population), and also during months when they were least ripe (December, 1973 for C. fissus; May, 1973 for B. glandula; and February, 1974 for T. squamosa controls). The latter series of ovary weights were used as a baseline for "unripe ovary weight," because some of the "ovary" was actually retractor muscles and tissue lining the mantle chamber. Because of the problems of ovarian tissue collection, the ripe ovary weights should be considered as underestimates of ripe ovary sizes.

The regressions for "ripe" and "unripe" ovary weight versus body weight as well as the brood weight versus body weight regressions are shown in Figure II-17. In C. fissus the unripe ovary was essentially non-existent and no tissue could be collected for weighing; as the ovary ripened it increased to a weight about equal to the brood size and no larger, indicating that not more than one brood was prepared at a time. In B. glandula the unripe ovary and associated tissues were significant in size and the ovary showed an increase of about 2.5 times the brood weight when ripe. This indicated that yolky material for a minimum of three broods and probably more was stored in the ovary, considering that

Figure II-17. Regressions of "ripe" ovary weight, "unripe" ovary weight, and brood weight versus body weight.



Chthamalus fissus

Balanus glandula

Tetraclita squamosa

much yolky ovarian tissue was left behind in the shell during collection. In T. squamosa although both ripe and unripe ovaries and the associated tissues weighed more than the brood, ripe ovaries were only slightly larger than unripe ovaries. Therefore, although these tissues were potentially sizeable storage areas in T. squamosa, not much nutrient storage in the form of yolky material detectable by weight-change actually occurred--at most one brood was prepared in advance.

4. Time per Brood and Number of Broods per Season:

Preliminary estimates of the time each brood was retained in the mantle chamber were made for C. fissus and B. glandula by keeping barnacles moist, but not submerged, in a 12°C cold room. Periodic samples of barnacles were inspected for the developmental stages of brooded embryos. Since copulation did not occur and no new broods were laid down unless the barnacles were submerged, only already-existing broods continued to develop without hatching. In C. fissus, 100% of the broods were judged ready to hatch in about two weeks. In B. glandula, all broods were ready to hatch after one month, but the adults were in poor condition after this much time without submergence. T. squamosa could not be maintained unsubmerged for any extended period of time.

Patel and Crisp (1960) showed that brooding time determined in vitro corresponded well with in vivo times for Chthamalus stellatus, Balanus balanus, B. crenatus, and Elminius modestus. To get a better estimate of the time per brood, freshly deposited eggs were removed from the mantle chambers of each species and maintained _in vitro_ where they could be observed until hatching occurred. _C. fissus_ nauplii did not in fact hatch _in vitro_ but development appeared to continue normally to a darkly pigmented, mobile, eyed nauplius stage which was judged to be ready to hatch by comparison to the most advanced brooded embryos. The reason hatching did not occur was not known, and whether the proper stimulus required parental presence, or some environmental factor, or both, was not investigated. At 12°C _C. fissus_ nauplii were judged to be ready to hatch in 14 days (S.D. = ± 3 days; n = 21 broods). At 19°C development time for _C. fissus_ was 12 days (S.D. = ± 2 days; n = 15 broods). Embryos of _B. glandula_ readily developed and hatched _in vitro_. At 12°C time to hatching was 27 days (S.D. = ± 6 days; n = 24 broods), and at 19°C _B. glandula_ hatched in 22 days (S.D. = ± 4 days; n = 15 broods). _T. squamosa_ nauplii hatched in 40 days (S.D. = ± 8 days; n = 20 broods) at 12°C and 30 days (S.D. = ± 7 days; n = 13 broods) at 19°C. In summary, "normal brooding time" (i.e., at 12°C) was estimated at about 0.5 mos. for _C. fissus_ ($Q_{10} = 0.80$), 1.0 mos. for _B. glandula_ ($Q_{10} = 0.75$), and 1.5 mos. for _T. squamosa_ ($Q_{10} = 0.66$).

To calculate a maximum number of broods per year produced by the control populations of each species, the length of the brooding season was divided by the estimated time required for each brood. This calculation made the assumption that there was no delay between broods, which was difficult to prove directly without extensive maintenance of individual barnacles in the laboratory. Probably at least a short period between broods in fact occurred, because less than 100% of any of the populations were brooding at any given time. However, there was very strong circumstantial evidence that each species put out several broods in rapid succession during a season. First, observations of barnacles growing on glass slides have been reported in the literature, and for *Chthamalus stellatus*, *Eliminius modestus*, *Balanus perforatus*, and *B. amphitrite* var. *denticulata* broods follow each other in rapid succession, limited only by the development time required for embryos to hatch (Crisp and Davies, 1955; Patel and Crisp, 1960). Second, the length of the brooding season for each species in the present study was clearly much longer than the developmental time for each brood, and most barnacles had ripe ovaries remaining while still brooding. Embryos in all stages of development were found throughout the brooding season of each species, and occasionally, a new brood was present in the mantle chamber while advanced embryos from a previous brood remained. For these reasons the assumption that there was no delay between broods appeared to be valid. For *C. fissus* the length of the brooding season from March through October was eight months with some low levels of activity at other times of the year. Therefore, eight plus months divided by 0.5 months per brood equals about 16 broods per season. For *B. glandula* the brooding season from December through May was six months, and six months divided by one month per brood equals about six broods per season. The control population of _T_. _squamosa_ brooded from late May or early June to late September or early October, or about 4.5 months. At 1.5 months per brood this resulted in about three broods per season for the control population.

It should be emphasized that these numbers of broods per season are probably maximum estimates. Any delay between broods would tend to decrease the number of broods produced in a season. For example, a lag of only 4-5 days between broods in _B_. _glandula_ would reduce from six to five the estimate of the number of broods produced over the six-month season, and this short lag could result in 15-20% of the population not brooding at any given time. On the other hand, any factor, such as temperature higher than 12°C, which shortens the brooding time would tend to make the production of more broods possible. It is thus very difficult to estimate the number of broods produced by the outfall populations. _B_. _glandula_, for example, tends to have a delayed, shorter brooding season in the outfall with a lower percent of the population brooding at any given time, but the higher temperatures probably shorten the time each brood is retained.

5. Patterns of Nutrient Storage and Energy Allocation to Reproduction:

It is now possible to form a deductive composite of barnacle reproductive effort throughout the year. For each species we have estimates of the following parameters: length of brooding season, time per brood, number and size of broods, and the amount of nutrient storage in the ovary. These parts of the deductive puzzle can now be fitted together along with information about environmental regulation of reproduction and rates of reproductive response of the barnacles to seasonal changes in the environment to show comparative patterns of nutrient storage and energy allocation to reproduction.

A schematic model of the patterns of nutrient storage is presented in Figure II-18 showing proportional changes in ovary size during the year relative to brood size for each species. Brooding in C. fissus is limited by food availability, so that as soon as enough nutrients for a brood are stored, the eggs are deposited, and the response time for changes in food levels is extremely rapid. As food availability increases during spring and summer, the rate of yolk accumulation increases and broods are produced more frequently, until at the peak of the summer brooding season nutrient buildup is so fast that the rate of brood production is probably only limited by the time required for brood incubation. In contrast, B. glandula rapidly stores nutrients in the ovary during the summer and remains full of yolky material during the fall until the proper cold temperature conditions are met and brooding begins in the winter. Yolk for at least three broods are 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 after about six broods. T. squamosa produces only three broods in the summer, and apparently only enough yolk for one brood at a time is accumulated before egg-laying.

Figure II-18. Schematic model of patterns of nutrient storage in ovary.

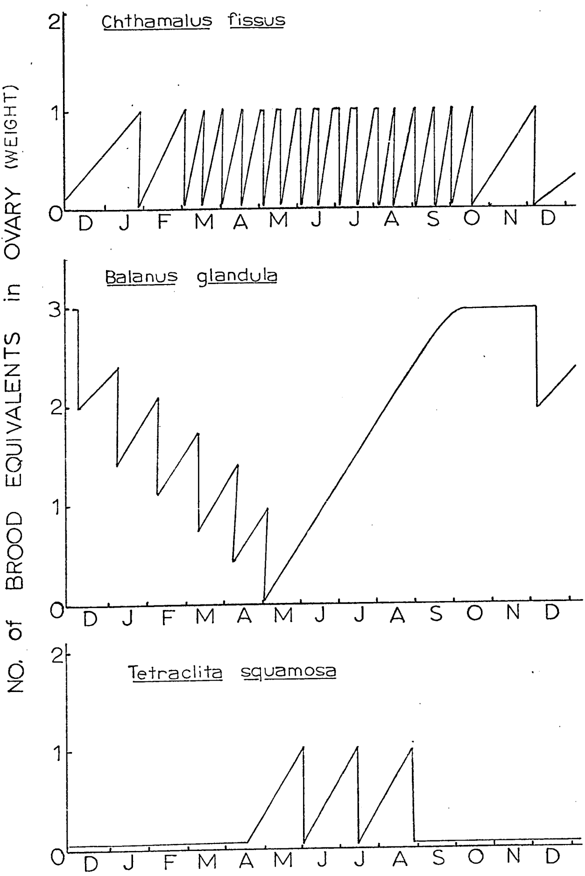
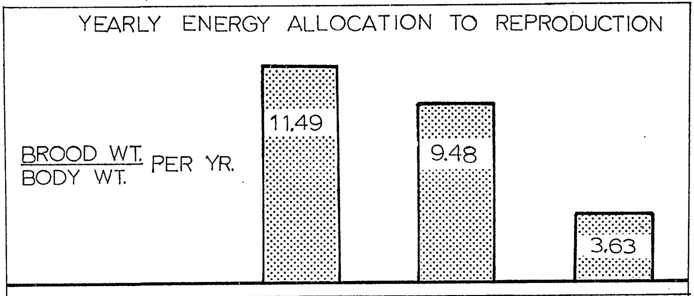

NO. of BROOD EQUIVALENTS in OVARY (WEIGHT)
Chthamalus fissus
2
1
0
D J F M A M J J A S O N D
Balanus glandula
3
2
1
0
D J F M A M J J A S O N D
Tetraclita squamosa
2
1
0
D J F M A M J J A S O N D

Figure II-19. Yearly energy allocation to reproduction. Number of broods per year times the slope of the brood weight versus body weight regression = brood weight/body weight per year.



YEARLY ENERGY ALLOCATION TO REPRODUCTION

	CHTHAMALUS FISSUS	BALANUS GLANDULA	TETRACLITA SQUAMOSA
length of season	8 mos.	6 mos.	4.5 mos.
time per brood	0.5 mos.	1 mos.	1.5 mos.
no. broods / yr.	16	6	3
brood wt./bodywt	0.718	1.58	1.21

Comparative energy allocations to reproduction measured as brood weight relative to body weight per year are shown in Figure II-19. For each species the measured length of the brooding season of the control population has been divided by the brood incubation time at 12°C in the laboratory to calculate the number of broods produced per year. The number of broods was then multiplied by the brood-weight to body-weight ratio (i.e., the slope of the regression of brood weight on body weight) to calculate the total size-specific brood weight expended during the year. _C_. _fissus_ had the highest proportional energy allocation to brood production--11.49 times the body weight produced as broods; _B_. _glandula_ expended an intermediate but large amount--9.48 times the body weight produced as broods; and _T_. _squamosa_ allocated the least amount of energy to brood production--3.63 times the body weight produced as broods--thus producing only about one-third the size-specific total brood weight of the other two species.

D. DISCUSSION

Very little information is available on the reproductive biology of _Chthamalus_ _fissus_. Straughan (1971) reports that she found brooding individuals the year round at Santa Barbara, California, but her sample sizes were small and she does not show a reproductive cycle for the species. Two other _Chthamalus_ species studied show distinct reproductive cycles, which appear to be temperature dependent. _C_. _stellatus_, an Atlantic and Mediterranean species, is reported to brood from May to

September in Great Britain (Crisp, 1950) and from February to October in Yugoslavia (Klepal and Barnes, 1975). It has a minimum breeding temperature of 14-16°C, below which brooding will not occur; brooding frequencies increase to an optimum temperature of 24-25°C, and fall off to a maximum temperature for brooding of 30-32°C, which is near the upper tolerance limit of 38°C for this species (Patel and Crisp, 1960; Klepal and Barnes, 1975). In contrast to the reproductive cycle of C. stellatus, C. depressus has a short brooding period from May through August in Yugoslavia, with a minimum temperature of 15-20°C for reproduction (Klepal and Barnes, 1975). C. fissus in the present study did not show any effect of temperature on brooding at 11.5°C and 20°C, nor did it show any difference in brooding cycles of the two field temperature regimes in the outfall and control areas. However, this high intertidal zone species surely normally encounters much wider extremes of temperatures than those tested, and reproduction may be affected when those extremes are reached. C. challengeri in Japan broods from March through October with a broad cycle very similar to that of C. fissus (Iwaki, 1975). Information available on gametogenesis in C. challengeri shows that the cycle of development of the male and female gametes mirrors the brooding cycle, but no experimental information is available on environmental factors controlling these cycles (Iwaki, 1975).

Clearly, food availability is normally the limiting factor for reproduction in C. fissus, with brooding frequency directly proportional to food availability at temperatures normally encountered. Patel and Crisp (1960) showed that nutrition also played a major role in allowing breeding to commence in *C. stellatus*. Starved *C. stellatus* which had not brooded even after having been kept for 30-40 days above critical breeding temperatures began brooding within 18-20 days after feeding liberally on *Artemia* larvae. Klepal and Barnes (1975) induced *C. depressus* to breed in the lab within one month by feeding them. This brooding response to increased food availability in *C. stellatus* and *C. depressus* is similar to the two-week response time for *C. fissus* in the present study.

C. stellatus is similar to *C. fissus* in that it exhibits a continuous succession of broods with the hatching of one brood followed immediately by the deposition of another during the breeding season (Crisp and Davies, 1955). For *C. stellatus* at 14.5°C the time for each brood from fertilization to hatching is about 15 days, and the rate of development is strongly temperature dependent: 29 days at 9°C to about seven days at 31°C for a $Q_{10} = 21.8$ (Patel and Crisp, 1960). This development time of about two weeks agrees well with that found in the present study for *C. fissus*, although the rate of development of *C. fissus* is not nearly so temperature sensitive. *C. fissus* is also similar to the warm-water species *Elminius modestus* which reproduces continuously over a broad range of temperature during the spring and summer when food supply is sufficient to allow a steady output of broods, the interval between broods being limited mainly by time taken by egg masses to develop (Crisp and Davies, 1955). The brooding period was temperature dependent in E. modestus: about 15 days at 15°C and as long as 60 days at 7-8°C. However, during late fall and winter, the rate of assimilation appeared to be limiting; the ovaries tended to be small and poorly developed, but the male organs were still present. Crisp and Davies therefore hypothesized that breeding in E. modestus was limited more by lack of food for the eggs than by any deficiency of the male reproductive system, but they did not prove this hypothesis as I have done for C. fissus.

Hatching in C. fissus may require the presence of a "hatching substance" which is frequently required for embryos of other barnacle species (Crisp, 1956; Crisp and Spencer, 1958; Barnes and Barnes, 1959; Patel and Crisp, 1960; Barnes and Stone, 1973). This substance may be the presence of diatoms associated with the spring plankton bloom or, in other cases, extracts of barnacles themselves may stimulate the release. Although a hatching substance is particularly important in boreo-arctic species, even embryos of some species which hatch on their own at higher temperatures will not hatch at low temperatures without the presence of a hatching substance. Thus the failure of C. fissus embryos to hatch their own in vitro is not surprising, although it is unusual for a warm-water barnacle and merits further study. C. fissus of all sizes above 1 mm reproduced in the present study, but there is no published information on size-dependent reproduction in other Chthamalus species.

Results of the present study agree well with the published reports on the reproductive cycle of Balanus glandula. At Morro Bay brooding occurred from December or January through May, and occasionally a few individuals brooded in the fall. Barnes and Barnes (1956) reported that B. glandula at Ladysmith, British Columbia, had a major brooding period from January through May, and a secondary brief autumn brooding period in August and September. At La Jolla, California, they reported B. glandula brooding from late November through May, but not in the early fall. Similarly, Connell (1970) reported B. glandula at San Juan Island, Washington, brooding from late fall to June; Hines (Unpublished) found it brooding from November to May at San Francisco Bay; and Straughan (1971) found it brooding from January to June and storing yolky material in the ovary during summer at Santa Barbara, California. Barnes and Barnes (1956) state that the first winter brood was a main brood which was followed by one or more smaller broods and that the early fall brood in northern populations was a minor, small brood with only a small percentage of the population brooding. However, they gave no data to support these evaluations of brood size. Connell (1970) and Straughan (1971) suggest that B. glandula produced two broods per year. These reports are in conflict with the present conclusion that B. glandula produces up to six broods of equal size, but they were based on guesses from field data which only indicated that more than one brood was released. The published percentages of samples brooding for B. glandula agree well with the levels of brooding activity found in the present study.

All of the published reports on B. glandula suggest that cold temperatures regulate the reproductive cycle and, thus, indirectly, the southern range of B. glandula. In this study, field differences between populations in the warm-water outfall and the control areas combined with the results of laboratory experiments showed clearly that a period of at least one month of cold temperatures is required in the fall to bring on brooding. Apparently a summer and early fall period of nutrient storage and gametogenesis is required before brooding can begin because brooding could not be induced during those months even though the barnacles appeared full or nearly full of yolky material by August. Brooding ceased in May apparently because the barnacles had depleted their ovarian reserves of yolky material, but it should be noted that there were always some individuals which still appeared ripe or partly ripe at that time. Since brood weight is apparently constant, perhaps these individuals were partly ripe but did not have sufficient yolk to produce a complete brood.

B. glandula is similar to the boreo-arctic species B. balanoides in its winter brooding season. Like B. glandula, Barnes (1963) showed that B. balanoides has a critical temperature near 10°C above which animals will not reproduce; and although increases in food availability and temperature changes during the earlier stages of oogenesis may advance by a few weeks the date when fertilization takes place, a really pronounced shift in reproductive period was not achieved.

He suggests that in B. balanoides biochemical processes during nutrient storage and development of the ovary limit the rate of reproduction so that a minimum time of five months is required from hatching of the previous brood until fertilization can recur. The time at which egg masses are laid could be manipulated by controlling the period when food was supplied to B. balanoides (Barnes and Barnes, 1967). Starvation periods of various times could delay brooding from November to January, and starvation early in oogenesis led to ovarian regression, but not so late in the season. The effects of starvation were not tested in the present study on B. glandula.

Of course, B. glandula is different from B. balanoides in many respects, especially since the former produces several broods while the later has only one brood per year. While brooding in B. glandula is apparently unaffected by photoperiod, constant light of even moderate intensity inhibits gonadal development in B. balanoides, and a period of 4-6 weeks in the fall with less than 12 hours light per day at a temperature below 10oC is essential for reproduction (Barnes, 1963). B. balanoides embryos develop to the point of being ready to hatch in 60-80 days depending on the temperature, but they may be retained by the parent for many weeks until the proper "hatching substance"--usually diatoms from the spring plankton bloom--is present (Crisp, 1956; Barnes, 1959). B. glandula, however, required no hatching substance for the release of embryos. These differences probably stem from the adaptation of B. balanoides to boreo-arctic conditions. In the extreme north the diatom bloom is sharply limited to the arctic spring, and only then is food available to either larvae or adults. The larvae of B. balanoides are thus released into an environment with abundant food, and the adults immediately proceed to accumulate metabolic reserves which are later utilized in gonad production (Barnes, Barnes, and Finlayson, 1963). Patterns of nutrient storage are reflected in changes of body weight and biochemical composition which are later followed by ovary changes in the boreo-arctic species B. balanoides and B. balanus and the warm temperate species Chthamalus stellatus and Verruca stroemia (Barnes, Barnes, and Finlayson, 1963; Barnes, 1972; Stone and Barnes, 1974). However, none of the three species in the present study showed any cycle of body weight, and nutrient storage in these species must take place in the ovary. Larvae of the temperate species, B. glandula, do not have nearly so restricted a plankton-rich period as B. balanoides, although the seasonality of temperate plankton productivity is sufficiently pronounced to select for a summer period of nutrient storage in the adults. Beyond simple nutrient storage in B. glandula, it is likely that other factors such as the time of settlement relative to competitors and predators and post-metamorphosic growth may select for larval hatching prior to, as well as during, the onset of the plankton increase. Since all sizes of B. glandula present during the brooding season brooded, it must reproduce in its first season, but B. balanoides and B. balanus do not reproduce the first winter after settlement.

There is practically no published information on the reproductive cycles of *Tetraclita squamosa*. Ricketts and Calvin (1962) state that it can be found brooding large egg masses in the summer, which agrees with the present findings. However, no other barnacle species has been described as similar to *T. squamosa* which show a reproductive pattern with a few broods each retained for a long period in the summer months. Those species that brood in the summer tend to produce numerous, frequent broods, while those species which put out only a few broods seem to be northern species which brood in the winter and/or spring. *T. squamosa* had a low energy allocation to reproduction compared to the other two species in the present study, and it did not store yolk for more than one brood at a time. Since little weight change could be detected in potential storage tissues, it appeared to be able to assimilate and metabolize energy into a brood rapidly in the summer when food availability was high without a prolonged build-up of reserves. The field evidence showing differences in reproduction in the outfall and control population was extremely suggestive that warm temperatures were required for reproduction, but the failure to induce brooding in the laboratory with any of the combinations of temperature, photoperiod, and food at various times of the year confused the issue. Without the ability to manipulate the reproductive cycle, it is difficult to speculate further about the control of reproduction in *T. squamosa*, aside from the fact that conditions in the warm-water outfall were very disruptive to both the ovarian and testicular cycles. *T. squamosa* is like the boreo-arctic species *Balanus balanoides* and *B. balanus* in that it does not begin to reproduce immediately but grows to a substantial size before it is fully mature. *Verruca stroemia* also shows a slightly delayed maturity and does not begin to reproduce until it is about 2 mm in basal diameter (Barnes and Stone, 1973).

Because there are no published reports on brood weights in barnacles, it is not possible to compare the allocation of energy to reproduction in the three species in the present study with other barnacles. Published studies on reproductive effort in barnacles are reports of fecundities and egg size (e.g., Barnes and Barnes, 1965); however, these aspects will be discussed in Chapter V.

CHAPTER III. SETTLEMENT

A. INTRODUCTION

Settlement in barnacles may or may not reflect the pattern of brooding seasonality shown by a species. Thus, the boreo-arctic species Balanus balanoides, B. balanus, and B. hameri which incubate a single large brood during winter, and which release nauplii into the plankton in synchrony with the spring diatom bloom, have a single large settlement in April (Barnes and Powell, 1953; Crisp, 1954; Barnes, 1963). Verruca stroemia incubates a large brood synchronously throughout the population in winter which hatches with the spring diatom bloom and is followed by several minor broods during summer. There is also a large peak of settlement in late spring followed by continual, small settlements in summer and early fall (Barnes, 1958; Barnes and Stone, 1973). Many temperate and warmer water species, such as Balanus crenatus, B. improvisus, Chthamalus challengeri, and Elminius modestus, which have reproductive seasons of repeated broods from late spring through early fall, show similar successive settlements over the same period (Barnes and Powell, 1953; Barnes and Barnes, 1962; Iwaki, 1975; Costlow and Bookhout, 1953). On the other hand, Chthamalus stellatus produces a number of broods during the summer, but settlement only occurs from September to October; presumably these settlers resulted from the late summer and early fall broods (Barnes, 1956; Connell, 1961a). Similarly, Balanus glandula releases broods during the winter and spring with occasional minor broods in the fall, but it shows a single major peak of settlement in May or June and may have minor settling from as early as January through as late as October at various places (Connell, 1970). Therefore, it is not always possible to predict the seasonal pattern of settlement of a species of barnacle from its seasonal pattern of brooding.

As in the time of settlement, the vertical pattern of settlement of barnacles may or may not follow the vertical distribution of adults in the population. For example, *Chthamalus stellatus* settles out over the entire vertical range of the intertidal zone, but because of crowding by *Balanus balanoides* in the lower zones, *C. stellatus* survives to adult age only in the highest zone (Connell, 1961a). *B. balanoides* and *B. glandula* settle in large numbers in all but the highest intertidal zone, although adults survive predation by snails and sea stars mainly in an upper mid-intertidal refuge zone (Connell, 1961b; 1970). *Balanus cariosus* settles only in about the lower half of the intertidal zones, and adults growing to sufficient size avoid predation in all but the lowest part of the zone of settlement (Connell, 1970). Cyprids of these four intertidal species apparently do not as a rule settle subtidally, although individuals of *B. cariosus* may occasionally be found in shallow subtidal waters (Barnes, 1955; Connell, 1961; Barnes and Barnes, 1956; Haderlie, 1974; personal observations). *Elminius modestus* settles and grows rapidly over the range from shallow subtidal to all but the highest intertidal zone (Barnes and Barnes, 1962). Subtidal species such as Balanus balanus and B. hameri appear to settle only subtidally (Barnes and Barnes, 1954; Crisp, 1954) while others such as Verruca stroemia, Balanus crenatus, and B. nubilis settle mainly subtidally but may sometimes settle and grow even in large numbers in low intertidal areas (Stone and Barnes, 1973; Barnes and Powell, 1953; Haderlie, 1974). Therefore, selective settlement in barnacles often accounts for only part of the vertical distribution of a species; differential survivorship after settling frequently further limits a population's distribution.

This chapter quantifies the seasonal patterns and vertical intertidal ranges of settlement in Chthamalus fissus, Balanus glandula, and Tetraclita squamosa by recording the appearance of new individuals in permanently marked quadrats. Settled barnacles were then followed in growth and survivorship studies presented in Chapters IV and V.

B. MATERIALS AND METHODS

As explained in the preceding chapters, the study was conducted at the Pacific Gas and Electric Company power plant at Morro Bay, California. During spring, 1973, several permanently marked, 10 x 15 cm quadrats were established at high, middle, and low intertidal positions in the outfall and in control areas unaffected by the warm-water discharge (see Figure III-1). Initially, newly recruited barnacles were counted directly in each 150 cm^2 quadrat during monthly

Figure III-1. Locations of permanently marked quadrats at Morro Bay, California.

Outfall: *Chthamalus fissus* and *Balanus glandula*: 1 high, 1 middle, and 1 low quadrats. *Tetraclita squamosa*: 14 low quadrats.

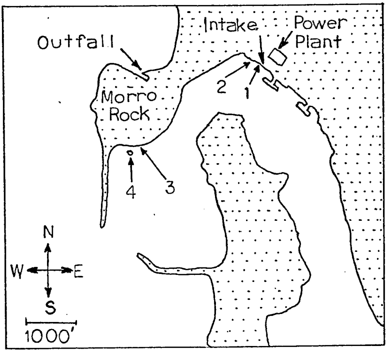
Control:

Area 1: *C. fissus*/*B. glandula*: 1 high, 1 low quadrat.

Area 2: *C. fissus*/*B. glandula*: 1 middle quadrat.

Area 3: *C. fissus*/*B. glandula*: 1 high, 1 low quadrat. *T. squamosa*: 4 low quadrats.

Area 4: *T. squamosa*: 6 quadrats.


Outfall
Intake
Power Plant
Morro Rock
1
2
3
4
N
W
E
S
1000′

collecting trips to Morro Bay. However, as the difficulties of keeping track of many quadrats and barnacles rapidly became apparent, photographic records of each quadrat were initiated in late summer and early fall of 1973 to conserve time in the field and to provide permanent records for later analysis. From late fall 1973 to mid-winter 1975 groups of 4-6 adjacent replicates at each intertidal level in each area, for a total of some 70 quadrats, were photographed monthly. All quadrats were examined qualitatively to ascertain any obvious differences between adjacent replicate quadrats. However, only the quadrats for which the longest continuous data were available (including field counts and photographs) were analyzed quantitatively (see Figure III-1 and description of quadrat locations below).

For Chthamalus fissus and Balanus glandula one high, one middle, and one low quadrat in the outfall and two high, one middle, and two low quadrats in the control areas were analyzed in detail. Tetraclita squamosa was present only in quadrats at lower intertidal levels, and all quadrats which contained individuals of this species were analyzed in order to obtain large enough sample sizes: 14 quadrats in the outfall, six quadrats in one control area, and four quadrats in another control area. Figure III-1 shows the location of these quadrats. All outfall quadrats for all three species were located on a vertical cement wall immediately south of the discharge tubes. One high and one low control quadrat for C. fissus and B. glandula were located on the corner of the vertical north-facing cement wall of the plant intake structure. The middle level control quadrat for *C. fissus* and *B. glandula* was located on a west-facing vertical surface of a granite boulder about five meters north of the intake structure. The second high and low control quadrats for *C. fissus* and *B. glandula* were located on a vertical south-facing granite outcrop on the south side of Morro Rock. This lower quadrat also marked the position of four adjacent control quadrats for *Tetraclita squamosa*. Finally, *T. squamosa* were analyzed from another control group of six adjacent quadrats located on a north-facing surface of another granite outcrop about five meters further west. *C. fissus* and *B. glandula* were not analyzed in this last location. For both outfall and control areas, high quadrats were located at about +5.5 to 6.0 feet above mean lower low water, middle quadrats at about +2.5 to 3.0 feet, and low quadrats at about 0 feet (mean lower low water). Quadrats in control area 4 for *T. squamosa* were located at about +2.5 feet rather than the usual "low" level; *T. squamosa* was able to survive at this higher position apparently because they were on a protected north-facing surface with a slight over-hang providing continuous shade.

Numbers of *B. glandula* and *T. squamosa* settling in the standard 150 cm^2 quadrats were counted; however, for settlement of *C. fissus* a smaller 50 cm^2 subquadrat in the center of each standard quadrat was counted. For summary comparisons between species, the data were then converted to correspond to a 100 cm^2 surface area.

Although generally quite successful, the use of photography to gather data on the quadrats involved several assumptions resulting in occasional difficulties in data processing. The data probably underestimate the numbers of cyprids actually settling because: (1) barnacles which had settled and died between monthly photographs leaving no trace of their presence obviously could not be counted; (2) in periods of very dense settlement, especially for _B_. _glandula_, it was difficult to distinguish every individual because of extreme crowding; and (3) photographic depth of field problems in quadrats where large _T_. _squamosa_ caused high relief made it difficult to keep all the substrate in focus. However, by observations of the quadrats during monthly samples and by working back and forth between successive monthly photographs, each individual barnacle was given a number as it appeared. In this way each barnacle could be later followed for growth and survival. Barnacles as small as 1-2 mm in basal diameter and about 1-3 weeks in age could readily be identified in the photographs.

C. RESULTS

Quadrat photographs showing examples of recently settled individuals of _Chthamalus_ _fissus_, _Balanus_ _glandula_, and _Tetraclita_ _squamosa_ are presented as Figures III-2 through III-4. Examination of photographic records and field notes for all 70 quadrats showed no obvious qualitative differences in barnacle recruitment, growth, and survivorship between adjacent replicate quadrats at each intertidal level for _C_. _fissus_

Figure III-2. Example of _Chthamalus fissus_ settlement: Control Middle quadrat, December 11, 1974. Arrow indicates recent settlement of _C. fissus_ on _Balanus glandula_ scars. Quadrat = 10 x 15 cm.


12-11-74
CONTROL
ROCK
SERIE

Figure III-3. Example of _Balanus glandula_ settlement: Outfall Middle quadrat, July 21, 1974. Arrow indicates barnacles which settled in June, 1974. Quadrat = 10 x 15 cm.

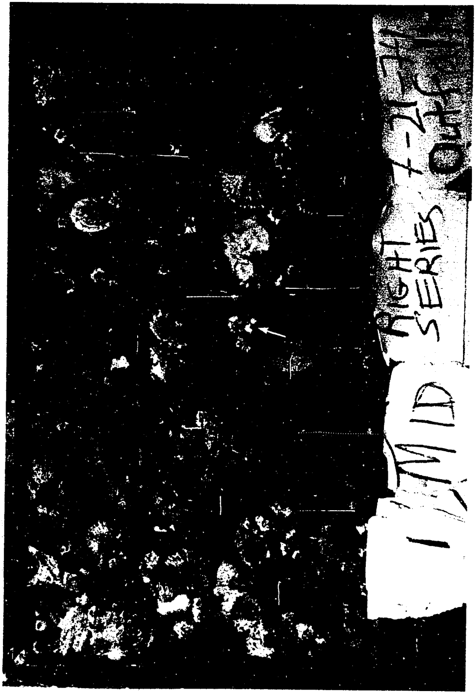
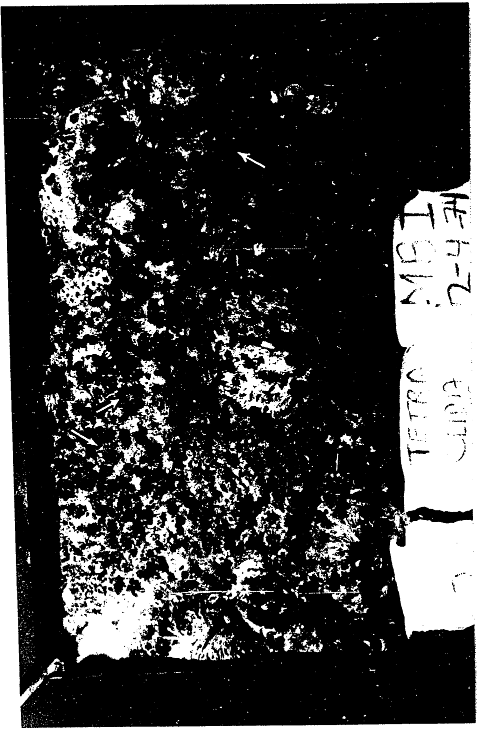

F-2
OUT
RIGHT SERIES
MID

Figure III-4. Example of Tetraclita squamosa settlement: Control area 4, February 4, 1974. Arrows indicate four-month old barnacles. Quadrat = 10 x 15 cm.


HE-G-7
TETRA

and B. glandula. Therefore, the quadrats which were quantitatively analyzed in detail were judged to be good representative samples of the populations of these two species. All data available are presented for T. squamosa.

The numbers of newly settled Chthamalus fissus appearing in each quadrat at the three levels in control and outfall areas from April, 1973 to January, 1975 are shown in Figure III-5. No obvious seasonality of settlement and no significant pattern of settlement relative to tidal height are apparent. Instead, C. fissus settles out erratically at all times of the year and at all tidal heights. Somewhat fewer C. fissus settled in the outfall quadrats than in the control quadrats, but the data are too variable to permit any significance to be attributed to this difference.

In contrast to Chthamalus fissus, Balanus glandula shows a markedly seasonal peak of settlement (see Figure III-6). In 1973 a few B. glandula settled as early as April, but in every quadrat peak settlement occurred in May with only a few additional barnacles settling in June. In 1974 the peak of settlement occurred slightly later, with a few recruits in May and most B. glandula settling in June, followed by some additional settlement in July in all quadrats. No settlement of B. glandula occurred at other times of year in any of the quadrats. In addition to the seasonal pattern of settlement, B. glandula showed a distinct pattern of greater settlement at lower intertidal levels: more barnacles settled in middle quadrats than high and many more settled in low quadrats than

Figure III-5. *Chthamalus fissus* settlement in control and outfall areas.

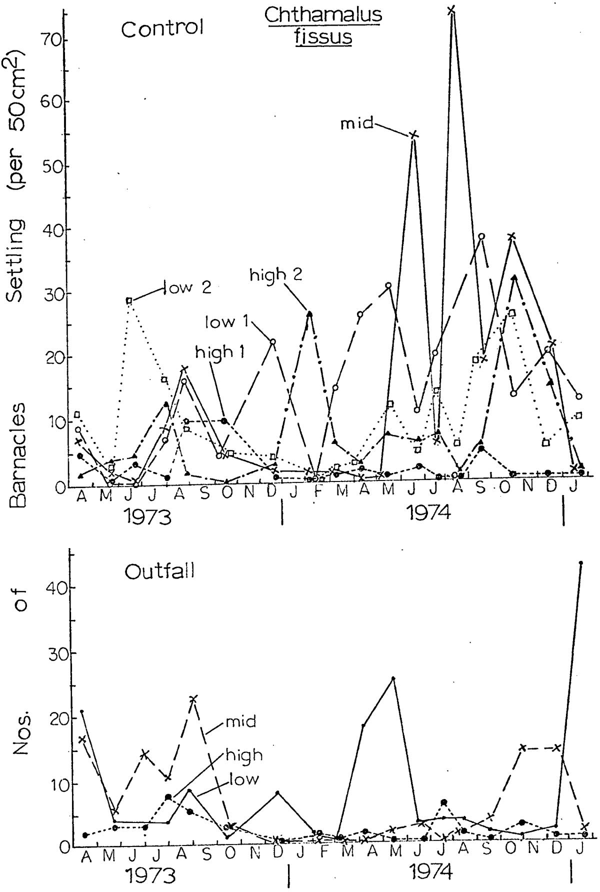
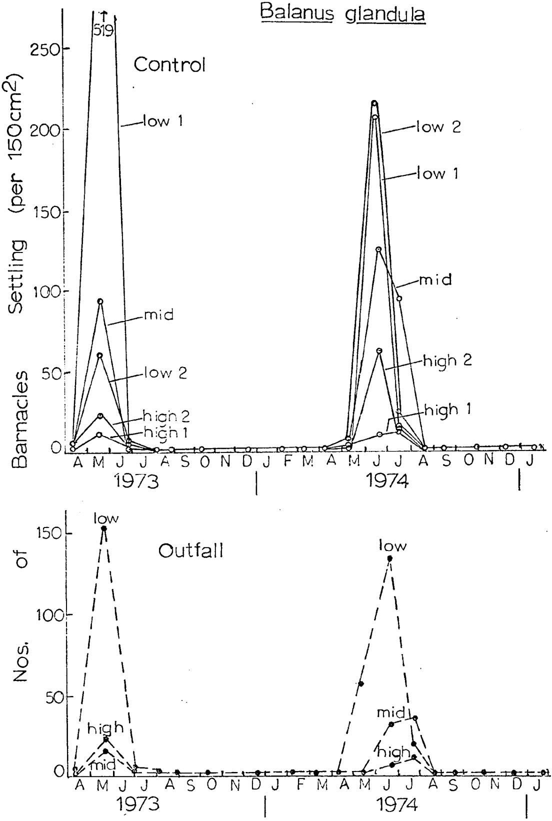

Control
Chthamalus fissus
Nos. of Barnacles Settling (per 50cm^2)
70
60
50
40
30
20
10
0
mid
high 2
low 2
low 1
high 1
A M J J A S O N D J F M A M J J A S O N D J
1973
1974
Outfall
40
30
20
10
0
mid
high
low
A M J J A S O N D J F M A M J J A S O N D J
1973
1974

Figure III-6. Balanus glandula settlement in control and outfall areas.



Balanus glandula

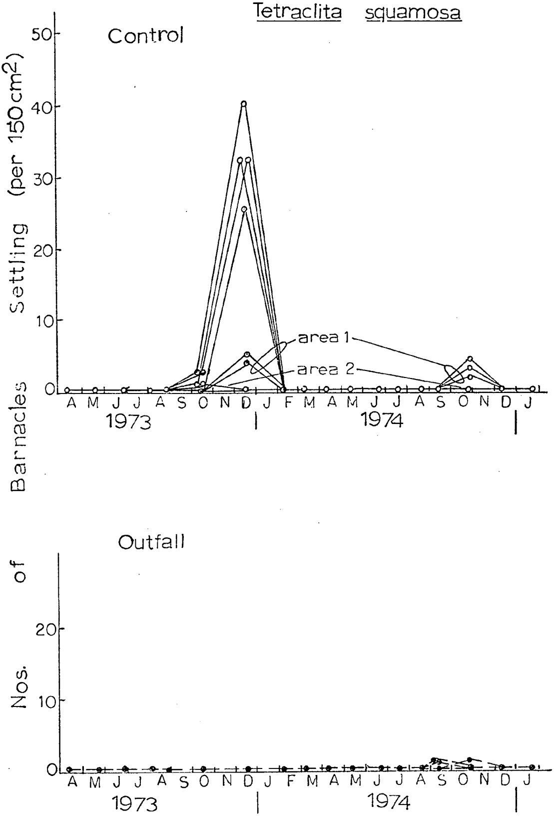
Control

Outfall

middle. There were some minor exceptions to this pattern--e.g., the control middle quadrat had more settlement than low quadrat number 2 in 1973 and the outfall high quadrat had more settlement than the middle quadrat in 1973--but the relationship of increasing density of settlement in lower zones was otherwise a consistent one. Just as the seasonal pattern of settlement was very repeatable in 1973 and 1974, the densities of barnacles settling at each tidal level were generally similar in both years. However, in 1973 control low qaudrat number one appears to have had exceptionally large numbers settling while control low 2 had rather few *B. glandula* settling in it, and the outfall middle quadrat had far fewer barnacles settling than the control middle quadrat in both years.

Like *Balanus glandula*, *Tetraclita squamosa* has a markedly seasonal period of recruitment (see Figure III-7) with peak settlement occurring in fall during late November or early December, 1973 and in October, 1974. Although a few individuals settled out as early as September, no *T. squamosa* were found settling at other times of the year. However, unlike *B. glandula*, no *T. squamosa* settled in any of the middle or high intertidal quadrats, and the distribution of *T. squamosa* settling in the lower areas was extremely patchy and annually variable. Thus, comparatively large numbers of *T. squamosa* settled out in all six control quadrats in area 4 in 1973, but only a few of this species settled in three of these quadrats in 1974. And in control area 3 only one new barnacle of this species was found in all four quadrats in 1973 and

Figure III-7. _Tetraclita_ _squamosa_ settlement in control and outfall areas.

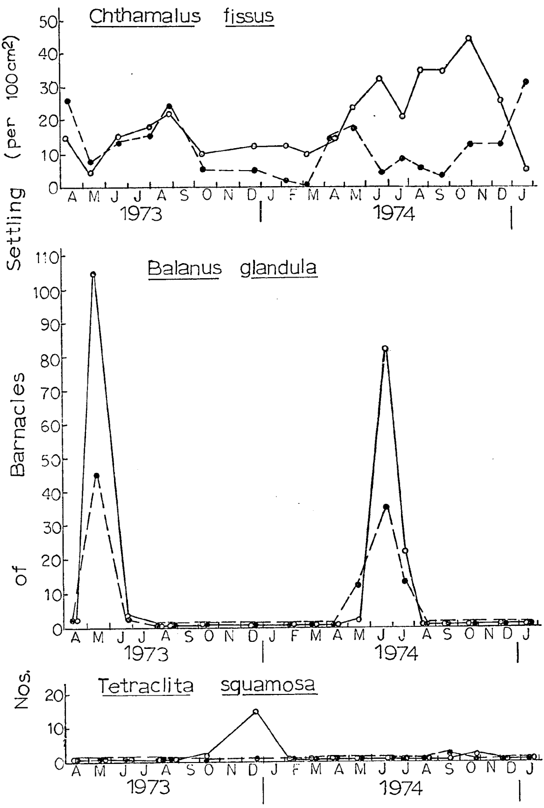

Tetraclita squamosa
Control
Nos. of Barnacles Settling (per 150cm^2)
50
40
30
20
10
0
area 1
area 2
A M J J A S O N D J F M A M J J A S O N D J
1973
1974
Outfall
20
10
0
A M J J A S O N D J F M A M J J A S O N D J
1973
1974

none was found in 1974. No T. squamosa settled in the 14 outfall quadrats in 1973 and only a very few in 1974. Given the extremely variable and patchy settlement of T. squamosa in the control areas, it would be wrong to conclude that the lack of settlement of this species in the outfall quadrats is the result of adverse conditions there. Probably it was a chance occurrence, since I observed T. squamosa successfully settling in other areas of the discharge canal in both 1973 and 1974.

Observations during dives on monthly collecting trips showed that only individual T. squamosa occasionally settled in shallow (less than 2 m) subtidal regions, and C. fissus and B. glandula were not found below about 1.5 feet below mean lower low water.

A summary of the seasonal patterns of settlement for the three species of barnacles is shown in Figure III-8. For each species the monthly means of barnacles settling in all outfall and in all control quadrats regardless of intertidal level were computed and converted for a standard 100 cm^2 surface area. Although there is a tendency for Chthamalus fissus to settle more frequently during summer and fall, settlement occurs year-round in quite variable numbers at all intertidal levels. Balanus glandula settlement is extremely seasonal with peak periods occurring in May, 1973 and June, 1974. The density of settlement of B. glandula is consistently high in both years compared to that of the other two species. Tetraclita squamosa also shows distinctly seasonal settlement with

Figure III-8. Comparative settlement summary of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa*. Means of all quadrats in outfall (closed symbols) and in control (open symbols) areas regardless of intertidal position, adjusted to 100 cm^2 surface area.


Chthamalus fissus
Balanus glandula
Tetraclita squamosa
Nos. of Barnacles Settling (per 100cm²)
0
10
20
30
40
50
60
70
80
90
100
110
A M J J A S O N D J F M A M J J A S O N D J
1973
1974

a peak in the fall, but apparently as a consequence of the patchy nature of settlement, the numbers of this species settling in marked quadrats in 1974 was very low. On the average, fewer barnacles of all three species settled in the outfall quadrats than in control quadrats.

D. DISCUSSION

Very little published information is available on settlement of Chthamalus fissus. Straughan (1971) reports that C. fissus had peaks in numbers settling in May and September, 1969 and June, 1970 on Santa Catalina Island, California, and settled at Santa Barbara in November, 1969. The northern congener, C. dalli, showed some settlement at Monterey, California, in December, 1971 (Haderlie, 1974), and is reported to settle mainly in late summer and early fall with some settlement year-round at neighboring Pacific Grove (Glynn, 1965). On the outer coast of Washington, C. dalli settles in about equal numbers (except for erratic heavy peaks) at all tidal levels from May through the summer, although in Puget Sound the set is lighter and begins later in summer (Dayton, 1971). C. challengeri in Japan broods from March through October and shows a corresponding season of settlement from May through December (Iwaki, 1975). C. depressus in Yugoslavia has a limited period of brooding in summer and, although I could find no published data on settlement in this species, it probably settles only in the fall. C. stellatus, however, has a limited period of settlement in fall in Great Britain even though it broods from early spring through early fall (Barnes, 1955; Connell, 1961a). C. stellatus also settles at all intertidal levels (Connell, 1961a), as does C. fissus and C. dalli (Dayton, 1971; Haderlie, 1974; personal observations). C. fissus in the present study showed year-round brooding activity with a broad peak season from spring through early fall (Chapter II). Although it tended to settle in greater numbers in summer and fall at all tidal levels, the amplitude of this season was not nearly as great as that of the brooding season. It is therefore difficult to extract a relationship between the pattern of brooding and settlement in species of this genus, and it is difficult to know whether this pattern of year-round settlement at Morro Bay is typical for C. fissus throughout its range.

Connell (1970) proposes that the season of settlement of Balanus glandula is related to water temperature: later, more restricted periods of settlement occur where temperatures are colder; and earlier, more prolonged settlement occurs in warmer waters. Thus, Connell observed that the main season of settlement of B. glandula at San Juan Island, Puget Sound, is from late May through August with some settling through October; and in an area of warmer water to the north at Ladysmith, Vancouver Island, Barnes and Barnes (1956) found settling in late March and nauplii in the plankton as late as September. However, in California this proposed relationship between settlement and temperature is unclear, perhaps because the trend of warmer water at more southerly latitudes is complicated by periods of upwelling of cold water. Thus, at Pacific Grove and Monterey, settlement begins in February or March and extends through October (Hewatt, 1935; Glynn, 1965; Haderlie, 1974). But to the south at Santa Barbara, *B. glandula* settles only between January and June (Connell, 1970; Straughan, 1971), and at La Jolla, settlement extends from January to May (Barnes and Barnes, 1956). The extremely narrow peaks of settlement of *B. glandula* observed in May and June in the present study in both warm-water outfall and control areas further confuse Connell's hypothesis. Other factors such as variations in phytoplankton productivity may be involved.

More important than the simple range of time over which individual *Balanus glandula* settle, however, is the apparently consistent observation at all locations where adequate samples are reported that there is a major peak of settlement, usually in late spring or early summer. Thus, Dayton (1971) reports that heavy settlement occurs on San Juan Island, Washington, from late May to July, although minor settling occurs as early as April to as late as September. At Pacific Grove, California, Hewatt (1935) showed only 95 *B. glandula* settling per cleared quadrat from about late February to early March, but 2,031 settled in March and April followed by additional minor settling in summer and fall. Glynn (1965) showed some minor settlement in the same region during much of the year but reported a large crop of new barnacles in September, indicating a peak of settlement in late summer. When examined in this fashion, these observations are much more consistent with the restricted season of settlement found in the present study. Like *Verruca stroemia*, *B. glandula* shows a seasonal pattern of settlement which is apparently a "modified version" of those patterns shown by such boreo-arctic species as *Balanus balanoides*, *B. hameri*, and *B. balanus*; these have a single settlement in spring capitalizing on seasonal food availability (Barnes, 1963; Barnes and Barnes, 1954; Barnes and Powell, 1953; Crisp, 1954). *Verruca stroemia* has a main spring peak followed by minor settling into summer (Barnes and Stone, 1973), and *B. glandula* may show an extension of this trend with minor settlement both earlier and later than the major peak.

Reports from other areas confirm the present finding that *B. glandula* settles in all but the highest intertidal (splash) zone (Connell, 1970; Dayton, 1971; Hewatt, 1935); it is similar to *B. balanoides* in this respect (Connell, 1961b). Dayton (1971) showed that in protected areas about equal numbers of *B. glandula* settle at all levels, but in areas of wave exposure, settlement tends to be greater at higher levels. This differs from the present pattern of much greater settlement in low zones in the protected areas at Morro Bay.

Little published information on settlement of *Tetraclita squamosa* is available. Hewatt (1935) showed a large settlement of *T. squamosa rubescens* in late fall or early winter at Pacific Grove, California, and Haderlie (1974) found *T. squamosa elegans* settling in the lower intertidal zone on pilings during fall at Monterey, California. Also at Pacific Grove, I have found T. squamosa rubescens settling in patches of three to 50 barnacles during late October, 1975 in the lower mid-intertidal zone. These findings agree with those of the present study that T. squamosa settles in the late fall in the low intertidal zone. The patchy nature of settlement of T. squamosa is very similar to that found in Balanus cariosus at San Juan Island, Washington, where B. cariosus has localized recruitment from May to July and is also patchy in space and in time from year to year (Dayton, 1971).

The reduced settlement of all three species in the outfall could perhaps be partly explained by peculiarities of the currents in the outfall, because the distribution of cyprids laterally and vertically in the water column is strongly related to currents (De Wolf, 1973). Although currents are very swift in the discharge canal, an eddy current frequently occurring next to the marked quadrats often produces decreased water movement, and it is possible that the reduced current would not keep cyprids up in the water column. On the other hand, Crisp (1953) studied the behavior of cyprids of Balanus balanoides and Elminius modestus in relation to water movement, and he found that maximum attachment occurs at velocities just great enough for the cyprid to maintain position by swimming against the current. Cyprids can migrate in all directions when exposed to moderate currents, but do so only with difficulty when velocities are high. Further, it should be noted that current velocities in all of the control areas are much less than those in the outfall. Another possible explanation is that cyprids passing through the condenser tubes of the power plant are killed or damaged, as observed in other plankton at other power plants (e.g., Carpenter, *et al*., 1974). Icanberry and Adams (1974) measured mortality of plankton passing through several power plants including that at Morro Bay, and they estimate cyprid mortality from entrainment to be around 2%, which is insufficient to account for the observed differences in settlement densities. It is more likely that the variability of individual quadrats with the peculiarities of spatial and temporal variations of settlement in each species could account for most of these differences. Thus, in the control areas the erratic settlements of *C. fissus* at all levels and months, the variable densities of *B. glandula* settling in the lower areas, and the patchy recruitment of *T. squamosa* all make it improper to conclude that conditions in the outfall are detrimental for settlement of these species.

Although the biology of the larval stages of the three species discussed here has not been studied, several general points about the planktonic period can be deduced by comparing the brooding pattern (see Chapter II) of a species with its settlement pattern. Thus, the sharp peak of brooding in August for *Tetraclita squamosa* is followed by a peak of settlement in October or November, indicating a larval life of about two to three months. Although *Balanus glandula* releases nauplii into the plankton several times from about January to May, it has only a single sharp peak of settlement in May or

June. This suggests that either B. glandula has a remarkable ability to delay metamorphosis until some general clue induces settlement, or there is a great loss of larvae due to hatching at the wrong time; and it is difficult to know what the environmental cue for settlement is if cyprids capable of settlement are present over such a long period. Chthamalus fissus releases larvae during much of the year and settles year-round, so that it is difficult to conclude much about the length of the planktonic period in this species. Because I do not know where larvae released by the Morro Bay populations go, where the cyprids settling at Morro Bay came from, these conclusions about the planktonic period remain highly speculative.

CHAPTER IV. GROWTH

A. INTRODUCTION

Barnacles generally grow very rapidly for a period following settlement, and then the growth rate becomes more moderate as size increases (Barnes and Barnes, 1959). Often there are seasonal growth patterns. For example, a number of temperate species of barnacles show a pattern of marked growth during spring and summer when food is available, but little or no growth during fall and winter (Barnes and Barnes, 1959). This annual pattern holds for Balanus balanoides, B. balanus, B. crenatus, Elminius modestus, and Verruca stroemia (see Barnes, 1953, 1955, 1958; Barnes and Barnes, 1954, 1962; Barnes and Powell, 1953; Crisp, 1954; and others). Growth in the north temperate species, Chthamalus stellatus, however, is more continuous, with the seasonal decreased rate during the winter (Barnes, 1956). Extrapolating from experimental manipulations of submergence time and food supply, the seasonal rhythm of growth in barnacles might be expected to be much less pronounced in warmer and in deeper waters where food supply is more constant (Barnes, 1958; Barnes and Barnes, 1959, 1962).

With adequate food supply, several species of barnacles often attain nearly their full size in the first growing season and show very little additional growth in subsequent years. This holds true for Balanus crenatus (Barnes and Powell, 1953; Haderlie, 1974), Verruca stroemia (Barnes, 1958), and Elminius *modestus* (Crisp and Patel, 1961). Other species, such as *Balanus balanoides* (Barnes and Powell, 1953) and *B. glandula* (Barnes and Barnes, 1956; Connell, 1970), grow rapidly in the first season but may also have substantial growth in subsequent years. Growth relative to full size is more gradual and continuous over several years in many of the larger barnacles, such as *Balanus balanus* (=*B. porcatus*) and *B. hameri* (Crisp, 1954), *B. carriosus* (Dayton, 1971), and *B. nubilus* (personal observations). *Chthamalus stellatus* also shows a slow and continuous growth over several years, even though the size of this species is always small (Barnes, 1956).

The purpose of this chapter is to compare the growth rates of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* at three intertidal levels in the warm-water outfall and in control areas unaffected by the discharge of a power plant. Crisp (1960) has shown that the basal diameter is both an easy measurement and a good parameter of size in barnacles indicating space occupied and biomass; in the present study changes in basal diameter were observed in barnacles occurring in permanently marked quadrats. The growth rates established for these species will then be used in Chapter V on demography to relate size-specific fecundity to age.

B. MATERIALS AND METHODS

These growth studies were conducted at the Pacific Gas and Electric Company power plant at Morro Bay, California, and utilized the same permanently marked quadrats established for the settlement studies in Chapter III. These 10 x 15 cm quadrats were positioned at high, middle, and low intertidal levels in the outfall and in control areas unaffected by the warm-water discharge. Details of the locations of these quadrats have been presented in the materials and methods of Chapter III and Figure III-1. Each quadrat was photographed monthly from late summer 1973 to mid-winter 1975. Barnacles in the photographs were measured to the nearest 0.1 mm along the rostral-carinal axis of the basal diameter; and these measurements were then adjusted to actual size by the proportion of the photographic print.

The growth of barnacles after settlement was followed in the successive monthly photographs. *Chthamalus fissus* does not have a sharp seasonal peak of settlement (Chapter III), so some individuals settling in each season were followed. There were many larger *C. fissus* initially present in the quadrats which had settled sometime before to the start of the study but which could not be aged. Growth of these individuals was measured by following two size groups of about 5 mm and 6 mm basal diameter respectively. *Balanus glandula* has a sharp peak of settlement in May or June (Chapter III), so distinct year-classes of this species could be identified. Two year-classes were followed from settlement during the study: that settling in 1974 was followed for seven months; and that settling in 1973 was followed for 19 months. Members of the 1972 year-class, which had settled the year prior to the beginning of the study, were readily identifiable and were followed from about age 14 months to 32 months. *B. glandula* which had settled prior to 1972 were lumped into a "1971 + year-class" and were followed from about age 27 months to 44 months. Thus, the growth of *B. glandula* could be determined for a time span of nearly four years. *Tetraclita squamosa* also has a seasonal peak of settlement in the fall, but recruitment of this species is patchy in space and in time from year to year (Chapter III). The seasonal settlement indicated that year-classes of this species could be followed, and members of four year-classes (from settlement in 1973 back to 1970) were identified by constructing a size-frequency histogram from all *T. squamosa* present in the February 1974 quadrat photographs; *T. squamosa* in these year-classes were followed for one year to provide growth information for a time span of more than four years.

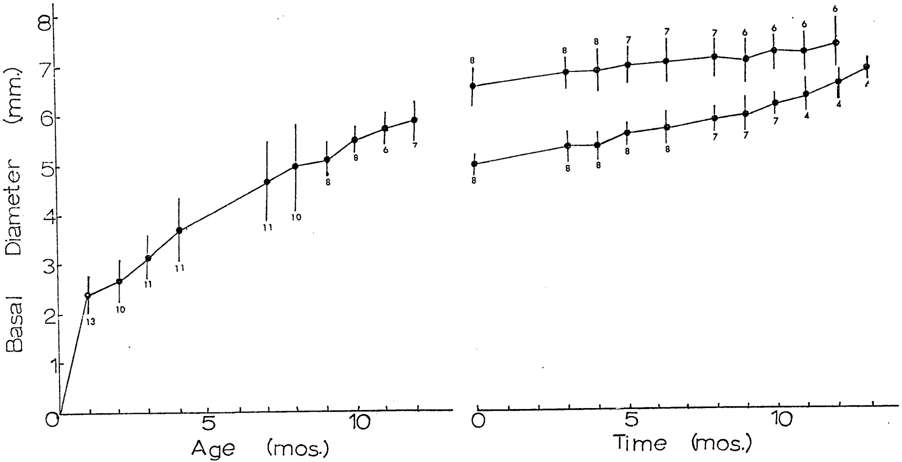
Several individuals of *Chthamalus fissus* and *Balanus glandula* which could be accurately measured and which lived for a fairly long time were followed in each quadrat. At frequent intervals the means and 95% confidence intervals of the basal diameters were calculated for each age-group in each quadrat. Because many barnacles died during the study, and because accurate measurements of some barnacles could not be taken in some months, the sample sizes in some quadrats at each age are not equal. For *T. squamosa* the mean and 95% confidence intervals were calculated for basal diameters of each age-group in all outfall quadrats and in all control quadrats in February, 1974 and again a year later. Other details of the treatment of data are presented in the results.

C. RESULTS

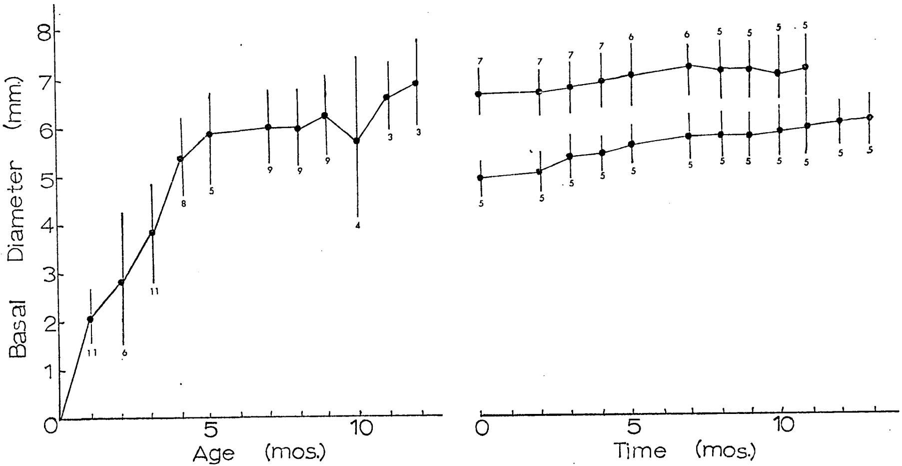
Growth of *Chthamalus fissus* from settlement and from two groups of larger barnacles which had settled prior to the start of the study is shown for each quadrat in Figures IV-1 to IV-8, and a summary plot of the means from all the quadrats is presented in Figure IV-9 on a different scale. *C. fissus* in all quadrats showed a similar pattern of rapid growth to about 3-4 mm basal diameter in the first six months, after which growth diminished to a more gradual, constant rate. *C. fissus* in the Outfall Middle quadrat (labelled "A" in Figure IV-9) grew exceptionally fast, attaining a mean basal diameter of 6 mm in five months. Growth in the other seven quadrats was more uniform, but by age ten months two groups of quadrats may be slightly different: one group (labelled "B" in Figure IV-9) including Outfall High, Outfall Low, Control Middle, and Control Low #1 had larger mean diameters (5 mm) than the other group (labelled "C" in Figure IV-9) including control quadrats High #1, High #2, and Low #2, which had means of about 4 mm. These differences in initial growth rates were not maintained in the growth of the two groups of larger barnacles, which showed very uniform gradual increases in basal diameter. Only *C. fissus* in Control Low #2 quadrat (labelled "D" in Figure IV-9) in the 5 mm group did not show any growth, and there were no larger *C. fissus* in Control High #1 quadrat. In general, *C. fissus* growing in the outfall tended to be larger than those in the control areas. However, because the larger barnacles did not show

Figures IV-1 through IV-8. Growth of Chthamalus fissus in each outfall and control quadrat. Mean basal diameter at each age is plotted, and sample sizes and 95% confidence intervals are shown. See text for further explanation.

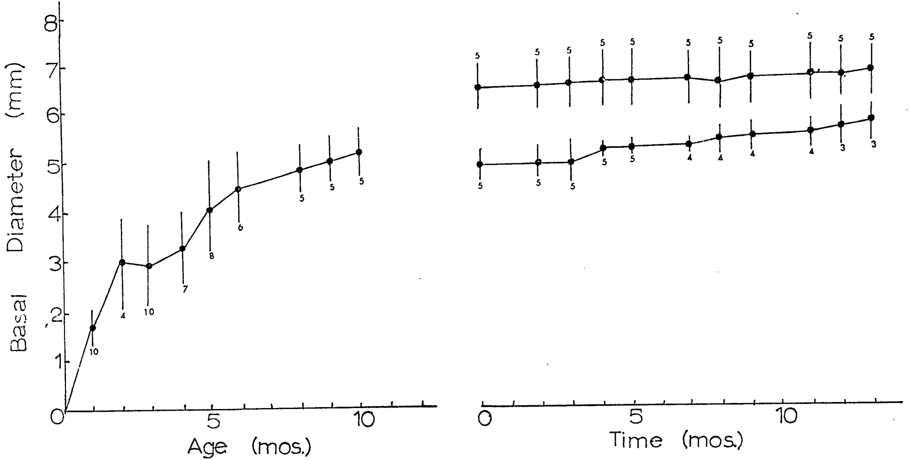
<u>Chthamalus</u> <u>fissus</u> Outfall High



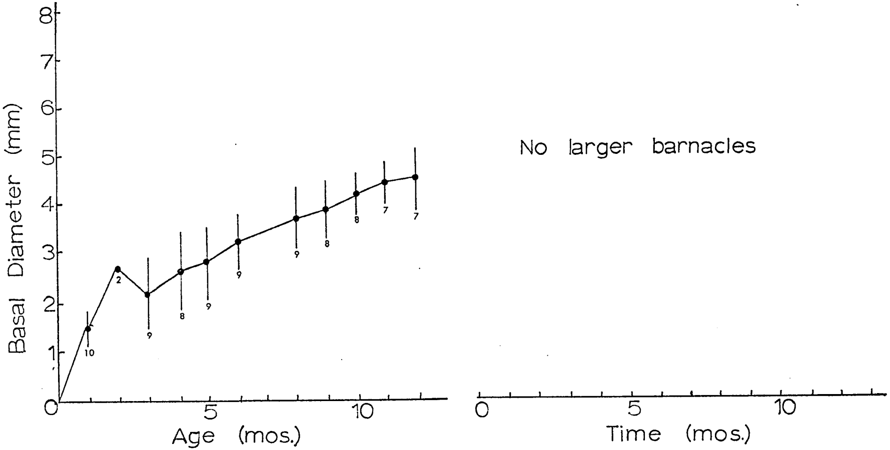
Chthamalus fissus Outfall Middle



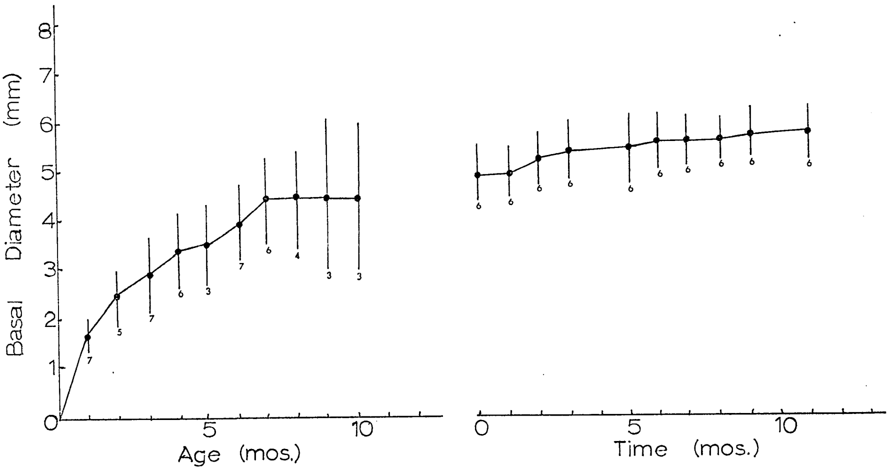
Chthamalus fissus Outfall Low



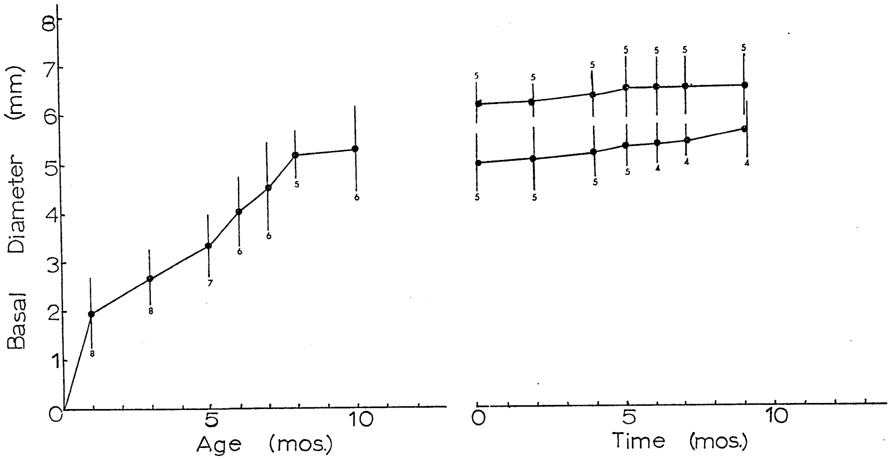
Chthamalus *fissus* Control High 1



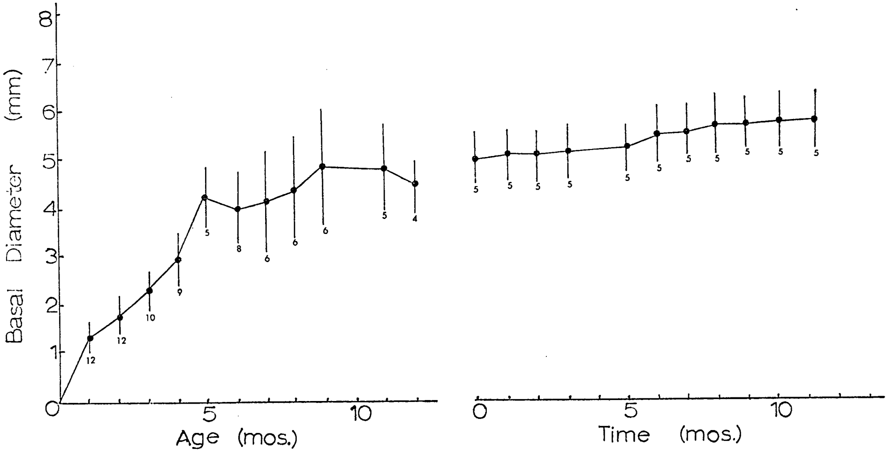
Chthamalus fissus Control High 2



Chthamalus fissus Control Middle



Chthamalus fissus Control Low 1



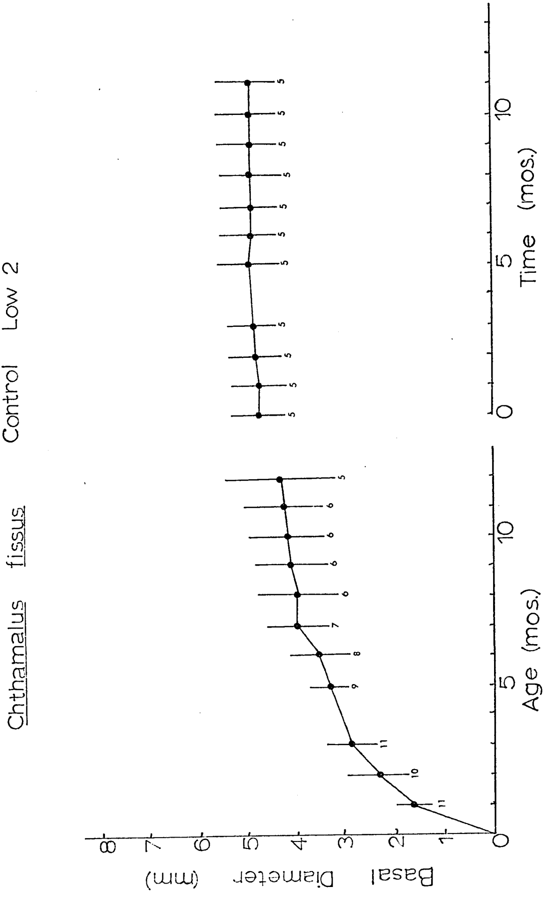
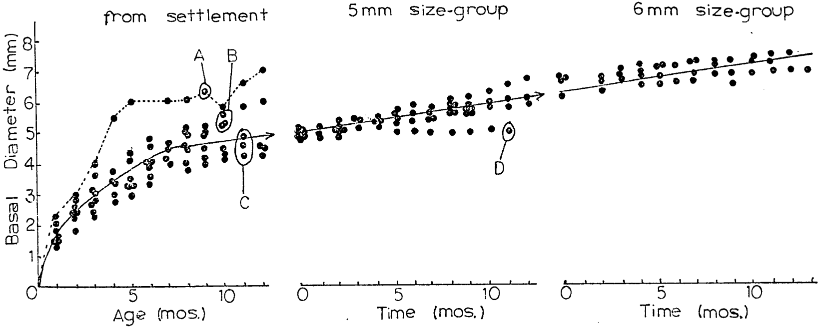

Chthamalus fissus
Control Low 2
Basal Diameter (mm)
0
1
2
3
4
5
6
7
8
Age (mos.)
0
5
10
Time (mos.)
0
5
10
11
10
11
9
8
7
6
6
6
6
5
5
5
5
5
5
5
5
5
5
5
5

Figure IV-9. *Chthamalus fissus* growth summary. Mean points from all the quadrats are plotted. A = Outfall Middle quadrat; B = Outfall High, Outfall Low, Control Middle, and Control Low #1 quadrats; C = Control High #1, Control High #2, Control Low #2 quadrats; and D = Control Low #2 quadrat. See text for further explanation.



CHTHAMALUS FISSUS GROWTH SUMMARY

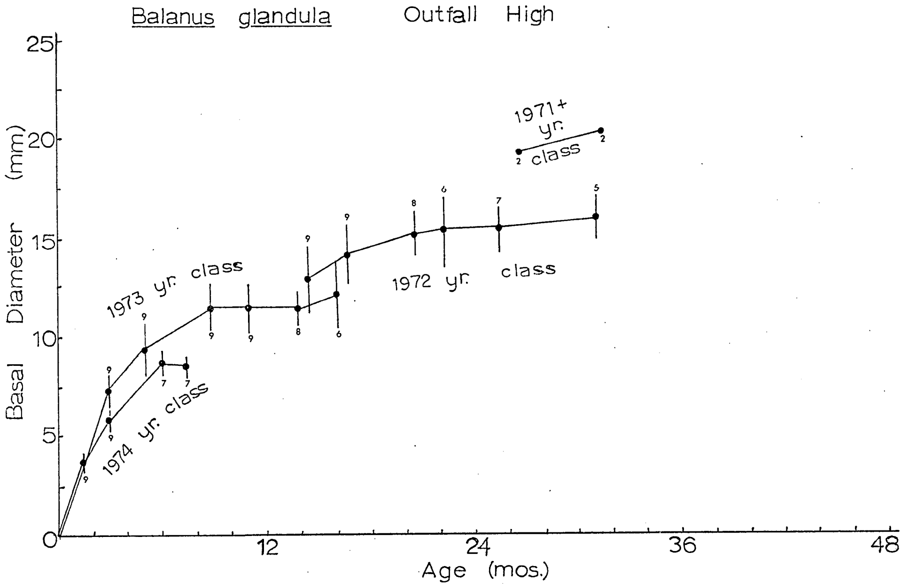
any important differences in growth, because there was no discernible pattern of quadrants with faster initial growth, and because the growth rates were quite variable, no significance was attributed to the differences in growth rates between quadrats. Therefore, a single growth curve for C. fissus was derived from the mean points in Figure IV-9 by fitting by eye the growth rate up to seven months and computing a linear regression from the points after seven months excluding the Outfall Middle quadrat and assuming a continuum of growth to the two groups of larger barnacles. The regression computed from these equally-weighted points is:

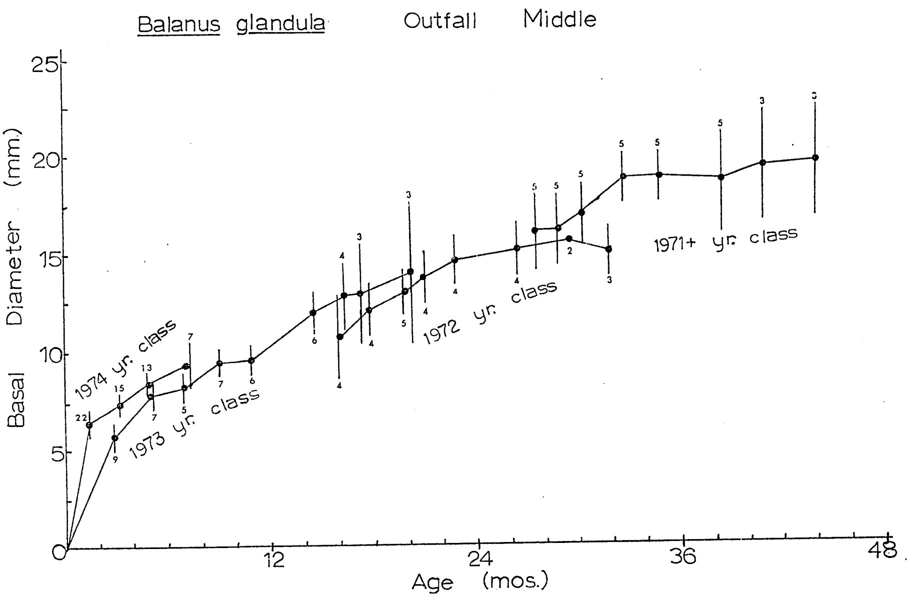
$$Y = 0.10X + 3.73$$

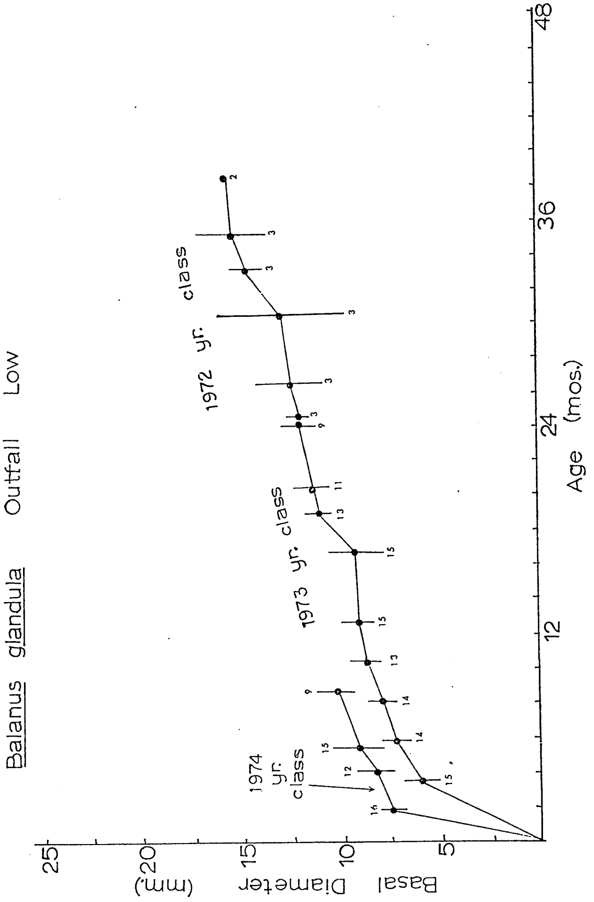
where Y = basal diameter in mm, X = age in months. The standard error of the slope = ± 0.04 and of the intercept = ± 0.79. The regression coefficient (r) = 0.88.

Growth of Balanus glandula in each quadrat is shown in Figure IV-10 to IV-17, and a summary plot of the means from all quadrats is presented in Figure IV-18. B. glandula in all quadrats show a similar pattern of extremely rapid growth to about 5.5 mm basal diameter in the first two months and to about 7.5 mm in the first five months after settlement. Although highly variable, the growth rate then diminishes and becomes more gradual. In all quadrats there is quite good correspondence in growth rates between year-classes, and there are no important differences in growth between outfall and control quadrats or between quadrats at different intertidal levels. Therefore, a single growth curve for B. glandula

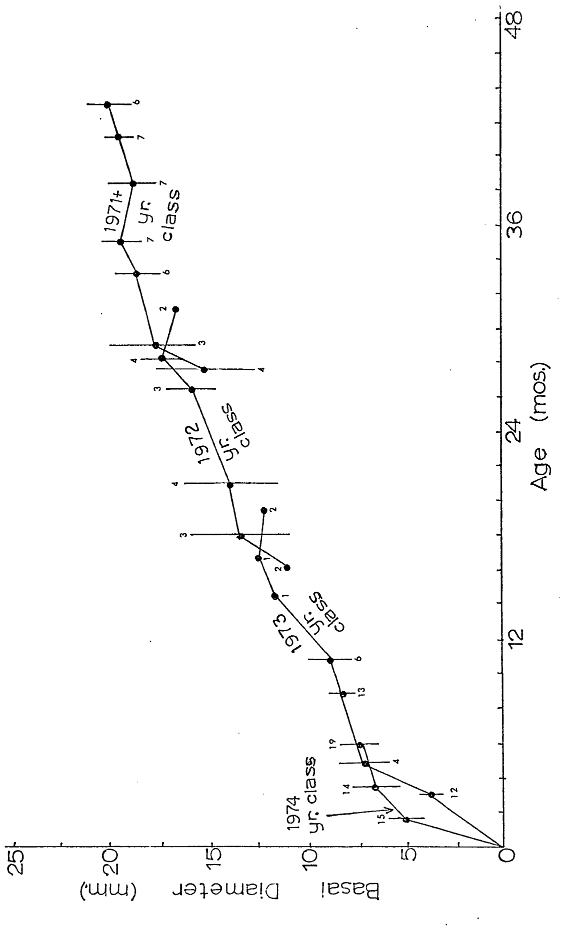
Figures IV-10 through IV-17. Growth of Balanus glandula in each outfall and control quadrat. Mean basal diameter at each age is plotted, and sample sizes and 95% confidence intervals are shown. See text for further explanation.


Balanus glandula Outfall High
Basal Diameter (mm)
0
5
10
15
20
25
Age (mos.)
12
24
36
48
1971+ yr. class
2
2
1972 yr. class
9
9
8
6
7
5
1973 yr. class
9
9
9
9
9
8
6
1974 yr. class
9
7
7

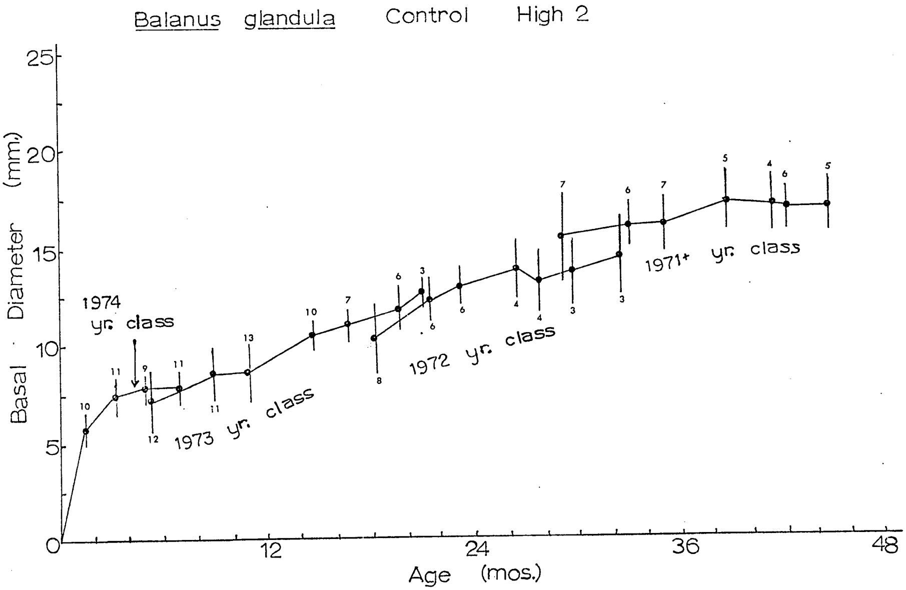

Balanus glandula Outfall Middle
Basal Diameter (mm.)
25
20
15
10
5
0
12
24
36
48
Age (mos.)
1974 yr. class
1973 yr. class
1972 yr. class
1971+ yr. class

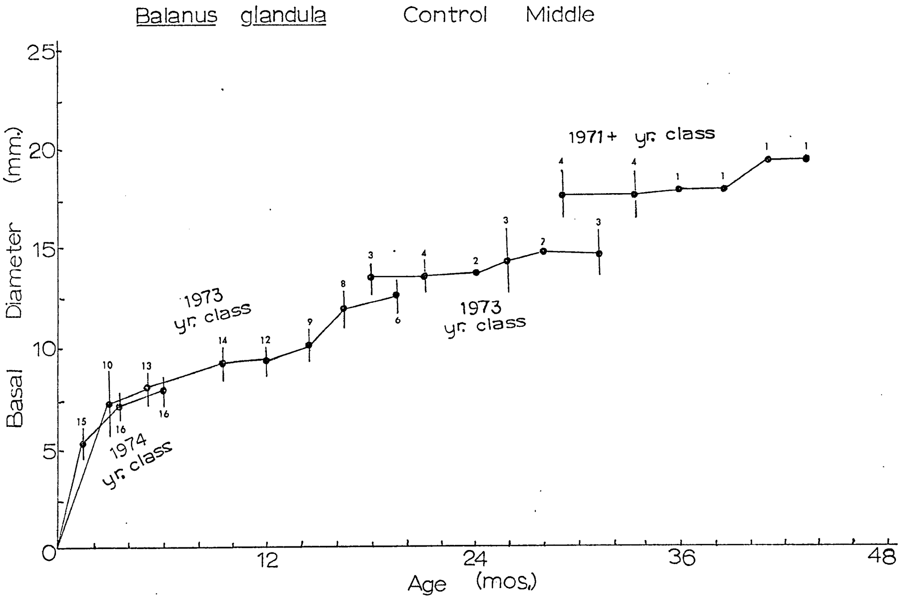


Balanus glandula Outfall Low



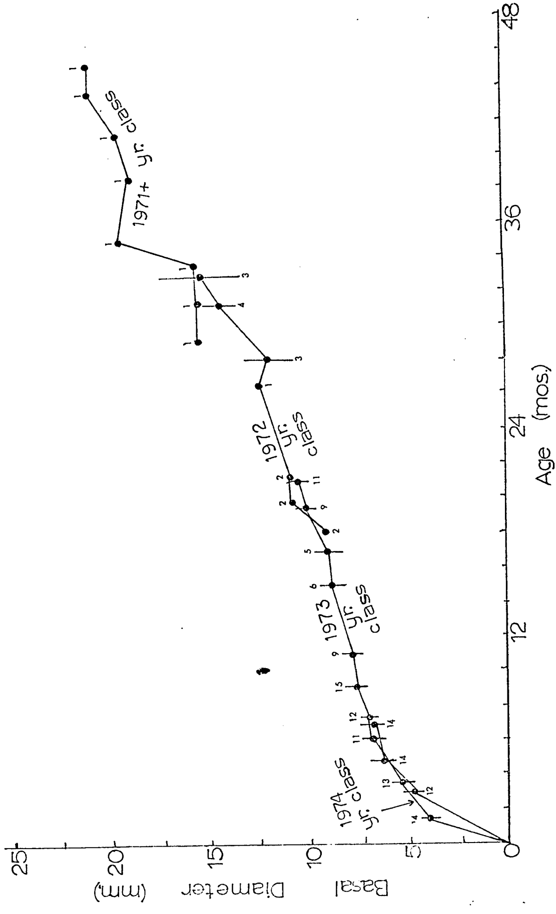
Balanus glandula Control High 1

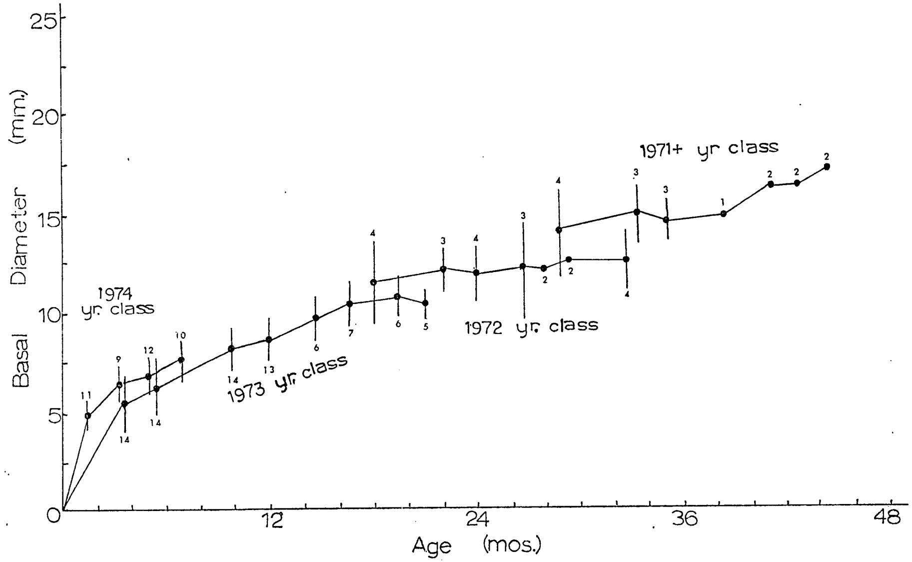

Balanus glandula Control High 2
Basal Diameter (mm.)
0
5
10
15
20
25
Age (mos.)
12
24
36
48
1974 yr. class
1973 yr. class
1972 yr. class
1971+ yr. class
10
11
9
11
11
12
13
10
7
8
6
3
6
6
4
4
7
3
3
6
7
5
4
6
5



Balanus glandula Control Middle

Balanus glandula Control Low 1

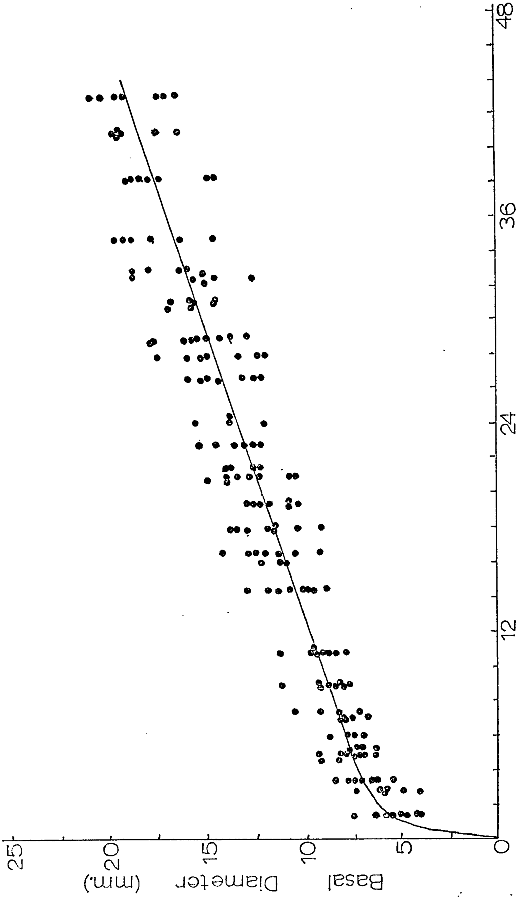




Balanus glandula Control Low 2

Figure IV-18. *Balanus glandula* growth summary. Mean points from all the quadrats are plotted. See text for further explanation.

Balanus glandula Growth Summary



was derived from the mean points in Figure IV-18 by fitting by eye the growth rate up to four months and computing a linear regression from the points after four months. The regression computed from these equally-weighted points is:

$$Y = 0.03X + 6.19$$

where Y = basal diameter in mm, X = age in months. The standard error of the slope = ± 0.01 and of the intercept = ± 0.24. The regression correlation coefficient (r) = 0.86.

Size-frequency histograms for Tetraclita squamosa in the control and in the outfall quadrats are shown in Figure IV-19. The basal diameters plotted in this figure were measured from the February 1974 quadrat photographs. Four year-classes of barnacles can be clearly seen in the control population: that settling in fall 1973, in 1972, in 1971, and in 1970, or earlier. There was no settlement of T. squamosa in the outfall quadrats in fall 1973 (see Chapter III), and only three year-classes can be seen in this population: 1972, 1971, 1970, or earlier. The members thus identified in each of these year-classes were then followed for one year, and their growth along with that of the few T. squamosa which settled in the outfall quadrats in fall 1974 is shown in Figure IV-20. Apparently, there are differences in growth rates between the year-classes such that each old year-class had attained a larger mean basal diameter than younger year-class at an equivalent age. Comparing growth in the outfall and control populations, too few data are available for the outfall to compare early growth rates, but growth rates are nearly the

Figure IV-19. Size-frequency histograms for *Tetraclita squamosa* in the control and in the outfall quadrats measured from February 1974 quadrat photographs. See text for further explanation.

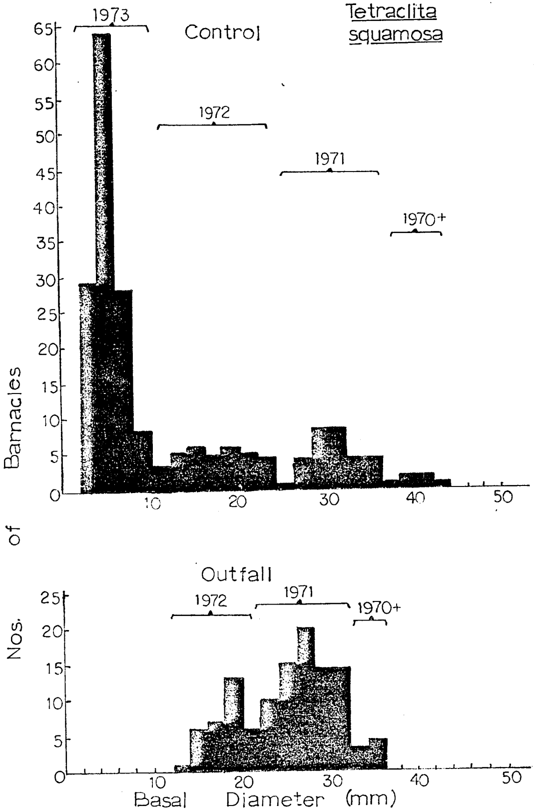
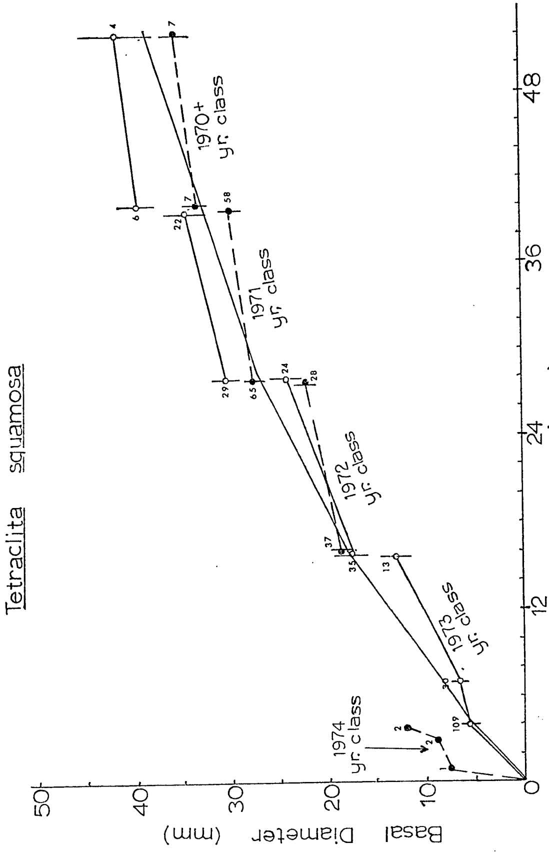

Tetraclita squamosa
Control
1973
1972
1971
1970+
65
60
55
50
45
40
35
30
25
20
15
10
5
0
10
20
30
40
50
Nos. of Barnacles
Outfall
1972
1971
1970+
25
20
15
10
5
0
10
20
30
40
50
Basal Diameter (mm)

Figure IV-20. Growth of <u>Tetraclita squamosa</u> in outfall (closed symbols) and control (open symbols) areas. Mean basal diameter at each age is plotted, and sample sizes and 95% confidence intervals are shown. See text for further explanation.


Tetraclita squamosa
Basal Diameter (mm)
0
10
20
30
40
50
Age (mos.)
0
12
24
36
48
1974 yr. class
1973 yr. class
1972 yr. class
1971 yr. class
1970+ yr. class
1
2
2
109
30
13
35
37
24
28
29
65
22
7
58
6
4
7

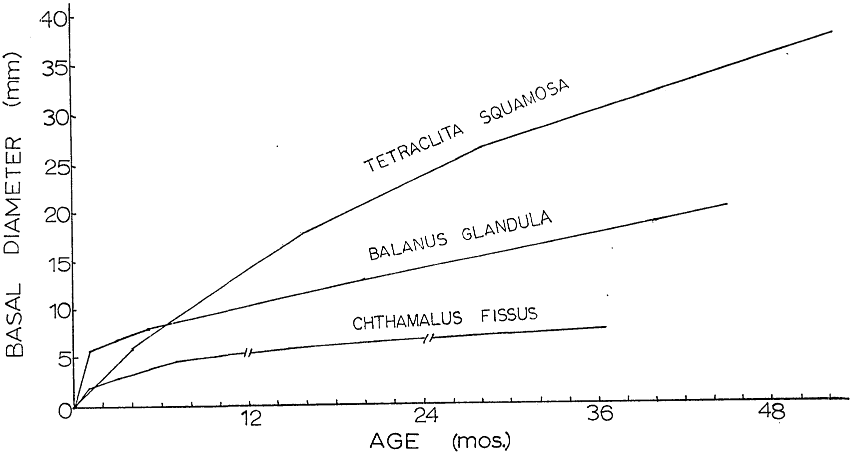
same in the 1972 year-class and the outfall barnacles perhaps grew somewhat more slowly and/or started at a smaller size than the controls in older year-classes. In spite of these differences, a single growth curve for T. squamosa was derived by plotting the mean basal diameter for all barnacles at equivalent ages regardless of year-class or outfall or control population. The curve is shown in Figure IV-20.

A summary graph comparing the derived growth curves for each of the three species is shown in Figure IV-21. Clearly, Tetraclita squamosa grows to a larger size than Balanus glandula, which in turn grows to be larger than Chthamalus fissus: at age 36 months T. squamosa is about 31 mm in basal diameter, B. glandula is about 18 mm, and C. fissus is about 7 mm. Of course, growth may continue beyond 36 months, and the growth rates in individuals of each species are highly variable. The largest individuals of each species which I observed during the course of this study were: 56 mm for T. squamosa; 28 mm for B. glandula; and 12 mm for C. fissus. B. glandula has the fastest initial growth rate, followed by C. fissus, and then T. squamosa. Relative to its "full size," C. fissus grows the fastest, followed by B. glandula and T. squamosa. There was no obvious seasonal aspect to growth in any of the three species.

D. DISCUSSION

A detailed explanation of the mechanism of shell and cuticle deposition by specialized regions of the hypodermis in barnacles is presented by Bourget and Crisp (1975b).

Figure IV-21. Summary comparison of the derived growth curves for *Tetraclita squamosa*, *Balanus glandula*, and *Chthamalus fissus*.

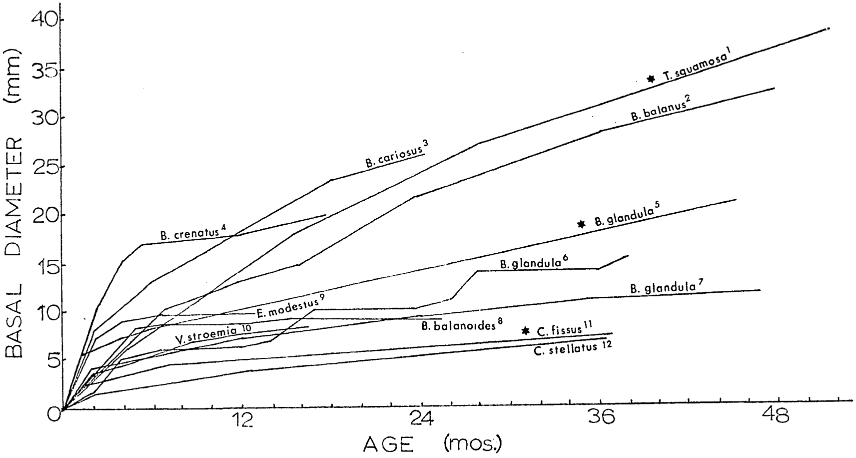

BASAL DIAMETER (mm)
40
35
30
25
20
15
10
5
0
12
24
36
48
AGE (mos.)
TETRACLITA SQUAMOSA
BALANUS GLANDULA
CHTHAMALUS FISSUS

Unlike the growth of malacostracans, growth in cirripedes is apparently not closely linked to the molting cycle (Costlow and Bookhout, 1953; 1956), and the rate of shell growth is relatively independent of the molt cycle and body growth (Costlow and Bookhout, 1957). The non-calcified cuticular exoskeleton is molted frequently. The body may or may not grow at each molt, and the shell grows whether or not body growth or molting is occurring. Also unlike malacostracans, which show much-increased oxygen consumption prior to ecdysis, barnacle respiration is independent of the molt cycle and is probably largely related to the metabolism of the tissues depositing calcium in the shell (Costlow and Bookhout, 1958). Like the control of molting in malacostracans, molting activity in barnacles is apparently regulated by crustecdysone (Tighe-Ford and Vaile, 1972), although this conclusion may be an artifact of the wound produced by the injection procedure for applying crustecdysone to a barnacle (Tighe-Ford and Vaile, 1974). Barnacles may have a period of anecdysis during brooding similar to that in malacostracans (Crisp and Patel, 1958; 1960; 1961). However, Barnes (1962) did not find a major effect of brooding on molting in the laboratory, and he suggests that the reduced molting frequency during a short period immediately following the onset of brooding is caused by a debilitated condition resulting from the discharge of gametes. No relationship of growth to reproductive season was observed in any of the three species in the present study, and individuals of each species were observed molting during their respective brooding season. However, it is noteworthy that the timing of recruitment in Balanus glandula and Tetraclita squamosa is such that the initial growth spurt following settlement is well in advance of the brooding season. B. glandula settles in May or June (Chapter III), and virtually all individuals of this species begin to brood in their first season in December or January, when they are about 7-8 mm in size. T. squamosa settles in October or November (Chapter III) and is about 11-12 mm in size by its first brooding season, at which size it is only beginning to mature sexually; and full reproductive maturity is not reached until it is about 18 mm in size, corresponding to about 19 months old and the time of the second potential brooding season in the juveniles second summer. (See Chapter II, Figure II-4 on brooding frequency vs. basal diameter, and Chapter V on fecundity schedules.) Chthamalus fissus apparently is able to begin to brood as soon as it is 1-2 mm in size, or about two months old.

Bourget and Crisp (1975a) present an outline summarizing many experimental studies on environmental factors influencing growth in barnacles. Basically, growth is largely regulated by food availability and by other environmental factors which affect, or are correlates of, food availability, such as: season, current, orientation to current, time of submergence, position on shore, quality of food, and parasitism. Other environmental factors, such as light and temperature, apparently do not have important or consistent effects on growth. It is not surprising, therefore, that there is no major difference in the growth of barnacles in the warm-water outfall and the control areas of the present study, since the food supply to the two areas is probably nearly the same in spite of the large temperature differential. The energetic requirements of barnacles in the two areas may be very similar because preliminary studies by me on Balanus glandula indicate that the respiratory rate of the outfall population measured at 20°C shows perfect acclimation compared to the control population measured at 12°C. It is unexpected, however, that there is no major difference in growth of barnacles at the three intertidal levels in the present study, since barnacles in the high intertidal zone have less submergence time to feed than those in the low zone. In the low zone higher densities of barnacles and crowding by other organisms may counter the longer feeding time and may reduce growth by physical crowding, by interference with the cirral feeding mechanism, and by greater competition for food (Connell, 1961a; Barnes, 1955; 1961; Barnes and Barnes, 1959; and others). Close crowding may cause barnacles to grow in a tall, columnar shape (Connell, 1961b; Haderlie, 1974; and many others), but I found this generally not to be the case in the present study, where barnacles usually died before the growth form changed under such crowded conditions (see Chapter V). Seasonal variation in food availability is pronounced enough at Morro Bay to regulate the brooding cycle of Chthamalus fissus (see Chapter II), so it is surprising that a seasonal variation in growth was not found in any of the three species in the present study. In addition to food availability, reduced salinity is an environmental factor which may restrict growth in barnacles, perhaps by limiting deposition of calcium and other minerals (Gordon, *et al.*, 1970; personal observations on *Balanus glandula* in San Francisco Bay).

Growth curves for several species of barnacles are shown in Figure IV-22 for comparison with the curves derived in the present study for *Tetraclita squamosa*, *Balanus glandula*, and *Chthamalus fissus*. These curves are extracted from growth data in the literature: species for which at least one year of data is averaged for several individuals were selected. Where more than one growth curve for a species has been published, the data were usually averaged to derive a single curve. However, two published growth curves for *Balanus glandula* are shown. *B. glandula* at San Juan Island, Washington, do not grow as large as those in the present study at Morro Bay, but the shape of the growth curve for the Washington population is otherwise very similar to that in the present study (Connell, 1970). *B. glandula* from Vancouver Island, British Columbia, and La Jolla, California, grow nearly as large as those in the Morro Bay population but, unlike those at Morro Bay, they show a pronounced seasonal cycle of rapid growth in spring and summer with no growth in winter (Barnes and Barnes, 1956). *Balanus balanoides* may also show a similar seasonal pattern of growth (Barnes and Barnes, 1959), and the growth curve for this species is similar to that of *B. glandula*,

Figure IV-22. Growth curves for several species of barnacles for comparison with the curves derived in the present study for *Tetraclita squamosa*, *Balanus glandula*, *Chthamalus fissus*. Curves are extracted from growth data in the literature. Species for which at least one year of data is averaged for several individuals were selected. Where more than one growth curve has been published for a species, the data were averaged to derive a single curve. (1) *Tetraclita squamosa*: present study; (2) *Balanus balanus*: averaged from Crisp, 1954; Barnes and Barnes, 1954; (3) *Balanus cariosus*: Dayton, 1971; (4) *Balanus crenatus*: averaged from Barnes, 1953; Barnes and Powell, 1953; and Haderlie, 1974; (5) *Balanus glandula*: present study; (6) *Balanus glandula*: Barnes and Barnes, 1956; (7) *Balanus glandula*: Connell, 1970; (8) *Balanus balanoides*: Barnes, Barnes, and Finlayson, 1963; (9) *Elminius modestus*: Barnes and Barnes, 1962; (10) *Verruca stroemia*: Barnes, 1958; (11) *Chthamalus fissus*: present study; (12) *Chthamalus stellatus*: Barnes, 1956.


BASAL DIAMETER (mm)
0
5
10
15
20
25
30
35
40
AGE (mos.)
12
24
36
48
★ T. squamosa¹
B. balanus²
B. cariosus³
B. crenatus⁴
★ B. glandula⁵
B. glandula⁶
B. glandula⁷
B. balanoides⁸
E. modestus⁹
V. stroemia¹⁰
★ C. fissus¹¹
C. stellatus¹²

although the amount of additional growth after the first year is much less than *B. glandula* (Barnes, Barnes, and Finlayson, 1963). No published growth data is available for *Tetraclita squamosa*, but growth in this species appears to be very similar to that in *Balanus cariosus* (Dayton, 1971) and *B. balanus* (Crisp, 1954; Barnes and Barnes, 1954). These three species get to be quite large, and their growth is continuous for several years. I could find no published growth studies on *Chthamalus fissus*; however, *C. stellatus* has a very similar growth pattern: both of these small barnacles have gradual, continuous growth. *Elminius modestus* and *Verruca stroemia* both grow rapidly and attain "full size" in their first year, so that their growth curves tend to level out after the initial growth spurt (Barnes and Barnes, 1962; Barnes, 1958). *Balanus crenatus* has a similar pattern of growth to "full size" in its first year, and this species has a remarkably fast initial growth rate before the curve levels out (Crisp, 1954; Barnes and Barnes, 1954). Thus, there seems to be four main patterns of growth in barnacles: (1) gradual and continuous growth to small size (*Chthamalus* spp.); (2) continuous growth over several years to large size (*Tetraclita squamosa*, *Balanus cariosus*, *B. balanus*); (3) rapid initial growth followed by continued growth at a more moderate rate (*Balanus glandula*, *B. balanoides*); and (4) very rapid initial growth with little or no additional growth (*Balanus crenatus*, *Elminius modestus*, *Verruca stroemia*).

CHAPTER V. DEMOGRAPHY

A. INTRODUCTION

The demographic characteristics of a population are described by its survivorship (l_x) and fecundity (m_x) rates, which are conveniently expressed in the format of a life table. From the schedules of its life table, several important parameters of a population's potential for growth can be computed: $l_x m_x$, the survivorship-weighted fecundity for each age group; R_o, the net reproductive rate per generation; G, the mean generation time; and r_m, the intrinsic rate of increase for the population for the particular environmental conditions. Excellent discussions of these population parameters may be found in Mertz (1970) and Krebs (1972).

Barnacles have long been viewed as nearly ideal animals for demographic studies because their intertidal, sessile habit make their populations readily accessible and easy to census. Hatton (1938) collected extensive data on survivorship of Balanus balanoides, and Deevey (1947) analyzed Hatton's data in life table format in a classic paper examining the methodology of life tables and patterns of survivorship schedules of a variety of animals. Connell (1961a,b) has extensively studied the survivorship of Chthamalus stellatus and Balanus balanoides and showed that the intertidal distributions of these two species can be largely explained by differential morality as a result of variable tolerance of physical factors, crowding, grazing, and predation. However, none of these previous studies included fecundity schedules in the life tables, making computation of the reproductive parameters of the populations impossible. Barnes and Barnes (1965; 1968) have presented many valuable data on egg size and numbers of eggs per brood in cirripedes. However, except for the boreo-arctic species *Balanus balanoides* and *B. balanus* which are known to produce only one brood per year, these data cannot be converted into a fecundity schedule without an estimate of the number of broods produced per year by a species; and Barnes and Barnes do not present survivorship data with their work. In an exemplary study, Connell (1970) presents life tables for *Balanus glandula* with both survivorship and fecundity schedules for eight years, and he presents experimental evidence on the effect of predation by snails as a major source of barnacle mortality. All of these studies on aspects of barnacle demography follow survivorship after settlement, ignoring the important, but difficult to measure larval period in the plankton.

The purpose of this chapter is to compare the demographic patterns of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa*. Post-settlement survivorship is assessed in permanently marked quadrats at high, middle, and low intertidal levels in the warm-water outfall and in control areas unaffected by the discharge of a power plant. A qualitative discussion of barnacle mortality in the study areas is presented. Fecundity schedules are estimated from egg counts per brood (this chapter), number of broods produced per year (from Chapter II), and size-age relationships (from Chapter IV).

Measurements of egg sizes are also given. Summary life tables comparing the demography of these species are presented, and several of the more important parameters of each population's potential for growth are computed and compared.

B. MATERIALS AND METHODS

These demographic studies were conducted at the Pacific Gas and Electric Company power plant at Morro Bay, California, and the survivorship aspects of the work utilized the same 150 cm^2 permanently marked quadrats established for the settlement and growth studies in Chapters III and IV. The quadrats were positioned at high, middle, and low intertidal levels in the outfall and in control areas unaffected by the warm-water discharge. Details of the locations of these quadrats have been presented in the Materials and Methods section of Chapter III and in Figure III-1. Survivorship of _Balanus glandula_ and _Tetraclita squamosa_ was followed in standard 150 cm^2 quadrats, however, the survivorship of _Chthamalus fissus_ was followed in smaller 30 cm^2 subquadrats in the center of each standard quadrat. Each quadrat was photographed monthly from late summer 1973 to mid-winter 1975. In addition, numbers of _B. glandula_ settling in the May 1973 peak were scored for each quadrat (see Chapter III). Each barnacle in the quadrats was given an identifying number and its survival was followed from its appearance after settlement or from the start of the study, and the month of each mortality was recorded. Deaths were usually easily observed because the barnacle simply disappeared from the quadrat, often, but not always, leaving a scar. Occasionally empty shells remained in the quadrats for several months, but these were still readily recognized as dead barnacles because they lacked scuta and terga closing the shell opening.

Chthamalus fissus does not have a sharp seasonal peak of settlement (Chapter III), so only those individuals which settled during the course of the study could be aged. There were many larger *C. fissus* initially present in the quadrats which had settled some time before the start of the study but which could not be aged. Survivorship of these individuals was followed as a group in each quadrat from the start of the study, and their survivorship schedule was treated as an extension of the schedule obtained for the aged individuals (see Results). *Balanus glandula* has a sharp peak of settlement in May or June (Chapter III), so distinct year-classes of this species could be identified and all individuals aged. Two year-classes were followed from settlement during the study: that settling in 1974 was followed for seven months; and that settling in 1973 was followed for 19 months. Members of the 1972 year-class, which had settled the year prior to the beginning of the study, were readily identifiable and were followed from about age 14 months to 32 months. *B. glandula* which had settled prior to 1972 were lumped into a "1971+ year-class" and were followed from about age 27 months to 44 months. Thus, the survivorship rate of *B. glandula* could be determined for a time span of nearly four years. *Tetraclita squamosa* also has a seasonal peak of settlement in fall, but recruitment of this species is patchy in space and in time from year to year (Chapter III). The seasonal settlement indicated that year-classes of this species could be followed, and members of four year-classes (from settlement in 1973 back to 1970) were identified by constructing a size-frequency histogram from all T. squamosa present in the February 1974 quadrat photographs (see Figure IV-19). T. squamosa in these year-classes were followed followed for one year to provide survivorship information for a time span of more than four years; however, no T. squamosa settled in the outfall quadrats during 1973, so no survivorship data is available for the first 12 months for the outfall population. For comparative purposes and for life tables, survivorship rates of all three species were prorated from an arbitrary 1000 to compensate for variations in numbers of barnacles starting and settling during the study.

Fecundity schedules used in the life tables for each species were derived using the following information. Brood weight varies linearly with adult body weight and does not change significantly during the brooding season in each species (see Chapter II on reproductive effort). Estimates of the maximum number of broods produced by each species during the brooding season of the control population are derived in Chapter II: 16 broods for C. fissus; six broods for B. glandula; and three broods for T. squamosa. Basal diameter-age relationships are derived for each species in Chapter IV on growth. Although the linear growth curves so derived are adequate for estimating size-age relationships over the life span of C.

fissus and *B. glandula*, the curvilinear growth curve of the longer lived *T. squamosa* had to be extended in time by eye as shown in Appendix Figure V-A. Egg numbers per brood of a wide range of sizes of barnacles available for each of the three species were counted using a Model A Coulter Counter. Each brood was first placed in about 5 ml of a weak solution of protease in seawater for three days to dissociate the eggs from each other; although broods of late developmental stage readily dissociated, early-stage broods required the full three days to dissociate. The dissociated eggs of each brood were then fixed in formalin and run through the Coulter Counter, which was equipped with a 1000 µ apperture and which was modified with the help of Mr. Bruce Hargreaves to count continuously, so that more electrolyte solution was added until virtually every egg in each brood was counted. The basal diameter and dry body weight (exclusive of ovary, mantle chamber lining, and retractor muscles) were recorded for the parental barnacle of each brood, and linear regressions for the egg numbers per brood on body weight and on basal diameter were computed. Therefore, the fecundity schedule (m_x) for each species could be estimated as follows: for each age (x) the basal diameter was computed from the growth curve; the basal diameter was then used in the linear regression of egg number per brood on basal diameter to obtain an estimate of the egg numbers per brood at age (x); and finally the egg numbers per brood were multiplied by the number of broods per season to estimate the maximum number of eggs produced per season. In addition, the length and width of about five fresh eggs in each brood used in the egg counts were recorded and their embryonic stage of development was noted as early if light yellow or red in color, or late if dark brown with eye spots present.

It is important to note that these fecundity schedules are derived from barnacles collected at about mean lower low water at the collecting sites described in Chapter II, and it is assumed that these fecundities apply to the populations spanning the entire intertidal zone. This assumption was not tested; however, Barnes and Barnes (1968) and others have shown that egg numbers per brood are generally greater in the lower intertidal zone in some species of barnacles. This assumption is probably most valid for _T. squamosa_, which was found only in a narrow intertidal band compared to the other two species.

The methods used in computing the life tables and parameters of potential population growth follow Mertz (1970) and Krebs (1972). Additional details for these computations are given in the Results.

C. RESULTS

1. Survivorship.

The survivorship of _Chthamalus fissus_ in the five control quadrats is shown in Table V-1 and in the three outfall quadrats in Table V-2. Survivorship of those barnacles settling during the study is indicated by age in months, and survivorship of those which were already present in the quadrats at

Table V-1. Survivorship of *Chthamalus fissus* in 30 cm^2 control quadrats at three intertidal levels. Survival of barnacles settling during the course of the study is indicated for ages in months. Survival of barnacles already present in the quadrats at the start of the study is indicated in time in months from the start of the study.

Chthamalus fissus

SURVIVORSHIP IN CONTROL QUADRATS

Age (mos.)	HIGH 1	HIGH 2	MIDDLE	LOW 1	LOW 2
0	16	56	83	128	73
1	-	50	53	66	38
2	10	43	20	-	30
3	3	37	19	33	23
4	2	23	18	-	17
5	2	19	15	16	12
6	2	14	12	12	9
7	2	9	11	7	5
8	2	-	6	6	4
9	2	6	6	5	4
10	1	5	6	4	3
11	1	5	6	3	2
12	1	5	5	3	2
13	1	3	2	3	2
14	1	1	2	3	2
15	1	1	2	3	2
Time (mos.)					
0	113	78	151	34	103
1	111	77	133	12	101
2	-	77	-	9	100
3	108	76	117	-	81
4	-	72	113	5	-
5	104	71	93	-	31
6	76	70	93	4	19
7	71	57	93	4	17
8	61	-	81	3	11
9	57	49	67	3	11
10	48	49	56	1	11
11	33	48	-	1	5
12	23	47	44	1	5
13	-	-	-	1	2
14	2	45	40	1	2
15	2	44	37	1	2
16	-	-	-	-	1
17	1	-	-	-	1

Table V-2. Survivorship of <u>Chthamalus</u> <u>fissus</u> in 30 cm^2 outfall quadrats at three intertidal levels. Survival of barnacles settling during the course of the study is indicated for ages in months. Survival of barnacles already present in the quadrats at the start of the study is indicated in time in months from the start of the study.

Chthamalus fissus

SURVIVORSHIP IN OUTFALL QUADRATS

Age (mos.)	HIGH	MIDDLE	LOW
0	13	22	40
1	-	-	-
2	4	13	5
3	-	6	-
4	2	5	2
5	-	4	2
6	2	4	2
7	1	3	1
8	1	3	1
9	1	2	1
10	1	1	1
11	1	1	1
12	1	1	1
13	1	1	1
14	1	1	1
15	1	1	1
Time (mos.)			
0	48	96	28
1	48	-	28
2	47	93	28
3	45	93	-
4	44	93	21
5	44	93	19
6	44	92	18
7	44	92	18
8	42	91	-
9	42	89	10
10	42	-	2
11	42	85	2
12	39	40	2
13	39	16	2
14	18	13	2
15	-	13	2
16	12	13	2
17	11	10	2

Table V-3. Survivorship of Chthamalus fissus in high, middle, and low intertidal level quadrats summed from control and outfall areas. Survival of barnacles settling during the course of the study is indicated for ages in months. Survival of barnacles already present in the quadrats at the start of the study is indicated in time in months from the start of the study. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals, and the survivorship rate of the barnacles present in the quadrats at the start of the study is treated as an extension of the survivorship of the barnacles settling during the study. These extended prorated survivorship rates are plotted in Figure V-1.

Chthamalus fissus

SURVIVORSHIP AT HIGH, MIDDLE, AND LOW INTERTIDAL LEVELS (Outfall plus Control Quadrats)

Age (mos.)	HIGH	Pro-rated	MIDDLE	Pro-rated	LOW	Pro-rated
0	85	1000	105	1000	241	1000
1	-	-	-	-	-	-
2	67	788	33	314	80	332
3	-	-	25	238	-	-
4	27	318	23	219	61	253
5	-	-	19	181	30	124
6	18	212	16	152	23	95
7	12	141	14	133	13	54
8	-	-	11	105	11	46
9	9	106	8	76	10	42
10	7	88	7	67	8	34
11	7	82	7	67	6	25
12	7	82	6	57	6	25
13	5	59	3	29	6	25
14	3	35	3	29	6	25
15	3	35	3	29	6	25

Time (mos.)		Pro-rated	↓		Pro-rated	↓		Pro-rated	↓
0	239	1000	35	247	1000	29	165	1000	25
1	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	137	830	21
3	229	958	34	210	850	25	-	-	-
4	-	-	-	206	834	25	-	-	-
5	-	-	-	-	-	-	54	327	8
6	190	795	28	185	749	22	41	248	6
7	172	720	25	185	749	22	39	236	6
8	-	-	-	172	696	20	-	-	-
9	148	620	22	156	631	18	24	145	4
10	139	582	21	-	-	-	14	85	2
11	123	515	19	-	-	-	8	49	1
12	109	456	17	84	340	10	8	49	1
13	-	-	-	-	-	-	5	31	0.6
14	65	272	10	53	215	6	5	31	0.6
15	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-

Figure V-1. Survivorship of Chthamalus fissus at high, middle, and low intertidal levels summed from control and outfall areas. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals, and the survivorship rate of the barnacles present in the quadrats at the start of the study is treated as an extension of the survivorship of the barnacles settling during the study.

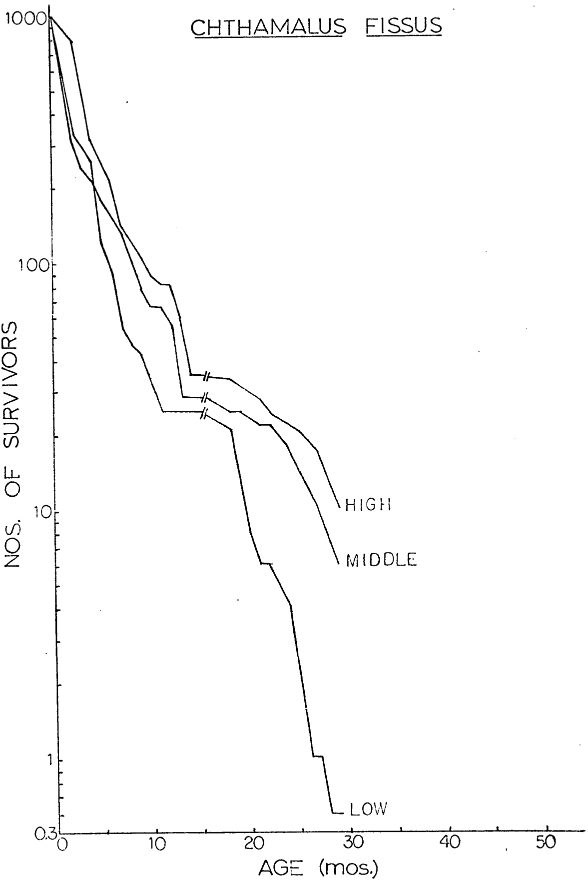

CHTHAMALUS FISSUS
NOS. OF SURVIVORS
1000
100
10
1
0.3
AGE (mos.)
0
10
20
30
40
50
HIGH
MIDDLE
LOW

Table V-4. Survivorship of <u>Chthamalus</u> <u>fissus</u> in all outfall and in all control quadrats and also in the total of all quadrats. For comparison of rates, survivorship rate of the barnacles present in the quadrats at the start of the study is treated as an extension of the survivorship of the barnacles settling during the study. These survivorship rates are plotted in Figures V-2 and V-6.

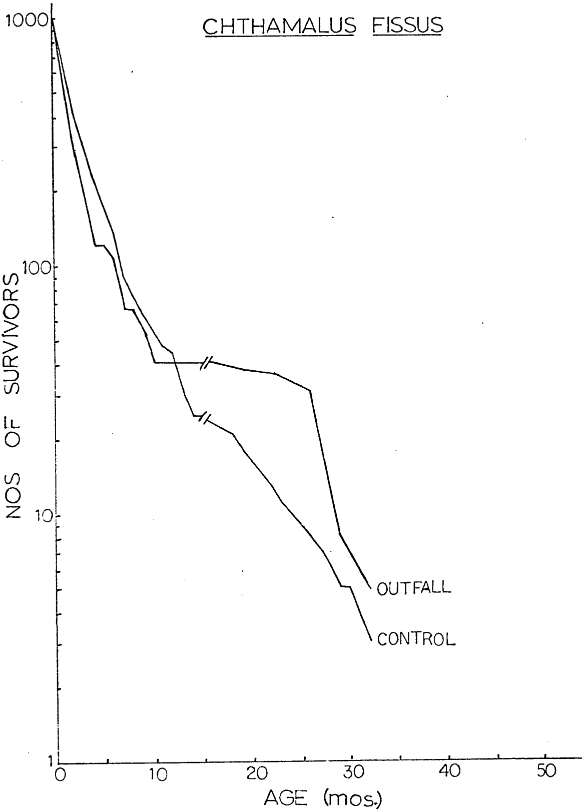
Chthamalus fissus

SURVIVORSHIP SUMMARY

Age (mos.)	OUTFALL	Pro-rated	CONTROL	Pro-rated	TOTAL	Pro-rated
0	75	1000	356	1000	431	1000
1	(40)	533	219	615	259	601
2	22	293	148	416	170	394
3	(14)	186	115	323	129	299
4	9	120	82	230	91	211
5	9	120	64	180	73	169
6	8	107	49	138	57	132
7	5	67	33	93	38	88
8	5	67	27	76	32	74
9	4	54	23	65	27	62
10	3	41	19	54	22	51
11	3	41	17	48	20	46
12	3	41	16	45	19	44
13	3	41	11	31	14	32
14	3	41	9	25	12	27
15	3	41	9	25	12	27

Time (mos.)		Pro-rated	↓		Pro-rated	↓		Pro-rated	↓
0	172	1000	41	479	1000	25	651	1000	27
1	(170)	988	41	434	906	23	604	928	25
2	168	976	40	(410)	856	22	578	888	24
3	(163)	947	39	389	812	21	552	848	23
4	158	918	38	(340)	710	18	498	765	21
5	(156)	906	38	(300)	626	16	456	700	19
6	154	894	37	262	547	14	416	639	17
7	154	894	37	242	505	13	396	608	16
8	(145)	842	35	(211)	440	11	356	547	14
9	141	819	34	187	390	10	328	504	13
10	132	767	32	165	344	9	297	456	12
11	129	750	31	(140)	292	8	269	413	11
12	81	471	19	120	250	7	201	309	8
13	57	331	13	(105)	219	6	162	249	6
14	33	192	8	90	188	5	123	189	5
15	(30)	175	7	86	180	5	116	178	5
16	27	158	6	(78)	163	4	105	161	4
17	23	135	5	(69)	144	3	92	141	3

Figure V-2. Survivorship of Chthamalus fissus in all outfall and in all control quadrats. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals, and the survivorship rate of the barnacles present in the quadrats at the start of the study is treated as an extension of the survivorship of barnacles settling during the study.


CHTHAMALUS FISSUS
1000
100
10
1
NOS OF SURVIVORS
0
10
20
30
40
50
AGE (mos.)
OUTFALL
CONTROL

the start of the study is indicated by time in months. The survivorship rate of the group already in the quadrats tended to be slightly higher than that of those settling during the study, but the former rate is treated as an extension of the rate from settlement in the presentation below. C. fissus in high intertidal quadrats showed a higher survivorship rate than those in the middle level, and the rate in the middle level quadrats was higher than that in the low quadrats. See Table V-3 for the comparative survivorship at the intertidal levels summed from outfall and control quadrats, and Figure V-1 plotting the rates at each level prorated from 1000 individuals. Thus, starting from 1000 individuals 10 C. fissus are alive in high quadrats after 30 months, six in middle quadrats, and only 0.4 in low quadrats. The survivorship of C. fissus in high quadrats was nearly the rate of survival of Balanus glandula in low quadrats (see below). C. fissus in the outfall quadrats had a higher survivorship than those in the control quadrats, although the rates in the two areas were very similar for the first year after settlement (see Table V-4 and Figure V-2).

Survival of Balanus glandula in the five control quadrats is given in Table V-5 and in the three outfall quadrats in Table V-6. B. glandula in high intertidal quadrats also showed a much higher survivorship rate than those in the middle quadrats, and the rate in the middle level quadrats was higher than that in the low quadrats. See Table V-7 for the comparative survivorship at the intertidal levels summed from outfall and

Table V-5. Survivorship of *Balanus glandula* in 150 cm^2 control quadrats at three intertidal levels. Year-classes from 1974 back to 1971 or earlier are indicated.

Balanus glandula

SURVIVORSHIP IN CONTROL QUADRATS

Age	HIGH 1				HIGH 2				MIDDLE				LOW 1				LOW 2			
(mos.)	1974	'73	'72	'71+	1974	'73	'72	'71+	1974	'73	'72	'71+	1974	'73	'72	'71+	1974	'73	'72	'71+
0	24	13	–	–	77	28	–	–	226	98	–	–	224	519	–	–	238	69	–	–
3	12	–	–	–	53	–	–	–	81	–	–	–	73	–	–	–	114	–	–	–
4	–	9	–	–	–	28	–	–	–	96	–	–	–	451	–	–	–	46	–	–
7	6	–	–	–	40	–	–	–	63	–	–	–	50	–	–	–	77	–	–	–
9	–	4	–	–	–	15	–	–	–	63	–	–	–	74	–	–	–	38	–	–
12	–	1	–	–	–	13	–	–	–	26	–	–	–	15	–	–	–	34	–	–
16	–	0	1	–	–	6	12	–	–	11	3	–	–	3	3	–	–	16	3	–
20	–	0	–	–	–	5	–	–	–	8	–	–	–	3	–	–	–	4	–	–
22	–	–	1	–	–	–	9	–	–	–	3	–	–	–	2	–	–	–	3	–
25	–	–	1	–	–	–	9	–	–	–	1	–	–	–	1	–	–	–	1	–
29	–	–	1	4	–	–	7	5	–	–	1	6	–	–	1	0	–	–	1	4
33	–	–	1	4	–	–	6	5	–	–	1	6	–	–	1	0	–	–	0	3
38	–	–	–	4	–	–	–	5	–	–	–	2	–	–	–	0	–	–	–	3
41	–	–	–	4	–	–	–	3	–	–	–	2	–	–	–	0	–	–	–	1
45	–	–	–	4	–	–	–	3	–	–	–	2	–	–	–	0	–	–	–	1

Table V-6. Survivorship of Balanus glandula in 150 cm^2 outfall quadrats at three intertidal levels. Year-classes from 1974 back to 1971 or earlier are indicated.

Balanus glandula

SURVIVORSHIP IN OUTFALL QUADRATS

Age (mos.)	HIGH				MIDDLE				LOW			
	1974	1973	1972	1971+	1974	1973	1972	1971+	1974	1973	1972	1971+
0	12	23	-	-	64	16	-	-	201	158	-	-
3	11	-	-	-	26	-	-	-	50	-	-	-
4	-	14	-	-	-	17	-	-	-	142	-	-
7	6	-	-	-	12	-	-	-	16	-	-	-
9	-	11	-	-	-	9	-	-	-	90	-	-
12	-	11	-	-	-	9	-	-	-	84	-	-
16	-	9	7	-	-	4	6	-	-	43	10	-
20	-	7	-	-	-	4	-	-	-	15	-	-
22	-	-	6	-	-	-	3	-	-	-	10	-
25	-	-	6	-	-	-	3	-	-	-	9	-
29	-	-	6	3	-	-	2	4	-	-	4	0
33	-	-	4	3	-	-	1	4	-	-	1	0
38	-	-	-	3	-	-	-	4	-	-	-	0
41	-	-	-	2	-	-	-	3	-	-	-	0
45	-	-	-	2	-	-	-	2	-	-	-	0

Table V-7. Survivorship of *Balanus glandula* in high, middle, and low intertidal quadrats summed from control and outfall areas. Year-classes from 1974 back to 1971 or earlier are indicated. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals. These survivorship rates are plotted in Figure V-3.

Balanus glandula

SURVIVORSHIP AT HIGH, MIDDLE, AND LOW INTERTIDAL LEVELS
(Control plus Outfall Quadrats)

Age (mos.)	HIGH					MIDDLE					LOW				
	1974	1973	1972	1971+	Pro-rated	1974	1973	1972	1971+	Pro-rated	1974	1973	1972	1971+	Pro-rated
0	113	64	-	-	1000	290	114	-	-	1000	660	746	-	-	1000
3	76	-	-	-	761	107	-	-	-	672	237	-	-	-	626
4	-	51	-	-	709	-	110	-	-	654	-	639	-	-	590
7	52	-	-	-	530	75	-	-	-	512	143	-	-	-	361
9	-	30	-	-	414	-	72	-	-	423	-	202	-	-	194
12	-	25	-	-	345	-	35	-	-	205	-	133	-	-	127
16	-	15	20	-	207	-	15	9	-	88	-	62	16	-	59
20	-	12	-	-	173	-	12	-	-	70	-	22	-	-	39
22	-	-	16	-	159	-	-	6	-	60	-	-	15	-	38
25	-	-	16	-	159	-	-	4	-	40	-	-	11	-	28
29	-	-	14	12	140	-	-	3	10	30	-	-	6	4	15
33	-	-	11	12	126	-	-	2	10	25	-	-	2	3	8
38	-	-	-	12	126	-	-	-	6	18	-	-	-	3	8
41	-	-	-	9	95	-	-	-	5	15	-	-	-	1	3
45	-	-	-	9	95	-	-	-	4	12	-	-	-	1	3

Figure V-3. Survivorship of Balanus glandula at high, middle, and low intertidal levels summed from control and outfall areas. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals.

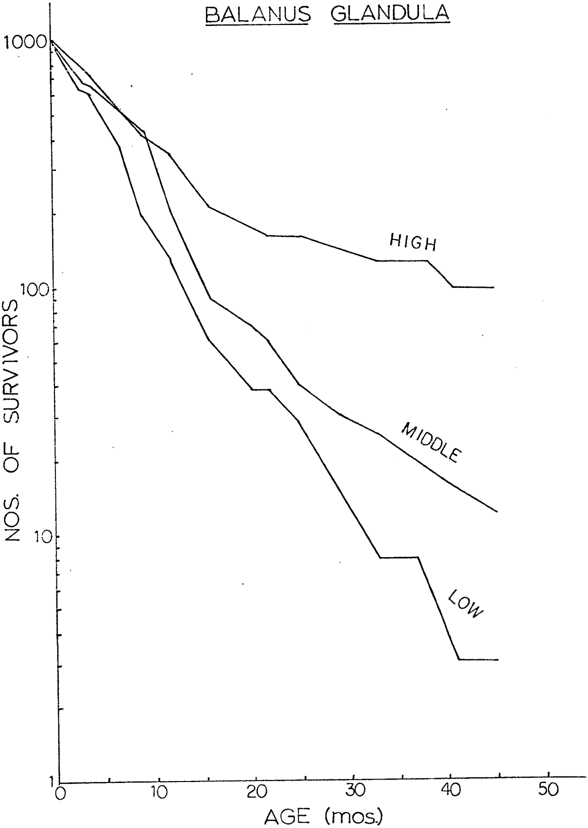

BALANUS GLANDULA
1000
100
10
1
NOS. OF SURVIVORS
HIGH
MIDDLE
LOW
0
10
20
30
40
50
AGE (mos.)

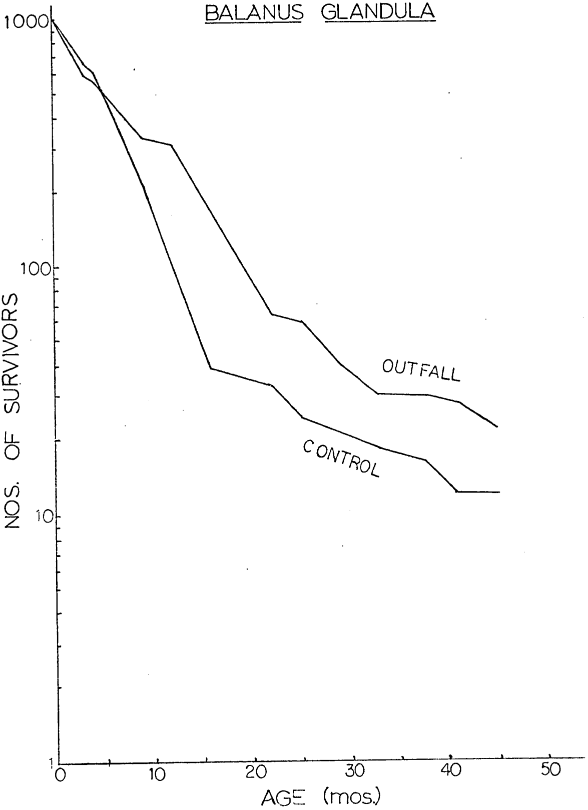
Table V-8. Survivorship of *Balanus glandula* in all outfall and in all control quadrats and also in the total of all quadrats. Year-classes from 1974 back to 1971 or earlier are indicated. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals. These survivorship rates are plotted in Figures V-4 and V-6.

Balanus glandula

SURVIVORSHIP SUMMARY

Age (mos.)	OUTFALL					CONTROL					TOTAL				
	1974	1973	1972	1971+	Pro-rated	1974	1973	1972	1971+	Pro-rated	1974	1973	1972	1971+	Pro-rated
0	277	197	-	-	1000	789	727	-	-	1000	1066	924	-	-	1000
3	86	-	-	-	604	333	-	-	-	655	419	-	-	-	641
4	-	170	-	-	563	-	617	-	-	620	-	787	-	-	605
7	34	-	-	-	402	236	-	-	-	400	270	-	-	-	396
9	-	110	-	-	330	-	194	-	-	214	-	304	-	-	242
12	-	104	-	-	312	-	89	-	-	98	-	193	-	-	154
16	-	56	23	-	168	-	36	22	-	39	-	92	45	-	74
20	-	26	-	-	88	-	20	-	-	35	-	46	-	-	51
22	-	-	19	-	64	-	-	18	-	33	-	-	37	-	48
25	-	-	18	-	60	-	-	13	-	24	-	-	31	-	40
29	-	-	12	7	40	-	-	11	19	21	-	-	23	26	30
33	-	-	6	7	30	-	-	9	18	18	-	-	15	25	24
38	-	-	-	7	30	-	-	-	14	16	-	-	-	21	20
41	-	-	-	5	28	-	-	-	10	12	-	-	-	15	14
45	-	-	-	4	22	-	-	-	10	12	-	-	-	14	13

Figure V-4. Survivorship of *Balanus glandula* in all outfall and control quadrats. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals.


BALANUS GLANDULA
1000
100
10
1
NOS. OF SURVIVORS
OUTFALL
CONTROL
0
10
20
30
40
50
AGE (mos.)

control quadrats, and Figure V-3 plotting the survivorship at each level prorated from 1000 individuals. Thus, starting from 1000 individuals 95 would remain at the high level after 45 months, 12 at the middle level, and only three would remain at the low level. The survival rate of *B. glandula* in the low quadrats approach that of *C. fissus* in the high quadrats (see above), and the survival of *B. glandula* at the high level was greater than that of *Tetraclita squamosa* (see below). *B. glandula* in the outfall quadrats had a higher survivorship rate than those in the control quadrats with 22 out of 1000 individuals alive in outfall quadrats after 45 months and only 13 alive in control quadrats (see Table V-8 and Figure V-4).

Tetraclita squamosa settled and lived only in the lower intertidal levels in the study areas, and survival of all *T. squamosa* in the 10 control quadrats and in the 14 outfall quadrats are summed in Table V-9. *T. squamosa* showed a higher survivorship in the control quadrats than in the outfall quadrats (Table V-9 and Figure V-5). Apparently as a result of the patchy nature of settlement of *T. squamosa*, recruitment of this species did not occur in the outfall quadrats in 1973 (see Chapter III on settlement). Survival in the outfall therefore could be compared to the control group only after about age 14 months. Thus, at age 52 months, 29 individuals of 1000 would remain alive in the control areas, and 21 would remain alive in the outfall area.

Comparing the overall survivorship of each species for all quadrats summed from all the intertidal levels in both

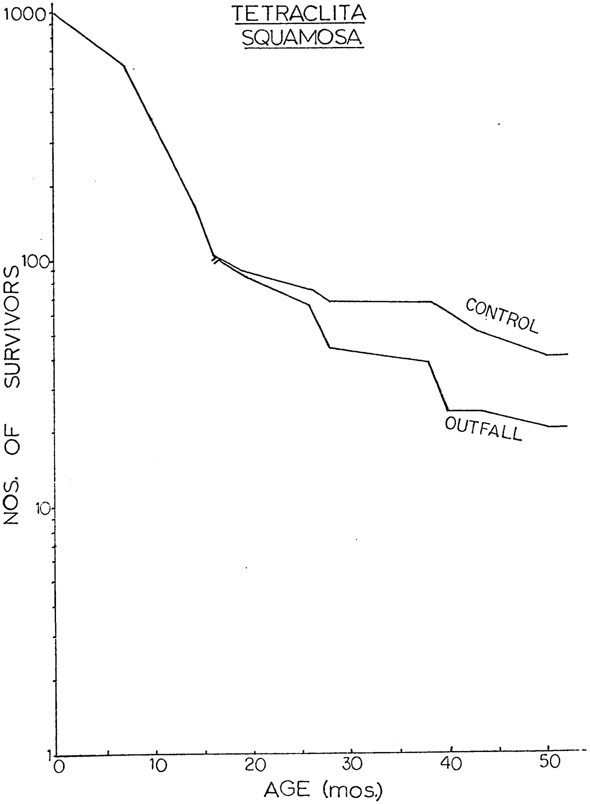
Table V-9. Survivorship of _Tetraclita_ _squamosa_ in all control and in all outfall quadrats and also in the total of all quadrats. Year-classes from 1973 back to 1970 or earlier are indicated. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals. No _T._ _squamosa_ settled in the outfall quadrats in 1973, so the initial survival rate of the control population was used. These survivorship rates are plotted in Figures V-5 and V-6.

Tetraclita squamosa

SURVIVORSHIP

Age	CONTROL					OUTFALL					TOTAL				
(mos.)	1973	1972	1971	1970+	Pro-rated	1973	1972	1971	1970+	Pro-rated	1973	1972	1971	1970+	Pro-rated
0	144	-	-	-	1000	-	-	-	-	1000	144	-	-	-	1000
4	109	-	-	-	757					→ (757)	109	-	-	-	757
7	89	-	-	-	618					→ (618)	89	-	-	-	618
14	24	-	-	-	167					→ (167)	24	-	-	-	167
16	15	35	-	-	104		33			→ (104)	15	68	-	-	104
19	-	30	-	-	89	-	28	-	-	88	-	58	-	-	89
26	-	26	-	-	77	-	21	-	-	66	-	47	-	-	72
28	-	23	29	-	68	-	14	73	-	44	-	37	102	-	57
31	-	-	29	-	68	-	-	72	-	42	-	-	101	-	56
38	-	-	29	-	68	-	-	66	-	38	-	-	95	-	53
40	-	-	26	6	61	-	-	42	7	24	-	-	68	13	38
43	-	-	-	5	51	-	-	-	7	24	-	-	-	12	35
50	-	-	-	4	41	-	-	-	6	21	-	-	-	10	29
52	-	-	-	4	41	-	-	-	6	21	-	-	-	10	29

Figure V-5. Survivorship of _Tetraclita_ _squamosa_ in all outfall and all control quadrats and in the total of all quadrats. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals. No _T_. _squamosa_ settled in the outfall quadrats, so the initial survival rate of the control population was used.


TETRACLITA SQUAMOSA
1000
100
10
1
NOS. OF SURVIVORS
CONTROL
OUTFALL
0
10
20
30
40
50
AGE (mos.)

outfall and control areas, *T. squamosa* had the highest survivorship rate, *B. glandula* an intermediate rate, and *C. fissus* the lowest rate. See Tables V-4, V-8, and V-9 for the total summary data for each species, and Figure V-6 plotting the survivorship rates of each species starting from 1000 individuals. These survivorship schedules are used in the life tables below for each species. However, because substantial numbers of each species were still alive at the end of the age intervals covered in the study, the survivorship curves of Figure V-6 were extended by eye with straight lines in Figure V-7 to complete the survivorship schedules to the last individual at about age 37 months for *C. fissus*, 88 months for *B. glandula*, and 140 months for *T. squamosa*. The simplistic assumption of straight-line extensions of these curves may produce unrealistically shortened survivorship schedules, particularly for *B. glandula* and *T. squamosa*. However, straight-line survivorship curves similar to these extensions have been reported for *B. glandula* (Connell, 1970), *C. stellatus* (Connell, 1961a), and *B. balanoides* (Connell, 1961b), although Deevey (1947) showed that the survivorship curves derived from Hatton's (1938) data for some populations of *B. balanoides* were hyperbolic in shape. Furthermore, based on the growth curves for the three species in the present study (Chapter IV), barnacles living much longer than these estimates of the ages of the last individuals would be expected to be larger than the maximum-sized individuals observed for each species in the study areas. A longer study is necessary to test the accuracy of these assumptions.

Figure V-6. Comparative survivorship of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* summed from all quadrats. For comparison of rates, survivorship is prorated from an arbitrary 1000 individuals. The survivorship rate of *C. fissus* present in the quadrats at the start of the study is treated as an extension of the survivorship of barnacles settling during the study.

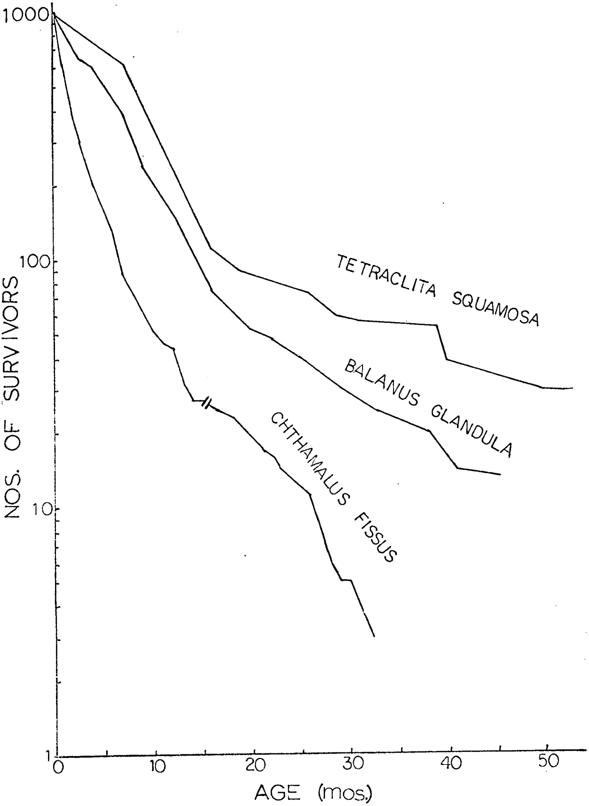
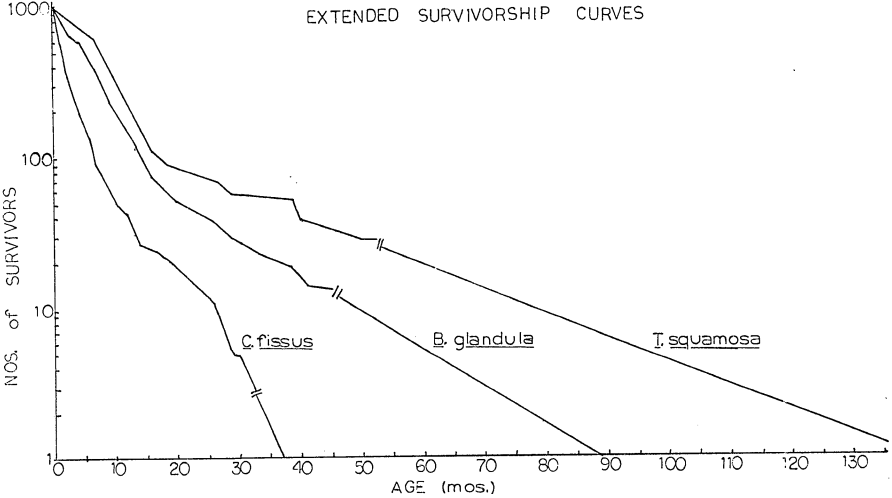

1000
100
10
1
NOS. OF SURVIVORS
0
10
20
30
40
50
AGE (mos.)
TETRACLITA SQUAMOSA
BALANUS GLANDULA
CHTHAMALUS FISSUS

Figure V-7. Extended survivorship rates for *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa*. The survivorship curves of Figure V-6 were extended by eye with straight lines to complete the survivorship schedules to the last individuals.


EXTENDED SURVIVORSHIP CURVES
NOS. of SURVIVORS
1000
100
10
1
0
10
20
30
40
50
60
70
80
90
100
110
120
130
AGE (mos.)
C. fissus
B. glandula
T. squamosa

2. Sources of Mortality.

During the course of this study several possible sources of barnacle mortality were observed in the study areas. These field observations are qualitative in nature, and no experiments or more extensive observations were made to quantify the effects of each source.

In control areas two major physical factors were observed to be important causes of mortality in the barnacles. First, desiccation, perhaps in combination with temperature stress, apparently occasionally killed *Chthamalus fissus* and *Balanus glandula* in the highest intertidal zone. This source of mortality may be especially significant in newly settled cyprids of all three species, although no observations of cyprids were made. *Tetraclita squamosa* was found only in moist conditions and was not observed in stressful desiccating or temperature conditions in the control areas; although in the laboratory it was the most sensitive of the three species to high temperatures, desiccation, and low oxygen levels. Second, scouring of the substrate by moving sand during early winter and early spring caused extensive mortality of barnacles in the low zones of some control areas. In the outfall areas the scouring by sand did not occur, but temperature stress in the heated water during peak plant loads and during heat treatment was undoubtedly very great (see Materials and Methods in Chapter II and Figure II-2). Desiccation stress in the outfall was also potentially greater than in control areas, because water levels in the discharge canal occasionally dropped as much as one meter for several days at a time when units in the power plant were shut down for repair. Chlorine was sometimes used by the power plant to reduce fouling of the cooling tubes, and this may have been a transient stress for the outfall populations, although I did not measure chlorine levels.

Many predators on barnacles are found in the control areas. Three species of neogastropods--*Acanthina spirata*, *Thais emarginata*, and *Ceratostoma foliatum*--were observed feeding on all three species of barnacle. *Thais* was found in all but the highest intertidal levels; *Acanthina* was in the middle and low levels; and *Ceratostoma* was only seen at low intertidal levels. Five species of sea stars--*Pisaster ochraceus*, *P. brevispinus*, *Leptasterias hexactis*, *Patiria miniata*, and *Pycnopodia helianthoides*--were found in low densities in the control areas, but only *P. ochraceus* and *L. hexactis* were actually observed feeding on barnacles in the low zones. The crab *Pachygrapsus crassipes* was occasionally observed eating *Balanus glandula* in control areas. Two species of fish--a perch *Micrometrus* sp. and the opaleye *Girella nigricans*--were seen browsing on hard substrates in control areas, but it was unclear whether they ever ate barnacles. Other possible vertebrate predators on barnacles in the control areas were birds, particularly turnstones *Arenaria* spp., and Norway rats *Rattus norwegicus*, but I did not actually observe barnacles being eaten by them. In addition, grazing acmaeid limpets probably caused barnacle mortality by bulldozing juvenile barnacles off the substrate.

There appeared to be significantly fewer predators on barnacles in the outfall area. No predatory gastropods were ever seen in the discharge canal, and only a few Pisaster ochraceus and Patiria miniata were occasionally observed in a limited area of the canal, never near the marked quadrats. Pachygrapsus crassipes is extremely abundant in the outfall, however, and it was seen breaking open Balanus glandula and Tetraclita squamosa on several occasions. Perch and opaleye are also abundant browsers in the outfall, but I did not actually observe them eating barnacles. Birds and rats, obviously, had access to the outfall as well as to the control areas. Acmaeid limpets, although present in the outfall, were not found in nearly such high abundance as in the control areas. However, I did observe them apparently bulldozing young barnacles in the outfall.

One of the major and most obvious sources of barnacle mortality is crowding by other barnacles in both the control and outfall areas. Chthamalus fissus was often overgrown and undercut by barnacles of the same species and by the other two species, especially in the lower and middle intertidal zones, where it settled in large numbers in May and June and grew rapidly in the summer (see Chapters III and IV on settlement and growth). Large sheets of B. glandula often fell off the substrate when crowding became especially severe in the lower zones. Only larger Tetraclita squamosa were relatively immune from crowding by B. glandula, but large T. squamosa crowded each other off the substrate and apparently competed for space with *Balanus nubilus* and *B. cariosus* in control areas. The cloning sea anemone *Anthopleura elegantissima* appeared to be a major competitor with barnacles for space in the lower zones of both study areas, and these sea anemones seemed to be much more tolerant of burial and abrasion by sand than the barnacles. Competition for space with other organisms was undoubtedly important in the low intertidal zones, but these interactions were difficult to document. Finally, the incidence of parasitic castration by the isopod *Hemioniscus* sp., which would effectively remove a barnacle from the breeding population, was not found at significant levels (<0.1%) at Mooro Bay.

3. Egg Size.

The size of embryos of all three species appeared to increase somewhat with advancing embryonic development, probably as a result of the formation of the naupliar shape from the compact egg. However, the size of newly deposited eggs and the size of advanced first stage nauplii varied only a few (±5) microns within each species. The dimensions of the embryonated eggs of each species before hatching are:

	length (μ)	width (μ)
Chthamalus fissus		
new egg	110	85
advanced nauplius	130	95
Balanus glandula		
new egg	220	160
advanced nauplius	245	175
Tetraclita squamosa		
new egg	310	180
advanced nauplius	340	195

These dimensions did not vary between the outfall and control populations for any of the species. Tetraclita squamosa has the largest, Balanus glandula an intermediate, and Chthamalus fissus the smallest egg.

4. Egg Numbers per Brood.

Numbers of eggs per brood increased linearly with dry body weight and with basal diameter of the parent barnacle (see Figure V-8 for Chthamalus fissus, Figure V-9 for Balanus glandula, and Figure V-10 for Tetraclita squamosa). The equations for the linear regressions of egg number per brood versus body weight and of the same egg counts versus the corresponding basal diameters are given below. The sample sizes (n), the square of the regression coefficients (r^2), and the regression slopes and intercepts ± one standard error are indicated.

Chthamalus fissus: $n = 24$

Egg No. vs. Body Wt.

$Y = 2.54(\pm 0.34)X + 0.28(\pm 0.27)$; $r^2 = 0.72$

Egg No. vs. Basal Diameter

$Y = 0.47(\pm 0.06)X - 1.12(\pm 0.43)$; $r^2 = 0.72$

Balanus glandula: $n = 33$

Egg No. vs. Body Wt.

$Y = 1.72(\pm 0.13)X - 0.37(\pm 0.98)$; $r^2 = 0.85$

Egg No. vs. Basal Diameter

$Y = 2.01(\pm 0.76)X - 14.13(\pm 9.54)$; $r^2 = 0.82$

Figure V-8. Chthamalus fissus: regressions of egg number per brood versus body weight, $Y = 2.54X + 0.28$; and the same egg counts per brood versus basal diameter, $Y = 0.47X - 1.12$.

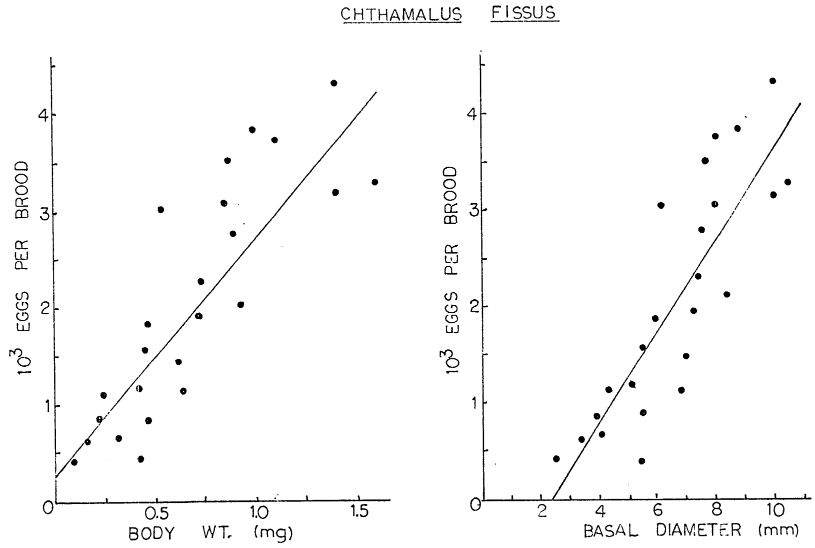

CHTHAMALUS FISSUS
10^3 EGGS PER BROOD
0
1
2
3
4
0.5
1.0
1.5
BODY WT. (mg)
10^3 EGGS PER BROOD
0
1
2
3
4
2
4
6
8
10
BASAL DIAMETER (mm)

Figure V-9. Balanus glandula: regressions of egg number per brood versus body weight, Y = 1.72X - 0.37; and the same egg counts per brood versus basal diameter, Y = 2.01X - 14.13.

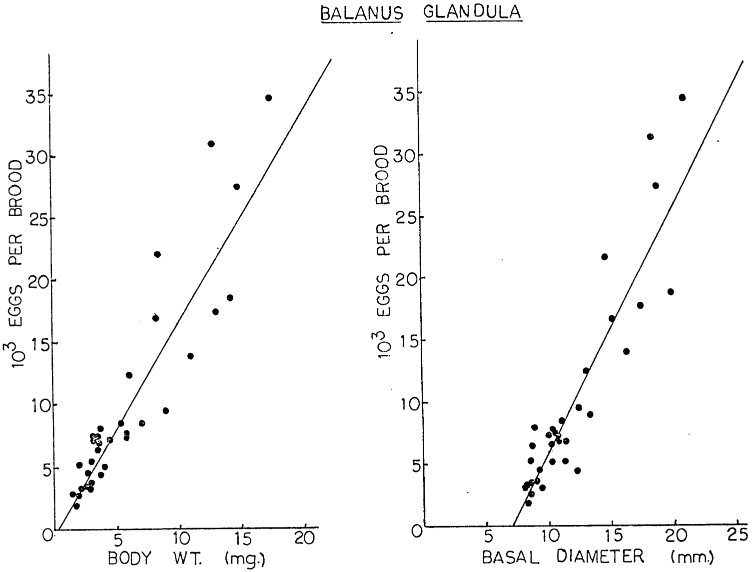
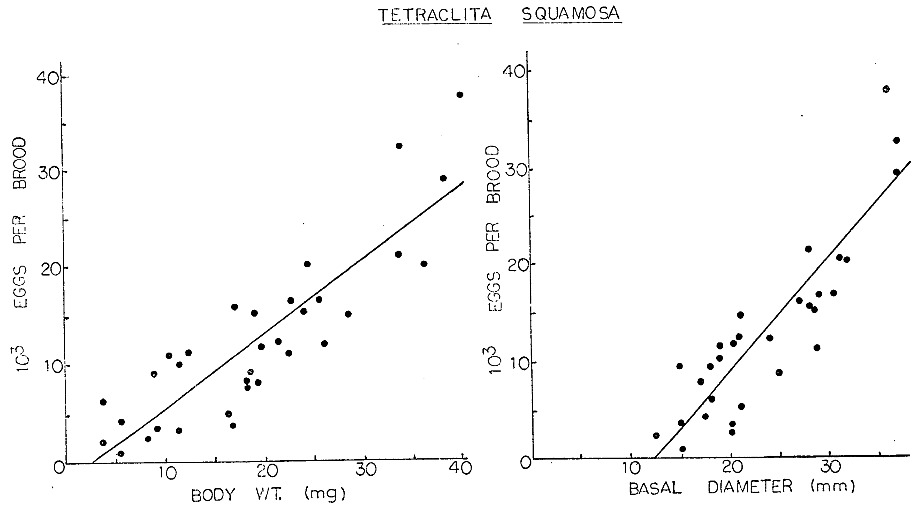

BALANUS GLANDULA
10^3 EGGS PER BROOD
0
5
10
15
20
25
30
35
BODY WT. (mg.)
0
5
10
15
20
10^3 EGGS PER BROOD
0
5
10
15
20
25
30
35
BASAL DIAMETER (mm.)
0
5
10
15
20
25

Figure V-10. *Tetraclita squamosa*: regressions of egg number per brood versus body weight, $Y = 0.75X - 2.05$; and the same egg counts per brood versus basal diameter, $Y = 1.14X - 14.31$.


TETRACLITA SQUAMOSA
10^3 EGGS PER BROOD
0
10
20
30
40
BODY WT. (mg)
0
10
20
30
40
10^3 EGGS PER BROOD
0
10
20
30
40
BASAL DIAMETER (mm)
10
20
30

Tetraclita squamosa: n = 33

Egg No. vs. Body Wt.

$Y = 0.75(\pm 0.08)X - 2.05(\pm 1.15);\ r^2 = 0.76$

Egg No. vs. Basal Diameter

$Y = 1.14(\pm 0.11)X - 14.31(\pm 2.59);\ r^2 = 0.79$

Note that the regressions of egg number on basal diameter intercept the X-axis at about 2 mm for C. fissus (Figure V-8), 7 mm for B. glandula (Figure V-9), and 12 mm for T. squamosa (Figure V-10). These basal diameters correspond well to the size of each species at the onset of brooding indicated by Figure II-5 and Chapter IV on growth.

5. Life Tables.

The life of Chthamalus fissus (Table V-10), Balanus glandula (Table V-11), and Tetraclita squamosa (Table V-12) are computed from age (x), survivorship (l_x), and fecundity (m_x) schedules as explained below.

The age schedule (x) used for each species is derived from the age of the barnacles at the middle of each brooding season of the control population (see Chapter II) following settlement (Chapter III). Thus, Balanus glandula settles in May or June; its brooding season is from about December through May; and all B. glandula begin to reproduce at about age 6-7 months in their first season at frequencies equal to those shown by older barnacles (Figure II-5 and Chapter IV). Tetraclita squamosa settles in October or November; it broods from about late May to early October; but it is usually not

Table V-10. Chthamalus fissus life table. See text for explanation. R_o = net reproductive rate per generation. G = generation time. r_m = intrinsic rate of increase of the population.

Chthamalus fissus

LIFE TABLE

Age (X) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood	X	No. broods per year	m_x	$(l_x)(m_x)$	$(x)(l_x)(m_x)$	$e^{-r_m x} l_x m_x$
6	0.1320	4.0	760		16	12,160	1,605	9,631	1.0010
18	0.0230	5.5	1,470		16	23,520	541	9,737	0.0000
30	0.0050	6.7	2,030		16	32,480	162	4,872	0.0000
42	(0.0005)	7.9	2,590		16	41,440	21	870	0.0000

$R_o = \Sigma(l_x)(m_x) = 2,329$ $\quad \Sigma = 1.0010$

$\Sigma(x)(l_x)(m_x) = 25,110$

$$G = \frac{\Sigma(x)(l_x)(m_x)}{R_o} = 10.78 \text{ mos.}$$

$r_m = 1.23$, as determined by solving $\Sigma e^{-r_m x} l_x m_x = 1$

Table V-11. *Balanus glandula* life table. See text for explanation. R_o = net reproductive rate per generation. G = generation time. r_m = intrinsic rate of increase of the population.

Balanus glandula

LIFE TABLE

Age (X) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood X	No. broods per year	m_x	$(l_x)(m_x)$	$(x)(l_x)(m_x)$	$e^{-r_m x} l_x m_x$
10	0.2100	10.3	6,573	6	39,438	8,282	82,820	1.0018
22	0.0480	13.1	12,201	6	73,206	3,514	77,306	0.0000
34	0.0230	16.7	19,437	6	116,622	2,682	91,198	0.0000
46	0.0120	20.5	27,075	6	162,450	1,949	89,672	0.0000
58	(0.0058)	24	34,110	6	204,660	1,187	68,848	0.0000
70	(0.0030)	27	40,140	6	240,840	722	50,576	0.0000
80	(0.0017)	30	45,170	6	271,020	461	36,858	0.0000

$R_o = \Sigma(l_x)(m_x) = 18,797$ $\Sigma = 1.0018$

$\Sigma(x)(l_x)(m_x) = 497,278$

$$G = \frac{\Sigma(x)(l_x)(m_x)}{R_o} = 26.45 \text{ mos.}$$

$r_m = 0.902$, as determined by solving $\Sigma e^{-r_m x} l_x m_x = 1$

Table V-12. *Tetraclita squamosa* life table. See text for explanation. R_o = net reproductive rate per generation. G = generation time. r_m = intrinsic rate of increase of the population.

Tetraclita squamosa

LIFE TABLE

Age (X) (mos.)	l_x	Basal diam. (mm)	No. eggs per brood x	No. broods per year	m_x	$(l_x)(m_x)$	$(x)(l_x)(m_x)$	$e^{-r_m x} l_x m_x$
9	0.4350	10.9	0	0	0	0	0	0
21	0.0840	21.4	10,090	3	30,270	2,543	53,396	0.9871
33	0.0550	29.7	19,550	3	58,650	3,226	106,450	0.0141
45	0.0330	34.3	24,790	3	74,370	2,454	110,439	0.0012
57	(0.0220)	41	32,430	3	97,290	2,140	122,002	0.0000
69	(0.0140)	45	36,990	3	110,970	1,554	107,197	0.0000
81	(0.0090)	48	40,410	3	121,230	1,091	88,377	0.0000
93	(0.0067)	51	43,830	3	131,490	881	81,931	0.0000
105	(0.0036)	52	44,970	3	134,910	486	50,996	0.0000
117	(0.0023)	53	46,110	3	138,330	318	37,225	0.0000
129	(0.0015)	56	49,530	3	148,590	223	28,752	0.0000
								$\Sigma = 1.0024$

$R_o = \Sigma(l_x)(m_x) = 14{,}916$

$\Sigma(x)(l_x)(m_x) = 786{,}765$

$$G = \frac{\Sigma(x)(l_x)(m_x)}{R_o} = 52.75 \text{ mos.}$$

$r_m = 0.374$, as determined by solving $\Sigma e^{-r_m x} l_x m_x = 1$

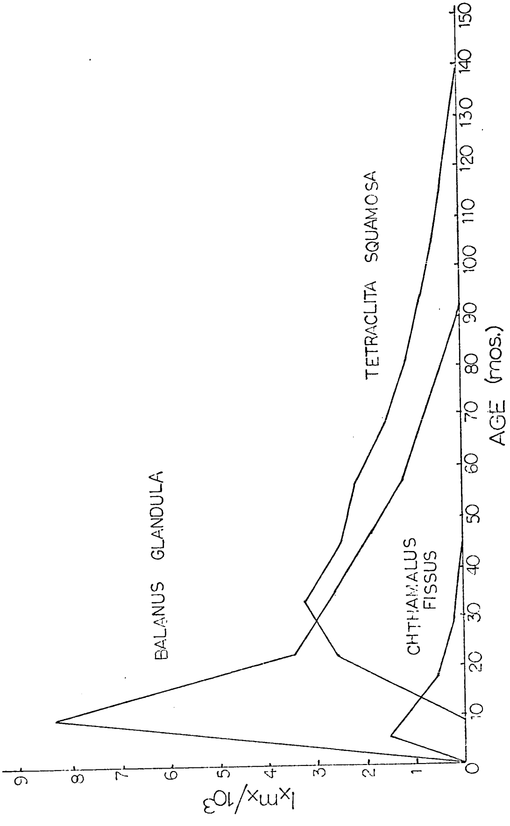
sexually mature in the first reproductive season and the onset of first brooding is delayed until the second summer of life at about age 19 months, and thereafter at equal frequencies for all ages (Figure II-5 and Chapter IV). *Chthamalus fissus*, however, may settle at any time of the year; it broods mainly from March through October; and it can begin to brood after about age two months at equal frequencies for all ages (Figure II-5 and Chapter IV). The year-round settlement of *C. fissus* is a complicating factor which is arbitrarily simplified in the computation of its life table by assuming a settlement time in January, two months before the start of the brooding season. It is thus assumed to be fully reproductive during the entire first brooding season.

The survivorship schedules (l_x) for each species are from the rates shown in the extended survivorship curves in Figure V-7 and are discussed in detail above in the Survivorship section (1) of the Results.

Fecundity schedules (m_x) for each species are calculated as the number of eggs per brood for the basal diameter at age (x) times the number of broods per season as explained in the Materials and Methods. *Balanus glandula* exhibits the highest annual fecundity; *Tetraclita squamosa* has an intermediate but high annual fecundity; and *Chthamalus fissus* shows the lowest.

The survivorship-weighted fecundity schedule (l_x)(m_x) indicates the expected reproductive contribution, or "reproductive value," of each age interval relative to the entire time of potential survival (see Figure V-11). Both *Chthamalus fis-*

Figure V-11. Survivorship-weighted fecundity versus age for *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* derived from their respective life tables. See text for explanation.


$l_x m_x/10^3$
0
1
2
3
4
5
6
7
8
9
AGE (mos.)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
BALANUS GLANDULA
TETRACLITA SQUAMOSA
CHTHAMALUS FISSUS

sus and Balanus glandula have maximum reproductive values in their first year. It is important to note that while B. glandula has a very high reproductive value in its first season, C. fissus reaches its peak value four months younger than B. glandula. Tetraclita squamosa does not begin reproducing until its second year and does not reach its peak reproductive value until its third year. Its reproductive contribution remains relatively high in its fourth and fifth years, declining gradually over a potentially long life span. As a result of the different survival expectancies of the three species, C. fissus has "lost" reproductive value after age 45 months, B. glandula after 93 months, and T. squamosa after 140 months.

The net reproductive rate per generation (R_o) is expressed as the sum of the $l_x m_x$ schedule and is highest for Balanus glandula (R_o = 18,797), intermediate but high for Tetraclita squamosa (R_o = 14,916), and lowest for Chthamalus fissus (R_o = 2,329).

The mean generation time (G) is calculated as the sum of the $(x)(l_x)(m_x)$ schedule divided by the net reproductive rate per generation (R_o). Chthamalus fissus has the shortest generation time (G = 10.78 months) as a result of beginning reproduction at an early age. Balanus glandula has an intermediate generation time (G = 26.45 months), more than twice that of C. fissus, even though it begins reproducing at an age of only four or five months older than C. fissus. Tetraclita squamosa has the longest generation time (G = 52.75 months) as a result of its delayed reproductive maturation.

A population's potential rate of increase in numbers is expressed as:

$$\frac{dN}{dt} = r_m N,$$

where r_m is the innate capacity for increase for the particular environmental conditions. The innate capacity for increase can be approximated for populations with overlapping generations by solving by trial and error the equation

$$e^{-r_m x} l_x m_x = 1.$$

The innate capacity for increase is highest for Chthamalus fissus ($r_m = 1.23$), intermediate but high for Balanus glandula ($r_m = 0.902$), and lowest for Tetraclita squamosa ($r_m = 0.374$). Put another way, under the environmental conditions at Morro Bay, C. fissus has the potential for fastest population growth, B. glandula has the potential for intermediate population growth, and T. squamosa has the slowest population growth potential. Because larval mortality is not included in the survivorship schedules, these estimates of the intrinsic rate of population growth are undoubtedly unrealistically high and should be examined for comparative purposes only.

D. DISCUSSION

The upper limits of intertidal zones are generally attributed to the variable tolerance of different species to the desiccation and temperature rigors of prolonged exposure to air (Rickets and Calvin, 1962; and many others). The lower limits of intertidal zones are usually defined by biological interactions of predation and competition (Dayton, 1971; Paine, 1969; and many others). Studies on the factors determining the patterns of the intertidal distribution of barnacles have provided much of the bases for these generalizations about intertidal zonation. 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). Connell (1961a) showed experimentally that the zonation pattern of *Chthamalus stellatus* living predominantly in high areas in Scotland was caused largely by competition for space with *Balanus balanoides*. *C. stellatus* settles in all zones but is severely limited in the lower zones where *B. balanoides* rapidly grows over and undercuts it each summer. When *B. balanoides* are removed from an area, *C. stellatus* survives well in the lower zones. *B. balanoides* exhibited much intraspecific competition for space as well, with crowding in the lower zones killing many of its own kind. A second major source of mortality in the lower range of *B. balanoides* is predation by *Thais lapillus*, a gastropod which feeds extensively on barnacles in the summer.

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. on young barnacles severely limits their survivorship in lower zones. *B. glandula* has a spatial refuge from predators in the upper mid-intertidal zone, however, where it has much higher survivorship. In contrast to *B. glandula*, *B. cariosus* may escape predation in the lower zones by growing to a size larger than most predators can attack. It is, therefore, 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).

Heavy predation pressure on barnacles in lower intertidal zones of western North America has been documented for a host of predators, the most important of which are several species of sea stars (Paine, 1966, 1969; Mauzey, 1967; Feder, 1970; Menge, B., 1972; and many others) and a variety of gastropods (Paine, 1963; Emlen, 1966; Connell, 1970; Dayton, 1971; Menge, J., 1974; and others). Deaths of young barnacles by grazing limpets and abrasion from algae have also been documented, and important competition for space from *Mytilus californianus* and *Anthopleura elegantissima* have also been shown to limit the distributions of barnacles (e.g., Dayton, 1971).

Field observations at Morro Bay on the sources of physiological stress, competition, and predation for barnacles indicate in a qualitative way that the aspects of differential mortality maintaining zonation patterns and community structure discussed above probably apply to community interactions in my study areas. The patterns of survivorship of the three species of barnacles in the present study are in general agreement with the analogous patterns in other communities. Thus, *Chthamalus fissus*, like *C. stellatus*, settles initially at all intertidal levels (Chapter III), but it 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. *B. glandula*, like *B. balanoides*, also survives best at the higher zone, where it settles only in low numbers (Chapter III). Inter-specific competition, predation, and sand abrasion undoubtedly account for much of the reduced survivorship in the lower zones, but intra-specific crowding following heavy settlement in the low levels seems to be the major cause of mortality of *B. glandula*. Because there appears to be more predators and competitors in the control areas, higher survival of barnacles in the outfall areas might be predicted. *C. fissus* and *B. glandula*, as expected, do show higher survival rates in the outfall than in control areas, but *Tetraclita squamosa* does not. It may be that *T. squamosa* is well adapted to the biological rigors of lower zones, but not as well to the temperature stress of the outfall since it would not normally encounter as great a stress in lower intertidal levels. *T. squamosa*, like *B. cariosus*, grows to a large size (Chapter IV) exempting it from much of the predation and competition pressures in the lower zone, and it has better overall survival than the other two species.

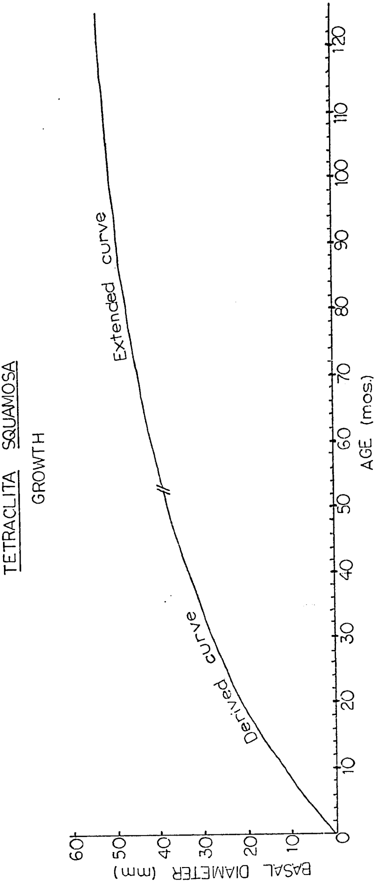
The egg sizes reported here for *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* are in good general agreement with those reported by Barnes and Barnes (1965) for nauplius sizes and would lead to very similar volume calculations (*C. fissus* = 0.54 x 10^{-6} ml; *B. glandula* = 2.99 x 10^{-6} ml; *T. squamosa* = 3.28 x 10^{-6} ml). Barnes and Barnes (1965) report that egg size in *Balanus balanoides* increases with parental basal diameter, but no such relationship was found by me. Although egg size and species size are positively correlated for the three species in the present study, Barnes and Barnes (1968) show in comparisons of many more species that most cirripede eggs fall into a size range of 100-300 u in length and that there is no consistent relation between egg size and species size. Thus, *Balanus balanoides*, a moderate-sized species, has a very large egg, but *B. nubilus*, perhaps the largest cirripede known, has only a medium-sized egg, and the largest reported egg size for a cirripede is for *B. hameri* (442 x 232 u), a large species. All of these cirripedes have a planktotrophic larva and most lack a truly lecithotrophic egg, so it is difficult to judge the significance of these egg sizes without a better estimate of the length of the larval period (see Chapter III). It may be that the length of the brooding period in the mantle chamber is as important as the length of the larval period in relation to egg size, such that *T. squamosa* retains its broods for 1.5 months, *B.* glandula one month, and *C. fissus* 0.5 months (see Chapter II).

Barnes and Barnes (1968) show that the egg number per brood of a species may vary from place to place geographically and vertically in the intertidal zone. The amount of regional variation in egg number per brood can be as much as an order of magnitude in some species, such as *Balanus balanoides*, and the variation appears to be dependent on local conditions rather than upon larger-scale latitudinal patterns. No attempt was made in the present study to look at variations in egg number per brood at different intertidal levels at Morro Bay or at other regions. However, this is an important variable which would affect all of the life table calculations and which needs much further study. Apart from these variations, *Chthamalus fissus* in the present study has numbers of eggs per brood very similar to those shown by Barnes and Barnes (1968) for *C. stellatus* and *C. depressus* of a 0.5 mg body weight. *Balanus glandula* has similar numbers of eggs per brood as *B. amphitrite*, *B. perforatus*, and *Elminius modestus* of equivalent body weight. *Tetraclita squamosa* has egg numbers per brood similar to *Pollicipes cornucopia* of equivalent body weight. *B. balanoides* and *B. improvisus* appear to have larger numbers of eggs per brood than the other species at equivalent body weight. Good published estimates of the numbers of broods per year are lacking for most barnacle species, with the exception of the boreo-arctic species such as *Balanus balanoides* which have only one brood each season. Without these estimates, it is difficult to compare the fecundity schedules of the three species in the present study with those of other species. However, *B. balanoides* with only a single large brood would probably have a much lower annual fecundity than either *B. glandula* or *T. squamosa*, but a higher fecundity than *C. fissus*.

The demographic characteristics presented here for

Chthamalus fissus, *Balanus glandula*, and *Tetraclita squamosa* provide considerable insight into the pattern of population dynamics for each species. *C. fissus* has poor survivorship and low fecundity relative to the other two species, but its early onset of reproduction results in a short generation time and a potential for rapid population increase. *B. glandula* has an intermediate survivorship rate but the highest fecundity. Although these rates result in the highest net reproductive rate per generation, its delayed onset of first reproduction until it is about four or five months older than *C. fissus* result in a generation time more than twice that of *C. fissus* and an intrinsic rate of population increase which is below that of *C. fissus*. *T. squamosa*, on the other hand, shows the best survivorship and an intermediate but high fecundity, resulting in an intermediate but high net reproductive rate per generation. In contrast, the delay in the onset of reproduction of *T. squamosa* until the second year, coupled with the delayed peak in survivorship-weighted fecundity until its third year results in a much longer generation time and much slower potential rate of population growth. These patterns emphasize the important effects of the age of first reproduction on the generation time and the intrinsic rate of population increase. These patterns confirm the predictions of Lewontin (1965) and others that the intrinsic capacity for increase in numbers is far more sensitive to changes in the age at first reproduction than to changes in fecundity or survivorship during the life history of an organism. However, what *T. squamosa* sacrifices in a longer generation time and slower intrinsic rate of population increase by delaying the onset of reproduction, is apparently gained in the adaptive advantage of having more energy to allocate to initial growth to a size large enough to escape mortality from many predators and competitors.

Appendix Figure V-1. *Tetraclita* *squamosa* growth. Curve extended by eye from the curve derived in Figure IV-20.


TETRACLITA SQUAMOSA
GROWTH
Extended curve
Derived curve
//
BASAL DIAMETER (mm)
0
10
20
30
40
50
60
AGE (mos.)
0
10
20
30
40
50
60
70
80
90
100
110
120

CHAPTER VI. SUMMARY

Chthamalus fissus is a small species tolerant of the physical rigors of high intertidal zones and well adapted to exploit open space opportunistically in the lower zones. It produces as many as 16 small broods in rapid succession during a long season from spring through early fall, and low food availability limits brood production to lower frequencies during the rest of the year. It does not store nutrients for more than one brood at a time, and it puts out a brood as soon as sufficient yolk reserves are required--approximately every two weeks during the brooding season. When food availability is high, the time between broods is limited only by the developmental time of the brood in the mantle chamber, and the next brood is deposited as soon as the larvae of the previous brood hatch into the plankton. This rapid turnover of broods results in a proportionally very high yearly allocation of energy to production of eggs.

Settlement of Chthamalus fissus occurs erratically throughout the year at all intertidal levels. However, it grows slowly to a small size, and its poor ability to compete for space results in a very high mortality in lower zones, where it is crowded by Balanus glandula and other species as well as being eaten by predatory snails and sea stars. It has better, but still low survival in the high intertidal zones where competition and predation are reduced. Although it has a low net reproductive rate per generation, C. fissus becomes sexually mature and begins to reproduce at an early age of about two months, resulting in a short generation time, an early peak in reproductive value, and a high intrinsic rate of population growth. These life history characteristics of *C. fissus* accommodate a rapid population turnover, compensating for its high mortality, and thus allowing it to exploit changing conditions and ephemeral open space quickly.

Balanus glandula is a species of moderate size which is well adapted to dominate large areas of the intertidal zone for part of the year. It produces as many as six large broods from mid-winter to late spring. It rapidly builds up yolky reserves for several broods during summer when food availability is high, and the ovary remains full of yolk through the fall until cold temperature stimulates brooding in the winter. Broods are incubated in the mantle chamber for about one month, with minimal delay between successive broods. Some additional nutrients are probably added to the ovary from feeding during the brooding season, but the ovary appears to be spawned out by June. *B. glandula*, thus, has an intermediate but high yearly allocation of energy to production of eggs.

A sharp peak of settlement of *Balanus glandula* occurs during May or June, and many more *B. glandula* settle in the low intertidal zones than in the high. Growth is very rapid for an initial period of about three months, after which the rate becomes more moderate and continuous for the rest of the barnacle's life. High settlement densities coupled with rapid initial growth during summer result in *B. glandula* crowding and smothering many other organisms in the lower zones, but this also produces intense intra-specific competition for space. The competition and predation by snails and sea stars causes high mortality in the lower zones, and the fewer barnacles of this species settling in the spatial refuge of the higher zones show a much higher survivorship.

Balanus glandula begin to reproduce and attain maximum reproductive value in their first season, but the delay of the onset of brooding until winter at about age six or seven months results in a generation time more than twice that of C. fissus. In spite of a very high net reproductive rate per generation, this longer generation time results in an intermediate, though high, intrinsic rate of population growth. This pattern of life history thus allows B. glandula to dominate a great deal of space in areas of the lower mid-intertidal zone during part of the year. Such dominance also probably effectively saturates the predator populations during the summer when many of the snails and sea stars are most active. 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; although information on the annual feeding cycles of the predators was gathered in Washington where winter temperatures are very cold, and similar data needs to be gathered for Morro Bay communities (Mauzey, 1967; Paine, 1969; Connell, 1970; Menge, B., 1972a,b; and Menge and Menge, 1974).

Tetraclita squamosa is a relatively large barnacle which is adapted for long-term competition for space and predator avoidance in lower intertidal zones. It produces about three intermediate, but still large broods during summer months when temperatures are warm. It does not appear to store up yolk for more than one brood at a time, but food availability is high during the brooding season and the incubation time of 1.5 months for each brood is apparently sufficiently long for the next brood to be manufactured. The few broods produced over a relatively short season result in a proportionally low yearly allocation of energy to production of eggs.

Settlement of _Tetraclita squamosa_ occurs in comparatively low densities in the lower intertidal zones over a limited fall period during October or November, but recruitment is patchy in space and in time from year to year. _T. squamosa_ grows rapidly and continuously over several years to a large size. Larger _T. squamosa_ are able to out-compete _B. glandula_ and many other species for space and attainment of large size reduces predation, resulting in a relatively high survivorship rate. The onset of reproduction is delayed in this species until the second brooding season at about 19 months of age, and maximum reproductive value is not reached until the third year. This long delay results in a generation time about twice that of _B. glandula_ and a relatively low intrinsic rate of population growth, in spite of an intermediate, though high net reproductive rate per generation.

However, the delay in reproduction of _Tetraclita squamosa_, the timing of its reproduction when food availability is high, and its low yearly allocation of energy to egg production would all facilitate the advantageous allotment of maximum energy for rapid growth to a size large enough to compete effectively for space and to avoid many predators. The timing of settlement in the fall is advantageous in that much of the initial smothering by B. 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 these smallest, and therefore, most susceptible individuals to predation will be available only when the predatory snails and sea stars tend to be quiescent. These barnacles will then have winter and early spring to grow before the major predators are active again and the 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 nearby availability of other T. squamosa for cross-fertilization.

Reproductive patterns in the context of life histories have been especially well studied in zooplankton (e.g., Hutchinson, 1967; Alan, 1976), birds (e.g., Lack, 1954; Skutch, 1967; Cody, 1966), lizards (e.g., Tinkle, 1969), and plants (e.g., Harper, 1967; Harper and Ogden, 1970; Gadgil and Solbrig, 1972). However, theoretical considerations of what have come to be called "reproductive strategies" and "life history tactics" have, in many respects, outstripped the data available to test the vast number of theoretical hypotheses generated over the last 20 years.

As early as 1930, Fisher defined and emphasized the importance of the relative reproductive value of different age classes, and Deevey (1947) introduced ecologists to the area of comparative demography. Cole (1954) emphasized the effect of delayed reproduction and longer generation time on lowering the intrinsic rate of population growth, and he arrived at a paradox that the gain in the intrinsic rate of population growth achieved by a species switching from an annual to a perenial reproductive habit would be exactly equivalent to adding only one offspring to the original annual fecundity. Lewontin (1965) also emphasized the important effect of the age at the onset of reproduction on the intrinsic rate of population growth for a colonizing species. However, Murphy (1968) suggested that repeated reproduction is advantageous when survival of pre-reproductive age-groups is uncertain and survival of reproductive age-groups is relatively stable, and Charnov and Schaffer (1973) revealed the hidden assumption which generated Cole's paradox by examining the importance of the ratio of juvenile to adult mortality.

MacArthur and Wilson (1967) introduced the term "r-selected" to characterize populations and species occurring at low densities relative to the carrying capacity of the environment and the term "K-selected" to characterize populations and species occurring at densities near the carrying capacity of the environment. Gadgil and Bossert (1970) indicated that r-selected species are expected to have high fecundity with small young early in life in a "big bang" strategy, while

K-selected species are expected to have lower fecundity with larger young and a longer life. Gadgil and Solbrig (1972) pointed out that r- and K-selections are relative terms and that only similar organisms should be compared. They emphasized the importance of density-independent mortality in selecting for r-strategists and showed that r-strategists will allocate greater proportions of their resources to reproduction than K-strategists. Pianka (1970) emphasized that species occur in a continuum of r- and K-strategies, but that r-strategists are found in environments of greater unpredictability and catastrophic, density-independent mortality and low competition, while K-strategists are found in relatively more predictable environments and have higher density-dependent mortality and rigorous competition. Pianka correlates the following life history characteristics with r-selection: low early survivorship with populations that recolonize each year, rapid development, high intrinsic rate of population growth, early reproduction, small body size, single reproduction, short life span of less than one year, leading to high productivity. And he correlates the following characteristics with K-selection: high early or constant survivorship rates, more stable populations with lesser fluctuations in recruitment, slow development, lower intrinsic rate of population growth, delayed reproduction, larger body size, longer life span, and efficiency.

Stearns (1976) suggests a third strategy in addition to r- and K-strategies may be called "bet-hedging," based on the arguments of Murphy (1968) and Schaffer (1974) that it is important for a species to minimize the chance of leaving no offspring under certain conditions. In this line of thought, a fluctuating environment that has its impact on juvenile mortality favors reduced reproductive effort, smaller clutches, and longer-lived organisms. While environmental variability that affects adult survival favors increased reproductive effort, larger clutches, and short-lived organisms.

Stearns (1976) provides an excellent critical review of most of the theoretical, and much of the empirical work up to 1974 on the evolution of life history phenomena, and no further attempt will be made here to analyze this extensive and controversial literature. However, a few important points about the patterns of reproduction and life history of the three species of barnacles in my study can be raised in closing. While *Chthamalus fissus* may generally fit the description of a colonizing species or r-strategist and *Tetraclita squamosa* that of a K-strategist, *Balanus glandula* clearly displays elements of both strategies and this mixture is therefore difficult to characterize with such labels. Furthermore, aspects of these patterns point out the inadequacies of many of the theoretical generalizations. For example, although *C. fissus* might be characterized as an r-strategist with its high mortality, low competitive ability, high allocation of energy to egg production, small body size, early reproduction, and high intrinsic rate of population growth, it also shows low fecundity and much of the success of its strategy derives from its repeated production of small broods. In face of extremely uncertain survival, then, C. fissus has elements of a bet-hedging strategy of leaving at least a few young rather than none. This pattern also effectively spreads out the reproductive effort, increasing the chance of encountering some period of favorable conditions, and increasing the dispersal of siblings (see Strathmann, 1974). On the other hand, T. squamosa also exhibits elements of bet-hedging with its strategy of short brooding and patchy settlement periods resulting in erratic recruitment. Therefore, it is important to examine the patterns of these species only as sets of co-adapted traits, because comparisons of isolated aspects of their life histories may lead to over-simplified conclusions about the adaptive signficance of a particular characteristic.

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