THE LIFE HISTORY OF THE INTERTIDAL BARNACLE,

BALANUS BALANOIDES (L.) IN PORT VALDEZ, ALASKA

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THE LIFE HISTORY OF THE INTERTIDAL BARNACLE, *BALANUS BALANOIDES* (L.) IN PORT VALDEZ, ALASKA

A

THESIS

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By

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ABSTRACT

The life history of the boreo-arctic barnacle *Balanus balanoides* was examined at three study sites in Port Valdez. Ovarian tissue development began in early summer. Fertilized eggs, evident by September, were brooded throughout the winter. Larval release was synchronous with the spring phytoplankton bloom. Settlement was observed in April and continued until June. Maximal shell growth occurred immediately subsequent to assimilation of organic material from the spring bloom. Seasonal fluctuations in body weight were noted and reflect feeding, spermatogenesis, and energy transfer to other biological processes (i.e., shell growth and reproduction). Mortality, greater for juveniles than adults, resulted from seasonal stresses (lowered salinity and heightened sedimentation), spatial competition, predation, and pollutants (hydrocarbons). Once life-history events were confirmed for barnacles in Port Valdez, comparisons of trends observed at the three sites were possible. Differences between populations were evident and were attributed to the unique micro-habitats of the study sites.

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INTRODUCTION

BACKGROUND

The life history of the intertidal barnacle *Balanus balanoides* (L.) was studied from 1980-1982 in Port Valdez, Alaska in association with a project carried out by the Institute of Marine Science, University of Alaska, Fairbanks and funded by Alyeska Pipeline Service Company. The specific purpose of the project was to design a monitoring program for the marine environment in the vicinity of the tanker terminal in Port Valdez. The data base accumulated would make it possible to identify the effects, if any, of the discharge of treated tanker ballast water on organisms inhabiting the intertidal and subtidal areas. Since tanker ballast is carried in unsegregated compartments, tankers docking at the Alyeska marine oil terminal must first pump oily ballast to a water treatment plant prior to taking on oil for transport to refineries in the south. The treated ballast water, containing < 10 ppm of hydrocarbon, is discharged into the Port from a diffuser located offshore from the terminal at 70 m.

In order to distinguish between natural environmental fluctuations and the deleterious effects resulting from industrial activity, a long-term monitoring program designed to accumulate a large data base must be established (Straughan, 1971; Lewis, 1972; Nelson-Smith, 1973). Monitoring for the possible effects of pollutants is especially critical in estuaries, bays, and other enclosed basins, since dissipation of oily residues requires a much longer period of time here than in open waters (Hyland and Schneider, 1976). Examination of the intertidal regime is essential to any monitoring study, since organisms inhabiting the area are highly susceptible to industrial pollutants such as oil (Olson and Burgess, 1967; Straughan, 1971; Nelson-Smith, 1973). An especially serious problem arises for sessile species, such as barnacles which are unable to escape the stress. The barnacle *B. balanoides*, a dominant intertidal organism in Port Valdez, is especially suitable for monitoring purposes. However, prior to establishing a program to monitor responses of an intertidal species to industrial pollutants, it is first necessary to understand all of the regional stresses, physical and biological, which would possibly have an effect on the organism. These include climatic conditions, freshwater input, suspended sediment loads, competition and predation. Also, basic events in the life history of the specific organism being studied should be worked out before undertaking a project of this nature. Thereafter the examination of critical aspects of the basic biology (reproduction, settlement, growth, mortality) of selected species, imperative to monitoring-type studies of the intertidal regime (Butler *et al.*, 1972; Lewis, 1972; Monastero, 1976), can be made.

Intertidal research in Port Valdez, prior to the present study was limited to the following:

1) A preliminary survey of rocky shores (McRoy and Stoker, 1969)
2) A meiofaunal study of sediment shores (Feder *et al.*, 1976a; Jewett and Feder, 1977; Feder and Paul, 1980)
3) An assessment of selected macrofaunal species on sediment beaches (Myren, 1973; Myren and Pella, 1977; Feder, unpub.)

4) A field examination of the effects of oil on the clam, *Macoma balthica* (Feder *et al.*, 1976a; Shaw *et al.*, 1976)
5) A base-line monitoring study of the abundance and zonation of selected faunal and floral species (Colonell, 1979; Feder and Keiser, 1980).
6) An examination of specific aspects of the biology of the blue mussel, *Mytilus edulis* (Keiser, 1978).

The specific objectives of the present thesis study were:

1) To document the biology of *B. balanoides* in the waters of Port Valdez.
2) To monitor populations of *B. balanoides* in Port Valdez to determine and identify the effects, if any, of chemically treated ballast water on these populations.
3) To identify short and/or long-term effects of tanker traffic, industrial activities, and oil spills on barnacle populations in the vicinity.
4) To determine the most useful monitoring tools for identifying biological responses of *B. balanoides* to environmental stress and industrial pollution.

LITERATURE REVIEW

The monograph of Charles Darwin (1854) on the Subclass Cirripedia is one of the earliest recorded descriptions of the Balanidae, to which *Balanus balanoides* belongs. Following Darwin, in the latter part of the nineteenth century, Koehler (1889, 1892) and Groom (1894, 1895) published the results of their investigations on the biology of barnacles. Koehler worked primarily on the physiology of Cirripedes while Groom concentrated on their developmental biology. However, most of the basic research on barnacles occurred during the early part of the present century (Pilsbry, 1907, 1916; Broch, 1922, 1936; Cornwall, 1925; Visscher, 1928; Bassindale, 1936). Moore (1933, 1934, 1935a and b, 1936) provided a substantial portion of the early life-history information for *B. balanoides*, including studies of distribution and growth. In subsequent years, Pyefinch (1948, 1949) working primarily with larvae, Smith (1946, 1949), Barnes and Powell (1950), and Knight-Jones (1953, 1955) studying settlement, Southward (1955) studying behavior, and Southward and Crisp (1956) studying abundance and distribution contributed to the rapidly accumulating wealth of barnacle literature. Over the past 30 years, H. Barnes, M. Barnes, and D. Crisp have published many significant papers on the biology, ecology, and biochemistry of barnacles, especially *B. balanoides*. The papers by H. Barnes and M. Barnes describe investigations of larval biology (e.g., Barnes and Barnes, 1958), reproductive biology (e.g., Barnes and Barnes, 1956), growth (e.g. Barnes and Barnes, 1959), distribution (e.g., Barnes, 1957), and energetics (e.g., Barnes *et al.*, 1963). Crisp and associates have also published a series of papers on barnacles, including studies of reproductive biology (e.g., Crisp, 1959), growth (e.g., Crisp, 1960), and feeding biology (e.g., Ritz and Crisp, 1970). Further research on *B. balanoides* includes the work of Connell (1961) on factors affecting distribution, Walley (1964, 1965, 1969) on larval and reproductive biology, and Petersen (1962, 1966) on the life history and distribution of the barnacle in Greenland. Recent additions to the data base on barnacles include reproductive studies (Hines, 1979), fecundity assessment (Hurley, 1973; Arnold, 1977), larval studies (Holland and Walker, 1975), settlement (Walker, 1973; Larman and Gabbott, 1975; Barnett *et al.*, 1979; Moyse and Hui, 1981; Kendall *et al.*, 1982), growth (Bourget, 1975, 1980; Bourget and Crisp, 1975) and energetics (Wu and Levings, 1978, 1979; Lucas *et al.*, 1979; Wu, 1980).

Much of the extensive literature base discussed above originated in northern Europe at latitudes similar to Port Valdez. However, little information is available on the life-history events of the boreo-arctic barnacle, *B. balanoides* in Alaskan waters. The present study was an attempt to fill the gap in the knowledge of this euryhaline species in northern regions.

PORT VALDEZ

The Physical Environment

Port Valdez is a deep, narrow, glaciated fjord located in the northeastern corner of Prince William Sound (61°06'N, 146°28'W) (Fig. 1). It is surrounded by the Chugach Mountains which are covered with ice fields and active glaciers. Port Valdez is approximately 20 km long and 4 to 6 km wide with a maximum depth of 230-250 m. The bottom topography is characterized by a smooth, flat channel-like depression, the largest and deepest in the Prince William Sound system. Two sills,

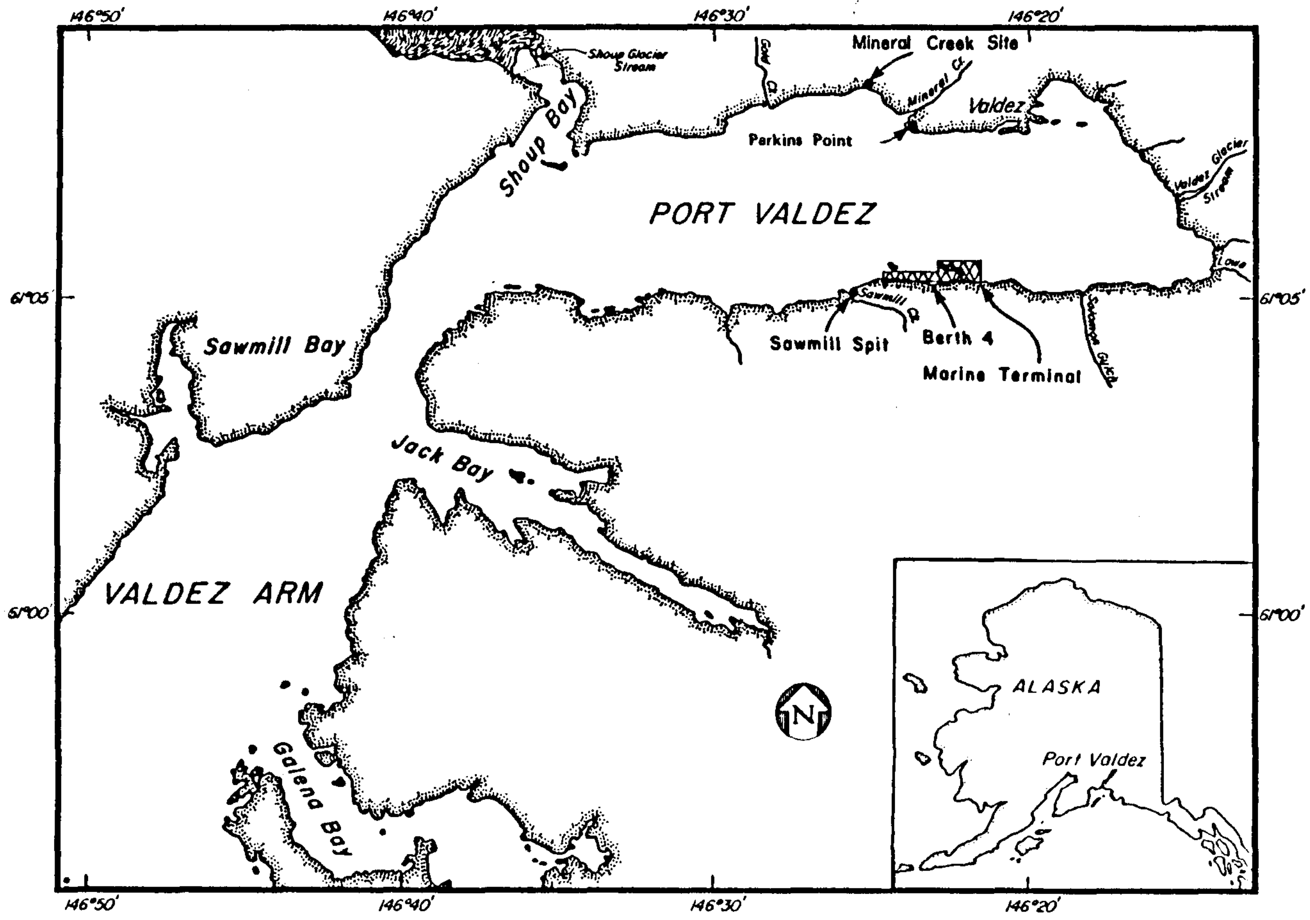

Figure 1. Map of Port Valdez showing the Sawmill Spit, Berth 4, and Mineral Creek sampling sites.

located in the Valdez Narrows at the mouth of the fjord are approximately 130 m in height.

Several sources of freshwater runoff empty into the Port during the summer season, particularly in July and August (Carlson *et al.*, 1969). These include the Lowe and Robe Rivers and the Valdez Glacier Stream from the head of the Port, Mineral Creek, Gold Creek, and the Shoup Glacier Stream from the north, and Solomon Gulch and Sawmill Creek from the south. The major contributors of suspended sediment to the Port are the Lowe River, the Valdez Glacier Stream, and Mineral Creek (Sharma and Burbank *in* Hood *et al.*, 1973). Due to the proximity of these three major sources, sedimentation rates are highest in the eastern end of the Port. Sediments originate from glacial deposits, and are characterized primarily by clay minerals. The suspended particles are transported into Port Valdez in a plume of low salinity surface water layered up to 10 m deep (Sharma and Burbank *in* Hood *et al.*, 1973). The surface lens of freshwater overlies a thick, deeper layer of highly saline, dense water. A stratification of temperature and salinity occurs in the waters during the summer. A pycnocline forms at the boundary between the two water masses. During the winter, when runoff is minimal, the pycnocline is absent and mixing occurs throughout the water column to the bottom (Muench and Nebert *in* Hood *et al.*, 1973).

Port Valdez is a classic example of a positive estuary that receives more freshwater runoff and precipitation annually than is lost through evaporation (Pritchard, 1952). Typical estuarine circulation occurs during the summer as a result of the freshwater runoff. This is characterized by a seaward movement of low density, brackish surface water and a landward movement of dense, deeper water. The latter water is often referred to as a salt wedge. In a classic estuarine circulation, as the freshwater lens moves seaward, entrainment of deep saline waters occurs, resulting in a gradient towards higher salinity water in the seaward direction. To satisfy continuity, as entrainment moves water out of the Port, water enters over the sill from outside to replace this water (Muench and Nebert *in* Hood *et al.*, 1973).

The general surface circulation of water in Port Valdez is counterclockwise and results from a combination of factors, including water discharge from rivers, wind, the Coriolis effect, and tides (Sharma and Burbank *in* Hood *et al.*, 1973). Tides are mixed and generally semidiurnal, with a tidal range of approximately 3 m. During spring tides however, a range up to 6 m occurs. Winds, though prevailing from the northwest in winter and from the southwest during the summer, are channeled in an east-west direction over the fjord by the mountains surrounding the area.

The maritime climate of Port Valdez is typically defined by mild winters and cool, wet summers. The mean air temperature is about 4°C in winter and 8.4°C during the summer months. Precipitation averages 150 cm annually with the months of September and October being the wettest. Winds are highest during the months of November to February with an average wind speed of 4.6 m/sec (10 mph) during this period.

The shoreline of Port Valdez is defined by steep, rocky walls in the western end, which are gradually replaced by gently sloping beaches and mud flats in the eastern end. Exposures are rugged and of two major types: dark gray to black slate-like shale and dark gray siltstone embedded with veins of quartz (Sharma and Burbank *in* Hood *et al.*, 1973).

Weather patterns observed over the course of the study (April 1980-August 1982) were variable and often responsible for conditions adversely affecting the intertidal biota. Weather data, provided by the National Weather Service Office in Valdez, Alaska, include mean daily air temperatures, precipitation, wind speed and direction, and the occurrence of clear vs. partly cloudy or cloudy days (summarized in Table 1). Monthly air temperatures over the course of the study (1980-1982) are included in Figure 2. Air temperatures between the years were compared by use of a Student's t-test in order to determine if the year-to-year variations differed significantly ($\alpha = 0.05$) from one another (results in Appendix 1). Temperatures were compared for the winters of 1980-81 and 1981-82, and for the summers of 1980, 1981, and 1982. Winters were arbitrarily considered to be the months of September-April and the summers, April-September. Results indicate that, in general, the winter of 1981-82 was more severe than the previous winter, 1980-81. Additional data support these results. The winter of 1981-82 was characterized not only by colder air temperatures, but, also by below normal amounts of precipitation (resulting in clear, cold days) and high winds accompanied by frequent ice formation. Each of these climatic parameters must be considered in order to compare seasons on a yearly basis. The only major summer difference, based on the criterion of air temperature

Table 1. Local climatological data from the National Weather Service Office, Valdez, Alaska for the period April 1980-September 1982.

						Number of		
Month	Mean monthly air temperature (°C)	Normal air temperature (°C)	Total monthly precipitation (cm)	Normal precipitation (cm)	Wind speed (m/sec)	Clear days	Partly cloudy days	Cloudy days
1980								
Apr	4.3	2.0	7.4	7.8	2.0	2	2	26
May	7.3	6.6	8.4	8.1	2.6	1	2	28
Jun	10.8	10.7	8.2	6.9	2.3	2	4	24
Jul	12.7	11.8	19.6	11.0	1.8	3	5	23
Aug	11.1	11.1	17.1	14.7	1.7	4	8	19
Sep	8.4	8.1	12.1	19.7	2.1	6	4	20
Oct	3.9	3.1	23.4	17.2	2.2	1	1	19
Nov	1.2	-3.3	12.0	14.4	3.0	5	2	23
Dec	-9.6	-6.9	12.9	13.7	5.1	15	2	14
1981								
Jan	1.0	-7.9	31.8	12.9	2.3	0	2	29
Feb	-2.8	-5.3	18.1	13.5	1.8	0	2	26
Mar	1.3	-2.9	17.5	11.0	2.0	6	5	20
Apr	3.2	2.0	1.5	7.8	3.0	13	4	13
May	9.9	6.6	4.8	8.1	2.2	3	9	19
Jun	11.5	10.7	11.6	6.9	2.5	3	9	18
Jul	11.9	11.8	22.8	11.0	1.6	1	1	29
Aug	10.9	11.1	46.3	14.7	1.7	5	2	24
Sep	8.1	8.1	15.9	19.7	2.1	3	4	23
Oct	4.3	3.1	30.0	17.2	2.5	5	5	21
Nov	-2.4	-3.3	17.2	14.4	3.3	6	4	20
Dec	-4.1	-6.9	19.7	13.7	3.4	9	0	22

Table 1. Continued.

						Number of		
Month	Mean monthly air temperature (°C)	Normal air temperature (°C)	Total monthly precipitation (cm)	Normal precipitation (cm)	Wind speed (m/sec)	Clear days	Partly cloudy days	Cloudy days
1982								
Jan	-9.1	-7.9	25.2	12.9	5.3	11	3	17
Feb	-4.5	-5.3	4.5	13.5	6.2	12	3	13
Mar	-1.4	-2.9	13.8	11.0	2.8	8	2	20
Apr	2.0	2.0	6.2	7.8	3.0	7	6	17
May	7.4	6.6	3.1	8.1	2.7	5	4	22
Jun	11.1	10.7	8.3	6.9	2.6	1	7	22
Jul	12.4	11.8	12.3	11.0	2.5	4	5	22
Aug	12.4	11.1	6.9	14.7	1.9	7	9	15
Sep	8.1	8.1	42.4	19.7	1.7	4	3	23

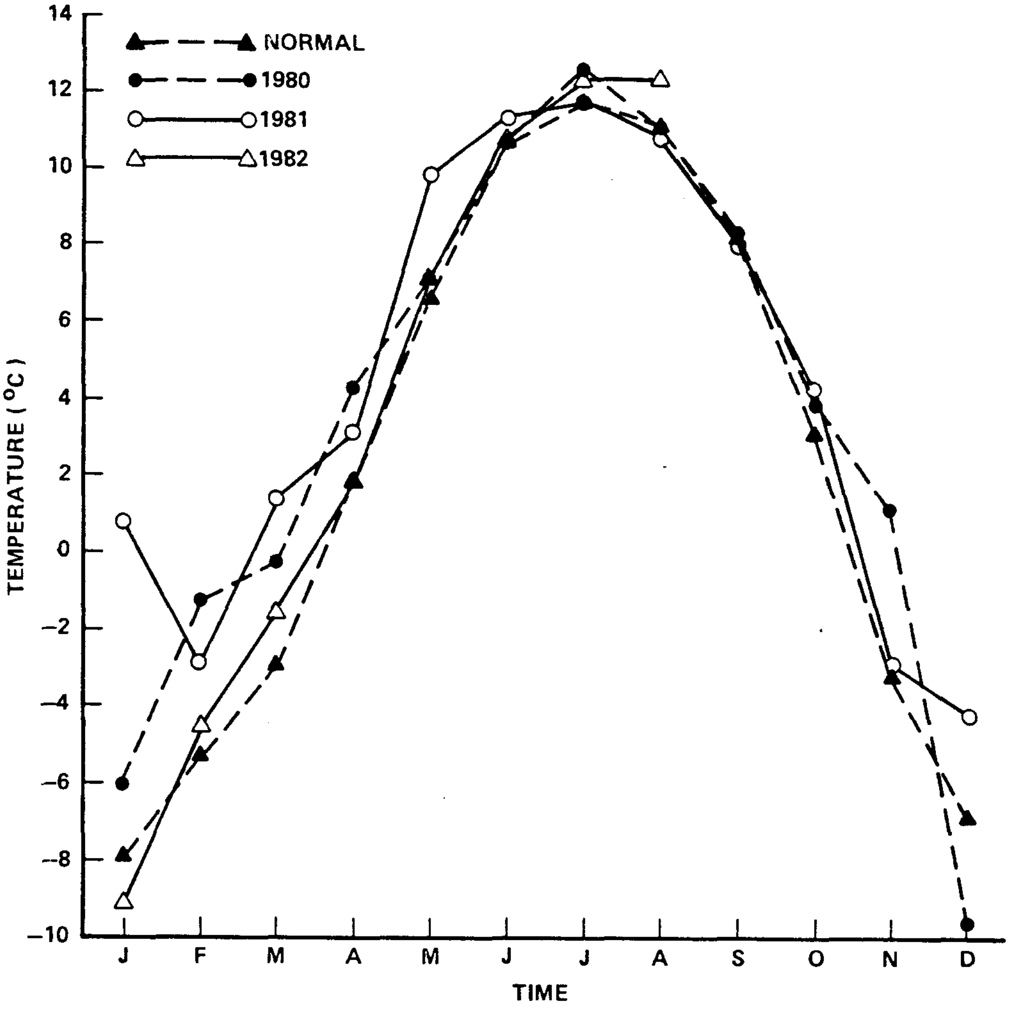

Figure 2. Annual fluctuations in air temperature for Port Valdez, Alaska, including the expected monthly average and actual monthly temperatures recorded over the course of the present study, 1980-1982. Data were provided by the National Weather Service Office, Valdez, Alaska.

alone, was between the summer of 1982 and the other two summer seasons (1980 and 1981). The late summer months of 1982 were significantly warmer than in previous summers. Furthermore, the levels of precipitation recorded for the summer of 1982 were lower than in the two preceding summers, indicating a warm, dry summer. The summer of 1981, though not significantly cooler than the other summers (with the late summer exception mentioned above for 1982) had unusually high levels of precipitation. The additional rainfall intensified major river runoff throughout the Port, which resulted in a greater suspended sediment load entering the waters of the area.

A further event which occurred in Port Valdez during the present study should be mentioned along with the climatic parameters discussed above. In April 1980, a small amount of crude oil (approximately 30 barrels) was spilled from the Berth 5 tanker site adjacent to the Berth 4 study area. The spill must be considered, along with environmental conditions, as a possible source of disturbance to the intertidal organisms in the vicinity of the tanker site.

Description of the Study Areas

In the present study, the biology of the barnacle *Balanus balanoides* was examined at three distinct intertidal study areas within Port Valdez. These sites are at Sawmill Spit (61°05.2'N, 146°25.2'W), Berth 4 (61°05.2'N, 146°23.9'W), and Mineral Creek (61°05.1'N, 146°25.6'W) (Fig. 1). All are typical rocky intertidal beaches characterized by similar assemblages of organisms. In addition to *B.*

balanoides, two other balanoid species inhabit the intertidal shores of Port Valdez. *Balanus glandula* overlaps the distribution of *B. balanoides* in the upper intertidal zone while *B. crenatus* overlaps it in the lower intertidal. Other major intertidal fauna include the following: the blue mussel *Mytilus edulis* (a prime competitor for space), the herbivorous gastropods *Littorina sitkana* and *L. scutulata*, the rock whelk *Thais (Nucella) lamellosa* (a common predator on *B. balanoides*), and the limpet *Collisella pelta*. Several species of algae inhabit the intertidal regions, as well. These include the green algae *Monostroma* spp., *Enteromorpha* spp., and *Ulothrix* spp., the brown algae *Fucus distichus* and *Pylaiella littoralis* and the red alga *Pterosiphonia bipinnata*. These fauna and flora occur in vertically distinct bands within the intertidal zone and reflect the universal scheme of intertidal zonation (Stephenson and Stephenson, 1949).

The three study sites differ in the topography or physical profile of the intertidal area. Sawmill Spit, located on the southern shore of the Port is somewhat exposed. The beach is gently sloping and composed primarily of flat cobblestones. A few large boulders are located in the upper intertidal region. The extreme reaches of the high intertidal form a vertical rock face which extends up into the adjacent wooded terrestrial regime. The Berth 4 area, also located on the southern shoreline east of Sawmill Spit is different from the latter site. Berth 4, situated behind Saw Island is more sheltered, and is defined primarily by vertical rock walls and the presence of large boulders located throughout the intertidal zone. Large rocks in the low intertidal form a small shelf giving way to a steep, vertical face plunging into subtidal depths. A relatively flat, but narrow tidepool area is located in the mid to lower intertidal region. The area immediately above and behind the boulder region is flat, but soon extends vertically up to the wooded area above the intertidal zone. Mineral Creek, on the northern shores of the Port is somewhat sheltered by Perkin's point to the east and a second point to the west. Although Mineral Creek is somewhat similar to Sawmill Spit, the sites differ since the Mineral Creek area forms the upper edge of an extensive flat located seaward of the beach. Large rocks are interspersed throughout the gently sloping intertidal, which is a combination of silty mud and small rocks. In the extremely high intertidal reaches of Mineral Creek, as at the other study sites, a vertical rock face connects the marine and rugged terrestrial regimes. The Mineral Creek study area, located adjacent to Mineral Creek, is seasonally subjected to physical stresses in the form of freshwater runoff and a heavy suspended sediment load. Despite the presence of a surface freshwater lens in the Port during the summer, the two sites on the shore opposite Mineral Creek are not subjected to physical stresses to the same extent as the Mineral Creek site. The Berth 4 site, located within the Alyeska Pipeline Terminal is subjected to industrial pollutants derived from discharged treated ballast water and tanker activity in the immediate vicinity. Sawmill Spit, although within a mile of the tanker terminal and in close proximity to Sawmill Creek, is the site apparently least affected by terminal activities and physical parameters, and for the purposes of this study, was considered to be the control site.

GLOSSARY

Since the reader may be unfamiliar with much of the terminology used in this thesis, a glossary of words and definitions pertaining to the biology of barnacles in included below. Important morphological features of a typical barnacle, as referred to throughout the text, are illustrated in Figure 3.

Aging technique (age) - method in which the age of a barnacle is determined by counting the number of winter disturbance rings on the surface of the outer shell plates; these rings are identified as distinct notches or overhangs of shell material, formed by the retreat of the mantle tissue when growth ceases for the winter; juveniles in their first year of growth possess no winter rings and comprise the first year class, true adults in their second year of growth possess one winter ring and comprise the second year class, those in their third year of growth comprise the third year class, etc.

Body tissue weight - the dry weight of the body proper, or prosoma, including the gastro-intestinal tract and male reproductive tissue but not ovarian or lamellar tissue; also referred to as somatic tissue weight.

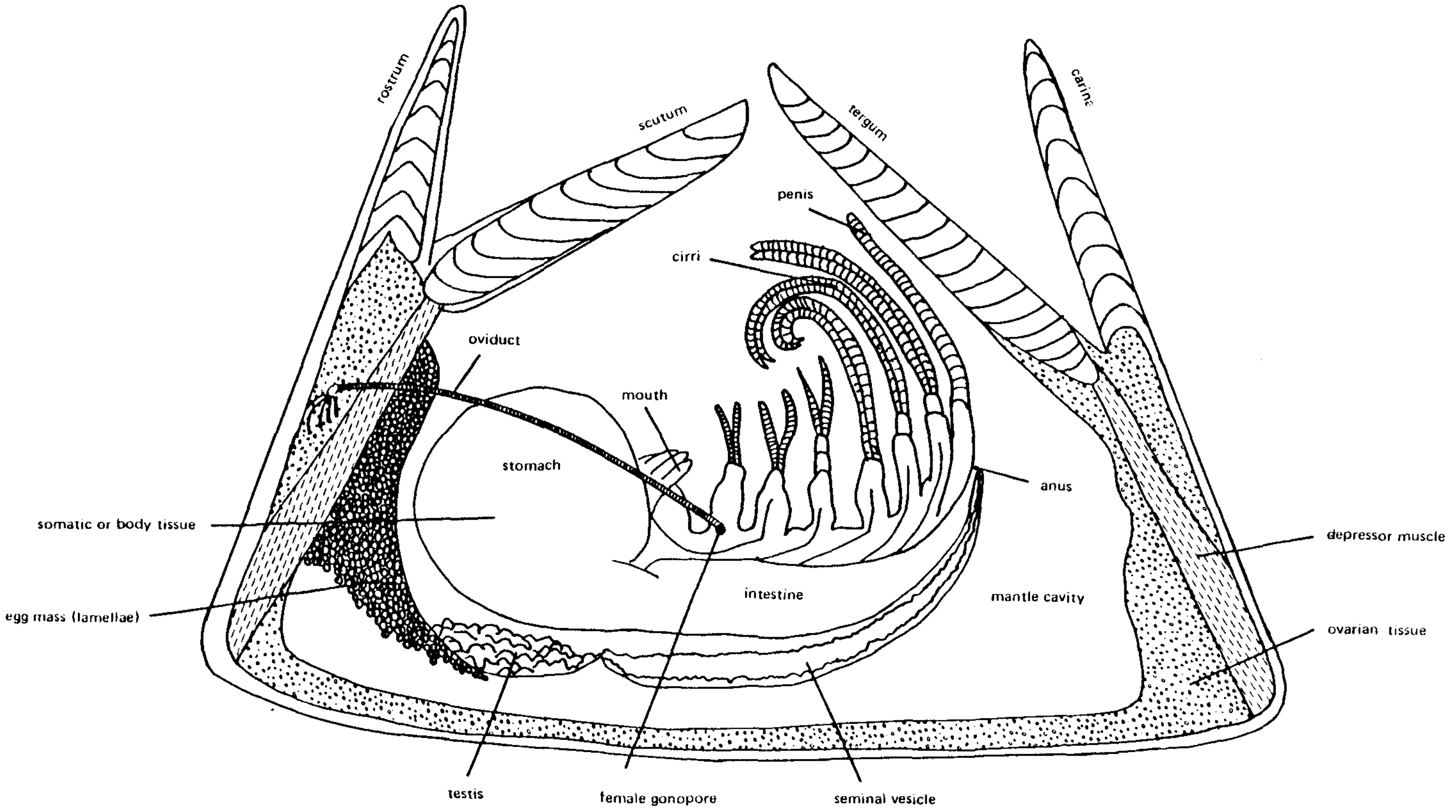

Figure 3. Diagram of a typical barnacle, illustrating morphological features referred to in the text of this thesis (modified from Barnes, 1980).

Cyprid - the non-feeding larval form which develops just prior to settlement and metamorphosis to a juvenile barnacle.

Disturbance ring - also referred to as winter ring; identified by a notch or overhang of shell material, formed by the retreat of the mantle tissue when growth has ceased for the winter months.

Energy partitioning - the periodic transfer of carbon from body (somatic) tissues to other regions of the organism, for utilization in various energy requiring processes, such as shell growth and gametogenic tissue development; can be recognized by fluctuations in body weight with time.

Fecundity - the number of fertilized eggs contained within lamellae in the mantle cavity prior to larval release.

Growth ring increment - the shell material formed annually by a barnacle between successive winter or disturbance rings.

Lamellae - the fertilized eggs and associated ovisac contained within the mantle cavity (Fig. 3).

Nauplii - any of the first six planktonic larval stages (all feeding except the first) through which the embryo develops.

Prosoma - the tissue comprising the body proper, including the gastrointestinal tract and male reproductive tissue.

R/C (Rostro-Carinal) diameter - the basal or widest barnacle diameter, measured from the base of the rostrum to the base of the carina on the shell plates (Fig. 4); also referred to as length (Barnes, 1953).

Recruitment - the settlement of cyprid larvae into a particular barnacle population, and the subsequent juvenile barnacle contribution, in numbers, to the population.

Somatic tissue weight - also referred to as body tissue weight.

Spat - a newly settled juvenile barnacle.

Spawning - the release of embryos or Stage I nauplii from the mantle cavity into the water column, initiated at the time of the spring diatom bloom.

Valve weight - the dry weight of the opercular valves (scuta and terga); utilized in energy partitioning analyses.

Vertical growth-ring height - a measure of the vertical addition of shell material for a given barnacle in each successive year of

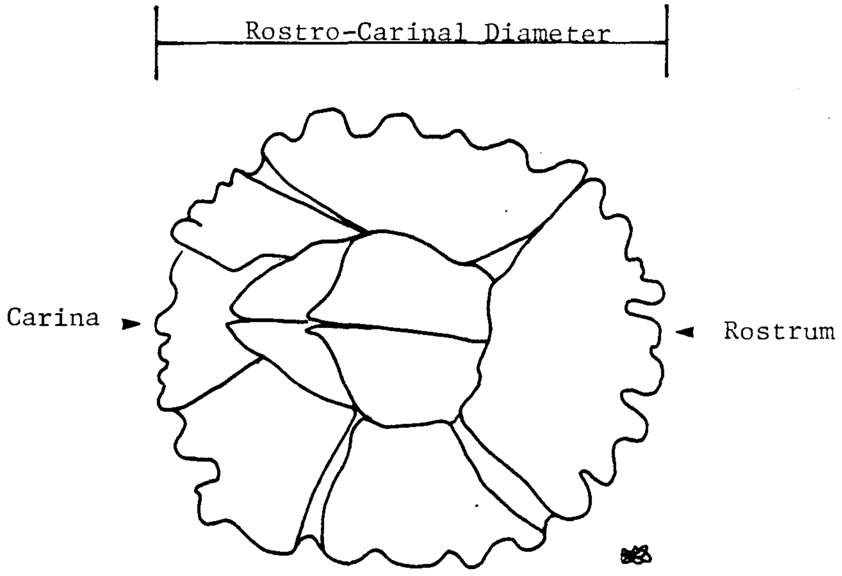

Figure 4. Diagram illustrating measurement of the rostro-carinal (R/C) diameter of a barnacle.

growth; taken as the distance between the top of the shell plate and the bottom edge of the disturbance or winter ring being measured (Fig. 5).

Winter ring - also referred to as disturbance ring.

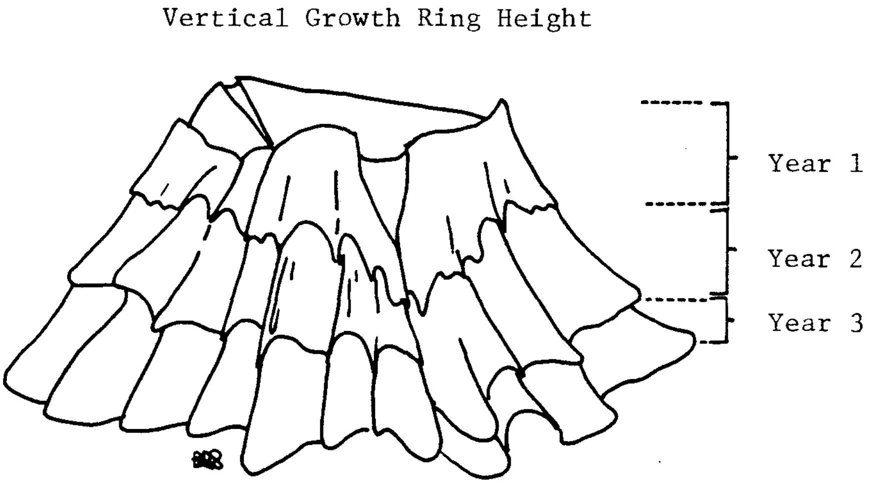

Figure 5. Diagram illustrating the structural criteria used for the recognition and measurement of successive vertical growth rings on shell plates of barnacles. The height of each year's shell accretion is determined for use in year-class growth determinations. Annual growth is considered as the increment of shell material between successive winter or disturbance rings. Winter rings are notches or overhangs of shell material formed by retreat of the mantle tissue in winter, when conditions no longer favor shell growth.

REPRODUCTIVE BIOLOGY

INTRODUCTION

The reproductive biology of *Balanus balanoides* in Port Valdez, Alaska was investigated in terms of annual ovarian and lamellar tissue production, reproductive staging, fecundity (the number of eggs present per individual), and cyprid settlement. From these data, seasonal and annual reproductive patterns of the barnacle were established and utilized as the basis for a long-term monitoring program in Port Valdez.

The weight of reproductive tissue varies throughout the year. Gametogenic tissue development, initiated during the spring phytoplankton bloom, continues into the summer months. Spermatogenesis occurs in late summer or early fall, immediately prior to copulation and fertilization (Barnes *et al.*, 1963). Upon being fertilized, eggs (now termed lamellae) are moved via the oviduct to the base of the mantle cavity (Fig. 3). Here, lamellae retained in ovisacs are brooded throughout the winter, and gradually develop into eyed nauplii. In late winter or early spring, larvae hatch and are spawned into the water column. After larvae (nauplii) are released from the mantle cavity of the parent, they spend approximately six weeks feeding in the water column, changing to non-feeding cyprids just prior to settlement.

Since *B. balanoides* produces only a single brood per year, the progression of development from stage to stage is easily followed and readily recognizable in a majority of barnacles at any given time. The annual breeding cycle of the boreo-arctic barnacle represents an adaptation to lower temperature regimes. Fertilized eggs of *B. balanoides* contain more yolk and are consequently larger than those of the more southern species. Many more eggs are produced by the boreo-arctic barnacle with only one annual brood (e.g., *B. balanoides*) than by those producing multiple bloods per year (e.g., *B. glandula* and *B. crenatus*). Embryos are brooded throughout the winter and larval release is synchronous with spring diatom production, ensuring food for developing planktonic offspring (Barnes, 1962; Barnes and Barnes, 1968).

A complete assessment of the fecundity of barnacles, including those of varying sizes, ages, tidal heights, and locations in Port Valdez is necessary in order to identify any fluctuations that may occur over time.

The observation of settlement patterns of juvenile barnacles is useful for determination of seasonal settlement trends as well as the preferred areas of intertidal settlement.

METHODS

Fifty *Balanus balanoides* from mid and lower zones of barnacle abundance and twenty-five from the upper zone (reduced sample size in the latter area was the result of low densities present in the upper zone) were collected from the intertidal areas of Sawmill Spit, Berth 4, and Mineral Creek for April, June, July, August, and September 1980, February-September 1981, and March-October 1982. Supplementary samples collected during the winter months (October 1980-January 1981, October 1981-February 1982, and October 1982) were provided by George Perkins.

Animals were removed from their rock substrate, frozen, and returned to Fairbanks.

The reproductive staging scheme employed by Keiser (Colonell, 1979 and Feder and Keiser, 1980; Table 2) was applied to the collected samples, and all stages present were noted. Reproductive material, located at the base of the mantle cavity (Fig. 3), was removed after staging, dried until weight loss was negligible (24 hrs, 60°C) and weighed. Reproductive material represented either ovarian or lamellar tissue, depending on the time of year relative to fertilization.

A one-way random-effects model of the analysis of variance (ANOVA) (Zar, 1974) was utilized to test the following null hypothesis (H_o): no difference exists between the weight of reproductive tissue in a given month for barnacles from Sawmill Spit, Berth 4, and Mineral Creek. A critical F value was determined for the null hypothesis and compared with tabled values of F at the 95 and 99% confidence levels to test the validity of the null hypothesis.

A Student's t-test was utilized to evaluate the following null hypothesis (H_o): no annual difference exists between the weight of reproductive tissue for a particular month at any site. In the event that the variance (SD^2) between two annual means differed significantly, an Aspin-Welch test was applied to the data (Snedecor and Cochran, 1980; also called the Behrens-Fisher test). Significance was determined at the 95% confidence level. Equations for the two tests are:

Table 2. The reproductive staging scheme used for *Balanus balanoides* in the present investigation in Port Valdez, Alaska (from Feder and Keiser, 1980).

Stage	Description
0	No reproductive forms evident — mantle cavity is empty and tissue is grayish in color
1	Developing female gametogenic tissue evident — whitish or yellowish ovarian tissue is present at the base of the mantle cavity
2	The ovarian tissue is fully ripe — present as a creamy white or yellow mass at the base of the mantle cavity. The female gametogenic tissue is evident — present as whitish tissue dorsal to the stomach. The penis is also evident — present as a long, transparent structure originating near the base of the sixth pair of cirri
3	Fertilized egg masses, lamellae, or ovisacs evident — present as yellowish paired lobes at the base of the mantle cavity
4	Eyed-embryos evident — as yet, unhatched
5	Mantle cavity distended with hatched nauplii (1st stage nauplii). (There may still be a few unhatched eyed-embryos or undeveloped eggs)

1) Student's t-test

$$t = \frac{\bar{x}_1 - \bar{x}_2}{Sp\ 1/n_1 + 1/n_2}$$

where:

$$Sp = \frac{(n_1 - 1)\ (S_1^2) + (n_2 - 1)\ (S_2^2)}{n_1 + n_2 - 2}$$

2) Aspin-Welch test

$$t = \frac{\bar{x}_1 - \bar{x}_2}{S_1^2/n_1 + S_2^2/n_2}$$

variables:

$\bar{x}$ = mean size

n = number of individuals (sample size)

S = standard deviation

Fecundity studies were initiated in February 1981, prior to the late winter/early spring release of nauplii. The method used for assessment of fecundity in *B. balanoides* was similar to that of Barnes and Barnes (1968) and Arnold (1977). A .0156 m^2 (12.5 cm x 12.5 cm) sampling frame was placed on a substrate of high barnacle density at each tidal height for the three beaches. All adult barnacles were collected from the chosen site and placed in whirlpaks. Upon returning from the field, all barnacles were examined under a dissecting microscope. The rostro-carinal diameter of each specimen was measured with calipers (Fig. 4) and the year class determined (see Growth Methodology section). Lamellae were dissected out, and placed in vials containing

3 ml of Gilson's fluid. Vials were coded and returned to the laboratory for further analyses. The shells, valves, and somatic tissue were combined for each barnacle and bagged and labeled separately.

In the laboratory, Gilson's fluid was replaced in each vial by Lugol's solution to remove the mercuric chloride content from the Gilson's preservative (see Humason, 1972 and Mueller, 1972 for formulas of solutions). After 24 hours, the Lugol's solution was replaced by 70% ethyl alcohol, and the vials agitated to break up any existing clumps of eggs. A Hensen-Stempel pipette was used to obtain 1 ml aliquots. Eggs were counted after suspension in a Sedgewick-Rafter counting cell. Four sub-sample counts were made for each specimen. The above procedure was repeated for barnacles collected in March 1982.

The body (prosoma) of each animal, located dorsal to the female reproductive tissue was separated from the shell plates. The resulting material (defined here as body or somatic tissue) was dried until weight loss was negligible (24 hrs, 60°C). Body weights were then obtained from the dried material (see also Methodology in the Energy Partitioning section).

Fecundity was examined at each site in terms of the mean value per tidal height, year class, mg body tissue, mm R/C diameter, and unit volume. Barnes (1953) estimates volume of a balanoid barnacle as the cube of the R/C diameter of the barnacle (referred to as "length" by Barnes, 1953), since the two parameters approximate a linear function. Volume was considered here to be the R/C diameter cubed (ℓ^3) in mm^3.

Fecundity values per year class were pooled for the three tidal heights at each site. The mean fecundity and the number of individuals present within the sampling area (0.0469 m^2, representative of the sum of the areas of the combined tidal levels) were extrapolated to the values expected in a m^2 plot. From these values, an estimation of egg production per m^2 at each of the three beaches was made for 1981 and 1982.

Data resulting from fecundity assessment (mean fecundity, mean body tissue weight, and mean R/C diameter) were compared for each site independently by use of a Student's t-test or an Aspin-Welch test, as appropriate. Between-year differences and between-height differences were tested. Significance was determined at the 95% confidence level.

Data from mortality plates provided recruitment information used in determining annual settlement patterns at each sampling site (see Barnacle Mortality section for methodology).

RESULTS-DISCUSSION

Reproductive Cycle

Samples from April, June, July, August, and September 1980, February-December 1981, and January-October 1982 were examined for extent of reproductive tissue development (Tables 3-5). The majority of adult barnacles observed in April were in the early stage of female gametogenic tissue development. Tissue appeared as a creamy mass, filling the space below the mantle cavity. Male reproductive structures became evident in May or June. Reproductive tissues continued to mature

Table 3. Summary of the occurrence (%) of adult *Balanus balanoides* in the reproductive stages at Sawmill Spit, Port Valdez, Alaska, April 1980-October 1982. n = number of barnacles examined.

	Reproductive Stages*					
Date	0	1	2	3	4	5
15 April 1980 n = 122	0.00	98.36	1.64	0.00	0.00	0.00
11 June 1980 n = 125	0.00	0.00	100.00	0.00	0.00	0.00
29 July 1980 n = 75	0.00	12.00	88.00	0.00	0.00	0.00
28 August 1980 n = 108	0.93	0.00	99.07	0.00	0.00	0.00
25 September 1980 n = 96	0.00	1.04	40.63	58.33	0.00	0.00
25 October 1980 n = 76	1.32	0.00	19.74	78.95	0.00	0.00
23 November 1980 n = 64	12.50	4.69	12.50	70.31	0.00	0.00
20 January 1981 n = 65	29.23	0.00	0.00	0.00	70.77	0.00
16 February 1981 n = 92	1.09	4.35	3.26	0.00	4.35	89.96
5 March 1981 n = 85	34.12	2.35	0.00	0.00	0.00	63.53

Table 3. Continued.

	Reproductive Stages*					
Date	0	1	2	3	4	5
3 April 1981 n = 80	12.50	87.50	0.00	0.00	0.00	0.00
5 May 1981 n = 106	1.89	3.77	94.34	0.00	0.00	0.00
2 June 1981 n = 90	0.00	2.22	97.78	0.00	0.00	0.00
1 July 1981 n = 76	0.00	0.00	100.00	0.00	0.00	0.00
1 August 1981 n = 52	5.00	0.00	95.00	0.00	0.00	0.00
30 August 1981 n = 96	0.00	0.00	100.00	0.00	0.00	0.00
15 September 1981 n = 88	0.00	0.00	96.67	3.33	0.00	0.00
30 October 1981 n = 23	13.00	0.00	0.00	87.00	0.00	0.00
29 November 1981 n = 25	4.00	0.00	4.00	92.00	0.00	0.00
12 January 1982 n = 26	0.00	0.00	3.80	0.00	96.20	0.00

Table 3. Continued.

Date	Reproductive Stages*					
	0	1	2	3	4	5
7 March 1982 n = 99	19.83	0.00	0.00	0.00	0.00	80.17
25 April 1982 n = 81	2.20	96.70	0.00	0.00	1.10	0.00
22 May 1982 n = 76	1.13	3.93	94.94	0.00	0.00	0.00
22 June 1982 n = 82	1.50	0.00	98.50	0.00	0.00	0.00
20 July 1982 n = 80	8.33	0.00	91.67	0.00	0.00	0.00
18 August 1982 n = 85	4.67	0.00	63.33	32.00	0.00	0.00
16 September 1982 n = 30	0.00	0.00	0.00	100.00	0.00	0.00
19 October 1982 n = 30	10.00	0.00	10.00	80.00	0.00	0.00

*For information on reproductive stages, see Feder *et al*. (1981a and b) and Table 2.

Table 4. Summary of the occurrence (%) of adult *Balanus balanoides* in the reproductive stages at Berth 4, Port Valdez, Alaska, April 1980-September 1982. n = number of barnacles examined.

Date	Reproductive Stages*					
	0	1	2	3	4	5
16 April 1980 n = 125	1.00	99.00	0.00	0.00	0.00	0.00
12 June 1980 n = 70	18.57	0.00	81.43	0.00	0.00	0.00
29 July 1980 n = 39	0.00	2.56	97.44	0.00	0.00	0.00
28 August 1980 n = 108	0.00	2.78	97.22	0.00	0.00	0.00
25 September 1980 n = 110	0.00	0.00	34.55	65.45	0.00	0.00
27 October 1980 n = 70	8.57	1.43	45.71	44.29	0.00	0.00
21 November 1980 n = 52	34.62	0.00	15.38	48.08	1.92	0.00
18 December 1980 n = 34	23.53	0.00	5.88	2.94	67.65	0.00
19 January 1981 n = 33	27.27	0.00	18.18	0.00	54.55	0.00
17 February 1981 n = 56	42.86	8.93	0.00	0.00	0.00	48.21
6 March 1981 n = 85	54.12	2.35	0.00	0.00	1.18	42.35

Table 4. Continued.

Date	Reproductive Stages*					
	0	1	2	3	4	5
4 April 1981 n = 73	31.51	68.49	0.00	0.00	0.00	0.00
6 May 1981 n = 73	4.11	31.51	64.38	0.00	0.00	0.00
3 June 1981 n = 78	1.28	2.57	93.59	1.28	1.28	0.00
2 July 1981 n = 73	0.00	0.00	100.00	0.00	0.00	0.00
2 August 1981 n = 34	3.55	0.00	96.45	0.00	0.00	0.00
31 August 1981 n = 73	2.23	0.00	91.97	5.80	0.00	0.00
14 September 1981 n = 76	0.00	0.00	91.67	8.33	0.00	0.00
29 October 1981 n = 22	0.00	0.00	0.00	100.00	0.00	0.00
29 November 1981 n = 23	8.70	0.00	0.00	91.30	0.00	0.00
12 January 1982 n = 23	8.70	0.00	0.00	91.30	0.00	0.00
8 March 1982 n = 80	26.63	10.57	0.00	0.00	1.63	61.17
26 April 1982 n = 88	43.03	39.20	15.57	0.00	0.00	2.20

Table 4. Continued.

Date	Reproductive Stages*					
	0	1	2	3	4	5
23 May 1982 n = 64	15.90	2.23	81.87	0.00	0.00	0.00
23 June 1982 n = 78	2.20	0.00	97.80	0.00	0.00	0.00
21 July 1982 n = 59	0.00	2.23	88.87	8.90	0.00	0.00
19 August 1982 n = 63	4.53	0.00	60.74	34.73	0.00	0.00
17 September 1982 n = 88	5.87	0.00	0.00	92.93	1.20	0.00

*For information on reproductive stages, see Feder *et al.* (1981a and b) and Table 2.

Table 5. Summary of the occurrence (%) of adult *Balanus balanoides* in the reproductive stages at Mineral Creek, Port Valdez, Alaska, April 1980-October 1982. n = number of barnacles examined.

Date	Reproductive Stages*					
	0	1	2	3	4	5
18 April 1980 n = 125	0.00	100.00	0.00	0.00	0.00	0.00
13 June 1980 n = 126	3.97	0.00	96.03	0.00	0.00	0.00
30 July 1980 n = 58	0.00	1.72	98.28	0.00	0.00	0.00
29 August 1980 n = 111	0.00	0.00	100.00	0.00	0.00	0.00
24 September 1980 n = 111	0.00	0.00	8.11	91.89	0.00	0.00
25 October 1980 n = 68	14.71	0.00	10.29	75.00	0.00	0.00
22 November 1980 n = 40	7.50	0.00	5.00	87.50	0.00	0.00
19 December 1980 n = 23	21.74	0.00	0.00	26.09	52.17	0.00
18 January 1981 n = 48	25.00	0.00	8.33	2.08	64.58	0.00
15 February 1981 n = 85	10.59	2.35	0.00	0.00	0.00	87.06
4 March 1981 n = 88	51.14	5.68	0.00	0.00	0.00	43.18

Table 5. Continued.

Date	Reproductive Stages*					
	0	1	2	3	4	5
2 April 1981 n = 66	24.24	75.76	0.00	0.00	0.00	0.00
4 May 1981 n = 90	0.00	6.67	93.33	0.00	0.00	0.00
1 June 1981 n = 86	0.00	0.00	100.00	0.00	0.00	0.00
30 June 1981 n = 90	2.20	3.33	94.47	0.00	0.00	0.00
31 July 1981 n = 69	4.17	4.17	91.66	0.00	0.00	0.00
29 August 1981 n = 75	1.77	0.00	98.23	0.00	0.00	0.00
16 September 1981 n = 85	0.00	0.00	94.23	5.77	0.00	0.00
27 October 1981 n = 25	8.00	0.00	4.00	88.00	0.00	0.00
27 November 1981 n = 25	12.00	0.00	0.00	88.00	0.00	0.00
10 January 1982 n = 25	4.00	0.00	0.00	96.00	0.00	0.00
19 February 1982 n = 25	20.00	4.00	4.00	0.00	20.00	52.00

Table 5. Continued.

Date	Reproductive Stages*					
	0	1	2	3	4	5
6 March 1982 n = 85	9.33	1.10	0.00	0.00	3.33	86.24
23 April 1982 n = 81	62.85	36.04	0.00	0.00	1.11	0.00
21 May 1982 n = 77	10.00	30.00	60.00	0.00	0.00	0.00
19 June 1982 n = 75	3.03	18.17	78.80	0.00	0.00	0.00
19 July 1982 n = 67	0.00	0.00	43.70	53.27	3.03	0.00
17 August 1982 n = 64	0.00	0.00	0.00	100.00	0.00	0.00
15 September 1982 n = 30	0.00	0.00	3.30	96.70	0.00	0.00
19 October 1982 n = 30	10.00	0.00	0.00	90.00	0.00	0.00

*For information on reproductive stages, see Feder *et al.* (1981a and b) and Table 2.

in the following months, but eggs were not generally fertilized until September, at which time over half of the adults contained fertilized eggs (lamellae). By December, unhatched eyed embryos were observed in the majority of barnacles. During the winter months (November-January), up to ∿35% of the specimens examined showed no signs of developing reproductive tissues (stage 0), and most likely represent individuals which were unsuccessful in their fertilization attempts, subsequently reabsorbing the mature gametogenic tissue (Barnes and Achituv, 1976). Hatched nauplii, appearing in the mantle cavity in February, were subsequently released into the water column in late February or early March, at the time of the spring diatom bloom (Barnes, 1962). In late March or early April, the mantle cavities of the majority of barnacles were either empty or just beginning to show evidence of redeveloping female gametogenic tissue.

Reproductive staging observations for barnacles at the three study sites, though generally following the above described sequence, occasionally revealed lags of up to one month in progression from stage to stage. The delays were most evident for barnacles at Berth 4 (Table 4). In June 1980 and May 1982, over 15% of the barnacles sampled at Berth 4 contained no developing ovarian tissue (still in Stage 0). A second lag in 1980 was observed subsequent to fertilization (late October-late November), when over 15% of the population sampled remained unfertilized (still in Stage 2).

Reproductive staging data also revealed that a few barnacles were not following the expected annual reproductive cycle. During the winter months, January-March 1981 and 1982, a small percentage of barnacles at each site were in Stage 1 or 2 (early developmental stages) as opposed to Stages 4 or 5 (as observed in the majority of barnacles) (Tables 3-5). The reproductive tissue of the latter barnacles represented either (1) remains of unfertilized material which had not been reabsorbed or (2) new reproductive tissue formed prematurely by individuals that had been able to secure adequate food supplies for development.

The annual reproductive cycle observed for *Balanus balanoides* in Port Valdez from 1980-1982 is in general agreement with that reported in previous studies of *B. balanoides* in the Port (Colonell, 1979 and Feder and Keiser, 1980). A major difference, however, involved the date of first detection of male reproductive structures. In the present study, development of male tissue (Stage 2) was detected as early as May. The penis, though still quite underdeveloped, was positively identified at this time. Earlier investigators (Feder and Keiser, 1980) did not recognize the penis until August, after substantial tissue development. Differing times of recognition of male reproductive tissue are probably due to varying interpretations.

Reproductive Tissue Development

Annual fluctuations in the weight of ovarian and lamellar material were observed for barnacles at Sawmill Spit, Berth 4, and Mineral Creek (April 1980-October 1982, Appendix 2, Table 1; and Figs. 6 and 7). Fluctuations in the weight of reproductive tissue followed an annual cyclic pattern. Ovarian weight generally increased from April until

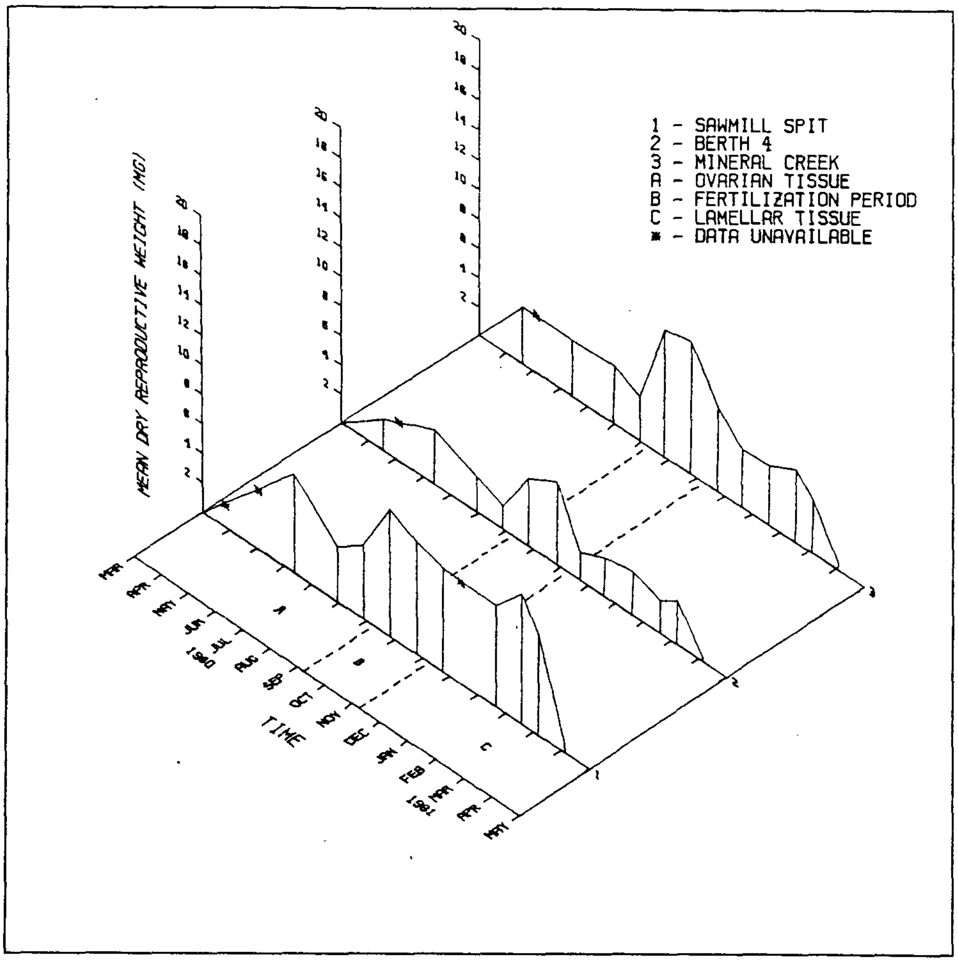

Figure 6. Mean dry reproductive tissue weight (mg) for *Balanus balanoides* mid zone specimens collected from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1981. Reproductive tissue represents either ovarian or lamellar tissue, depending on the time of year relative to fertilization.

Mean dry reproductive weight is read for any month by following a line parallel to the x-axis (abscissa) for the monthly value in question to the y-axis (ordinate).

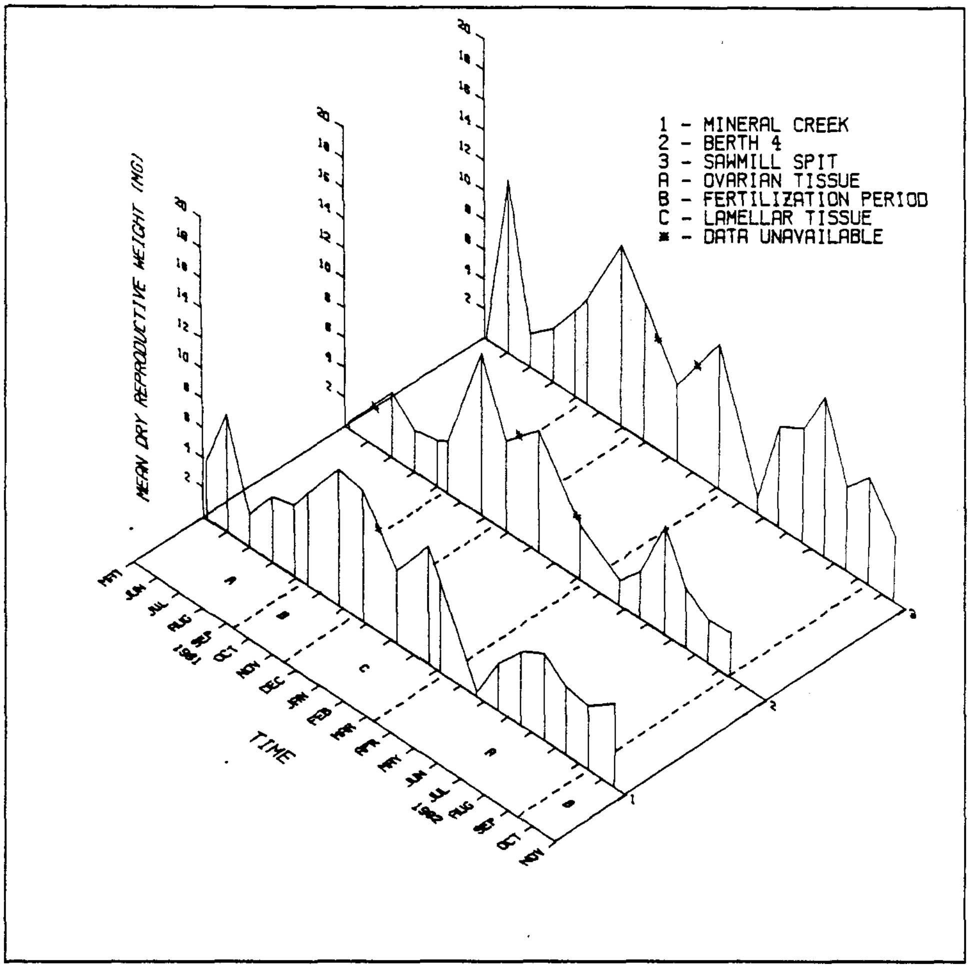

Figure 7. Mean dry reproductive tissue weight (mg) for *Balanus balanoides* mid zone specimens collected from Mineral Creek, Berth 4, and Sawmill Spit, Port Valdez, Alaska, May 1981-October 1982. Reproductive tissue represents either ovarian or lamellar tissue, depending on the time of year relative to fertilization.

Mean dry reproductive weight is read for any month by following a line parallel to the x-axis (abscissa) from the monthly value in question to the y-axis (ordinate).

June, after which time it decreased somewhat. By August, the ovarian tissue was increasing in weight again. The reproductive tissue weight (lamellar weight) reached a maximum following fertilization in late September or early October. A second decline in weight (lamellar tissue) occurred in late October, followed by a gradual weight increase until December or January. In February, another period of weight loss occurred. The weight of the reproductive tissue in April (<1.0 mg) was the lowest observed during the year. Although weight fluctuations in 1980-81 and 1981-82 followed the same general pattern, a lag of up to one month was occasionally observed in the reproductive cycle at all sites.

Data were compared for barnacles from all tidal heights at each site to determine if between-height differences could be detected in the reproductive cycle (Appendix 2, Table 1). At Sawmill Spit, organisms in the lower-tidal zone generally contained the greatest amount of reproductive tissue, followed by individuals in the mid and high zones, respectively. The above trend is to be expected, and reflects the longer submersion period and associated increased feeding time of barnacles in low intertidal areas. The only exception to this trend at Sawmill Spit was observed for barnacles of the mid zone in May 1981, at which time a very low ovarian weight was determined for barnacles here. The reduced ovarian weight noted for these mid-zone barnacles was the result of the large number of two-year old barnacles in that month's sample. These young individuals were less productive and contained less reproductive tissue than older individuals. Barnacles from Berth 4 and Mineral Creek displayed no differences in the weight of reproductive tissue relative to tidal height. In fact, the reproductive tissue of low-zone organisms often weighed less than that of organisms from mid and high-tidal heights. The above observation for the latter two areas may be indicative of disturbance within these populations, possibly in the form of seasonal environmental stress (lowered salinity and a heightened suspended sediment load) at Mineral Creek and chronic low-level exposure to pollutants (hydrocarbon in origin) at Berth 4. The organisms must possibly attain a larger size in upper intertidal reaches in order to adapt to longer periods of exposure to the various stresses.

Fluctuations in the weight of gametogenic tissues are related to seasonal availability of food. The spring diatom bloom occurs in Port Valdez in March or April (see Hood *et al.*, 1973 and Colonell, 1979). During the latter period barnacles feed intensively and store a large proportion of the assimilated material in the ovarian and somatic tissues. Although caloric values were not determined for the present study, a related species, *B. glandula*, has a higher caloric value for ovarian than somatic tissue (Wu and Levings, 1978). Rapid assimilation and storage of material by *Balanus balanoides* in Port Valdez is an adaptation for life in northern waters. Food is limited to a very few months of the year in northern latitudes, and must be assimilated while available (Barnes *et al.*, 1963). In the winter when food is scarce or during times of starvation, energy stored in tissues is remobilized (Wu and Levings, 1978). Thus, barnacles cope with fluctuating food supplies by utilizing reserves stored during the spring and early summer. Data indicate that barnacles in Port Valdez follow the above discussed behavioral adaptations observed for *B. balanoides* elsewhere (Barnes *et al.*, 1963).

Although fluctuations in the mean weight of reproductive tissue were generally the same at all sites in 1980-81, the maximum weight of this tissue for any month was typically greater at Sawmill Spit than at either Mineral Creek or Berth 4. Results of the analysis of variance (ANOVA) comparing mean monthly reproductive weights for the three sites indicate that Sawmill Spit barnacles had a significantly higher weight value ($\alpha = 0.05$ and $\alpha = 0.01$) than those from Berth 4 in June, September, and November 1980 and in February 1981 (Appendix 2, Table 2). Sawmill Spit barnacles weighed significantly more than barnacles from Mineral Creek, as well, in June 1980 and February 1981. In 1981-82, no obvious difference in the weights at the three sites was observed, with the exception of July 1981 (Appendix 2, Table 2). During this period, the ovarian weight at Berth 4 was significantly less than at the other two sites. During the last six months of the study (April-September 1982), barnacles from Sawmill Spit contained significantly more reproductive tissue than those from Mineral Creek in June, than those from Berth 4 in August, and than those from either Berth 4 or Mineral Creek in September (Appendix 2, Table 2).

Comparisons between the reproductive weight data for 1980-1981 and 1981-82 are included for barnacles from each sampling location in Appendix 2, Table 3 and Figures 8-10. In general, the same pattern was followed by Sawmill Spit and Mineral Creek barnacles in both years, though a slight lag in the reproductive cycle was noticeable at each

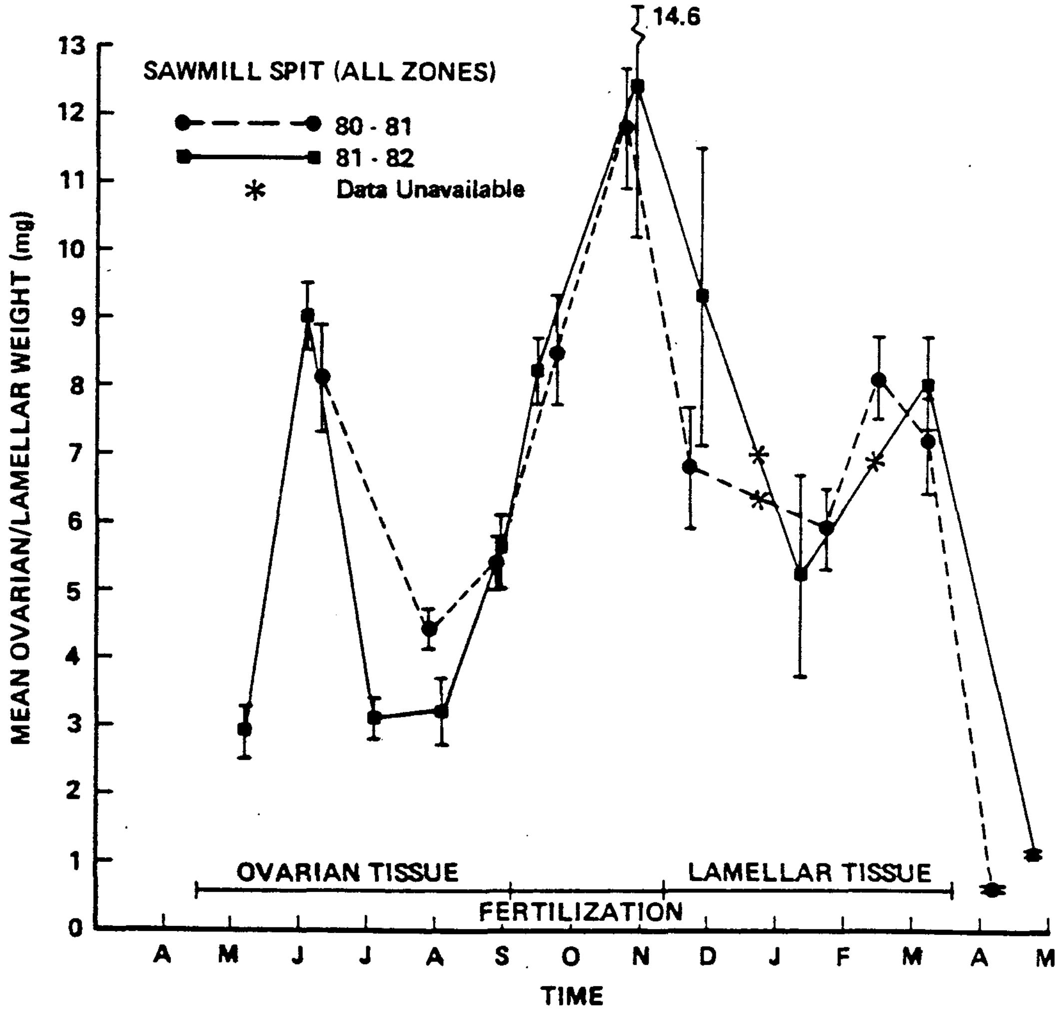

Figure 8. Monthly reproductive tissue weight fluctuations of *Balanus balanoides* for the sampling periods 1980-81 and 1981-82 at Sawmill Spit, Port Valdez, Alaska. Error bars represent standard error of the mean.

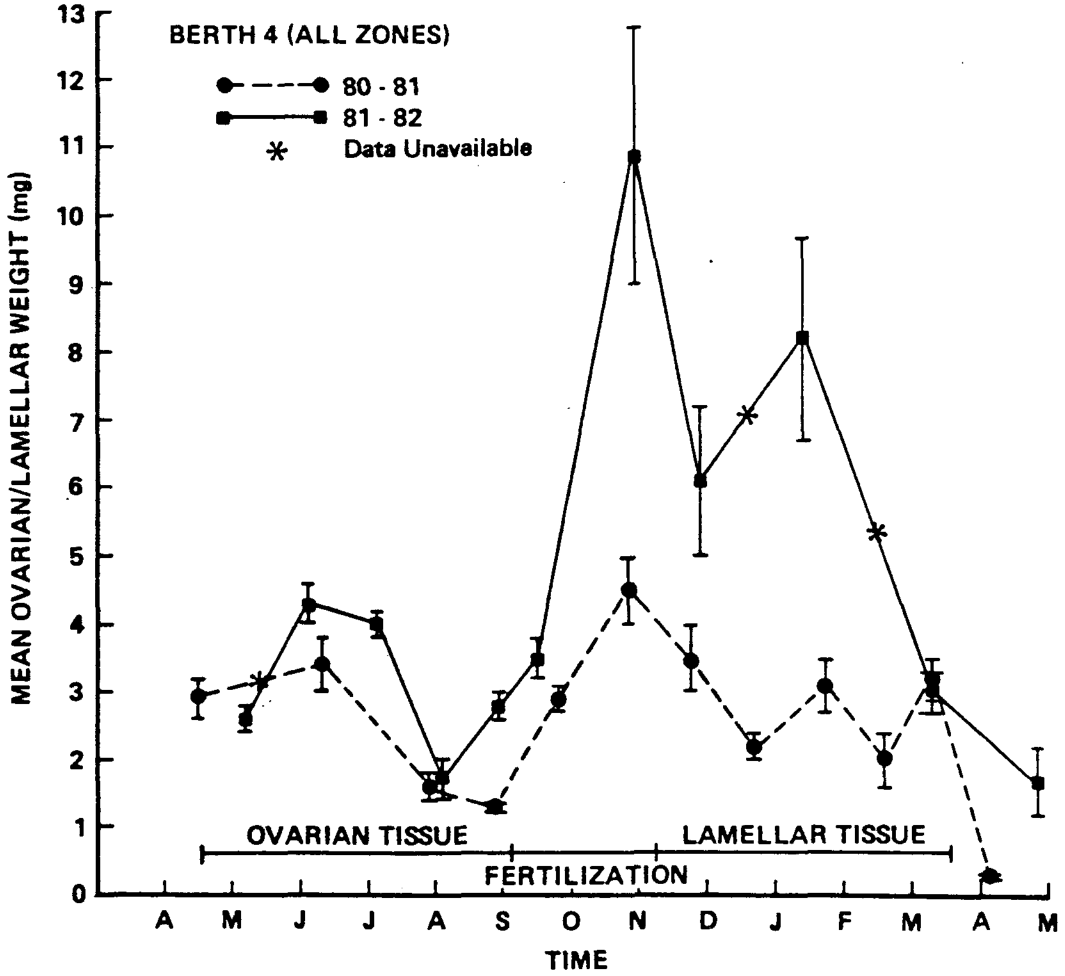

Figure 9. Monthly reproductive tissue weight fluctuations of *Balanus balanoides* for the sampling periods 1980-81 and 1981-82 at Berth 4, Port Valdez, Alaska. Error bars represent standard error of the mean.

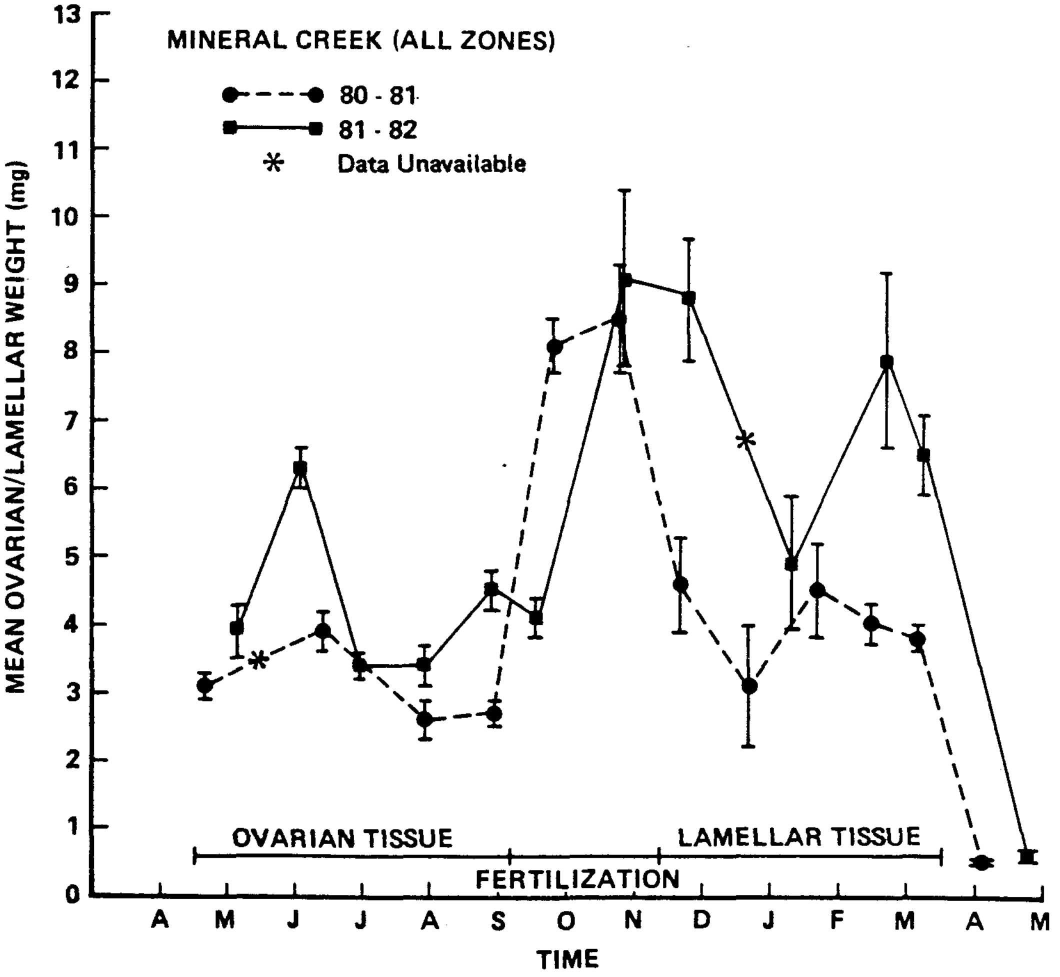

Figure 10. Monthly reproductive tissue weight fluctuations of *Balanus balanoides* for the sampling periods 1980-81 and 1981-82 at Mineral Creek, Port Valdez, Alaska. Error bars represent standard error of the mean.

site in the latter months of the 1981-82 season. Results of the t-test used for between-year comparisons of mid-zone data (Appendix 2, Table 3) indicate that at Sawmill Spit, no significant difference ($\alpha = 0.05$) exists between mean monthly data for 1980-81 and 1981-82, with the exception of the months of June and March (Fig. 8). In the latter cases, values were always higher in 1981-82 than in the preceding year. Although the results representing the Mineral Creek data reveal significant differences between months in 1980-81 and 1981-82, the difference can be attributed to the evident lag observed in the reproductive development pattern during the latter year at this site (Fig. 10). Berth 4 barnacles, on the other hand, displayed a significant difference in reproductive weight patterns between 1980-81 and 1981-82, especially during the months subsequent to fertilization (Appendix 2, Table 3 and Fig. 9). Weight values for August 1980-January 1981 were significantly lower than in the following year (Appendix 2, Table 3), although the same basic trend was observed for both years. Environmental conditions were apparently unfavorable at Berth 4 in 1980, possibly as a result of the small oil spill in the vicinity in April. Either the phytoplankters in the spring bloom were affected by the disturbance and were temporarily unavailable as a food source or subsequent gametogenic tissue production was reduced due to metabolic problems. Statistical results indicate that significantly less ovarian tissue was produced in 1980 at Berth 4 in comparison with other sites (ANOVA results, Appendix 2, Table 2) and in comparison with the ovarian weight at Berth 4 in 1981 (t-test results, Appendix 2, Table 3).

Fecundity

The fecundity of barnacles in Port Valdez was examined in relation to dry body weight, size (R/C diameter), volume (length^3), and year class. The number of eggs present per individual generally increased as weight, size, volume, and year class increased (Figs. 11-14). Deviations from the above relationships could often be explained by the small sample size representing these data points. The number of eggs contained in an indiviudal is a function of adult size (Moore, 1935), since, within wide limits, fecundity is a linear function of the mass of the parent (Barnes and Barnes, 1968).

Tables 6-8 provide sample size, mean fecundity, mean dry body weight, mean R/C diameter, and mean volume $(\ell)^3$ data for barnacles from each tidal height, and for the three heights combined at Sawmill Spit, Berth 4, and Mineral Creek, during February 1981 and March 1982. Figures 11-14 compare for the three sampling sites the relationship between fecundity and body weight, size, volume, and year class. The resulting trends are illustrated for 1981 in Figures 11-14a and for 1982 in Figures 11-14b. A discussion of general trends emerging in 1981 and 1982 for the three study sites follows. Discussion concerning the fecundity differences from year to year at a particular site will be discussed later.

Differences between sampling areas were evident from fecundity data. In 1981, the barnacles from Sawmill Spit (all intertidal heights combined) had the greatest mean fecundity ($\bar{x}$ = 5680 eggs per individual) in comparison with Berth 4 ($\bar{x}$ = 2001 eggs per individual) and Mineral

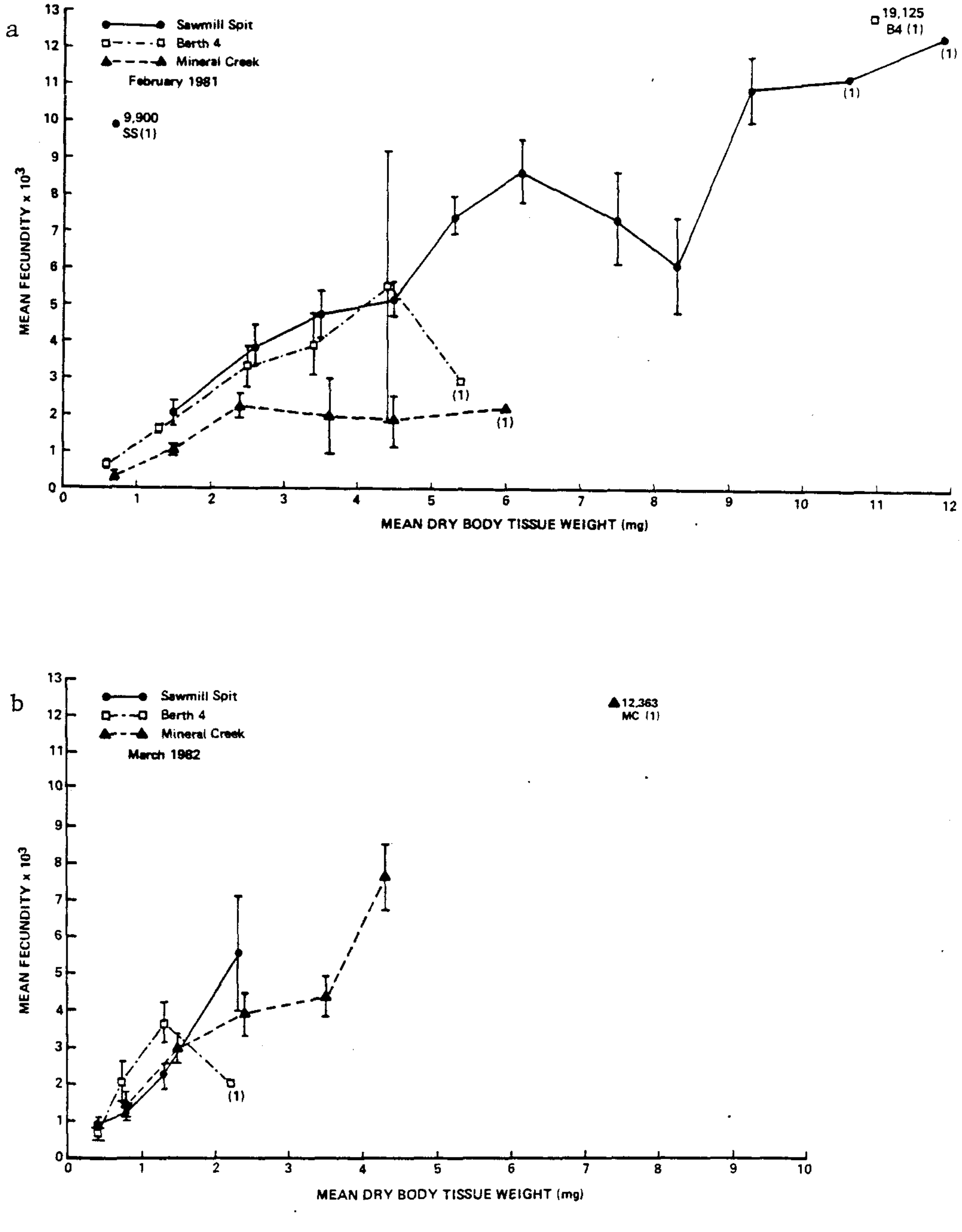

Figure 11. Fecundity as a function of dry body tissue weight (mg) for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

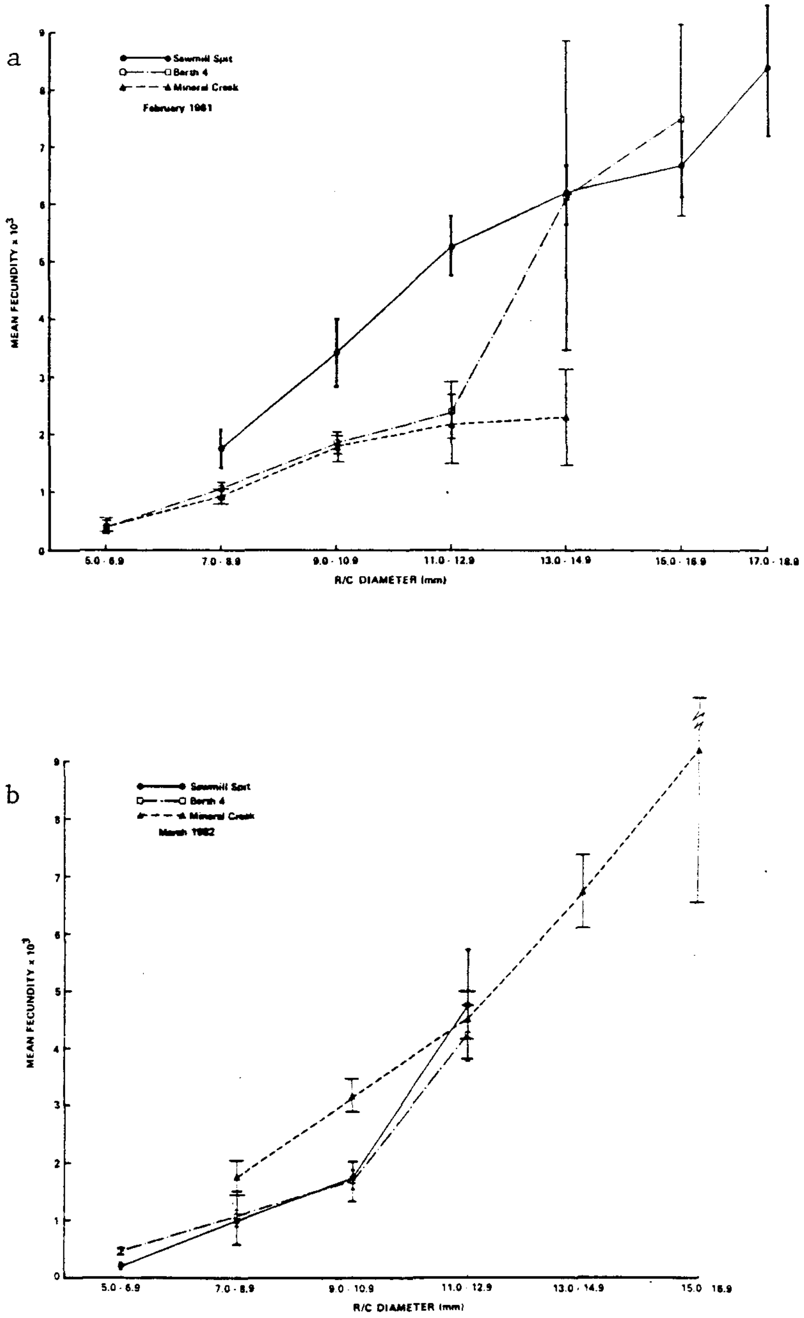

Figure 12. Fecundity as a function of R/C diameter (mm) for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represents standard error of the mean.

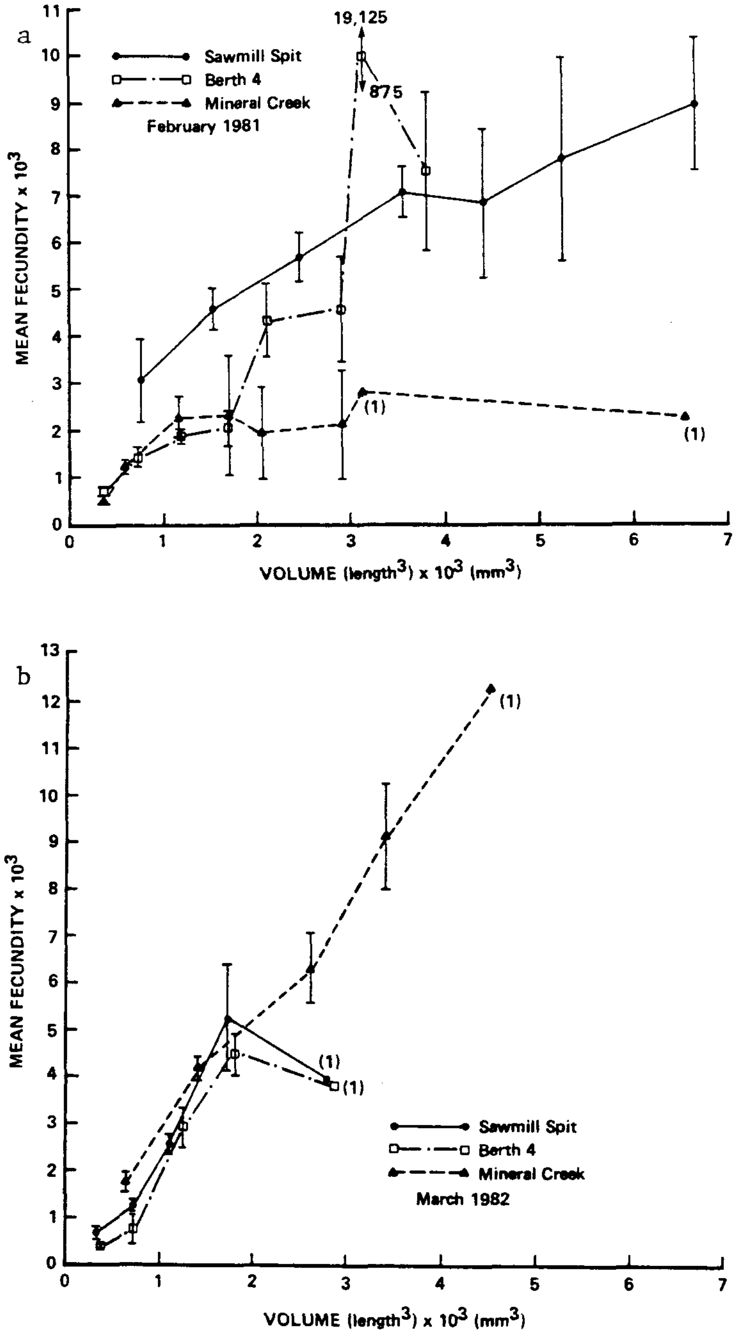

Figure 13. Fecundity as a function of volume or length^3 (mm^3) for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

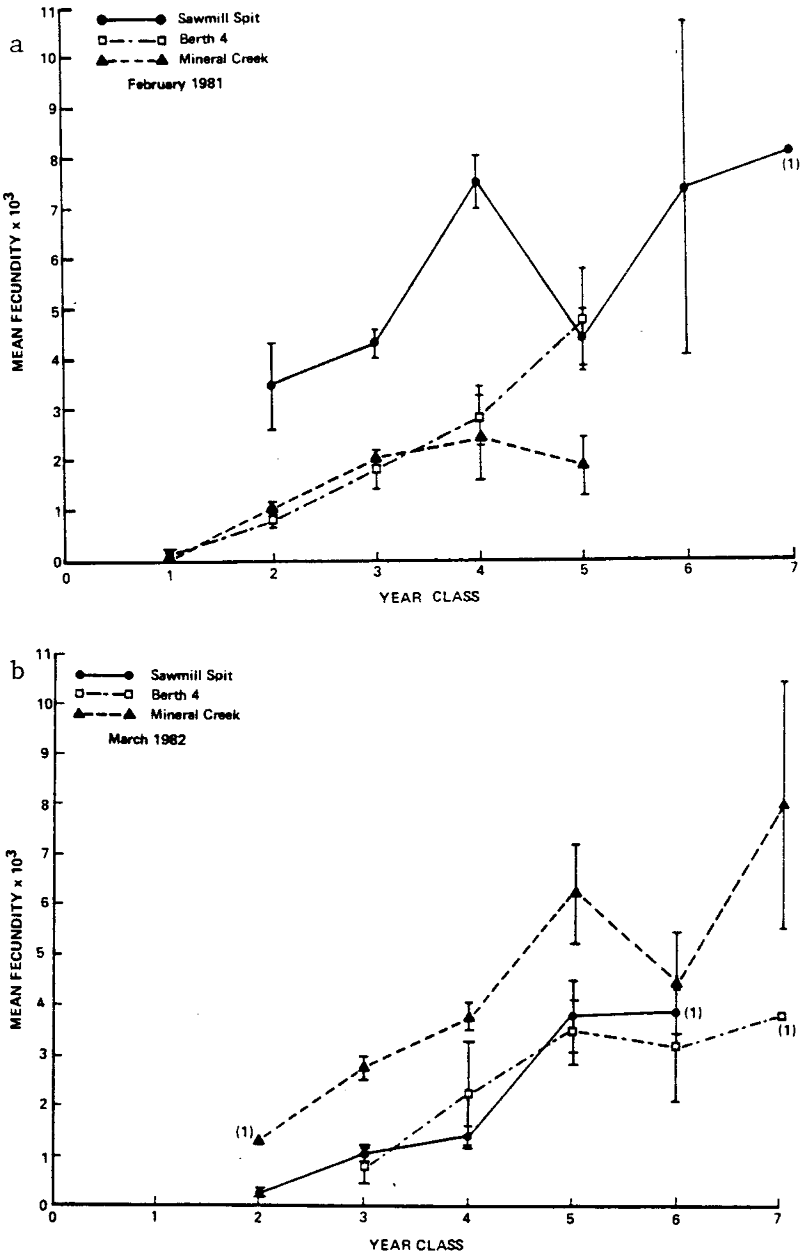

Figure 14. Fecundity as a function of year-class for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

Table 6. Mean fecundity, mean dry body tissue weight, mean rostro-carinal (R/C) diameter, and mean volume (length^3) for *Balanus balanoides* from Sawmill Spit, Port Valdez, Alaska, February 1981 and March 1982. n = number of individuals sampled, SD = standard deviation, SE = standard error of the mean.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	18	13	49	25	40	26	107	64
$\bar{x}$ fecundity	4303	757	4926	2079	7223	1291	5680	1490
SD	2805	1024	2631	1374	3054	1198	3051	1324
SE	661	284	376	274	483	235	295	166
Range								
Lo	1231	113	1187	144	794	88	794	88
Hi	10244	3981	12068	7156	12350	5444	12350	7156
$\bar{x}$ body weight	4.1	0.7	3.9	0.8	5.3	0.8	4.5	0.8
SD	2.2	0.6	1.6	0.4	2.3	0.4	2.1	0.4
SE	0.5	0.2	0.2	0.1	0.4	0.1	0.2	0.1
Range								
Lo	1.0	0.2	1.1	0.3	2.0	0.2	1.0	0.2
Hi	8.1	2.6	8.9	2.0	11.9	1.8	11.9	2.6
$\bar{x}$ R/C diameter	12.4	8.3	13.5	9.3	13.5	8.7	13.3	8.9
SD	2.6	2.0	2.5	1.2	2.1	1.5	2.4	1.5
SE	0.6	0.6	0.4	0.2	0.3	0.3	0.2	0.2
Range								
Lo	8.3	5.9	8.3	6.9	9.4	5.7	8.3	5.7
Hi	16.2	14.1	18.6	11.9	19.0	12.4	19.0	14.1

Table 6. Continued.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	18	13	49	25	40	26	107	64
$\bar{x}$ length^{3}	2142	668	2718	850	2624	721	2586	761
SD	1152	659	1450	322	1203	392	1319	435
SE	272	183	207	64	190	77	128	54
Range								
Lo	287	205	804	329	831	185	287	185
Hi	4252	2803	6751	1685	4742	1907	6751	2803

Table 7. Mean fecundity, mean dry body tissue weight, mean rostro-carinal (R/C) diameter, and mean volume (length^3) for *Balanus balanoides* from Berth 4, Port Valdez, Alaska, February 1981 and March 1982. n = number of individuals sampled, SD = standard deviation, SE = standard error of the mean.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	21	2	50	12	20	22	91	36
$\bar{x}$ fecundity	3572	2935	1459	3999	1706	907	2001	2050
SD	2180	1313	697	1365	4134	1144	2385	1894
SE	476	928	99	394	924	244	250	316
Range								
Lo	585	2006	207	1563	69	44	69	44
Hi	9225	3863	3525	6875	19125	4488	19125	6875
$\bar{x}$ body weight	2.7	1.9	1.3	1.0	2.0	0.6	1.6	0.8
SD	1.1	0.4	0.4	0.4	2.9	0.3	1.4	0.5
SE	0.2	0.3	0.1	0.1	0.6	0.1	0.1	0.1
Range								
Lo	0.8	1.6	0.7	0.4	0.2	0.2	0.2	0.2
Hi	4.5	2.2	2.8	1.7	10.9	1.7	10.9	2.2
$\bar{x}$ R/C diameter	12.0	12.7	9.8	11.0	7.9	8.9	9.9	9.8
SD	2.2	2.1	1.2	1.1	2.2	1.4	2.2	1.8
SE	0.5	1.5	0.2	0.3	0.5	0.3	0.2	0.3
Range								
Lo	8.6	11.2	7.5	8.7	5.2	6.4	5.2	11.2
Hi	15.8	14.2	11.8	12.4	14.7	11.3	15.8	14.2

Table 7. Continued.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	21	2	50	12	20	22	91	36
$\bar{x}$ length[3]	1877	2134	977	1380	619	737	1106	1046
SD	1005	1031	345	371	699	385	770	551
SE	219	729	49	107	156	82	81	92
Range								
Lo	636	1405	422	659	141	301	141	301
Hi	3944	2863	1643	1907	3177	1443	3944	2863

Table 8. Mean fecundity, mean dry body tissue weight, mean rostro-carinal (R/C) diameter, and mean volume (length^3) for *Balanus balanoides* from Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. n = number of individuals sampled, SD = standard deviation, SE = standard error of the mean.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	22	22	35	32	32	8	89	62
$\bar{x}$ fecundity	1361	4893	844	3327	1914	3276	1356	3876
SD	1633	3024	761	1669	1340	3897	1308	2624
SE	348	645	129	295	237	1378	139	333
Range								
Lo	63	675	50	588	350	313	50	313
Hi	6037	12363	2812	5963	7347	11369	7347	12363
$\bar{x}$ body weight	2.1	3.0	1.9	2.0	1.7	2.0	1.9	2.4
SD	1.4	1.5	1.2	1.0	0.5	1.2	1.1	1.3
SE	0.3	0.3	0.2	0.2	0.1	0.4	0.1	0.2
Range								
Lo	0.2	0.5	0.7	0.8	0.7	0.7	0.2	0.5
Hi	4.7	7.4	6.0	3.8	2.7	4.4	6.0	7.4
$\bar{x}$ R/C diameter	9.9	12.0	9.3	10.0	8.8	9.8	9.3	10.7
SD	2.4	2.2	2.5	1.7	1.3	2.7	2.1	2.2
SE	0.5	0.5	0.4	0.3	0.2	1.0	0.2	0.3
Range								
Lo	6.4	8.3	6.2	6.5	6.1	7.6	6.1	6.5
Hi	14.4	16.5	18.7	13.9	11.9	15.6	18.7	16.5

Table 8. Continued.

	High Zone		Mid Zone		Low Zone		All Zones	
	1981	1982	1981	1982	1981	1982	1981	1982
n	22	22	35	32	32	8	89	62
$\bar{x}$ length^3	1146	1902	1002	1101	731	1145	940	1391
SD	815	1014	1162	571	331	1125	864	901
SE	174	216	196	101	59	398	92	114
Range								
Lo	262	572	238	275	227	439	227	275
Hi	2986	4492	6539	2686	1685	3796	6539	4492

Creek ($\bar{x}$ = 1356 eggs per individual) (Tables 6-8). The trend was also obvious in the relationships between fecundity and body weight, R/C diameter, volume, and year class (Figs. 11-14). In general, the greatest fecundity relative to the above parameters was observed for barnacles from Sawmill Spit, followed by those from Berth 4 and Mineral Creek, respectively. The results observed in 1981 (i.e., Sawmill Spit with the highest fecundity value, followed by Berth 4 and Mineral Creek) can be explained by the differences in body weight, size, and volume of barnacles in the collections from the three areas. Sawmill Spit barnacles from any tidal height were larger and weighed more than individuals from any height at Berth 4 or Mineral Creek. The collection from Sawmill Spit was composed of a greater number of older individuals as well, especially four year olds. These older individuals at Sawmill Spit were typically more fecund than the younger barnacles common from other sites, especially in comparison to those from the Mineral Creek collection.

The 1982 data (for all intertidal heights combined) indicate that of the three sites, Mineral Creek barnacles produced the most eggs ($\bar{x}$ = 3876 per individual), in comparison with Berth 4 ($\bar{x}$ = 2050 per individual) and Sawmill Spit ($\bar{x}$ = 1490 per individual) (Tables 6-8). The same trend, relative to most other parameters observed was noted for Mineral Creek barnacles, which typically contained more eggs per mm R/C diameter, per mm^3 volume, and per year class than either barnacles from Berth 4 or Sawmill Spit (Figs. 11-14). The latter two sites had similar fecundity values relative to these parameters and contained, within wide limits, equal numbers of eggs per mm R/C diameter, mm^3 volume, and year class. However, in relation to body weight, Berth 4 barnacles, which with one exception, weighed only up to 1.5 mg, possessed the greatest number of eggs per mg body weight relative to the other two areas (Fig. 11b). The 1982 barnacle collections from Sawmill Spit and Mineral Creek contained a number of individuals with weight values greater than the 1.5 mg body-weight maximum for barnacles at Berth 4. The latter weights explain higher fecundity values (extending beyond 1.5 mg), especially for barnacles at Mineral Creek (Fig. 11b).

Figures 15-18 compare independently for each site the 1981 and 1982 relationships between fecundity and volume, dry body weight, and year class. The trends in fecundity at each site, based on these data, indicate that in general, fecundity was greater for barnacles at Sawmill Spit in 1981 in comparison with 1982, and was greater at Mineral Creek in 1982 in comparison with 1981. The between-year comparisons of fecundity relationships for barnacles at Berth 4 were not entirely clear-cut. However, barnacles in any year class contained more eggs in 1981 than in 1982.

Sawmill Spit barnacles collected in 1981 ($\bar{x}$ = 5680 eggs per individual) displayed a significantly greater fecundity (α = 0.05) than those collected in 1982 ($\bar{x}$ = 1490 eggs per individual) based on t-test results comparing the mean values for all tidal heights. The same trend was observed independently for each tidal height as well (Appendix 2, Table 4). The greater mean egg production observed for barnacles at

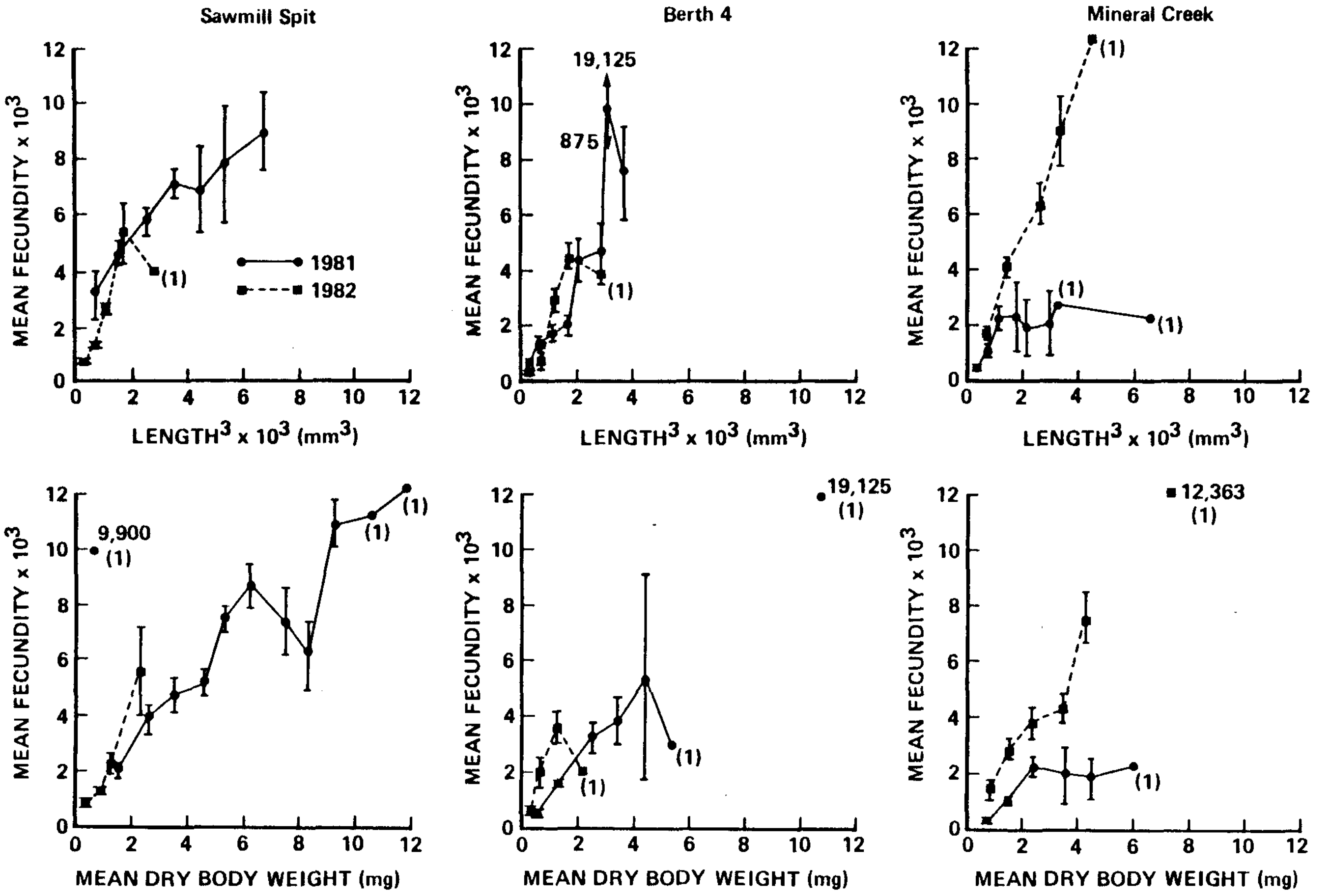

Figure 15. The relationship between mean fecundity and length^3 (volume), and mean fecundity and dry body weight for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

	Year Class						
	1	2	3	4	5	6	7
Sawmill Spit							
February 1981							
n	0	5	43	45	11	2	1
$\bar{x}$ fecundity	*	3330	4223	7555	4253	7322	8131
SD	*	2161	2232	2959	2002	4786	*
SE	*	965	340	441	603	3394	*
Range							
Lo	*	1337	794	1187	1313	3938	*
Hi	*	6494	11818	12350	7825	10706	*
March 1982							
n	0	2	22	40	5	1	
$\bar{x}$ fecundity	*	169	1095	1430	3814	3981	
SD	*	115	904	1059	1924	*	
SE	*	82	233	226	859	*	
Range							
Lo	*	88	88	167	2194	*	
Hi	*	250	2900	5444	7156	*	

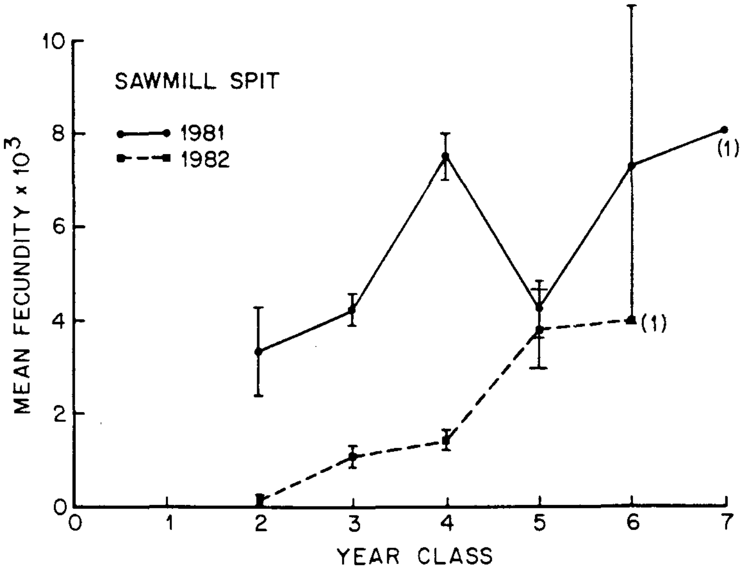

Figure 16. Fecundity as a function of year-class for *Balanus balanoides* from Sawmill Spit, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

	Year Class						
	1	2	3	4	5	6	7
Berth 4							
February 1981							
n	2	16	50	16	6		
$\bar{x}$ fecundity	75	827	1832	2836	4733		
SD	9	433	2593	1984	2520		
SE	6	108	367	496	1029		
Range							
Lo	69	350	207	150	2419		
Hi	81	1744	19125	6081	9225		
March 1982							
n	0	0	19	7	10	2	1
$\bar{x}$ fecundity	*	*	888	2244	3668	3216	3863
SD	*	*	1209	2581	1103	1710	*
SE	*	*	277	974	349	1213	*
Range							
Lo	*	*	44	181	1563	2006	*
Hi	*	*	4488	6875	5825	4425	*

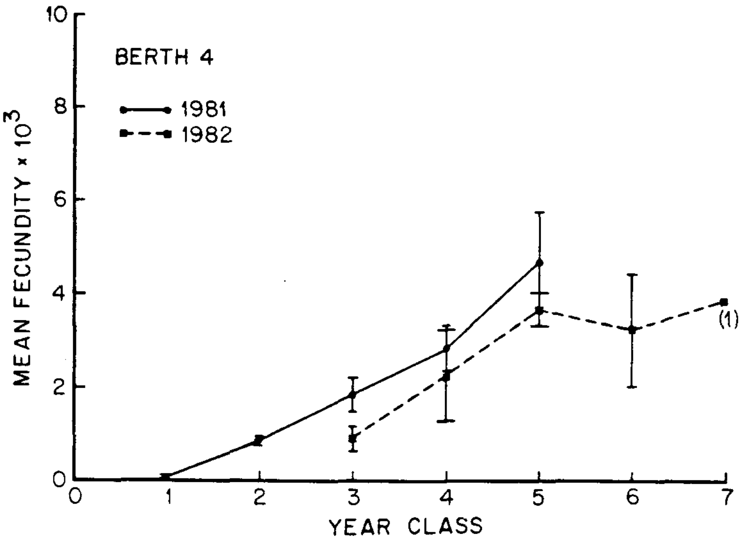

Figure 17. Fecundity as a function of year-class for *Balanus balanoides* from Berth 4, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

	Year Class						
	1	2	3	4	5	6	7
Mineral Creek							
February 1981							
n	2	51	30	4	2		
$\bar{x}$ fecundity	66	966	1947	2308	1828		
SD	4	1146	1318	1674	632		
SE	3	161	241	837	448		
Range							
Lo	63	50	213	425	1381		
Hi	68	7347	6037	4350	2275		
March 1982							
n	0	1	34	12	8	7	3
$\bar{x}$ fecundity	*	1250	2798	3880	6288	4641	8121
SD	*	*	1784	1713	2727	2804	4225
SE	*	*	306	495	964	1058	2442
Range							
Lo	*	*	313	675	3294	1344	3913
Hi	*	*	7019	5669	11369	8456	12363

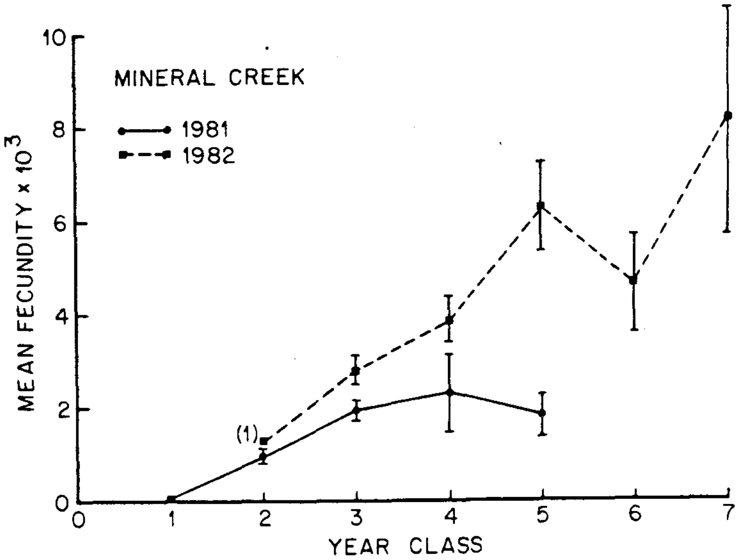

Figure 18. Fecundity as a function of year-class for *Balanus balanoides* from Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982. Error bars represent standard error of the mean.

Sawmill Spit in 1981 (3.8 times that in 1982, Table 9), may be partially attributed to the difference in the size of barnacles in the 1981 and 1982 collections. The barnacles collected from all intertidal heights in 1981 were larger and weighed more than corresponding samples in 1982 (Table 6 and Appendix 2, Table 4; Fig. 15). The above results suggest the presence of larger barnacles (and therefore, more fecund individuals) in any year class in 1981 as compared with 1982. Year-class data (Fig. 16) indicate that for most year classes common to both years (the exception being the fifth), significantly more eggs were produced per individual in 1981 than in 1982 ($\alpha = 0.05$) (Appendix 2, Table 5). The barnacle samples from the 1982 fecundity collection did not contain a proportionately greater number of young barnacles than the 1981 collection (Fig. 16). Thus, reduced overall fecundity for 1982 was not related to the presence of large numbers of young individuals in the sample. The difference may instead be related to the effects of climatic conditions on the population from 1981 to 1982. During the winter months of 1981-82, a high percent mortality was observed for the Sawmill Spit adult barnacle population (see Mortality discussion). The high mortality was probably a result of the harsh winter (low temperatures with clear skies, wind, and ice) (discussed in Physical Environment section). Evidently, only smaller individuals in every year class survived the winter of 1981-82, which explains the lowered fecundity observed for barnacles at Sawmill Spit in 1982 in comparison with 1981 (Table 6).

Table 9. Year-class abundance, fecundity, and egg production per 0.0469 m^2 (12.5 cm^2 x 3 – total sampling area for high, mid, and low intertidal zones) and per m^2 for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, February 1981 and March 1982.

Year Class	n/0.0469 m^2		Approximate n/m^2		Mean Fecundity/0.0469 m^2		Approximate Mean Fecundity/m^2		Egg Production/0.0469 m^2 (n x mean fecundity)		Approximate Egg Production/m^2 (n x mean fecundity)	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Sawmill Spit												
1	0	0	-	-	-	-	-	-	-	-	-	-
2	5	2	107	43	3,300	169	71,154	3,611	16,650	338	355,769	7,222
3	43	22	919	470	4,223	1,095	90,235	23,397	181,589	24,090	3,880,107	514,744
4	45	40	962	855	7,555	1,430	161,432	30,556	339,975	57,200	7,264,423	1,222,222
5	11	5	235	107	4,253	3,814	90,876	81,496	46,783	19,070	999,637	407,479
6	2	1	43	21	7,322	3,981	156,453	85,064	14,644	3,981	312,906	85,064
7	1	0	21	-	8,131	-	173,739	-	8,131	-	173,739	-
TOTAL ALL YEAR CLASSES	107	70	2,287	1,496					607,772	104,679	12,986,581	2,236,731
MEAN ALL YEAR CLASSES					5,680	1,490	121,368	31,838				

3.8 times more eggs produced in 1981 than in 1982

Table 9. Continued.

Year Class	$n/0.0469\ m^2$		Approximate n/m^2		Mean Fecundity/$0.0469\ m^2$		Approximate Mean Fecundity/m^2		Egg Production/$0.0469\ m^2$ (n x mean fecundity)		Approximate Egg Production/m^2 (n x mean fecundity)	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Berth 4												
1	2	0	43	-	75	-	1,603	-	150	-	3,205	-
2	15	0	342	-	827	-	17,671	-	13,232	-	282,735	-
3	50	19	1,068	406	1,832	888	39,145	18,974	91,600	16,872	1,957,265	360,513
4	16	7	342	150	2,836	2,244	60,598	47,949	45,376	15,708	969,573	335,641
5	6	10	128	214	4,733	3,668	101,132	78,376	28,398	36,680	606,795	783,761
6	0	2	-	43	-	3,216	-	68,718	-	6,432	-	137,436
7	0	1	-	21	-	3,863	-	82,543	-	3,863	-	82,543
TOTAL ALL YEAR CLASSES	90	39	1,923	834					178,756	79,555	3,819,573	1,699,894
MEAN ALL YEAR CLASSES					2,001	2,050	42,756	43,803				
					Approximately same number of eggs in 1981 and 1982							

Table 9. Continued.

Year Class	$n/0.0469\ m^2$		Approximate n/m^2		Mean Fecundity/$0.0469\ m^2$		Approximate Mean Fecundity/m^2		Egg Production/$0.0469\ m^2$ (n x mean fecundity)		Approximate Egg Production/m^2 (n x mean fecundity)	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Mineral Creek												
1	2	0	43	-	66	-	1,410	-	132	-	2,821	-
2	51	1	1090	21	966	1,250	20,641	26,709	49,266	1,250	1,052,692	26,709
3	30	34	641	726	1,947	2,798	41,603	59,786	58,410	95,132	1,248,077	2,032,735
4	4	12	85	256	2,308	3,880	49,316	82,906	9,232	46,560	197,265	994,872
5	2	8	43	171	1,828	6,288	39,060	134,359	3,656	50,304	78,120	1,074,872
6	0	7	-	150	-	4,641	-	99,167	-	32,487	-	694,167
7	0	3	-	64	-	8,121	-	173,526	-	24,363	-	520,577
TOTAL ALL YEAR CLASSES	89	65	1,902	1,388					120,696	250,096	2,578,975	5,343,932
MEAN ALL YEAR CLASSES					1,356	3,876	28,974	82,821				

2.9 times more eggs produced in 1982 than in 1981

The observed fecundity at Mineral Creek, based on the mean of samples from all tidal heights was approximately 2.8 times greater in 1982 ($\bar{x}$ = 3876) than in 1981 ($\bar{x}$ = 1356) (Tables 8 and 9). A significantly greater fecundity ($\alpha = 0.05$) was observed in the high and mid tidal heights when considered separately, as well (Appendix 2, Table 4). A significant difference in mean body weight of barnacles collected for the two years was observed in the high zone and for all heights combined (1982 weight greater than 1981). The above results explain the data in Figure 15, since the fecundity per mg body weight was noticeably greater in 1982. The mean R/C diameter of high zone and combined samples collected in 1982 was significantly larger that that of corresponding barnacles sampled in 1981 (Table 8 and Appendix 2, Table 4). The observed R/C diameter difference was reflected in volume, as well. In 1982, at any volume, fecundity was higher than in 1981 (Fig 15). Year-class data (Fig. 18) indicate that the mean fecundity for year classes common to both years was greater in 1982 than in 1981, although only significantly for three year olds (Appendix 2, Table 5). The majority of barnacles examined in 1982 were older than those in 1981 as well, which further explains the fecundity difference observed between 1981 and 1982 collections here. During the summer of 1981, an extremely high mortality percentage was observed for individuals at Mineral Creek (see Mortality section for further discussion). The many deaths resulted from a heavy sediment and algal accumulation, which presumably covered the barnacles completely (see discussion in the Physical Environment section). The organisms surviving were apparently larger individuals which were not covered as thoroughly. These larger barnacles collected in 1982 were more fecund in comparison with 1981 Mineral Creek barnacles.

Berth 4 fecundity values, based on the mean of all three tidal heights, were approximately the same in 1981 ($\bar{x}$ = 2001) and 1982 ($\bar{x}$ = 2050) (Table 7 and Appendix 2, Table 4). Values, although not significantly different in the high and low zones between 1981 and 1982, varied greatly between the years for mid tidal-height barnacles (Appendix 2, Table 4). The R/C diameter data reflect fecundity data for mid-zone organisms — smaller and less fecund individuals in 1981 in comparison with 1982. Mean fecundity per mg dry body weight was typically greater for pooled samples of barnacles collected from all heights at Berth 4 in 1982 in comparison with those collected in 1981 (Fig. 15). The barnacles in 1982, though possessing more eggs than those in 1981 weighed less on the average than 1981 barnacles sampled (Table 7 and Fig. 15). Only barnacles from the high zone failed to weigh significantly more in 1981 than in 1982 (Appendix 2, Table 4), probably as a result of the low number examined in the latter year. Year-class data indicate that a somewhat greater number of eggs were produced for any year class in 1981 than in 1982 (Fig. 17). These data also indicate that younger individuals were collected at Berth 4 in 1981 than in 1982. The mean fecundity at Berth 4 was the same in 1981 and 1982 probably only due to the inclusion of younger (probably smaller individuals) in 1981 and older (larger barnacles) in 1982. Upon examination of fecundity values for three, four, and five year olds (the year classes common to both the 1981 and 1982 collections), mean fecundity was greater in 1981 than in

1982, though only significantly greater ($\alpha = 0.05$) for three year olds (Appendix 2, Table 5).

The fecundity results discussed above for barnacles at Berth 4, unlike those observed for barnacles at Sawmill Spit and Mineral Creek, were difficult to interpret based on knowledge of the biology of the barnacle in Port Valdez and the environmental conditions present during the study period. It is conceivable that the chronic low-level exposure of barnacles at Berth 4 to hydrocarbons subject these organisms to uncommon stresses, the results of which are reflected by the inconsistencies observed in the fecundity data here.

Based on data in Table 9 and Figures 16-18, fecundity generally increased with year class at every site (i.e., as barnacles grow older, they become more fecund). However, comparisons of egg production values (Table 9) (number of individuals in a particular year class times the mean fecundity of the year class) between the sites reveal that in both years assessed, production reached its maximum by the fourth year at Sawmill Spit and by the third year at Mineral Creek. No pattern emerged for barnacles at Berth 4. In 1981, the third year class was the most productive, while in the following year it was the fifth year class which produced the most eggs. Although only two years of the above discussed data are available for analysis, the inconsistencies in the egg production data for barnacles at Berth 4 may further reflect chronic problems within the population here which have resulted from exposure to continuing low levels of hydrocarbons.

Upon examination of size, volume, weight, and fecundity data from each tidal height at the three sampling sites (Tables 6-8), several trends become apparent. At Sawmill Spit, barnacles in general increase in diameter, volume, dry body weight, and fecundity in the lower intertidal areas. The above trend is to be expected, since barnacles in lower zones are submerged for longer periods of time, and presumably feed longer (Crisp, 1959). Also, barnacles from all heights at Sawmill Spit mirror the same annual trend, since barnacles throughout the intertidal zone were larger, weighed more and contained more eggs in 1981 than in 1982. At Berth 4, no trend due to tidal height emerged. For example, although individuals from all heights were smaller in diameter in 1981 than in 1982, those in every zone weighed more the former year. In 1981, fecundity values were greater for these smaller, but heavier barnacles inhabiting high and low zone areas, but lower for mid-zone barnacles. Unlike individuals at Sawmill Spit, the barnacles at Berth 4 did not grow exceedingly larger in the lower intertidal zone. In fact, the opposite was observed. High-zone barnacles were larger, weighed more, and for at least 1981, were more fecund. Mineral Creek barnacles from the high, mid, and low intertidal displayed the same trend within any year, as was observed for barnacles from Sawmill Spit. In 1981, barnacles from all zones were generally smaller, weighed somewhat less, and were less productive in terms of fecundity than in 1982. However, as for Berth 4, the larger and, in general, more fecund individuals were observed in high zone areas. The larger barnacle size in high intertidal areas at Berth 4 and Mineral Creek may indicate an adaptive response to stress, since in order to overcome environmental problems, the organisms must reach a particular critical size.

It is obvious that a more extensive investigation, including a long-term fecundity data set is needed in order to assess what is "typical" for a particular area, especially at Berth 4, where continuing exposure to low levels of hydrocarbons occurs. Also, the quality and quantity of food available to barnacles in the study areas are not known for the two years, but undoubtedly influenced the reproductive output. Barnes and Barnes (1968) observed marked fluctuations in fecundity values over a two year period as well. They believe that these differences may have reflected long-term cyclic changes, since year-to-year fluctuations in the level of reproduction, due to unknown origins, have been observed in many marine invertebrates.

Settlement

Settlement of juvenile *Balanus balanoides* in Port Valdez first occurs in April, approximately six weeks after the liberation of nauplii into the water column (personal observation). Following release, the larvae metamorphose through six naupliar stages and one cyprid stage. During the non-feeding cyprid stage, larvae settle out of the water column to search for a suitable substratum on which to settle (Stubbings, 1975; Barnes, 1980). Behavior during settlement includes extensive crawling of cyprids back and forth on the substrate, pivoting away from neighboring barnacles, and eventual establishment of a suitable site determined by a "nearest neighbor distance" of 1-3 mm from the closest

B. balanoides (Knight-Jones and Moyse, 1961). Cyprids are able to detect and pivot away from other members of their species, but settle indiscriminantly beside and on barnacles of other species, responding to previously settled barnacles as only irregularities on the rock (Crisp, 1961; Knight-Jones and Moyse, 1961; Moyse and Hui, 1981). Knight-Jones (1955), Crisp and Meadows (1962), and Larman and Gabbott (1975) suggest the detection of a settling factor by young cyprids in search of an optimum attachment site. *Balanus balanoides* cyprids apparently detect intertidal heights best supporting other members of their species by recognition of a proteinaceous settling factor (Crisp and Meadows, 1962), since larvae subsequently choose areas already populated by *B. balanoides* for their attachment. Cyprids transform into young barnacle "spat" upon cementing their antennae to the substratum.

In Port Valdez, cyprids were observed crawling around on rocks from early to mid-April in 1980-1982. Gregarious settlement occurred in April of each year, with recruitment continuing through June (Appendix 2, Table 6 and Fig. 19). A few newly settled juveniles were recognized at other times of year, especially in lower zones. These juveniles represent a portion of the continual reproductive efforts of *B. crenatus*, which produces several broods annually. High zone settlement at times of year other than that expected for *B. balanoides* is due to *B. glandula*, the other intertidal barnacle living in high intertidal regions in Port Valdez (for further discussion, see Feder and Keiser, 1980). Figures 20-22 illustrates annual settlement patterns at each location for barnacles living throughout the intertidal zone.

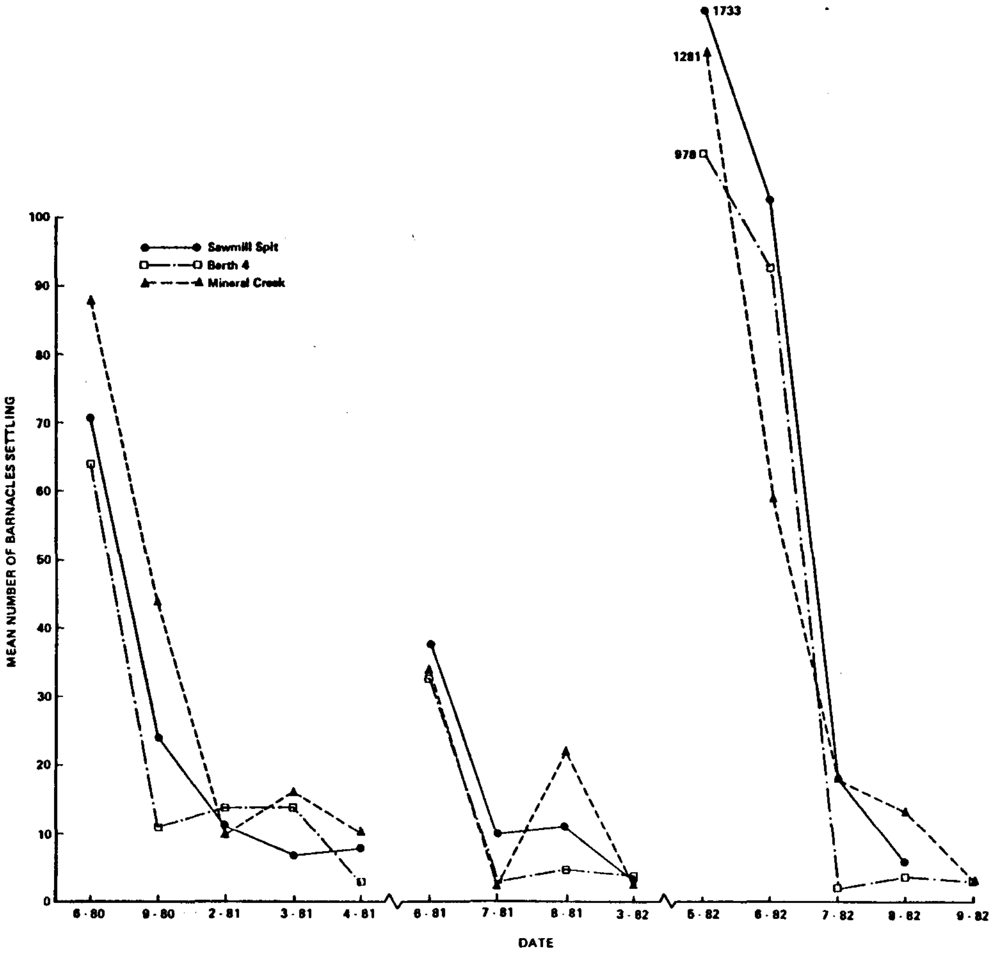

Figure 19. Annual recruitment of juvenile *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Months illustrated represent times of data collection, with the exception of 3-82 at Sawmill Spit, from which data were actually collected in 4-82.

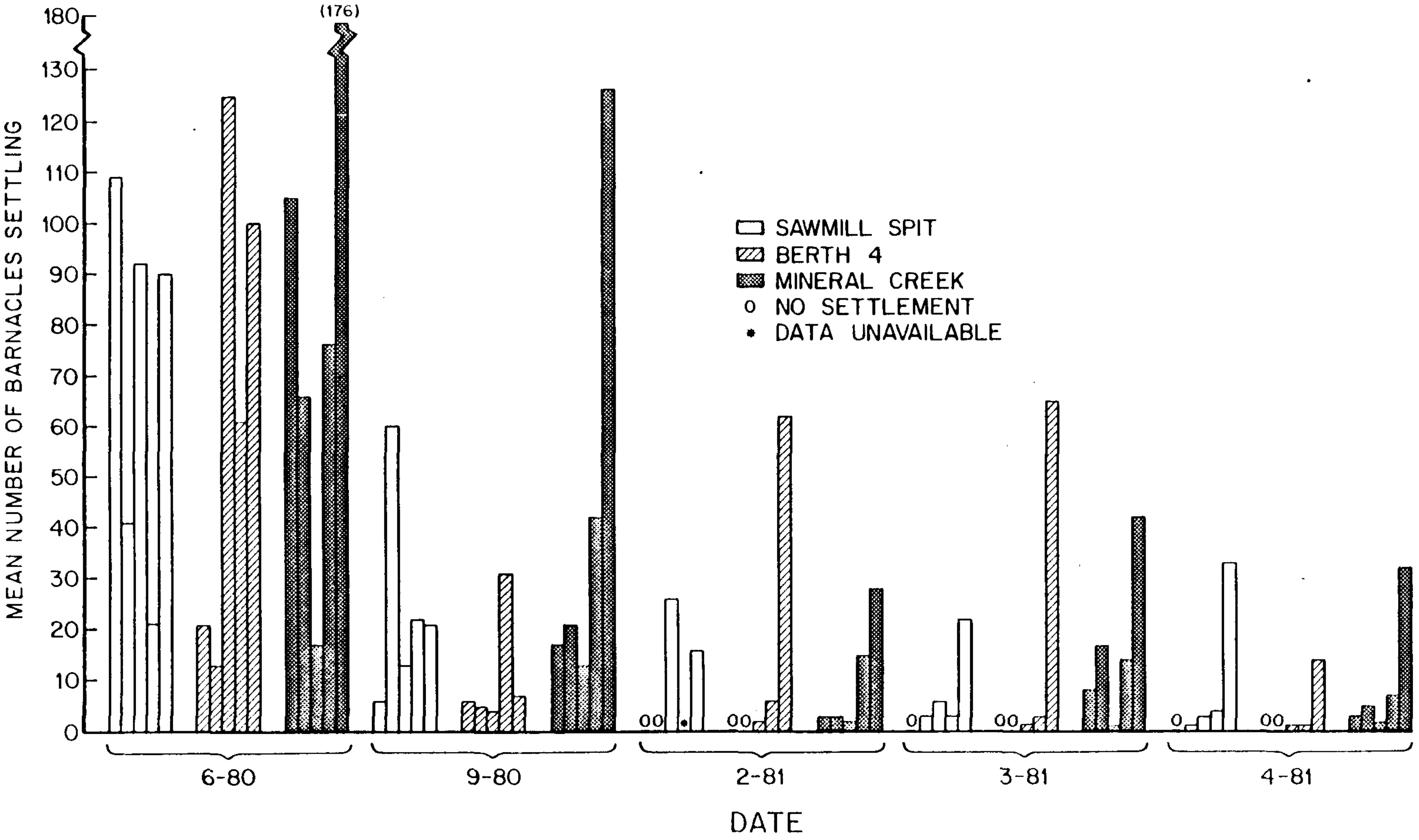

Figure 20. Cyprid settlement of *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, during the sampling period June 1980-April 1981. Five tidal heights are examined for each location — highest tidal area to the left, lowest to the right. For actual tidal heights, refer to Table 23.

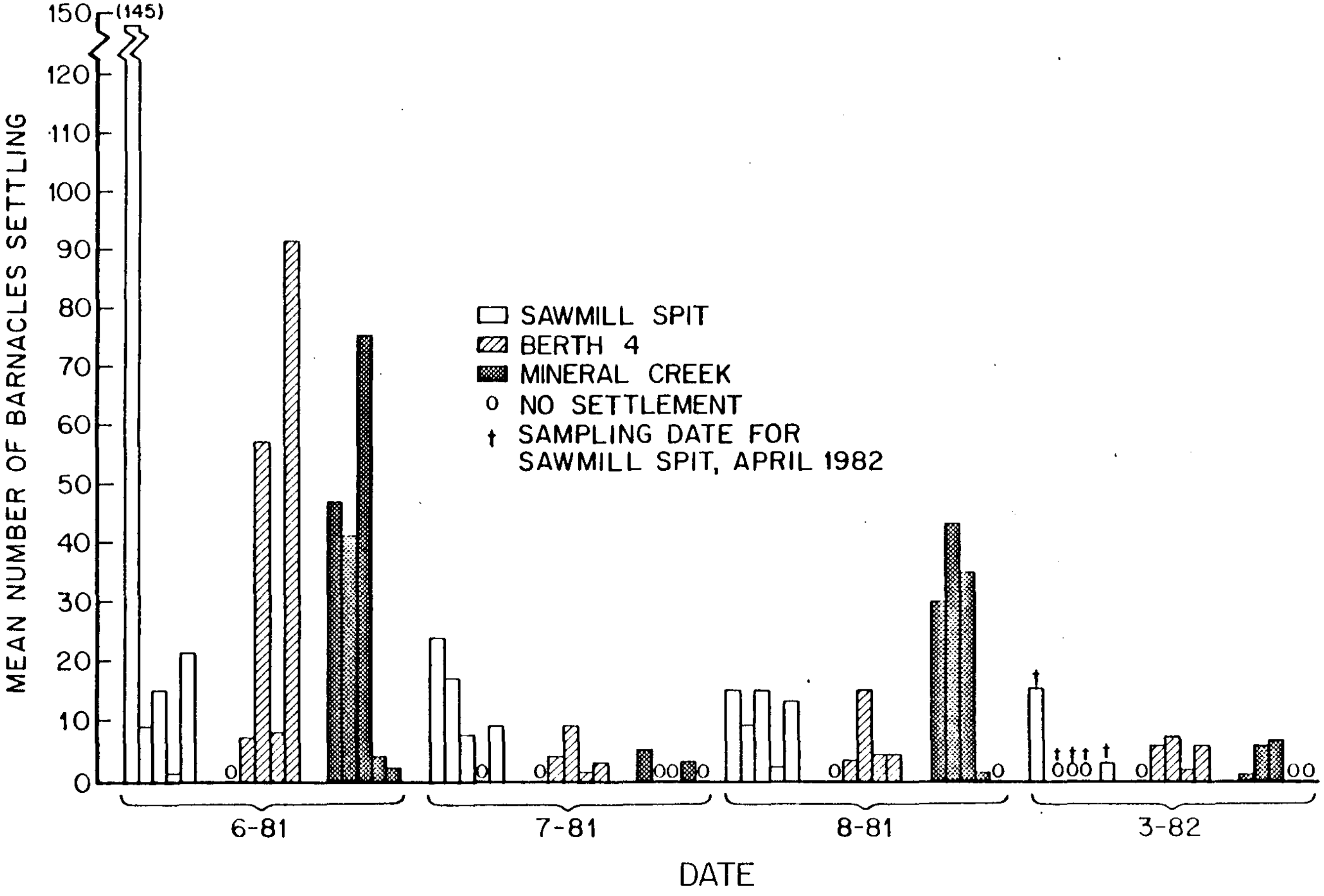

Figure 21. Cyprid settlement of *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, during the sampling period June 1981–March 1982. Five tidal heights are examined for each location — highest tidal area to the left, lowest to the right. For actual tidal heights, refer to Table 23.

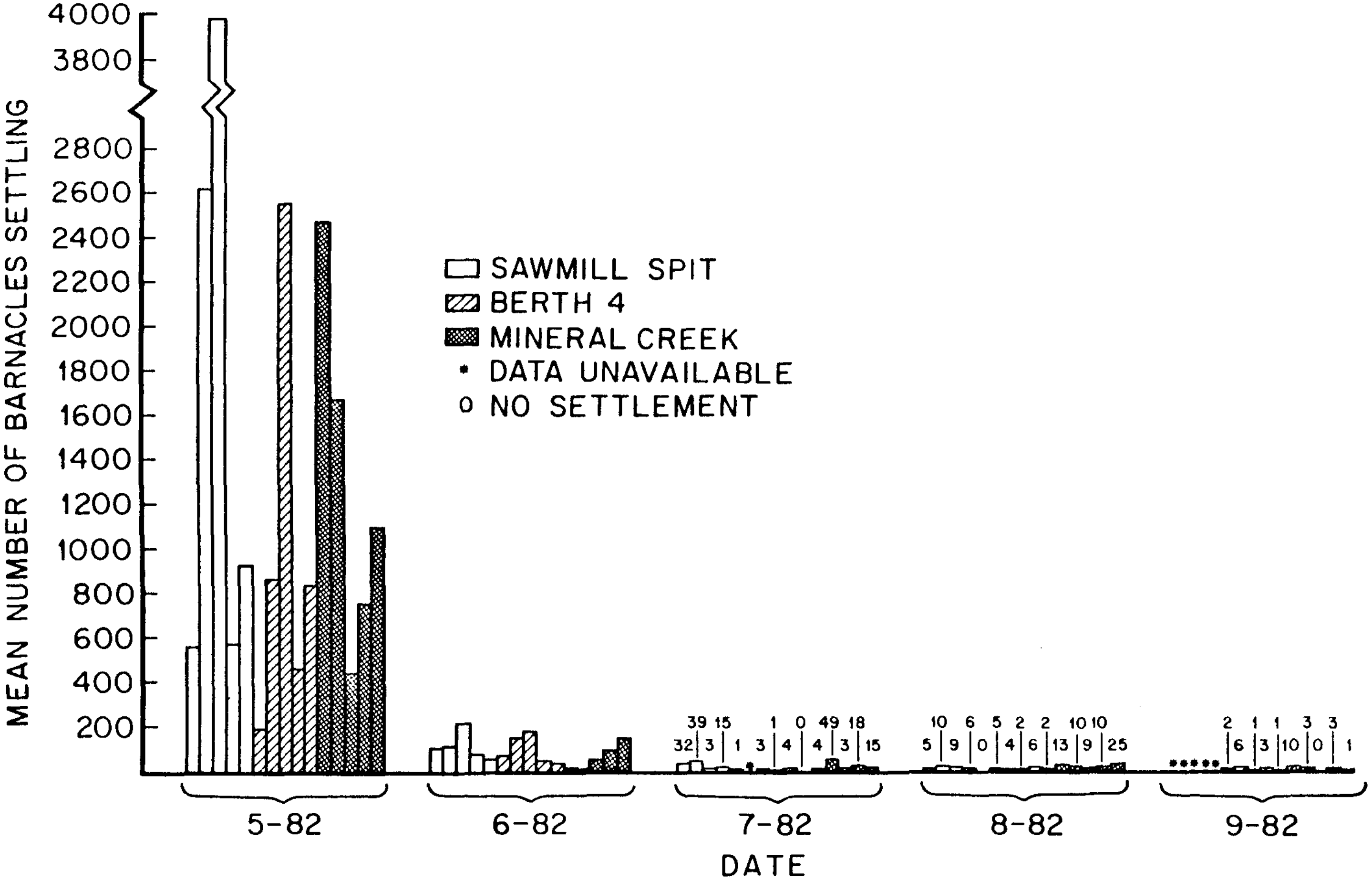

Figure 22. Cyprid settlement of *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska during the sampling period May-September 1982. Five tidal heights are examined for each location — highest tidal area to the left, lowest to the right. For actual tidal heights, refer to Table 23.

Seasonal settlement patterns of *B. balanoides*, observed over a three year period indicate that greatest recruitment of spat occurred during the spring of 1982, followed by 1980 and 1981, respectively. No apparent trend due to location emerged, since in some years more juveniles settled at one site and in other years greater numbers were observed at another site. However, settlement of spat at times of year other than expected for *B. balanoides* more frequently occurred at Mineral Creek than at the other sites, although high and low zone settlement due to *B. glandula* and *B. crenatus* occurred throughout the year at all locations.

CONCLUSIONS

Balanus balanoides, a hermaphroditic intertidal barnacle, produces a single brood of individuals each year. Ovarian tissue becomes evident in early April following the spring diatom bloom. Male reproductive structures appear in May or June, and development of these structures and of female gametogenic tissue continues throughout the summer. Spermatogenesis begins in August with fertilization commencing in late August to mid September. Upon fertilization, eggs are moved via the oviduct to the base of the mantle cavity. Here the embryos are brooded until February or March, at which time the larvae hatch and are liberated as eyed nauplii into the water column. After approximately six weeks, and following a transition through six naupliar stages, a non-feeding cyprid is formed, which drops from the water column and settles head first onto the hard substrate to develop into a juvenile barnacle.

Annual patterns of reproductive tissue development at the three study areas generally appear to follow the above described sequence (see Tables 3, 4, and 5). During the winter months (November-January), up to ∿35% of the barnacles examined showed no signs of developing reproductive tissue. These barnacles most likely represent individuals which were unsuccessful in their fertilization attempts.

Fluctuations in ovarian and/or lamellar weight (Fig. 6) indicate that for a typical barnacle, ovarian weights prior to fertilization in 1980 were somewhat higher at Sawmill Spit and Mineral Creek than at Berth 4. Barnacles from the latter area displayed lower than typical values throughout the year. In addition, following fertilization in 1980, the Sawmill Spit and Mineral Creek values for lamellar weight were higher than those for Berth 4 (Fig. 6). However, values for reproductive weight in 1981-82 were approximately the same at all sites. The reduced reproductive weights observed at Berth 4 throughout 1980-81 were significantly lower ($\alpha = 0.05$) than corresponding weights for the site in 1981-82 (Appendix 2, Table 3) and may indicate a response to the small oil spill in the vicinity of Berth 4 in April 1980. In 1982, Sawmill Spit ovarian tissue weight was the greatest of the three sites. Although similar annual reproductive patterns emerge for each site, lags of up to one month are occasionally evident in the reproductive cycle at all sites.

Results of between-height comparisons of reproductive tissue weight indicate that barnacles from the low zone of Sawmill Spit generally produced the most reproductive tissue annually, followed by those from mid and high-zone areas, respectively (Appendix 2, Table 1). The above is to be expected, and reflects the longer submersion period and associated increased feeding time for barnacles in low tidal areas. No pattern relative to tidal height emerged for organisms from Berth 4 or Mineral Creek, since often the greatest observed weights were for barnacles in the higher intertidal zone. The latter observation may be indicative of disturbance within the populations at Berth 4 and Mineral Creek, in the form of seasonal environmental stresses (lowered salinity and a heightened suspended sediment load) at the latter site and continuing low-level exposure to pollutants (i.e., hydrocarbons) at the former.

Fecundity, the number of eggs released by the parent into the water column in late February or early March, is, in general, related to the size of the barnacle (R/C diameter), the volume (ℓ^3), the year class, and the body weight (Figs. 11-14). Since fecundity values often show marked fluctuations from year to year, it is only possible to examine general trends in this type of data, unless numerous consecutive years of data are available.

In 1981, Sawmill Spit barnacles contained the greatest number of eggs, based on the mean of individuals from all tidal heights ($\bar{x}$ = 5680), followed by barnacles at Berth 4 ($\bar{x}$ = 2001) and Mineral Creek ($\bar{x}$ = 1356). One year later, Mineral Creek barnacles were the most fecund ($\bar{x}$ = 3876), as compared with those at Berth 4 ($\bar{x}$ = 2050) and Sawmill Spit ($\bar{x}$ = 1490). During 1981, Sawmill Spit barnacles, in general, maintained a higher fecundity at any given size, volume, body weight, or year class than either Berth 4 or Mineral Creek barnacles

(Figs. 11-14a). Based on size, volume, and year-class data, barnacles from Mineral Creek generally displayed the highest fecundity values in 1982, followed by barnacles from Berth 4 and Sawmill Spit, the latter two groups having similar values for every size, volume, and year class (Figs. 12-14b). However, in 1982, Berth 4 barnacles as compared with those at other sites, displayed the greatest fecundity value relative to body weight, up to approximately 1.5 mg (Fig. 11b). Mineral Creek barnacles > 1.5 mg contained the greatest number of eggs per mg tissue, as compared with those at Sawmill Spit.

Year-to-year fluctuations in fecundity indicate that for barnacles at Sawmill Spit, fecundity was greater in 1981 than in 1982. Organisms in the former year were larger and weighed more at every tidal height than in the latter year (Table 6). Year class data revealed no significant shift in numbers in any year-class from 1981 to 1982 (Fig. 16); thus, samples collected in 1981 were not necessarily older. The size-weight reduction (and subsequent lowered fecundity) observed for barnacles in 1982 indicate that only the smaller individuals in any year class were present. The mortality of larger barnacles probably occurred during the severe winter of 1981-82, since a high mortality was observed for Sawmill Spit adults during the latter period.

The fecundity for barnacles from all intertidal heights at Mineral Creek was greater in 1982 than in 1981. Year-class data indicate that younger individuals were present in the 1981 collection (Fig. 18). Barnacles at Mineral Creek in 1982 were larger and weighed more throughout the intertidal zone than they did in 1981 (Table 8). The fecundity difference between 1981 and 1982 was undoubtedly due to the difference in size of barnacles in these years. The lack of survival of smaller individuals in 1982 can probably be attributed to the mass mortality observed for barnacles at Mineral Creek during the summer of 1981. The mortality resulted from the combined accumulation of large amounts of sediment and the algae, *Monostroma* spp., which completely covered a large number of barnacles (especially smaller ones).

The mean fecundity (based on all individuals from all tidal heights) was the same at Berth 4 in 1981 and 1982. However, year-class data indicate that a somewhat greater egg production occurred in 1981 (in comparison with 1982) for year classes common in both years (third, fourth, and fifth year classes) (Appendix 2, Table 5; Fig. 17). These data also indicate that younger individuals were collected in 1981 than in 1982. Thus, the mean fecundity was the same at Berth 4 in 1981 and 1982 only due to the inclusion of younger barnacles in 1981 and older barnacles in 1982, the fecundity values of which averaged out to similar means. Upon inspecting fecundity values per tidal height, it was observed that the only major difference between 1981 and 1982 was in the mid-zone data. In 1982, a significantly greater number of eggs were assessed for these organisms than in 1981 (Appendix 2, Table 4). The inconsistencies within the fecundity data set for barnacles throughout the intertidal zone at Berth 4 appear to be a reflection of the continuing low-level exposure of these organisms to hydrocarbon pollutants. However, in order to accurately assess the expected annual fecundity for these barnacles, a much longer-term study, identifying natural cyclic fluctuations, should be undertaken.

The examination of egg production values revealed that the fourth year class at Sawmill Spit and the third year class at Mineral Creek were the most productive in both years examined (Table 9). A similar annual trend did not emerge for barnacles from Berth 4. In 1981, the third year class was the most productive and in 1982, it was the fifth year class which produced the greatest amount of eggs. Although, further data are needed before long-term patterns become apparent, the inconsistency at Berth 4, in view of other inconsistencies observed for the data set here, may reveal problems within the barnacle population at this site.

A final observation emerging from the fecundity data is related to biological differences between barnacles at high, mid, and low-tidal heights for each site. Barnacles at Sawmill Spit in general grow larger, weigh more, and are more fecund in lower intertidal areas than in high zones (Table 6), as would be expected, since the organisms of the low intertidal are submerged for longer periods of time and presumably feed longer. However, for barnacles at Berth 4 and Mineral Creek the opposite trend was observed with larger and more fecund individuals present in the high intertidal. The presence of larger individuals in the high zones of these two sites (both apparently subject to stress) may represent a selection for individuals with a greater chance of survival in the stressed, upper regions.

Juvenile settlement of *B. balanoides* initially occurs in April, with recruitment often continuing through June. Settlement observed at other times of year were attributed to spat of the other two common intertidal barnacles, *B. glandula* in the high zone and *B. crenatus* in the low zone, both of which produce several broods annually. Observed settlement patterns in Port Valdez indicate that recruitment was significantly greater during the spring of 1982 at all sites than in either 1980 or 1981 (Fig. 19). The greatest number of recruits during 1982 was observed at Sawmill Spit, followed by Berth 4 with a few less spat, and Mineral Creek with significantly fewer.

SEASONAL AND ANNUAL GROWTH

INTRODUCTION

In order to determine trends in seasonal and annual growth for *Balanus balanoides*, several parameters are considered — age, size, and the increment of seasonal and annual growth. The outer surfaces of barnacle shell plates have clearly visible disturbance rings, which appear as distinct overhangs or notches. These rings result from the reduction in growth and the retreat of the growing edge of the mantle when conditions are no longer favorable for growth. These "winter rings", utilized in the present investigation for age analysis of barnacles in Port Valdez have served as the basis for aging in studies conducted elsewhere (Crisp, 1954; Petersen, 1966; Klepal and Barnes, 1975; Bourget, 1980). "Winter ring" formation was documented in the present study via monthly examination of recruits of the year in the field and through scanning electron microscopy studies. Most investigations concerned with growth in barnacles, including the present study, employed a commonly measured dimension, the basal or rostro-carinal (R/C) diameter (Fig. 4). It is a satisfactory measurement, since it is readily accomplished in the field, is accurate, and does not destroy the individual during measurements (Barnes *et al.*, 1963). However, when barnacles are removed from the substrate and brought into the laboratory, growth rates can be better estimated by a measurement technique developed for the present study. In this technique, measurements of the distance or the vertical height between successive age rings on the shell plates are made (Fig. 5). Individuals collected in the field are frequently crushed or broken, and the damaged shell plates of these specimens are unsatisfactory for measurement of R/C diameter. The vertical growth-ring measurement utilized here is easily obtainable, accurate, and can be applied to partially broken or crushed individuals.

METHODS

Age determination and rostro-carinal diameter (maximum barnacle diameter) data were obtained for all individuals collected for reproductive and energy partitioning studies (see Methods in the sections on Reproductive Biology and Energy Partitioning). Age was determined by counting winter disturbance rings on the surface of the outer portion of the shell when the skeletal plates were observed with a dissection microscope (Bourget, 1980). Age was assessed as follows: barnacles in their first year of growth comprise the first year-class, those in the second year of growth the second year-class, etc. Rostro-carinal (R/C) diameter was measured for each animal using vernier calipers accurate to 0.05 mm. Animals were measured either in the field or the laboratory. Results obtained from the R/C diameter data were used to compare growth patterns for the three study areas.

In February 1981, an additional means of examining growth was begun. Three replicate destructive plots (removal of all organisms) were taken monthly from the mid-tidal height at each study area (Sawmill Spit, Berth 4, Mineral Creek) for age assessment and seasonal and annual growth determinations. A 0.0156 m^2 (12.5 cm x 12.5 cm) sampling frame was randomly tossed onto the substrate, and all barnacles within the frame collected and preserved in 10% formalin buffered with hexamine. Samples were returned to the laboratory for examination. Barnacles with elongated or irregular growth rings were eliminated from the analysis. Yearly winter disturbance rings were identified, and the vertical distance between the top of the first growth ring and successive disturbance rings were measured using vernier calipers (Fig. 5, termed vertical growth-ring height). One edge of the calipers was placed on top of the first growth ring and the other edge at the base of the growth ring for which a measurement was being taken. The measurement of vertical growth-ring height is cumulative in that the size attained at year 2 includes the growth height for the second year plus the previous or first year's growth, etc. Growth curves were developed for barnacles from each site based on these values.

A value for the average yearly shell growth (the annual growth-ring increment) was determined for growth rings of all individuals examined. The increment was calculated from vertical growth-ring height measurements by subtracting the ring-height value prior to new annual growth from the ring-height value following cessation of annual growth.

Growth-history tables, also based on vertical growth-ring height, were constructed using age-growth data modified after the method of Feder and Paul (1974) and Feder *et al.* (1976b). Mean growth-ring heights in the tables include measurements taken between all rings for each year-class. Each year's shell growth is read by following the sequential values for any year-class across the table. Shell growth of all year-classes in a particular year can be obtained by reading up the diagonal from the desired year. The tables allow for quick comparisons between annual growth values of the different year-classes at any site. Also, site to site comparisons of specific values can easily be accomplished. Seasonal shell-growth data were attained by measuring the increment of new shell material formed below the last detectable winter disturbance ring.

Growth-ring height values were tested for between-site differences in a given year and for within-site differences between the two years sampled by use of a Student's t-test. In the event that the variance (SD^2) differed significantly between the two values in question, an Aspin-Welch test was applied to the data. Significance was determined at the 95% confidence level. See Methods in the Reproductive Biology section for equations.

RESULTS-DISCUSSION

Year-Class Composition

Barnacles from destructive plots used in growth analyses were examined monthly from May-November 1981 and from January-September 1982. Year class-composition data for populations of barnacles at each of the three sampling sites are presented for 1981 in Table 10 and Figure 23 and for 1982 in Table 11. In 1981, a single barnacle at Sawmill Spit (0.09% of the total population sampled) was found to be 13 years old, the oldest specimen observed at any of the Port Valdez sites. The oldest individuals from Berth 4 were 8 years old (0.18% of

Table 10. Year-class composition for growth samples of *Balanus balanoides* in Port Valdez, Alaska, May-November 1981. n = number of individuals examined.

Year-Class	n	% of Total Population
Sawmill Spit		Total sample size = 1,138
1	596	52.37
2	224	19.68
3	12	1.05
4	21	1.85
5	136	11.95
6	69	6.06
7	30	2.64
8	31	2.72
9	11	0.97
10	5	0.44
11	2	0.18
12	0	0.00
13	1	0.09
Berth 4		Total sample size = 1,119
1	709	63.36
2	35	3.13
3	8	0.71
4	45	4.02
5	281	25.11
6	34	3.04
7	5	0.45
8	2	0.18

Table 10. Continued.

Year-Class	n	% of Total Population
Mineral Creek		Total sample size = 1,870
1	817	43.69
2	116	6.20
3	349	18.66
4	281	15.03
5	199	10.64
6	64	3.42
7	25	1.34
8	15	0.80
9	4	0.21

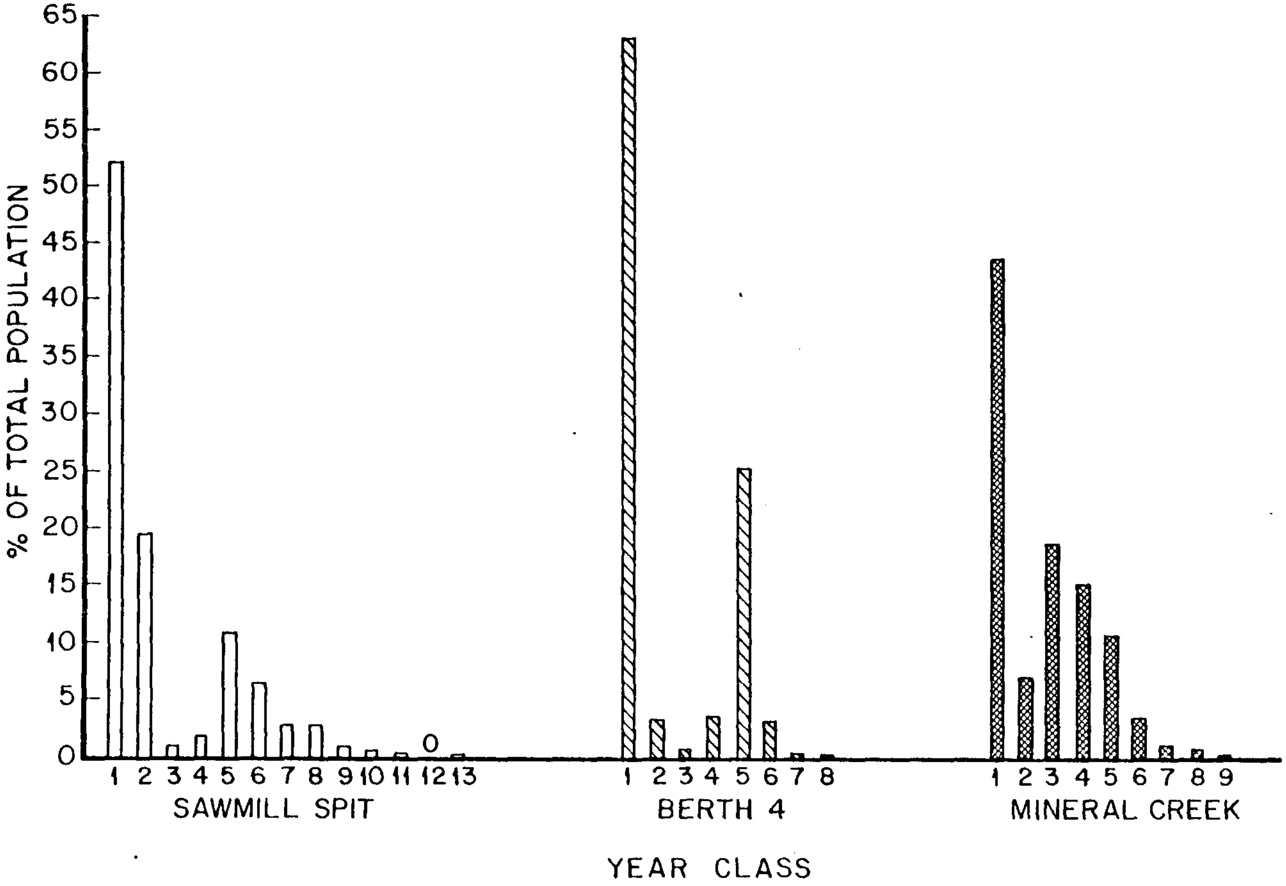

Figure 23. Year-class composition of populations of *Balanus balanoides* sampled for growth studies at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, May-November 1981.

Table 11. Year-class composition for growth samples of *Balanus balanoides* in Port Valdez, Alaska, January-September 1982. n = number of individuals examined.

Year-Class	n	% of Total Population
Sawmill Spit		Total sample size = 1,125
1	627	55.73
2	243	21.60
3	148	13.16
4	47	4.18
5	9	0.80
6	26	2.31
7	8	0.71
8	5	0.44
9	9	0.80
10	3	0.27
Berth 4		Total sample size = 1,061
1	425	40.06
2	391	36.85
3	71	6.69
4	21	1.98
5	72	6.79
6	69	6.50
7	12	1.13

Table 11. Continued.

Year-Class	n	% of Total Population
Mineral Creek		Total sample size = 1,102
1	530	48.09
2	193	17.51
3	86	7.80
4	153	13.88
5	73	6.62
6	30	2.72
7	33	2.99
8	4	0.36

the total population). The oldest barnacles at Mineral Creek were 9 years of age (0.21% of the total population in 1981). In 1982, the oldest individuals, again from Sawmill Spit, were 10 years old (0.27% of the total population). The oldest barnacles at Berth 4 were 7 years of age (1.13% of the total population) and at Mineral Creek, 8 years of age (0.36% of the total population).

In 1981, greatly reduced numbers of three-year old barnacles were observed at Sawmill Spit and Berth 4, representing less than 2% of the total population at either location (Table 10). The lowered abundance of barnacles in the third year-class was a result of unsuccessful reproductive efforts (reproductive development, lowered fecundity, and subsequent settlement) and/or high mortality rates (juvenile and larval) in 1978-79 in comparison with other years. Three-year old barnacles at Mineral Creek did not demonstrate a similar year-class failure. The third year-class comprised almost 30% of the total barnacle population there. The reduced numbers observed in 1981 for the third year-class at Sawmill Spit and Berth 4 as well as an evident reduction in numbers of the fourth year-class from Sawmill Spit suggest a disturbance in the vicinity of these sites in 1977-1979. Large numbers of *Balanus balanoides* in the first year-class at all sites were attributed to the gregarious nature of settlement of the barnacle (Knight-Jones, 1953). Barnacles from Mineral Creek were present in relatively large numbers up to 5 or 6 years of age, with the exception of the second year-class in 1981. The failure of this particular year-class was most likely the result of physical stress (lowered salinity and/or heavy sedimentation) which would affect primarily recruits of the year.

The apparent year-class failures of 1978 and 1979 at Sawmill Spit, as reflected by the reduced numbers of three and four-year old barnacles in 1981, were also observed for four and five-year old barnacles in 1982 (Table 11). The reduced numbers for the third year-class at Berth 4 in 1981 were reflected by the lowered numbers of four-year old barnacles at the site in 1982. These individuals, in their fourth year of growth in 1982 made up only 1.98% of the total population at Berth 4. The reduction in abundance of two-year old barnacles at Mineral Creek in 1981 was also reflected in the data of 1982, at which time a lowered percentage (7.80%) of three-year old individuals was observed here.

Annual Shell Growth

Annual shell-growth measurements (vertical growth-ring heights) for pooled samples of barnacles from all year-classes examined in 1981 are included in Table 12 for each sampling site. Growth curves of these data are presented in Figures 24-26.

During their first year of growth, young barnacles at Sawmill Spit attained a mean vertical growth-ring height of 1.24 mm, at Berth 4 juveniles grew to 1.12 mm, and at Mineral Creek barnacles reached a height of 1.04 mm. In subsequent year-classes, barnacles continued to be significantly larger ($\alpha = 0.05$) at Sawmill Spit than at the other two sites, suggesting that conditions governing growth were best at the former site (Table 12 and Appendix 3, Table 1; Figs. 24-26). As expected,

Table 12. Annual shell growth for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, sampling period May-November 1981. Data are derived from a pooled sample of individuals from all year-classes. For example, from Sawmill Spit, 649 barnacles were measured to obtain the first growth ring values. Since 107 barnacles were only 1 year old, the second year of growth ring values were taken from the remaining individuals which were at least 2 years old, in this case, 542 barnacles. n = number of individuals measured, SD = standard deviation, SE = standard error of the mean (see Growth Methodology for growth measurement techniques).

Year Class	n	Mean Growth Ring Height (mm)	SD	SE	Range L	Range H	Annual Growth Ring Increment (mm)
Sawmill Spit, sample size = 649							
1	649	1.24	0.33	0.01	0.40	2.30	1.24
2	542	3.05	0.89	0.04	1.00	5.50	1.82
3	318	4.29	1.01	0.06	2.20	7.40	1.24
4	306	5.86	1.07	0.06	3.00	9.70	1.57
5	285	7.33	1.20	0.07	4.00	11.30	1.47
6	149	8.57	1.38	0.11	5.20	12.20	1.24
7	80	9.64	1.50	0.17	6.40	14.00	1.06
8	50	10.87	1.75	0.25	7.40	16.20	1.23
9	19	11.72	1.61	0.37	8.40	13.60	0.85
10	8	13.00	1.28	0.45	10.20	14.50	1.28
11	3	14.57	1.58	0.91	13.20	16.30	1.57
12	1	13.70	-	-	-	-	-0.87
13	1	14.60	-	-	-	-	0.90

Table 12. Continued.

Year Class	n	Mean Growth Ring Height (mm)	SD	SE	Range		Annual Growth Ring Increment (mm)
					L	H	
Berth 4, sample size = 543							
1	543	1.12	0.32	0.01	0.40	2.20	1.12
2	410	2.52	0.72	0.04	0.90	4.60	1.40
3	375	3.61	0.89	0.05	1.60	6.40	1.09
4	367	4.70	0.98	0.05	2.20	8.40	1.09
5	322	6.18	1.04	0.06	3.50	10.00	1.48
6	41	6.89	1.24	0.19	4.60	9.60	0.71
7	7	6.56	1.13	0.43	5.30	8.60	-0.34
8	2	6.80	1.41	1.00	5.80	7.80	0.24
Mineral Creek, sample size = 1,176							
1	1,176	1.04	0.28	0.01	0.40	2.20	1.04
2	1,053	2.50	0.80	0.02	0.80	5.30	1.46
3	937	4.05	1.10	0.04	1.40	7.80	1.54
4	588	4.90	1.12	0.05	2.10	8.40	0.85
5	307	5.53	1.02	0.06	2.80	9.30	0.63
6	108	6.37	1.07	0.10	3.80	9.40	0.84
7	44	7.04	1.23	0.19	4.50	10.00	0.66
8	19	7.77	1.30	0.30	5.80	10.20	0.74
9	4	8.52	1.47	0.73	7.50	10.70	0.75

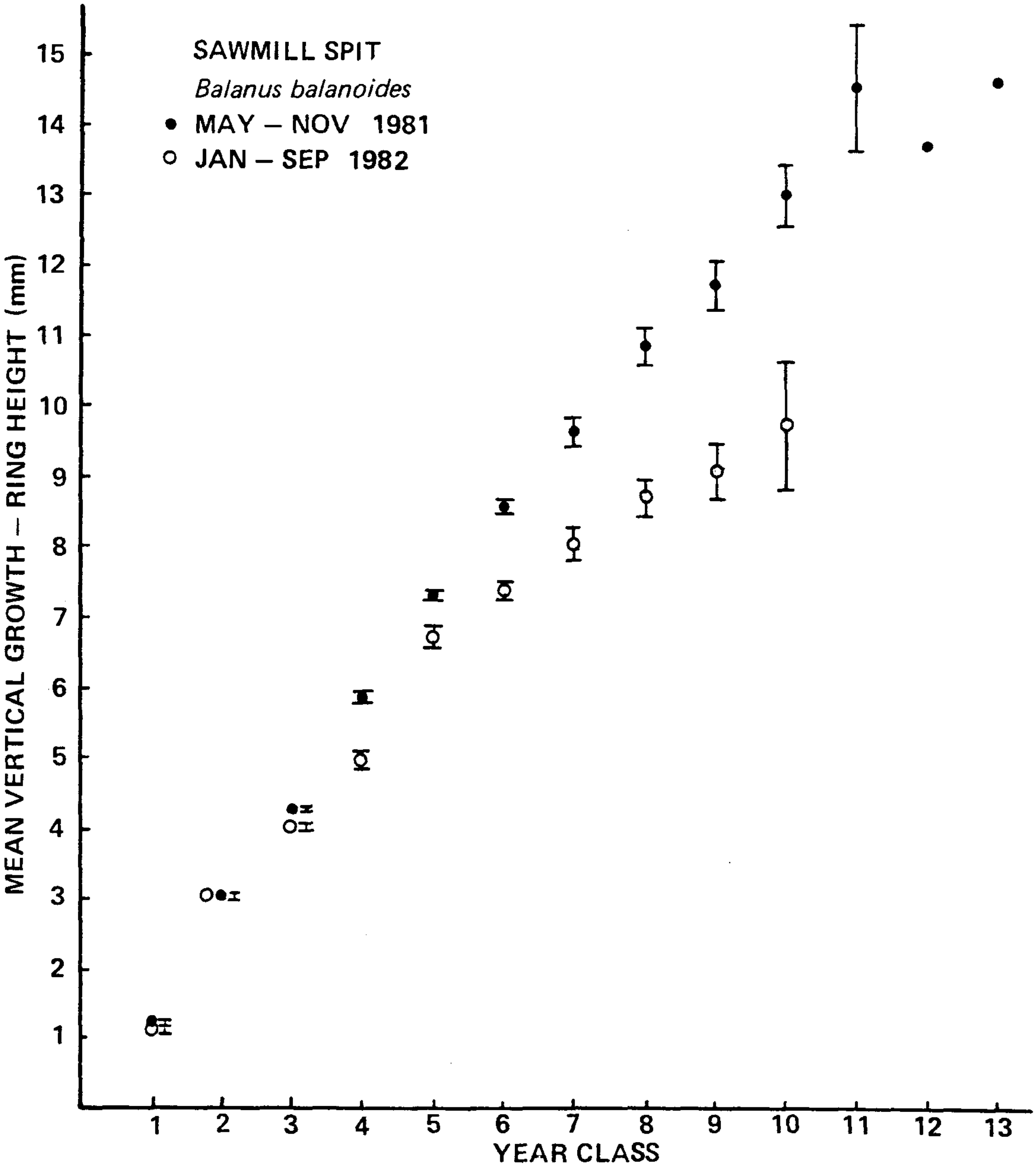

Figure 24. Growth curves for *Balanus balanoides* from the mid-zone of Sawmill Spit, Port Valdez, Alaska, 1981 and 1982. Error bars represent standard error of the mean. Error bars located to the side of data points represent errors smaller than size of data points.

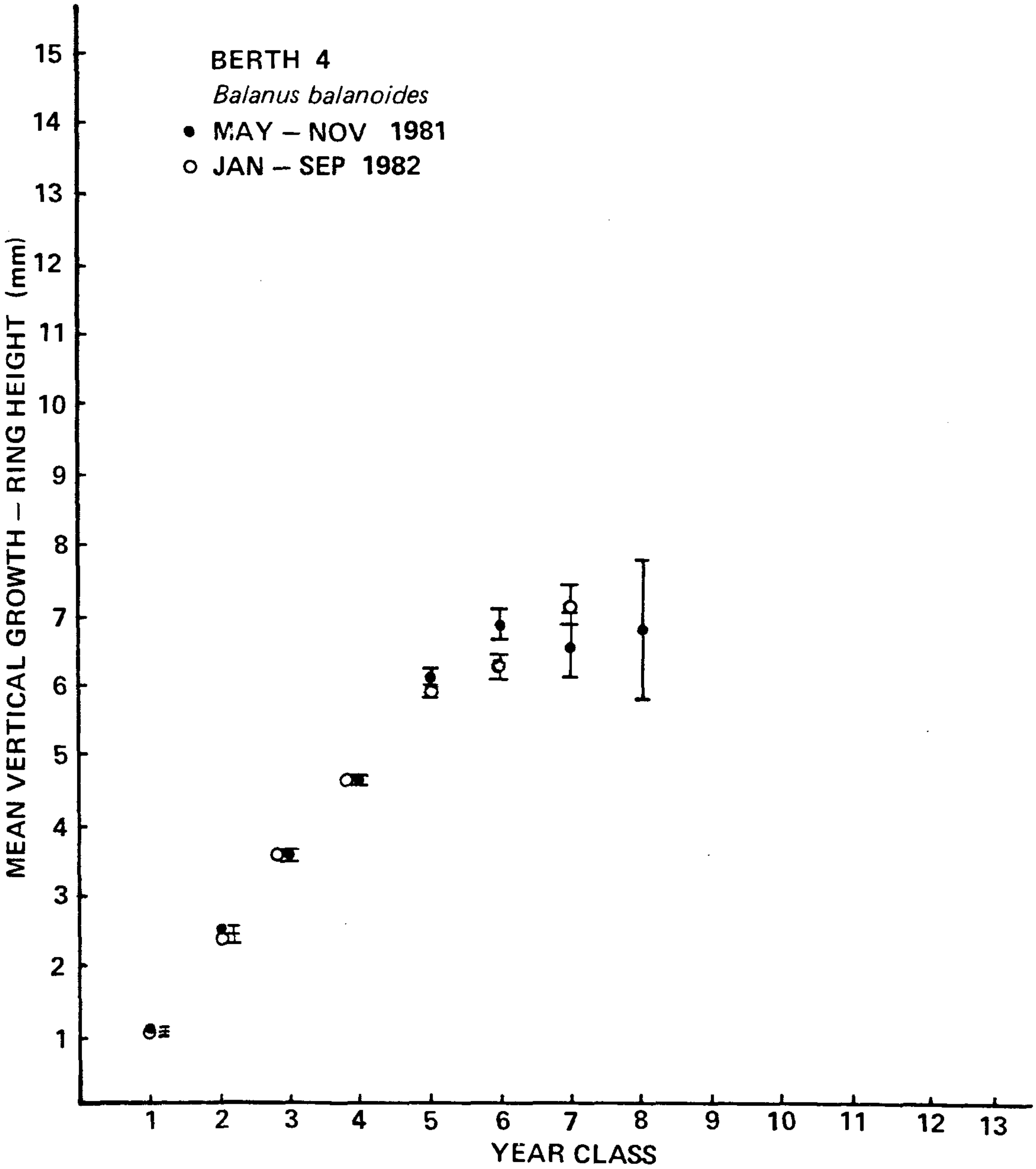

Figure 25. Growth curves for *Balanus balanoides* from the mid-zone of Berth 4, Port Valdez, Alaska, 1981 and 1982. Error bars represent standard error of the mean. Error bars located to the side of data points represent errors smaller than size of data points.

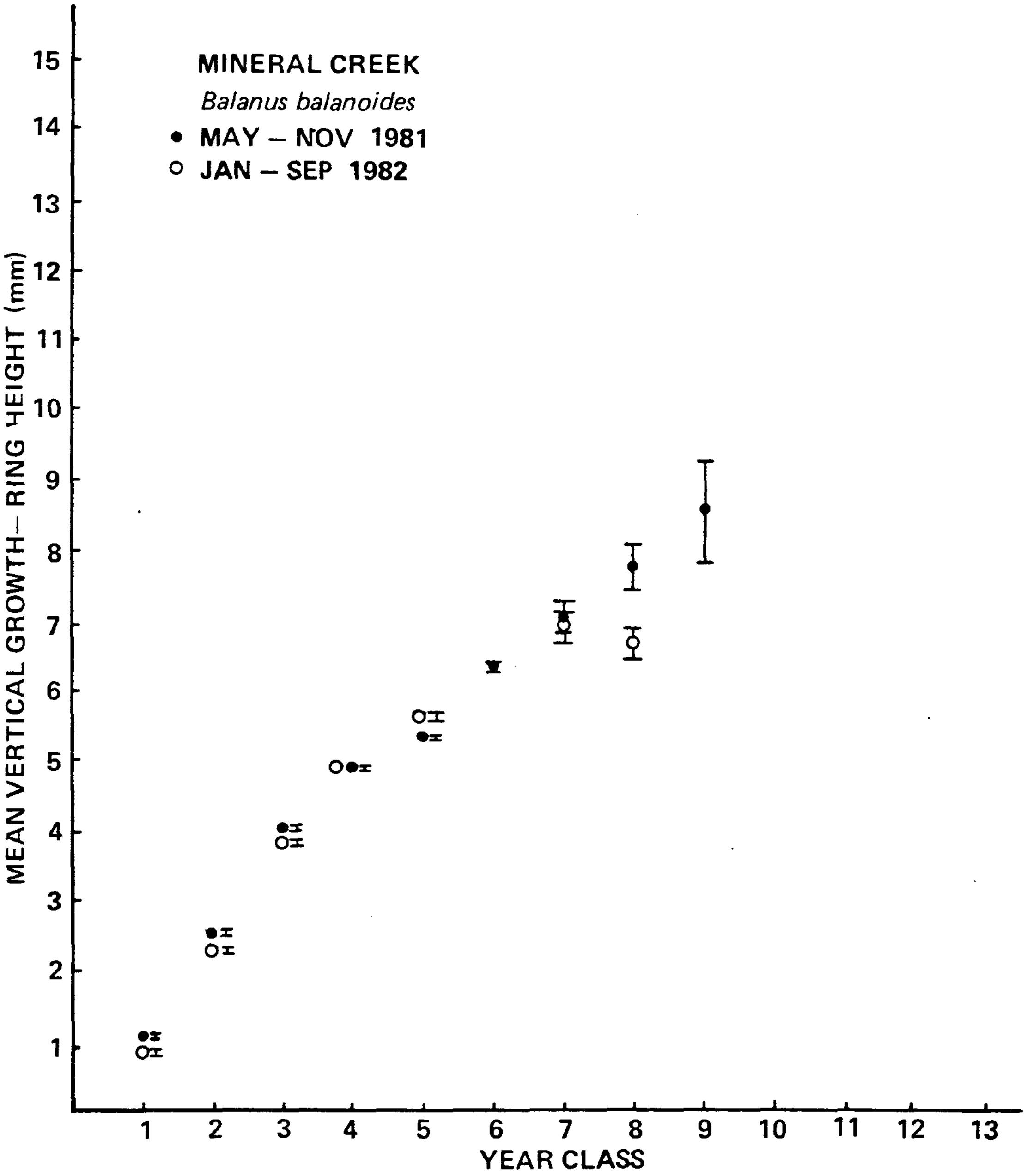

Figure 26. Growth curves for *Balanus balanoides* from the mid-zone of Mineral Creek, Port Valdez, Alaska, 1981 and 1982. Error bars represent standard error of the mean. Error bars located to the side of data points represent errors smaller than size of data points.

annual growth-ring increment values indicate that the rate of growth for barnacles at Sawmill Spit was generally greater than that for individuals at the other sites. The only exception was in the third year-class, in which case the rate of growth was less than that observed for barnacles of the same year-class at Mineral Creek (1.24 mm/year as compared with 1.54 mm/year). The reduced growth rate for the third year-class at Sawmill Spit in 1981 is probably another reflection of the problems encountered by barnacles here in 1979 (the year the third year-class was recruited). The few barnacles that survived the stresses present in 1979 may have been individuals in poor condition. These barnacles might be expected to have a reduced rate of growth relative to that expected for barnacles from Sawmill Spit. Growth rates (growth-ring increment values) for year-classes at Berth 4 and Mineral Creek varied between years. Significantly greater growth was observed for barnacles at Berth 4 in some years and for those at Mineral Creek in others, though growth was always reduced at both sites relative to Sawmill Spit (Table 12). Sawmill Spit barnacles grew at the rate of over 1.00 mm per year ($\bar{x}$ = 1.37 mm/yr) through their eleventh year, with the exception of the ninth year of growth. Berth 4 barnacles added over 1.00 mm of shell material yearly ($\bar{x}$ = 1.24 mm/yr) until age 6, at which time the growth rate decreased in comparison with barnacles from Sawmill Spit. At Mineral Creek, barnacles added greater than 1.00 mm of shell material yearly for only the first four years ($\bar{x}$ = 1.35 mm/yr). In subsequent years at Mineral Creek, vertical ring growth decreased to between 0.63 and 0.85 mm (note change in slope in Fig. 26). It is apparent that barnacles from each site grow at a relatively constant rate up to a particular age. The age at which the growth rate declines is variable between sites, and may reflect the differing stresses to which barnacles are subjected at the sites (i.e., Berth 4 to low levels of hydrocarbons and Mineral Creek to physical problems).

Annual vertical growth-ring increment data for 1982 (Table 13) indicate that barnacles at Sawmill Spit added more shell material yearly than those from Berth 4 or Mineral Creek, with the exception of the third and fourth year-classes. In addition, growth-ring height measurements were significantly greater ($\alpha = 0.05$) at Sawmill Spit with the exception of the fourth year-class (barnacles recruited in 1979). The growth value for this year-class, though significantly greater than that for Berth 4 barnacles of this age, was not statistically different from that observed for the fourth year-class at Mineral Creek. No obvious trends emerged when comparing growth data for Berth 4 and Mineral Creek.

The growth rates of barnacles in 1982 were similar to those of 1981, with Sawmill Spit barnacles generally displaying the greatest annual increments of growth. However, the amount of shell growth for barnacles at Sawmill Spit was somewhat reduced in 1982 from that observed in 1981 (Appendix 3, Table 2; Fig. 24). The exception was found in young, fast growing individuals of the second year-class. For older individuals, growth was less in any year-class in 1982 in comparison with 1981. The latter trend seems to suggest the absence of larger individuals from every year-class in 1982 and implies that these larger

Table 13. Annual shell growth for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, sampling period January-September 1982. Data are derived from a pooled sample of individuals from all year classes. For example, from Sawmill Spit, 548 barnacles were measured to obtain the first growth ring values. Since 80 individuals were only 1 year old, the second year of growth ring values were taken from the remaining individuals which were at least 2 years old, in this case, 468 barnacles. n = number of individuals measured, SD = standard deviation, SE = standard error of the mean (see Growth Methodology for growth measurement techniques).

Year Class	n	Mean Growth Ring Height (mm)	SD	SE	Range L	Range H	Annual Growth Ring Increment (mm)
Sawmill Spit, sample size = 548							
1	548	1.14	0.26	0.01	0.60	2.10	1.14
2	468	3.11	0.89	0.04	1.10	5.50	1.97
3	255	4.05	0.83	0.05	1.90	6.20	0.93
4	107	4.93	1.04	0.10	2.80	7.20	0.89
5	60	6.60	0.84	0.11	4.00	8.30	1.67
6	51	7.16	0.74	0.10	5.30	9.50	0.55
7	25	7.90	0.99	0.20	6.20	10.30	0.74
8	17	8.72	1.16	0.28	7.30	11.10	0.82
9	12	9.12	1.38	0.40	7.30	11.60	0.40
10	3	9.83	1.57	0.91	8.60	11.60	0.72

Table 13. Continued.

Year Class	n	Mean Growth Ring Height (mm)	SD	SE	Range L	Range H	Annual Growth Ring Increment (mm)
Berth 4, sample size = 540							
1	540	1.07	0.30	0.01	0.60	2.30	1.07
2	464	2.38	0.78	0.04	1.00	4.10	1.31
3	245	3.56	0.92	0.06	1.70	6.00	1.18
4	174	4.66	0.81	0.06	2.20	6.80	1.10
5	153	5.96	1.10	0.09	4.20	8.00	1.30
6	81	6.21	1.57	0.17	4.90	9.00	0.26
7	12	7.07	1.06	0.31	5.90	9.00	0.86
Mineral Creek, sample size = 574							
1	574	0.94	0.18	0.01	0.50	1.60	0.94
2	502	2.37	0.63	0.03	0.80	4.80	1.42
3	379	3.87	0.86	0.04	1.90	6.70	1.50
4	293	4.93	0.92	0.05	3.00	8.80	1.06
5	140	5.55	0.89	0.08	3.30	8.50	0.62
6	67	6.32	0.77	0.09	4.50	8.40	0.77
7	37	6.92	0.87	0.14	5.30	8.90	0.60
8	4	6.63	0.30	0.15	6.30	7.00	-0.30

individuals suffered a high rate of mortality during the months between the 1981 and 1982 samplings (see Mortality section for further discussion). Growth-ring height comparisons at Berth 4 and Mineral Creek, when significantly different from each other, were always greater in 1981 than in 1982 (Appendix 3, Table 2). This was especially noticeable for the first few growth rings at each site. Most likely, conditions promoting growth were better in 1981 than in 1982.

Growth-history tables for *Balanus balanoides* (Tables 14-16) were compiled by site from vertical growth-ring measurements of all barnacles collected from May-November 1981. Data contained in the growth-history tables, unlike the pooled data in Tables 12 and 13, are measurements of the growth rings of individual barnacles from each year-class. As observed for data in Table 12, Sawmill Spit barnacles displayed the greatest increments of annual growth as compared to the other sites, with the exception of low values in growth-ring height for the third year-class. These low values, in conjunction with the reduced numbers observed in the third year-class at Sawmill Spit (Table 10; Fig. 23, and discussion in section on Year-Class Composition) suggest that unusual circumstances influenced the population of barnacles at that site in 1979. As observed with the pooled growth data, no trend emerged from comparisons of growth for barnacles at Berth 4 and Mineral Creek. Growth was sometimes greater for individuals at Berth 4 and sometimes greater for those at Mineral Creek. The 1982 growth-history data (Tables 17-19) reflect trends dicussed above for the 1981 data.

Table 14. Growth-history table for *Balanus balanoides* from Sawmill Spit, Port Valdez, Alaska, sampling period May-November 1981.

Sawmill Spit **1981** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	GRH for Ring 8	GRH for Ring 9	GRH for Ring 10	GRH for Ring 11	GRH for Ring 12	GRH for Ring 13	Number in Year Class
1	1.43													107
2	1.27	3.57												224
3	0.90	2.33	4.12											12
4	1.22	2.85	4.59	6.44										21
5	1.12	2.61	3.92	5.59	7.42									136
6	1.15	2.75	4.77	5.90	6.95	8.44								69
7	1.13	2.69	4.43	6.21	7.27	8.07	9.01							30
8	1.21	2.79	4.51	6.15	7.76	9.05	9.81	10.66						31
9	1.36	2.68	4.25	5.87	7.44	8.96	9.81	10.55	11.12					11
10	1.36	3.18	4.54	5.94	7.88	9.18	11.10	11.88	12.16	12.54				5
11	1.60	3.10	4.65	5.85	7.45	9.50	11.45	13.10	13.55	14.10	15.25			2
12	+	+	+	+	+	+	+	+	+	+	+	+		0
13	1.30	2.60	5.50	6.90	7.30	8.50	9.90	11.20	12.40	13.10	13.20	13.70	14.61	1
	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
	YEAR OF GROWTH RING FORMATION													649

*GRH = GROWTH RING HEIGHT

+ = NO INDIVIDUALS IN 12th YEAR CLASS FOUND

Table 15. Growth-history table for *Balanus balanoides* from Berth 4, Port Valdez, Alaska, sampling period May-November 1981.

Berth 4 **1981** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	GRH for Ring 8	Number in Year Class
1	1.36								133
2	1.17	3.12							35
3	1.09	2.51	4.51						8
4	1.07	2.52	3.78	5.65					45
5	1.03	2.44	3.51	4.53	6.26				281
6	1.04	2.66	4.05	4.92	5.65	7.13			34
7	0.70	1.54	2.76	4.06	5.26	5.76	6.74		5
8	1.10	2.50	4.45	4.90	5.30	5.70	6.10	6.80	2
	1974	1975	1976	1977	1978	1979	1980	1981	Total
	YEAR OF GROWTH RING FORMATION								543

*GRH = GROWTH RING HEIGHT

Table 16. Growth-history table for *Balanus balanoides* from Mineral Creek, Port Valdez, Alaska, sampling period May-November 1981.

Mineral Creek **1981** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	GRH for Ring 8	GRH for Ring 9	Number in Year Class
1	0.99									123
2	1.03	3.23								116
3	1.19	2.88	4.87							349
4	0.95	1.99	3.68	5.38						281
5	0.96	2.26	3.23	4.21	5.47					199
6	1.03	2.30	4.12	4.87	5.43	6.27				64
7	0.94	2.10	3.40	5.18	5.86	6.42	6.96			25
8	1.03	2.18	3.43	4.77	6.13	6.56	7.03	7.74		15
9	1.17	2.68	3.43	4.25	5.63	7.13	7.60	7.90	8.52	4
	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
	YEAR OF GROWTH RING FORMATION									1176

*GRH = GROWTH RING HEIGHT

Table 17. Growth-history table for *Balanus balanoides* from Sawmill Spit, Port Valdez, Alaska, sampling period January-September 1982.

Sawmill Spit **1982** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	GRH for Ring 8	GRH for Ring 9	GRH for Ring 10	Number in Year Class
1	1.11										80
2	1.22	3.37									213
3	1.10	3.26	4.19								148
4	0.94	2.35	3.73	4.41							47
5	1.16	2.52	4.27	6.08	6.31						9
6	1.15	2.47	3.77	5.18	6.87	6.88					26
7	1.05	2.20	3.73	4.71	5.66	7.15	7.26				8
8	1.14	2.48	4.20	5.60	6.80	7.52	8.26	8.26			5
9	1.18	2.49	4.11	5.53	6.91	7.52	8.07	8.88	8.88		9
10	1.03	2.17	3.80	5.23	6.47	7.90	8.50	9.00	9.83	9.83	3
	1973	74	75	76	77	78	79	80	81	82	Total
	YEAR OF GROWTH RING FORMATION										548

*GRH = GROWTH RING HEIGHT

Table 18. Growth-history table for *Balanus balanoides* from Berth 4, Port Valdez, Alaska, sampling period January-September 1982.

Berth 4 **1982** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	Number in Year Class
1	0.95							76
2	1.18	2.14						219
3	1.00	2.94	3.49					71
4	0.95	2.10	3.25	4.54				21
5	0.98	2.48	3.64	4.66	5.82			72
6	1.06	2.53	3.57	4.67	6.14	6.41		69
7	1.03	2.52	3.98	4.80	5.71	6.85	7.07	12
	1976	77	78	79	80	81	82	Total
	YEAR OF GROWTH RING FORMATION							540

*GRH = GROWTH RING HEIGHT

Table 19. Growth-history table for *Balanus balanoides* from Mineral Creek, Port Valdez, Alaska, sampling period January-September 1982.

Mineral Creek **1982** ***Balanus balanoides***

Year Class	*GRH for Ring 1	GRH for Ring 2	GRH for Ring 3	GRH for Ring 4	GRH for Ring 5	GRH for Ring 6	GRH for Ring 7	GRH for Ring 8	Number in Year Class
1	0.83								72
2	0.98	2.59							123
3	0.99	2.53	4.16						86
4	0.96	2.36	4.13	5.25					153
5	0.93	2.07	3.48	4.82	5.59				73
6	0.96	2.10	3.30	4.35	5.74	6.28			30
7	0.92	2.08	3.36	4.32	5.36	6.41	7.00		33
8	0.92	2.15	3.38	4.38	4.98	5.85	6.33	6.63	4
	1975	76	77	78	79	80	81	82	Total
	YEAR OF GROWTH RING FORMATION								574

*GRH = GROWTH RING HEIGHT

Another method of assessing growth, although not as satisfactory for collected specimens brought into the laboratory, is through examination of year-class/rostro-carinal diameter (R/C) relationships. Year-class assessment and R/C diameter measurements for barnacles used in reproductive and energy partitioning studies from 1980-1982 are included for each site in Appendix 3, Table 3 and in Figure 27. Shell growth data (from R/C diameter measurements) indicate a similar pattern for barnacles from the three sites. During the first two years, growth appeared to be exponential at all sites. In contrast, data derived from measurements of vertical shell growth demonstrated a linear increase in growth each year throughout the life of the barnacle. Thus, during the early years of growth, young barnacles increase in diameter faster than they increase in height. This relationship between R/C diameter and vertical shell height explains differences observed in growth patterns when comparing measurements of height and diameter. By the third year, based on R/C diameter values, growth at every site was linear rather than exponential, probably as a result of metabolic changes which occur at the onset of maturity (Crisp, 1960). The size attained by the third and older year-classes was always greater for barnacles at Sawmill Spit than for those at either Berth 4 or Mineral Creek. The observation of larger barnacles at Sawmill Spit is in agreement with the trend resulting from assessment of vertical shell growth. Growth-increment data (expressing the rate of growth) indicate that after the first year, barnacles from Sawmill Spit added more shell material yearly than those from either Berth 4 or Mineral Creek (Fig. 27). The increment of

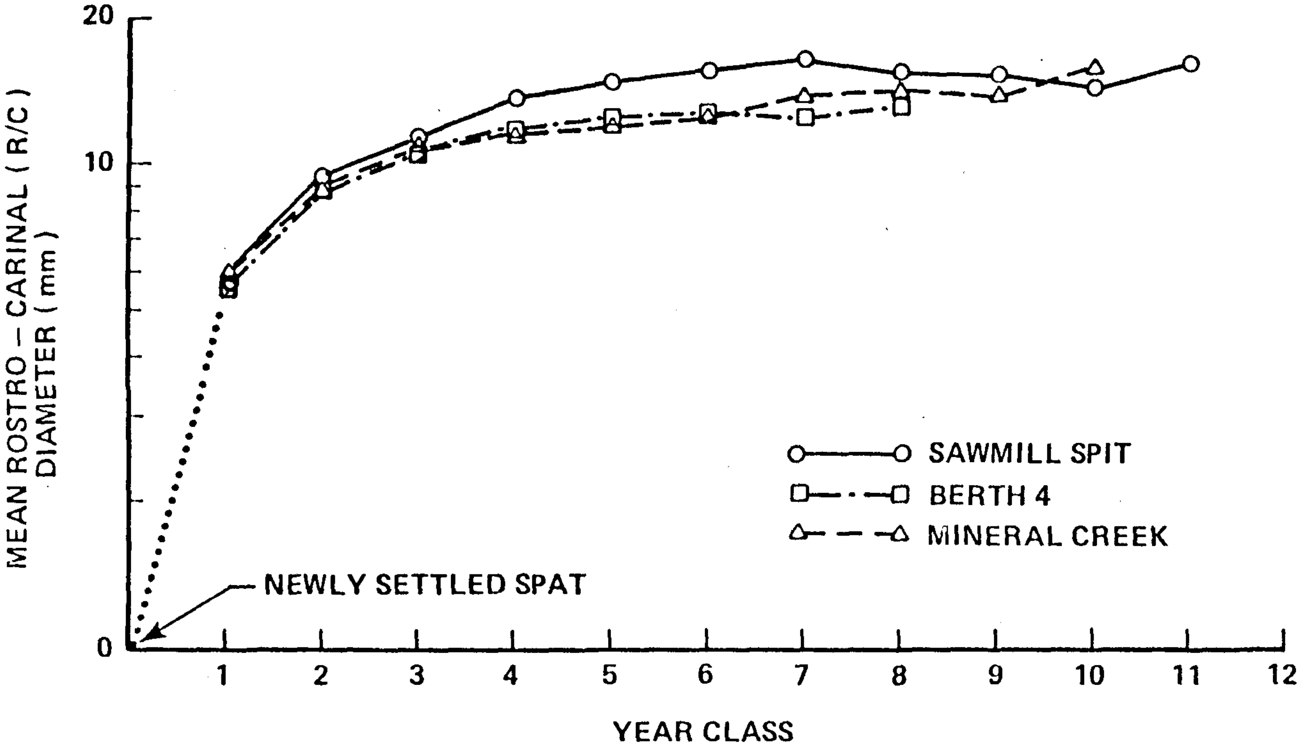

Figure 27. Growth curve for *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, based on measurements of R/C diameter per year-class.

growth generally decreased at the three sites in each successive year. Growth was similar for individuals at Berth 4 and Mineral Creek until the seventh year; subsequently, barnacles from Mineral Creek grew more rapidly.

Juveniles made up only a small percentage of the total number of barnacles collected at each site, since mature, reproducing adults were the only ones taken for the reproductive and energy partitioning studies (Appendix 3, Table 3). The year-class containing the most individuals at each site was the third year-class, followed by the fourth, second, and fifth year-classes. The reduced numbers in the third year-class at Sawmill Spit and Berth 4 for 1981 (as previously discussed in the Year-Class Composition section) were not observed for these particular individuals. The present assessment included data pooled from barnacles collected over the course of the study (1980-1982) and did not represent annual data. The oldest barnacle observed, a 14 year old, was collected from Sawmill Spit. Barnacles reached age 8 at Berth 4 and age 10 at Mineral Creek. The presence of older barnacles at Sawmill Spit (followed by Mineral Creek and Berth 4, respectively) reflects the trend observed for barnacles collected for growth-ring height analysis.

Seasonal Shell Growth

Seasonal shell growth data were obtained from barnacles collected in destructive samples. The period of major shell growth occurs in late spring or early summer, immediately following the spring diatom bloom, when food is readily available. In 1981, the major period of seasonal growth was missed, since growth assessment did not begin until May. Additional shell material was added between May and June at Berth 4 and Mineral Creek, and between June and July at Berth 4. No additional material, based on random observation was added at Sawmill Spit during the summer of 1981. In 1982, the largest monthly increment of new growth was recorded between the months of April and May. Adult barnacles at Sawmill Spit added the most shell material (1.08 mm) during this time, followed by those at Berth 4 (0.88 mm) and Mineral Creek (0.66 mm). No obvious increment was noted during the summer months of 1982, with an exception for Sawmill Spit barnacles from June to July, when approximately 0.25 mm of new shell material was added.

CONCLUSIONS

Annual growth data derived from vertical growth-ring measurements provided population age structure, annual growth patterns, growth-ring increments, and growth-history tables for barnacles at each study site.

The oldest individuals were observed at Sawmill Spit in both years sampled (13 years old in 1981, 10 years old in 1982). In comparison, Berth 4 barnacles reached a maximum age of 8 years in 1981 and 7 years in 1982 and were observed up to 9 years of age at Mineral Creek in 1981 and 8 years of age in 1982. Age structure data (Table 10 and Fig. 23) indicate that in 1981, greatly reduced numbers of 3 year old barnacles (recruited in 1979) were present at Sawmill Spit and Berth 4, less than 2% of the total population at either location. Also, a reduction in the abundance of 4 year olds at Sawmill Spit was revealed. The above trend may suggest unsuccessful reproductive efforts (reduced reproductive development, lowered fecundity, and subsequent settlement) or high mortality (juvenile or larval) on the southern side of the Port for these years. The trend observed in 1981 (reduced numbers of three-year-old barnacles at Berth 4 and three and four-year old barnacles at Sawmill Spit) was reflected in the lowered number of fourth year-class barnacles at Berth 4 and fourth and fifth year-class barnacles at Sawmill Spit in 1982 (Table 11). The observation of lowered numbers of individuals in the year-class originating in 1979 was further substantiated by the higher than typical mortality observed in Port Valdez for *Mytilus edulis* individuals of this same year-class (Feder *et al.*, 1983). Barnacles at Mineral Creek displayed year-class failure for two-year olds in 1981. The trend was observed in the following year for barnacles of the third year-class. The reduced abundance of individuals in this year-class (barnacles recruited in 1980) was presumably the result of problems encountered by newly settled juveniles (lowered salinity and heightened sedimentation).

Growth curves derived from 1981 data (Figs. 24, 25, and 26) identify a linear pattern of shell growth for barnacles at the three areas. Sawmill Spit barnacles generally displayed the greatest yearly increment of growth (Table 12) (with the exception of the third year-class), vertically adding > 1.00 mm of shell material until age 11. Berth 4 barnacles accumulated > 1.00 mm of shell material until age 6, at which time growth leveled off. At Mineral Creek, barnacles grew at a rate of

> 1.00 mm annually up to age 4, after which time growth decreased somewhat but continued until age 9. The differences in the annual increment of growth at the three sites is most likely a reflection of the varying conditions to which barnacles at each of the study sites are exposed. For example, barnacles from the control site, Sawmill Spit are subjected to few stresses, and subsequently grew at a constant rate for a longer period of time than those at other sites. Conversely, individuals at Mineral Creek are seasonally subjected to freshwater runoff and associated glacial sediments and those at Berth 4 to continual low-levels of hydrocarbons resulting from the proximity of the tanker berths. The apparent disturbance of these latter two areas is mirrored in the growth-increment data.

Growth data for 1982 indicate that more shell material was added by barnacles at Sawmill Spit during this year than by those at either Berth 4 or Mineral Creek, with the exception of the third and fourth year-classes (Table 13). The growth trends in 1982 are in general agreement with those observed for barnacles in 1981. However, a comparison of growth data for individuals at Sawmill Spit in 1981 and 1982 reveals that growth values in the latter year were reduced from those of the former year (Fig. 24). Larger individuals were missing from all year-classes in 1982, suggesting that these larger individuals suffered high mortalities during the months between the 1981 and 1982 samplings.

The data displayed in the growth-history tables (Tables 14-19), based on individual measurements for each year-class, substantiate the trends demonstrated by the pooled data. Thus, the greatest increments of growth occurred at the Sawmill Spit site, with the exception of the third year-class in 1981. The reduced growth in 3 year olds together with the previously discussed reduction in numbers in this year-class suggest that the population has experienced some type of disturbance. Smaller than typical growth increments were also observed in 1981 for the third year-class at Berth 4.

The growth results which emerged from the assessment of year class-R/C diameter data are similar to those observed from measurements of vertical growth-ring height (Fig. 27). After the first two years of apparent exponential growth (approximately the same for the three sites), barnacles at Sawmill Spit were larger in any year-class and added more shell material annually than individuals from Berth 4 or Mineral Creek. The barnacles from the latter two sites grew at the same rate until the seventh year, at which time those from Mineral Creek possessed the greater increment of growth.

It is obvious from growth trends discussed above that barnacles from Sawmill Spit grow for a longer period of time and to a larger size than those from either Berth 4 or Mineral Creek. Apparently, conditions governing growth are better at Sawmill Spit than at the other two, somewhat disturbed sites. Barnacles from the latter sites are exposed to a poorer set of living conditions than those from Sawmill Spit (i.e., possible hydrocarbon contamination at Berth 4 and physical stress at Mineral Creek) and the organisms reflect via their growth patterns the difficulties encountered at these sites.

ENERGY PARTITIONING

INTRODUCTION

Annual events in the life history of *Balanus balanoides*, such as formation of reproductive tissue and addition of shell material, are dependent on energy stored in the somatic tissue during a few critical weeks in the spring and fall, the periods of primary productivity. This stored energy is slowly allocated to the mantle and gametogenic tissues for eventual utilization in growth and reproductive processes. Based on an understanding of seasonal ovarian dry-weight fluctuations and shell growth increments, the period of maximal partitioning of energy from somatic to reproductive and mantle tissues can be identified. The development of a total energy budget (identification of the carbon requirements for each biological process) is not possible from the available data. (See Wu and Levings, 1978, for the methodology utilized in the energy budget determination of the intertidal barnacle, *B. glandula*). However, an estimate of temporal energy expenditure to reproductive tissue development and shell growth is obtainable.

A fluctuation in the weight of somatic tissue occurs throughout the year as the result of periodic demands on food reserves stored here (Barnes *et al.*, 1963). Since change in somatic weight is predictable (Barnes *et al.*, 1963; Rucker *in* Feder *et al.*, 1983), any significant variation from this expected trend could indicate environmental stress on a barnacle population. For example, a decrease in body weight is expected subsequent to the spring phytoplankton bloom. Failure for this decrease to occur suggests a delay in the allocation of energy to other tissues. This delay or blocking of energy transfer may reflect unusual environmental conditions at the time.

METHODS

The specimens collected for age-size determinations and studies of reproductive biology were also used in the energy partitioning studies (see Reproductive Biology methodology). The methods utilized are similar to those of Barnes *et al.* (1963). The body of each animal was removed from the shell plates and separated from the ovarian tissue or the lamellae (Fig. 3). The tissues were dried until weight loss was negligible (24 hrs in a 60°C oven). Opercular valves were separated from the plates and boiled for 30 minutes in test tubes containing 10% KOH to insure removal of adhering muscle tissue. After a rinse in distilled water, the valves were dried until no further weight loss was recorded (24 hrs, 60°C). If dried material could not be weighed immediately, it was stored in a desiccator until weights could be taken.

Values for valve weight and body weight were utilized to examine the month-to-month fluctuation in dry body weight per 20 mg valve weight (Barnes *et al.*, 1963). Changes in the weight of the body (representing energy utilization) were plotted through time for a typical adult barnacle with a standard shell size.

A one-way random-effects model of the analysis of variance (ANOVA) (Zar, 1974) was utilized to test the following null hypothesis (H_o): no difference exists between the weight of somatic (body) tissue in a given month for barnacles from Sawmill Spit, Berth 4, and Mineral Creek. A critical F value was determined for the null hypothesis and compared with tabled values of F at the 95 and 99% confidence levels to test the validity of the null hypothesis.

A second approach for assessment of energy flux was considered as well. Dry valve weight was utilized as the independent variable for plots which illustrate changes in time relative to a dependent variable, dry body weight. This approach is useful, since monthly fluctuations in dry body weight, as related to feeding, partitioning of energy to reproductive and growth processes, spermatogenesis, and fertilization can be readily identified. Valve weight is a suitable variable in this type of relationship, since the monthly increase in valve weight is small in comparison with the weight change occurring each month in somatic tissue.

Slopes (A) and y-intercepts (B) were calculated for linear regressions of body weight vs. valve weight by use of the following equations:

$$A = \frac{n\Sigma xy - \Sigma x\Sigma y}{n\Sigma x^2 - (\Sigma x)^2}$$

$$B = \frac{\Sigma y\Sigma x^2 - \Sigma x\Sigma xy}{n\Sigma x^2 - (\Sigma x)^2}$$

A correlation coefficient was calculated for each regression in order to determine the closeness of fit of the data points to a linear relationship. An analysis of covariance (ANOCOVA) (Zar, 1974) was utilized to test the following null hypothesis (H_o): no difference exists between the slopes of linear regressions illustrating body weight vs. valve weight in a given month for barnacles from Sawmill Spit, Berth 4, and Mineral Creek. A critical F value was determined for the null hypothesis and compared with tabled values of F at the 95% confidence level to test the validity of the null hypothesis.

The relationships discussed above were utilized for barnacles from Sawmill Spit, Berth 4, and Mineral Creek, to identify energy partitioning patterns of the organisms at the three areas on a temporal basis. The method of determining the pattern of somatic tissue fluctuation based on a barnacle of 20 mg valve weight is discussed first, followed by results of linear regression analysis of body weight changes with time.

By comparing the dry ovarian weight of barnacles to the dry body (somatic) tissue weight, a value representing the Reproductive Effort Index (REI) was obtained. The REI, $\frac{\text{dry ovarian weight}}{\text{dry body weight}}$ (modified from Hines, 1979) gives roughly the allocation of energy to egg production, thus, approximates the reproductive component of the total energy budget for *Balanus balanoides*.

Seasonal shell growth-increment data are useful for the identification of periods of maximum energy transfer from somatic tissue to the mantle. Seasonal shell growth increments were determined by measuring the new shell material formed below the last detectable winter disturbance ring. Increments included in the following discussion were determined only for adult barnacles due to the problems encountered in attempting to collect and successfully measure fragile, young barnacles.

RESULTS-DISCUSSION

Annual Patterns of Energy Partitioning

Dry somatic (body) tissue weight (mg body weight per 20 mg valve weight) for *Balanus balanoides* was plotted from two and a half years of data (April 1980-November 1982) for each sampling area in Port Valdez. Figures 28 and 29 illustrate annual fluctuations in body weight and suggest patterns of energy partitioning by the barnacle. A general description of the expected annual changes in body weight, as reflected by energy storage and allocation follows. Body weight was highest in the month of April as a result of assimilation of organic material during the spring phytoplankton bloom. In the early summer, ovarian tissue began to develop (Fig. 6) and shell growth was initiated. Subsequently, a sharp decline in body weight was observed, and persisted until late July or early August. During the latter period, a time of reduced food abundance, energy was channeled from the body to the developing ovary and to the mantle. In August or September, body weight increased as a result of spermatogenesis within the prosoma (body). It was not possible to separate male gametogenic tissue from the prosoma. Following sperm formation in late August to early or mid September, fertilization and a corresponding loss of body weight occurred. Throughout the winter (late October-February) food was greatly reduced in the water column (see Hood *et al.*, 1973, for a general discussion on the seasonal cycle of primary productivity), body weight remained relatively constant, and virtually no shell accretion occurred. Fertilized eggs were brooded as lamellae in the mantle cavity during the latter period.

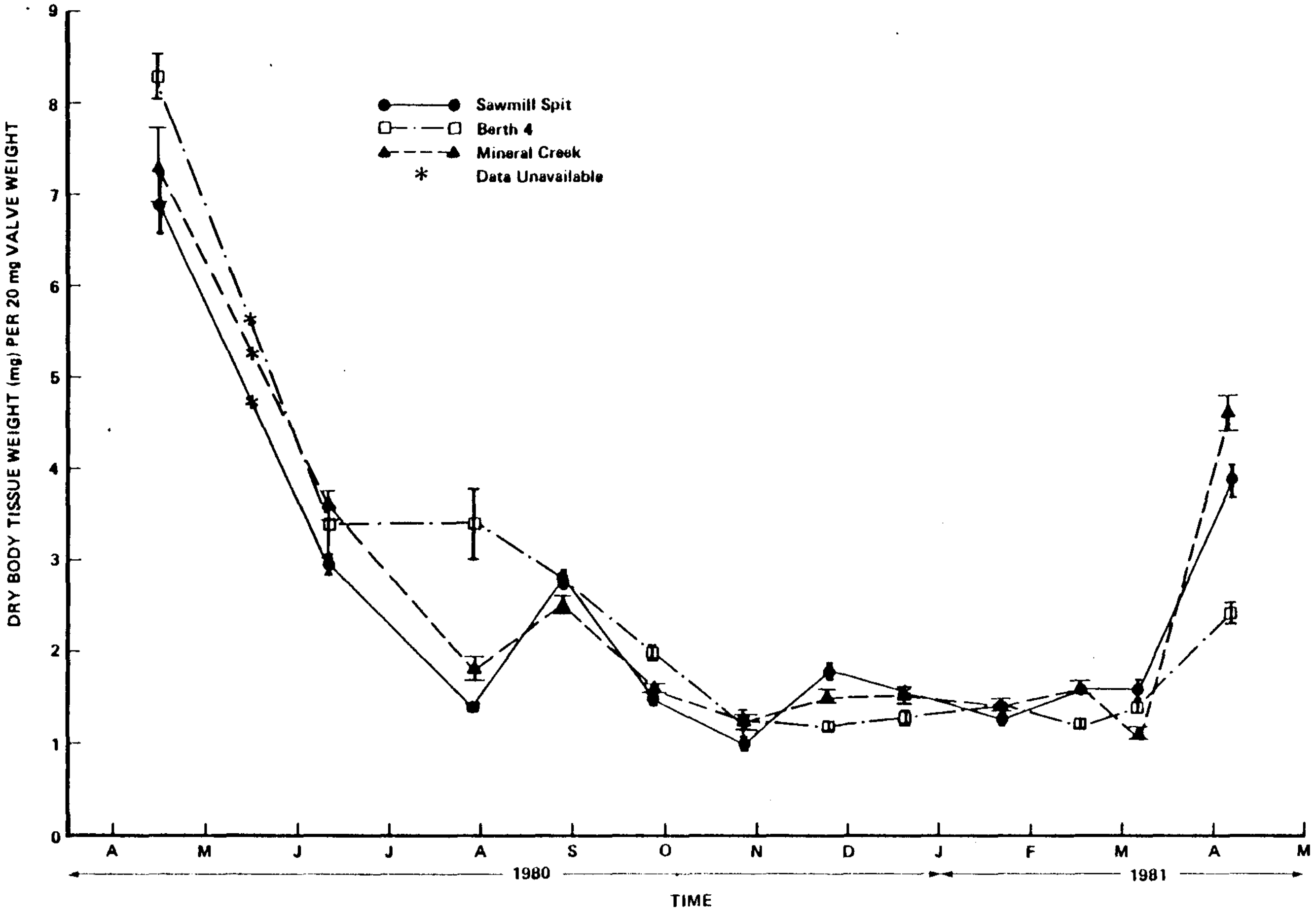

Figure 28. Annual fluctuations in dry body tissue weight (mg) per 20 mg valve weight for *Balanus balanoides* from the mid zone of Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1981. Error bars represent standard error of the mean.

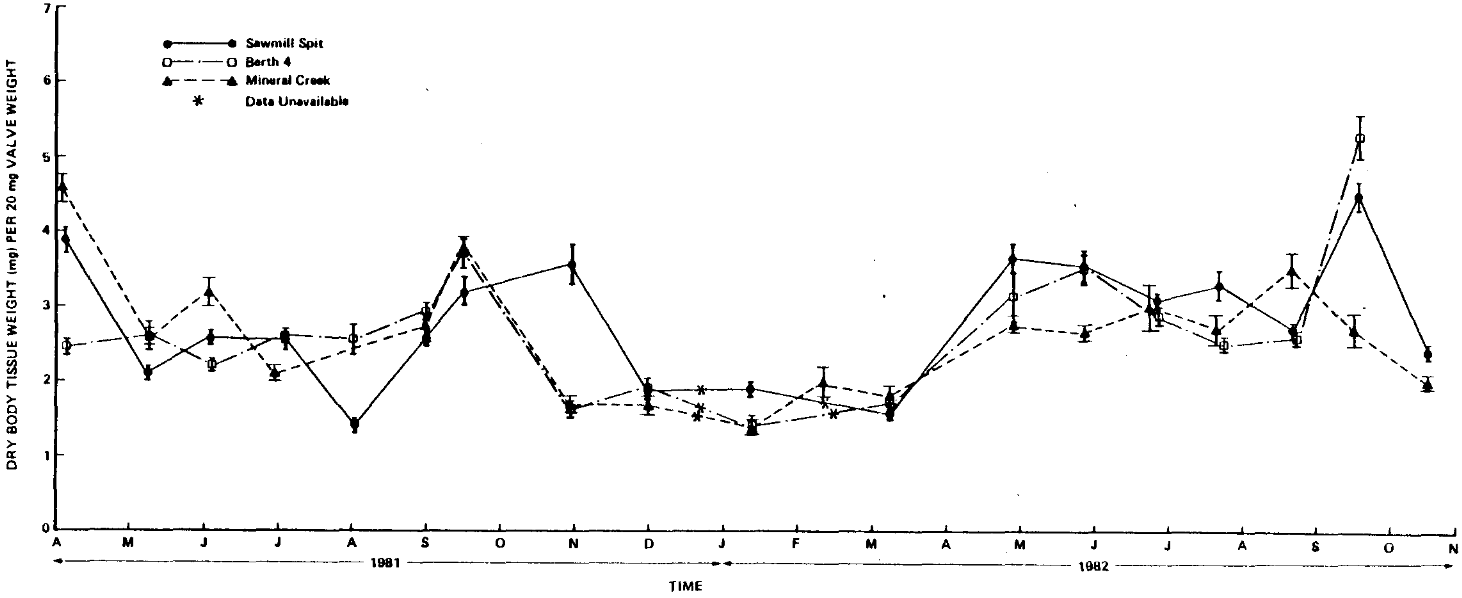

Figure 29. Annual fluctuations in dry body tissue weight (mg) per 20 mg valve weight for *Balanus balanoides* from the mid zone of Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1981-October 1982. Error bars represent standard error of the mean.

As observed from the above, annual fluctuations in body weight are related to other biological processes (especially ovarian tissue development and shell growth) that occur within the barnacle from spring until early fall. Wu and Levings (1978), working with a related species, *B. glandula*, estimated that the barnacle annually partitions 12.3% of its energy to egg production and 6.6% to new shell growth. Other processes together make up a smaller percentage of the energy needs of a barnacle, 3.9% for body tissue production, 2.3% for molting, and 7.5% for fecal pellet production. Respiration accounts for 67.4% of the annual utilization of energy (52.9% for aquatic respiration and 14.5% for aerial respiration).

In general, the annual pattern of fluctuation in weight was similar for barnacles at all sampling sites during 1980-81 (Fig. 28). One substantial difference, however, was observed. The body weight of barnacles at Berth 4 was significantly higher ($\alpha = 0.05, 0.01$) in July 1980 than the corresponding weight for individuals at either Sawmill Spit or Mineral Creek (Appendix 4, Table 1) which suggests that these barnacles were not shunting energy from somatic tissue to the same degree as individuals at the other two sites. Body weight was high for barnacles at all sites in April 1980 (Fig. 28). The latter observation eliminates the possibility of a lag in energy transfer at Berth 4 as a result of the unavailability of food in the waters of the area during the spring phytoplankton bloom. Most likely, enough carbon was stored by the Berth 4 barnacles during the bloom, but was allocated more slowly here than at Sawmill Spit or Mineral Creek. It is possible that conditions of stress at Berth 4 during the spring of 1980 interfered with transfer of energy to ovarian tissue. The above delay is substantiated by the fact that ovarian tissue weighed less at Berth 4 than at Sawmill Spit or Mineral Creek during the same period (July 1980) (Fig. 6) and continued to weigh less until spawning occurred in March 1981 (Appendix 4, Table 1; see also discussion in Reproductive Biology section). Body tissue weight at Berth 4 in subsequent months (after July 1980) again followed the general fluctuating pattern noted for Sawmill Spit and Mineral Creek barnacles (Fig. 28).

A few other differences were observed between the sites during 1980-81. The weight of somatic tissue for barnacles at Berth 4 in April 1980 was significantly greater than that of individuals from Sawmill Spit (Appendix 4, Table 1). The above either implies that barnacles from Berth 4 stored greater amounts of organic material during the bloom or that barnacles from Sawmill Spit had already partitioned energy for growth and reproductive processes. In September 1980, the weight of barnacles at Berth 4 remained significantly higher than corresponding weights at the other two sites, which possibly suggests a delay in ovarian development and the subsequent fertilization process at this site (Appendix 4, Table 1).

The various anomalies in the Berth 4 data seem to reflect the effects of a small oil spill (April 1980) on the barnacle population at Berth 4, which was located adjacent to the spill site.

The basic pattern of energy flux, as described above, was followed during the 1981-82 developmental period and in 1982 following the spring bloom (Fig. 29). However, differences from the 1980-81 fluctuating body-weight cycle were observed and are discussed in the following. A reduced increment in body weight for barnacles at Berth 4 occurred in April 1981 in comparison with that observed at Sawmill Spit or Mineral Creek (significant at $\alpha = 0.05, 0.01$; Appendix 4, Table 1). Although somatic tissue weight dropped significantly at Sawmill Spit and Mineral Creek in May 1981, the body weight of barnacles at Berth 4 remained virtually the same as the preceding month, and was significantly greater than for barnacles at Sawmill Spit ($\alpha = 0.05$) (Appendix 4, Table 1). By June, somatic tissue weight at Berth 4 had dropped slightly. However, during the latter period, a second increase in body weight was observed at Sawmill Spit and Mineral Creek. The weight increase may indicate that an additional food supply was available at these areas. The body-weight increase in early summer for barnacles at Sawmill Spit and Mineral Creek was not observed for barnacles at Berth 4 until the next month (July) which suggests a lag in the pattern at the latter site. By July 1981, body weight was again decreasing at Mineral Creek, suggesting transfer of additional material for growth and reproduction. Somatic weight had dropped at Sawmill Spit by August. No further decrease in weight was observed at Berth 4 subsequent to the slight June decline. A gradual increase in weight occurred at all sites in late summer due to spermatogenesis. By late October, following fertilization, body tissue weight at Berth 4 and Mineral Creek had decreased to a weight of $\sim$ 2.0 mg which is typical during the winter months. Body tissue weight remained high at Sawmill Spit until November (significantly higher than other sites, $\alpha = 0.05, 0.01$) (Appendix 4, Table 1). The delayed weight loss here implies postponement of fertilization, possibly a result of prolonged feeding activity, as suggested by Crisp (1959). Throughout the winter, somatic tissue weights remained low, but again rose characteristically in April 1982, following the spring bloom. By May, Sawmill Spit and Mineral Creek barnacles were beginning to partition energy to ovarian and mantle tissues, as supported by loss in somatic weight at this time. Berth 4 barnacles continued to increase in weight through May (as in May 1981), however, their weight decreased in June, as did that of barnacles at the other two sites. In June, no difference in somatic weight was noted between sites (Appendix 4, Table 1). Ovarian weight for Berth 4 barnacles was observed to increase substantially in June 1982 as well, suggesting that energy transfer was now taking place.

Based on two and a half years of data, it appears that, in general, Berth 4 barnacles lag in their body-weight cycle more often than do the barnacles from the other sites. In 1980, 1981, and 1982, following the spring bloom, a delay in loss of somatic-tissue weight occurred at Berth 4, suggesting either an insufficient storage of available energy for shunting to needed areas or an interference with the transfer process. However, once spermatogenesis and subsequent fertilization had occurred (1980-82), Berth 4 barnacles followed the same basic pattern as that observed for barnacles from Sawmill Spit and Mineral Creek.

An alternate way to examine patterns of somatic tissue weight fluctuation is via linear regression analysis, which compares dry body weight to dry valve weight monthly. Samples collected at the three sampling sites from April 1980-April 1981 provided somatic tissue and valve weight data for the regressions (Figs. 30-32). Regression lines above 5 mg valve weight appear to be linear for the three areas at all times of year. Although data are unavailable for barnacles below approximately 5 mg valve weight, the curves representing these data could be better explained exponentially, since barnacles of these lesser weights represent young, rapid growing juveniles. These juveniles have neither reached maturity nor attained a reduction in their metabolic rate (Crisp, 1960). The latter behavior is reflected by data in curves depicting the growth rate as exponential rather than linear (Figure 27 and Discussion in section on Annual Shell Growth).

The slope, correlation coefficient, and y-intercept for each regression are included in Table 20. The slope values representing the regression lines reflect monthly changes in the extent of energy allocation by barnacles. The changes in slope observed in Figures 30-32 are related to the occurrence of events in the life history of *B. balanoides*. At all sites, the slopes of the regressions representing the April 1980 data were greater than for any of the other months examined, and indicate that body weight at any given valve weight was greater in April than in the other months sampled. Thus, as previously observed (Figs. 28 and 29), the amount of energy stored in the somatic tissue of *B. balanoides* was highest in April, immediately following the spring bloom and prior to the transfer of energy to gametogenic and/or mantle tissue. The slope values in June 1980 (Table 20) were lower at Sawmill

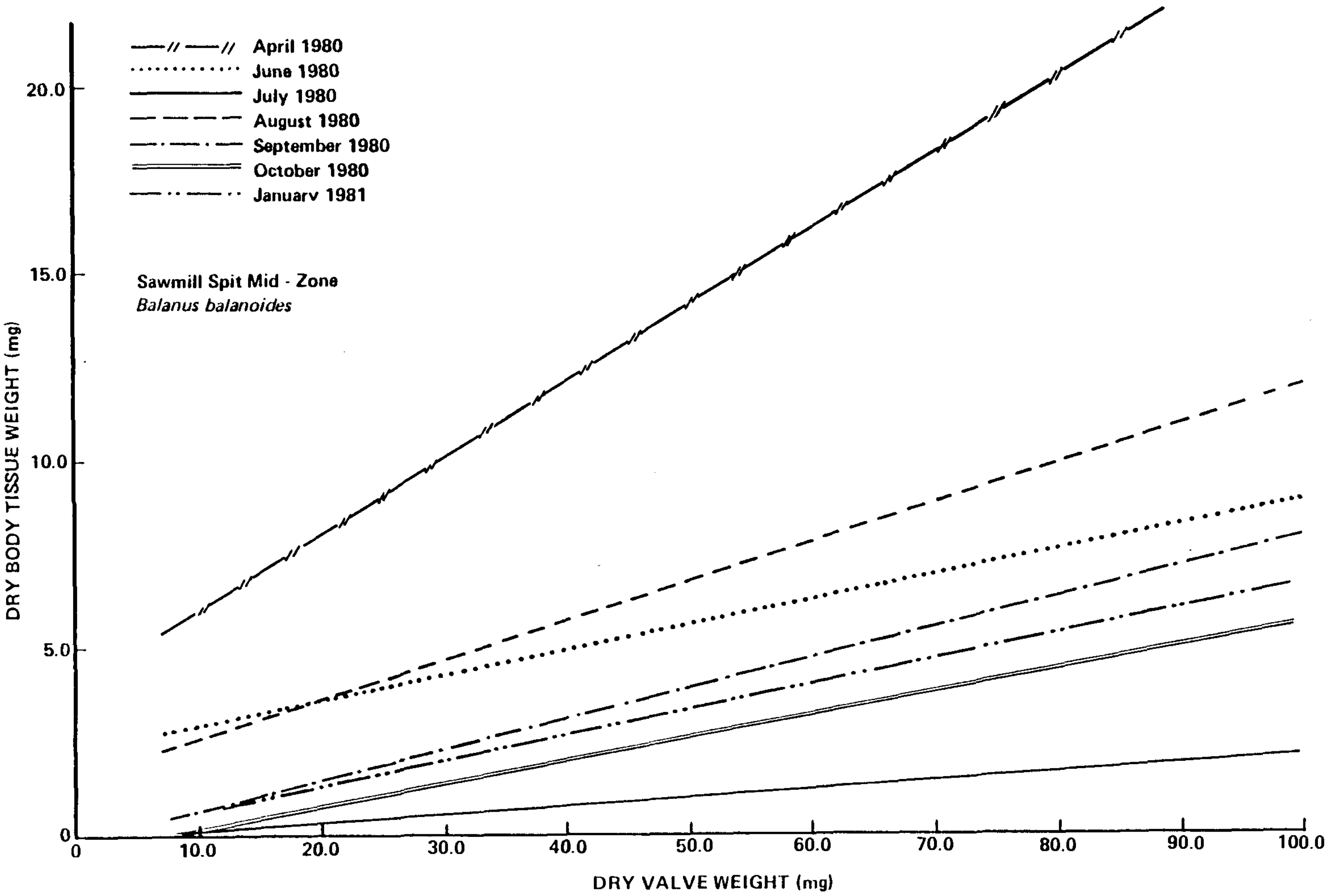

Figure 30. Dry body (somatic) tissue weight fluctuations of *Balanus balanoides* from the mid zone of Sawmill Spit, April 1980-January 1981.

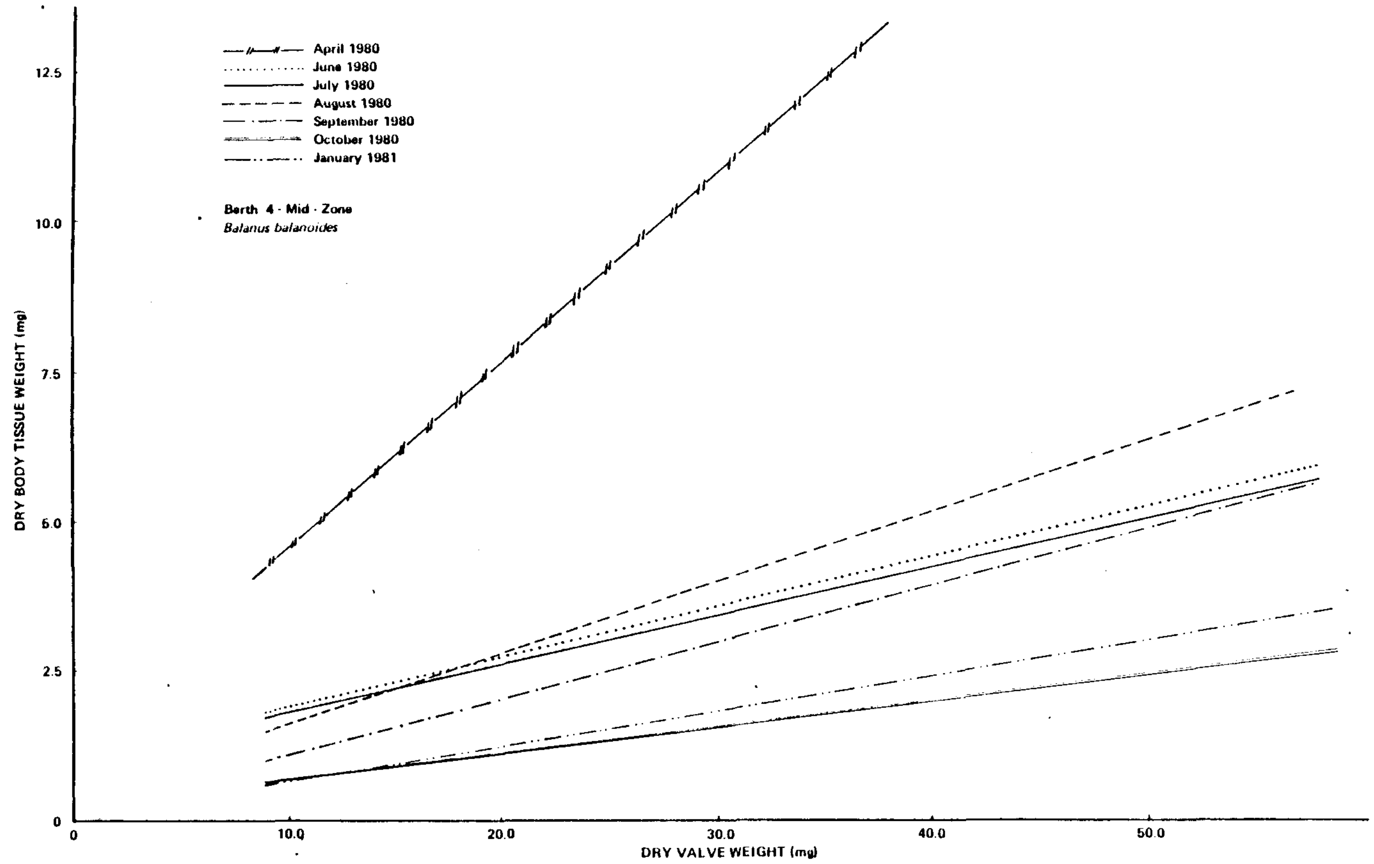

Figure 31. Dry body (somatic) tissue weight fluctuations of *Balanus balanoides* from the mid zone of Berth 4, April 1980-January 1981.

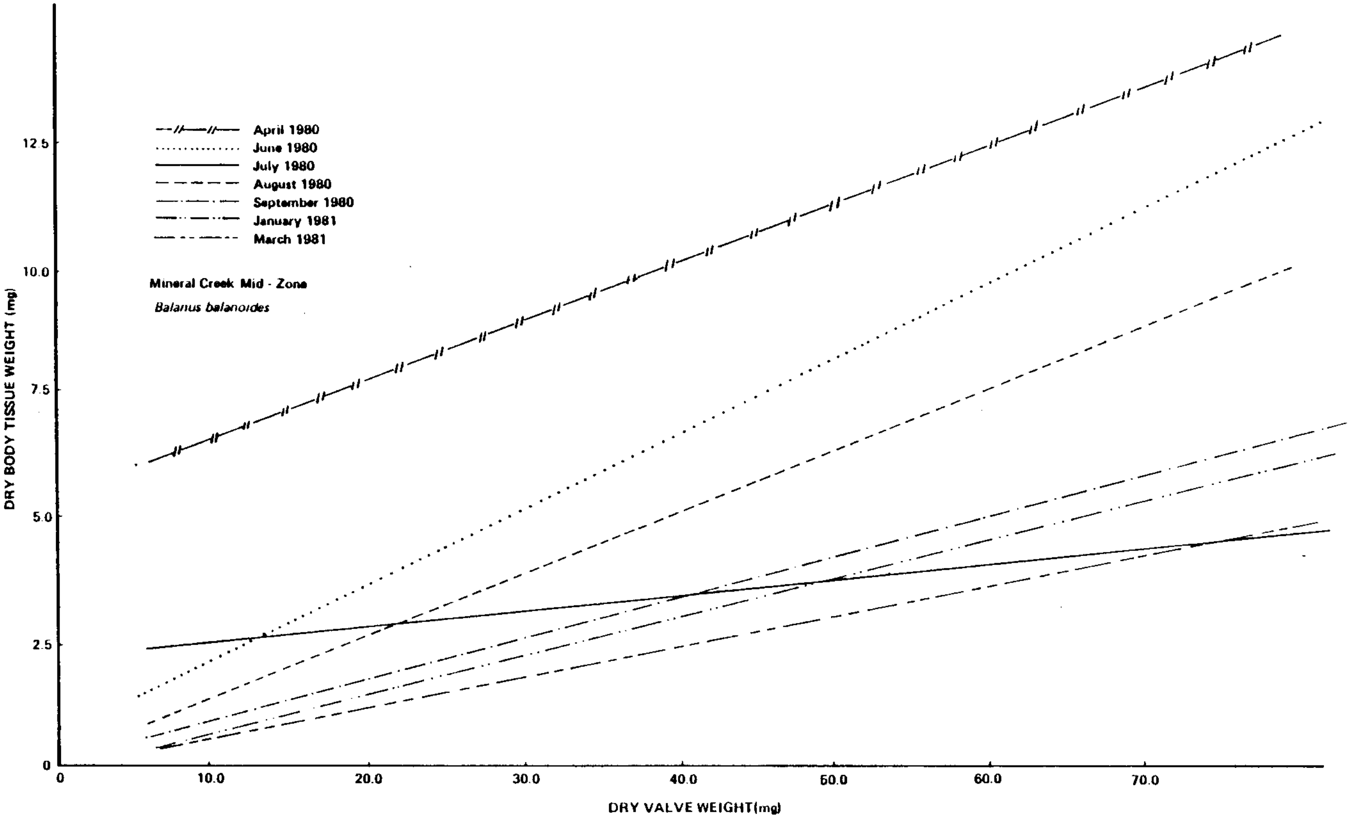

Figure 32. Dry body (somatic) tissue weight fluctuations of *Balanus balanoides* from the mid zone of Mineral Creek, April 1980-March 1981.

Table 20. Energy partitioning values (slope) correlation coefficients (C.Co.) and Y-intercepts for *Balanus balanoides* from the mid-zone of Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1981.

Sawmill Spit				Berth 4				Mineral Creek			
Date	Slope	C.Co.	Y-int.	Date	Slope	C.Co.	Y-int.	Date	Slope	C.Co.	Y-int.
15 Apr 80	0.203	0.799	3.955	16 Apr 80	0.309	0.856	1.370	18 Apr 80	0.157	0.588	4.827
11 Jun 80	0.066	0.730	2.244	12 Jun 80	0.078	0.614	1.099	13 Jun 80	0.149	0.890	0.566
29 Jul 80	0.071	0.890	-0.046	29 Jul 80	0.074	0.751	0.968	30 Jul 80	0.033	0.279	2.092
28 Aug 80	0.103	0.674	1.554	28 Aug 80	0.113	0.640	0.414	29 Aug 80	0.124	0.849	0.029
25 Sep 80	0.080	0.759	-0.106	25 Sep 80	0.085	0.726	0.256	24 Sep 80	0.080	0.863	0.055
25 Oct 80	0.059	0.756	-0.381	27 Oct 80	0.091	0.577	-0.478	18 Jan 81	0.080	0.974	-0.084
20 Jan 81	0.066	0.954	-0.001	19 Jan 81	0.064	0.837	0.103	4 Mar 81	0.062	0.760	-0.169
3 Apr 81	0.231	0.747	-1.297	4 Apr 81	0.141	0.867	-0.327	2 Apr 81	0.172	0.874	1.305

Spit and Berth 4 than they were in April. The slope of the regression for the Mineral Creek data in June 1980, although having a significantly higher value than for Sawmill Spit and Berth 4 (Appendix 4, Table 2), was lower than the April slope at this site as well. The reduction in slope for the regressions at all sites suggests allocation of energy from body storage areas to gametogenic tissue and to mantle tissue. In July, the slope value representing the data at Sawmill Spit was slightly higher than in June (Appendix 4, Table 3). However, the y-intercept was much lower. Figure 30 illustrates the decrease in weight of somatic tissue from June to July. The slope of the July regression at Berth 4 (Fig. 31) was not significantly different than that in June (Appendix 4, Table 3), suggesting a temporal lag in transfer of energy to mantle and ovarian tissues. This agrees with previously discussed results obtained by examining body weight through time (Fig. 28). By July, the slope value had dropped significantly at Mineral Creek (Appendix 4, Table 3), once again reflecting the shunting of energy from body tissues to other areas (Fig. 32). In August 1980, the slopes increased somewhat, reflecting formation and storage of spermatozoa within body tissues (prosoma). A decrease in slope of the regression lines for the three sites was observed in September 1980, at which time gametes were released, body tissue weight decreased, and fertilization occurred. During the winter, little food was available and the weight of somatic tissue remained low. This is reflected by the low slope values at each site. Following the spring bloom in April 1981, somatic tissue weight was once again increasing, as indicated by higher slope values (Table 20), due to the assimilation of organic matter derived from the phytoplankton bloom.

Figure 30 compares dry body weight-dry valve weight relationships between the three sites in the months of April, June, and August 1980, and January 1981. In April, the slope of the Berth 4 regression was highest in comparison to the other sites (Appendix 4, Table 2). However, the Sawmill Spit and Mineral Creek regressions extended to include larger individuals (see Growth discussion for further information on size). In June 1980, the Sawmill Spit and Berth 4 slopes were significantly lowered, which indicates that body-weight loss via energy partitioning to reproductive and mantle tissues had occurred. Mineral Creek barnacles, though maintaining a higher dry body weight per valve weight than barnacles at the other sites (suggesting a delay in energy channeling) (Appendix 4, Table 2), weighed less than they did in April (Fig. 32). By August, the slopes of all regressions were nearly identical (Appendix 4, Table 2), although the body-weight values per valve weight for Sawmill Spit barnacles were slightly greater than those for the other two sites. In comparison to the June values, slopes for regressions at all three sites were greater in August, and reflected body weight gain due to spermatogenesis. The values for barnacles at all sites were low in January 1981.

An important observation emerged from the above discussed slope comparisons between sites. The barnacles collected at Berth 4 (Figs. 31 and 33) never included individuals with valve weights much greater than 50 mg. However, at Sawmill Spit and Mineral Creek, barnacles of

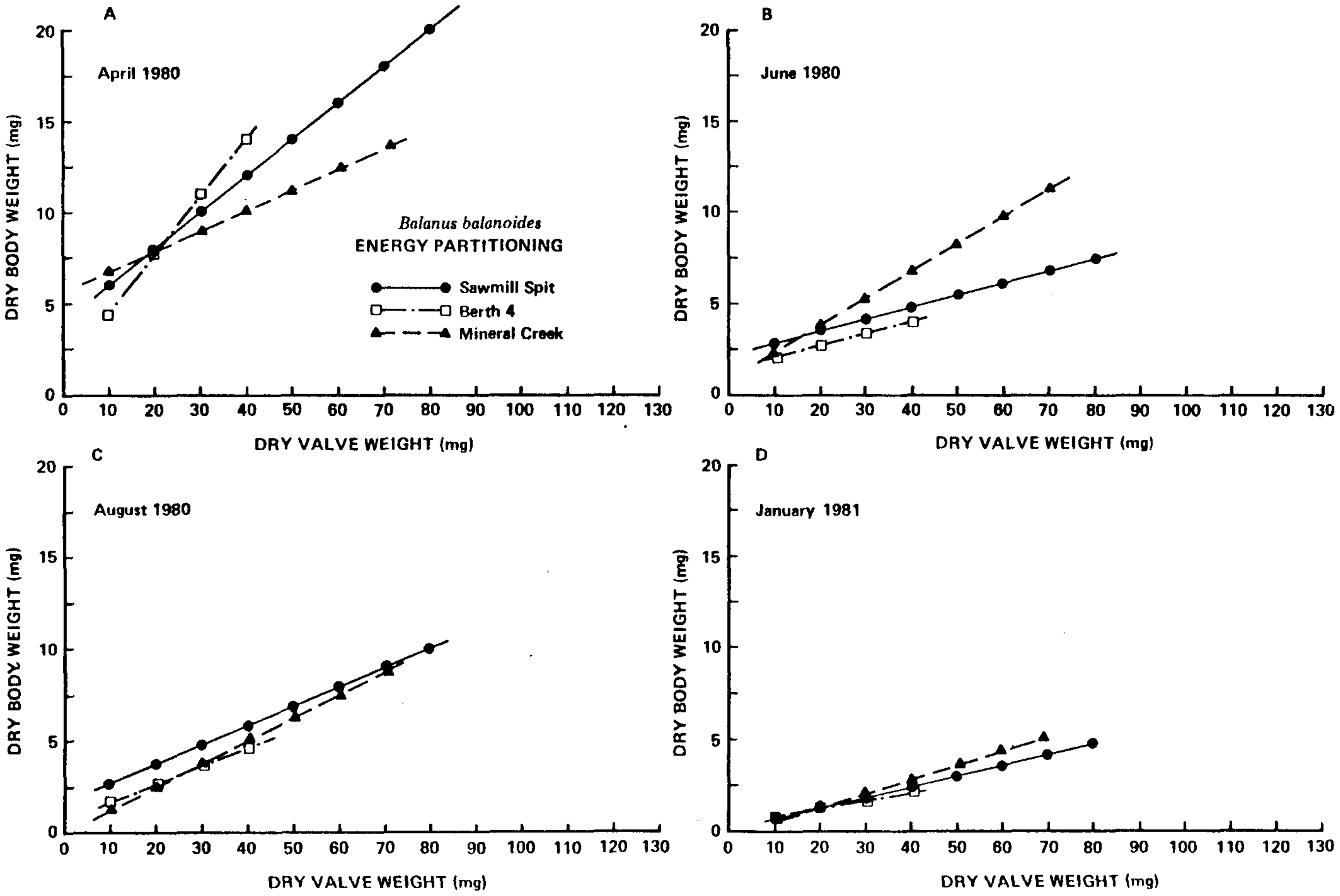

Figure 33. Comparisons of regression slope values (representing body or somatic tissue weight relative to valve weight) for mid zone samples of *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April, June, and August 1980 and January 1981.

at least 70 mg valve weight were represented in each regression and at times valve weights up to 100 mg were observed. The body-tissue weights at Sawmill Spit and Mineral Creek were often greater than at Berth 4 as well, implying that barnacles at the former two sites were typically larger than those at Berth 4. The size differences discussed above, as those which emerged from the shell-growth studies, indicate that the largest barnacles were observed at Sawmill Spit. The trend for larger individuals at Mineral Creek relative to Berth 4 was not obvious from shell-growth data.

Energy Partitioning and Reproduction

By observing monthly changes in the weight of reproductive and somatics tissues, assessment of the pattern and extent of energy transfer in *Balanus balanoides* throughout the year can be made. The increase in ovarian weight observed through June (Figs. 6 and 7 in Reproductive Biology section) reflected stored energy made available to the ovarian tissue by partitioning from body tissues. Throughout the early months of the summer, female gametogenic tissue developed and became more compact and dense. The development was reflected by the weight increment of the tissue during this period. A decrease in ovarian weight occurred in July and suggested internal redistribution of energy from the female gonadal material. During this period, food in the water column was greatly reduced. Since barnacles require additional energy for shell growth, somatic growth, and sperm production in July, energy may have been transferred from ovarian tissue to required areas.

Ovarian tissue is higher in caloric content than somatic tissue (Wu and Levings, 1978) and may have been the best potential source of energy for the additional metabolic needs. A second weight gain that occurred between August and October may be due to storage of additional material acquired through a fall phytoplankton bloom (Hood *et al.*, 1973). Data to substantiate this occurrence, however, were not available from the present study. A second weight loss occurred following fertilization, since spermatozoa, stored in seminal vesicles within the prosoma were expelled during copulation. During the incubation period, lasting until spawning in February or March, yolk of the fertilized eggs was utilized by developing embryos, and accounted for the decrease in lamellar weight. The weight gain observed in the embryos in winter, prior to spawning, has not been previously described. The increase in weight cannot be explained by energy partitioning from somatic tissue, since no metabolic exchange between parents and embryos occurs subsequent to fertilization (Barnes and Achituv, 1976). The possibility of uptake of dissolved organic carbon (DOC) from the surrounding water by embryos could contribute to the greater weight values recorded for the lamellar tissue at this time of year. Manahan (in press) has described uptake of amino acids by eggs developing within the mantle cavity of the oyster *Crassostrea gigas*, and a similar process could be occurring in the fertilized *B. balanoides* eggs. A possible source of DOC in Port Valdez sufficient to account for the increase in lamellar weight was not identified for the present study.

The Reproductive Effort Index, REI = $\left(\frac{\text{dry ovarian weight}}{\text{dry body weight}}\right)$, approximates the degree of energy allocation from the body (somatic tissue) to ovarian tissue for egg production. Data representing REI values for barnacles from each site during the 1980, 1981, and 1982 periods of gametogenesis are included in Table 21. As an example, the REI for barnacles from the mid zone of Sawmill Spit was 1.48 in June 1980, which means, that in terms of overall energy stored, approximately 1.5 times the somatic tissue weight was partitioned as energy to reproductive tissue for development.

The REI generally increased from April until June or July at which time a maximum was reached. The increase reflected the continual transfer of energy from somatic reserves to gametogenic tissue. In July or August, the REI, and corresponding extent of energy allocation to ovarian tissue development decreased. The decrease in the REI was a result of spermatogenesis, which began at about this time. The process of sperm formation occurring within the tissues of the body, resulted in a gain in somatic tissue weight. In 1981, following a decrease in the REI in July, a second increase was observed in most cases. The major exception occurred in barnacles at Berth 4. The increased values in August at Sawmill Spit and Mineral Creek were observed in the mid and low intertidal areas and may be indicative of a supplemental food source available to barnacles in these two areas at the time. An identical trend was reflected in somatic tissue weight (Fig. 29) during the summer of 1981. An uncharacteristic rise in body weight was observed in barnacles during this period. The additional food source conceivably

Table 21. Reproductive Effort Index (REI) data for *Balanus balanoides* from the high, mid, and low intertidal heights at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April-August 1980-1982. * = data unavailable.

	Sawmill Spit			Berth 4			Mineral Creek		
	High	Mid	Low	High	Mid	Low	High	Mid	Low
1980									
April	*	*	*	0.36	0.15	*	0.17	0.34	0.20
June	0.79	1.48	*	0.84	0.79	*	0.53	0.92	1.16
July	*	1.55	1.47	*	1.05	1.05	1.07	1.30	1.16
August	1.04	0.80	0.85	0.68	0.67	0.55	0.69	0.84	0.66
1981									
April	0.08	0.08	0.06	0.04	0.04	0.09	0.12	0.03	0.14
May	2.07	0.51	1.65	1.08	*	1.71	1.67	1.12	1.74
June	2.01	2.02	1.95	1.50	*	2.03	1.64	1.77	1.33
July	1.08	1.37	0.71	0.79	0.94	1.09	1.52	1.32	1.12
August(1)	0.83	1.48	0.82	*	0.70	0.19	1.14	1.53	1.31
(2)	0.77	0.73	0.76	0.53	0.72	0.56	0.85	1.48	1.16
1982									
April	0.28	0.29	0.31	0.17	0.14	0.26	0.01	0.09	0.44
May	0.81	0.76	0.91	1.24	0.73	0.41	0.47	0.65	0.88
June	0.96	0.89	1.15	1.14	1.05	0.75	0.59	1.23	*
July	0.58	1.11	0.92	0.46	0.98	*	*	1.19	1.24
August	*	0.78	0.55	*	0.71	*	*	*	*

provided supplemental energy to developing female gametogenic tissue as well, as reflected in the REI data. The REI data also indicate that typically a greater proportion of energy was available for ovarian development in organisms at Sawmill Spit (higher REI value), followed by those at Berth 4 and Mineral Creek. The only exception to the latter trend occurred during the 1982 developmental period. At this time, barnacles from Sawmill Spit were observed in several cases to have lower REI values than organisms from the other sites. This observation apparently reflects the altered structure of the adult barnacle population at Sawmill Spit which resulted from high adult mortality here during the 1981-82 winter season (see Discussion in Adult Mortality section).

Energy Partitioning and Shell Growth

As noted previously, energy stored in body tissues during the spring bloom are partitioned to mantle and ovarian tissues throughout the late spring and summer. The energy within the mantle is available for use in the process of deposition of shell material. Additional energy may be stored as a result of a fall phytoplankton bloom (Hood *et al.*, 1973), and channeled to the mantle tissue for additional growth before "winter ring" formation occurs. By measuring growth ring increments periodically throughout the growing season, determination of the times of maximum energy usage for shell accretion can be made.

Seasonal shell growth-increment data for adults (Table 22) indicate that the maximal increment of shell material occurred in the period from

Table 22. Seasonal shell growth-increment data for adult *Balanus balanoides* from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska. n = number of individuals examined, $\bar{x}$ = mean seasonal shell-growth increment, SD = standard deviation.

	Sawmill Spit Total n = 306			Berth 4 Total n = 378			Mineral Creek Total n = 409		
Month	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
March	16	0.55	0.23	25	0.51	0.18	0	*	*
April	10	0.47	0.25	17	0.48	0.28	24	0.68	0.35
May	50	1.55	0.54	57	1.32	0.41	56	1.34	0.78
June	22	1.65	0.37	104	1.16	0.44	122	0.99	0.59
July	25	1.90	0.69	30	1.36	0.40	30	1.02	0.60
August	51	1.95	0.44	33	1.32	0.60	53	0.93	0.64
September	32	1.88	0.46	37	1.34	0.53	18	0.83	0.44
January	100	2.96	0.56	75	1.60	0.61	106	2.23	0.67

April to May, at a time immediately following assimilation of organic material from the spring phytoplankton bloom (see Growth section for additional discussion). Throughout the remaining months of the summer, little growth occurred, and most of the available energy was utilized in reproductive tissue development. A second major shell increment was observed between the months of September and January. The latter shell growth most likely resulted from additional energy acquired during a small phytoplankton bloom in the fall. Based on data from the three study areas, the greatest monthly growth was observed in most instances for barnacles from Sawmill Spit, followed by those from the other two sites (as was discussed in the section on Growth).

CONCLUSIONS

Fluctuations in the weight of somatic tissue (per 20 mg valve weight) throughout the year reflect feeding, energy storage, and subsequent energy allocation to other regions of the barnacle as needed (such as to reproductive and mantle tissues) (Figs. 28 and 29). In April, following the spring phytoplankton bloom, body tissue weight was high. In June, reproductive tissue development and shell growth were occurring. A corresponding decrease in body weight at this time reflected partitioning of energy to ovarian tissue and mantle. In August, body weight increased as spermatogenesis occurred within the body (prosoma). Fertilization typically commenced in September. At this time, a loss of body weight occurred as a result of expulsion of spermatozoa from the prosoma. During the winter months, when little was available, body weight remained relatively constant.

A few substantial differences from the annual fluctuation in somatic weight described above were noted. In July 1980, the weight of barnacle tissue at Berth 4 remained as high as in June (Fig. 28). The difference at Berth 4 may represent a delay in either the channeling of energy to ovarian tissue or subsequent development of the tissue. The body weight anomaly appears to reflect a transient biological response to the small oil spill that occurred in the Berth 4 area in April 1980. However, in following months, barnacles at Berth 4 again displayed weight fluctuations similar to those observed as Sawmill Spit and Mineral Creek.

In April 1981, somatic weight was lower at Berth 4 in comparison to the weight here the previous year (Figs. 28 and 29). The observed weight was also lower than for barnacles at Sawmill Spit and Mineral Creek. Body weight at Berth 4 did not decrease during the summer of 1981, as expected, which suggest that energy partitioning from this tissue was reduced as compared to that at other sites. In mid-summer of 1981, an increase in somatic weight was observed for individuals at all sites, although delayed by a month for barnacles at Berth 4. The weight increment implies the availability of a supplemental food resource. This weight increment did not occur during the summer of 1980. In 1981 at Sawmill Spit, the loss of body weight subsequent to fertilization was delayed until November (usually late September through early October), and indicates a delay in the time of fertilization at this site. The delay was probably the result of prolonged feeding activity by Sawmill Spit barnacles in late summer or early fall.

The pattern of somatic-tissue fluctuation which emerged from the relationship considered above (body weight per 20 mg valve weight) was reflected in linear regression plots, as well (dry body weight vs. dry valve weight) (Figs. 30-32). By following changes with time in slope values for the regressions, patterns of energy flux could be recognized and were related to critical events in the life history of the barnacle, as previously mentioned (feeding, reproductive tissue development, and shell growth).

A comparison of slope values for 1980-81 revealed that the regression slope representing data for barnacles at Berth 4 remained the same in July as 1980 in June (Fig. 31). The latter observation was previously noted from the other relationship uitilized for assessing energy transfer patterns (body weight per 20 mg valve weight). The failure for the somatic tissue to decrease in weight in July suggests that environmental disturbance may have interrupted the transfer of energy from somatic reserves.

An important observation from the regression plots confirmed the growth trends perviously discussed for barnacles at the three sites (see discussion in Annual Shell Growth section). Upon examination of regressions for 1980-81, it became evident that plots for barnacles at Berth 4 never included valve weights above 50 mg. At Sawmill Spit and Mineral Creek, valve weights of up to 100 mg were common, and in all regressions, barnacles attained a valve weight of at least 70 mg. Body weights were often greater for the latter individuals as well, suggesting a size difference in barnacles from Sawmill Spit and Mineral Creek in comparison with those from Berth 4. Data from the shell growth study indicated that barnacles were larger at Sawmill Spit than at the other sites (Table 12 and 13; Fig. 27). Barnacles were often larger at Mineral Creek than at Berth 4 as well, although the trend was not as evident as for barnacles at Sawmill Spit.

Seasonal fluctuations in the weight of ovarian tissue were primarily a result of energy transfer from somatic tissue reserves. The REI (Reproductive Effort Index) revealed roughly the amount of material allocated to egg production by the body each month (Table 21), thus described the energetic relationship between body and ovarian tissues. The REI generally rose as ovarian tissue development was initiated in late spring/early summer. A maximum value was attained in mid-summer, followed by a decrease in mid to late summer. The decrease at this time was a reflection of somatic-weight gain which resulted from spermatogenesis within the body. In August 1981, a second rise in the REI occurred and may be a reflection of the assimilation of supplemental organic material within the water column. The latter increase occurred at Sawmill Spit and Mineral Creek, but was not observed at Berth 4. The highest REI values were typically observed for barnacles at Sawmill Spit, and may suggest a more productive population here.

Seasonal shell growth-increment data (Table 22) were utilized to identify periods of major shell accretion. The maximal increment occurred from April to May, immediately following the spring bloom. A second period of shell accretion was observed from September until January and may be indicative of additional energy acquired through a fall bloom. The greatest seasonal increments were generally observed for individuals from Sawmill Spit.

MORTALITY

INTRODUCTION

Inter- and intraspecific competition for space in the intertidal zone is intense, and represents a major factor limiting population size. Physical environmental stresses are also important variables that limit survival of intertidal species (Connell, 1961). High air temperatures with little precipitation, lowered salinity, a high suspended sediment load in the spring and summer, and low air and water temperatures and wind in the winter are environmental parameters that could stress intertidal organisms in Port Valdez. Predation seems to play a minor role in barnacle mortality at the three sampling sites (personal observation), and on the few occasions observed, was the result of feeding activity by the gastropod *Thais (Nucella) lamellosa*. A nudibranch, *Onchidoris*, feeds exclusively on barnacles along most of the north Pacific coast (Carefoot, 1977) but does not occur in Port Valdez. Sea stars feed extensively on barnacles in more temperate regions (Feder, 1959, 1970), but are not a major consumer of barnacles in protected Alaskan waters. Studies from southeastern and southcentral Alaska, inclusive of Port Valdez, indicate that intertidal and shallow subtidal sea stars feed primarily on clams, mussels, and other mollusks (Paul and Feder, 1975; Feder and Jewett, 1980; Feder, unpub.). The sea star *Pycnopodia helianthoides* (Brandt) occasionally utilizes barnacles for food, although Paul and Feder (1975) report an unusual observation of a single *P. helianthoides* containing 84 juvenile balanoids. Preliminary mortality data for barnacles in Port Valdez, prior to the operation of the Alyeska Pipeline Terminal, is presented in Colonell (1979) and Feder and Keiser (1980).

METHODS

A series of five permanently marked sites located throughout the intertidal areas of Sawmill Spit, Berth 4 and Mineral Creek were established in April 1980. Actual tidal heights (meters above MLLW) are included for the five sites at each sampling area in Table 23. Five clear plexiglass plates, 0.0625 m^2 (25 cm x 25 cm) were cut and drilled to fit over small pins projecting from sampling frames of the same size. For each observation, the frames and plates were lined up with the permanent markers (rebar or spikes), and the location of barnacles marked on the plexiglass plates with an indelible marking pen. Different symbols were used to denote adults and juveniles. Changes with time in the numbers of barnacles (recruitment of juveniles and/or death of juveniles and adults) were noted upon examination of plates in the laboratory.

The first annual observation period was initiated in April 1980. Plates were subsequently marked in June and September 1980 and monthly from February-April 1981, to complete a data set for the first year of mortality assessment (April 1980-April 1981). In May 1981, new, unmarked plates were used. Monthly observations were made from May until September 1981, and in March and April, 1982. Data from May 1981-April 1982 comprise a second year of mortality observations. A third observation period, using new plates, was initiated in April 1982. Mortality

Table 23. Approximate tidal heights in meters above MLLW for *Balanus balanoides* mortality plots at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska.

Tidal Level	Approximate Tidal Height (meters above MLLW)
Sawmill Spit	
1	2.1
2	1.1
3	0.8
4	0.4
5	0.1
Berth 4	
1	2.7
2	2.5
3	1.7
4	1.2
5	0.7
Mineral Creek	
1	2.6
2	2.1
3	1.6
4	1.3
5	1.0

observations and recruitment information were recorded monthly thereafter until September 1982.

The two and a half years of mortality data (April 1980-September 1982) were examined seasonally in order to identify trends relative to summer and/or winter stresses. Data were divided into approximate six month "summer" and "winter" periods as follows, based on dates of collection: summer 1980 (April-September 1980), winter 1980-81 (September 1980-April 1981), summer 1981 (May-August 1981), winter 1981-82 (August 1981-April 1982), and summer 1982 (April-September 1982 for adults, May-September 1982 for juveniles).

Barnacles mortality was assessed on a "monthly" basis, as well. The frequency of calculation of these "monthly" percentages reflects the actual dates of data collection in the field, although not strictly on a monthly basis. For example, during the summer of 1980, data were collected in April, June, and September, but not in other summer months; thus, "monthly" percentages were determined for the periods from April to June and from June to September only.

At Sawmill Spit in February 1981, the sampling site at 0.4 m was not located. The site was recovered the following month, and individuals were marked as before. In March 1982, no Sawmill Spit sampling sites were located due to heavy snow cover on the beach. Therefore, data for March were estimated from counts recorded on new mortality plates deployed in April 1982. In April 1981 and 1982, due to active cyprid larval movement on the substratum prior to attachment, it was not possible to make counts of juveniles of the year. By May of both years, the majority of spat had metamorphosed into juvenile barnacles, and a new growing season for the population had begun. Juveniles from the previous year were now marked as adults, and the newly settled spat marked as juveniles.

Mortality percentages for adults and juveniles were calculated from the number of individuals surviving by use of the following equations (Ricker, 1975):

$$S = \frac{N_{t+1}}{N_t} (100)$$

$$M = 100 - S$$

where S = survivorship

N_t = number of individuals counted during the initial sampling

N_{t+1} = number of individuals counted during the next or subsequent sampling

M = mortality

Negative juvenile mortality values occur, and represent net recruitment of juveniles to a particular location (i.e., a greater number of juveniles settling than dying at the site).

The Z-test of proportions (Zar, 1974) was used to compare between-site survivorship at any given time and within-site survivorship for differing time periods. These survivorship comparisons express comparisons of percent mortality as well, since survivorship is a function of mortality ($M = 100 - S$). Thus, statistical tests of differences in percent mortality referred to throughout the text are always based on comparisons of survivorship proportions. Significance was determined at the 95% confidence level. The equation used for the analysis is as follows:

$$Z = \frac{\hat{p}_1 - \hat{p}_2}{\frac{\hat{p}\hat{q}}{n_1} + \frac{\hat{p}\hat{q}}{n_2}}$$

where $\hat{p}$ and $\hat{q}$ = proportions of individuals surviving

n = number of individuals (sample size)

RESULTS-DISCUSSION

Adult Mortality

Annual, seasonal, and monthly mortality percentages were determined for adult barnacle populations at five tidal levels from Sawmill Spit, Berth 4, and Mineral Creek during the sampling period April 1980-September 1982 (Tables 24-26). Figure 34 displays mortality percentages calculated for each month of observation at each study site. Mortality results for any year are discussed in the following order: annually, seasonally, and monthly.

Annual adult mortality percentages, which were generally much lower than juvenile percentages, were significantly less ($\alpha = 0.05$) at Sawmill Spit than at Berth 4 or Mineral Creek from April 1980-April 1981 (Table 24 and Appendix 5, Table 1). For example, adult barnacles at Sawmill Spit had a mean annual mortality of 10.4% in 1980-1981 as compared with 46.3% at Berth 4 and 21.7% at Mineral Creek.

Seasonal adult mortality was calculated for the periods April-September 1980 (summer season) and September 1980-April 1981 (winter

Table 24. Annual percent (%) mortality for *Balanus balanoides* adults from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23. N_t represents the number of individuals at a given time and $N_t + 1$ represents the number of individuals surviving until the subsequent sampling period.

Tidal Level	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
Sawmill Spit	Apr 80-Apr 81		May 81-Apr 82	
1	66.7	1/3	66.7	1/3
2	no adults	0/0	75.8	8/33
3	0.0	3/3	53.3	14/30
4	13.5	128/148	67.8	46/143
5	1.5	66/67	47.5	104/198
Total	10.4	198/221	57.5	173/407
Berth 4	Apr 80-Apr 81		May 81-Mar 82	
1	85.9	9/64	28.6	5/7
2	26.7	22/30	4.0	24/25
3	39.2	104/171	36.9	65/103
4	40.7	16/27	15.0	17/20
5	40.8	61/103	37.8	125/201
Total	46.3	212/395	33.7	236/356
Mineral Creek	Apr 80-Apr 81		May 81-Mar 82	
1	20.4	113/142	6.2	122/130
2	10.0	117/130	6.3	120/128
3	9.4	289/319	3.2	269/278
4	34.6	89/136	16.8	144/173
5	64.4	32/90	95.1	21/427
Total	21.7	640/817	40.5	676/1136

Table 25. Seasonal percent (%) mortality for *Balanus balanoides* adults from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-September 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23.

Tidal Level	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
Sawmill Spit	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Apr 1982		Apr-Sep 1982	
1	0.0	3/3	66.7	1/3	66.7	1/3	0.0	1/1	20.0	28/35
2	no adults	0/0	no adults	0/0	9.1	30/33	73.3	8/30	82.6	4/23
3	0.0	3/3	0.0	3/3	3.3	29/30	51.7	14/29	70.0	12/40
4	5.4	140/148	8.6	128/140	2.8	139/143	66.9	46/139	24.5	77/102
5	0.0	67/67	1.5	66/67	5.6	187/198	44.4	104/187	8.4	306/334
Total	3.6	213/221	7.0	198/213	5.2	386/407	55.2	173/386	20.0	427/534
Berth 4	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Mar 1982		Apr-Sep 1982	
1	81.2	12/64	25.0	9/12	28.6	5/7	0.0	5/5	46.7	8/15
2	20.0	24/30	8.3	22/24	0.0	25/25	4.0	24/25	6.3	30/32
3	22.2	133/171	21.8	104/133	11.7	91/103	28.6	65/91	40.2	70/117
4	22.2	21/27	23.8	16/21	0.0	20/20	15.0	17/20	15.4	22/26
5	20.4	82/103	25.6	61/82	30.4	140/201	10.7	125/140	47.0	107/202
Total	31.1	272/395	22.1	212/272	21.1	281/356	16.0	236/281	39.5	237/392
Mineral Creek	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Mar 1982		Apr-Sep 82	
1	10.6	127/142	11.0	113/127	2.3	127/130	3.9	122/127	21.2	204/259
2	6.2	122/130	4.1	117/122	2.3	125/128	4.0	120/125	4.9	214/225
3	1.6	314/319	8.0	289/314	2.2	272/278	1.1	269/272	7.5	408/441
4	14.7	116/136	23.3	89/116	12.1	152/173	5.3	144/152	34.4	99/151
5	5.6	85/90	62.4	32/85	93.2	29/427	27.6	21/29	65.4	9/26
Total	6.5	764/817	16.2	640/764	37.9	705/1136	4.1	676/705	15.2	934/1102

Table 26. Monthly percent (%) mortality for *Balanus balanoides* adults from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23. N_t represents the number of individuals at a given time and N_{t+1} represents the number of individuals surviving until the subsequent sampling period.

Time	Tidal Level	Sawmill Spit		Berth 4		Mineral Creek	
		% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
1980-81							
Jun 1980	1	0.0	3/3	0.0	64/64	0.0	142/142
	2	no adults	0/0	0.0	30/30	3.9	125/130
	3	0.0	3/3	2.3	167/171	0.3	318/319
	4	0.0	148/148	0.0	27/27	5.2	129/136
	5	0.0	67/67	0.0	103/103	2.2	88/90
	Total	0.0	221/221	1.0	391/395	1.8	802/817
Sep 1980	1	0.0	3/3	81.3	12/64	10.6	127/142
	2	no adults	0/0	20.0	24/30	2.4	122/125
	3	0.0	3/3	20.4	133/167	1.3	314/318
	4	5.4	140/148	22.2	21/27	10.1	116/129
	5	0.0	67/67	20.4	82/103	3.4	85/88
	Total	3.6	213/221	30.4	272/391	4.7	764/802
Feb 1981	1	0.0	3/3	16.7	10/12	4.7	121/127
	2	no adults	0/0	4.2	23/24	0.0	122/122
	3	0.0	3/3	16.5	111/133	5.4	297/314
	4	†	†	4.8	20/21	18.1	95/116
	5	0.0	67/67	9.8	74/82	25.9	63/85
	Total	0.0	73/73	12.5	238/272	8.6	698/764
Mar 1981	1	66.7	1/3	10.0	9/10	4.1	116/121
	2	no adults	0/0	0.0	23/23	2.5	119/122
	3	0.0	3/3	2.7	108/111	2.7	289/297
	4	6.4	131/140	10.0	18/20	5.3	90/95
	5	1.5	66/67	16.2	62/74	20.6	50/63
	Total	5.6	201/213	7.6	220/238	4.9	664/698
Apr 1981	1	0.0	1/1	0.0	9/9	2.6	113/116
	2	no adults	0/0	4.4	22/23	1.7	117/119
	3	0.0	3/3	3.7	104/108	0.0	289/289
	4	2.3	128/131	11.1	16/18	1.1	89/90
	5	0.0	66/66	1.6	61/62	36.0	32/50
	Total	1.5	198/201	3.6	212/220	3.6	640/664
1981-82							
Jun 1981	1	0.0	3/3	0.0	7/7	0.0	130/130
	2	0.0	33/33	0.0	25/25	0.0	128/128
	3	0.0	30/30	4.9	98/103	0.4	277/278
	4	0.0	143/143	0.0	20/20	1.2	171/173
	5	2.5	193/198	6.5	188/201	86.0	60/427
	Total	1.2	402/407	5.1	338/356	32.6	766/1136
Jul 1981	1	0.0	3/3	0.0	7/7	0.8	129/130
	2	0.0	33/33	0.0	25/25	0.8	127/128
	3	0.0	30/30	2.0	96/98	0.0	277/277
	4	2.1	140/143	0.0	20/20	5.3	162/171
	5	0.0	193/193	16.0	158/188	28.3	43/60
	Total	0.8	399/402	9.5	306/338	3.7	738/766

Table 26. Continued.

Time	Tidal Level	Sawmill Spit % Mortality	Sawmill Spit N_{t+1}/N_t	Berth 4 % Mortality	Berth 4 N_{t+1}/N_t	Mineral Creek % Mortality	Mineral Creek N_{t+1}/N_t
1981-82 (cont'd)							
Aug 1981	1	66.7	1/3	28.6	5/7	1.6	127/129
	2	9.1	30/33	0.0	25/25	1.6	125/127
	3	3.3	29/30	5.2	91/96	1.8	272/277
	4	0.7	139/140	0.0	20/20	6.2	152/162
	5	3.1	187/193	11.4	140/158	32.6	29/43
	Total	3.3	386/399	8.2	281/306	4.5	705/738
Mar 1982*	1	0.0	1/1	0.0	5/5	3.9	122/127
	2	73.3	8/30	4.0	24/25	4.0	120/125
	3	51.7	14/29	28.6	65/91	1.1	269/272
	4	66.9	46/139	15.0	17/20	5.3	144/152
	5	44.4	104/187	10.7	125/140	27.6	21/29
	Total	55.2	173/386	16.0	236/281	4.1	676/705
1982							
May 1982	1	0.0	35/35	0.0	15/15	0.0	259/259
	2	0.0	23/23	0.0	32/32	0.4	224/225
	3	0.0	40/40	2.6	114/117	0.5	439/441
	4	5.9	96/102	3.9	25/26	8.0	139/151
	5	0.6	332/334	5.5	191/202	23.1	20/26
	Total	1.5	526/534	3.8	377/392	1.9	1081/1102
Jun 1982	1	0.0	35/35	6.7	14/15	1.5	255/259
	2	4.4	22/23	0.0	32/32	1.8	220/224
	3	0.0	40/40	7.0	106/114	6.8	409/439
	4	6.3	90/96	0.0	25/25	16.6	116/139
	5	2.4	324/332	8.4	175/191	55.0	9/20
	Total	2.8	511/526	6.6	352/377	6.7	1009/1081
Jul 1982	1	0.0	35/35	†	†	0.0	255/255
	2	0.0	22/22	3.1	31/32	0.0	220/220
	3	0.0	40/40	6.6	99/106	0.0	409/409
	4	4.4	86/90	0.0	25/25	5.2	110/116
	5	0.0	324/324	16.0	147/175	0.0	9/9
	Total	0.8	507/511	10.7	302/338	0.6	1003/1009
Aug 1982	1	11.4	31/35	35.7	9/14	1.6	251/255
	2	31.8	15/22	3.2	30/31	0.5	219/220
	3	37.5	25/40	16.2	83/99	0.0	409/409
	4	7.0	80/86	8.0	23/25	9.1	100/110
	5	2.8	315/324	20.4	117/147	0.0	9/9
	Total	8.1	466/507	13.3	262/302	1.5	988/1003
Sep 1982	1	9.7	28/31	11.1	8/9	18.7	204/251
	2	73.3	4/15	0.0	30/30	2.3	214/219
	3	52.0	12/25	15.7	70/83	0.2	408/409
	4	3.8	77/80	4.4	22/23	1.0	99/100
	5	2.9	306/315	8.6	107/117	0.0	9/9
	Total	8.4	427/466	9.5	237/262	5.5	934/988

* data from Sawmill Spit collected in April of 1982.
† data unavailable.

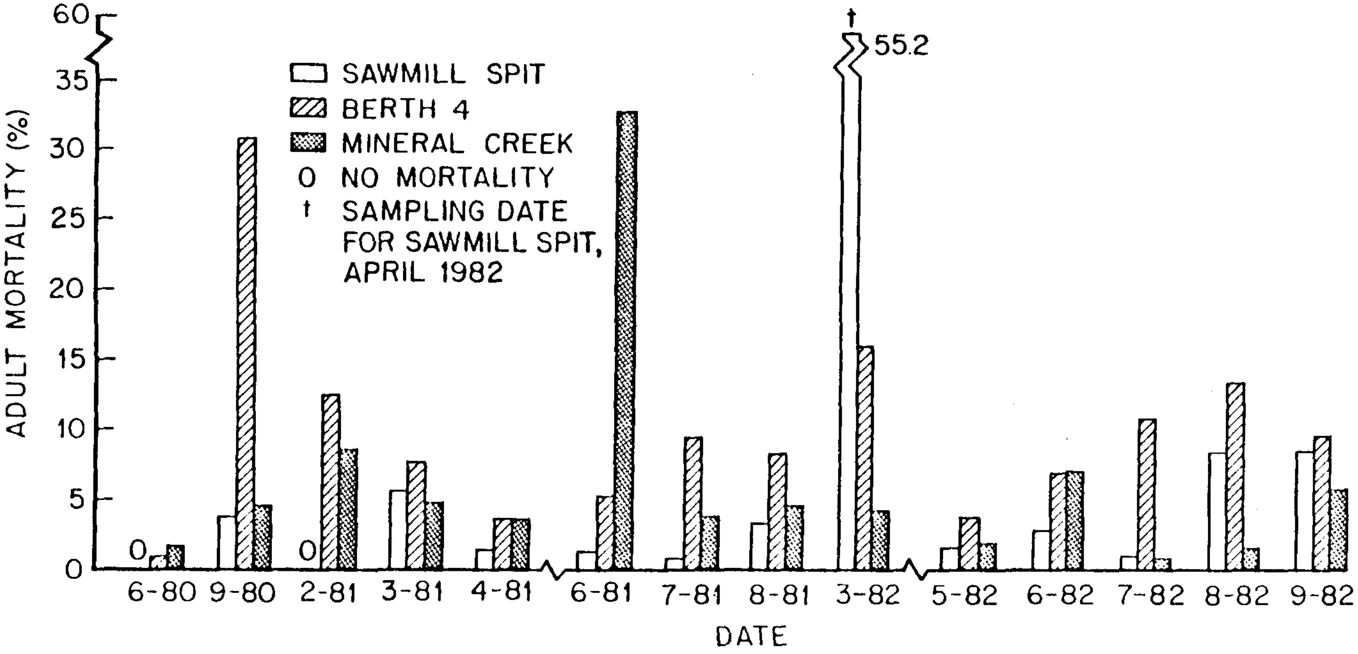

Figure 34. Adult percent mortality for *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Months illustrated represent times of data collection.

season). Data are included in Table 25. Sawmill Spit and Mineral Creek sites displayed a higher percent mortality during the winter season of 1980-81, as compared with the summer of 1980. In contrast, Berth 4 barnacles died in greater numbers in the summer of 1980, during which time over 30% of all adults present failed to survive (see also monthly mortality data, Table 26; Appendix 5, Table 2; Fig. 34). Less than 10% of all adults present died at either of the other sites from April to September 1980. The high adult mortality at Berth 4 suggests that environmental conditions were more severe at Berth 4 than at the other two sites during the summer of 1980, possibly as a result of the small oil spill that occurred in the vicinity of Berth 4 in April 1980. Possible environmental disturbance at Berth 4 during this period was reflected by other biological responses of *Balanus balanoides* as well. Reduced ovarian weights of barnacles from Berth 4 in 1980 in comparison with other sites (Fig. 6 and discussion in the section on Reproductive Tissue Development) suggest that critical biological activities were affected by stress at the time. Statistical data from the Z-test of proportions (Appendix 5, Table 3) indicate that no significant difference existed between adult mortality values at Sawmill Spit and Mineral Creek during the summer season (April-September 1980), and that the mortality for barnacles at these sites was significantly less than at Berth 4 during the same time period ($\alpha = 0.05$).

During the next year, 1981-82 (May 1981-March 1982, except Sawmill Spit which was sampled through April 1982), the annual percent adult mortality was greatest as Sawmill Spit (57.5%), followed by Mineral

Creek (40.5%) and Berth 4 (33.7%) (Table 24). The mortality percentages at the three study sites were statistically different from one another. Sawmill Spit barnacle mortality was higher ($\alpha = 0.05$) than that at either of the other sites (Appendix 5, Table 1).

Mortality percentages derived from seasonal and monthly data for 1981-82 indicate that most Sawmill Spit adult barnacles that died during this period did so during the winter season, August 1981-April 1982 (Tables 25 and 26; Appendix 5, Table 2; Fig. 34). During the severe winter of 1981-82, the National Weather Service Office in Valdez, Alaska recorded a period of clear, cold weather, characterized by above average wind speeds and frequent ice formation (local climatological data, NOAA, WSO, Valdez, Alaska and personal observation; see also the section discussing physical environmental characteristics). These factors appear to have affected barnacle mortality only at Sawmill Spit, since unlike Berth 4 or Mineral Creek, the former area is relatively unprotected. The intertidal organisms at Sawmill Spit were likely influenced by low air temperatures in conjunction with high winds and ice effects (substrate abrasion) to a greater degree than organisms at either of the two more sheltered areas. A similar degree of mortality occurred at Berth 4 during summer and winter seasons of 1981-82, although the greatest percent mortality (21.1%) occurred during the summer months (Appendix 5, Table 2). The majority of Mineral Creek barnacles died during the summer season (May-August 1981, especially June) (Tables 25 and 26; Appendix 5, Table 2; Fig. 34). The mortality, primarily in the low zone, was the result of a heavy silt load (due to excess runoff from

Mineral Creek during the wet summer, see discussion in Physical Environment section) and a great abundance of the green algae *Monostroma* spp. covering the sampling site. Many of the barnacles were completely covered by sediment and algae during this period, and were presumably unable to feed.

The seasonal mortality percentages for adults at the three study sites differed significantly from one another ($\alpha = 0.05$) (Appendix 5, Table 3). During the 1981 summer period, fewer barnacles ($\alpha = 0.05$) died at Sawmill Spit (5.2%) than at Berth 4 (21.1%) or Mineral Creek (37.9%). In comparing percentages for the latter two sites, the mortality observed at Mineral Creek was significantly higher than that observed at Berth 4. In the winter of 1981-82, a greater number of adults died at Sawmill Spit (55.2%) as compared with Berth 4 (16.0%) or Mineral Creek (4.1%). The latter two mortality percentages, although much lower than at Sawmill Spit, were significantly different from one another, as well.

During the 1982 summer season (April-September 1982) Berth 4 adult barnacles died in greater numbers than those at either Sawmill Spit or Mineral Creek (Tables 25 and 26). Approximately 40% of the adult population at Berth 4 was dead by September, as compared to 20% at Sawmill Spit and 15% at Mineral Creek. A significant difference occurred between the mortality percentages at each of the three sites, although the difference between Sawmill Spit and Mineral Creek was less than between these sites and Berth 4 (Appendix 5, Table 3). The high mortality observed at Berth 4 in the summer of 1982 (as well as the somewhat higher than typical mortality observed at Sawmill Spit for this time of year) was probably the result of unusually severe environmental conditions within Port Valdez at this time. Lowered precipitation and high air temperatures, conditions promoting desiccation, occurred during this period (see Physical Environment section for discussion).

Significant year-to-year differences in annual percent adult mortality at a particular site emerge when comparisons are made (Appendix 5, Table 4). For example, at Sawmill Spit, mortality was higher in 1981-82 (58%) than in 1980-81 (10%) (Table 24), presumably because of the great losses during the severe winter season of 1981-82 (Table 25; see also discussion in Physical Environment section). A similar trend was observed for barnacles at Mineral Creek, when in 1981-82 many adults (40%) died in comparison with 1980-81 (22%) (Table 24). Unlike Sawmill Spit, however, the greatest mortality at Mineral Creek occurred during the summer of 1981 (as a consequence of sediment and algae covering) as opposed to the winter of 1981-82 (Table 25). The summer of 1981 was a period of heavy precipitation, accompanied by major river outflow (see Physical Environment section). Although percent mortality at Berth 4 was relatively high in both years, in 1980-81 significantly greater barnacle losses occurred (46% in 1980-81 as opposed to 34% in 1981-82) (Appendix 5, Table 4). The extensive mortality at Berth 4, primarily during the summer months of 1980 (Table 25) may have resulted from stressed conditions in the vicinity at the time. Between the months of April and September 1980, air temperatures were not significantly warmer than normal, precipitation was close to the summertime average, and in general, few clear, sunny days were recorded. Since environmental conditions were not extreme during this period, barnacle mortality most likely did not result from desiccation. Adult losses similar to those observed at Berth 4 did not occur at either Sawmill Spit or Mineral Creek. Thus, the resulting mortality at Berth 4 was probably the reflection of an accumulation of pollutants within the Berth 4 intertidal zone, since a small oil spill occurred in April 1980 at the adjacent Berth 5 tanker site.

Statistical values indicate that for all sites significant differences in adult mortality existed between the three summer seasons sampled (Appendix 5, Table 5). At Sawmill Spit, mortality during the summer of 1982 was significantly higher than during either the summer of 1980 or 1981. Wintertime mortality was statistically higher during the 1981-82 winter season than in the preceding winter. These results agree with trends discussed previously for barnacles at Sawmill Spit. At Berth 4, summer mortalities varied significantly from one year to another, although in all summers mortality was greater than 20%. Results of the Z-test indicate that the summer of 1982 had the greatest number of barnacle deaths, followed by 1980 and 1981, respectively. No difference in winter mortality at Berth 4 emerged. The summer mortality at Mineral Creek was significantly higher in 1981 than in 1980 or 1982, reflecting the mass mortality at this time due to silt and algal covering. Results of the 1980 and 1982 comparison indicate a higher mortality during the 1982 summer season. The mortality during the winter of 1980-81 tested significantly higher than the mortality the following winter.

Juvenile Mortality

At all locations, the annual mortality rate of juveniles was extremely high as a result of problems encountered in the months after settlement. The highest annual juvenile mortality in 1980-81 occurred at Berth 4 (95% mortality), followed by Sawmill Spit (88%) and Mineral Creek (81%) (Table 27). A significant difference ($\alpha = 0.05$) among the three annual mortality values for 1980-81 was revealed (Berth 4 significantly greater than Sawmill Spit or Mineral Creek and Sawmill Spit significantly greater than Mineral Creek) (Appendix 5, Table 6). Mortality was typically greater at the higher tidal levels, since the longer periods of exposure placed additional stresses on the organisms. A net recruitment of juveniles occasionally occurred (i.e., a greater number of juveniles settled than died) as in 1980-81 for the low zone of Mineral Creek. Data for these barnacles are expressed as negative juvenile mortality values.

Seasonal mortality data for Sawmill Spit and Berth 4 indicate that in 1980-81, significantly more juveniles died at each site during the summer (70.4% and 93.9%, respectively) than in the winter (57.9% and 20.8%, respectively) (Table 28 and Appendix 5, Table 7). However, over 75% of the juveniles at Mineral Creek died between the months of September 1980 and April 1981 (the winter period), primarily from September 1980 to February 1981 (Tables 28 and 29; Appendix 5, Table 7; Fig. 35). Significant statistical differences in percent mortality occurred between the three sites seasonally in 1980-81 (Appendix 5, Table 8). During the summer, juvenile mortality at Berth 4 was significantly

Table 27. Annual percent (%) mortality for *Balanus balanoides* juveniles from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23. N_t represents the number of individuals at a given time and N_t + 1 represents the number of individuals surviving until the subsequent sampling period.

Tidal Level	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
Sawmill Spit	Apr 80-Apr 81		May 81-Apr 82	
1	99.7	2/757	94.5	28/509
2	91.7	30/363	90.6	5/53
3	95.0	39/774	97.8	2/89
4	79.9	27/134	72.2	5/18
5	25.9	186/251	83.2	60/357
Total	87.5	284/2279	90.3	100/1026
Berth 4	Apr 80-Apr 81		May 81-Mar 82	
1	100.0	0/119	33.3	2/3
2	99.8	1/546	-133.3*	14/6
3	99.7	5/1887	87.5	51/408
4	97.1	7/245	77.2	18/79
5	87.3	196/1543	89.9	128/1263
Total	95.2	209/4340	87.9	213/1759
Mineral Creek	Apr 80-Apr 81		May 81-Mar 82	
1	98.8	27/2272	85.5	113/778
2	97.6	27/1146	86.4	67/494
3	98.2	17/924	78.5	160/743
4	77.7	143/640	62.5	30/80
5	-24.0*	843/680	100.0	0/20
Total	81.3	1057/5662	82.5	370/2115

* negative mortality values indicate a net recruitment of juveniles, i.e., a greater number of juveniles settled than died.

Table 28. Seasonal percent (%) mortality for *Balanus balanoides* juveniles from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-September 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23.

Tidal Level	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
Sawmill Spit	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Apr 1982		May-Sep 1982	
1	98.5	11/757	81.8	2/11	74.7	129/509	78.3	28/129	95.3	27/577
2	79.1	76/363	60.5	30/76	-20.8*	64/53	92.2	5/64	98.1	50/2634
3	73.9	204/774	80.9	39/204	10.1	80/89	97.5	2/80	99.3	30/3987
4	20.9	106/134	74.5	27/106	0.0	18/18	72.2	5/18	93.0	40/569
5	-10.8*	278/251	33.1	186/278	10.4	320/357	81.3	60/320	99.2	7/916
Total	70.4	675/2279	57.9	284/675	40.5	611/1026	83.6	100/611	98.2	154/8683
Berth 4	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Mar 1982		May-Sep 1982	
1	95.0	6/119	100.0	0/6	0.0	3/3	33.3	2/3	87.4	23/182
2	98.9	6/546	83.3	1/6	-150.0*	15/6	6.7	14/15	98.5	13/870
3	99.5	9/1887	44.4	5/9	65.7	140/408	63.6	51/140	99.7	9/2566
4	85.3	36/245	80.6	7/36	22.8	61/79	70.5	18/61	96.9	14/452
5	86.6	207/1543	5.3	196/207	44.2	705/1263	81.8	128/705	99.3	6/827
Total	93.9	264/4340	20.8	209/264	47.5	924/1759	76.9	213/924	98.7	65/4897
Mineral Creek	Apr-Sep 1980		Sep 1980-Apr 1981		May-Aug 1981		Aug 1981-Mar 1982		May-Sep 1982	
1	43.3	1287/2272	97.9	27/1287	10.7	695/778	83.7	113/695	97.8	54/2479
2	47.8	598/1146	95.5	27/598	8.9	450/494	85.1	67/450	98.6	24/1665
3	12.2	811/924	97.9	17/811	9.2	675/743	76.3	160/675	90.8	40/434
4	-16.9*	748/640	80.9	143/748	47.5	42/80	28.6	30/42	-2.4*	766/748
5	-43.8*	978/680	13.8	843/978	90.0	2/20	100.0	0/2	-8.2*	1181/1092
Total	21.9	4422/5662	76.1	1057/4422	11.9	1864/2115	80.1	370/1864	67.8	2065/6418

* negative mortality values indicate a net recruitment of juveniles, i.e., a greater number of juveniles settled than died.

Table 29. Monthly percent (%) mortality for *Balanus balanoides* juveniles from Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Tidal level refers to vertical position in the intertidal zone - Level 1 is the highest on the shoreline, Level 5 the lowest. For actual distances above MLLW, see Table 23. N_t represents the number of individuals at a given time and N_{t+1} represents the number of individuals surviving until the subsequent sampling period.

Time	Tidal Level	Sawmill Spit		Berth 4		Mineral Creek	
		% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
1980-81							
Jun 1980	1	8.3	694/757	0.8	118/119	0.1	2269/2272
	2	17.4	300/363	20.0	437/546	0.0	1146/1146
	3	26.4	570/774	0.3	1882/1887	0.0	924/924
	4	24.6	101/134	0.0	245/245	0.5	637/640
	5	4.0	241/251	2.0	1512/1543	0.4	677/680
	Total	16.4	1906/2279	3.4	4194/4340	0.2	5653/5662
Sep 1980	1	99.4	5/803	100.0	0/139	46.5	1270/2374
	2	95.3	16/341	99.8	1/450	52.4	577/1212
	3	71.2	191/662	99.8	5/2007	15.2	798/941
	4	31.2	84/122	98.4	5/306	1.0	706/713
	5	22.4	257/331	87.6	200/1612	0.2	851/853
	Total	75.5	553/2259	95.3	211/4514	31.0	4202/6093
Feb 1981	1	81.8	2/11	100.0	0/6	98.9	15/1287
	2	57.9	32/76	66.7	2/6	99.0	6/598
	3	90.7	19/204	88.9	1/9	98.0	16/811
	4	†	†	94.4	2/36	82.6	130/748
	5	54.0	128/278	34.3	136/207	2.2	957/978
	Total	68.2	181/569	46.6	141/264	74.6	1124/4422
Mar 1981	1	0.0	2/2	no juveniles	0/0	5.6	17/18
	2	6.3	30/32	0.0	2/2	22.2	7/9
	3	22.2	35/45	0.0	3/3	11.1	16/18
	4	72.6	29/106	0.0	8/8	3.5	140/145
	5	4.9	137/144	26.3	146/198	11.8	869/985
	Total	29.2	233/329	24.6	159/211	10.7	1049/1175
Apr 1981	1	0.0	2/2	no juveniles	0/0	4.0	24/25
	2	12.1	29/33	50.0	1/2	8.3	22/24
	3	12.2	36/41	0.0	4/4	11.8	15/17
	4	28.1	23/32	45.5	6/11	11.7	136/154
	5	3.8	153/159	13.7	182/211	11.0	811/911
	Total	9.0	243/267	15.4	193/228	10.9	1008/1131
1981-82							
Jun 1981	1	3.9	489/509	0.0	3/3	7.6	719/778
	2	7.6	49/53	0.0	6/6	9.1	449/494
	3	4.5	85/89	10.5	365/408	6.2	697/743
	4	16.7	15/18	13.9	68/79	6.3	75/80
	5	3.6	344/357	14.8	1076/1263	100.0	0/20
	Total	4.3	982/1026	13.7	1518/1759	8.3	1940/2115
Jul 1981	1	2.5	618/634	0.0	3/3	1.8	752/766
	2	3.5	56/58	0.0	13/13	0.0	490/490
	3	19.0	81/100	5.5	399/422	0.0	772/772
	4	0.0	16/16	11.8	67/76	30.4	55/79
	5	2.7	355/365	8.1	1073/1167	0.0	2/2
	Total	4.0	1126/1173	7.5	1555/1681	1.8	2071/2109

Table 29. Continued.

Time	Tidal Level	Sawmill Spit		Berth 4		Mineral Creek	
		% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t	% Mortality	N_{t+1}/N_t
1981-82 (cont'd)							
Aug 1981	1	82.2	114/642	0.0	3/3	12.2	665/757
	2	24.7	55/73	29.4	12/17	16.9	407/490
	3	24.4	65/86	69.4	125/408	17.1	640/772
	4	0.0	16/16	16.2	57/68	29.3	41/58
	5	15.0	307/361	34.9	701/1076	0.0	2/2
	Total	52.7	557/1178	42.9	898/1572	15.6	1755/2079
Mar 1982*	1	89.9	13/129	33.3	2/3	83.9	112/695
	2	92.2	5/64	46.7	8/15	86.4	61/450
	3	97.5	2/80	68.6	44/140	77.3	153/675
	4	72.2	5/18	73.8	16/61	28.6	30/42
	5	81.9	58/320	82.7	122/705	100.0	0/2
	Total	86.4	83/611	79.2	192/924	80.9	356/1864
1982							
May 1982	1	0.0	17/17	no juveniles	0/0	0.0	9/9
	2	no juveniles	0/0	12.5	7/8	0.0	2/2
	3	no juveniles	0/0	no juveniles	0/0	0.0	3/3
	4	no juveniles	0/0	0.0	1/1	no juveniles	0/0
	5	0.0	2/2	no juveniles	0/0	no juveniles	0/0
	Total	0.0	19/19	11.1	8/9	0.0	14/14
Jun 1982	1	10.1	519/577	6.0	171/182	1.1	2453/2479
	2	6.8	2454/2634	2.3	850/870	0.8	1651/1665
	3	64.9	1401/3987	4.4	2452/2566	10.6	388/434
	4	42.7	326/569	12.2	397/452	7.0	696/748
	5	77.8	203/916	22.4	642/827	0.9	1082/1092
	Total	43.5	4903/8683	7.9	4512/4897	2.3	6270/6418
Jul 1982	1	24.4	464/614	†	†	0.0	2459/2459
	2	9.4	2315/2555	75.8	242/1000	0.2	1651/1655
	3	6.8	1499/1608	96.8	85/2628	0.0	434/434
	4	16.2	330/394	32.7	297 441	0.1	785/786
	5	65.3	86/248	46.1	363/673	0.2	1229/1231
	Total	13.4	4694/5419	79.2	987/4742	0.1	6558/6565
Aug 1982	1	97.0	15/496	92.4	18/237	88.0	296/2463
	2	96.6	81/2354	97.6	6/245	33.2	1136/1700
	3	92.9	107/1502	84.9	13/86	13.5	378/437
	4	90.4	33/345	90.0	30/301	3.9	772/803
	5	47.1	46/87	97.0	11/363	5.5	1176/1244
	Total	94.1	282/4784	93.7	78/1232	43.5	3758/6647
Sep 1982	1	†	†	8.7	21/23	85.8	44/309
	2	†	†	30.0	7/10	98.2	21/1146
	3	†	†	46.7	8/15	89.7	40/387
	4	†	†	69.4	11/36	2.4	763/782
	5	†	†	61.5	5/13	1.8	1180/1201
	Total	†	†	46.4	52/97	46.5	2048/3825

* data from Sawmill Spit collected in April of 1982.
† data unavailable.

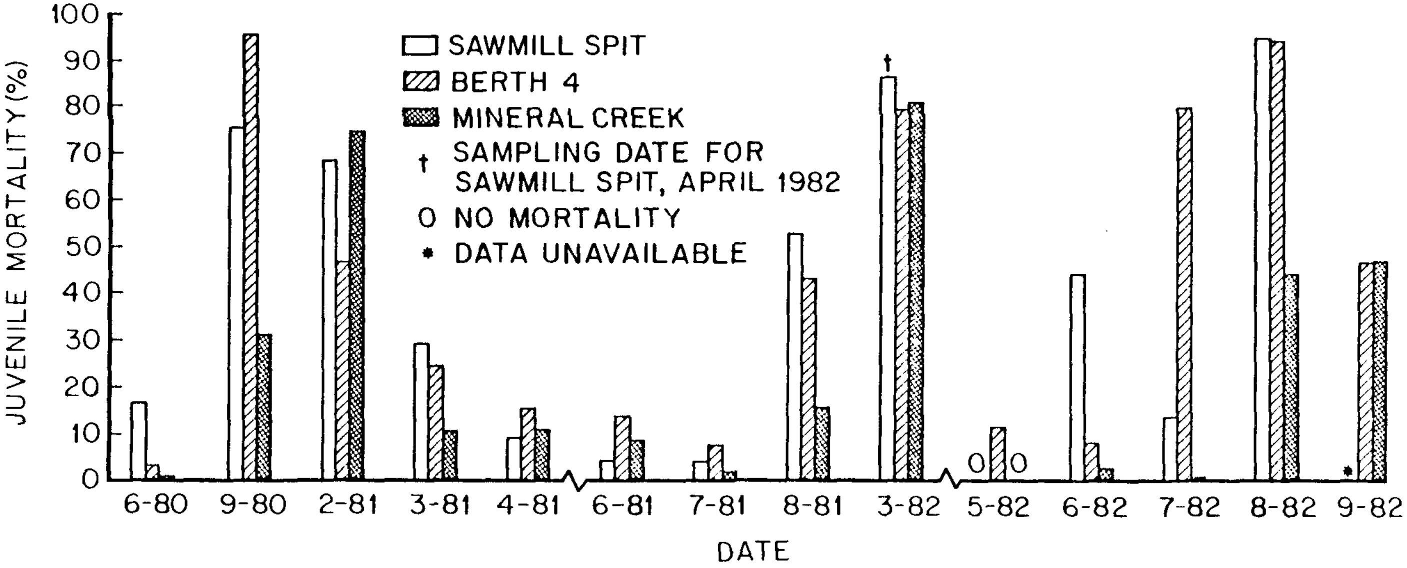

Figure 35. Juvenile percent mortality for *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Months illustrated represent times of data collection.

greater than at the other sites. Throughout the winter, however, juveniles at Mineral Creek died in significantly greater numbers than those at Sawmill Spit or Berth 4. The higher summer mortality at Sawmill Spit and Berth 4 occurred between the months of June and September 1980, when 75 and 95%, respectively, of all juveniles died (Table 29 and Fig. 35). The unusually high juvenile mortality occurring at Sawmill Spit and Berth 4 in the summer of 1980 was presumably the result of environmental stresses not ordinarily encountered by barnacles at the two sites. The high juvenile mortality at these sites may have resulted from the small oil spill which occurred within the Berth 4 area in April 1980.

The highest annual mortality of juveniles, from May 1981-March 1982 (April 1982 at Sawmill Spit) occurred at Sawmill Spit (90%), followed by Berth 4 (88%) and Mineral Creek (83%) (Table 27). No statistical difference emerged in comparisons of juvenile percent mortality from the Sawmill Spit and Berth 4 sites during 1981-82 (Appendix 5, Table 6). Both areas, however, were statistically different than Mineral Creek, each having a greater number of juvenile deaths annually than the latter area. No apparent trend in juvenile mortality relative to tidal position was noted, but, in general, barnacles between the mid and low tidal zones (tidal level 4) experienced the least annual mortality.

The greatest seasonal mortality for juveniles at all three sites occurred during the 1981-82 winter season (August 1981-March 1982) as opposed to the summer of 1981 (May-August 1981), at which time approximately 80% of juveniles at each location died (Table 28 and Fig. 35). Statistical differences in mortality between Sawmill Spit and Berth 4 are evident for the winter of 1981-82 (Appendix 5, Table 8). The percentage dying was significantly higher at Sawmill Spit (83.6%) than at Berth 4 (76.9%). No difference in juvenile mortality was observed for the winter of 1981-82 between either the Sawmill Spit or Berth 4 sites and Mineral Creek (80.1%). Mortality at both Sawmill Spit and Berth 4 during the summer season of 1981, although not as extreme as in the winter of 1981-82, was considerably higher than at Mineral Creek over the same time span. Barnacles at Berth 4 died in greater numbers during the summer season than did those from Sawmill Spit (47.5% as compared with 40.5%) (Appendix 5, Table 8).

Seasonal mortality values for the summer of 1982 indicate extremely high mortalities for juveniles at Sawmill Spit and Berth 4 and somewhat higher than typical summer mortalities for juveniles at Mineral Creek (Tables 28 and 29). Although results of Z-test analyses indicate significant differences in seasonal percent mortality for the three sites, the most apparent difference, based on p value comparisons, was between Mineral Creek and the other two sites, with the former site having a significantly lower percentage of deaths than either Sawmill Spit or Berth 4 (Appendix 5, Table 8). High mortality at Mineral Creek was observed in the mid to high zones only. A net recruitment of spat was observed at the lower levels. The high mortality values recorded for the three sites in the summer of 1982 were probably a result of warmer than average air temperatures and reduced precipitation in Port Valdez during this period (see Physical Environment section for further discussion).

A comparison of annual juvenile mortality data for 1980-81 and 1981-82 indicate that significant differences occurred between years at Sawmill Spit and Berth 4. A higher mortality was observed in 1981-82 at the former site (90.3% in 1981-82 as compared with 87.5% in 1980-81). At Berth 4, a higher mortality of juveniles occurred in 1980-81 (95.2% in 1980-81 as compared with 87.9% in 1981-82). No annual variation in mortality was observed for juveniles at Mineral Creek (81.3% in 1980-81, 82.5% in 1981-82) (Appendix 5, Table 9).

The percent mortality of juveniles at Sawmill Spit varied significantly between the three summer seasons sampled (Appendix 5, Table 10). The highest summer mortality (98.2%) occurred in 1982. The 1980 mortality (70.4%), though less than that observed in 1982 was significantly higher than during the summer of 1981 (40.5%). The same yearly trend was reflected by Berth 4 and Mineral Creek juveniles — the highest seasonal mortality occurred during the summer of 1982, followed by 1980 and 1981. See Appendix 5, Table 10 for data representing mortalities at Berth 4 and Mineral Creek. The summer of 1982 was warmer than average, with below normal levels of precipitation. The combined conditions of physical stress affected juveniles from all areas. The juveniles presumably died due to desiccation.

Winter percent mortality also varied between the years sampled (Appendix 5, Table 10). Extreme winter conditions in 1981-82 were responsible for a greater number of juvenile deaths at all sites than were condition in the winter of 1980-81.

CONCLUSIONS

Mortality of barnacles in Port Valdez is the result of a combination of (1) physical factors such as extreme temperatures, heavy suspended sediment load, and fluctuating salinity due to freshwater runoff, (2) biological factors such as inter- and intraspecific competition for food and space and predation, and (3) industrial activity.

Based on mortality values calculated for barnacles observed from April 1980-September 1982, it is apparent that adult mortality is considerably lower than that of juveniles at the three study sites. Sawmill Spit adult barnacles displayed somewhat lower mortality percentages than those from Berth 4 or Mineral Creek in 1980-81 (Table 24). For example, during 1980-81 the Sawmill Spit adult barnacles exhibited a mean mortality of 10.4% as compared to 46.3% and 21.7% at Berth 4 and Mineral Creek, respectively. Seasonal mortality data for 1980-81 (Table 25) reveal that most adults at Sawmill Spit and Mineral Creek died during the winter of 1980-81 (7.0% and 16.2%, respectively). However, over 30% of the adult population died during the summer of 1980 at Berth 4, possibly as a result of the small oil spill which occurred in the vicinity of Berth 4 in April 1980. In 1981-82, adult mortality rates (Table 24) averaged 33.7% at Berth 4 and 40.5% at Mineral Creek. Sawmill Spit adult barnacles displayed the highest mortality of the three sites in 1981-82, 57.5%. Adult mortality was highest during the summer of 1981 at Berth 4 (21.1%) and Mineral Creek (37.9%), but was more significant in the winter of 1981-82 at Sawmill Spit (55.2%) (Table 25), probably as the result of severe temperatures, wind, and ice accumulation occurring at this relatively exposed region of Port Valdez during this time (see Physical Environment section for further discussion). The mass adult mortality in the summer of 1981 at Mineral Creek (37.9%) was most likely the result of a large accumulation of silt and algae (see also discussion in Physical Environment section). In the summer of 1982, adult mortality was relatively high at all three locations (Table 25), possibly due to the extreme summer temperatures and low precipitation recorded for this period.

Annual juvenile mortality rates were extremely high (> 80%) at all sampling sites (Table 27) due to problems encountered subsequent to settling. Seasonal mortality data for juveniles (Table 28) indicate that during 1980-81, the majority of barnacles from Sawmill Spit and Berth 4 died during the summer months (70.4% and 93.9%, respectively). The greatest number of deaths at Mineral Creek (76.1%) occurred during the winter period (September 1980-April 1981). The many deaths in the summer of 1980 at Sawmill Spit and Berth 4 may have resulted from complications arising from the small oil spill which occurred in April 1980 in the vicinity of the Berth 4 site. During 1981-82, most juveniles died during the winter (Table 28). The summer of 1981, which was comparatively wet, provided the juveniles with improved conditions for survival (i.e., fewer desiccatory problems). However, during the winter, which was severe in 1981-82, many deaths were recorded, presumably as a result of the clear, cold weather accompanied by high winds and frequent ice formation (see Discussion in the section on the Physical Environment for further information). A high percentage of juveniles died from each site during the summer of 1982 (April-September 1982) (Table 28). The latter time period was characterized, in general, by warm, sunny days (high air temperatures with little precipitation). Juveniles died primarily as a result of desiccation. The high rate of mortality observed each year for juveniles indicates that newly settled spat are extremely susceptible to fluctuating environmental parameters.

SUMMARY

The boreo-arctic barnacle *Balanus balanoides* displays several behavioral adaptations and responses to life in northern waters, including the following:

(1) A rapid assimilation of organic material acquired during the limited period of food availability in the spring, resulting in a rapid increase in body weight.

(2) Reproduction limited to only one brood per year due to a seasonally limited food supply.

(3) Formation of larger, more yolky eggs than southern species of acorn barnacles, ensuring a food source for the developing embryos during the winter incubation period.

(4) Precise larval release synchronous with initiation of the spring phytoplankton bloom, providing offspring with potential for survival due to availability of food.

(5) Rapid juvenile growth rate (exponential) which is an adaptive advantage, since the intense spatial competition with other juveniles would favor more rapidly growing spat.

(6) No reproduction by the barnacles during the first year; thus, juveniles are able to partition all accumulated energy to shell growth.

(7) Continued annual shell growth at onset of maturity. Thus, greater egg production is possible in larger and older individuals. The continual shell growth is a reproductive strategy as well as a strategy of growth.

(8) Annual mortality is greater for juveniles (∿85%) than for adults (∿35%). Barnacle mortality results from a combination of physical environmental stresses (freshwater runoff, heightened sedimentation, desiccation), biological factors (inter- and intraspecific competition for food and space, and predation) and industrial pollutants (hydrocarbons).

The various biological parameters discussed in this thesis suggest that the barnacle population at Sawmill Spit is more successful than populations from either Berth 4 or Mineral Creek. Data derived from growth ring-increment measurements and body and reproductive tissue weights indicate that barnacles at Sawmill Spit, in contrast to individuals at Berth 4 and Mineral Creek, grow at a faster rate, live longer, produce more reproductive tissue, and partition energy more efficiently to needed areas. Mortality data reveal that survivorship, especially in the stable adult populations, is somewhat higher for Sawmill Spit barnacles than for those at the other two sites in most cases. Populations from Berth 4 and Mineral Creek demonstrate the same trends as observed at Sawmill Spit. However, biological activities (addition of shell material and formation of ovarian tissue) are typically reduced at Berth 4 and to a lesser extent at Mineral Creek in comparison with Sawmill Spit.

A major exception to the basic trends for *Balanus balanoides* as presented in this thesis was observed during the summer of 1980 at Berth 4. The decrease in body weight that generally occurs in early summer, as ovarian weight increases (indicative of energy transfer), did not occur to the same extent at Berth 4 as it did at Sawmill Spit and Mineral Creek (Fig. 30). The above anomaly was also reflected in the lowered REI value and the low mean ovarian weight displayed by Berth 4 barnacles in June and July of 1980. The reproductive weight values at Berth 4 throughout 1980-81, lower than the respective Sawmill Spit and Mineral Creek values (Fig. 6), were also greatly reduced in comparison with ovarian/lamellar weights for Berth 4 during 1981-82 (Figs. 7 and 9). A further consequence of the lowered ovarian weight at Berth 4 was reflected in the February 1981 fecundity data for mid-zone barnacles (Table 7). The fecundity in 1981 was less than for barnacles at this tidal height in the subsequent year. Barnacles at Berth 4 with these lowered fecundity values had higher than typical somatic tissue weights, which suggests the retention rather than transfer of storage components from the body to the ovary. Adult and juvenile mortality values at Berth 4 were also noticeably higher during the summer of 1980 than at other sites or times, as well (Tables 25, 26, 28, and 29; Figs. 28 and 29). All of these irregularities probably represent a biological response to the small oil spill which occurred in the immediate vicinity of Berth 4 in April 1980. Data indicate, however, that in the months following the spill, ovarian tissue development returned to normal and was similar to that observed for barnacles at the other two sites. Mortality decreased considerably at Berth 4 in subsequent months as well.

Data in other years also appear to reflect problems for the barnacles at Berth 4. The loss in somatic weight which typically occurs during the early summer (indicating energy transfer to ovarian and mantle tissue) was delayed for Berth 4 individuals during 1981 and 1982 (as was previously mentioned for 1980) (Fig. 31). The effects of the delay in transfer are reflected in the smaller growth-ring increment values (Tables 12 and 13) and lowered fecundities (Table 7) typical of the barnacles at Berth 4. Although biological activities for organisms here follow trends exhibited by barnacles from Sawmill Spit and Mineral Creek, in general, it seems that the intensity with which the processes occur is somewhat reduced in comparison with the other Port Valdez areas, possibly indicative of stress.

It should be re-emphasized that a major difference exists between the environments of the three locations. Sawmill Spit and Mineral Creek are characterized by typically flat or gently sloping substrates, while Berth 4 is distinct in having a vertical rocky shelf. The Mineral Creek site is seasonally influenced as well, by Mineral Creek itself, which is in very close proximity to the study site established here. These factors must be considered when discussing apparent biological differences between barnacle population at the three locations. Biological and physical differences at each site must be considered on a temporal basis. Year-to-year fluctuations can only be useful once general trends have been established. The lack of food availability data (i.e, primary productivity values) limits the discussion of annual and seasonal variations observed between sites. It is unknown to what extent seasonal bloom fluctuations influence biological processes of the barnacle in Port Valdez, but it is suspected that any such fluctuation would have a significant effect on the populations.

A timetable summarizing the expected annual physical and biological events in the life cycle of *Balanus balanoides* in Port Valdez, Alaska is included in Table 30.

Table 30. Timetable of expected annual events in the life cycle of *Balanus balanoides* in Port Valdez, Alaska.

January

Low temperatures - water and air

Low turbidity or suspended sediment load

Salinity high, > 30°/₀₀

No shell growth

Eyed embryos brooding in mantle cavity

Lamellar tissue weight increasing

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

February

Temperatures remain low

Turbidity remains low

Salinity high, > 30°/₀₀

No shell growth

Stage I Nauplii ready for spawning

Lamellar tissue weight increasing to winter maximum

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

March

Temperatures increasing

Turbidity increasing

Table 30. Continued.

Salinity high, > 30°/₀₀

Phytoplankton bloom detected

Shell growth initiated

Larvae are spawned, mantle cavity appears empty

Lamellar tissue weight decreasing rapidly

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

April

Temperatures increasing

Turbidity increasing

Salinity remains high, > 30°/₀₀

Intensive phytoplankton bloom continues

Shell growth continues

Ovarian tissue develops and weight increases

B. balanoides cyprids begin to settle and develop into spat

Somatic tissue weight rapidly increasing to annual maximum

May

Temperatures increasing rapidly

Turbidity increasing

Salinity decreasing

Phytoplankton bloom decreasing

Shell growth continues

Table 30. Continued.

Ovarian tissue weight reaches spring maximum

Male gametogenic tissue development begins

Major cyprid settlement occurs, spat abundant

Somatic tissue weight decreasing

June

Temperatures continue to rise

Turbidity high

Salinity decreasing rapidly

Phytoplankton bloom no longer observed

Shell growth continues

Ovarian tissue weight decreasing

Male gametogenic tissue development continues

Cyprid settlement continues, but to lesser degree

Somatic tissue weight decreasing

July

Temperatures rising

Turbidity remains high

Salinity continues to decrease

Shell growth continues

Ovarian tissue weight remains low

Male gametogenic tissue development continues

Cyprid settlement reduced

Somatic tissue weight increasing

Table 30. Continued.

August

Temperatures highest of the year

Turbidity starts to decrease

Salinity lowest of the year

Shell growth decreasing

Ovarian tissue weight increasing

Male gametogenic tissue reaches maturation

Fertilization of ovarian tissue begins

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Mass mortality of spat occurs

Somatic tissue weight increasing

September

Temperatures start to decline

Turbidity decreasing

Salinity increasing rapidly

Small fall bloom begins

Shell growth decreasing

Ovarian/lamellar tissue weight increasing

Fertilization continues

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight decreasing

Table 30. Continued.

October

Temperatures declining

Turbidity low

Salinity increasing rapidly

Small fall bloom reaches peak

Shell growth ceases

Lamellar tissue weight decreasing

Fertilization completed

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

November

Temperatures declining

Turbidity low

Salinity continues to increase

Small fall bloom declines

No shell growth

Lamellar tissue weight continues to decrease

Male gametogenic tissue deteriorates

Fertilized eggs are brooded in mantle cavity

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

Table 30. Continued.

December

Temperatures low

Turbidity low

Salinity high, > 30°/₀₀

No shell growth

Lamellar tissue weight reaches low and begins to increase again

Male gametogenic tissue absent

Eyed embryos present, as yet unhatched

Cyprid settlement low (probably settlement of *B. crenatus* and *B. glandula*)

Somatic tissue weight low

SUGGESTIONS FOR FUTURE STUDIES

The following is a review of the "biological tools" utilized in the present study for documentation of events in the life history of the barnacle, *Balanus balanoides* and for identification of difficulties encountered by the barnacle in the Port Valdez environment.

Reproductive tissue staging and ovarian/lamellar weight measurements are useful for the monitoring of barnacle populations, since data from these studies follow a general, predictable trend. Year-to-year fluctuations in these established patterns are readily recognizable and may indicate environmental disturbance of populations at a particular time. Fecundity studies reveal that a generally linear relationship exists between egg numbers and size (rostro-carinal diameter), volume (ℓ^3), body tissue weight, and year class. Annual variations in fecundity values are typical; thus, more than two years of data are needed in order to assess the "norm" for a given population. It is suggested that to be useful in a monitoring sense, fecundity values should be measured over several years to establish general trends. Thereafter, fluctuations which are substantially different from the basic fecundity pattern may reveal difficulties encountered by the barnacles during reproductive tissue development, and may indicate stress. A different technique for egg counting might be helpful in reducing error, such as use of a particle Coulter counter. Another parameter which may possibly identify stress is mean egg size for a particular location for any year. Settlement appears to be important for monitoring in a qualitative sense only. However, assessment of yearly patterns of settlement is useful for determining the success of reproductive efforts in any given year, and may indicate to what extent larvae have survived their period as plankters in the water column.

Aging and measurement techniques used in establishing growth-history tables and growth curves may provide evidence of stress or disturbance and are considered valuable for monitoring purposes. For example, the reduction in numbers in the 3rd year-class (barnacles spawned in 1979) at Sawmill Spit and Berth 4 in 1981 and the smaller growth-ring heights observed for the barnacles in this year-class indicate that these populations were subjected to unfavorable conditions. Growth-history tables are valuable in that annual growth for any year-class is clearly displayed, and can easily be read and compared to values for other year-classes at other sites. Growth curves illustrate typical patterns to be expected at each site and differences which may occur between sites and from year to year. In future monitoring programs, it is suggested that permanent sampling sites be established and individual barnacles marked for monthly R/C (rostro-carinal) diameter measurements in the field. This would be beneficial for seasonal growth determinations and for the establishment of specific growth rates, especially for juveniles. Growth measurements for the present study were conducted in the laboratory on specimens taken from replicate destructive plots. Vertical growth-ring height (a new technique developed for this study) was used, since it is easier and more accurate to measure for specimens taken to the laboratory for examination; these specimens are often crushed or broken.

The employment of mortality plates to determine the degree of survivorship of adult and juvenile barnacles is a highly satisfactory tool for the monitoring of barnacle populations. The season of greatest mortality, and the tidal height or location with the greatest barnacle losses are readily discernible from the data provided by the plates. Differences in percent mortality from year to year may be indicative of stress or disturbance in an area. For example, the high degree of adult and juvenile mortality observed during the summer of 1980 at Berth 4 probably reflects transient effects of a small oil spill which occurred within the area in April of that year. It may be desirable statistically in the future to establish two replicate plates in the high, mid-, and low intertidal zone of each beach instead of choosing 5 sites on a transect. Some investigators prefer photography as a tool in assessing percent mortality. However, in the current study, the method in use appears to be the only technique applicable to Port Valdez, since at some locations extensive algal covering present in the plots would make photographic methods difficult. The algae obviously should not be removed, in order to ensure maintenance of an undisturbed environment.

Body-weight measurements of *Balanus balanoides* taken throughout the year are useful for establishing yearly patterns of fluctuation in body weight and in determining the timing in the allocation of energy from body tissue storage sites to various metabolic processes. The use of body weight measurements in the calculation of a Reproductive Effort Index (REI) is another example of the value of body-weight measurements.

The linear regression-slope values established in the present study via regression analyses (dry body vs. dry valve weight) assess fluctuations in somatic tissue weight of barnacles in time. Identification of fluctuations in body weight appears to be one of the most useful monitoring tools in the present study. Since body weight depends on other well-documented life history events (feeding, reproduction, growth), significant variation from established trends should indicate that disturbances have occurred which have altered the expected progression of biological events.

Increments of seasonal shell growth and patterns of reproductive tissue fluctuation are important in order to estimate the major period of energy partitioning by somatic tissue. Energy from the body is allocated to the mantle and ovarian tissues during the summer months for shell growth and gametogenic tissue development.

Other studies which may have been desirable include the establishment of an annual energy budget to identify the degree of energy expenditure to other biological processes not considered here (i.e., respiration, fecal pellet production, moulting). Also, an estimate of larval survivorship would be of interest. Finally, in the future, it is recommended that a quantitative assessment of primary productivity be considered. The quality and quantity of food available to a population is of great importance, especially when attempting to explain variations from the annual expected life-history events of the population.

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APPENDIX 1

Statistical Analysis of Weather Data

Table 1. Between-year comparisons of monthly air temperatures (°C) recorded for Valdez, Alaska, April 1980-September 1982. AW = Aspin-Welch test, t = Student's t-test, * = significant at $\alpha = 0.05$, NS = not significant.

Date	Mean air temperature (°C)	SD	Test used	Test statistic
January				
1981	1.0	1.8	A-W	12.063*
1982	9.1	4.3		
February				
1981	-2.8	3.7	A-W	1.374NS
1982	-4.5	5.4		
March				
1981	1.3	1.8	A-W	4.754*
1982	-1.4	2.6		
April				
1980	4.3	1.7	A-W	1.940NS
1981	3.2	2.6		
1980	4.3	1.7	A-W	4.055*
1982	2.0	2.6		
1981	3.2	2.6	t	1.788NS
1982	2.0	2.6		
May				
1980	7.3	0.9	A-W	-6.090*
1981	9.9	2.2		
1980	7.3	0.9	A-W	-0.217NS
1982	7.4	2.4		
1981	9.9	2.2	t	4.275*
1982	7.4	2.4		
June				
1980	10.8	1.8	t	-1.349NS
1981	11.5	2.2		
1980	10.8	1.8	t	-0.611NS
1982	11.1	2.0		
1981	11.5	2.2	t	0.737NS
1982	11.1	2.0		
July				
1980	12.7	1.7	A-W	2.141*
1981	11.9	1.2		

Table 1. Continued.

Date	Mean air temperature (°C)	SD	Test used	Test statistic
July (continued)				
1980	12.7	1.7	t	0.758NS
1982	12.4	1.4		
1981	11.9	1.2	t	-1.510NS
1982	12.4	1.4		
August				
1980	11.1	1.7	t	0.437NS
1981	10.9	1.9		
1980	11.1	1.7	t	-3.100*
1982	12.4	1.6		
1981	10.9	1.9	t	-3.362*
1982	12.4	1.6		
September				
1980	8.4	1.7	t	0.591NS
1981	8.1	2.2		
1980	8.4	1.7	t	0.683NS
1982	8.1	1.7		
1981	8.1	2.2	t	0.000NS
1982	8.1	1.7		
October				
1980	3.9	2.3	t	-0.685NS
1981	4.3	2.3		
November				
1980	1.2	1.6	A-W	4.891*
1981	-2.4	3.7		
December				
1980	-9.6	5.5	t	-4.271*
1981	-4.1	4.6		

APPENDIX 2

Supplemental Reproductive Biology Data and Statistical Analyses

Table 1. Reproductive tissue weight data for *Balanus balanoides* from the high, mid, and low intertidal of Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-October 1982. n = number of individuals examined, SD = standard deviation, * = data unavailable.

	High			Mid			Low		
Date	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Sawmill Spit									
4-80	0	*	*	0	*	*	0	*	*
6-80	20	1.9	1.5	48	6.6	3.8	45	12.1	6.9
7-80	0	*	*	40	3.7	3.2	35	5.4	3.2
8-80	16	2.1	1.7	53	4.8	2.9	43	7.2	4.3
9-80	19	3.2	3.7	44	8.6	5.9	36	11.3	9.9
10-80	25	6.1	4.3	25	7.3	5.0	26	17.9	7.3
11-80	21	4.3	3.0	22	5.8	5.7	19	6.9	9.5
12-80	0	*	*	0	*	*	0	*	*
1-81	22	2.1	3.0	23	5.6	4.7	19	5.0	5.0
2-81	29	4.4	2.8	30	8.5	6.0	35	9.2	5.5
3-81	25	2.2	2.9	30	4.5	4.5	30	8.3	10.9
4-81	20	0.3	0.3	28	0.6	0.4	28	0.6	0.4
5-81	27	4.5	4.1	30	0.4	0.6	49	3.0	3.5
6-81	30	7.3	5.7	56	11.7	4.4	56	7.3	7.8
7-81	21	5.8	3.0	28	2.8	3.2	25	2.0	1.2
8-81a	15	2.6	2.3	24	3.5	4.3	12	2.6	2.1
b	25	4.7	3.0	40	4.9	3.4	30	6.8	6.3
9-81	28	5.8	3.6	30	7.1	3.3	30	11.6	5.6
10-81	0	*	*	23	10.8	10.0	0	*	*
11-81	0	*	*	25	9.0	11.3	0	*	*
1-82	0	*	*	26	5.2	7.9	0	*	*
2-82	0	*	*	0	*	*	0	*	*
3-82	18	1.5	2.9	51	9.1	6.8	30	5.7	5.3
4-82	21	0.7	0.5	30	1.2	1.0	30	1.4	2.1
5-82	15	5.3	4.8	28	6.6	3.8	28	5.0	4.0
6-82	22	3.2	3.0	30	7.7	3.8	30	9.8	7.3
7-82	19	3.1	2.8	30	10.7	4.2	29	4.1	2.6
8-82	25	5.8	3.5	26	5.6	2.8	27	1.7	1.1
9-82	0	*	*	30	6.8	3.9	0	*	*
10-82	0	*	*	29	4.1	3.0	0	*	*
Berth 4									
4-80	20	3.2	1.7	7	5.4	5.9	0	*	*
6-80	20	2.3	2.0	39	3.0	3.3	0	*	*
7-80	0	*	*	24	2.4	1.1	16	0.3	0.3

Table 1. Continued.

	High			Mid			Low		
Date	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Berth 4 (continued)									
8-80	22	1.2	0.5	42	1.6	0.9	47	1.0	0.6
9-80	24	1.1	1.1	50	4.6	1.7	38	1.8	1.7
10-80	24	3.7	5.0	25	5.0	4.7	24	4.0	3.0
11-80	16	4.5	4.6	19	1.5	2.0	24	1.8	2.3
12-80	6	1.3	1.0	14	2.3	1.5	15	1.2	1.2
1-81	22	2.4	2.5	17	2.2	2.3	0	*	*
2-81	14	0.3	0.5	26	1.4	2.0	13	1.1	2.0
3-81	28	1.8	2.3	29	1.8	2.2	30	1.1	1.9
4-81	19	0.2	0.2	22	0.1	0.1	24	0.2	0.2
5-81	20	1.9	1.8	0	*	*	30	2.7	1.3
6-81	18	3.0	2.1	0	*	*	29	5.1	2.1
7-81	13	2.5	1.0	30	4.4	2.2	30	4.2	1.7
8-81a	0	*	*	9	2.9	1.9	20	1.2	0.9
b	13	1.7	0.8	29	3.1	1.9	30	2.9	2.3
9-81	17	4.1	3.5	28	3.5	2.2	29	3.0	2.0
10-81	0	*	*	22	10.9	8.9	0	*	*
11-81	0	*	*	23	6.2	6.7	0	*	*
1-82	0	*	*	22	7.8	7.2	0	*	*
2-82	0	*	*	0	*	*	0	*	*
3-82	9	2.8	3.4	40	2.2	2.9	29	4.0	3.2
4-82	28	1.3	1.8	30	0.9	1.7	30	1.0	1.6
5-82	13	7.6	7.9	21	3.2	1.6	29	1.0	1.3
6-82	18	3.7	2.5	30	7.0	5.0	30	3.2	2.0
7-82	6	2.6	1.9	23	4.1	2.2	29	5.3	3.7
8-82	17	4.3	3.2	22	2.5	2.2	24	2.4	1.1
9-82	28	3.4	2.5	30	3.0	1.6	30	3.2	1.4
10-82	0	*	*	0	*	*	0	*	*
Mineral Creek									
4-80	14	2.5	2.6	42	3.9	1.7	28	2.3	1.2
6-80	22	2.1	2.8	46	3.6	4.0	52	4.5	3.1
7-80	8	1.7	1.2	23	3.9	2.9	28	1.8	0.9
8-80	18	1.9	1.1	43	3.0	2.0	50	2.7	2.5
9-80	22	7.7	4.1	47	7.1	5.2	50	9.2	4.7
10-80	24	6.2	5.9	22	8.6	4.6	21	7.0	7.8
11-80	5	0.7	0.4	19	5.1	4.3	15	4.4	4.5
12-80	4	1.2	2.5	11	3.6	4.6	6	1.0	0.7
1-81	12	4.0	4.0	22	3.5	4.3	13	2.5	3.2
2-81	28	3.6	3.1	29	4.7	2.8	26	2.4	1.5

Table 1. Continued.

	High			Mid			Low		
Date	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Mineral Creek (continued)									
3-81	28	3.7	3.9	30	1.3	2.2	29	0.6	1.2
4-81	18	0.5	0.3	30	0.2	0.3	16	0.5	0.7
5-81	30	5.7	4.8	30	3.8	1.7	29	2.1	1.4
6-81	27	6.8	3.6	30	7.9	2.7	30	4.2	2.0
7-81	29	4.2	2.1	29	2.0	0.9	29	3.7	2.4
8-81a	24	2.9	3.1	19	4.4	3.2	24	2.7	1.5
b	17	4.6	3.2	29	4.7	2.0	26	3.9	1.8
9-81	22	3.1	1.5	30	6.2	2.1	30	2.7	2.4
10-81	0	*	*	25	8.4	6.6	0	*	*
11-81	0	*	*	25	7.8	4.9	0	*	*
1-82	0	*	*	25	4.7	4.9	0	*	*
2-82	0	*	*	25	6.3	6.0	0	*	*
3-82	25	6.7	5.5	30	5.7	4.1	30	6.8	5.8
4-82	21	0.1	0.5	30	0.3	0.8	30	1.4	0.8
5-82	15	3.0	2.3	29	3.2	2.7	29	4.0	2.6
6-82	22	3.1	2.7	29	4.9	2.4	24	5.2	3.4
7-82	10	3.2	2.4	29	5.8	4.2	26	3.9	1.9
8-82	14	3.8	2.9	29	4.6	3.2	21	3.0	1.5
9-82	0	*	*	30	4.1	3.4	0	*	*
10-82	0	*	*	30	5.1	3.0	0	*	*

Table 2. Results of an analysis of variance (ANOVA) used to compare reproductive tissue weights of barnacles from Sawmill Spit, Berth 4, and Mineral Creek for selected times in 1980, 1981, and 1982. df = degrees of freedom, SS = sum of squares, MS = mean square.

Source of variation	df	SS	MS	Computed F	Tabled F
June 1980					
"Between" groups	2	264	132.0	9.30	($\alpha=0.05$) 3.07
"Within" groups	124	1764	14.2		($\alpha=0.01$) 4.78
Total	126	2028			
Result: SS significantly different B4, MC					
September 1980					
"Between" groups	2	443	221.5	11.97	($\alpha=0.05$) 3.07
"Within" groups	127	2348	18.5		($\alpha=0.01$) 4.78
Total	129	2791			
Result: SS, MC significantly different B4					
November 1980					
"Between" groups	2	227	113.5	6.24	($\alpha=0.05$) 3.20
"Within" groups	47	857	18.2		($\alpha=0.01$) 5.09
Total	49	1084			
Result: SS significantly different B4					
February 1981					
"Between" groups	2	516	258.0	15.45	($\alpha=0.05$) 3.13
"Within" groups	71	1186	16.7		($\alpha=0.01$) 4.92
Total	73	1702			
Result: SS significantly different B4, MC					
April 1981					
"Between" groups	2	1.07	0.54	1.50	($\alpha=0.05$) 4.04
"Within" groups	49	17.76	0.36		($\alpha=0.01$) 7.18
Total	51	18.83			
Result: No significant difference between SS, B4, MC					
July 1981					
"Between" groups	2	102	51.0	12.14	($\alpha=0.05$) 3.96
"Within" groups	86	358	4.2		($\alpha=0.01$) 6.96
Total	88	460			
Result: B4 significantly different SS, MC					

Table 2. Continued.

Source of variation	df	SS	MS	Computed F	Tabled F
October 1981					
"Between" groups	2	116	58.0	0.83	
"Within" groups	62	4356	70.3		F < 1; NS
Total	64	4472			
Result: No significant difference between SS, B4, MC					
January 1982					
"Between" groups	2	235	117.5	2.65	(α=0.05) 3.14
"Within" groups	68	3015	44.3		(α=0.01) 4.94
Total	70	3250			
Result: No significant difference between SS, B4, MC					
June 1982					
"Between" groups	2	131	65.5	4.43	(α=0.05) 3.11
"Within" groups	85	1255	14.8		(α=0.01) 4.88
Total	87	1386			
Result: SS significantly different MC					
August 1982					
"Between" groups	2	83	41.5	5.32	(α=0.05) 3.13
"Within" groups	71	553	7.8		(α=0.01) 4.92
Total	73	636			
Result: SS significantly different B4					
September 1982					
"Between" groups	2	295	147.5	14.60	(α=0.05) 3.11
"Within" groups	86	870	10.1		(α=0.01) 4.88
Total	88	1165			
Result: SS significantly different B4, MC					

Table 3. Results of between-year comparisons (1980-81 vs 1981-82) in reproductive tissue weight for barnacles in the mid zone of Sawmill Spit, Berth 4, and Mineral Creek. n = number of individuals examined, $\bar{x}$ = mean, SD = standard deviation, t = Student's t-test, A-W = Aspin-Welch test, * = significant at α = 0.05, NS = not significant.

Dates of comparison	n	$\bar{x}$	SD	Test used	Test statistic
Sawmill Spit					
11 June 1980	50	6.7	3.8	t	-6.225*
2 June 1981	56	11.7	4.4		
29 July 1980	40	3.7	3.2	A-W	0 NS
1 August 1981	23	3.7	4.3		
28 August 1980	50	5.0	2.9	A-W	-0.811NS
30 August 1981	39	5.8	5.6		
25 September 1980	44	8.6	5.9	A-W	1.396NS
15 September 1981	30	7.1	3.3		
25 October 1980	24	7.6	4.8	A-W	-1.844NS
30 October 1981	19	12.2	10.0		
23 November 1980	18	7.0	5.5	A-W	-0.895NS
29 November 1981	25	9.3	11.1		
20 January 1981	19	6.8	4.3	A-W	0.871NS
12 January 1982	26	5.2	7.9		
5 March 1981	20	6.8	3.9	A-W	-2.261*
7 March 1982	49	9.8	7.0		
Berth 4					
16 April 1980	5	2.1	5.5	A-W	0.768NS
4 April 1981	10	0.2	0.8		
29 July 1980	24	2.4	1.1	A-W	-0.654NS
2 August 1981	10	2.8	1.8		
28 August 1980	42	1.6	0.9	A-W	-3.956*
31 August 1981	29	3.1	1.9		
25 September 1980	50	4.6	1.7	t	2.462*
14 September 1981	28	3.5	2.2		
27 October 1980	22	5.6	4.6	A-W	-2.481*
29 October 1981	22	10.9	8.9		
21 November 1980	15	1.9	2.1	A-W	-3.393*
29 November 1981	21	6.1	5.1		

Table 3. Continued.

Dates of comparison	n	$\bar{x}$	SD	Test used	Test statistic
Berth 4 (continued)					
19 January 1981	13	2.9	2.2	A-W	-3.183*
12 January 1982	21	8.2	7.1		
6 March 1981	18	2.9	2.1	t	-0.996NS
8 March 1982	25	3.7	2.9		
Mineral Creek					
13 June 1980	44	3.8	4.0	A-W	-5.264*
1 June 1981	30	7.9	2.7		
30 July 1980	23	3.9	2.9	t	-0.531NS
31 July 1981	19	4.4	3.2		
29 August 1980	43	3.0	2.0	t	-3.783*
29 August 1981	30	4.8	2.0		
24 September 1980	36	8.6	4.9	A-W	2.660*
16 September 1981	30	6.2	2.1		
25 October 1980	21	9.0	4.3	A-W	-0.062NS
27 October 1981	23	9.1	6.3		
22 November 1980	17	5.7	4.1	t	-2.309*
27 November 1981	22	8.8	4.2		
18 January 1981	19	4.0	4.4	t	-0.625NS
10 January 1982	24	4.9	4.9		
15 February 1981	28	4.9	2.6	t	-2.196*
19 February 1982	20	7.9	5.7		
4 March 1981	11	3.6	2.3	A-W	-2.470*
6 March 1982	28	6.1	3.9		

Table 4. Results of between-year comparisons of fecundity, body weight, and R/C diameter data for *Balanus balanoides* from high, mid, low, and combined intertidal heights at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska. $\bar{x}$ = mean, SD = standard deviation, n = number of individuals examined, AW = Aspin-Welch test, t = Student's t-test, * = significant at $\alpha = 0.05$, NS = not significant.

Year-Zone	$\bar{x}$	SD	n	Test used	Test statistic
SAWMILL SPIT					
Fecundity					
1981-High	4303	2805	18	A-W	4.928*
1982-High	757	1024	13		
1981-Mid	4926	2631	49	A-W	6.115*
1982-Mid	2079	1374	25		
1981-Low	7223	3054	40	A-W	11.046*
1982-Low	1291	1198	26		
1981-All	5680	3051	107	A-W	12.389*
1982-All	1490	1324	64		
Body Weight					
1981-High	4.1	2.2	18	A-W	6.243*
1982-High	0.7	0.6	13		
1981-Mid	3.9	1.6	49	A-W	12.801*
1982-Mid	0.8	0.4	25		
1981-Low	5.3	2.3	40	A-W	12.096*
1982-Low	0.8	0.4	26		
1981-All	4.5	2.1	107	A-W	17.696*
1982-All	0.8	0.4	64		
R/C Diameter					
1981-High	12.4	2.6	18	t	4.753*
1982-High	8.3	2.0	13		
1981-Mid	13.5	2.5	49	A-W	9.761*
1982-Mid	9.3	1.2	25		
1981-Low	13.5	2.1	40	A-W	10.820*
1982-Low	8.7	1.5	26		
1981-All	13.3	2.4	107	A-W	14.750*
1982-All	8.9	1.5	64		

Table 4. Continued.

Year-Zone	$\bar{x}$	SD	n	Test used	Test statistic
BERTH 4					
Fecundity					
1981-High	3572	2180	21	t	0.401NS
1982-High	2935	1313	2		
1981-Mid	1459	697	50	A-W	-6.253*
1982-Mid	3999	1365	12		
1981-Low	1706	4134	20	A-W	0.836NS
1982-Low	907	1144	22		
1981-All	2001	2385	91	t	-0.110NS
1982-All	2050	1894	36		
Body Weight					
1981-High	2.7	1.1	21	t	1.004NS
1982-High	1.9	0.4	2		
1981-Mid	1.3	0.4	50	t	2.333*
1982-Mid	1.0	0.4	12		
1981-Low	2.0	2.9	20	A-W	2.149*
1982-Low	0.6	0.3	22		
1981-All	1.6	1.4	91	A-W	4.740*
1982-All	0.8	0.5	36		
R/C Diameter					
1981-High	12.0	2.2	21	t	-0.431NS
1982-High	12.7	2.1	2		
1981-Mid	9.8	1.2	50	t	-3.157*
1982-Mid	11.0	1.1	12		
1981-Low	7.9	2.2	20	A-W	-1.738NS
1982-Low	8.9	1.4	22		
1981-All	9.9	2.2	91	t	0.242NS
1982-All	9.8	1.8	36		

Table 4. Continued.

Year-Zone	$\bar{x}$	SD	n	Test used	Test statistic
MINERAL CREEK					
Fecundity					
1981-High	1361	1633	22	A-W	-4.820*
1982-High	4893	3024	22		
1981-Mid	844	761	35	A-W	-7.714*
1982-Mid	3327	1669	32		
1981-Low	1914	1340	32	A-W	-0.974NS
1982-Low	3276	3897	8		
1981-All	1356	1308	89	A-W	-6.982*
1982-All	3876	2624	62		
Body Weight					
1981-High	2.1	1.4	22	t	-2.057*
1982-High	3.0	1.5	22		
1981-Mid	1.9	1.2	35	t	-0.369NS
1982-Mid	2.0	1.0	32		
1981-Low	1.7	0.5	32	A-W	-0.692NS
1982-Low	2.0	1.2	8		
1981-All	1.9	1.1	89	t	-2.549*
1982-All	2.4	1.3	62		
R/C Diameter					
1981-High	9.9	2.4	22	t	-3.025*
1982-High	12.0	2.2	22		
1981-Mid	9.3	2.5	35	A-W	-1.350NS
1982-Mid	10.0	1.7	32		
1981-Low	8.8	1.3	32	A-W	-1.018NS
1982-Low	9.8	2.7	8		
1981-All	9.3	2.1	89	t	-3.952*
1982-All	10.7	2.2	62		

Table 5. Results of between-year comparisons of fecundity for a given year class at Sawmill Spit, Berth 4, and Mineral Creek. $\bar{x}$ = mean, SD = standard deviation, n = number of individuals examined, A-W = Aspin-Welch test, t = Student's t-test, * = significant at $\alpha = 0.05$, NS = not significant.

Year class	Year	$\bar{x}$	SD	n	Test used	Test statistic
Sawmill Spit						
2	1981	3330	2161	5	A-W	3.259*
	1982	169	115	2		
3	1981	4223	2232	43	A-W	7.997*
	1982	1095	904	22		
4	1981	7555	2959	45	A-W	12.982*
	1982	1430	1059	40		
5	1981	4253	2002	11	t	0.411NS
	1982	3814	1924	5		
Berth 4						
3	1981	1832	2593	50	A-W	2.053*
	1982	888	1209	19		
4	1981	2836	1984	16	t	0.602NS
	1982	2244	2581	7		
5	1981	4733	2520	6	A-W	0.980NS
	1982	3668	1103	10		
Mineral Creek						
3	1981	1947	1318	30	A-W	-2.186*
	1982	2798	1784	34		
4	1981	2308	1674	4	t	-1.597NS
	1982	3880	1713	12		
5	1981	1828	632	2	t	-2.203NS
	1982	6288	2727	8		

Table 6. Cyprid settlement of *Balanus balanoides* at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, June 1980-September 1982. Numbers of individuals settling at each of five tidal heights and the mean numbers for all tidal heights are included. Tidal height 1 is the highest intertidal height, 5 the lowest.

	Tidal Height																	
	Sawmill Spit						Berth 4						Mineral Creek					
Time	1	2	3	4	5	$\bar{x}$	1	2	3	4	5	$\bar{x}$	1	2	3	4	5	$\bar{x}$
6-80	109	41	92	21	90	71	21	13	125	61	100	64	105	66	17	76	176	88
9-80	6	60	13	22	21	24	6	5	4	31	7	11	17	21	13	42	127	44
2-81	0	0	26	*	16	11	0	0	2	6	62	14	3	3	2	15	28	10
3-81	0	3	6	3	22	7	0	0	1	3	65	14	8	17	1	14	42	16
4-81	0	1	3	4	33	8	0	0	1	1	14	3	3	5	2	7	32	10
5-81	507	23	50	*	171	188	3	5	403	72	1067	310	751	467	726	*	*	648
6-81	145	9	15	1	21	38	0	7	57	8	91	33	47	41	75	4	2	34
7-81	24	17	5	0	6	10	0	4	9	1	3	3	5	0	0	3	0	2
8-81	15	9	15	2	13	11	0	3	15	4	4	5	30	43	35	1	0	22
3-82†	15	0	0	0	2	3	0	6	7	2	6	4	1	6	7	0	0	3
5-82	560	2634	3987	569	914	1733	182	863	2566	451	827	978	2470	1663	431	748	1092	1281
6-82	95	101	207	68	45	103	66	150	176	44	31	93	6	4	46	90	149	59
7-82	32	39	3	15	1	18	*	3	1	4	0	2	4	49	3	18	15	18
8-82	5	10	9	6	0	6	5	4	2	6	2	4	13	10	9	10	25	13
9-82	*	*	*	*	*	*	2	6	1	3	1	3	10	3	0	3	1	3

* data unavailable.

5-81 numbers are estimated, based on 4-81 settlement data.

† sampling date for Sawmill Spit, April 1982.

APPENDIX 3

Supplemental Annual Growth Data and Statistical Analyses

Table 1. T-test statistics for between-site comparisons of annual shell growth for *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, 1981 and 1982. SD = standard deviation, n = number of individuals measured, t = Student's t-test, A-W = Aspin-Welch test, * = significant at α = 0.05, NS = not significant.

Growth-Ring	Location	Mean growth ring height	SD	n	Test used	Test statistic
1981						
1	SS	1.24	0.33	649	t	6.339*
	B4	1.12	0.32	543		
	SS	1.24	0.33	649	A-W	13.061*
	MC	1.04	0.28	1176		
	B4	1.12	0.32	543	A-W	5.007*
	MC	1.04	0.28	1176		
2	SS	3.05	0.89	542	A-W	10.151*
	B4	2.52	0.72	410		
	SS	3.05	0.89	542	A-W	12.091*
	MC	2.50	0.80	1053		
	B4	2.52	0.72	410	A-W	0.462NS
	MC	2.50	0.80	1053		
3	SS	4.29	1.01	318	A-W	9.323*
	B4	3.61	0.89	375		
	SS	4.29	1.01	318	A-W	3.578*
	MC	4.05	1.10	937		

Table 1. Continued.

Growth-Ring	Location	Mean growth ring height	SD	n	Test used	Test statistic
1981 (continued)						
3	B4	3.61	0.89	375	A-W	-7.542*
	MC	4.05	1.10	937		
4	SS	5.86	1.07	306	t	14.664*
	B4	4.70	0.98	367		
	SS	5.86	1.07	306	t	12.346*
	MC	4.90	1.12	588		
	B4	4.70	0.98	367	A-W	-2.902*
	MC	4.90	1.12	588		
5	SS	7.33	1.20	285	A-W	12.539*
	B4	6.18	1.04	322		
	SS	7.33	1.20	285	A-W	19.591*
	MC	5.53	1.02	307		
	B4	6.18	1.04	322	t	7.909*
	MC	5.53	1.02	307		
6	SS	8.57	1.38	149	t	7.049*
	B4	6.89	1.24	41		
	SS	8.57	1.38	149	A-W	14.387*
	MC	6.37	1.07	108		
	B4	6.89	1.24	41	t	2.534*
	MC	6.37	1.07	108		

Table 1. Continued.

Growth-Ring	Location	Mean growth ring height	SD	n	Test used	Test statistic
1981 (continued)						
7	SS	9.64	1.50	80	t	5.291*
	B4	6.56	1.13	7		
	SS	9.64	1.50	80	t	9.819*
	MC	7.04	1.23	44		
	B4	6.56	1.13	7	t	-0.968NS
	MC	7.04	1.23	44		
8	SS	10.87	1.75	50	t	7.008*
	MC	7.77	1.30	19		
1982						
1	SS	1.14	0.26	548	A-W	4.110*
	B4	1.07	0.30	540		
	SS	1.14	0.26	548	A-W	14.915*
	MC	0.94	0.18	574		
	B4	1.07	0.30	540	A-W	8.703*
	MC	0.94	0.18	574		
2	SS	3.11	0.89	468	A-W	13.319*
	B4	2.38	0.78	464		
	SS	3.11	0.89	468	A-W	14.850*
	MC	2.37	0.63	502		

Table 1. Continued.

Growth-Ring	Location	Mean growth ring height	SD	n	Test used	Test statistic
1982 (continued)						
2	B4	2.38	0.78	464	A-W	0.218NS
	MC	2.37	0.63	502		
3	SS	4.05	0.83	255	A-W	6.245*
	B4	3.56	0.92	245		
	SS	4.05	0.83	255	t	2.621*
	MC	3.87	0.86	379		
	B4	3.56	0.92	245	t	-4.278*
	MC	3.87	0.86	379		
4	SS	4.93	1.04	107	A-W	2.292*
	B4	4.66	0.81	174		
	SS	4.93	1.04	107	t	0.000NS
	MC	4.93	0.92	293		
	B4	4.66	0.81	174	A-W	-3.309*
	MC	4.93	0.92	293		
5	SS	6.60	0.84	60	A-W	4.563*
	B4	5.96	1.10	153		
	SS	6.60	0.84	60	t	7.773*
	MC	5.55	0.89	140		
	B4	5.96	1.10	153	A-W	3.520*
	MC	5.55	0.89	140		

Table 1. Continued.

Growth-Ring	Location	Mean growth ring height	SD	n	Test used	Test statistic
1981 (continued)						
6	SS	7.16	0.74	51	A-W	4.682*
	B4	6.21	1.57	81		
	SS	7.16	0.74	51	t	5.970*
	MC	6.32	0.77	67		
	B4	6.21	1.57	81	A-W	-0.555NS
	MC	6.32	0.77	67		
7	SS	7.90	0.99	25	t	2.334*
	B4	7.07	1.06	12		
	SS	7.90	0.99	25	t	4.115*
	MC	6.92	0.87	37		
	B4	7.07	1.06	12	t	0.492NS
	MC	6.92	0.87	37		
8	SS	8.72	1.16	17	A-W	6.555*
	MC	6.63	0.30	4		

Table 2. T-test statistics for within-site comparisons of annual shell growth for *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, 1981 and 1982. SD = standard deviation, n = number of individuals measured, A-W = Aspin-Welch test, t = Student's t test, * = significant at α = 0.05, NS = not significant.

Growth ring	Year	Mean growth ring height	SD	n	Test used	Test statistic
Sawmill Spit						
1	1981	1.24	0.33	649	A-W	5.861*
	1982	1.14	0.26	548		
2	1981	3.05	0.89	542	t	-1.068NS
	1982	3.11	0.89	468		
3	1981	4.29	1.01	318	A-W	3.122*
	1982	4.05	0.83	255		
4	1981	5.86	1.07	306	t	7.795*
	1982	4.93	1.04	107		
5	1981	7.33	1.20	285	A-W	5.630*
	1982	6.60	0.84	60		
6	1981	8.57	1.38	149	A-W	9.194*
	1982	7.16	0.74	51		
7	1981	9.64	1.50	80	A-W	6.706*
	1982	7.90	0.99	25		
8	1981	10.87	1.75	50	A-W	5.738*
	1982	8.72	1.16	17		

Table 2. Continued.

Growth ring	Year	Mean growth ring height	SD	n	Test used	Test statistic
Sawmill Spit (Continued)						
9	1981	11.72	1.61	19	t	4.168*
	1982	9.12	1.38	12		
10	1981	13.00	1.28	8	t	3.469*
	1982	9.83	1.57	3		
Berth 4						
1	1981	1.12	0.32	543	t	2.652*
	1982	1.07	0.30	540		
2	1981	2.52	0.72	410	A-W	2.759*
	1982	2.38	0.78	464		
3	1981	3.61	0.89	375	t	0.675NS
	1982	3.56	0.92	245		
4	1981	4.70	0.98	367	A-W	0.500NS
	1982	4.66	0.81	174		
5	1981	6.18	1.04	322	t	2.114*
	1982	5.96	1.10	153		
6	1981	6.89	1.24	41	A-W	2.609*
	1982	6.21	1.57	81		
7	1981	6.56	1.13	7	t	-0.988NS
	1982	7.07	1.06	12		

Table 2. Continued.

Growth ring	Year	Mean growth ring height	SD	n	Test used	Test statistic
Mineral Creek						
1	1981	1.04	0.28	1176	A-W	9.013*
	1982	0.94	0.18	574		
2	1981	2.50	0.80	1053	A-W	3.476*
	1982	2.37	0.63	502		
3	1981	4.05	1.10	937	A-W	3.161*
	1982	3.87	0.86	379		
4	1981	4.90	1.12	588	A-W	-0.423NS
	1982	4.93	0.92	293		
5	1981	5.53	1.02	307	A-W	-0.210NS
	1982	5.55	0.89	140		
6	1981	6.37	1.07	108	A-W	0.359NS
	1982	6.32	0.77	67		
7	1981	7.04	1.23	44	A-W	0.512NS
	1982	6.92	0.87	37		
8	1981	7.77	1.30	19	A-W	3.415*
	1982	6.63	0.30	4		

Table 3. Annual shell growth for *Balanus balanoides*, based on rostro-carinal (R/C) diameter measurements. Data are from pooled samples collected April 1980-October 1982 at Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska. Percent composition of year classes and diameter growth increments are also included. n = number of individuals measured.

Year class	n	Percentage of animals observed	Mean R/C diameter (mm)	Diameter growth increment
Sawmill Spit (n = 2184)				
1	18	0.82	5.84	5.84
2	364	16.67	9.51	3.67
3	591	27.06	11.52	2.01
4	529	24.22	13.70	2.18
5	407	18.64	14.79	1.09
6	184	8.42	15.45	0.66
7	54	2.47	16.18	0.73
8	28	1.28	15.33	
9	4	0.18	15.19	
10	3	0.14	14.33	
11	1	0.05	16.05	
12	0	-	-	
13	0	-	-	
14	1	0.05	17.60	

Table 3. Continued.

Year class	n	Percentage of animals observed	Mean R/C diameter (mm)	Diameter growth increment
Berth 4 (n = 1816)				
1	30	1.65	5.62	5.62
2	239	13.16	8.73	3.11
3	723	39.81	10.49	1.76
4	531	29.24	11.67	1.18
5	223	12.28	12.28	0.61
6	47	2.59	12.81	0.53
7	18	0.99	12.38	
8	5	0.28	13.08	
Mineral Creek (n = 2029)				
1	14	0.69	5.92	5.92
2	362	17.84	9.09	3.17
3	511	25.18	10.77	1.68
4	427	21.04	11.39	0.62
5	350	17.25	11.98	0.59
6	216	10.65	12.45	0.47
7	90	4.44	13.85	1.40
8	44	2.17	14.06	0.21
9	12	0.59	13.75	
10	3	0.15	15.37	

APPENDIX 4

Statistical Analyses of Energy Partitioning Data

Table 1. Results of an analysis of variance (ANOVA) used to compare somatic (body) tissue weights of barnacles from Sawmill Spit, Berth 4, and Mineral Creek for selected times in 1980, 1981, and 1982. df = degrees of freedom, SS = sum of squares, MS = mean square.

Source of variation	df	SS	MS	Computed F	Tabled F
April 1980					
"Between" groups	2	51	25.3	4.70	(α=0.05) 3.07
"Within" groups	137	735	5.4		(α=0.01) 4.77
Total	139	786			
Result: SS significantly different B4 (α=0.05)					
June 1980					
"Between" groups	2	11	5.7	3.41	(α=0.05) 3.07
"Within" groups	125	209	1.7		(α=0.01) 4.78
Total	127	220			
Result: SS significantly different MC (α=0.05)					
July 1980					
"Between" groups	2	46	23.1	36.67	(α=0.05) 3.11
"Within" groups	85	54	0.6		(α=0.01) 4.88
Total	87	100			
Results: B4 significantly different SS, MC					
September 1980					
"Between" groups	2	6	3.1	13.48	(α=0.05) 3.06
"Within" groups	144	34	0.2		(α=0.01) 4.75
Total	146	40			
Result: B4 significantly different SS, MC					
October 1980					
"Between" groups	2	3	1.6	5.60	(α=0.05) 3.14
"Within" groups	68	20	0.3		(α=0.01) 4.94
Total	70	23			
Result: SS significantly different B4, MC					

Table 1. Continued.

Source of variation	df	SS	MS	Computed F	Tabled F
January 1981					
"Between" groups	2	0.2	0.1	1.25	(α=0.05) 3.16
"Within" groups	58	4.5	0.1		(α=0.01) 4.99
Total	60	4.7			
Result: No significant difference between sites					
April 1981					
"Between" groups	2	62	30.9	30.85	(α=0.05) 3.11
"Within" groups	78	78	1.0		(α=0.01) 4.88
Total	80	140			
Result: B4 significantly different SS, MC (α=0.05, α=0.01) SS significantly different MC (α=0.05)					
May 1981					
"Between" groups	2	4	1.8	3.46	(α=0.05) 3.12
"Within" groups	78	41	0.5		(α=0.01) 4.91
Total	80	45			
Result: SS significantly different B4, MC (α=0.05)					
June 1981					
"Between" groups	2	14	6.8	12.7	(α=0.05) 3.10
"Within" groups	87	46	0.5		(α=0.01) 4.85
Total	89	60			
Result: MC significantly different SS, B4					
August 1981					
"Between" groups	2	16	7.9	21.8	(α=0.05) 3.19
"Within" groups	48	17	0.4		(α=0.01) 5.08
Total	50	33			
Result: SS significantly different B4, MC					
September 1981					
"Between" groups	2	7	3.4	3.5	(α=0.05) 3.11
"Within" groups	86	82	1.0		(α=0.01) 4.86
Total	88	89			
Result: SS significantly different MC (α=0.05)					

Table 1. Continued.

Source of variation	df	SS	MS	Computed F	Tabled F
October 1981					
"Between" groups	2	60	29.8	42.5	(α=0.05) 3.14
"Within" groups	67	47	0.7		(α=0.01) 4.94
Total	69	107			
Result: SS significantly different B4, MC					
January 1982					
"Between" groups	2	4	2.0	9.75	(α=0.05) 3.15
"Within" groups	62	13	0.2		(α=0.01) 4.98
Total	64	17			
Result: SS significantly different B4, MC					
April 1982					
"Between" groups	2	11	5.5	3.78	(α=0.05) 3.10
"Within" groups	87	126	1.4		(α=0.01) 4.85
Total	89	137			
Result: SS significantly different MC (α=0.05)					
June 1982					
"Between" groups	2	2	0.8	0.61	
"Within" groups	86	113	1.3		F < 1; NS
Total	88	115			
Result: No significant difference between sites					
August 1982					
"Between" groups	2	14	7.1	11.0	(α=0.05) 3.12
"Withing" groups	77	49	0.6		(α=0.01) 4.89
Total	79	63			
Result: MC significantly different SS, B4					
September 1982					
"Between" groups	2	101	50.3	27.9	(α=0.05) 3.10
"Within" groups	87	157	1.8		(α=0.01) 4.85
Total	89	258			
Result: MC significantly different SS, B4					

Table 2. Results of an analysis of covariance (ANOCOVA) used to compare slope values of linear regressions which illustrate somatic (body) weight vs. valve weight for barnacles from Sawmill Spit, Berth 4, and Mineral Creek for selected times during the 1980-81 sampling period. SS = sum of squares, df = degrees of freedom.

Date	Common SS	Pooled SS	Pooled df	Computed F	Tabled F ($\alpha=0.05$)
April 1980	1115	1029	134	5.60	3.07
Result: B4 significantly different SS, MC					
June 1980	264	217	119	12.89	3.07
Result: MC significantly different SS, B4					
July 1980	58	38	82	21.58	3.11
Result: B4 significantly different SS, MC					
August 1980	327	325	130	0.40	3.07
Result: No significant difference between sites					
September 1980	80	76	127	3.34	3.07
Result: B4 significantly different SS, MC					
January 1981	9	8	56	3.50	3.17
Result: MC significantly different SS, B4					
April 1981	236	186	75	10.08	3.12
Result: B4 significantly different SS, MC					

Table 3. Month-to-month comparisons of slope values of linear regressions (body vs. vlave weight) for barnacles at Sawmill Spit, Berth 4, and Mineral Creek, April 1980-April 1981. SS = sum of squares, df = degrees of freedom, * = significant (α=0.05) difference between months, NS = no significant difference.

Dates of comparison	Residual SS	Residual df	Computed t	Tabled t (α=0.05)
SAWMILL SPIT				
April 1980 June 1980	468 91	41 46	11.64	2.00*
June 1980 July 1980	91 15	46 38	7.46	1.99*
July 1980 August 1980	15 246	38 48	-6.67	1.99*
August 1980 September 1980	246 31	48 34	5.15	1.99*
September 1980 October 1980	31 12	34 22	5.45	2.00*
October 1980 January 1981	12 4	22 21	-4.88	2.02*
January 1981 April 1981	4 128	21 28	-11.40	2.01*
BERTH 4				
April 1980 June 1980	95 77	45 29	15.14	1.99*
June 1980 July 1980	77 8	29 23	-1.12	2.01NS
July 1980 August 1980	8 27	23 41	0	2.00NS
August 1980 September 1980	27 10	41 48	4.41	1.99*
September 1980 October 1980	10 59	48 23	2.25	1.99*
October 1980 January 1981	59 2	23 15	0.67	2.02NS
January 1981 April 1981	2 15	15 20	-6.94	2.03*

Table 3. Continued.

Dates of comparison	Residual SS	Residual df	Computed t	Tabled t ($\alpha=0.05$)
MINERAL CREEK				
April 1980	466	48	7.39	1.99*
June 1980	49	44		
June 1980	49	44	11.39	2.00*
July 1980	15	21		
July 1980	15	21	-5.41	2.00*
August 1980	52	41		
August 1980	52	41	6.56	1.99*
September 1980	35	45		
September 1980	35	45	0	2.00NS
January 1981	2	20		
January 1981	2	20	3.77	2.01*
March 1981	11	28		
March 1981	11	28	-15.63	2.00*
April 1981	52	27		

APPENDIX 5

Statistical Analysis of Mortality Data

Table 1. Z-test statistics for between-site comparisons of annual % survivorship, as a function of mortality, for adult *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1981 and May 1981-March 1982. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
April 1980-April 1981					
SS	10.4	198	221	0.896	9.06*
B4	46.3	212	395	0.537	
SS	10.4	198	221	0.896	3.76*
MC	21.7	640	817	0.783	
B4	46.3	212	395	0.537	-8.81*
MC	21.7	640	817	0.783	
May 1981-March 1982					
SS	57.5	173	407	0.425	-6.57*
B4	33.7	236	356	0.663	
SS	57.5	173	407	0.425	-5.92*
MC	40.5	676	1136	0.595	
B4	33.7	236	356	0.663	2.29*
MC	40.5	676	1136	0.595	

Table 2. Z-test statistics for within-site comparisons of summer and winter seasonal % survivorship, as a function of mortality, for adult *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$, NS = not significant.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Sawmill Spit					
Apr-Sep 1980	3.6	213	221	0.964	1.59NS
Sep 1980- Apr 1981	7.0	198	213	0.930	
May-Aug 1981	5.2	386	407	0.948	15.44*
Aug 1981- Apr 1982	55.2	173	386	0.448	
Berth 4					
Apr-Sep 1980	31.1	272	395	0.689	-2.58*
Sep 1980- Apr 1981	22.1	212	272	0.779	
May-Aug 1981	21.1	281	356	0.789	-1.62NS
Aug 1981- Mar 1982	16.0	236	281	0.840	
Mineral Creek					
Apr-Sep 1980	6.5	764	817	0.935	6.14*
Sep 1980- Apr 1981	16.2	640	764	0.838	
May-Aug 1981	37.9	705	1136	0.621	-16.30*
Aug 1981- Mar 1982	4.1	676	705	0.959	

Table 3. Z-test statistics for between-site comparisons of seasonal % survivorship, as a function of mortality, for adult *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-September 1982. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at α = 0.05, NS = not significant.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
April-September 1980					
SS	3.6	213	221	0.964	8.01*
B4	31.1	272	395	0.689	
SS	3.6	213	221	0.964	1.61NS
MC	6.5	764	817	0.935	
B4	31.1	272	395	0.689	-11.42*
MC	6.5	764	817	0.935	
September 1980-April 1981					
SS	7.0	198	213	0.930	4.54*
B4	22.1	212	272	0.779	
SS	7.0	198	213	0.930	3.39*
MC	16.2	640	764	0.838	
B4	22.1	212	272	0.779	-2.16*
MC	16.2	640	764	0.838	
May-August 1981					
SS	5.2	386	407	0.948	6.61*
B4	21.1	281	356	0.789	
SS	5.2	386	407	0.948	12.47*
MC	37.9	705	1136	0.621	
B4	21.1	281	356	0.789	5.87*
MC	37.9	705	1136	0.621	
August 1981-March 1982					
SS	55.2	173	386	0.448	-10.26*
B4	16.0	236	281	0.840	
SS	55.2	173	386	0.448	-19.41*
MC	4.1	676	705	0.959	
B4	16.0	236	281	0.840	-6.40*
MC	4.1	676	705	0.959	

Table 3. Continued.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
April-September 1982					
SS	20.0	427	534	0.800	6.51*
B4	39.5	237	392	0.605	
SS	20.0	427	534	0.800	-2.43*
MC	15.2	934	1102	0.848	
B4	39.5	237	392	0.605	-10.04*
MC	15.2	934	1102	0.848	

Table 4. Z-test statistics for within-site comparisons of annual % survivorship, as a function of mortality, for adult *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, 1980-81 and 1981-82. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at α = 0.05.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Sawmill Spit					
Apr 1980- Apr 1981	10.4	198	221	0.896	11.46*
May 1981- Apr 1982	57.5	173	407	0.425	
Berth 4					
Apr 1980- Apr 1981	46.3	212	395	0.537	-3.52*
May 1981- Mar 1982	33.7	236	356	0.663	
Mineral Creek					
Apr 1980- Apr 1981	21.7	640	817	0.783	8.76*
May 1981- Mar 1982	40.5	676	1136	0.595	

Table 5. Z-test statistics for within-site comparisons of seasonal % survivorship, as a function of mortality, for adult *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, Summer 1980, 1981, and 1982 and Winter 1980-81 and 1981-82. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$, NS = not significant.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Sawmill Spit					
Apr-Sep 1980	3.6	213	221	0.964	0.88NS
May-Aug 1981	5.2	386	407	0.948	
Apr-Sep 1980	3.6	213	221	0.964	5.71*
Apr-Sep 1982	20.0	427	534	0.800	
May-Aug 1981	5.2	386	407	0.948	6.60*
Apr-Sep 1982	20.0	427	534	0.800	
Sep 1980- Apr 1981	7.0	198	213	0.930	11.62*
Aug 1981- Apr 1982	55.2	173	386	0.448	
Berth 4					
Apr-Sep 1980	31.1	272	395	0.689	-3.13*
May-Aug 1981	21.1	281	356	0.789	
Apr-Sep 1980	31.1	272	395	0.689	2.47*
Apr-Sep 1982	39.5	237	392	0.605	
May-Aug 1981	21.1	281	356	0.789	5.47*
Apr-Sep 1982	39.5	237	392	0.605	
Sep 1980- Apr 1981	22.1	212	272	0.779	-1.81NS
Aug 1981- Mar 1982	16.0	236	281	0.840	

Table 5. Continued.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Mineral Creek					
Apr-Sep 1980	6.5	764	817	0.935	15.88*
May-Aug 1981	37.9	705	1136	0.621	
Apr-Sep 1980	6.5	764	817	0.935	5.94*
Apr-Sep 1982	15.2	934	1102	0.848	
May-Aug 1981	37.9	705	1136	0.621	-12.12*
Apr-Sep 1982	15.2	934	1102	0.848	
Sep 1980-Apr 1981	16.2	640	764	0.838	-7.60*
Aug 1981-Mar 1982	4.1	676	705	0.959	

Table 6. Z-test statistics for between-site comparisons of annual % survivorship, as a function of mortality, for juvenile *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-April 1981 and May 1981-March 1982. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$, NS = not significant.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
April 1980-April 1981					
SS	87.5	284	2279	0.125	11.26*
B4	95.2	209	4340	0.048	
SS	87.5	284	2279	0.125	-6.68*
MC	81.3	1057	5662	0.187	
B4	95.2	209	4340	0.048	-20.65*
MC	81.3	1057	5662	0.187	
May 1981-March 1982					
SS	90.3	100	1026	0.097	-1.90NS
B4	87.9	213	1759	0.121	
SS	90.3	100	1026	0.097	-5.71*
MC	82.5	370	2115	0.175	
B4	87.9	213	1759	0.121	-4.67*
MC	82.5	370	2115	0.175	

Table 7. Z-test statistics for within-site comparisons of summer and winter seasonal % survivorship, as a function of mortality, for juvenile *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Sawmill Spit					
Apr-Sep 1980	70.4	675	2279	0.296	-6.07*
Sep 1980-Apr 1981	57.9	284	675	0.421	
May-Aug 1981	40.5	611	1026	0.596	17.05*
Aug 1981-Apr 1982	83.6	100	611	0.164	
Berth 4					
Apr-Sep 1980	93.9	264	4340	0.061	-39.97*
Sep 1980-Apr 1981	20.8	209	264	0.792	
May-Aug 1981	47.5	924	1759	0.525	14.68*
Aug 1981-Mar 1982	76.9	213	924	0.231	
Mineral Creek					
Apr-Sep 1980	21.9	4422	5662	0.781	54.21*
Sep 1980-Apr 1981	76.1	1057	4422	0.239	
May-Aug 1981	11.9	1864	2115	0.881	43.31*
Aug 1981-Mar 1982	80.1	370	1864	0.199	

Table 8. Z-test statistics for between-site comparisons of seasonal % survivorship, as a function of mortality, for juvenile *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, April 1980-September 1982. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at $\alpha = 0.05$, NS = not significant.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
April-September 1980					
SS	70.4	675	2279	0.296	26.08*
B4	93.9	264	4340	0.061	
SS	70.4	675	2279	0.296	-40.76*
MC	21.9	4422	5662	0.781	
B4	93.9	264	4340	0.061	-71.53*
MC	21.9	4422	5662	0.781	
September 1980-April 1981					
SS	57.9	284	675	0.421	-10.23*
B4	20.8	209	264	0.792	
SS	57.9	284	675	0.421	9.99*
MC	76.1	1057	4422	0.239	
B4	20.8	209	264	0.792	19.64*
MC	76.1	1057	4422	0.239	
May-August 1981					
SS	40.5	611	1026	0.596	3.59*
B4	47.5	924	1759	0.525	
SS	40.5	611	1026	0.596	-18.38*
MC	11.9	1864	2115	0.881	
B4	47.5	924	1759	0.525	-24.56*
MC	11.9	1864	2115	0.881	
August 1981-March 1982					
SS	83.6	100	611	0.164	-3.18*
B4	76.9	213	924	0.231	
SS	83.6	100	611	0.164	-1.91NS
MC	80.1	370	1864	0.199	
B4	76.9	213	924	0.231	1.96NS
MC	80.1	370	1864	0.199	

Table 8. Continued.

Location	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
May-September 1982					
SS	98.2	154	8683	0.018	1.98*
B4	98.7	65	4897	0.013	
SS	98.2	154	8683	0.018	-52.16*
MC	67.8	2065	6418	0.322	
B4	98.7	65	4897	0.013	-41.59*
MC	67.8	2065	6418	0.322	

Table 9. Z-test statistics for within-site comparisons of annual % survivorship, as a function of mortality, for juvenile *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, 1980-81 and 1981-82. p̂i = estimated individual proportion, ts = test statistic, * = significant at α = 0.05, NS = not significant.

Date	% Mortality	Nt + 1	Nt	p̂i	ts
Sawmill Spit					
Apr 1980- Apr 1981	87.5	284	2279	0.125	2.25*
May 1981- Apr 1982	90.3	100	1026	0.097	
Berth 4					
Apr 1980- Apr 1981	95.2	209	4340	0.048	-10.17*
May 1981- Mar 1982	87.9	213	1759	0.121	
Mineral Creek					
Apr 1980- Apr 1981	81.3	1057	5662	0.187	1.19NS
May 1981- Mar 1982	82.5	370	2115	0.175	

Table 10. Z-test statistics for within-site comparisons of seasonal % survivorship, as a function of mortality, for juvenile *Balanus balanoides*, Sawmill Spit, Berth 4, and Mineral Creek, Port Valdez, Alaska, Summer 1980, 1981, and 1982 and Winter 1980-81 and 1981-82. $\hat{p}i$ = estimated individual proportion, ts = test statistic, * = significant at α = 0.05, NS = not significant.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Sawmill Spit					
Apr-Sep 1980	70.4	675	2279	0.296	-16.33*
May-Aug 1981	40.5	611	1026	0.596	
Apr-Sep 1980	70.4	675	2279	0.296	44.75*
May-Sep 1982	98.2	154	8683	0.018	
May-Aug 1981	40.5	611	1026	0.596	64.96*
May-Sep 1982	98.2	154	8683	0.018	
Sep 1980-Apr 1981	57.9	284	675	0.421	10.06*
Aug 1981-Apr 1982	83.6	100	611	0.164	
Berth 4					
Apr-Sep 1980	93.9	264	4340	0.061	-41.49*
May-Aug 1981	47.5	924	1759	0.525	
Apr-Sep 1980	93.9	264	4340	0.061	12.31*
May-Sep 1982	98.7	65	4897	0.013	
May-Aug 1981	47.5	924	1759	0.525	51.79*
May-Sep 1982	98.7	65	4897	0.013	
Sep 1980-Apr 1981	20.8	209	264	0.792	16.80*
Aug 1981-Mar 1982	76.9	213	924	0.231	

Table 10. Continued.

Date	% Mortality	Nt + 1	Nt	$\hat{p}i$	ts
Mineral Creek					
Apr-Sep 1980	21.9	4422	5662	0.781	-10.00*
May-Aug 1981	11.9	1864	2115	0.881	
Apr-Sep 1980	21.9	4422	5662	0.781	50.51*
May-Sep 1982	67.8	2065	6418	0.322	
May-Aug 1981	11.9	1864	2115	0.881	44.78*
May-Sep 1982	67.8	2065	6418	0.322	
Sep 1980-Apr 1981	76.1	1057	4422	0.239	3.50*
Aug 1981-Mar 1982	80.1	370	1864	0.199	