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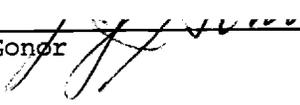
Harold Parker Batchelder for the degree of Master of Science

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Title: POPULATION CHARACTERISTICS OF THE INTERTIDAL GREEN SEA ANEMONE,
ANTHOPLEURA XANTHOGRAMMICA, ON THE OREGON COAST

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Chapter One

Field population censuses with a photographic quadrat method were used to describe the density and size structure of intertidal populations of the green sea anemone, Anthopleura xanthogrammica, on different types of rocky intertidal habitats on the Oregon coast. Anemone populations in marked plots were monitored for individual motility, growth, mortality, and recruitment. Experiments were performed to evaluate anemone population responses to simulated harvesting. Laboratory experiments were conducted to determine size-specific growth rates under known conditions. Rocky intertidal locations with dense populations of the green anemone are not abundant along the Oregon coast. No detectable fluctuations in anemone population density or size-frequency distribution were found during the two year study. Adult anemones showed little movement in either disturbed or undisturbed populations. No natural mortality or recruitment was found in study plots at any Oregon coastal location between July, 1977, and May, 1979. Removal of adult anemones from rock surfaces did not promote recruitment from the plankton onto the newly available surface, nor did anemones adjacent to depopulated plots rapidly immigrate into the cleared areas. Individual growth is inferred to be very slow in intertidal populations, requiring an estimated minimum of sixteen

years for an individual to grow from 2 cm to 10 cm diameter. Field and laboratory studies indicate that A. xanthogrammica is a long-lived, slow growing species with limited, low or erratic recruitment and highly stable intertidal adult populations. This study indicates that harvest of A. xanthogrammica will probably not be possible on a continuing basis.

Chapter Two

Anthopleura xanthogrammica populations within mussel beds were surveyed at several locations during the summers of 1978 and 1979. Oxygen consumption of anemones was measured at various experimental conditions. Theoretical rates of water evaporation during tidal exposure were calculated for anemones at several rates of insolation. Some mussel beds were found to have high numbers of anemones ($1600/m^2$), while others had lower densities ($200/m^2$). Calculated rates of water loss by evaporation indicate that loss of 75% of the water from a small anemone is possible during spring and summer, when daylight low tides are coincident with high insolation rates. Results from the measurements of anemone respiration, together with the time available for feeding at different tidal levels, suggest that on a vertical wall, the size gradient of anemones with tidal height is the result of height related differential growth.

It is proposed that chance factors during the planktonic, settlement, and early post-settlement periods largely determine the large scale distribution and abundance of intertidal A. xanthogrammica populations and that mortality from desiccatory water loss is of primary importance in determining the distribution of anemones within local populations

Population Characteristics of the Intertidal
Green Sea Anemone,
Anthopleura xanthogrammica,
on the Oregon coast

by

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POPULATION CHARACTERISTICS OF THE INTERTIDAL GREEN SEA ANEMONE,
ANTHOPLEURA XANTHOGRAMMICA, ON THE OREGON COAST

GENERAL INTRODUCTION

The population ecology of sea anemones has rarely been investigated. The absence of hard skeletal parts in anemones prevents accurate adult age determination. The lack of effective rapid tagging methods suitable for field study of large numbers of individuals has also contributed to the difficulties in studying the population ecology of sea anemones. Furthermore, growth of many individual anemones is often slow, life spans are long, and short term temporal variation in individual size is so great that field studies of only a few years duration are not sufficiently long to adequately ascertain the population parameters desired.

A few field studies of anemone populations have focused on behavior (Francis, 1973a, b, 1976; Hart and Crowe, 1977; Brace and Pavey, 1978), reproductive cycles (Ford, 1964; Chia and Rostron, 1970; Dunn, 1975, 1977a; Rostron and Rostron, 1978; Jennison, 1979a; Ottaway, 1979), and motility (Dunn, 1977b; Ottaway, 1978), and recently, on the seasonality of lipid content (Hill-Manning and Blanquet, 1979; Jennison, 1979b) and population structure (Sebens, 1977; Ottaway, 1979).

In order to assess factors determining habitat suitability, Sebens (1977) attempted to determine basic individual and population characteristics such as the time and intensity of recruitment, immigration rates into experimentally disturbed plots, and size-dependent fecundity and growth rates of Anthopleura xanthogrammica and A. elegantissima. The works of Ottaway (1973, 1978, 1979a,b) and Ottaway and Thomas (1971) on Actinia tenebrosa are the most comprehensive studies currently available on the population ecology of anemones.

Many diverse modes of reproduction are found in actinians and many species utilize several methods of reproduction. Previous work on the ecology of anemones has generally dealt with species such as Anthopleura elegantissima and Actinia tenebrosa, which have an asexual as well as sexual mode of reproduction, or Epiactis prolifera, which has internal fertilization and broods its young. Sebens' (1977) investigation of the ecology of A. xanthogrammica is the only previous population study to have dealt with an anemone having external fertilization and pelagic larvae as its only means of reproduction.

Many aspects of the physiological ecology of sea anemones have been investigated. Previous studies concerning the tolerance of anemones to extremes of temperature and desiccation, and the effects of sublethal extremes of temperatures, salinity, and aerial exposure on metabolic rate and presumably growth are pertinent to the problem being studied here. Actinia equina exhibited acclimation of metabolic rate to different water temperatures (Griffiths, 1977b). The southern extent of the distribution of each of three anemones along the Atlantic coast of North America was correlated with the experimentally determined upper lethal temperature of each species (Sassaman and Mangum, 1970). Stotz (1979) related the tidal zonation of three anemones to their morphology and ability to retain water within their coelenteron during tidal exposure. Griffiths (1977a) found adult Actinia equina to be very tolerant of desiccation and high temperature in laboratory experiments. Ottaway (1973) found small Actinia tenebrosa to be very susceptible to death from the effects of desiccation; the effect of temperature on mortality was relatively unimportant although adult A. tenebrosa moved away from areas of high temperature.

The present study was designed to assess the density, biomass, and size-structure of intertidal Anthopleura xanthogrammica populations on the Oregon coast. The rate of growth of individuals, individual motility, and mortality and recruitment were examined through periodic field sampling of selected sites. The density and size-structure of anemones in mussel beds were determined in order to test the hypothesis proposed by Sebens (1977) that recruitment of A. xanthogrammica larvae is spatially directed into upper intertidal mussel beds. Oxygen consumption of anemones was measured at different experimental conditions. Theoretical heat budgets and evaporative water loss rates were calculated using environmental insolation data.

The first chapter presents the results of surveys of anemone populations and laboratory experiments, designed to determine the population characteristics of A. xanthogrammica, especially those relevant to future decisions concerning the utilization and management of this intertidal sea anemone resource. Chapter two presents additional results which are used to evaluate the mechanisms controlling the population characteristics of A. xanthogrammica.

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CHAPTER ONE

POPULATION CHARACTERISTICS OF THE INTERTIDAL
GREEN SEA ANEMONE, ANTHOPLEURA XANTHOGRAMMICA,
ON THE OREGON COAST

H. P. Batchelder and J. J. Gonor

POPULATION CHARACTERISTICS OF THE INTERTIDAL GREEN SEA ANEMONE,
ANTHOPLEURA XANTHOGRAMMICA, ON THE OREGON COAST

INTRODUCTION

The potential for discovering new pharmacologically active substances from marine organisms has lead to extensive research efforts on biologically active substances from marine coelenterates. Searches for such compounds among the anthozoa have been especially productive (see reviews by: Norton, et al. 1978; Beress, 1978; Kulkarni et al. 1978). Shibata (1974, 1975, 1976), and Norton (1976, 1978) of the University of Hawaii and their associates have shown that at very low concentrations, extracts from common sea anemones of the Pacific coast of North America have potent selective stimulatory effects on mammalian heart muscle. Their research on extracts from Anthopleura xanthogrammica and A. elegantissima lead to the isolation and pharmacological characterization of three cardiogenic agents, Anthopleurins A and B from the first species and C from the second (AP-A, AP-B, AP-C). They have also shown that these substances are polypeptides and have determined the amino acid sequences of Anthopleurin A (Tanaka et al. 1977) and C (Bennett, 1977) which are very similar. Of the three substances, the pharmacological properties of AP-A have been most thoroughly investigated. AP-A has very favorable properties as a cardiogenic agent and fewer undesired effects compared to the cardiac glycosides such as digitalis in current clinical use. In his review of this work, Norton et al. (1978) stated: "All the pharmacological work so far indicates AP-A is a good candidate for clinical study in the treatment of the failing heart with potential for considerable advantage over currently used drugs".

In considering the possibility of clinical trials of this drug in humans, the potential source of future supplies is of concern. The AP-A molecule is a polypeptide with a chain length of 49 amino acids and chemical synthesis of the entire molecule is presently not commercially feasible. The only potential source of supply would therefore be the natural populations of the anemones. In A. xanthogrammica from the coasts of California, Oregon, Washington, and British Columbia, AP-A is present in quantities ranging from 10 to 48 parts per million of wet preserved (alcohol) weight of anemone (Norton, et al. 1978). The feasibility of relying upon harvest of natural populations as a source for a material in such low concentration can be questioned. While the anemones are known to be relatively common, little was known about their population biology and no information on actual abundance was available to use in evaluating this question. It was not possible from previously published information to estimate the quantity of available stocks nor adequately predict the impact of harvesting on the anemones or the intertidal community of which they are a part.

It was known that Anthopleura xanthogrammica is common on rocky shores and headlands on wave exposed open coasts from Sitka, Alaska to Punta Baja on the outer coast of Baja California, Mexico (Sebens, 1977). Larger individuals are abundant in lower tide pools and channels below mussel beds. Hand (1955) and others have noted that small, sexually immature individuals are common within mussel beds or in crevices around them. In addition, A. xanthogrammica is also found in the shallow subtidal on rocky shores (McLean, 1962). Predation by A. xanthogrammica

on a broad range of prey species was shown by Dayton (1973, 1975) to be important in intertidal community processes. Reproduction is exclusively by sexual means (Siebert, 1974). No other information on population biology of this species was available until the unpublished work of Sebens (1977) became known to us after the start of our work.

An estimate of the availability of the natural source is required before production of AP-A can begin. Efficient commercial utilization will require detailed information on natural population abundances.

The purpose of the research described here was to provide information needed to effectively utilize and manage intertidal green sea anemone resources. The distribution, abundance, size structure and dynamics of intertidal A. xanthogrammica populations were studied along the coast of Oregon. Seasonal sampling of some field areas provided data to estimate migration, motility, mortality, recruitment and individual growth in undisturbed populations. Laboratory populations were maintained to provide information on size-specific growth rates under known conditions. Field experiments were performed to evaluate population responses to simulated harvesting.

MATERIALS AND METHODS

FIELD POPULATION SURVEYS

Samples were obtained using a quantitative photographic method in order to estimate the density, spatial distribution and size structure of anemone populations. Photography was done with a 35 millimeter reflex camera on color transparency film to utilize the advantage of color contrast. To obtain uniform sharp and shadow-free exposures under all field conditions including darkness during winter low tides, an electronic flash unit was used for all photography. Quadrat sampling frames with flat, yellow borders and a white string grid were held closely against the rock surface to be photographed. The camera was held approximately normal to the surface to minimize parallax. A square frame, 1.0 m^2 in area, and a rectangular frame, 60 cm by 80 cm were used. Both were strung with white string at 10 cm intervals along the edges to produce a grid. The rectangular frame is proportional to the 35 mm film frame and was used at closer camera distances to improve resolution of the smaller anemones in the samples. The grids of the sampling frames provide a scale in two dimensions regardless of camera angle, and permitted close corrections in later measurements for both size and parallax. (Gonor and Kemp, 1978).

At the scale used in most of this work, on typical rock surfaces, accurate enumeration of A. xanthogrammica in the photographs is possible for all sizes down to individuals 0.7 cm in diameter. In photographs of relatively smooth rock surfaces or surfaces with good color contrast, anemones smaller than 0.7 cm diameter can be distinguished and measured. In the field, direct searches of most study areas found few anemones

less than 0.7 cm in diameter. The photographic technique yields large, unbiased and accurate samples of the anemone population on most rock faces.

Each transparency was projected at a convenient working size onto white paper and the quadrat frame boundaries and grid intervals marked on the paper. The outline of each anemone present was then drawn in, following the grid rows for systematic coverage. This provided a readily accessible graphic record for later comparisons or for gathering additional data. The anemone outlines were later counted and their diameters measured, using a scale correction made for each horizontal grid row. Some diameters and counts were made directly on projected images, but most of the work was done as described.

Wide horizontal intertidal benches having low densities of A. xanthogrammica were sampled in transects both parallel and vertical to shore by nondestructive, in-situ counting and measuring of diameters. Since the anemone density per sample unit was low compared to other sampled habitats, no significant reduction in sampling time would have resulted from using the photographic sampling method.

Tidal heights at each sampling area were estimated in the field with a hand level and stadia rod, using water level at predicted times of low tide for reference. The height of the frame was thus usually known for each photograph and the data could be subdivided by tidal height intervals.

POPULATION DYNAMICS

Periodic sampling of marked plots within five natural anemone aggregations was conducted to describe seasonal or other temporal changes detectable within one year. Two groups of anemones (one of 20 and one

of 40 individuals) on a basalt boulder were photographed during July, 1977 and January, April, June, and August of 1978 to assess seasonal events or changes in these populations. All net anemone movements into, out of, or within defined boundaries were measured. The limit of the photographic method for relocating an anemone on the rock was approximately ± 2 cm. These areas were also searched for new recruits to the adult population and for the disappearance of anemones from the marked plots and adjacent areas, as evidence of mortality of adults.

An estimate of short term changes in diameter of individual anemones in three groups was obtained over 55, 57 and 81 day periods respectively, between June and September, 1978. Diameters of contracted anemones were measured in the field at low tide on an irregular wall at the Strawberry Hill location. The precision of repeated in-situ measurements was assessed by repeating measurements on one group of anemones over successive 3, 13, and 15 day intervals. All groups were also measured over two successive 26 to 29 day periods, and one group over three such intervals. Each set of successive measurements on individuals in each anemone group was compared using the Wilcoxon matched pairs signed ranks test. All individuals were tagged with numbered t-bar tags for identification.

The response of anemone populations to harvesting was evaluated by removing all individuals from small areas of rock surfaces. The corners of areas to be cleared were marked with concrete nails, the areas photographed, and all Anthopleura xanthogrammica within the marked plots removed. Some of these anemones were used in the laboratory to provide data for conversions among diameter, fresh wet weight, and ash-free dry

weight. Ten to twelve months later, marked areas were re-photographed and all anemones located within them removed and their diameters measured.

SIZE-SPECIFIC GROWTH RATES IN THE LABORATORY

Anemones ranging from 0.4 cm to 12.0 cm in diameter were maintained from September, 1977 to May, 1979 in tanks of running ambient seawater. Temperature in the tanks varied from a low of 4.0°C in December, 1978 to 15.5°C in October of 1978, with mean monthly temperatures of 8 to 12°C for most months. Mean monthly salinities and salinity ranges were seasonally variable. Mean salinity remained high (above 30‰) from June to November; this period also exhibited a monthly salinity range of approximately 4‰, the smallest monthly range of the year. From December to May, salinity of the laboratory seawater pumped from lower Yaquina Bay fluctuates markedly with the tidal cycle. Mean monthly salinities less than 28‰ are common from December to May. In late winter and early spring, especially in February and March, salinity of the seawater supply during low tide falls as low as 10‰. Consequently, the seawater supply to the tanks containing anemones was shut off when the salinity dropped below 25‰ and turned on when the salinity again exceeded this level, usually 3 to 4 hours later, but in winter occasionally extending to 14 hours. All tanks were aerated.

Anemones maintained in the seawater tanks with natural daylength lighting from August to November of 1977, were not fully expanded and appeared to be losing their symbiotic algae. After November of 1977, all anemones were maintained with 24 hour light from overhead fluorescent lights and the deep green color and behavior returned to normal.

Anemones maintained in the laboratory were fed fresh mussels, Mytilus californianus, or frozen herring once each week from August, 1977 to June, 1978. After June of 1978 each individual anemone was fed three times per week. Tests indicated no difference in acceptance of the two food sources by A. xanthogrammica. Using entire M. californianus of a standard size as a food source for large anemones provided a convenient qualitative method of assessing the extent of digestion by examining the mussel valves after egestion. Because of this advantage, mussels were the major food source for the anemones during laboratory growth studies. During growth investigations, feeding at a rate of three times per week was used because larger anemones required 35 to 45 hours to ingest a mussel, digest all of the soft tissue and egest the shell. The results were usually recorded two days after feeding, as the number of completely digested, partially digested, and undigested mussels in the tank. Anemones ranging from 0.6 cm to 12.0 cm in diameter were fed an estimated 5 to 10% of their own weight in mussel tissue at each feeding.

Anemones smaller than 3 cm to 4 cm diameter were kept individually in containers appropriate for their size. Trays with compartments of 28 ml volume each were used to culture most individuals smaller than 1.1 cm in diameter. Anemones 0.7 cm to 1.9 cm in diameter were maintained individually in 100 ml plastic cups. Individuals kept in tray compartments and plastic cups standing in running sea water required water changes every 48 hours. Anemones 1.5 cm to 3.0 cm in diameter were placed in shallow glass bowls which were then submerged in running seawater tanks. Anemones greater than 3.0 cm were individually tagged

with numbered t-bar tags (Floy Tag Co., Seattle) with knotted vinyl ends. Until December of 1978, tagged individuals were permitted to attach directly to the fiberglass surfaces of the sea water tanks. To avoid damage during detachment for weighing, attempts were made to attach the large, individually tagged anemones permanently to tared glass plates with slightly roughened surfaces. These attempts were unsuccessful, because the anemones moved as soon as possible to any available surface which had a rougher texture than the glass. In December of 1978, 87 large anemones were successfully attached permanently to separate tared ceramic tiles. They were maintained on these tiles until May, 1979, when the growth experiments were terminated.

Growth of the sea anemones was measured by periodically weighing them while they were suspended in sea water. This reduced weight measure was used to quantify growth of all anemones larger than 2 cm diameter, including the large tagged individuals and those maintained in submerged glass bowls. Reduced weight is defined as the weight of an individual when suspended in water of known density. It is the actual weight of the tissues minus the weight of the volume of water displaced by the tissues. Most reduced weights of anemones were taken using ambient sea water from the tanks as the suspending fluid to eliminate problems caused by salinity differences between the ambient sea water used and the water contained within the coelenteron of the anemones. Variations in anemone weights caused by different states of contraction and water expulsion are eliminated using a submerged or reduced weight technique if the suspending medium and coelenteron water have equal density. The method presumes that the relative amounts of body chemical constituents

remains constant. If an increase in body lipid were to take place, this assumption would lead to underestimated actual weight.

Wet weight in air, measured in closed containers to reduce evaporative water loss, was used to quantify growth in anemones less than 2 cm in diameter. Replicate weighings of anemones in air indicated that wet weight could be determined with a precision of 6% or less for most individuals of this size. The precision of wet weights obtained for anemones larger than 2 cm diameter was only 20%. The greater precision of repeated wet weights for small anemones was probably related to their small coelenteron volume and thin body walls which permitted more standardized contraction and blotting.

Since weights of large and small individuals were measured by different methods, an equation relating the two was obtained to allow comparison. The blotted wet weight (WW) and reduced weight (RW) of 93 large anemones were determined and related by the equation:

$$WW(g) = 24.883 + 21.263 RW(g) \quad R^2 = .65 \quad N=93.$$

The diameter of 66 anemones collected from Strawberry Hill during June, 1978 were measured and the individual blotted dry and weighed. The dry weights were determined after oven drying at 80°C for 7 days. Weights were obtained after ashing at 550°C for 5 days and the dry weights adjusted for ash content. Regression of ash-free dry weight (AFDW) on wet weight (WW), and diameter (D) on ash-free dry weight provided the following conversions:

$$WW(g) = 0.532 + 6.187 AFDW(g) \quad R^2 = 0.97 \quad N=66$$

$$AFDW(g) = 0.043 D(cm) + 2.823 \quad R^2 = 0.93 \quad N=60.$$

RESULTS

POPULATION STRUCTURE

Sampling to describe population characteristics of Anthopleura xanthogrammica was conducted at Boiler Bay, Yaquina Head, Yachats, Neptune State Park, Bandon and Port Orford along the central and southern Oregon Coast. Preliminary surveys were also done at Rocky Creek State Park, Seal Rock State Park, Sunset Bay, Cape Arago, and Cape Blanco, areas which were found not to have large populations of A. xanthogrammica. Only areas with relatively high population densities were studied in detail. The locations sampled extensively are described below (Fig. 1).

Boiler Bay is an open coastal cove with basaltic breccia, soft sandstone and siltstone substrates. Wide intertidal siltstone benches and basaltic boulders were sampled to describe the anemone populations. A wide intertidal shelf dissected by channels and tidepools was sampled at Yaquina Head, an exposed basaltic headland. The basaltic bench at Yachats, Oregon is very exposed to waves which severely restricted access and sampling during winter months. Many surge channels run parallel to shore, but few tidepools are present. Two different habitat types are predominant at Yachats; vertical rock walls with rock below them, and flat horizontal surfaces, some of which can become covered by sand. The Strawberry Hill location at Neptune State Park is a wide rocky intertidal area. The basalt substrate is very dissected and contains numerous stacks, surge channels, tide pools and ridges. Extensive sampling was done within a length of shoreline, about 46 m long, where the density of anemones is relatively high. Anemone populations of tide pools, horizontal rock surfaces and vertical surfaces were sampled.

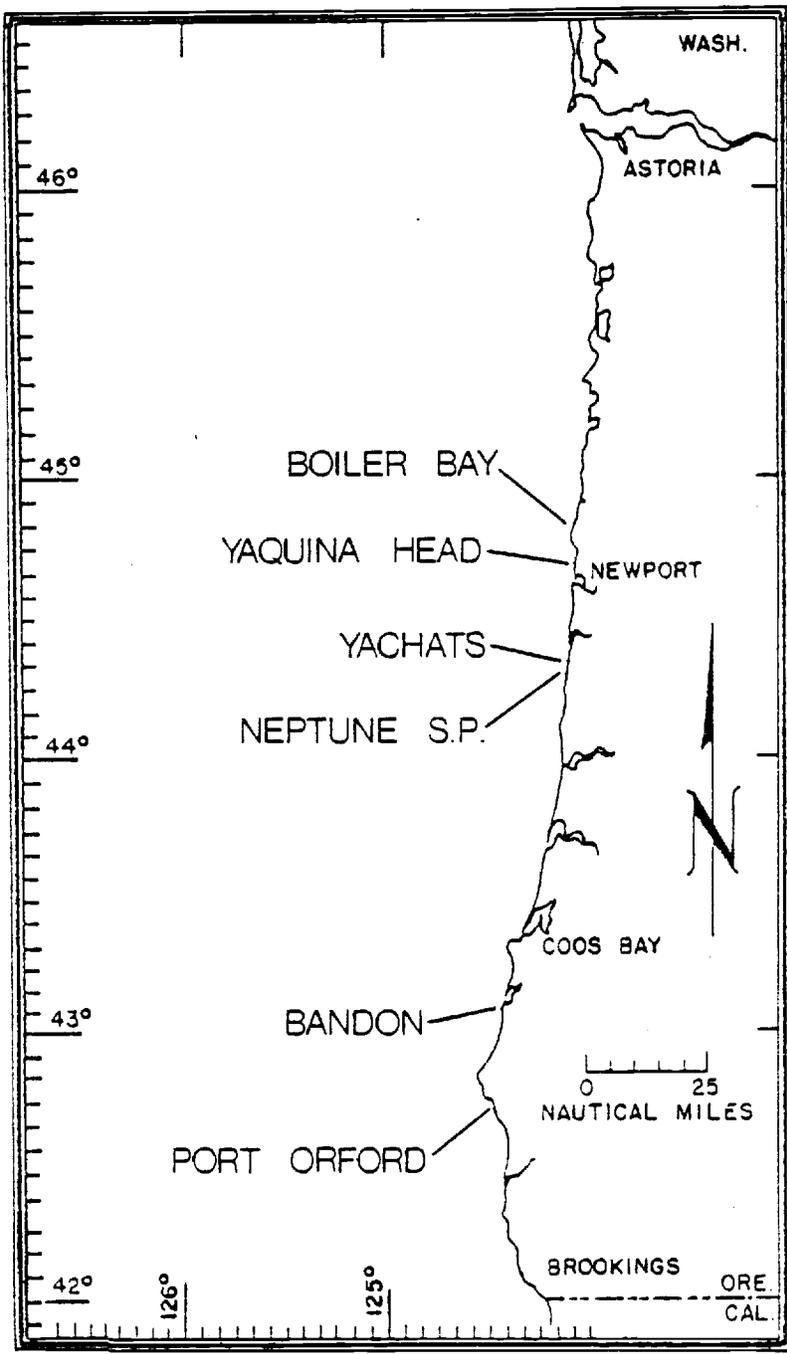


Figure 1. Sampling locations along Oregon coast.

Coquille Point, near the town of Bandon, Oregon, is a large rocky headland with intertidal rock substrates limited to the steep sides of the headland and scattered boulders embedded in sand at its base. The predominant habitat type is rock wall with sand below it. The sand appears to be very mobile and during some periods of the year may cover a substantial part of the anemone populations present on the rocky substrates.

Battle Rock, located just south of Port Orford, Oregon, is a narrow steep sided outcrop perpendicular to shore. The southeast facing intertidal wall of this outcrop is covered by a dense population of Anthopleura xanthogrammica from the level of the sand below the walls up to approximately 80 cm above the sand level. It is probable that these anemones, like those at Bandon, are covered by sand either seasonally or aperiodically. This habitat has also been classified as a rock wall with sandy substrate below it.

Mean density, biomass and mean diameter of anemones sampled from the five habitat types studied are summarized in Table 1. Figures 2 and 3 show the distribution of numbers of individuals and biomass, respectively, by size class for each of the habitat types. The size-frequency comparisons in Fig. 2 indicate that wall-rock, wall-sand, and horizontal surfaces are similar in mean anemone diameter and size distribution. However, in the wall-sand habitats the mean biomass of A. xanthogrammica per square meter (Table 1) is less than in either of the other two habitats. The relatively few large individuals which contribute a substantial part to the total biomass of the horizontal flats and wall-rock habitats are entirely absent from the lower levels of rock walls with sand below them (Figure 3).

TABLE 1. Mean density, mean biomass, and mean anemone diameter of A. xanthogrammica populations of different habitats.

HABITAT TYPE	AREA SAMPLED (m ²)	MEAN DENSITY (#/m ²)	MEAN DIAMETER (cm)	MEAN BIOMASS (gAFDW/m ²)
Wall-rock	32.94	185.2	3.4	584.5
Wall-sand	15.72	137.3	3.4	290.6
Horizontal Surfaces	10.95	145.4	3.5	427.0
Pools	4.69	86.1	6.5	1067.5
Wide horizontal benches	92.16	3.4	5.2	23.2

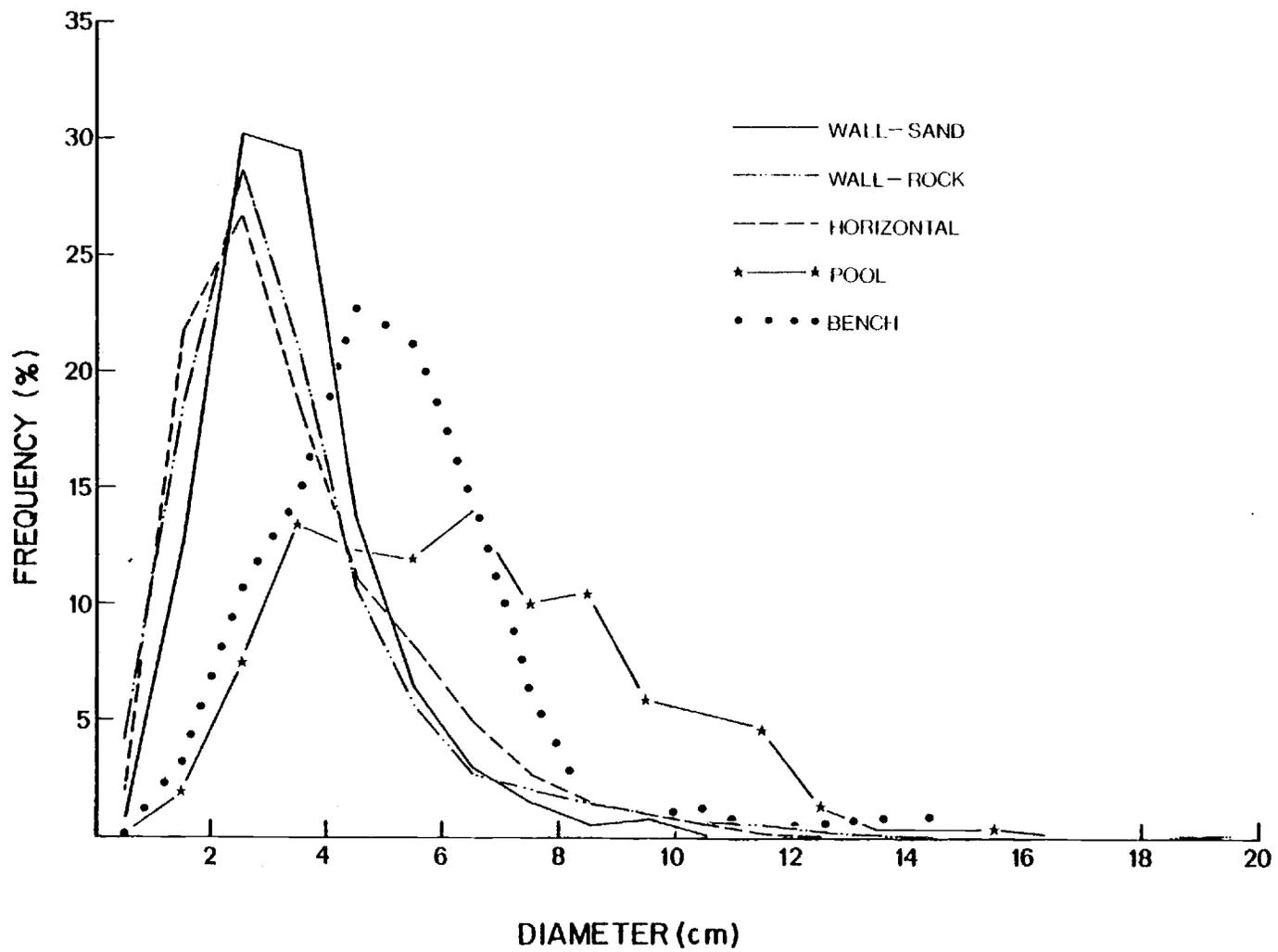


Figure 2. Size-frequency distributions of *A. xanthogrammica* inhabiting different habitats. See Table 1 for absolute numbers.

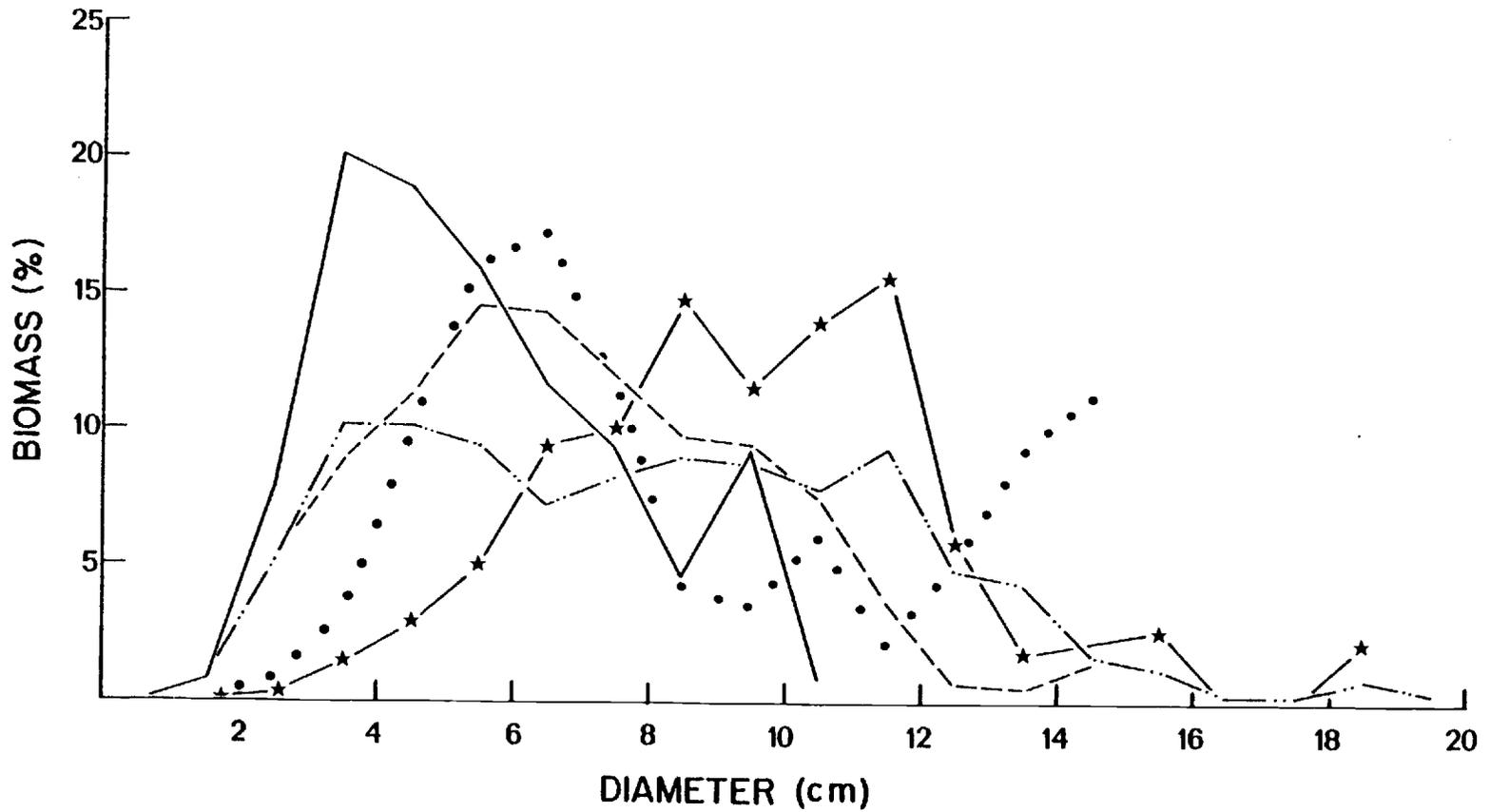


Figure 3. Size-biomass distributions of *A. xanthogrammica* inhabiting different habitats. (Symbols as in Figure 2). See Table 1 for absolute values of biomass per square meter.

The majority of the individuals on the horizontal surfaces, wall-sand and wall-rock habitats were restricted to a narrow size range (Fig. 2). On wide horizontal benches the modal diameter was larger than on the three previously mentioned habitat types and the majority of individuals fell into a broader size range. A large size range of anemones, with no well defined peak, was present in pool habitats. The anemone size-frequency distributions for all habitat types were unimodal whereas the size-biomass curves had multiple modes because of the power relationship between diameter and biomass (Fig. 2, 3). In all habitat types the major mode of the size-biomass curve occurs at a larger diameter than the corresponding size-frequency mode. A major portion of the biomass exists in the fewer but larger individuals. This is most evident in the biomass curve for wide horizontal benches (Fig. 3).

Vertical walls, which span a tidal range of one meter or more exhibit a well defined size gradient of Anthopleura xanthogrammica. The exposed walls at Yachats, Strawberry Hill and Boiler Bay exhibit such a size gradient, with larger individuals located lower on the wall (Figures 4, 5, 6). On all three of these walls, the rock surface is relatively smooth and the anemone size gradient is well defined. Other walls at Strawberry Hill, which have high surface relief, do not have a clearly defined vertical size gradient. Concavities, cracks and other protected areas in the upper regions of such walls contain large anemones which confuse the overall size gradient found on walls with little surface relief. A consequence of the anemone size gradient with tidal height on walls with little surface relief is that lower areas of walls contain considerably more biomass than the upper areas of the walls provided that anemone density does not differ markedly with height.

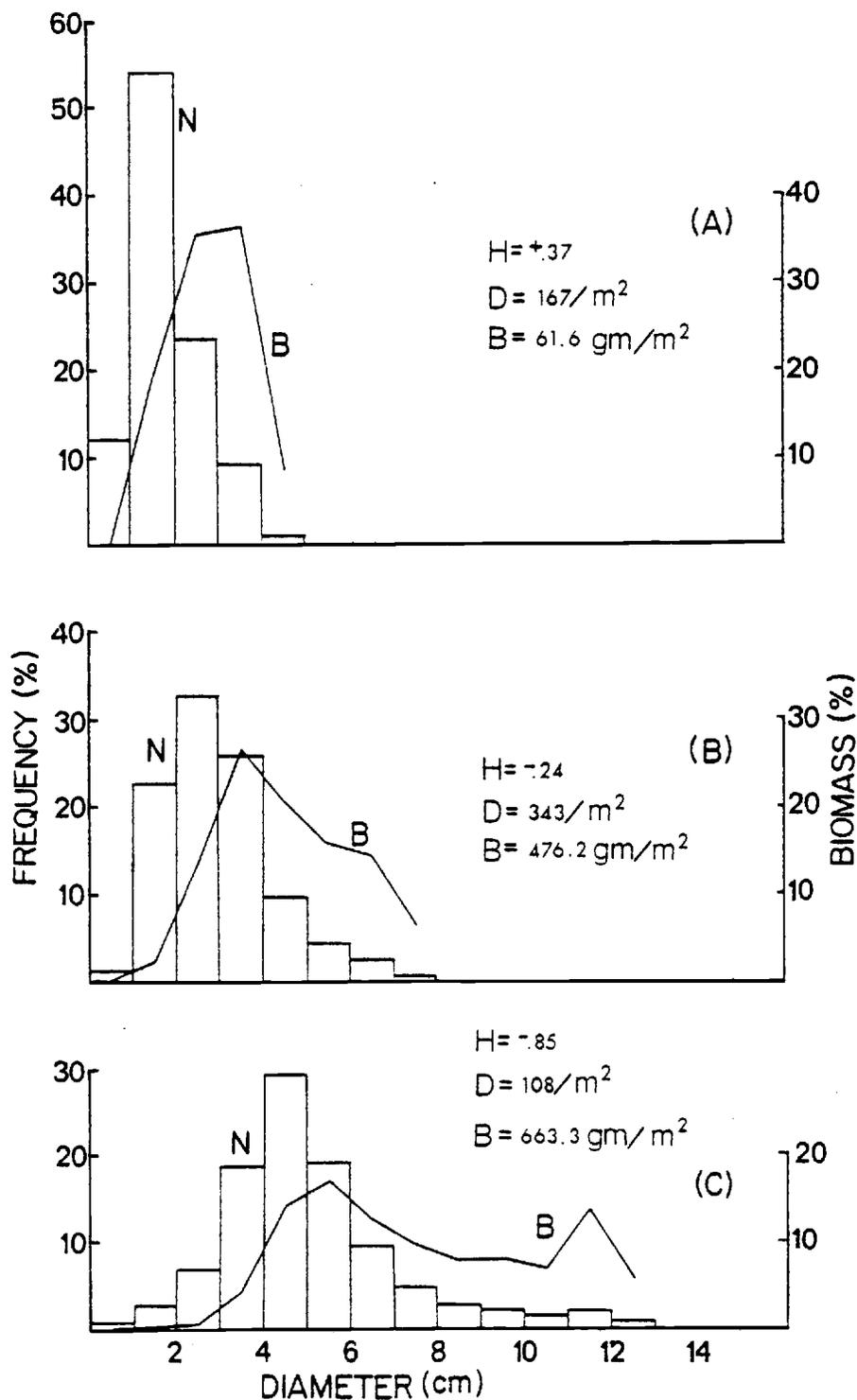


Figure 4. Size-frequency (N) and size-biomass (B) distributions for A. xanthogrammica as a function of tidal height on a vertical wall (YH 2) at Yachats (H - height relative to MLLW; D - mean density; B - mean biomass (gm AFDW/m²)).

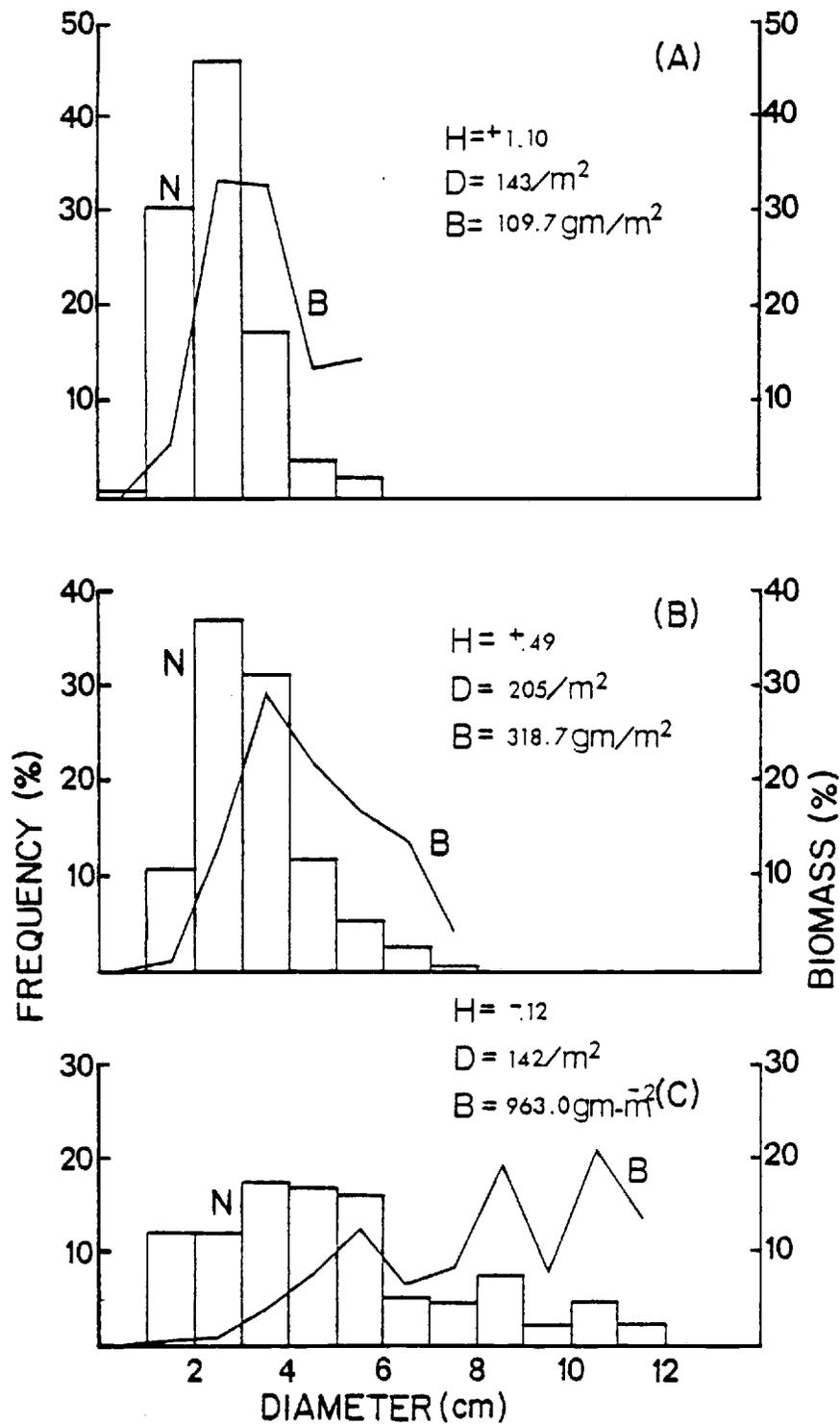


Figure 5. Size-frequency (N) and size-biomass (B) distributions for A. xanthogrammica as a function of tidal height on a vertical wall (SH 1) at Neptune State Park.

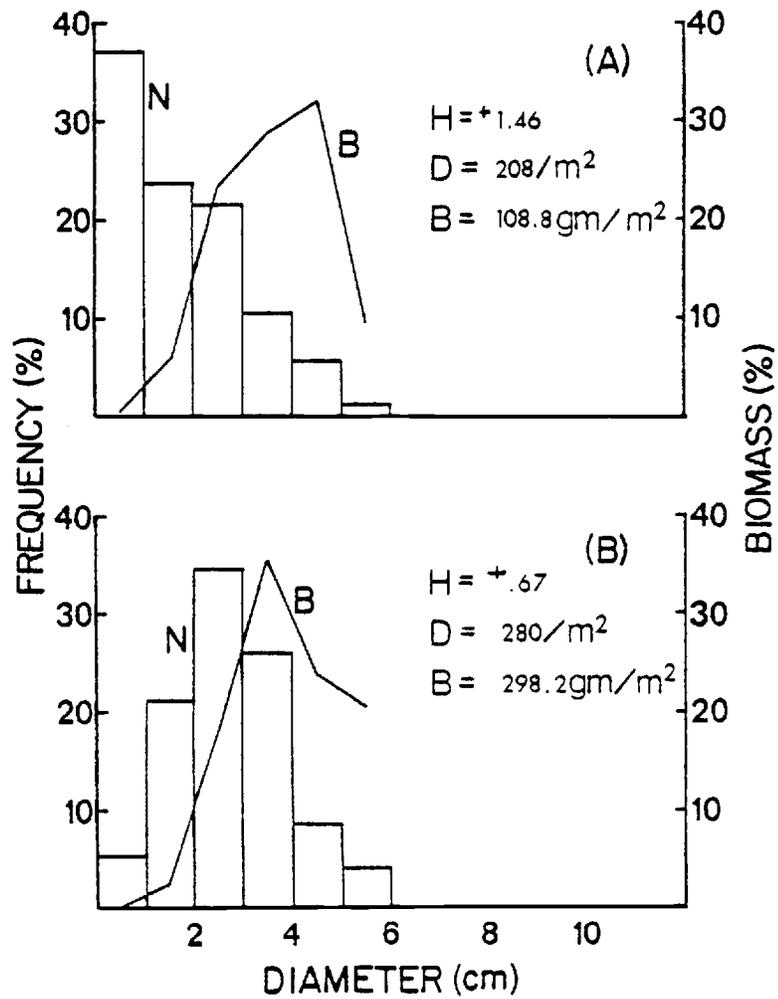


Figure 6. Size-frequency (N) and size-biomass (B) distributions for A. xanthogrammica as a function of tidal height on a vertical wall (BB 1) at Boiler Bay.

Figure 7 shows a general trend of increasing biomass per square meter with lower tidal level.

The size-frequency and size-biomass curves for walls at different study sites are more similar at the same relative position (upper, middle, lower) on the wall than at similar tidal levels among the walls. For example, the upper level (+.37m) of the exposed wall at Yachats (Fig. 4) appears more similar, in its distribution of number and biomass with respect to diameter, to the upper level (+1.10 m) of a similar wall at Strawberry Hill (Fig. 5) than it is to the middle level (+.49m) of this wall. The middle levels of these two walls are also very similar in number and biomass distribution although the tidal heights differ by more than 0.61 meters. Table 2 summarizes the density, mean diameter, and biomass of each site sampled.

POPULATION DYNAMICS

Movements within, into, and out of the two defined plots at Boiler Bay were very restricted during the twelve month monitoring period. Eighty percent of the identified individuals showed no measurable movement during this period. Within the plots, ten percent of the individuals moved 5 to 10 centimeter distances. Only three individuals (5%) could not be found within the plots or adjacent to them; they either died or moved more than 30 cm away from the boundaries of the plots. Five individuals (1.7 to 3.6 cm diameter) moved into the plots, probably from adjacent areas, having moved at least 15 cm into the plots from the boundary. These individuals appeared in the plots at different times of the year, and because of their size are interpreted as having moved from elsewhere on the rock rather than as recruits from the

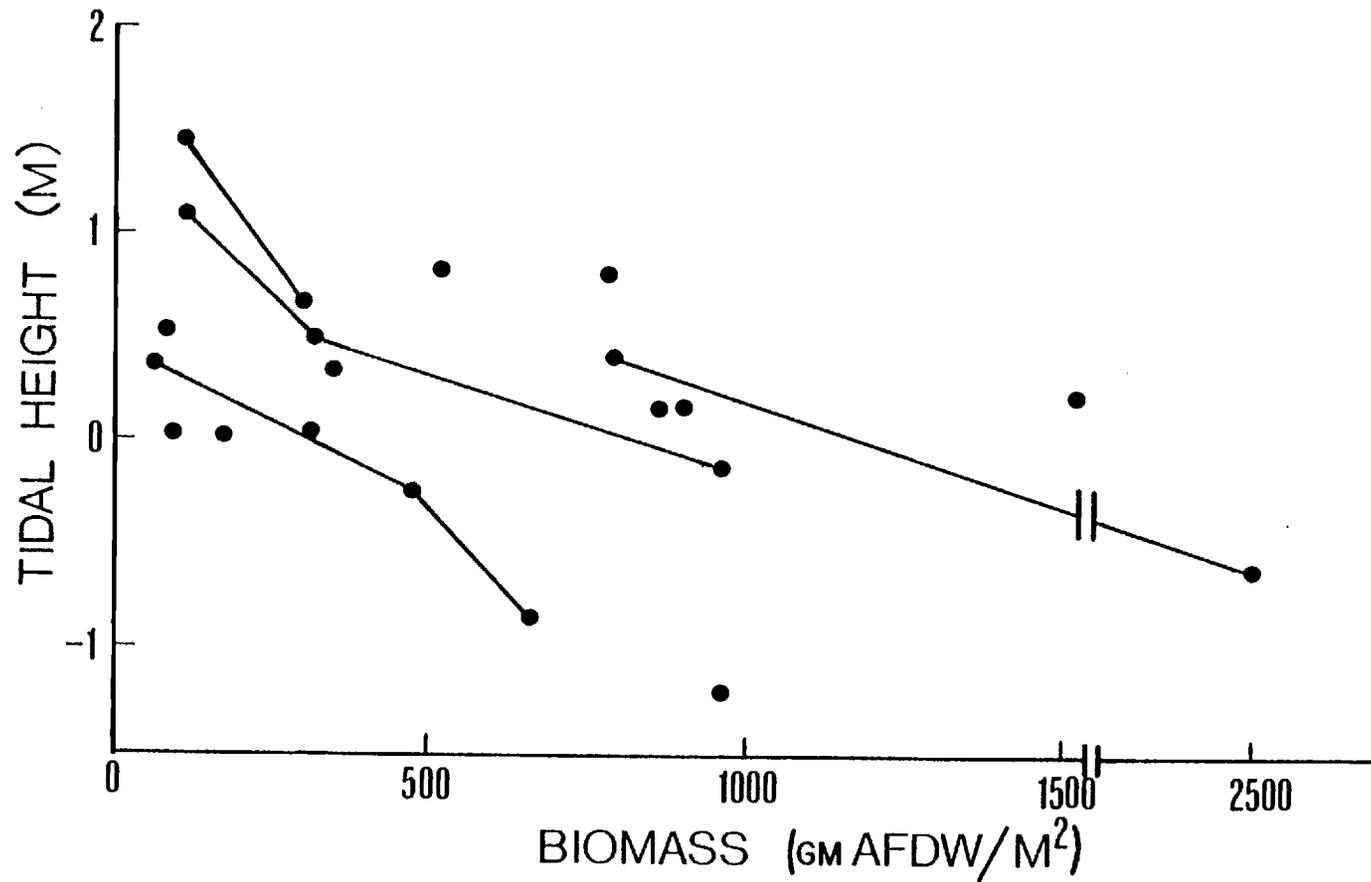


Figure 7. Relationship between tidal height and standing crop of anemones. (Lines connect points from different levels of a single wall).

TABLE 2. Characteristics of *A. xanthogrammica* populations for each site sampled. Mean and (in parentheses) 95% C.I. of density, biomass and anemone diameter are shown.

Site ^a	# of ^d samples	Tidal ht. m. relative to MLLW	Density/m ²	Biomass gAFDW/m ²	Diameter (mm)	Diameter range (mm)
WALL-ROCK SITES						
SH 1	8	+ .18-.68	112.0(19.0)	706.5(345.3)	45.5(2.6)	7-178
SH 2	9	+ .18-.68	144.8(49.0)	302.8(183.5)	34.2(1.5)	9-141
SH 3	5	-.40+.60	250.4(92.3)	346.1(142.3)	31.9(0.8)	9- 84
SH 4	6	-.43+1.37	160.0(51.9)	464.7(425.8)	36.0(1.7)	9-120
SH 5	4	+ .39-.64	246.2(69.2)	405.1(258.0)	31.3(1.2)	6-134
SH 6	8	-.40+.90	85.9(22.5)	907.2(306.0)	28.8(8.4)	11-153
YH 1	15	-.76+.50	129.7(20.5)	1945.7(551.0)	66.5(2.2)	7-191
YH 2	12	-.85+.40	207.1(85.0)	413.1(223.9)	30.2(1.0)	6-127
BB 1	7	+ .52-1.40	207.1(123.0)	198.0(141.1)	25.7(1.1)	4- 60
WALL-SAND SITES						
BN 1	6	b	76.7(36.7)	173.3(85.6)	35.4(2.0)	8- 84
BN 2	3	b	103.3(70.3)	469.9(581.0)	44.5(3.3)	12- 97
BN 3	5	b	67.6(38.3)	121.9(87.1)	31.7(2.1)	8- 90
BN 4	5	b	133.8(52.4)	221.9(153.5)	32.6(1.3)	11-103
BR 1	14	b	302.6(78.5)	496.2(130.8)	32.7(0.5)	6- 89
POOL SITES						
SH 7	3	c	132.0(35.22)	720.6(274.8)	48.1(3.0)	14-118
SH 8	2	c	39.5	714.4	76.6(6.2)	30-181
SH 9	3	c	139.0(122.5)	1738.1(1482.0)	66.2(3.9)	17-120
HORIZONTAL SITES						
SH 10	1	+ .15	247.0	860.3	40.2(2.3)	8-110
SH 11	3	+ .03	101.3(178.4)	167.1(160.7)	30.4(2.0)	8- 73
SH 12	2	+ .03	143.5	307.4	35.2(2.4)	10- 98
SH 13	3	+ .50	194.9(86.4)	302.1(286.4)	28.1(1.9)	5-103
YH 3	7	+ .21	142.7(39.2)	1546.1(412.6)	59.7(2.7)	7-146
YH 4	3	+ .81	141.7(117.5)	779.7(835.3)	44.8(3.5)	9-114
YH 5	2	+ .03	135.5	92.8	21.5(2.0)	7- 70
YH 6	3	+ .53	53.7(31.5)	82.1(94.6)	29.6(3.4)	10- 67
BN 5	1	b	179.0	257.7	33.3(1.9)	14- 67

a. SH - Strawberry Hill, BN - Bandon, YH - Yachats, BR - Battle Rock, BB - Boiler Bay.

b. tidal heights not determined.

c. permanently submerged.

d. Confidence intervals not calculated for sites with less than 3 samples.

plankton. No individuals which could be interpreted as recently metamorphosed larvae were detected in any of the rock surface plots at any location during this study.

The in-situ measurements over 3, 13, and 15 day intervals indicated that diameter measurements of individuals were replicable within 0.5 cm. This variability is caused by different amounts of water being retained within individual contracted anemones at different times. Each set of successive measurements on individuals in each anemone group was compared using the Wilcoxon matched pairs signed ranks tests. Individuals in these groups ranged in size from 3.5 cm to 11.7 cm. The greatest group difference in mean diameter measured over any 28 day period was not greater than the error estimated for replicate measurements. No significant changes in mean diameter of the populations at the $p=0.05$ level were therefore detectable during the summer, the period in which growth is most rapid (Sebens, 1977).

Estimates of changes in mean diameter of individual anemones over 4 to 13 month periods were made from successive scaled photographs of defined plots at Boiler Bay and Strawberry Hill. In three sites at Strawberry Hill and two at Boiler Bay, undisturbed and untagged individual anemones were identified in successive photographs taken throughout these periods. Only diameter measurements of these individuals were used in comparisons. The plots at Boiler Bay were located on the vertical face of a large basalt boulder. The three plots monitored at Strawberry Hill were on a vertical wall with anemones 2.2 cm to 6.0 cm in diameter, and on two horizontal surfaces with anemones 1.5 cm to 9.0 cm in diameter. Most individuals at other sites within these locations are included within these diameter ranges.

Differences between diameter measurements of individuals in successive samples were evaluated using the Wilcoxon signed ranks test. In photographs taken at two month intervals, the mean difference between repeated diameter measurements of the same individuals was 0.02 cm to 0.4 cm, and over longer intervals mean differences were between 0.1 cm and 0.4 cm. These figures approximate the precision of the method for repeated measurements. At none of the sites were the mean group differences, measured over 11 to 13 month periods, greater than the differences found in short term, in-situ replicate diameter measurements from other Strawberry Hill sites.

After approximately one year, some A. xanthogrammica were found in three of the four cleared areas. Only a large pool at Boiler Bay, cleared in February, 1977, was devoid of anemones in May, 1979. This pool was located in the soft sandstone bench at Boiler Bay. In all cleared areas with anemones, the mean size of immigrants was less than the mean size of the anemones originally removed (Table 3). The smallest anemones found in cleared areas after 12 months were 0.5 to 0.6 cm in diameter. Most of the anemones found were near the periphery of the plots, probably having immigrated into the clearing from surrounding rock surfaces rather than having settled as planktonic larvae, since the latter are only 150 μ m in diameter (Siebert, 1974). In all cases, the new density in the cleared areas was less than 35% of that originally found in that location.

TABLE 3. Dimensions of Experimental Anemone Removal Areas. Mean and (in parentheses)
Range of Anemone Diameters

Location	Perimeter length (m)	Area cleared (m ²)	Immigration time (yrs)	Before Removal		After Immigration	
				Original number present	Diameter (cm)	Number of immigrants	Diameter (cm)
Channel wall	3.2	0.57	1	74	2.3 (0.4-7.5)	26	1.4 (0.6-3.3)
shallow pool	1.8	0.17	1	34	1.1 (0.5-2.9)	11	1.0 (0.5-1.7)
wall-adjacent to mussel bed	1.3	0.10	1	56	1.7 (0.4-5.8)	13	0.8 (0.5-1.1)
large pool	ca. 12.8	ca. 10.0	2	265	6.4 (2.4-12.6)	none apparent	---

GROWTH RATE ESTIMATES FOR LABORATORY POPULATIONS

Table 4 summarizes the growth rates of A. xanthogrammica obtained from laboratory growth studies. Instantaneous growth rates were calculated using the exponential relation:

$$G = [\ln(W_t/W_o)]/t$$

where W_o is the initial weight, and W_t the weight after t days. Anemones 1.0 cm to 3.0 cm in diameter had the greatest rate of growth. Positive growth rates calculated for anemones maintained in the laboratory were inversely related to anemone size for individuals greater than 1.0 cm in diameter (Fig. 8).

The negative growth rates calculated for anemones maintained in cups from October, 1977 to March, 1978 probably reflect the low level of feeding, and the low salinity conditions prevailing in February, 1978. The periods of greatest growth of anemones were during summer for anemones less than 3.0 cm diameter, kept in cups and bowls, and during the fall for the largest, individually tagged anemones. These periods had the highest salinity of all times during which growth on those sizes of anemones was studied. Large anemones required more than two months for reattachment to a substrate and a return to normal behavior. During the summer preceding the fall period of high growth, the large anemones had been detached for weighing and the resulting abnormal behavior prevented feeding even though the summer salinity was high.

Overall, only 26% of the large anemones attached to ceramic tiles ingested the food provided them during January to May of 1979. Failure to feed was probably caused by the low salinities prevalent during this period. Unlike the large anemones, 85% or more of the anemones less than

TABLE 4. Summary of Anemone Growth Obtained in Laboratory Experiments.

	Number of Individuals	Duration of Experiment (Days)	Diameter Range (cm)	Culture Vessel	Feeding rate per week	% of Individuals Feeding	Growth ^a Rate (day ⁻¹)
<u>1977</u>							
October- December	32	72	0.5-2.0	Cup	1	N/A	-.0006
<u>1978</u>							
January- March	32	87	0.5-2.0	Cup	1	N/A	-.0020
June-	26	56	0.5-1.8	Cup	3	59	+.0044
August	24	56	1.0-3.0	Bowl	3	N/A	+.0060
August-	7	137	0.5-2.0	Cup	3	79	+.0006
December	24	137	1.2-3.0	Bowl	3	86	+.0033
	91	111	4.0-11.9	Tagged in Tanks	3	82	+.0027
<u>1979</u>							
January-	54	109	0.3-1.0	Tray	3	85	-.0036
May	61	100	0.5-2.0	Cup	3	91	-.0032
	24	100	1.5-3.5	Bowl	3	94	-.0012
	87	100	3.2-10.0	Ceramic Tiles	3	26	+.0013

^aInstantaneous growth rates calculated using $G = [\ln(Wt/Wo)]/t$.

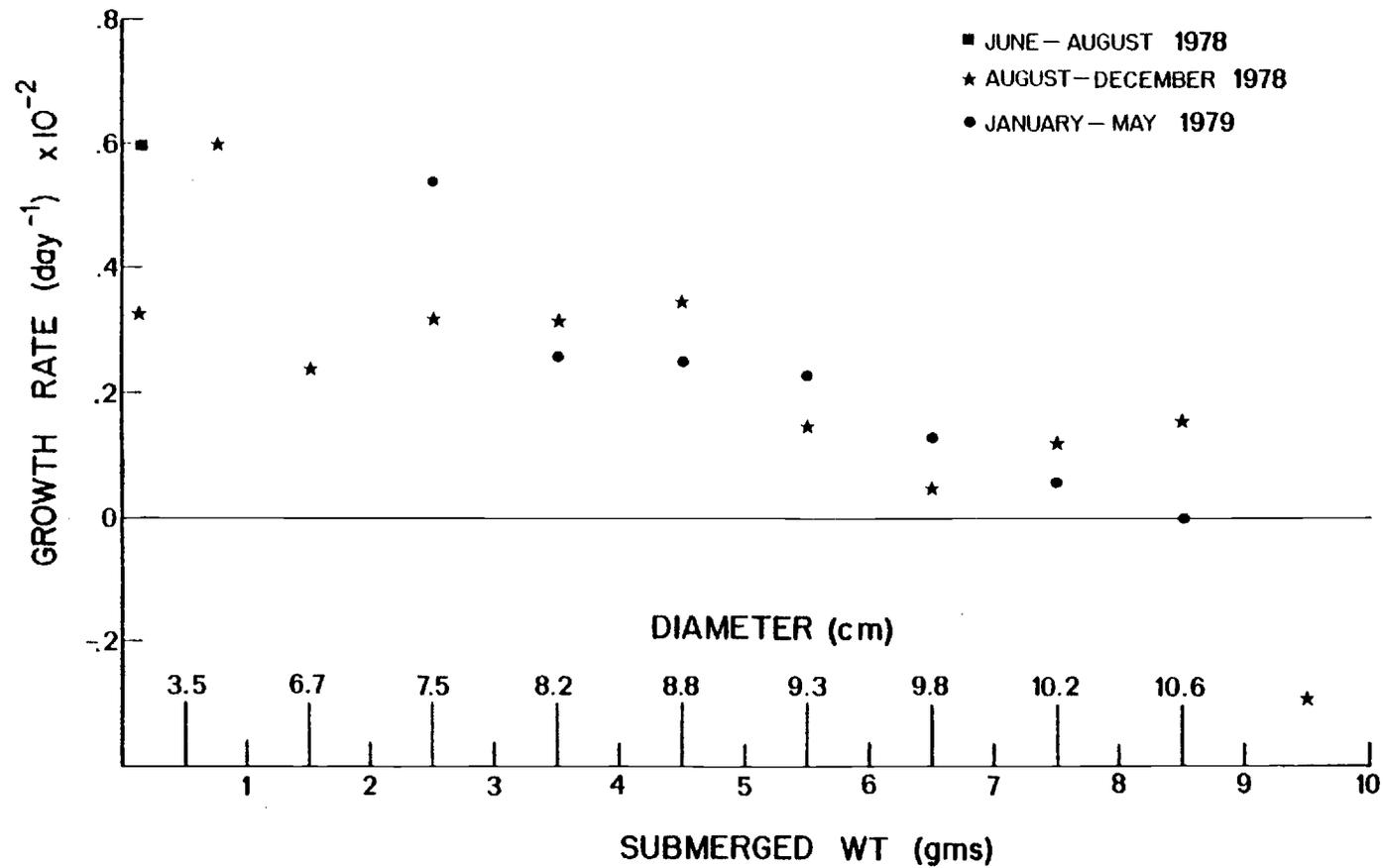


Figure 8. Growth rates observed for laboratory populations of *A. xanthogrammica* as a function of size.

3.0 cm in diameter continued to ingest the food provided during this period.

The maximum size-specific growth rate obtained from laboratory populations of A. xanthogrammica was used to plot the growth of anemones initially 2.0 cm in diameter (Fig. 9). These two curves are derived from the size specific growth rates shown in Figure 8. The curves in Figure 10 show the growth of anemones initially 0.6 cm in diameter using the maximum and minimum non-negative growth rates obtained from laboratory populations. There is a six-fold difference between maximum and minimum growth rates for anemones less than 2.0 cm in diameter and a two-fold difference for sizes larger than 2.0 cm. Additionally, even though the small anemones fed more consistently than larger anemones, the growth rate of small anemones decreased more than the growth rate of larger anemones, during the low salinity conditions of winter and spring, 1979. The metabolic implications of this inconsistency are not understood. Growth of small anemones is more sensitive to changes in environmental conditions, such as food availability and salinity, than is the growth of large anemones.

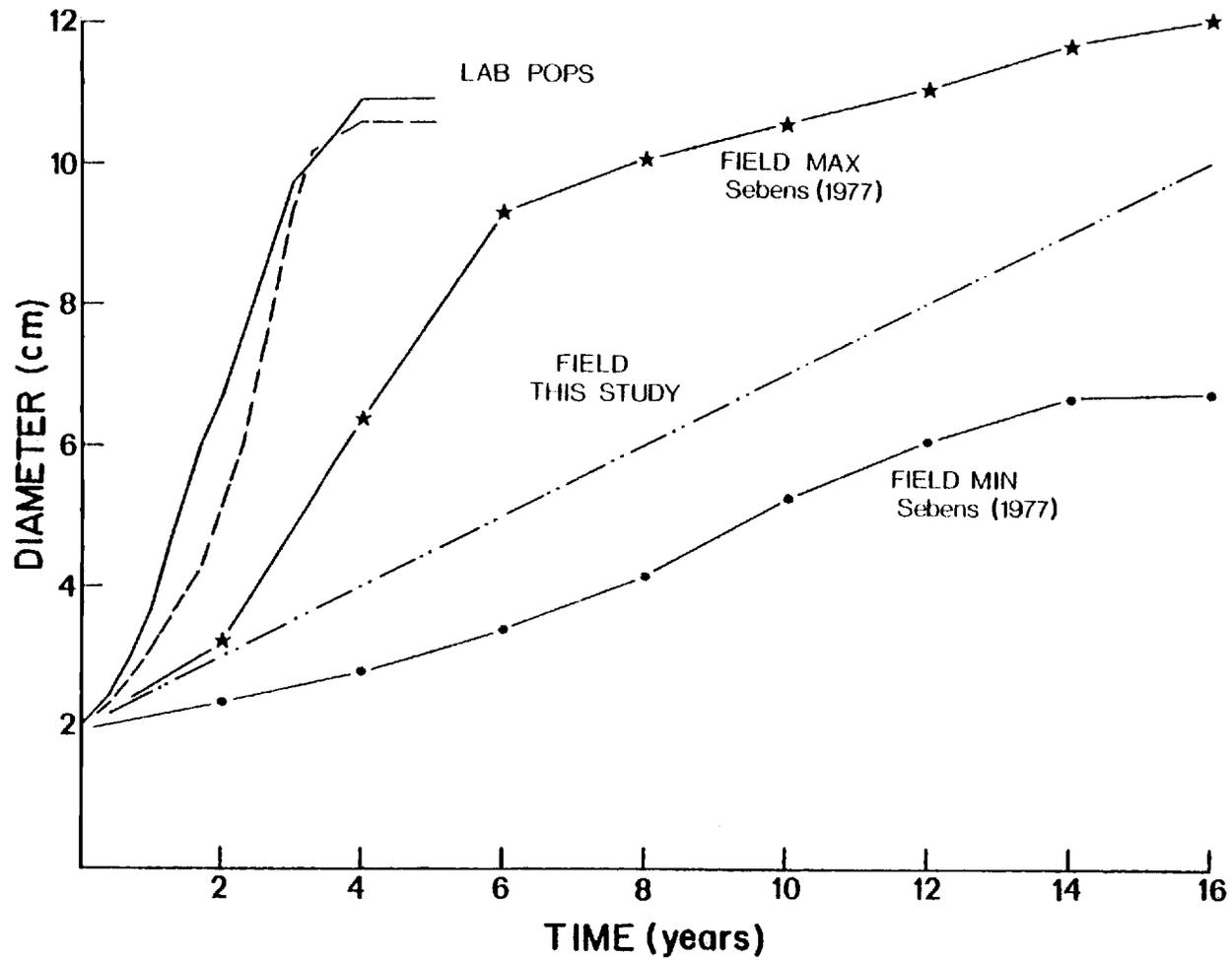


Figure 9. Hypothetical growth of *A. xanthogrammica* calculated from observed laboratory and field size-specific growth rates.

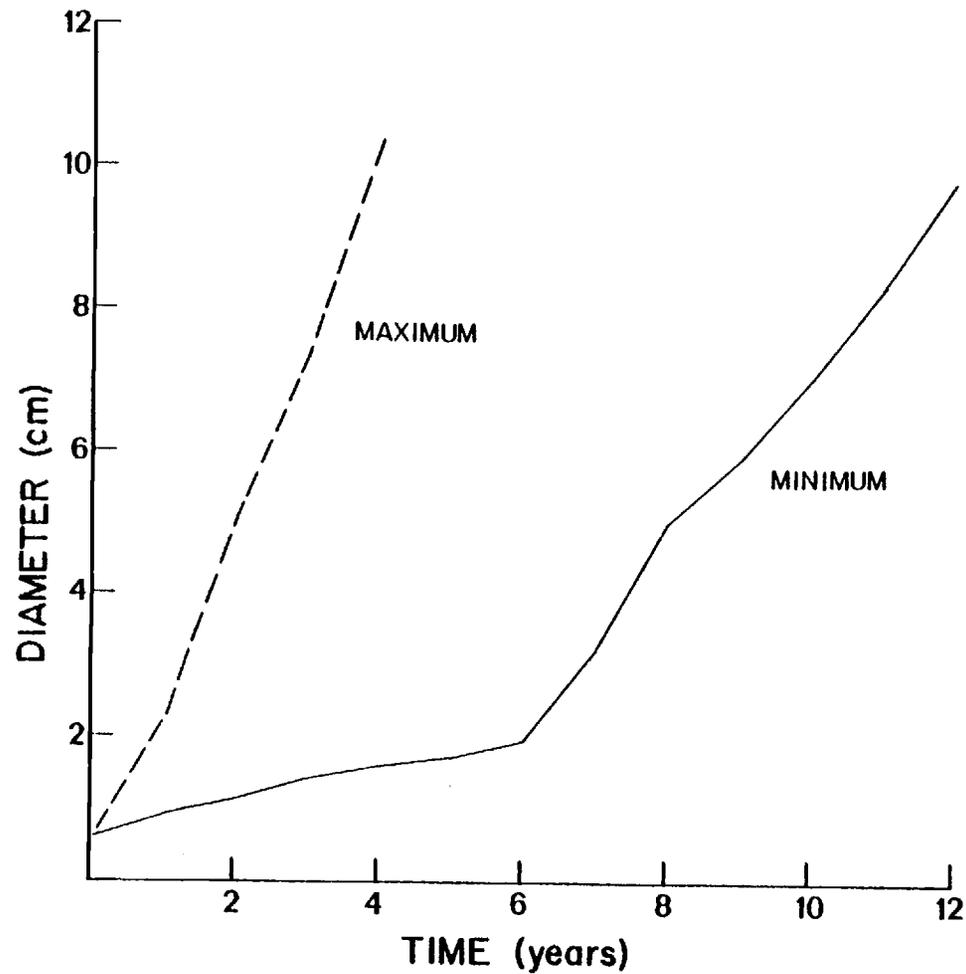


Figure 10. Hypothetical growth curves of A. xanthogrammica 0.6 cm in diameter using maximum and minimum non-negative growth rates obtained from laboratory populations.

DISCUSSION

Few rocky intertidal areas with high population densities of Anthopleura xanthogrammica were found along the Oregon coast. Locations with dense populations were very restricted in area but had high standing crops per square meter. At most rocky intertidal areas examined, anemone population density was low. No fluctuations in population density or changes in size frequency distribution were detected during this study. Sebens (1977) found no changes in the size distributions of A. xanthogrammica in mapped areas of Tatoosh Island, Washington, in two years. An absence of fluctuations in density of adult anemone populations was also reported by Ottaway (1979), who found populations of Actinia tenebrosa to be very stable; the net change in three years being a decrease of 2.4% of the original number present. In the A. xanthogrammica populations studied here, there was very little disappearance of anemones which could be ascribed to mortality of established adults.

Since each anemone must be removed individually from the substrate and the time and effort required per individual is relatively independent of size, a harvest by removing the largest individuals of a population would yield the greatest biomass of anemones for the effort required. The effect of harvesting large individuals can be estimated from the data in Figures 2, 3, 11 and Table 1. For example, removing 50% of the population biomass by selective harvest of the largest individuals will affect populations in different habitats to different extents. This type of selective harvest of the largest individuals would lower the maximum anemone diameter in wall-sand habitats from 11.0 cm to 5.2 cm (Fig. 11). Sebens (1977) reported that A. xanthogrammica

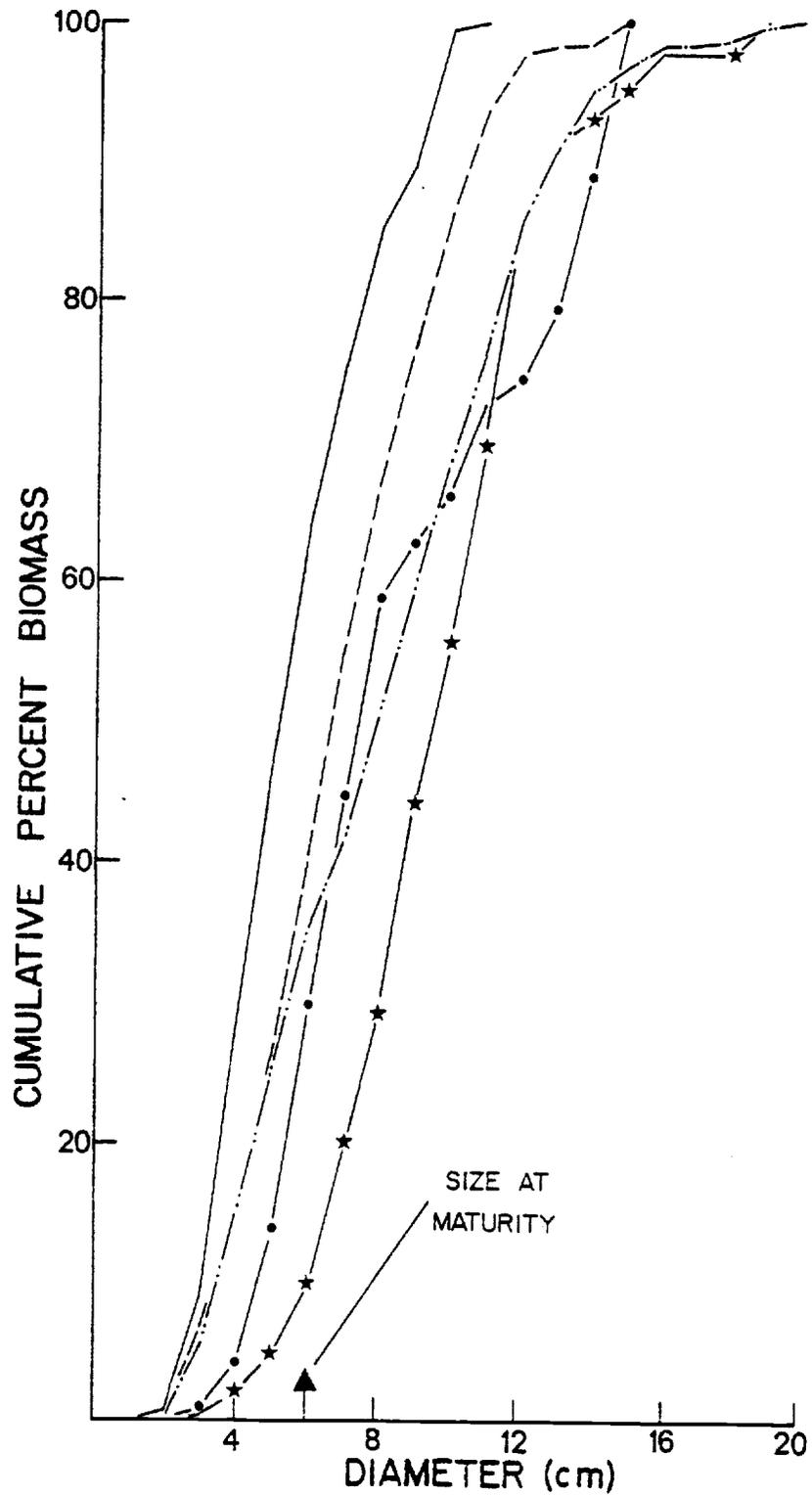


Figure 11. Cumulative size-biomass distributions of *A. xanthogrammica* in different habitats. (Symbols as in Figure 2)

less than 6.0 cm in diameter were never reproductively mature. Consequently, no reproductively mature anemones would remain. A similar harvest in pools, on the other hand, would lower the maximum diameter to 9.6 cm, leaving some reproductive individuals in the population.

Within populations of A. xanthogrammica of the size range (1.4 cm to 4.6 cm contracted diameter) monitored for movement, individuals moved at most 10 cm to 20 cm net distances in 12 months. However, only about 5% to 10% of the individuals monitored showed detectable movement. Motility of this magnitude is similar to movements and displacements reported for other intertidal anemone species. In an Actinia tenebrosa population monitored for two years, 76.3% of the anemones greater than 15mm in diameter moved less than 25 cm with the majority of individuals having net displacements less than 3 cm from their original location (Ottaway, 1978). Dunn (1977) reported locomotion by Epiactis prolifera to be nondirectional with net displacements after 76 days to be only 36% of traveled-path distance. Since the A. xanthogrammica population on the rock surface studied occupies only 22% of the surface area, with much of the remaining surface unoccupied, it is improbable that motility is space limited here. It is therefore unlikely that extensive redistribution of smaller anemones would occur following removal of the larger ones from a population.

Siebert (1974) has shown that A. xanthogrammica has a relatively long-lived planktonic planula larva. No appearance of small individuals indicative of successful settlement of larvae from the plankton was found in plots of undisturbed populations of anemones. Sebens (1977) concluded that larvae settle in mussel beds and then move downward as

they grow; this hypothesis could not be substantiated in this study. More thorough seasonal sampling in mussel beds is required to resolve this question. However, we have found adult anemone populations on flat rock benches remote from the nearest mussel bed so it is unlikely that mussel beds are the only site of recruitment. Under relatively normal natural conditions, the growth of an undisturbed adult anemone population through recruitment of juveniles derived from larval settlement must be balanced by natural deaths of adults, yet no evidence of either process was found in the two year course of the study.

Repeated diameter measurements of individuals, either in the field or from photographic records indicated that in natural populations of anemones ranging from 1.5 cm to 9.0 cm in diameter, growth over a year is less than can be detected by the methods used. Lack of detectable long-term diameter changes greater than the error estimate of short-term replicates implies that growth of individuals in the anemone populations studied was no greater than the error estimate of 0.5 cm per year. Using 0.5 cm per year as the maximum possible growth rate for this population of anemones, the minimum time required for an individual greater than 1.5 cm in diameter to attain a larger diameter can be estimated. An example of such a growth estimate for an anemone initially 2.0 cm in diameter is given in Figure 9. Curves showing the maximum and minimum growth rates for natural populations of anemones, derived from data reported by Sebens (1977), are also included in Fig. 9.

At Oregon coastal locations, intertidal populations of A. xanthogrammica have very low recruitment and death rates and are evidently not

subjected to severe mortality from extrinsic causes such as predation or severe physical stresses. The well established intertidal adult populations of this species appear to be poorly adapted to recovering from the large scale removals which harvesting would entail.

This is substantiated by the lack of response of populations to the small-scale removals, simulating harvests, done in this study. Recovery of small cleared areas after complete removal of the A. xanthogrammica population was very slow and occurred primarily through immigration from nearby areas. Harvesting does not, as in many exploited populations, appear to allow more recruitment to the adult population. Instead, the effect of a limited A. xanthogrammica harvest appears to be slight changes in the distribution of anemones already present on the rock surfaces during the first year after clearing. Since density after one year of immigration is related to the periphery and not the area of a cleared plot, the larger a cleared area is, the lower will be immigrant density near its center.

The possibility that a limited or selective removal of larger anemones would result in increased growth of remaining anemones adjacent to or moving into cleared areas could not be demonstrated in the two year period of this study. Sebens (1977) however, reported that individuals moved from the periphery into small areas cleared of their original anemone populations, and that these immigrants showed accelerated growth. His results can be interpreted to mean that space and food is limiting growth in some dense populations. At the rates of movement we observed both in the field and in the laboratory, immigration would be only an edge effect in larger harvested areas. Competition for food and its

availability are probably not major limitations on individual or population growth in most open coast populations of average density. In most of the areas monitored in this study, population density is sufficiently low so that individual anemones are surrounded by open surface. However, in these places we measured neither growth of individuals nor migration which could have brought individuals to new positions more advantageous for feeding. A few large areas were cleared of anemones to provide material for AP-A research. Movement within these large cleared areas was restricted to some individuals emerging from crevices in the rock; extensive movements into the cleared area from the margins were not observed in over two years. This suggests that a harvest method selectively removing only the largest anemones from a population would not lead to accelerated growth of smaller immigrating individuals or enhance recruitment sufficiently to sustain continued commercial harvesting on the Oregon coast.

In natural intertidal populations, growth of A. xanthogrammica individuals is slow, requiring an estimated 16 years for growth from 2 cm to 10 cm diameter at the fastest growth rate estimated from field populations at Oregon coastal locations. The growth rates obtained under known laboratory conditions indicate that individuals 2 cm in diameter could possibly attain a diameter of 10 cm in four years. However, collecting a large number of small anemones in the field and maintaining them for four years in the manner used in this study would be an expensive undertaking.

Our preliminary estimate of the entire standing crop of A. xanthogrammica at Strawberry Hill, where anemones are both large and abundant

is 7,100 kg wet weight in an area of 1950 m². This population, if harvested completely would probably take a very long time to recover, given the apparent slow population dynamics of the species. In harvested areas, anemone populations may never return to the density and size structure present before harvesting. Other faster recruiting and growing species, which utilize the same space in the habitat, such as surfgrass (Phyllospadix scouleri) or sea urchins (Strongylocentrotus purpuratus) may colonize the surfaces previously occupied by anemones. More needs to be learned about community interactions in the intertidal habitat of the anemones before extensive harvesting begins. Large anemones and surf grass clumps are often crowded together in mosaic fashion in channels and tide pools, suggesting direct competition for surface space. Large anemones, commonly scattered about in pools with dense populations of sea urchins, feed extensively on the urchins, yet small anemones were never found in this situation. This suggests that small anemones rarely survive here to grow to a size large enough to prey upon urchins.

If a species is to sustain a commercial fishery over the long term it must have a high and successful recruitment to the fishery and/or fast density-dependent growth. Anthopleura xanthogrammica populations along the central Oregon coast have neither of the above necessary criteria. We found no evidence in any of our study areas of successful recruitment to the rock surface. Recruitment may have occurred along the Oregon coast during the period of this study, yet be so spatially patchy that none of the study areas experienced successful larval settlement from the plankton. Alternatively, anemone recruitment may be temporally patchy, occurring in some years only, and that none occurred

between August, 1977 and May, 1979. A species, such as A. xanthogrammica, that is adapted to achieve success through high individual survival is a poor prospect for a commercial fishery.

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CHAPTER TWO

CONTROL OF POPULATION CHARACTERISTICS IN
ANTHOPLEURA XANTHOGRAMMICA

H. P. BATCHELDER

CONTROL OF POPULATION CHARACTERISTICS IN ANTHOPLEURA XANTHOGRAMMICA

INTRODUCTION

The most striking features of Anthopleura xanthogrammica populations are apparently erratic patterns of distribution and abundance, and inconsistent size structures. An absence of recurrent patterns in size structure, abundance, and distribution in intertidal species is usually attributed to local differences in the availability of food, wave exposure, surface relief, aspect and tidal height. However the lack of recurrent patterns among samples separated by a meter or less at the same tidal height, on surfaces with similar exposure, aspect and surface relief suggests that chance factors may be important in determining the characteristics of A. xanthogrammica populations. Lewis (1964) defined chance factors as physical and biological influences of the past which were important in determining the present local structure of a population or community. Two types of chance factors operate: those which influence reproduction, settlement, and establishment on the shore and those which control later survival. Important chance factors of the first type are initial larval supply, and oceanographic and meteorological conditions during the pelagic and early post-settlement stages. The latter stochastic processes are very important in governing survival and recruitment of benthic invertebrates which produce huge numbers of small eggs and pelagic larvae. A great majority of pelagic larvae are lost through a variety of biological and physical processes. The chance occurrence of onshore waves when larvae are ready to set may enhance recruitment, whereas offshore currents or severe wave conditions may result in extensive mortality of larvae by transporting them offshore or onto upper

intertidal surfaces where survival is poor. Settlement coincident with warm, dry weather may fail because of death of recently settled juveniles from desiccation. The extremes of physical stresses at settlement sites may be very important in determining survival and the eventual distribution of adults.

The second type of chance factors include grazing, predation, and competition and are those important in controlling later survival on the shore. Previous episodes of intense grazing, predation, or competition have been demonstrated to determine local distributions in many intertidal invertebrate populations (Connell, 1961a, b; Dayton, 1971; Menge, 1976). Chance battering by drift logs is important in determining the distribution of many sessile invertebrates in upper intertidal communities on the coast of Washington (Dayton, 1971). Substrate stability is of additional importance to populations of long-lived sessile marine invertebrates. Substrates such as sandstone, having easily eroded surfaces are not suitable for survival of slow growing, long-lived immobile species because substrate turnover may occur at a time scale shorter than the generation length of the species.

The purpose of this research was to determine the processes and mechanisms controlling the population characteristics of Anthopleura xanthogrammica. The distribution, abundance, and size structure of anemones inhabiting mussel beds at several locations are described. Size specific respiration of anemones was measured at various conditions and heat budgets calculated for anemones of various sizes for a range of environmental insolation values. Combining laboratory determined rates with theoretically derived limits has aided in ascertaining the factors

resulting in the observed population characteristics of Anthopleura
xanthogrammica.

MATERIALS AND METHODS

SURVEY OF ANEMONE POPULATIONS WITHIN AND ADJACENT TO MUSSEL BEDS

Destructive sampling of mussel beds at Boiler Bay (44°50'N), Yachats (44°18'N), and Strawberry Hill (44°15'N) along the central Oregon coast provided estimates of the density, distribution, and size structure of anemone populations in mussel beds. A square sampling quadrat, 0.1 m² in area, was placed on the mussel bed and all mussels and associated fauna within the sampling quadrat removed. The contents of each sample were kept in the laboratory in running seawater until the anemones could be measured and enumerated. Diameters of anemones found in mussel bed samples were measured after blotting on dry paper towelling. All samples were sorted within one week of collection.

At Strawberry Hill, several samples, 0.1 m² in area, were obtained from the uppermost tidal levels of a vertical channel wall, immediately below mussel beds.

SIZE-SPECIFIC OXYGEN CONSUMPTION

Starved Anthopleura xanthogrammica ranging in size from 0.002 gm to 0.530 gm dry weight were allowed to attach to Warburg flasks of 20 to 100 ml capacity containing 31‰ sea water at 15°C. Oxygen consumption was measured in air and in water at different salinities and temperatures, using a Gilson differential respirometer. An external refrigerated water bath was used to regulate temperature during measurements. Water of 20, 26, and 31‰ was prepared by dilution with distilled water and filtered through Whatman GF/A filter paper. After one to two hours of equilibration, three to size oxygen consumption measurements were made at 45 to 60 minute intervals for each anemone. All experiments were conducted in low

light conditions to reduce any effect the symbiotic algae present in the anemones might have had on respiration. The effect of exposure to air on the respiration of A. xanthogrammica was determined from oxygen consumption measurements of anemones without water in the flask. Anemones were probed with a pipette until they were strongly contracted and the flasks were then drained of water. Anemones not covered by water were assumed to be in an atmosphere of 100% relative humidity. At the conclusion of the experiment the anemones were blotted, weighed wet, oven dried at 85°C and then weighed dry.

SIZE-SPECIFIC HEAT BUDGETS

The time required for 75% water loss by evaporation was calculated for anemones ranging from 0.5 cm to 3.0 cm in diameter, under various rates of heating by direct insolation. Estimates of insolation (ly/min) were obtained from unshielded pyrhelimeter recordings made at the Marine Science Center dock in Yaquina Bay (44°37'N), Oregon during the summer of 1968. The total water content of anemones was determined from wet and dry weights. It was assumed that 585 calories were required to evaporate one gram of water from an anemone, and that an anemone having lost 75% of its total water content during tidal exposure would not survive, even after re-submergence in water. For purposes of calculation, the surface area of an anemone subject to direct insolation was assumed to be equal to the area of a circle having a diameter equal to that of the anemone, a large underestimation of surface area available for heat exchange and evaporation.

RESULTS

ANEMONE POPULATIONS WITHIN AND ADJACENT TO MUSSEL BEDS

Large variations in density of Anthopleura spp. were found in samples from beds of the mussel, Mytilus californianus (Table 5). Maximum anemone densities were found at Boiler Bay in a mussel bed located above a vertical face occupied by numerous larger anemones. The density of anemones in Boiler Bay mussel bed samples taken in 1978 and 1979 did not differ significantly at the $p=0.10$ level (Mann-Whitney test). In all but two mussel bed samples, the mean diameter of anemones was less than 1.0 cm; few anemones from within mussel beds were greater than 1.5 cm in diameter (Fig. 12). An analysis of variance of anemone diameter sample means indicated that mean diameter did not differ significantly between years at Boiler Bay. The absence of a change in density and mean anemone diameter suggests that during this interval, either recruitment from the plankton did not occur at this location or recruitment occurred but was balanced by mortality and emigration of anemones from the mussel bed.

Anemone density within mussel beds at other sampling locations along the Oregon coast rarely approached the high densities found in mussel beds above the vertical rock wall at Boiler Bay (Table 5).

Very few anemones were found in samples adjacent to the lower margins of mussel beds at the Strawberry Hill sampling area; a total of only three individuals was found in three 0.1 m^2 samples. At lower levels, anemone density at this location is among the highest found at Oregon study areas.

TABLE 5. Density and mean diameter of anemones in samples from mussel beds.

MUSSEL BED SITE ^a	YEAR/MONTH	MEAN DIAMETER (cm)	DENSITY (#/0.1m ²)
BB-boulder	1978 Jul	.28	122
	1978 Jul	.33	213
	1978 Jul	.38	100
	1978 Jul	.31	108
	1978 Jul	.30	223
	1978 Jul	.37	78
	1979 Apr	.36	221
	1979 Jul	.38	205
	1979 Jul	.33	200
BB - north cove	1978 Oct	.23	21
	1978 Oct	.28	37
YH-center of horiz. beds	1978 Jul	1.07	25
	1978 Jul	.89	24
YH-beds above YH 1	1979 Mar	.60	82
	1979 Mar	.61	97
SH-beds above SH 4	1978 Jul	.59	15
	1979 Jul	1.63	15
	1979 Jul	.70	23
SH-beds above SH 1	1978 Jul	.50	21
	1979 Jul	.68	26
	1979 Jul	.55	15
SH-barnacle zone above SH 1	1979 Apr	---	0
	1979 Apr	---	0
	1979 Apr	.77	3

a. BB - Boiler Bay; YH - Yachats; SH - Strawberry Hill.

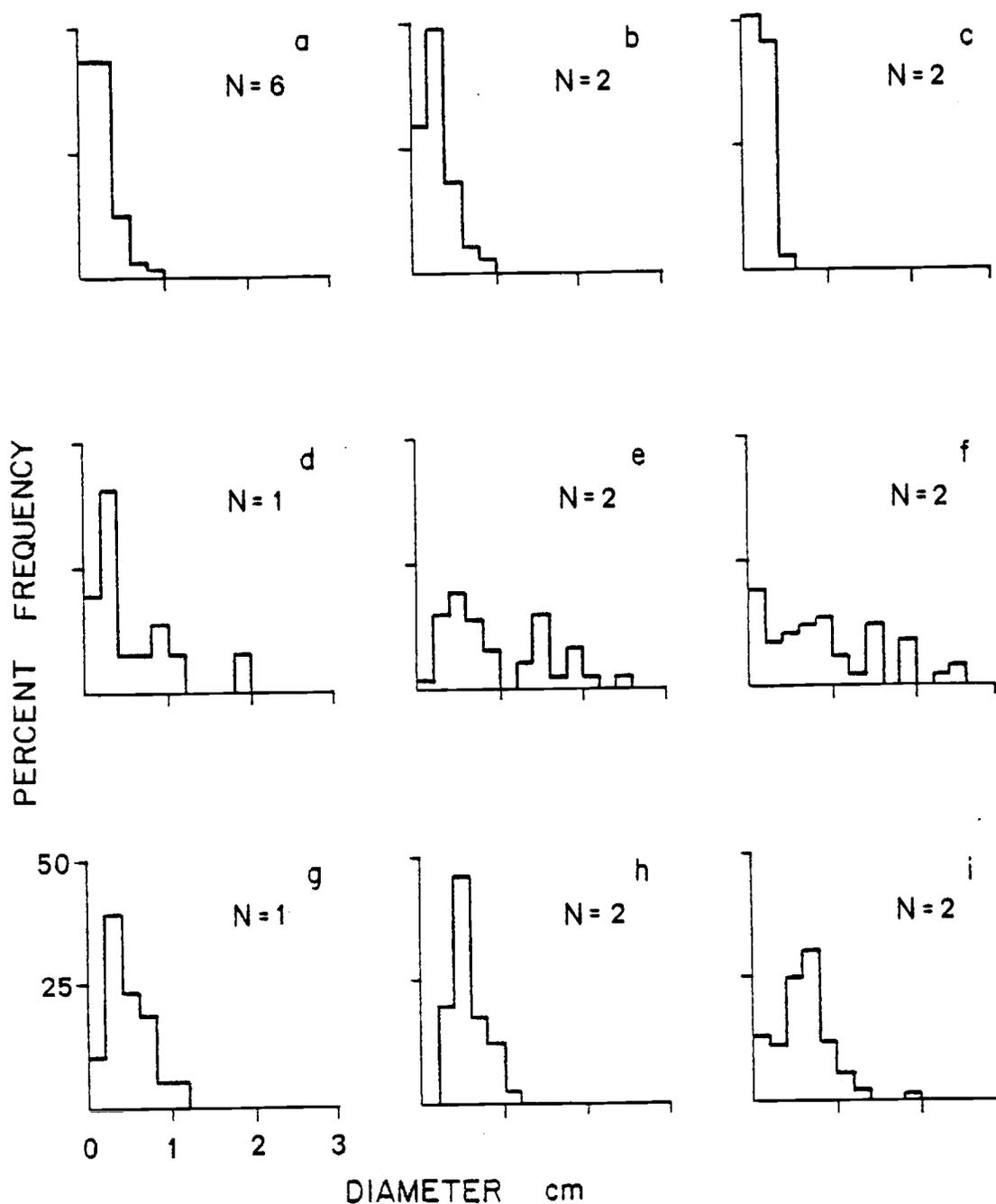


Figure 12. Size-frequency distributions of anemones from samples of mussel beds. a. Boiler Bay boulder, 1978; b. Boiler Bay boulder, 1979; c. Boiler Bay North Cove, 1978; d. Strawberry Hill above SH 4, 1978; e. Strawberry Hill above SH 4, 1979; f. Yachats, center of horizontal mussel beds, 1978; g. Strawberry Hill above SH 1, 1978; h. Strawberry Hill above SH 1, 1979; i. Yachats above YH 1, 1979. (N is number of samples).

SIZE-SPECIFIC OXYGEN CONSUMPTION

Oxygen consumption of anemones was measured in the laboratory to investigate the effect of temperature, salinity, and emersion on the metabolic rate and growth of A. xanthogrammica. The relationship between body weight and oxygen consumption ($\mu\text{l/hr}$) at three water temperatures is shown in Figure 13. Oxygen consumption varies logarithmically with the log of body weight, as expected from previous measurements of oxygen consumption of other anemones (Newell and Northcroft, 1967; Griffiths, 1977; Shumway, 1978).

Water salinity had little effect on respiration by A. xanthogrammica at any temperature (Fig. 14). This differs from the results of Shumway (1978) on Metridium senile, in which oxygen consumption decreased with decreasing salinity because contraction at low salinities resulted in less surface area for gas exchange. Although a similar contraction in response to lowered salinity has been observed in populations of A. xanthogrammica maintained in seawater tanks during this study, all anemones in respiration vessels remained fully expanded throughout the measurement period at all salinities used.

Oxygen consumption (Fig. 15) rose with increased water temperature; this increase is most marked in the smallest individuals tested. Respiratory rate of anemones in air at 20°C was two to three times greater than that of similar sized anemones emersed in water at 20°C . Actinia equina in air exhibited a similar increase in oxygen consumption, which gradually declined to levels similar to those of constantly submerged individuals at the same temperature (Griffiths, 1977).

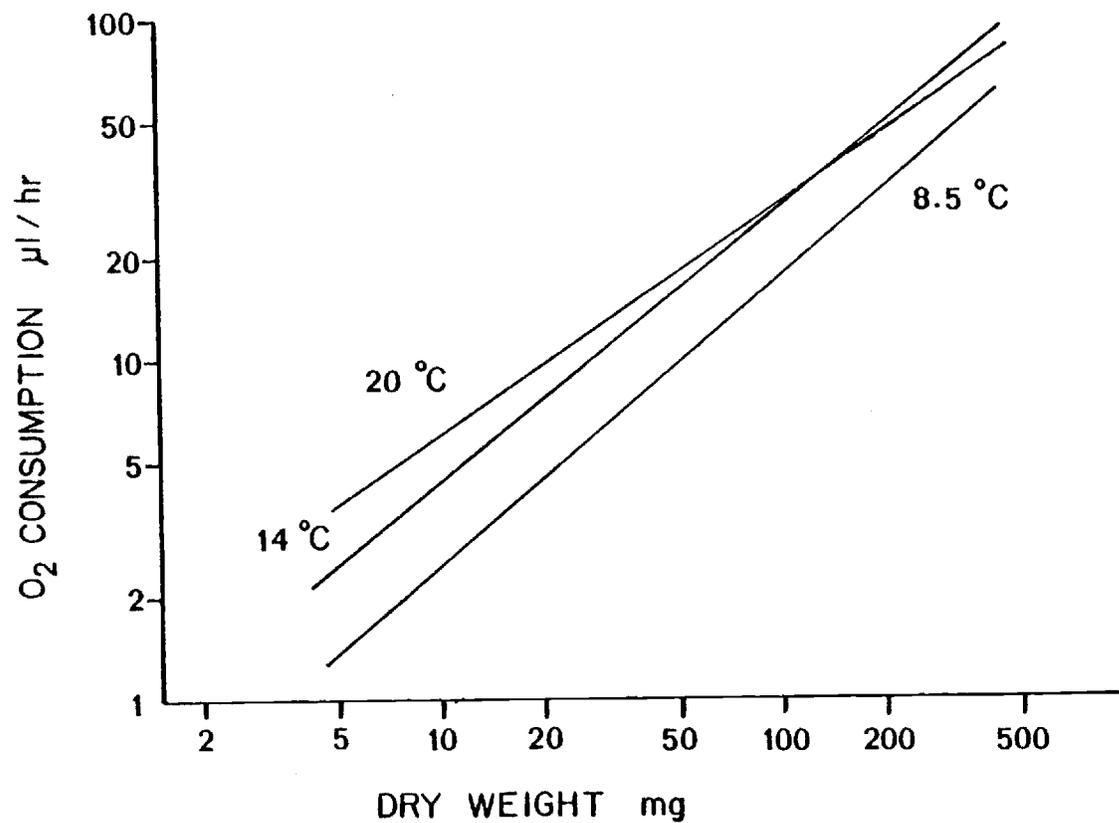


Figure 13. Relationship of oxygen consumption and weight of *A. xanthogrammica* at three temperatures.

$$\begin{array}{l}
 (8.5^{\circ}\text{C} \quad R = .347 W^{.855} \quad r^2 = 0.94; \\
 14^{\circ}\text{C} \quad R = 6.59 W^{.808} \quad r^2 = 0.92; \\
 20^{\circ}\text{C} \quad R = 1.227 W^{.690} \quad r^2 = 0.94)
 \end{array}$$

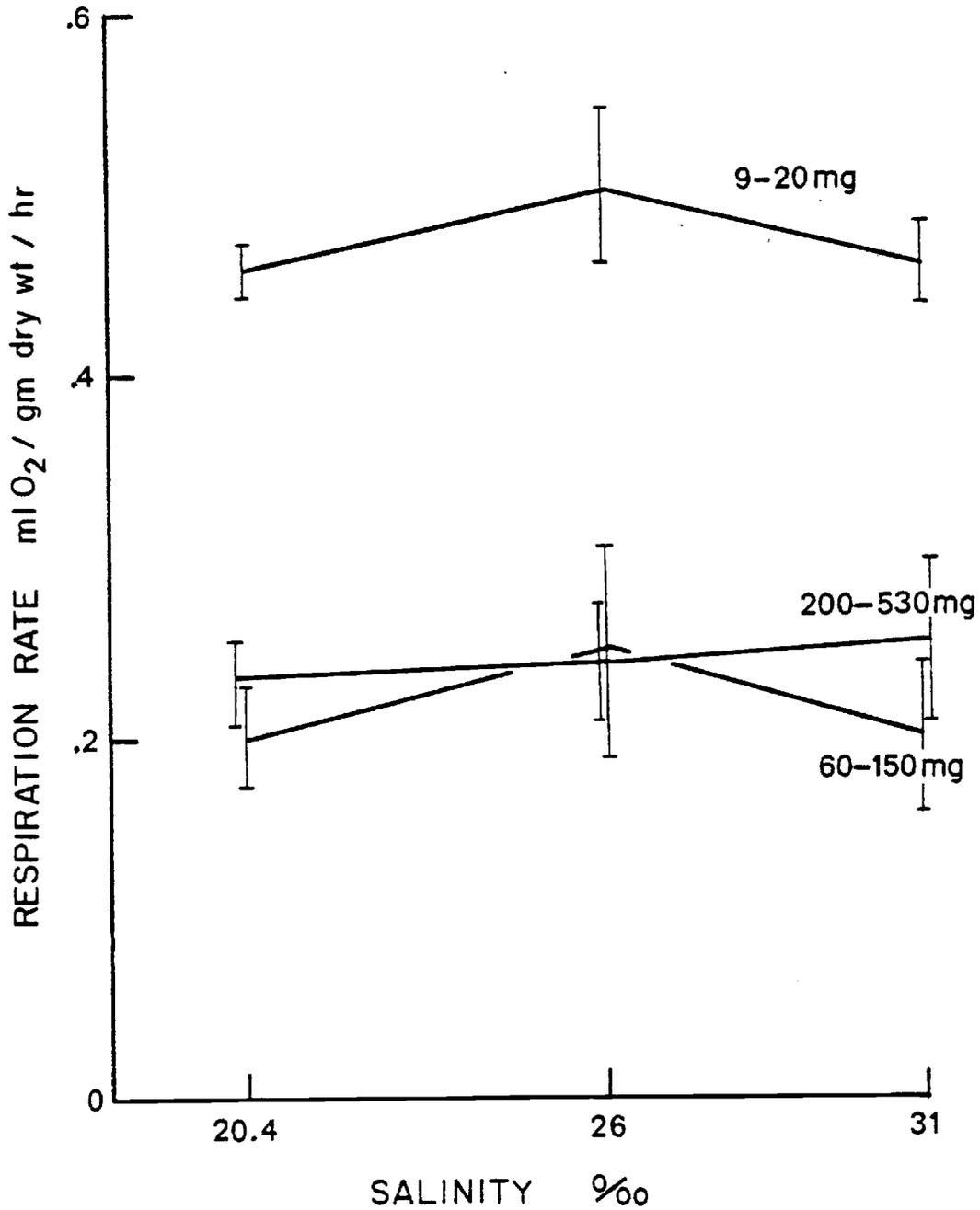


Figure 14. Relationship between water salinity and oxygen consumption of *A. xanthogrammica* at 14°C. Three curves represent three size classes (dry wt) of anemones. (Mean and SE bars given).

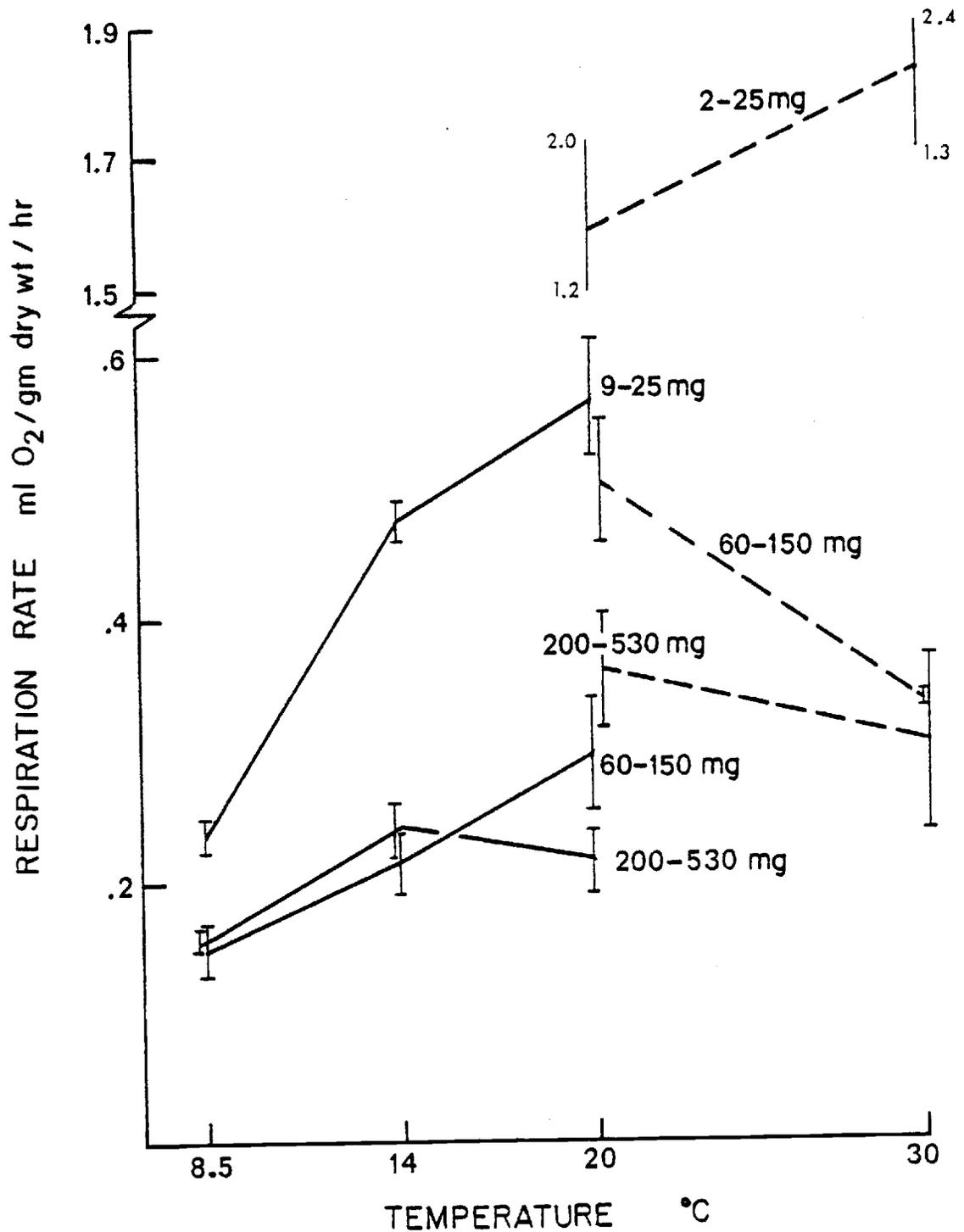


Figure 15. Effect of temperature and aerial exposure on respiration by *A. xanthogrammica*. (Solid lines--anemones submerged in seawater; dashed lines--anemones without water in flasks), Three size classes (dry wt) of anemones are represented. (Mean and SE bars given)

SIZE-SPECIFIC HEAT BUDGETS

Heat budgets calculated for anemones of various sizes indicate that loss of water by evaporation during emergence and exposure to direct insolation can cause 75% water loss and presumably death. Evaporative water loss will prevent intense heating of surface tissue. But, at the rates of insolation measured on the Oregon coast during summer, evaporative water loss within a single period of tidal exposure can also result in greater than 75% water loss from an individual anemone.

Susceptibility to death by water loss during the same time period decreases with increasing anemone size (Fig. 16) because large anemones contain and retain greater quantities of water per unit area subject to insolation than small anemones. Total water capacity of an anemone increases at a rate close to the cube of the radius, whereas the surface area of an anemone subject to direct insolation increases as the square of the radius. The most important factors governing the amount of water lost from an individual anemone are the rate and duration of heating. At an insolation of 1.3 ly/min, the maximum summer rate recorded on the Oregon coast in 1968, 75% of the water of an anemone 0.4 cm in diameter can evaporate in less than two hours. Longer periods of less intensive heating can also evaporate 75% of an individual's water; five hours direct heating at 0.45 ly/min could result in death of an individual 0.4 cm in diameter (Fig. 16). Both this level of insolation and this duration of exposure are frequently coincident on the Oregon coast in spring and summer at mid and upper intertidal levels.

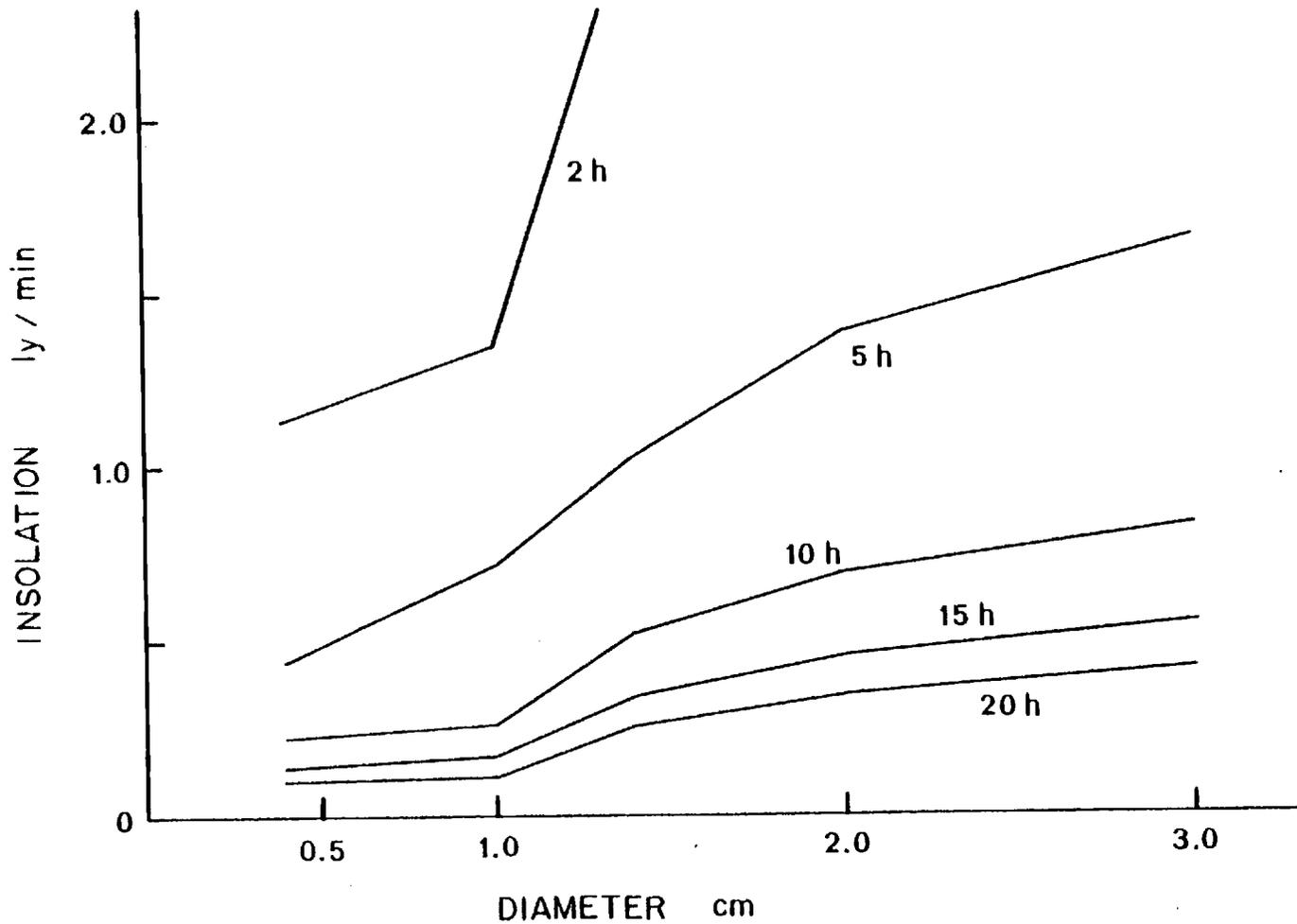


Figure 16. Calculated time in hours to 75% water loss as a function of insolation rate and anemone size.

DISCUSSION

Sebens (1977) concluded that recruitment in A. xanthogrammica was temporally and spatially unpredictable; he hypothesized that Anthopleura larvae selectively settle in mussel beds and subsequently migrate downward to lower tidal levels where they grow more rapidly. The observable size gradient of anemones with tidal height was therefore explained as a reflection of growth, active migration, and the availability of space.

An alternative hypothesis is that larval settlement in A. xanthogrammica is non-selective, with site-specific differential mortality operating upon the recently settled larvae and resulting in the observed distribution of adults. In addition to site-specific mortality and infrequent non-selective recruitment, site-specific growth and limited movement of juveniles are also assumptions of this model.

The assumption that anemone movement is very limited is supported by the results, described in Chapter 1, from seasonal monitoring of selected sites and from experimental removals. The results reported here on the distribution and abundance of anemones within mussel beds, oxygen consumption measurements, and calculations of heat budgets for individual anemones will be used to support the additional assumptions required by the model.

Dayton (1971) found the upper intertidal limit of Anthopleura elegantissima to be determined by desiccation, and Ottaway (1973, 1979) found juveniles of Actinia tenebrosa to be much less tolerant of desiccation than adults. Ottaway (1979) concluded that juvenile A. tenebrosa require for survival microhabitats where they are protected from desiccation. Rates of water loss calculated for A. xanthogrammica of

various sizes at different rates of heating (Fig. 16) suggest that desiccation resulting from evaporative cooling during tidal exposure can be a significant cause of mortality of small anemones. The observed microgeographic distribution of anemones in the field, where anemones are primarily confined to depressions or cracks in rock surfaces and mussel beds, probably reflects site-specific juvenile mortality from desiccation.

Anemones occupying high intertidal surfaces which drain at low tide and lack a canopy are subject to severe desiccation during tidal exposure. Within the intertidal range normally occupied by A. xanthogrammica the conditions of severest desiccation occur at the level just below the lowest extent of mussels and on protruding rock surfaces below this level. Desiccation is less severe at lower tidal levels, in crevices, and within the protective canopy offered by beds of Mytilus. Mussel beds and crevices, as locations of moist conditions in the upper intertidal, may be favorable for survival of juvenile anemones.

Air and rock temperatures in the Oregon intertidal at low tide during summer are significantly higher than ambient sea temperatures, while in winter sea temperatures are frequently higher than air temperatures. Rock temperatures during winter are often higher than air temperatures because the high specific heat of rock acts as a buffer to cooling during exposure to low air temperatures at low tide (Gonor, 1968). During summer, intertidal organisms experience an abrupt temperature change from approximately 12°C when covered by water to 10°C to 22°C when uncovered and exposed to air. Upper intertidal rock surfaces during summer low tides can heat 9°C to 10°C above ambient air temperature through direct insolation (Gonor, 1968). Low intertidal surfaces

and continually shaded surfaces do not undergo such intensive heating during aerial exposure.

Because higher intertidal levels experience greater temperature extremes during emergence than lower levels, organisms occupying different tidal levels encounter different thermal regimes. During summer, individuals present at high levels attain warmer temperatures during tidal exposure than similar size individuals at low levels, and small individuals attain higher temperatures during aerial exposure than large individuals at the same tidal level because they retain less water and therefore heat more rapidly (Elvin and Gonor, 1979).

The results of experiments on oxygen consumption by A. xanthogrammica suggest that individuals in the upper intertidal cannot grow as rapidly as individuals at lower levels because the metabolic energy expenditure of anemones at 20°C is greater during periods of aerial exposure than while covered by water (Fig. 15). Direct insolation during tidal exposure in the summer can heat A. xanthogrammica and other intertidal anemones to temperatures significantly greater than ambient air and sea temperature (Table 6). In this study, A. xanthogrammica ranging in size from 0.009 gm to 0.150 gm dry weight had $Q_{10} = 2.00$ while submerged over a temperature range from 8.5°C to 20°C (Fig. 15); heating of anemones by direct insolation during tidal exposure as indicated in Table 6, would increase metabolic expenditure significantly.

In addition to having higher respiratory rates because of prolonged exposure to air, anemones at upper intertidal levels have less feeding time available than those lower in the intertidal because anemones are capable of feeding only while submerged.

TABLE 6. Summary of anemone temperatures in the field in summer.

SPECIES	LOCATION	MAX. BODY TEMP. (°C)	MAX. DIFF. ANEMONE TEMP.-AIR TEMP. (°C)	REFERENCE
<u>Actinia equina</u>	South Africa	32.4	11.2	Griffiths (1977a)
<u>Anthopleura xanthogrammica</u>	Oregon	11.7	2.3	Gonor (1968)
<u>Anthopleura xanthogrammica</u>	Oregon	19.1	7.4	Gonor (1968)
<u>Anthopleura elegantissima</u>	Washington	33.6	13.3	Dayton (1971)

The observed size gradient of anemones with tidal height on intertidal vertical walls may be adequately explained by metabolic considerations involving the thermal regime and available feeding time, which vary with tidal height. Height on the shore, as it reflects time available for feeding, has been suggested as a mechanism controlling the population structure of mussels (Seed, 1969). Sebens' (1977) hypothesis that larvae selectively settle in mussel beds and migrate downward to lower levels is not necessary to explain the observed gradient of anemone size with tidal height. Sebens cites the presence of numerous small anemones (< 2.0 cm) in mussel beds and the emigration of anemones from mussel beds after experimental removal of anemones from adjacent rock surfaces as evidence in support of his hypothesis. The presence of small A. xanthogrammica in mussel beds probably results from favorable conditions for survival coupled with short feeding times at high tidal levels. Along the Oregon coast, no locations were found which had dense populations of anemones immediately below and adjacent to mussel beds.

Three sites in particular provide evidence supportive of the model proposed here. At these sites, a zone free of anemones and varying from approximately 20 cm to 50 cm in tidal height is found below the lowest edges of mussel beds and above dense populations of larger anemones along the base of the wall. Sebens' model requires that anemones leaving mussel beds for the more suitable lower habitats actively migrate through this empty zone. Yet few anemones were found on the barnacle dominated surfaces adjacent to mussel beds at these sites (Table 5). Space below mussel beds did not appear to be limiting, yet anemones were never observed migrating into this zone from the mussel beds.

At sufficiently rapid rates of downward movement, Sebens' hypothesis would predict that large numbers of small anemones should be found crowding about and competing for space with larger established adults in low pools and channels. No locations having numerous small anemones adjacent to aggregations of large individuals were found in this study. Except for lower tidepools where anemones were large, abundant and crowded together, no evidence of extreme intraspecific competition for the available space resources could be detected in A. xanthogrammica populations along the coast of Oregon.

In neither this study nor that of Sebens (1977) on A. xanthogrammica was unequivocal evidence of recruitment to the benthic habitat obtained. All evidence to date indicates that recruitment of this species is discontinuous in time, space, or both. Sporadic recruitment, in either time or space, raises the problem of how this species maintains its rocky intertidal populations.

Large annual fluctuations in recruitment intensity of other marine benthic invertebrates are known. Recruitment intensity of Patella vulgata, an intertidal limpet, was monitored for seven years in Great Britain (Bowman and Lewis, 1977). Both the between-sites and between-years variance in recruitment were found to be significant indicating the presence of temporal as well as spatial heterogeneity. Annual variation in set of Patella larvae was explained by the susceptibility of recently settled juveniles to low air temperatures, frost and snow.

Other benthic species in which large annual fluctuations in the level of recruitment are known are Crassostrea virginica (Loosanoff, et al., 1955; Loosanoff, 1966), Asterias forbesi (Loosanoff, et al., 1955), Cucumaria elongata, Amphiura chiajei, and Echinocardium cordatum

(Buchanan, 1967). A single successful heavy settlement of Amphiura chiajei formed a very stable feature of the bottom fauna over an eight year observational period, during which little subsequent recruitment occurred (Buchanan, 1967).

Populations of Donax gouldii and Tivela stultorum, two intertidal bivalves, undergo large fluctuations in population size (Coe, 1956). Declines in population density of these clams were attributed to failure of young clams to establish themselves at the end of the larval period. The occasional return of these populations to high densities was attributed to chance combinations of suitable conditions during the pelagic larval period and favorable onshore currents when the larvae were ready to set.

A species can maintain stable populations over long periods in spite of infrequent recruitment, if adult mortality is low and individuals are long lived. Lewis and Bowman (1975) found no widely applicable major external cause of mortality of Patella vulgata after the initial vulnerable period at settlement. Similarly, no extensive mortality of established adult Anthopleura xanthogrammica has been observed in this study or that of Sebens (1977). A. xanthogrammica, having extreme longevity, few causes of extrinsic mortality of large adults, and repeated annual spawning can maintain large populations in spite of sporadic recruitment.

It is concluded that the sporadic distribution and erratic abundance of intertidal A. xanthogrammica populations result from the importance of stochastic processes in structuring populations of this anemone. The frequency and initial level of recruitment are more important in controlling the distribution and abundance of A. xanthogrammica than

are mortality influences acting on the population subsequent to the early post-settlement period. Furthermore, it is concluded that the size structure pattern in A. xanthogrammica populations, showing a clearly defined gradient with tidal height on a vertical wall, may result from the interaction between physiological and habitat restraints to growth and age (time since recruitment occurred) rather than movement.

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SUMMARY

1. The density, distribution and size structure of intertidal Anthopleura xanthogrammica populations were described from field surveys using a photographic quadrat method. Periodic sampling was conducted from July 1977 to August 1978 at selected intertidal sites to document the dynamics of anemone populations. The main study locations were Boiler Bay (44°50'N), Yachats (44°18'N), and Strawberry Hill (44°15'N) along the central Oregon coast. Population surveys were also done at Yaquina Head (44°40'N), Bandon (43°6'N), and Port Orford (42°44'N).
2. Intertidal locations having dense populations of A. xanthogrammica are not abundant; most intertidal locations examined did not have high anemone density. Neither the population density nor the size structure of intertidal anemone populations was found to change at sites monitored during this study. Little movement of adult anemones was observed. Mortality of established adults was low or nonexistent.
3. Removal of the anemone populations at several locations did not stimulate settlement of planula larvae from the plankton, nor did adults from locations adjacent to the experimental removal locations rapidly immigrate into the areas cleared of anemones.
4. Attempts to determine size-specific growth rates in the laboratory at known levels of feeding produced inconsistent results. Generally, growth of continually submerged individuals decreased with increasing anemone size. It is inferred from the results of laboratory and field studies that individual growth in intertidal populations of A. xanthogrammica is very slow.

5. Anemone density within mussel beds was usually greater than on adjacent rock surfaces at lower tidal levels, but sizes were smaller. The mean diameter of anemones from mussel beds was usually less than 1.0 cm. The density and mean diameter of anemones in mussel beds did not change significantly in one year.
6. Calculations indicate that upper intertidal anemone populations should have lower rates of growth than lower tidal level populations because of the combined effects of shorter feeding times, and higher metabolic expenditures as measured by oxygen consumption.
7. It is inferred from calculations of heat budgets and rates of evaporative water loss during tidal exposure that desiccation during a single period of tidal exposure can result in death of small anemones and may be responsible for the observed small-scale distribution of the population.
8. No evidence of settlement of A. xanthogrammica larvae from the plankton onto rocky intertidal surfaces was found at any study location during the study period.
9. The evidence presented in this study supports the hypothesis that the erratic large-scale distribution and abundance of intertidal A. xanthogrammica populations is primarily a result of the initial level and location of recruitment. The small-scale distribution of anemones, which are primarily located in depressions and crevices in rock surfaces, results from the mortality of small anemones on surfaces which experience intense desiccation. The size gradient of anemones with tidal height on a vertical wall results from greater rates of growth of individuals at lower levels.

10. The results of studies directed toward detecting recruitment to the benthic habitat and toward obtaining individual growth rates indicate that recruitment is unpredictable and individual growth is neither fast nor density dependent in A. xanthogrammica populations. The population characteristics of intertidal A. xanthogrammica populations are not suitable to allow commercial harvest on a sustained basis.