

AN ABSTRACT OF THE THESIS OF

Frank Douglas Ratti for the degree of Master of Science  
(Name) (Degree)  
in Oceanography presented on July 21, 1977  
(Major) (Date)

Title: REPRODUCTION AND GROWTH OF THE PACIFIC BASKET -  
COCKLE, CLINOCARDIUM NUTTALLII CONRAD, FROM  
INTERTIDAL AND SUBTIDAL ENVIRONMENTS OF  
NETARTS BAY

Abstract approved: Redacted for Privacy  
James E. McCauley

Age structure and growth of shells of the Pacific basket-cockle, Clinocardium nuttallii in Netarts Bay, Oregon, were investigated with special emphasis on the differences between subtidal and intertidal populations. The cockle was chosen for study because its growth is highly sensitive to physical factors in the environment. Evidence is presented which suggests that stresses of the physical environment and biological factors result in oldest individuals being in the subtidal, and that growth of shells is correlated with the amount of tidal submergence. A short-term tagging study was done at two sites and most of yearly growth occurred in the Spring months.

Collections were made from July, 1975, through September, 1976, from six sites to study synchronism of gonadal development

and fecundity of populations by histological examination of gonads. Synchronism of gonadal development to the ripe stage occurs among intertidal and subtidal populations in the same area, while populations from different areas of the bay do not reach the ripe condition at the same time. There is evidence of protandric spawning behavior, and the hermaphroditic nature of C. nuttallii is compared to that of the Family Tridacnidae. The fecundity of the subtidal populations, in terms of percentages of the populations producing ripe gonads, was greater than fecundity of the intertidal populations. The subtidal environment is suggested to serve as 'refugia' for adult breeding populations.

Reproduction and Growth of the Pacific  
Basket-cockle, Clinocardium nuttallii Conrad, from  
Intertidal and Subtidal Environments of Netarts Bay

by

Frank Douglas Ratti

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

June 1978

APPROVED:

Redacted for Privacy

---

Associate Professor of Oceanography  
in charge of major

Redacted for Privacy

---

Acting Dean of School of Oceanography

Redacted for Privacy

---

Dean of Graduate School

Date thesis is presented July 21, 1977

Typed by Margie Wolski for Frank Douglas Ratti

## ACKNOWLEDGEMENT

Deo gratias!

## TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION	1
Scope	1
Approach	2
The Pacific Basket-Cockle	6
Taxonomy	6
Reproduction	7
Growth	10
Symbiosis with Zoochlorellae	13
Netarts Bay	14
II. MATERIALS AND METHODS	16
Sample Sites	16
Site Elevations	16
Collection of Cockles	21
Abiotic Data	24
Growth Data	25
Symbiosis	29
Processing Samples	30
Criteria for Gonad Condition	30
III. RESULTS	34
Gonadal Development	34
Synchronism of Ripeness	46
Age of Ripeness	47
Sample Site Differences in Percentage of Ripeness	47
Growth	49
Analysis of Variance of Sample Site Means	49
Intertidal Versus Subtidal Growth	51
Allometric Growth	51
Tide Level and Zoochlorellae	55
Tide Level and Shell Algae	63
Growth Data from Specific Sites	63
Shell Tagging Data	68
Abiotic Data	71
Hydrology	71
Intertidal Sample Site Elevations	72
Sediment Parameters	74
Associated Benthos	75

Table of Contents, continued:

IV. DISCUSSION	77
Physical Environment and Growth Rates	78
Distribution of Symbiosis	83
Age Distribution	84
Population Density	89
Reproduction and Synchronous Spawning	90
SUMMARY	97
BIBLIOGRAPHY	99

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Sample collection data for <u>Clinocardium nuttallii</u> from Netarts Bay, 1975-1976.	22
2	Stages of gonadal development of individuals in each sampling period.	42
3	Rankings of sample sites according to biological and physical parameters.	50
4	Growth data of tagged cockles retrieved from site intertidal I-East.	70

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Distribution of <u>Clinocardium nuttallii</u> in Netarts Bay.	17
2	Location of sample sites in Netarts Bay, Oregon.	19
3	Shell measurements of <u>C. nuttallii</u> .	26
4	Percentages of follicular tissue in tissue sections.	35
5	Numbers of oocytes per follicle.	36
6	Diameters of oocytes and oocyte nuclei.	37
7	Ratios of numbers of male follicles to numbers of female follicles.	38
8	Means of percentages of follicular tissue in tissue sections, Netarts Bay, 1975-1976.	39
9	Means of numbers of oocytes per follicle, Netarts Bay, 1975-1976.	40
10	Percentages of the number of individuals collected with ripe male/female gonads at each age.	48
11	Absolute growth of shell heights and weights in the subtidal and intertidal environments, Netarts Bay.	52
12	Age-frequency histograms of <u>C. nuttallii</u> from the intertidal and subtidal environments, Netarts Bay.	54
13	Linear regressions of lengths on heights on logarithmic axes from the intertidal and subtidal environments, Netarts Bay.	56

List of Figures, continued:

14	Linear regressions of widths on heights on logarithmic axes from the intertidal and subtidal environments, Netarts Bay.	58
15	Allometric plots of shell weights and heights from the intertidal and subtidal environments, Netarts Bay.	60
16	Mean degrees of infection of zoochlorellae in cockles from the intertidal and subtidal environments, Netarts Bay.	62
17	Mean degrees of epiphytic algae on shells of cockles from the intertidal and subtidal environments, Netarts Bay.	62
18	Age-frequency histograms of <u>C. nuttallii</u> from the six sampling sites, Netarts Bay.	64
19	Absolute growth of shell heights in the six sampling sites, Netarts Bay.	65
20	Absolute growth of shell heights in three subtidal sites, Tillamook Bay.	66
21	Age-frequency histograms of <u>C. nuttallii</u> from three subtidal sites, Tillamook Bay.	69
22	Heights of the four intertidal sites above mean lower low water, Netarts Bay.	73

Netarts Love

Hundred miles driving to the coast,  
Nodding out enough to keep on the road,  
Always a different partner,  
A task nevertheless.

Arrival loses sight of home.  
Time speaks in the running of tides.  
Wind measures the day.

We came for slack water,  
Bare sand shoulders,

Taking home salt animal roses.

REPRODUCTION AND GROWTH OF THE PACIFIC  
BASKET-COCKLE, CLINOCARDIUM NUTTALLII CONRAD,  
FROM INTERTIDAL AND SUBTIDAL ENVIRONMENTS OF  
NETARTS BAY

I. INTRODUCTION

Scope

Beds of subtidal clams may be important seed producing areas for the intertidal clam beds of estuaries. Subtidal stocks could provide recruits in times of extreme stress or mortality to populations in other habitats. This hypothesis is the rationale for this research. The idea of a zone of refuge for a marine species was discussed by Connell (1971) concerning the population of the barnacle, Balanus glandula, in the high, rocky intertidal. He described the population above the high water line as the breeding population, because the recruits below that zone are limited by a predator snail, Thais emarginata.

The objective of this thesis is to make a comparative autecological study of intertidal and subtidal populations of the Pacific basket-cockle, Clinocardium nuttallii, in Netarts Bay. Much of the assessment of benthic habitats has been made by interpreting the species or dominance diversity of assemblages of organisms collected in random samples (Sanders, 1968). In an examination of the impacts of dredging in estuaries, Slotta et al. (1974) added the need to

arbitrarily choose certain areas for intensive study, such as dense clam beds. Since dredging artificially alters the ratio of intertidal to subtidal area, the reproductive importance of one or the other of these habitats could be a principal concern in gauging dredging impacts in dense clam beds. This is a study of the differences in age, growth and reproduction of populations of a bivalve species from these two levels of submergence in an undredged estuary.

### Approach

One way of addressing the question of the importance of the contribution of subtidal populations in repopulating the estuary is to study larval setting. Such a study entails sampling the plankton for a specific pelecypod larvae and also collecting spat from the sediment. Cerastoderma (=Cardium) edule has been studied in this way by Baggerman (1953), and Mercenaria mercenaria by Carriker (1961). These studies observed vertical and horizontal distribution, time of occurrence, and wastage of larvae in the water column. Another approach to the question is an experimental study using laboratory spawning techniques. This will also furnish descriptive knowledge of a particular species larval form. Laboratory studies such as one concerning the setting behavior of Mya arenaria toward various substrates have been made (Keck, Maurer, and Malouf, 1974). A third approach questions the degree of separation between

subtidal and intertidal populations through a biochemical assay such as an electrophoretic separation of enzymes (Reid, P., 1968; Smoker, 1976). This technique estimates the degree of genetic isolation between populations. Also glycogen analysis has been used to follow the reproductive cycle of a clam population (Montgomery, 1957; Viles and Silverman, 1949; Westenhouse, 1968). The depletion in winter of gonadal glycogen in Tresus capax has been associated with its spawning period, although it was accentuated by winter starvation as well (Reid, R., 1969). All of these approaches were considered.

Instead it was decided after weighing facilities, time, guidance, and funding available, that the reproductive cycle of C. nuttallii was to be followed histologically. By directly observing the stages of gametogenesis one can observe the time of ripeness for a species, and by collecting samples from several areas in an estuary including subtidal and intertidal environments one can compare times of ripeness of populations. Synchronism of ripeness within populations was compared to that among populations, and the percent of sexually mature individuals from each environment was obtained through the histological method. From these data and measurements of age and growth taken from shells, conclusions can be stated concerning the relative production of gametes by either population.

By investigating a reproductive cycle in terms of its histology, larval ecology was to be ignored. The study of gonad condition,

then, could only yield information about the potential amount and time of spawning of gametes. It was decided, however, that this information would be sufficient to discuss the different spawning potentials of populations.

Gametogenesis in bivalves has been followed by many investigators. Coe and Turner (1938) described the gamete development of Mya arenaria in detail, although the period of development and time of spawning were not addressed. Ropes and Stickney (1965) expressed the need to determine the times and duration of spawning in M. arenaria, took periodic samples and histologically examined gonads. They noted the unreliability of fresh unstained smears for examining gonad material, and endorsed the practice of fixing and staining gonad tissue for histological examination. Ropes (1968) used histological techniques to describe the reproductive cycle of the surf clam, Spisula solidissima. The reproductive cycles of Tresus capax by Machell and DeMartini (1971) and the manila clam, Venerupis japonica by Holland and Chew (1974) have also been described by this method. It was decided that the histological approach was the best procedure for investigating the reproductive characteristics of a bivalve species.

None of the above studies, however, compared reproductive cycles from different populations of the species they studied, as they were mainly descriptive studies. Gonor (1972) compared ratios of

dry gonad weight to total dry weight of sea urchins, Strongylocentrotus purpuratus, from three oceanic intertidal locations, and found that gonad index differed between habitats. This study is unique in using a histological approach to assess differences in gamete production within an estuary. Subtidal bivalve populations are rarely studied.

A bivalve species was chosen for a comparative study of the intertidal and subtidal environments, because the most outstanding feature of growth in mulluscs is its variation in rate, and environmental conditions are a significant cause of that variability (Wilbur and Owen, 1964). Therefore data on growth were studied as well as a description of habitats. Because the degree of genetic isolation would be unknown, it would be assumed that variability in features of growth between populations would be environmentally caused. The Pacific basket-cockle has extreme variability in its growth parameters due to its sensitivity to environmental factors (Weymouth and Thompson, 1931; Taylor, 1960). It occurs in estuaries in Oregon in sufficient abundance, and its reproductive biology is unique and has not been well described. The Pacific cockle has a negligible importance as a commercially harvested clam, but is a major catch of sports diggers (Marriage, 1964).

Netarts Bay was chosen for the study area because it is pristine and has never been disturbed by dredging, and because the

basket-cockle occurs in several intertidal and subtidal areas. Also the physical characteristics and some biological data have been recently examined there (Glanzman, Glenne, and Burgess, 1971; Shabica et al., 1976).

### The Pacific Basket-Cockle

#### Taxonomy

The Pacific basket-cockle was first described by Martyn (1782) and named Cardium corbis in his "Universal Conchologist." Several years later it was renamed Cardium nuttallii by Conrad (1837) who with others saw inconsistencies in Martyn's binomial naming method and thus rejected his nomenclature. Conrad described this species with other Cardium species from the West Coast of the United States. He gave the habitat of this cockle as 'muddy salt marshes, a few miles from the estuary of the Columbia River'. Conrad's description came from a collection of marine shells belonging to Thomas Nuttall; hence, the origin of several species names.

Until 1935 authors used either name to describe the species, which may have led to some confusion of its biology. In 1936, Keen designated a new genus, Clinocardium, to include the Pacific basket-cockle and at least ten other Western American cardiid species previously under the genus Cardium. She identified at least 89 species

of the family Cardiidae in the area between Peru and Alaska, including two-thirds fossil species. Most of the living species occurred south of California. Clinocardium was identified as a cool water genus.

She recognized nuttallii as the first available species name citing Winkworth's (1939) and Conrad's (1869) criticisms of Martyn's original naming procedures. According to Keen's Molluscan Genera of Western North America (1963) the present taxonomic classification of Clinocardium nuttallii became as follows:

Class Pelecypoda

Subclass Teleodesmata

Order Heterodontida

Suborder Cyclodontida

Superfamily Cardiacea

Family Cardiidae

Subfamily Laevicardiinae

Genus Clinocardium Keen, 1936

Species nuttallii Conrad, 1837

### Reproduction

The Pacific basket-cockle was identified as a monoecious bivalve by Edmonson (1919, 1920). He retained Martyn's nomenclature, Cardium corbis. Its hermaphroditism was substantiated by histologically sectioning gonads during the spawning period and finding ripe spermaries surrounding ripe ovaries. Edmonson stated

that sexual products begin to form in the early spring, and that spawning occurs in September.

Fraser (1931) reported that individuals are mature at two years old. He said that ova and spermatozoa seem to be shed during the same period, but if there is a difference it is that the ova are shed first, because some partially spent individuals contain a larger portion of remaining spermatozoa than ova. The first spent individuals were found on May 31. He reported a long spawning period among cockles from the same beach, but between beaches in the same vicinity there were even greater differences in spawning periods. He found well-filled gonads in late July on several beaches. Whatever the physical or chemical conditions are that influence spawning, Fraser believed they must have persisted through spring and summer.

Butler, Milleman, and Stewart (1968) were able to obtain larvae for assaying the acute effects of insecticide Sevin. They induced ripe cockles to spawn by holding them in standing sea water at 20 degrees C and 25 parts per thousand, in which limited spawning occurred after 48 hours. The larvae were not described. In 1968 Silvey published another physiological study of the regulation of the heartbeat of cockles through interganglionic pathways. The natural history of Clinocardium nuttallii was reviewed by Quayle and Bourne (1972), along with other clam fisheries of British Columbia, but no

recent work on its reproductive biology has been published.

More study has been done on other members of the family Cardiidae, especially with the European cockle, Cerastoderma edule, which has been an important fishery for Northern Europe. Baggerman (1953) studied larval transport and setting on the Dutch Wadden Sea. Cerastoderma edule has been spawned in the laboratory and its larval development has been described by Creek (1960). Boyden (1971) made a comparative study of the reproductive cycles of C. edule and C. glaucum, two closely related species from the Crouch estuary. He, however, made only macroscopic examination of the appearance of gonads and microscopic examination of wet smears of gonads, so no detailed histological study of C. edule gametogenesis is available. The European cockle cannot be compared reproductively with Clinocardium nuttallii in any case, because it is distinctly dioecious. Other characteristics of the European and Pacific cockles can be related in this present study.

The Pacific basket-cockle is closely related in its reproductive characteristics to the family Tridacnidae (Superfamily: Cardiacea). Several species of the giant tridacnid clams of the tropical Pacific are protandric functional hermaphrodites (Wada, 1952), including the genera Tridacna and Hippopus. Besides sharing the same superfamily these species are among the four percent of Bivalvia, which do not have separate sexes, and are of the very few bivalve species

in which hermaphroditism is simultaneous (Fretter, 1964).

Another pelecypod, which was originally described as a simultaneous hermaphrodite by Weymouth (1923) is the pismo clam, Tivela stultorum. However, Coe (1947) showed it definitely had separate sexes with only occasional hermaphroditic individuals.

### Growth

Fraser (1931) collected 760 specimens of C. nuttallii from 32 intertidal beaches along the coast of British Columbia, and noted a great variation in the size of individuals at any particular age. Age was determined by counting winter growth checks on the shells, which Fraser found to be strongly marked on cockles of British Columbia. Orton (1926) in an experiment with tagged C. edule, observed that checks were made on shells every time he disturbed them to make measurements of growth. Both Orton and Fraser concurred that the disturbance checks were weakly marked in comparison to winter annuli. Fraser found a predominance of three and four year old classes in his collection and a maximum age of seven years (six specimens). Weymouth (1951) examined age and growth of C. nuttallii from a collection of 1,800 taken from nine intertidal beaches along 2,200 miles of Pacific Coast ranging in latitude from Tillamook Bay, Oregon to Port Moller, Alaska, near the northern limit of the species. He noted much better defined winter growth

checks on the northern specimens of the species than on those forms from southern beaches, where winter growth is less retarded. He had justified the method of aging clams by their winter growth checks in detail in his earlier work on Tivela stultorum, the pismo clam (Weymouth, 1923), and Siliqua patula, the razor clam (Weymouth, 1925, 1931).

Weymouth (1931) graphed absolute and relative curves of shell length vs. age and found the shapes of growth curves of the cockle from different areas matched very well with those obtained for the razor clam. In comparing growth from different latitudes he showed that the northern forms grow slowly in contrast to the southern, but reach greater maximum age and size. In 1960, Taylor examined Weymouth's data further, and showed growth parameters to be quantitatively associated with the decreasing mean air temperatures of latitude. He used Bertalanffy's growth equation ( $L = L_{\infty} (1 - e^{-k(t-t_0)})$ ) to estimate growth coefficients ( $k$ ) and an index of longevity. He found a significant linear correlation between the log of  $k$  and mean air temperatures, and was able to estimate the maximum lengths and ages of the oldest cockles based on the growth coefficients from geographic area.

Mitchell (1935) described three shell layers of C. nuttallii, an outer periostracum of conchyolin, and two inner layers of aragonite. Evans (1972) analyzed shell microstructure of Clinocardium and

correlated growth lines with the mixed semi-diurnal pattern of the tidal cycle of the eastern Pacific coast. Lines were formed during the period of exposure each day caused by the lower of the two daily low tides. Evans noted that the only other species showing the same pattern of daily low tide increments of growth was Tridacna squamosa.

The distribution and growth of C. edule has been extensively studied by Kreger (1940), Verwey (1952), Cole (1956), Kristensen (1957), Eisma (1965), Hancock (1973), and others. Particular attention has been paid to the effects of the physical environment upon growth characteristics. The most distinctive characteristic of Cerastoderma has been the wide variation of its parameters of growth. This characteristic has often been attributed to its shallow depth of burial and subsequent high exposure to the surface conditions of its substrate. Specifically studied environmental factors which effect C. edule size, weight, and population density have been the influence of light, oxygen, salinity sea temperature, the time of submergence and exposure, sediment characteristics as well as current velocities. Biotic factors which affect recruitment and growth, which have been investigated, include the effects of the existing stock density upon recruitment, and the effects of exploitation, predation, and 'migration'. From these studies coupled with my observations from Netarts Bay, Oregon of C. nuttallii populations,

an explanation is presented of the factors influencing the age and size distribution of the Pacific cockle in an estuary.

#### Symbiosis with Zoochlorellae

In 1972, Hartman reported the green algal symbiont found in some individuals of Clinocardium nuttallii to be a chlorophyte algae of the genus Chlorella. This symbiont, infecting cockles older than two years as a facultative parasite, was found in 35 percent of 1,290 individuals collected intertidally from Yaquina Bay, Oregon. The zoochlorellae were harbored in the siphonal and mantle tissues in sometimes large colonies. The algae was cultured separately and uninfected animals were infected in his experiments.

The tridacnid clams have been related to Clinocardium nuttallii in another way besides in simultaneous hermaphroditism. Yonge (1975) reported that the symbiosis between the giant tridacnids and zooxanthellae is a similar relationship to reef building corals and their dinoflagellate symbiont, Gymnodinium. He noted that the only molluscan species which host this kind of symbiosis were six tridacnid species and one other related species, presumably Clinocardium nuttallii.

### Netarts Bay

Netarts Bay is an undisturbed moderate-sized shallow estuary on the Northern Oregon Coast. Its biology and physical characteristics have recently been summarized by Shabica et al. (1976). It is Oregon's fifth largest estuary encompassing 2,300 acres total, 1,500 acres of tidelands, and 16 square miles of watershed. The bay, characterized by extensive mudflats and sandflats, is bisected by a main channel which winds almost eight miles south from the mouth. The channel is naturally formed and shallow, covering the only submerged lands of the bay at the lowest tides. The bay is fed by 12 small creeks, which have little effect upon the well-mixed high-salinity characteristics throughout the year. The tidal range is seven feet with respect to mean lower low water, and the average prism is estimated to be 75 percent of the total water volume contained in the bay during each tidal cycle (Glanzman et al., 1971). The total water volume in the bay at mean high water is approximately 10,000 acre feet. The sediments contain fine-grained materials from stream flow through the watershed, and large-grained sands from the tidal flow through the mouth. There has been an accretion of sediments and a ten percent decrease in the bay volume at high water in the years from 1957 to 1969 according to Glanzman et al. (1971), who attributed this to high erosion of adjacent lands due to logging,

construction, and land filling operations. The bay has been currently used for sport fishing, crabbing, and clamming. The inlet is not navigable, and there has been no dredging within the bay.

## II. MATERIALS AND METHODS

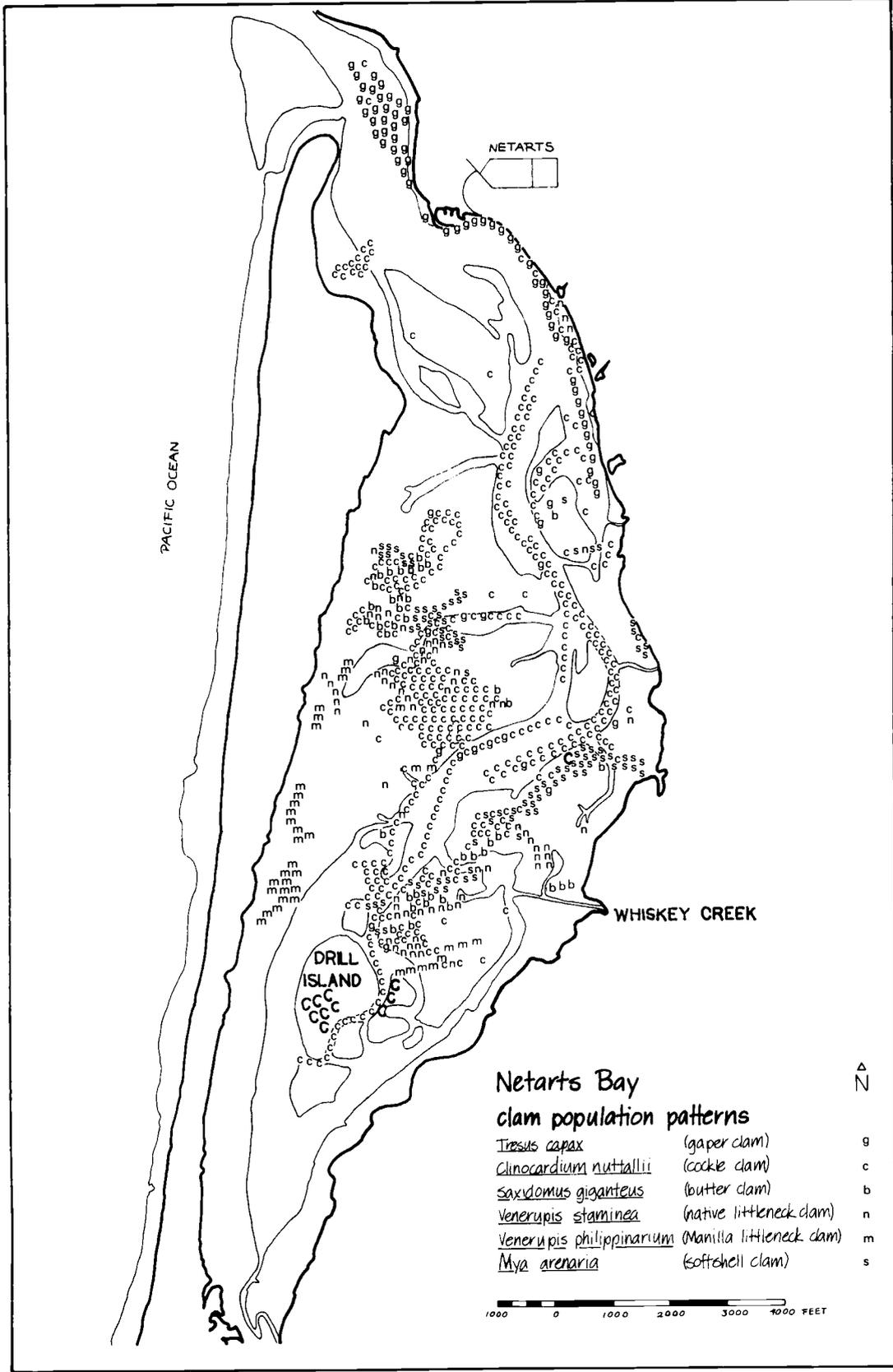
### Sample Sites

Six sample 'sites' were chosen in Netarts Bay, which met the following criteria: 1) each had an abundance of cockles sufficient to meet sampling requirements for a year, 2) each intertidal site was isolated from the others at low tide, and 3) intertidal and subtidal sites had distinct boundaries between them. The subtidal distribution of C. nuttalli in Netarts Bay had previously been determined by the Oregon Department of Fish and Wildlife (ODFW) (Figure 1). Intertidal sites were separated by the main channel into east and west intertidal sites, while subtidal sites were located in the channel. The bay was divided geographically into two 'stations': I, downbay, and II, upbay, which were 4.35 and 6.10 miles upbay from the mouth, respectively. Each station contained two intertidal sites on opposite beaches of the subtidal channel site (Figure 2). The location of these stations coincided with stations D and E of Glanzman et al. (1971).

### Site Elevations

Sampling dates were chosen to coincide with spring tides and the time of low tides on those days, which exposed all but the channels of Netarts Bay. The intertidal was that area exposed at low tide.

Figure 1. Distribution of Clinocardium nuttallii in Netarts Bay, Oregon (After Oregon Department of Fish and Wildlife).



Netarts Bay  
clam population patterns

- Tresus capax* (gaper clam) g
- Clinocardium nuttallii* (cockle clam) c
- Saxidomus giganteus* (butter clam) b
- Venerupis staminea* (native littleneck clam) n
- Venerupis philippinarum* (Manilla littleneck clam) m
- Mya arenaria* (softshell clam) s

1000 0 1000 2000 3000 4000 FEET

Δ  
N

Figure 2. Location of sample sites in Netarts Bay, Oregon (After Oregon Department of Fish and Wildlife).



The channels were six to ten feet deep and were bordered by steep banks at the intertidal boundary, so that subtidal and intertidal were sharply divided.

Heights above mean lower low water of the four intertidal sites were determined using a surveyor's rod and land level on July 31, 1976. The height of the low tide on that morning was predicted to be 0.3 feet above mean lower low water at 8:49 from the NOAA tide table for Humbolt Bay, CA. Heights at five to twelve points along transects from 100 to 500 feet long were taken at the four intertidal sites. Since the measurements were taken at slack water on a calm day, a crude estimate of the heights of the tide flats above MLLW was calculated taking into account the corrections for Netarts Bay from the predicted height of the tide. These measurements determined the difference in heights of the intertidal beaches from each other.

#### Collection of Cockles

Twelve collections of cockles were made during the year from July, 1975 to September, 1976 (Table 1). Sampling strategy was to get monthly samples, but the logistics, weather, and tides prevented evenly spaced sampling periods. Samples were collected during the low tide period over one or two days. Sites were identified by their geographic position in the estuary in relation to the channel and were

Table 1. Sample collection data for Clinocardium nuttallii from Netarts Bay, 1975-1976.

Date	Predicted Tide*		Station I		Station II		Number of Cockles Collected
	Time	Height	Salinity (%)	Temp. (C)	Salinity (%)	Temp. (C)	
July 11, 1975	844	-2.0	--	--	--	--	57
Aug. 8, 1975	739	1.8	--	--	--	--	112
Aug. 15, 1975	1325	2.8	34.1	15.8	33.8	17.1	70
Sept. 5, 1975	629	-1.1	30.9	16.7	30.4	17.7	137
Oct. 3, 1975	1744	0.1	31.7	12.2	31.3	12.4	226
Nov. 5, 1975	647	2.4	29.8	12.4	--	--	30
Nov. 29, 1975	1528	0.0	29.4	8.3	26.4	7.3	91
Jan. 27, 1976	1557	-0.4	29.1	9.3	26.8	9.2	139
Mar. 11, 1976	1443	0.6	28.3	9.3	26.2	10.3	157
May 4, 1976	1026	-0.4	28.2	14.6	26.4	16.5	161
June 15, 1976	933	-1.7	31.6	16.5	31.5	18.7	134
July 31, 1976	958	-0.2	34.9	16.6	--	--	60
Sept. 11, 1976	832	1.3	--	--	34.6	17.0	60

-----  
 \* Predicted tide data from Newport Marine Science Center (Oregon State University).

not designated as marked 'plots'. Station I was located in an intensely dug sport clamming area of the estuary and Station II was located in a zone upbay restricted by the ODFW to no clam digging.

In the intertidal areas, cockles were collected with clam rakes, three centimeter spacing between prongs. There was some bias toward large animals, but with repeated raking over an area many individuals smaller than the space between prongs were found. No attempt to quantify either abundance or distribution of the area was made. Ten cockles from each site provided gonad samples, and the excess cockles were kept for the growth study so that no cockles were thrown back. Over the year, each sample site was well sampled for its age and size distribution above the juvenile stage.

For the subtidal areas, two scuba divers picked up cockles by hand in the channel between East and West intertidal sites at the two stations. The divers found cockles half-exposed in the sand and by random raking with a hand rake. The divers had a difficult time collecting when the tide was running, resulting in a considerable bias toward large individuals, which were often almost fully exposed on top of the sandy bottom. One subtidal sample (August 15, 1975) was collected with the clam suction-dredge used by the ODFW. In that sample some small sized individuals were found, indicating their presence in the subtidal, and the bias toward missing them in a sample collected by hand.

A supplemental collection was made on October 3 and 4, 1975, consisting of 65 cockles from Intertidal I-East and Subtidal II, which were tagged and returned to their areas in order to retrieve and measure their growth on a later date, as well as assess their 'migration' or transport away from those sites. The 65 were buried in a perimeter around permanent auger spikes as markers of both sites.

#### Abiotic Data

Salinity and temperature measurements were taken in the channels at both stations on each trip (Table 1). In addition to these data use was made of other hydrographic and climatological data of conditions in Netarts Bay (Glanzman, 1971). Some isolated observations were taken in the course of this study such as temperature of sediments in various conditions of sunlight, and times of lag between predicted and observed tidal movements. The physical data taken on this study were used to compare with more comprehensive results from other sources.

Sediment cores were taken on May 4, 1976, from each site for measurement of water content and volatile solids. These two parameters are used to describe differences among the sediments and the hydrodynamics of tidal flushing at each site. The sediment parameters of pore water and organic content can be correlated with characteristics such as grain size and current velocity. Sediment

data were also taken from Glanzman et al. (1971), whose transects for sediment cores correspond to Station I and II.

Two parameters of sediment, percentages of water and volatile solids, were compared among sample sites using analysis of variance, F-tests, and contrasts comparing means. The samples were ranked according to these sediment parameters.

### Growth Data

Age was determined by counting concentric rings which mark seasonal growth checks and other disturbances in pelecypods as concluded by Weymouth (1923, 1931), Wilbur and Owen (1964), and others. The yearly growth checks were not always clearly evident (Figure 3). Fraser and Weymouth noted in 1931 that the southern populations of Clinocardium nuttallii have less severe winters, and less prominent rings than the northern members of the species. The formation of rings began with the year zero, which was marked by the first check put down by a cockle after setting in the spring, summer, or fall. The age of the shell was determined by counting the number of rings after the zero check. Also important was the time of collection in estimating age. In the early winter the last check was recently made and thus was an accurate age marker. Collections in the late summer showed the growth of a year, but no check marked the age until the season changed. A year was added to

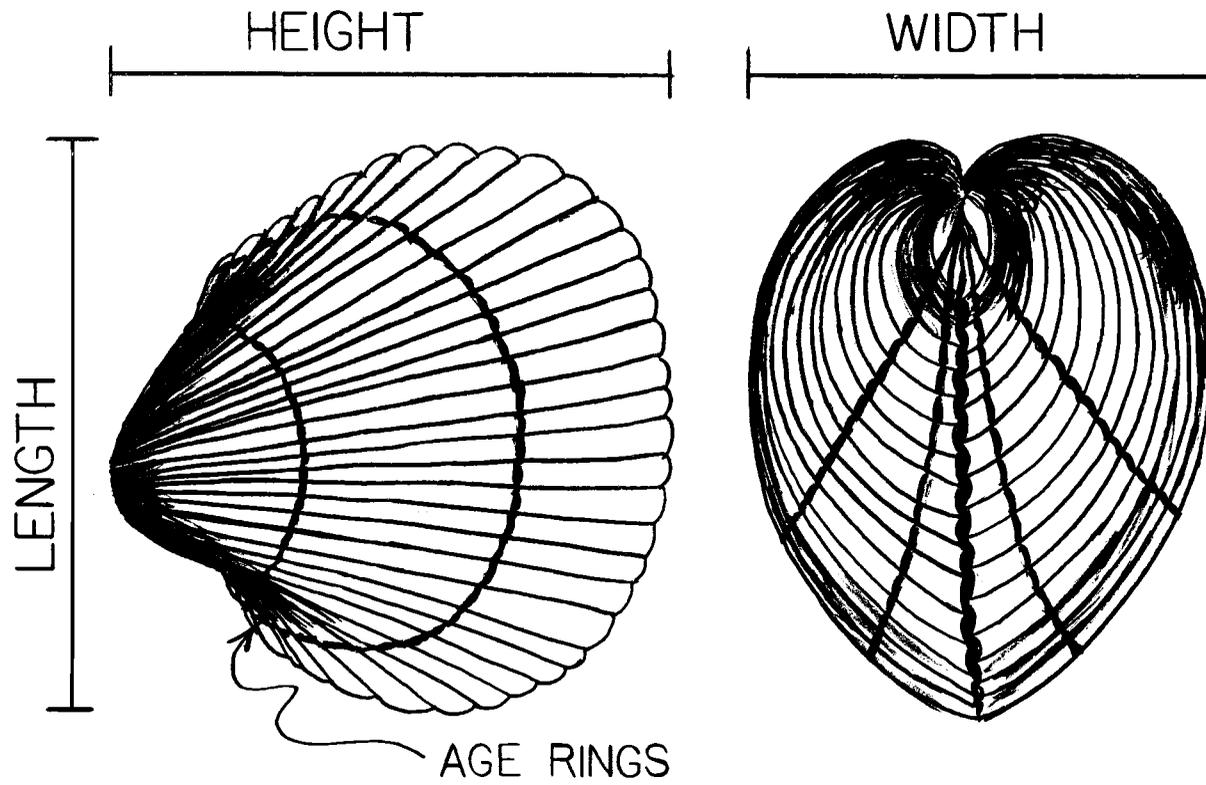


Figure 3. Clinocardium nuttallii shell measurements.

the number of checks in the summer. The number of disturbance checks was not known. Age was used as the independent variable on all graphs which displayed absolute growth.

Mean lengths and heights of the shells at each age were determined in a different manner from those of other Clinocardium studies (Fraser, 1931; Weymouth, 1931). Those studies considered individual growth rates by measuring the length of each ring of each specimen, which determined average yearly growth from several year-classes. The method employed in this study was to measure the total length of each cockle at its shell edge and then estimate its age at the time it was collected (Figure 3), which determined the average growth of cohorts of animals, which set in the eight years before 1976. Each age was represented by only two year-classes, as cockles were collected over two growing seasons during this study. By dividing the collections into cohorts the effects of annual climatic variability upon growth was isolated into age classes, and so the geographic environment as a source of variability of growth was compared within each cohort.

The ODFW measured shell height and estimated age in the same manner as this study in a series of collections of subtidal cockles from Tillamook Bay (September, 1974; August, 1975; April, 1976). Comparison of Netarts subtidal growth data was made with data on those subtidal samples collected with the suction dredge.

Additional growth data were obtained concerning juvenile C. nuttallii taken from the cement fish ponds of Oregon Aquafoods, Inc. in Newport. A year after the ponds were filled in November 1973, cockles were collected from the sediments which had accumulated in them, and shell heights were taken as heights of the year class 1974. Samples of 1975 and 1976 year classes have been collected on September 27, 1976 and January 3, 1977. These subtidal data allow comparison of first year growth with Netarts samples.

The size and age of 1,434 cockles was coded for analysis with the Statistical Interactive Programming System (SIPS) on the OS3 computer operating system (Guthrie, Avery, and Avery, 1974; Rowe, 1975). An analysis of variance was made of means of age, dimension, and shell weight from the six sample sites of this study. The cockle samples, which were used for gonad assessment, were used for this analysis, because they had equal sample sizes of eight to ten individuals. The hypothesis that there is no significant difference between the means of measurements of cockle parameters was tested using the F test. A contrast of means of age, length and height was made for three samples, representing the largest and smallest calculated F values at the beginning and end of the sampling program. The contrast of means tested the significance of differences between means of sets of sample sites and between means of individual sites. Six contrasts were made:

- 1) East vs West Intertidal
- 2) Station-I vs Station-II
- 3) Intertidal vs Subtidal
- 4) I-E vs II-E
- 5) S-I vs S-II
- 6) I-W vs II-W

Ranks of sample sites for age, length, and shell weight were made.

Shell data were organized according to sample sites and according to subtidal versus intertidal comparison. Means of shell weights and dimensions were calculated using the data from all the specimens collected over the study. Plots and age histograms were made from these data. Absolute, relative, and allometric forms were used as ways of presenting growth data.

#### Symbiosis

The incidence of zoochlorellae in the siphon and mantle tissues of the cockle and the amount of epizoic red or green algae attached to the shell was observed in the lab. The degree of infection was translated to a scale of 0) none, 1) light, 2) heavy. Plots were made of the occurrence of these symbionts with age. Subtidal and intertidal sites were compared.

### Processing Samples

For most sample periods 60 cockles, the ten largest from each site, were processed for histological examination of gonads. Ten individuals were chosen as the sample size to simplify comparison with other studies (Ropes and Stickney, 1965; Matchell and DeMartini, 1971). The largest were chosen to eliminate the effect of the variable bias against small specimens in sampling.

Gonad tissue was removed from above the "knee" or middle portion of the foot of each cockle. If the animal was a juvenile or its foot was completely flaccid, a cross section of the foot was taken including dermis, muscle, and any gut tissue present. Tissue was fixed in Bouin's solution and stored from 48 hours to several months. The tissue was dehydrated, embedded in paraplast, sectioned from seven to ten microns thick, and mounted on slides. The sections were stained with Mayers haematoxylin and eosin using standard techniques (Davenport, 1960). A Fisher Tissuematon was used for automated processing and staining of the slides.

### Criteria for Gonad Condition

Each cockle was analyzed for its male and female gonad condition. This was done by examining tissue sections under a dissecting microscope and then under a compound microscope at 100 and 400

power. Follicles of both sexes were present in each section, making separate judgements difficult, because male and female condition were interdependent. Several measurements were used to assist the subjective assessment of gonadal stages.

1) Percentage of follicles. The area of follicular tissue contained within a stained section of the foot tissue of the cockle was estimated in ten percent increments. Follicular tissue was defined as male and female follicles in any stage of development. It also included free spermatozoans or oocytes on the outside of ruptured follicles in the section. The amount of follicular tissue ranged from zero to one hundred percent. Other tissues present were connective, gut, muscle, and nerve. Some sections were cross sections of the foot and included dermal layers of muscle and epithelium. Percentage of follicular tissue in the section was an estimate of overall ripeness of the individuals.

2) Male to female ratio. The ratio of numbers of male follicles to the number of female follicles was also estimated by observation. The ratios were estimated in increments of one. The mean ratio was determined by dividing the sums of both sides:

$$\begin{array}{r}
 1: 1 \\
 1: 1 \\
 1: 2 \\
 1: 2 \\
 2: 1 \\
 \hline
 1: 3 \\
 7: 10 = 1: 1.43
 \end{array}$$

The ratio of male to female follicles helped to show the sequence of male and female development during the year. It addressed the questions of protandrous or protogynous development of this hermaphrodite.

3) Number of oocytes per follicle. This measurement quantitatively assessed oocyte development from the time when female follicles first appeared. In each section all developing female gonidia were counted in five adjacent follicles. This included primary and secondary oocytes and smaller oogonia at the follicle walls. When different sized follicles were found in different parts of a section of tissue, ten follicles were counted. In a few cases a major discrepancy in stages of development within a single individual was noted.

4) Diameter of oocyte and nucleus. The mean diameters of eggs and their nuclei within follicles were measured using an ocular micrometer at four hundred power. The five largest oocytes with visible nuclei within a single female follicle were measured across their narrowest diameters. Five oocytes seemed to give a representative mean of the largest oocytes present in the section. The mean diameters of eggs and nuclei were factors in separating gonadal stages early in development.

With these quantitative measurements and a comparative inspection of each slide, their ranges were categorized into five

general gonad stages for both male and female. This has been done by other authors (Holland and Chew, 1974). Seven hundred four slides were inspected representing individual cockles from the twelve samples taken over the year from July, 1975 to September, 1976. Not every sample produced ten gonads from each site due to occasional sampling difficulties (Table 1).

Ripe gonad condition was the focus of the analysis, and was designated as the indicator of fecundity of individuals, since the time or amount of actual spawning was not measured. Spawning period was established by dates of samples containing ripe male or female gonads, while the distribution of ripe individuals over the spawning period was compared among populations, which were represented by the sample sites. A chi-square test was used to address the hypothesis that the populations of this cockle did not spawn synchronously even in adjacent areas (Snedecor and Cochran, 1968).

Fecundity of each population was established by determining the percent of ripe individuals found during the spawning period of the total collected in those samples, and sites were ranked accordingly. The percentage of ripe individuals at each site was also analyzed in relation to its age distribution. Statements were made concerning the efficiency of each population in producing gametes, even though quantities of larvae were not measured.

### III. RESULTS

#### Gonadal Development

Examination of sectioned material revealed five categories of gonadal development. Each gonad was characterized separately for the stage of development of its male and female follicles. These stages were identified by examination of the following criteria: the percentage of follicular tissue in the section; the number of oocytes per follicle; oocytes and nuclei diameters; and ratio of the number of male to female follicles. Mean values of each of these criteria were calculated for each of the six sample sites for each gonadal stage (Figures 4-7). There was a high degree of consistency among the sites in the mean values of the criteria used in staging.

Percentage of follicular tissue showed a distinct mean for each gonadal stage. Number of oocytes per follicle and male to female ratio had distinct values only for the ripe stage, while values at other stages overlapped. The early active stage is most clearly distinguished by the criteria of oocytes and nuclei diameters.

Gonadal development was followed over time by plotting monthly sample means of percentages of follicular tissue and number of egg per follicle, and development was compared among sites by separating these values into monthly means from each site (Figures 8 and 9). The male and female gonad conditions of 704

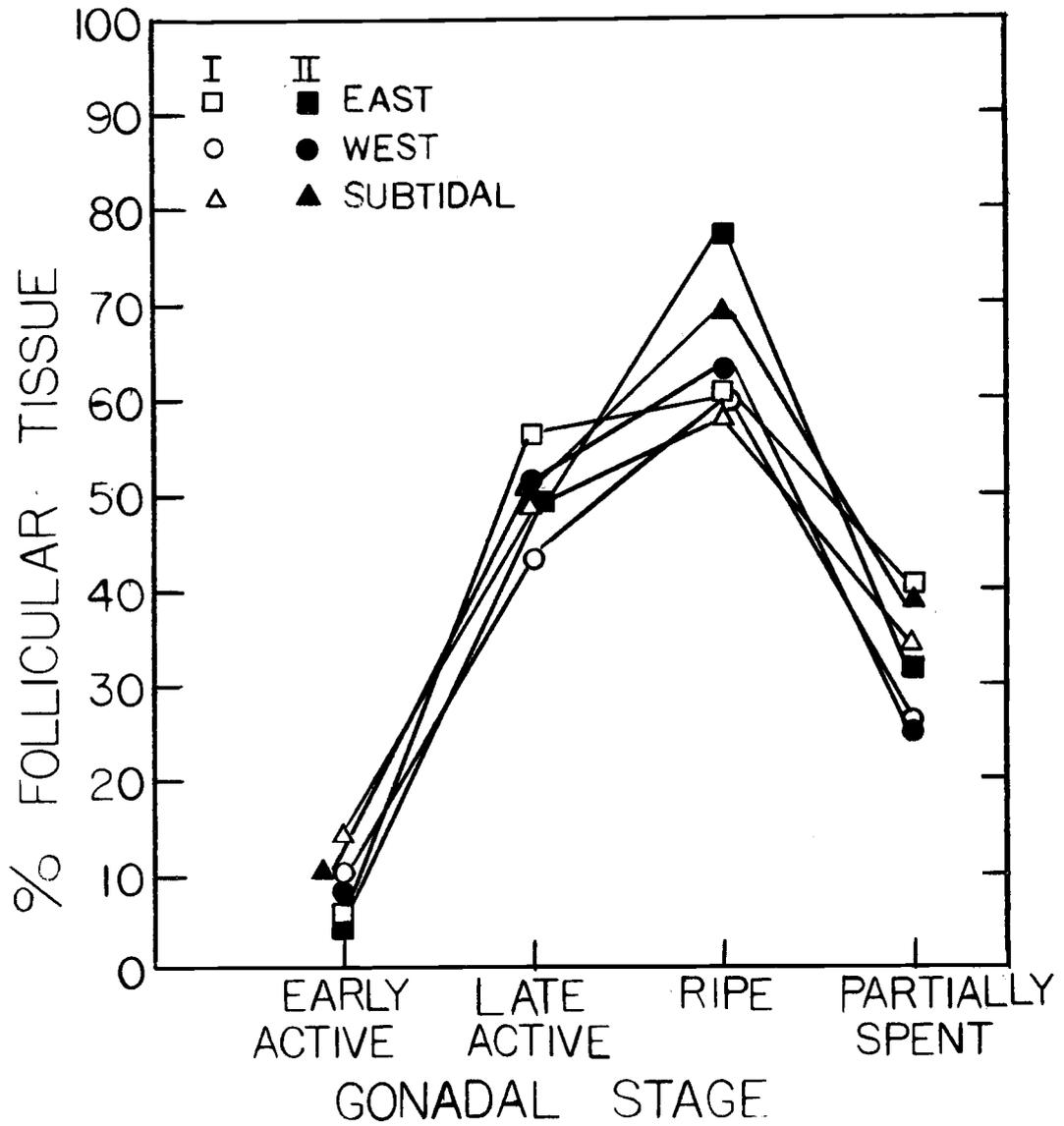


Figure 4. Percentages of follicular tissue in tissue sections.

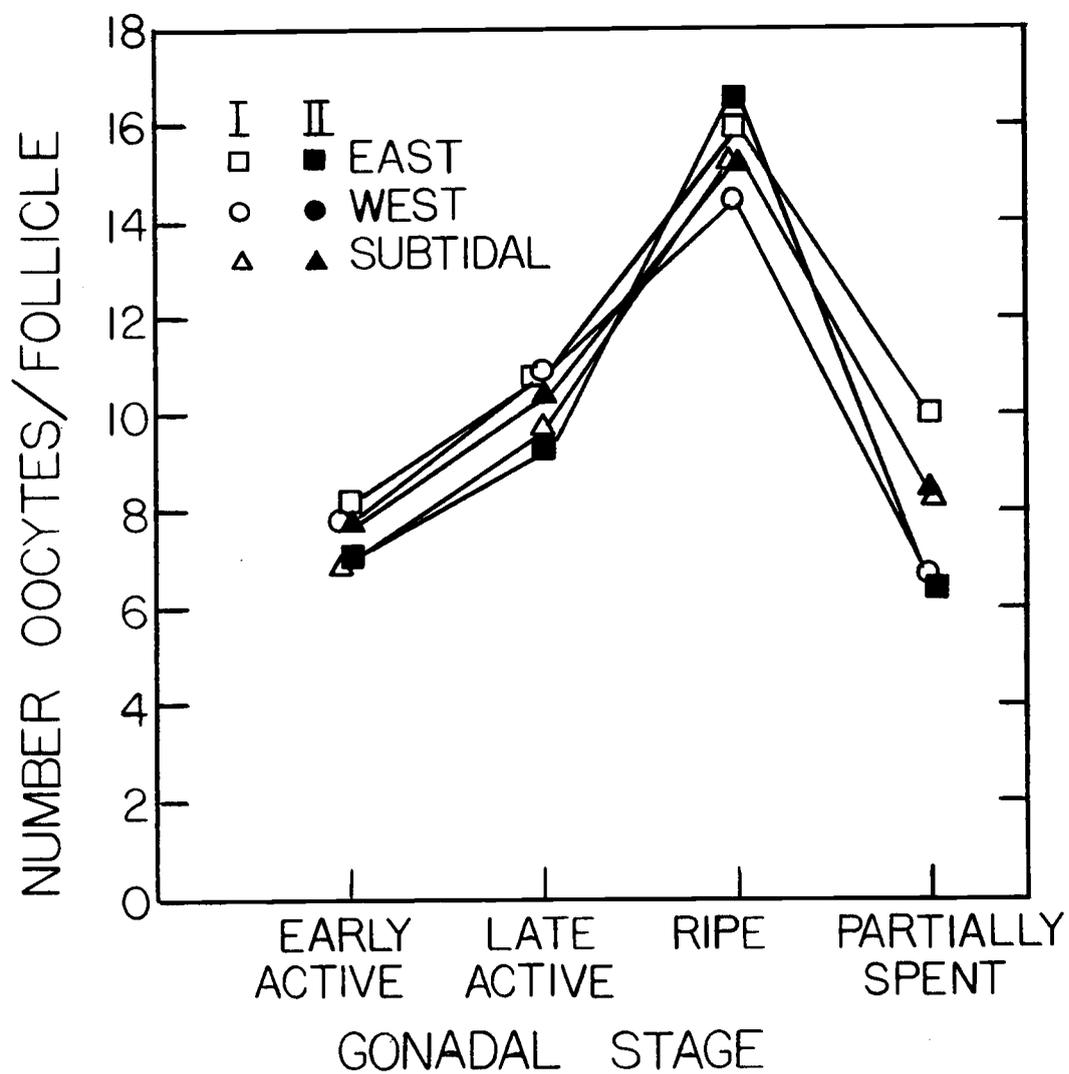


Figure 5. Numbers of oocytes per follicle.

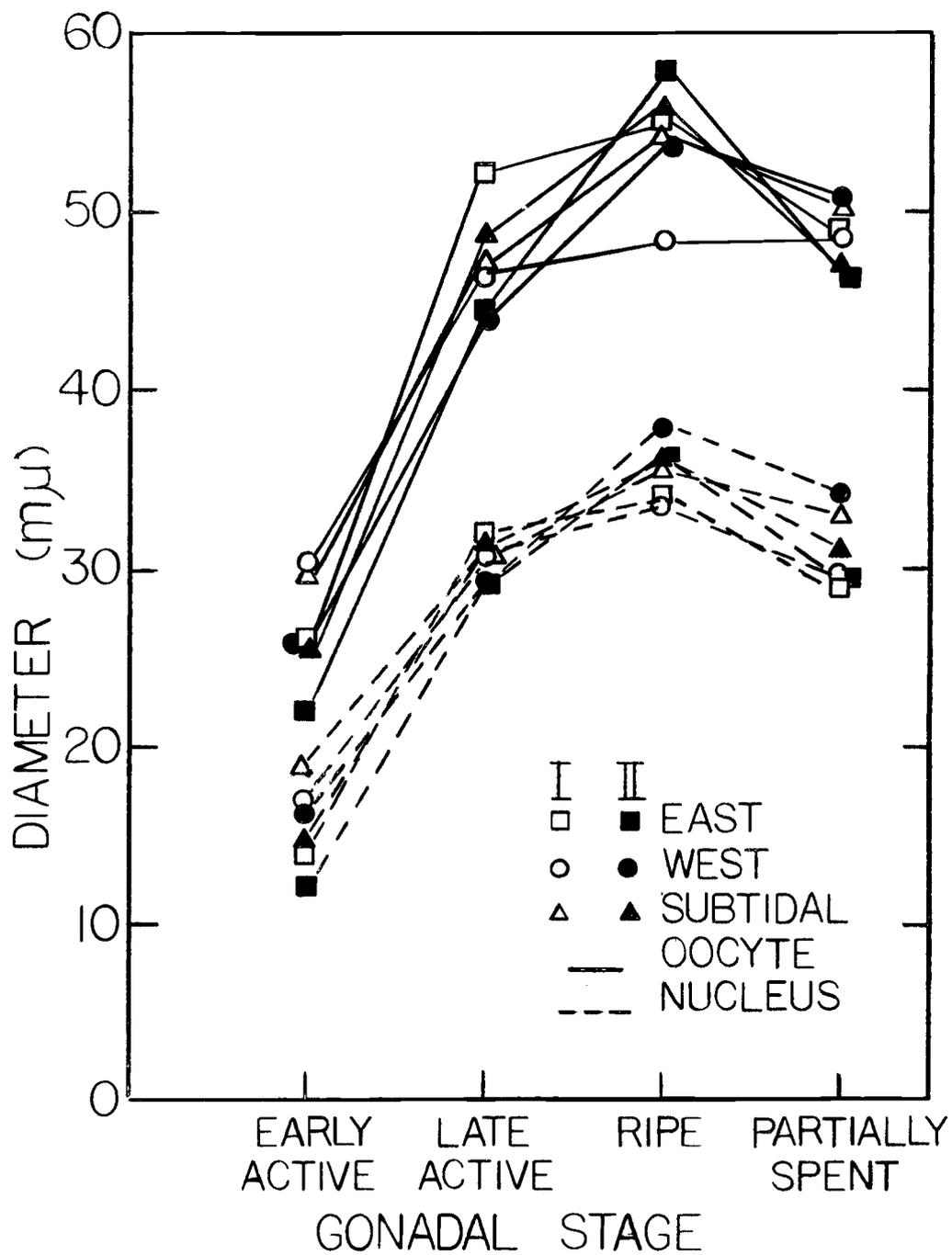


Figure 6. Diameters of oocytes and oocyte nuclei.

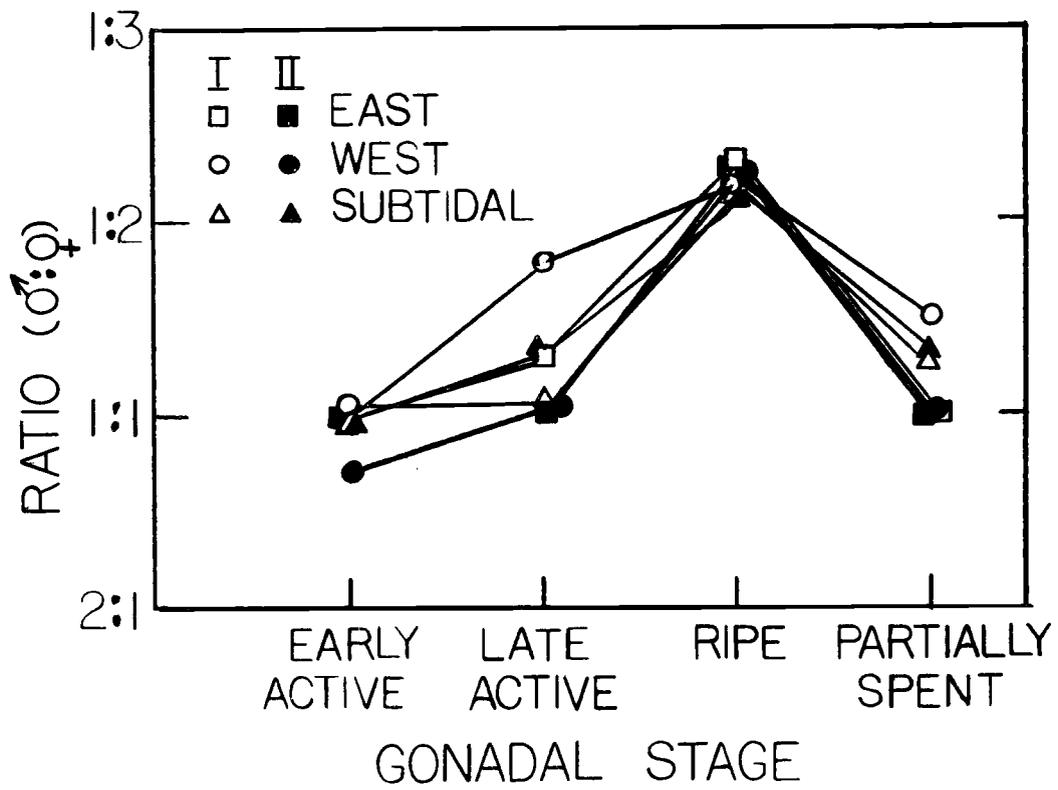


Figure 7. Ratios of numbers of male follicles to number of female follicles.

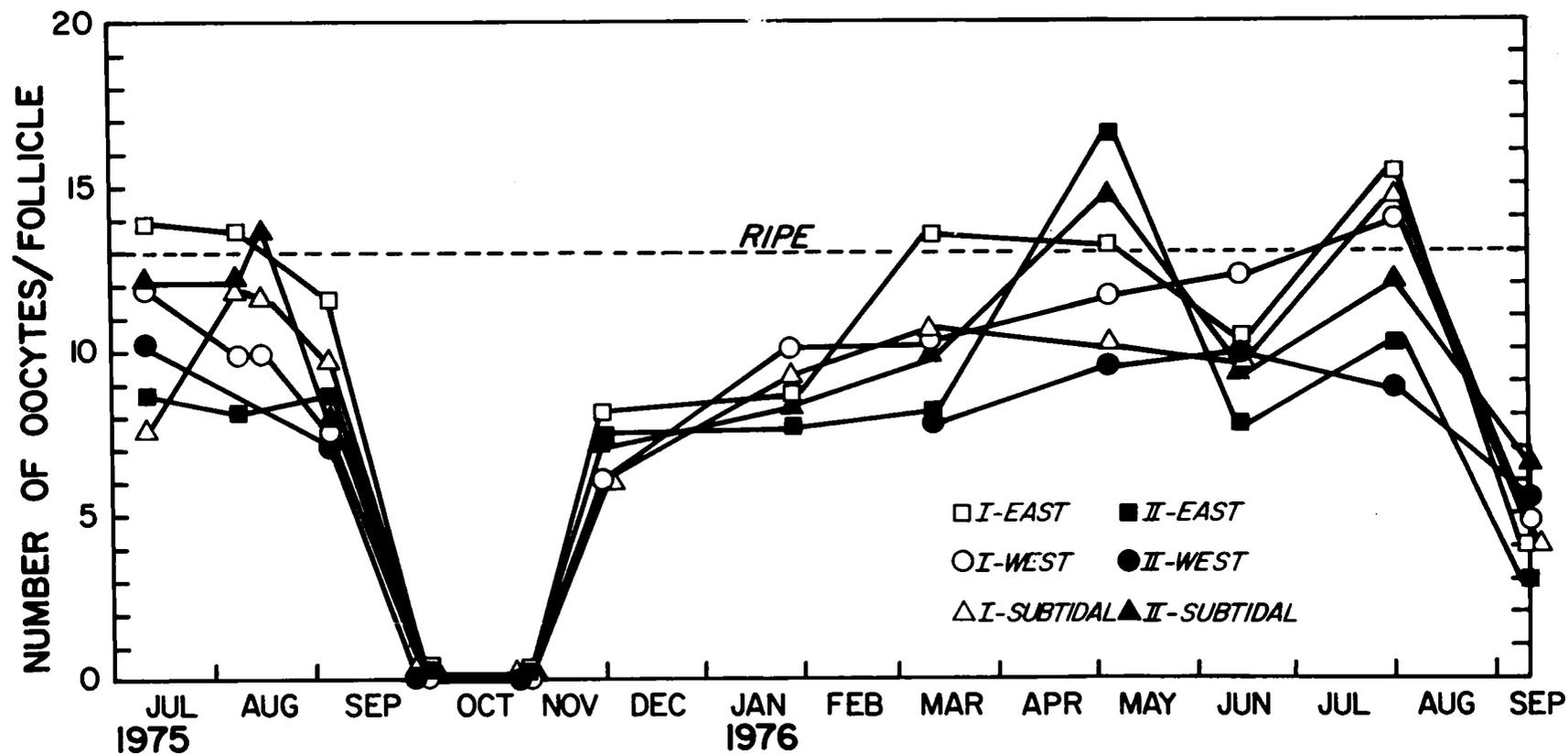


Figure 8. Means of percentages of follicular tissue in tissue sections, Netarts, 1975-1976.

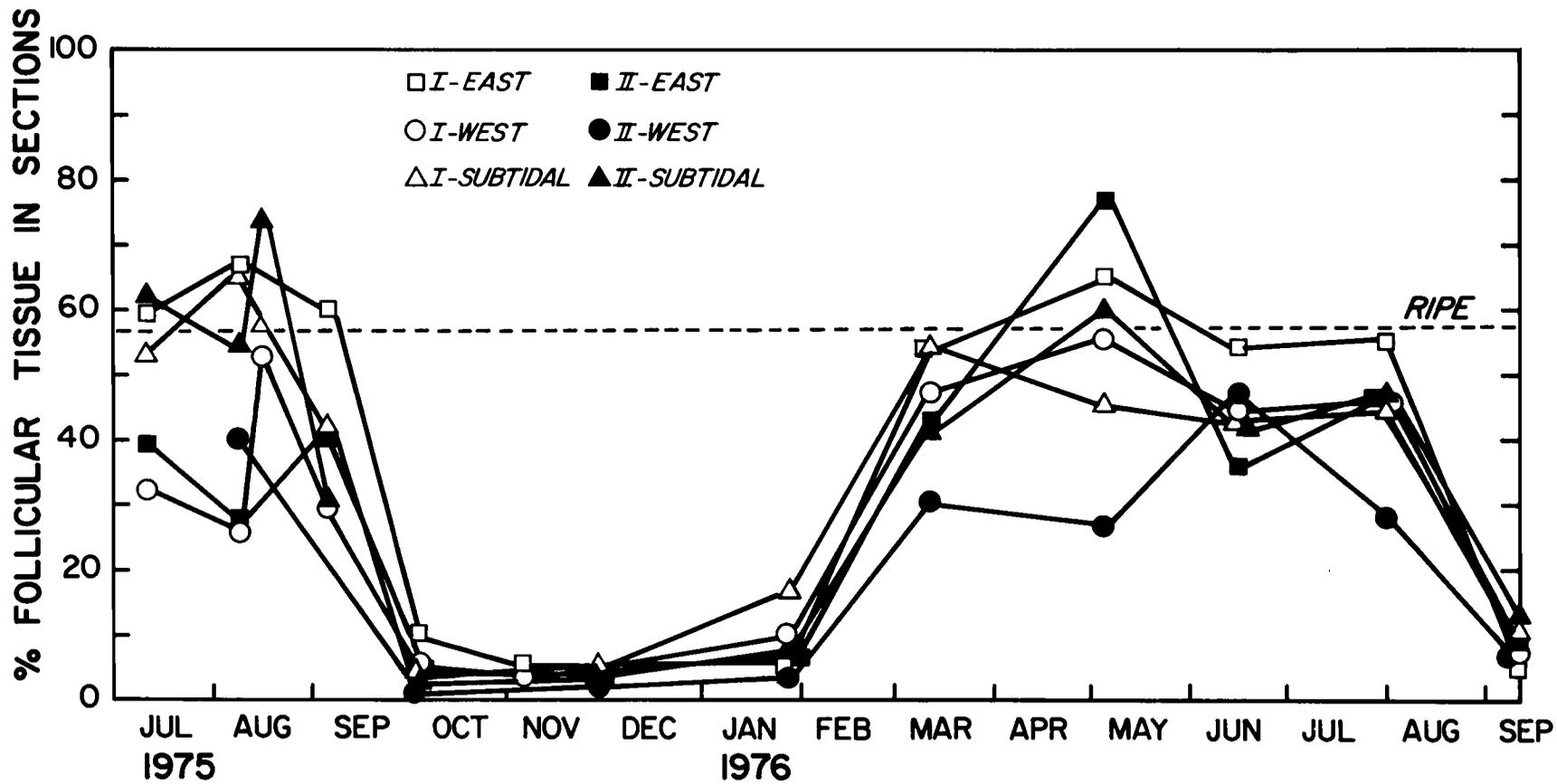


Figure 9. Means of numbers of oocytes per follicle, Netarts Bay, 1975-1976.

specimens from the study were recorded (Table 2).

The five categories of gonadal development are described as follows:

1) Early active stage. The early active stage marks the initiation of visible gonadal development. The stage is characterized by a small percentage of reproductive tissue present in a section (Figure 4).

The individuals earliest in development have female follicles but no differentiable male follicles. The follicular tissue stains slightly darker than surrounding tissue. The oogonia first become recognizable when the basophilic nuclei are visible before there is evidence of spermatogenesis. Spermatogonia first become visible in the sections containing the larger of the early active oogonia. Spherical spermatogonia and primary spermatocytes stain darkly. Both male and female follicles mature from the outside toward the center. When both male and female follicles are observed in the early active stage, the ratio between follicles is one to one.

2) Late active stage. The late active stage of the gonads is characterized by follicles partially full with some ripe gametes. The percentage of follicular tissue and number of eggs per follicle increases from the early active stages (Figures 4 and 5). Female follicles include developing oogonia in the follicular walls, primary oocytes and secondary oocytes. Most oogonia and oocytes are still

Table 2. Stages of gonadal development of individuals in each sampling period.

Sample Date	71175	80875	81575	90575	100375	110575	112975	12776	31176	50476	61576	73176	91176	Total															
Gonadal Condition	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F													
Intertidal I-East	Partially Spent (PS)	3	-	1	-	-	-	-	1	-	-	-	-	-	8	2	1	1	5	3	18	7							
	Ripe (R)	9	7	9	4	-	-	10	3	-	-	-	-	-	2	2	9	4	2	1	9	6	-	-	50	27			
	Late Active (LA)	-	5	-	5	-	-	-	7	-	-	-	-	-	8	8	1	6	-	7	-	3	-	-	-	9	41		
	Early Active (EA)	-	-	-	1	-	-	-	-	-	-	-	-	-	9	6	10	-	-	-	-	-	-	-	-	-	6	20	
	Spent (S)	-	-	-	-	-	-	-	-	10	9	10	10	10	1	4	-	-	-	-	-	-	-	-	5	7	39	27	
	Total (N)	12		10		0		10		10		10		10		10		10		10		10		10		10		122	
Intertidal I-West	P. S.	3	-	5	3	2	-	5	6	-	-	-	-	-	-	-	-	2	7	1	7	4	29	16					
	R.	4	1	3	2	8	2	5	1	-	-	-	-	-	-	-	1	2	2	2	2	5	-	-	25	15			
	L. A.	5	11	-	2	-	7	-	3	-	-	-	-	-	9	9	9	8	6	6	-	3	-	-	29	49			
	E. A.	-	-	-	-	-	1	-	-	-	-	-	-	-	3	9	10	1	1	-	2	-	1	-	-	12	16		
	S.	-	-	1	2	-	-	-	-	10	10	10	10	10	7	1	-	-	-	-	-	-	-	3	6	36	35		
	N.	12		9		10		10		10		10		10		10		10		10		10		10		10		131	
Subtidal-I	P. S.	-	-	-	-	-	-	6	8	1	1	1	1	-	-	-	-	-	-	8	8	5	7	21	17				
	R.	11	5	10	3	10	4	2	1	-	-	-	-	-	-	3	1	-	3	2	1	2	-	-	38	25			
	L. A.	1	7	-	7	-	6	-	-	-	-	-	-	-	2	6	7	8	10	6	8	-	-	-	-	21	49		
	E. A.	-	-	-	-	-	-	-	-	-	-	-	-	4	7	7	4	1	1	-	-	-	-	-	-	13	12		
	S.	-	-	-	-	-	-	2	1	9	9	2	2	8	4	3	1	-	-	-	-	1	-	5	3	30	20		
	N.	12		10		10		10		10		3		8		10		10		10		10		10		10		123	
Subtidal-II	P. S.	-	-	3	2	2	2	7	7	-	-	-	-	-	-	-	-	9	5	10	7	6	6	37	29				
	R.	8	3	6	5	8	6	1	1	-	-	-	-	-	-	2	2	9	7	1	1	-	3	-	35	28			
	L. A.	3	6	-	3	-	2	-	-	-	-	-	-	-	1	1	6	6	1	2	-	4	-	-	-	9	24		
	E. A.	-	-	-	-	-	-	-	-	-	-	-	-	7	3	9	1	1	-	1	-	-	-	-	-	4	18		
	S.	-	-	-	-	-	-	2	2	10	10	-	-	11	4	6	-	1	1	-	-	-	-	4	4	35	21		
	N.	9		10		10		10		10		0		11		10		10		10		10		10		10		120	
Intertidal II-East	P. S.	5	9	4	4	-	-	5	6	-	1	-	-	-	-	-	-	5	4	2	1	3	3	24	28				
	R.	6	1	2	1	-	-	4	1	-	-	-	-	-	-	-	-	10	9	1	-	6	-	-	29	12			
	L. A.	-	1	-	1	-	-	-	2	-	-	-	-	-	-	-	1	8	-	1	4	5	1	8	-	6	26		
	E. A.	-	-	-	-	-	-	-	-	-	-	-	-	3	1	9	7	1	-	-	-	-	-	-	-	8	13		
	S.	-	-	3	3	-	-	1	1	10	9	-	-	10	7	9	1	1	-	-	1	1	1	7	7	42	30		
	N.	1		9		0		10		10		0		10		10		9		10		10		10		10		109	
Intertidal II-West	P. S.	-	-	7	7	-	-	8	8	1	-	-	-	-	-	-	-	2	-	3	1	3	2	24	18				
	R.	-	-	3	3	-	-	1	-	-	-	-	-	-	-	-	-	2	2	1	1	2	-	-	9	6			
	L. A.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	4	4	4	4	5	7	-	5	-	13	21		
	E. A.	-	-	-	-	-	-	-	-	-	-	-	-	2	3	9	4	6	2	3	1	1	2	2	-	12	23		
	S.	-	-	-	-	-	-	1	1	9	10	-	-	9	7	7	1	2	-	2	1	1	1	3	2	7	8	41	31
	N.	0		10		0		10		10		0		9		10		10		10		10		10		10		99	

attached to their follicular walls by micropyles. The larger oocytes are conical or pyriform.

Late active male follicles mature more rapidly than female follicles. Male follicles in the late active stage contain at least some spermatids or free spermatozoans in the central lumina. Most male gametes are spermatocytes. Male follicles are larger in diameter than those from the early active stages.

Late active individuals were identified in every sample except those from October 3, 1975 to January 27, 1976. Late active female gonads were identified from two to four times as often as male gonads. The late active stage was observed primarily in the late winter and early spring, but was also observed after the peak in spawning and became confused with the partially spent stages.

3) Ripe stage. The ripe stage of gonads is separated from the late active and partially spawned stages by having the greatest amounts of follicular tissue and having follicles full of ripe oocytes. More than 58 percent of follicular tissue in a section and 13 or more oocytes per follicle were the criteria used in identifying the ripe stage (Figures 4 and 5). The largest female follicles contained up to 27 oocytes. The diameters of oocytes and nuclei could not be used to distinguish ripe oocytes from late active or partially spent stages.

Ripe male follicles were characterized by being at least

three-quarters full of mature spermatozoans. The spermatozoa were arranged in concentric circles, head to head, with rod-shaped bodies and trailing flagella oriented toward the central lumen of the follicle.

Twenty percent of the ripe female gonads occurred with spent or partially spent male follicles. Some late active female gonads were found with ripe male gonads and even occurred with partially spent male follicles. The mean ratio of male to female follicles was 1:2 (Figure 7). The greater number of female follicles suggests earlier male spawning.

Ripe specimens were observed in July, August, and early September of 1975. In 1976, ripe individuals were collected from March 11 through July 31. None were observed from the September 11, 1976 collections (Table 2). The amount of follicular tissue and the number of eggs per follicle showed peaks through the summers of both years (Figures 8 and 9). Not all sample sites were ripe at the same time. Since the ripe condition of gonads was accepted as an indication of spawning, a very long spawning period was observed in this study.

4) Partially spent stage. Some of the characteristics of the partially spent stage overlap those of ripe and late active stages. The amount of follicular tissue tends to be less than in late active or ripe sections (Figure 4). Although some oocytes remain in the

ripe condition, the average number of oocytes per follicle is more variable (Figure 5), and overlaps the characteristics of the late active and ripe stages. Mean oocyte diameters vary within a range covering late active to ripe stages (Figure 6).

Recently-spawned male follicles are as large as ripe ones, but contain fewer spermatozoans. The partially spawned follicle contains spermatocytes and can be confused with late active follicles.

Seventeen percent of the number of partially spawned female gonads occurred with ripe male gonads, which contradicted the observation that male gonads spawned first. The ratio of male to female follicles, 1:1.0 to 1:1.4, may suggest a catching up of female spawning to male spawning toward the end of the spawning period. Eventually in the gametogenic process unspawned follicles disorganize, diminish in size, and are resorbed.

5) Spent stage. Spent individuals are easily recognized, as the tissue sections contain no follicles. Some slightly basophilic tissue remains, from zero to five percent, through the spent season but it is not sexually differentiable. In some cases a few remaining oocytes or free spermatozoa are in the sections, but none are in follicles. The spent phase seems to be reached simultaneously by both sexes.

Spent gonads were found occasionally in every sample among immature and degenerate individuals. The populations as a whole

were in spent phase during the fall and early winter.

### Synchronism of Ripeness

Occurrence of many individual male and female gonads in the same condition within a sample is an indication of synchronism of development in a population. In this study, gametogenesis is followed in the bay population as a whole and in sample sites separately (Figures 8 and 9). The entire bay population develops synchronously from the spent through the early active stage, but local populations reach the final stages of gonad maturity at different times.

Simultaneous occurrence of many ripe gonads in a sample is an indication of synchronous spawning of a population, and several sample sites show a majority of gonads in the ripe stage in one or more samples during the spawning period. However, there is no sample when more than three sites are simultaneously ripe.

The distribution of ripe individuals over the sampling period was compared using a chi-square test to indicate which sites were ripening synchronously. The populations at the up (Station II) and down (Station I) bay sites have different spawning peaks. Station II precedes Station I in initiating spawning, and also discontinues reproductive activity earlier in the summer. Subtidal and intertidal sites at each station are synchronous in their gonadal development. The West site populations develop gonadal material somewhat

autonomously from the others.

The occurrence of ripeness in male and female gonads is synchronous, when the cockles in the bay are taken as a single population, even though there are examples of uneven development of male and female gonads within individual cockles.

#### Age of Ripeness

The age of distributions of the samples collected for gonad observation and the age distribution of ripe individuals are compared (Figure 10). During the months when ripe gonads were observed, 443 cockles were sectioned and examined. The modal age for the whole bay was four years, which comprised 30 percent of the collection. Of those collected, 186 male gonads (42 percent) and 113 female gonads (25 percent) were ripe. Younger ages contained higher percentages of ripe male and female gonads than older ages. Two year olds had 53 percent ripe males and 31 percent ripe females, while the percentage of ripe gonads diminished consistently with increasing age after two years. Zero and one year cockles were immature; only 15 percent of one year male gonads and no females were observed to be ripe.

#### Sample Site Differences in Percentage of Ripeness

There was a large range in the values of the percentage of ripe

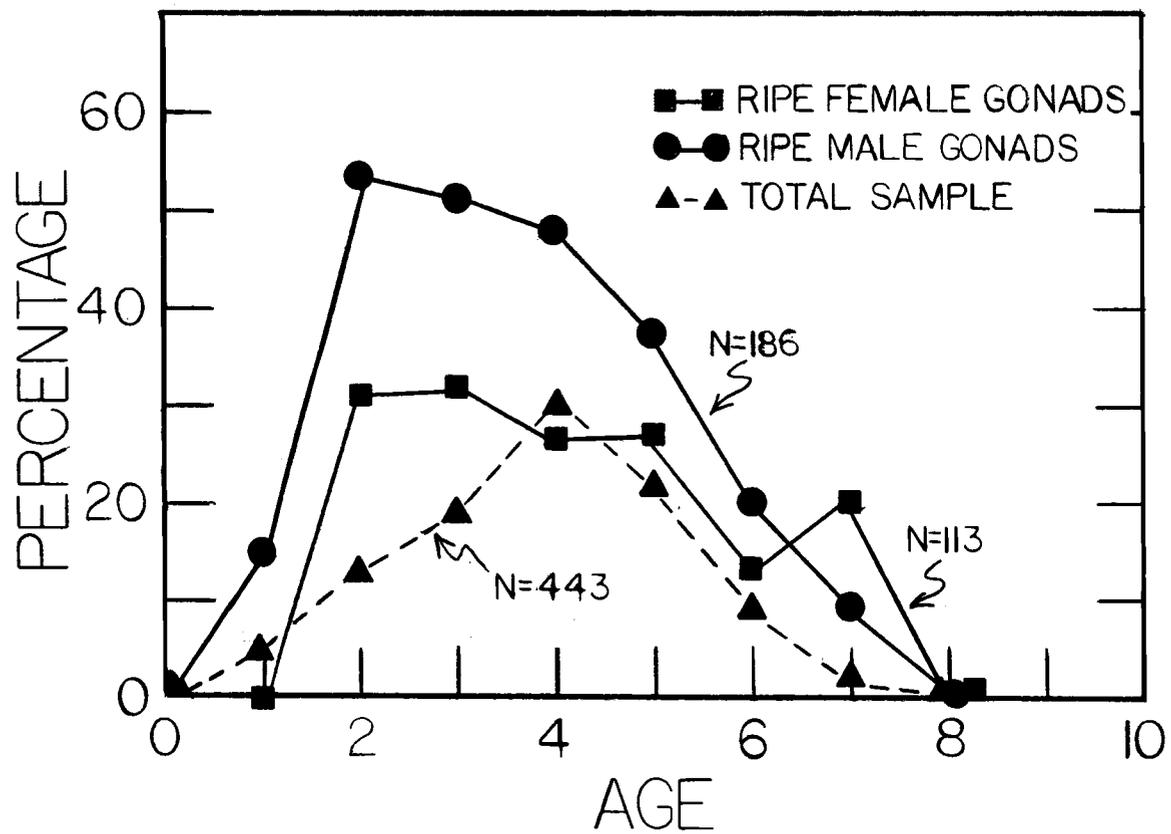


Figure 10. Percentages of the number of individuals collected with ripe male/female gonads at each age.

male and female gonads observed at each sample site (Table 3). Compared to the intertidal sites (except I-East), the two subtidal locations were characterized by higher percentages of individuals with ripe male and female gonads. Subtidal collections included 45 percent ripe male and 33 percent ripe female gonads. Intertidal collections (excluding I-East) included 29 percent ripe male and 15 percent ripe female gonads.

### Growth

#### Analysis of Variance of Sample Site Means

Age, size, and shell weight of Clinocardium nuttallii varies with location in Netarts Bay. Random samples of ten cockles from each site for each shell measurement were tested for the null hypothesis that the population means from each sample site are equal. The alternative hypothesis was that at least one mean is significantly different from the others with 99 percent confidence. The null hypothesis was tested for parameters of age, length, height, width, and shell weight using F-tests.

For age, length, and shell weight the most significant differences in means occurs between the intertidal and subtidal sites. The subtidal sites rank first and second in all three parameters (Table 3). The combination of means from the three sites at Station I is

Table 3. Rankings of sample sites according to biological and physical parameters.

---

Means of age and shell growth.

	I-East	I-West	Subtidal I	Subtidal II	II- East	II- West
Age	5	3	1	2	4	6
Length	3	4	1	2	5	6
Shell Weight	3	4	1	2	5	6

---

Individuals with ripe gonads.

Male Gonads

Percentage	69	31	46	44	42	15
Rank Order	1	5	2	3	4	6

Female Gonads

Percentage	38	19	30	35	17	10
Rank Order	1	4	3	2	5	6

---

Means of sediment parameters.

Organic Content	3	6	2	1	4	5
Water Content	3	6	1	2	4	5

---

significantly greater than those of Station II, and in some samples the East populations have greater means of size and shell weight than West populations. The rank of intertidal II-West is sixth in every parameter, while the other intertidal sites vary in rank between age, size, and weight.

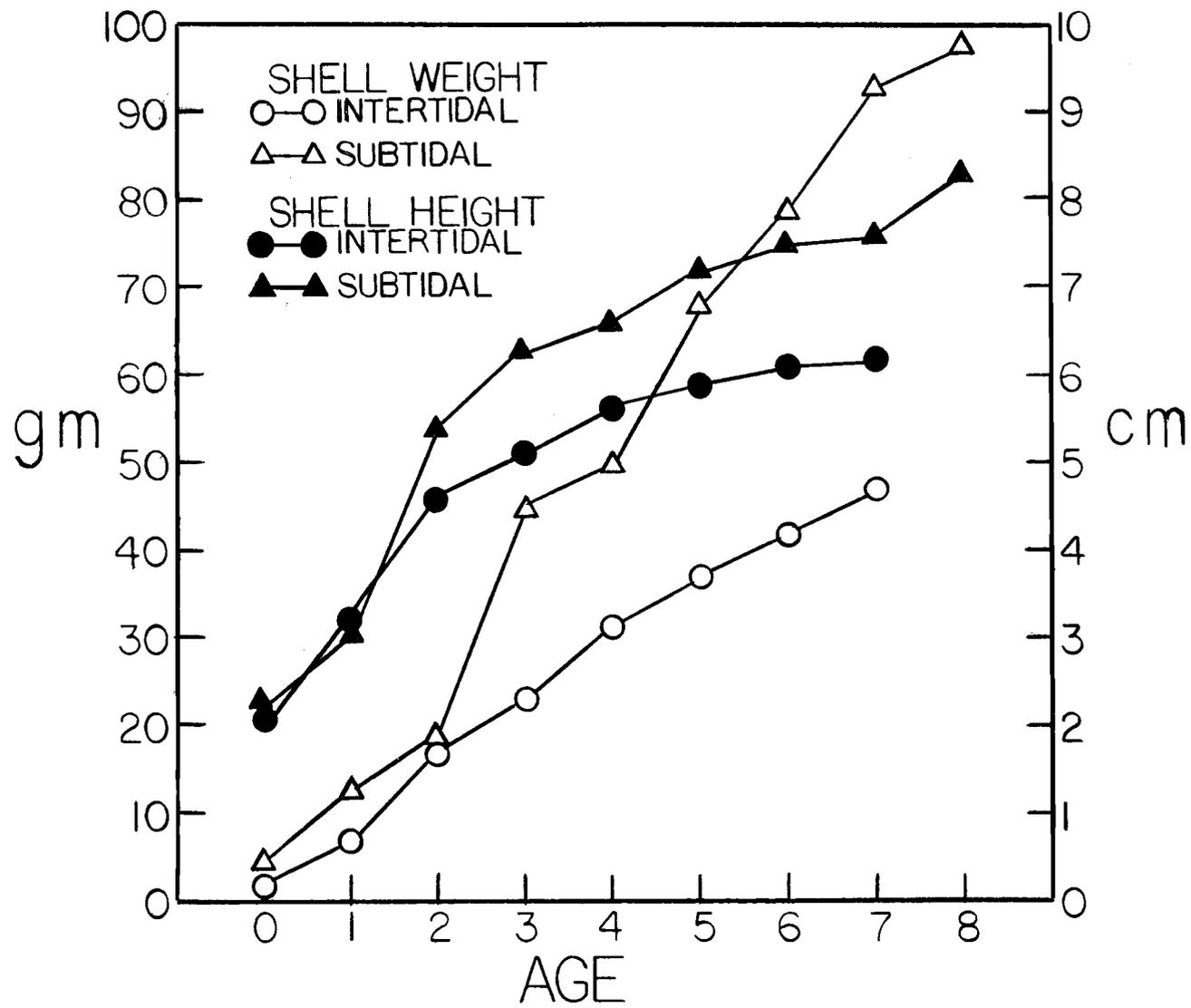
#### Intertidal versus Subtidal Growth

Subtidal cockle shells grow much faster and become much heavier than intertidal cockles after two years (Figure 11). Comparison of age distributions from these two environments shows a greater proportion of cockles above four years in the subtidal, and almost all the concentration of juveniles below three years in the intertidal (Figure 12). These plots of absolute growth are calculated from the measurement of all cockles collected in the study, and the numbers of cockles used to estimate means at each age are shown by the age histograms.

#### Allometric Growth

The shape of the cockle shell remains essentially the same throughout its growth. Plots of length against height, and width versus height show a nearly constant relationship between these shell parameters throughout the life of C. nuttallii using the allometric growth equation ( $Y = aX^b$ ) (Dame, 1972). The relationship

Figure 11. Absolute growth of shell heights and weights in the subtidal and intertidal environments, Netarts Bay.



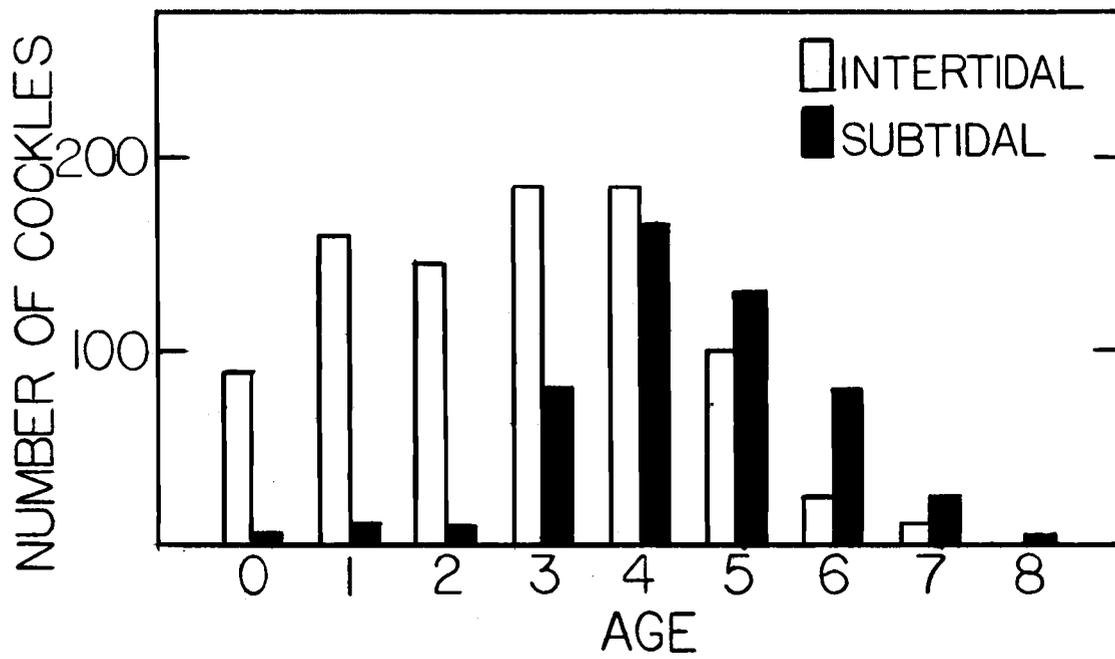


Figure 12. Age-frequency histograms of C. nuttallii from the intertidal and subtidal environments, Netarts Bay.

of these dimensions are the same for intertidal and subtidal collections. Linear regressions of length on height and width on height plot almost rectilinearly on logarithmic axes, and produce identical lines for the intertidal and subtidal (Figures 13 and 14).

There is an inherent relationship between height and shell weight, but the slope of this relationship changes with age, and differs between tide levels. The regression of shell weight on height gives two different slopes (b) for the subtidal and intertidal populations (Figure 15). Part of the difference is due to the different age distributions in these two areas, and part is due to the heavier shells at a given age in the subtidal.

#### Tide Level and Zoochlorellae

Zoochlorellae symbiosis is a characteristic which markedly differentiates subtidal from intertidal cockles in Netarts Bay (Figure 16). The four intertidal sites produce virtually no infected cockles. The subtidal environment produces medium to heavy zoochlorellae infections which increases with age. In the intertidal animals older than three years show a slightly higher percentage of infection.

Figure 13. Linear regressions of lengths on heights on logarithmic axes from the intertidal and subtidal environments, Netarts Bay.

[ log Intertidal Length = 0.107+.963 (log Intertidal Height);  
log Subtidal Length = 0.141+.950 (log Subtidal Height)]

$R^2 = 0.950$

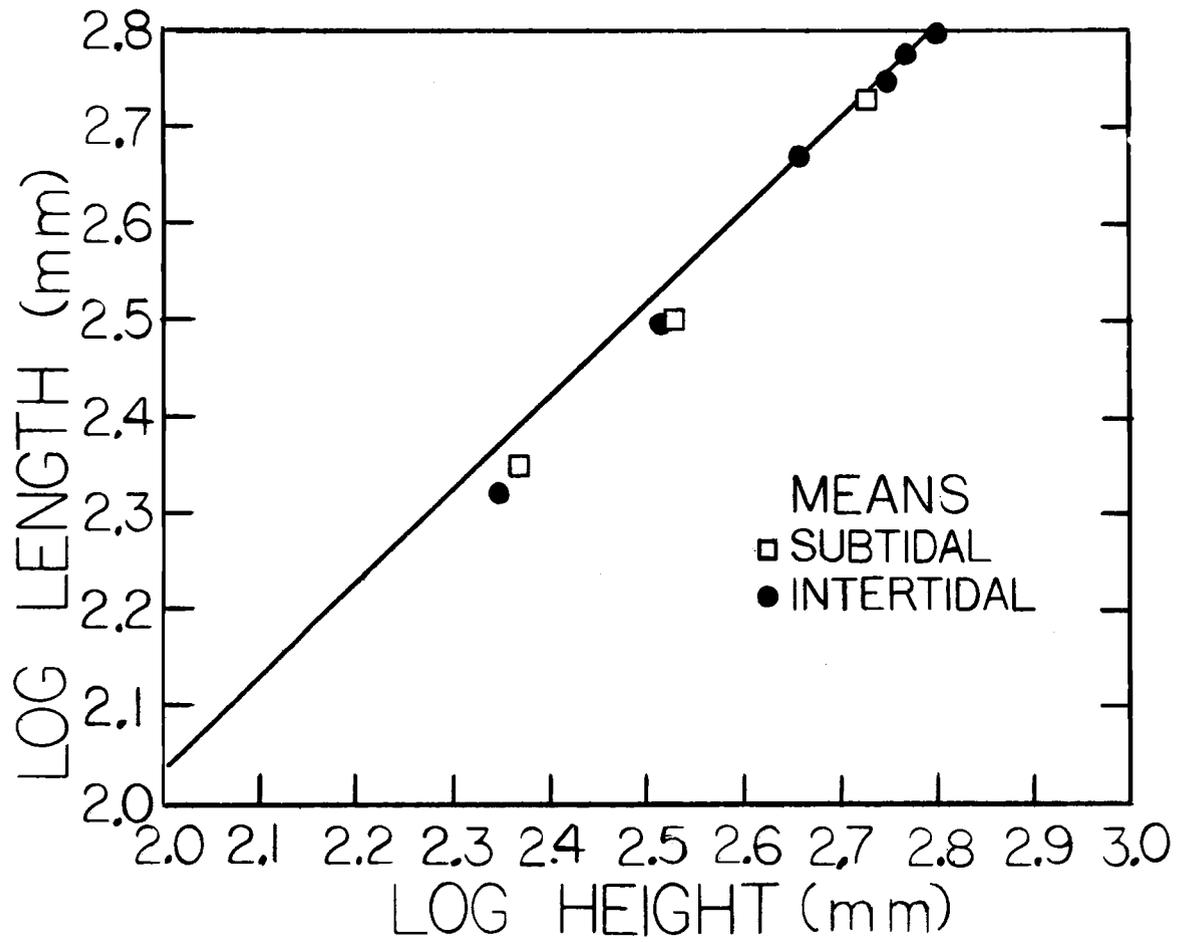


Figure 14. Linear regressions of widths on heights on logarithmic axes from the intertidal and subtidal environments, Netarts Bay.

[ log Intertidal Width =  $-0.00267 + .955 (\log \text{ Intertidal Height})$ ; log Subtidal Width =  $-0.00215 + .951 (\log \text{ Subtidal Height})$ ]

$$R^2 = 0.950$$

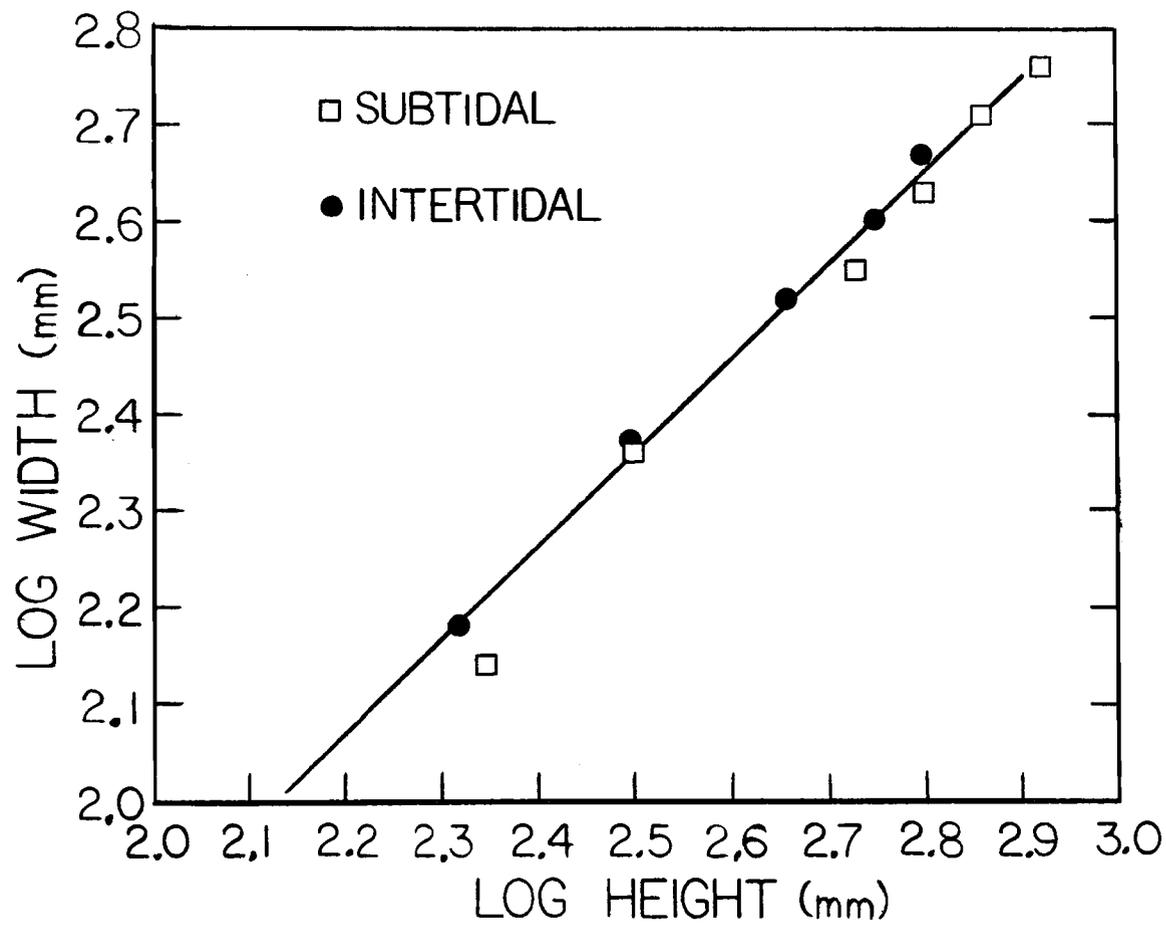
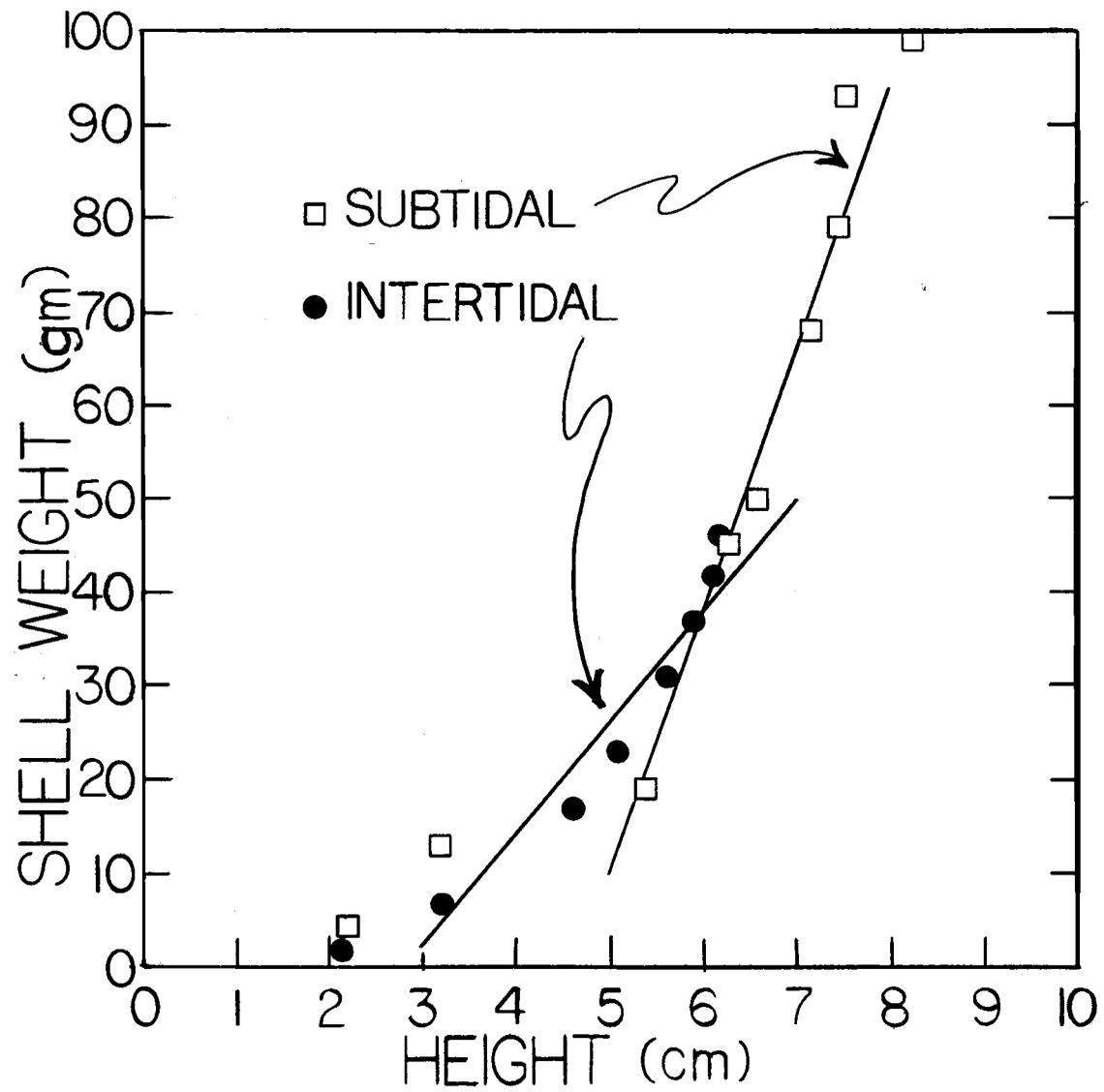


Figure 15. Allometric plots of shell weights and heights from the intertidal and subtidal environments, Netarts Bay.

[ log Intertidal Shell Weight =  $-6.07 + 2.74 (\log \text{Intertidal Height})$ ; log Subtidal Shell Weight =  $-6.62 + 2.95 (\log \text{Subtidal Height})$ ]



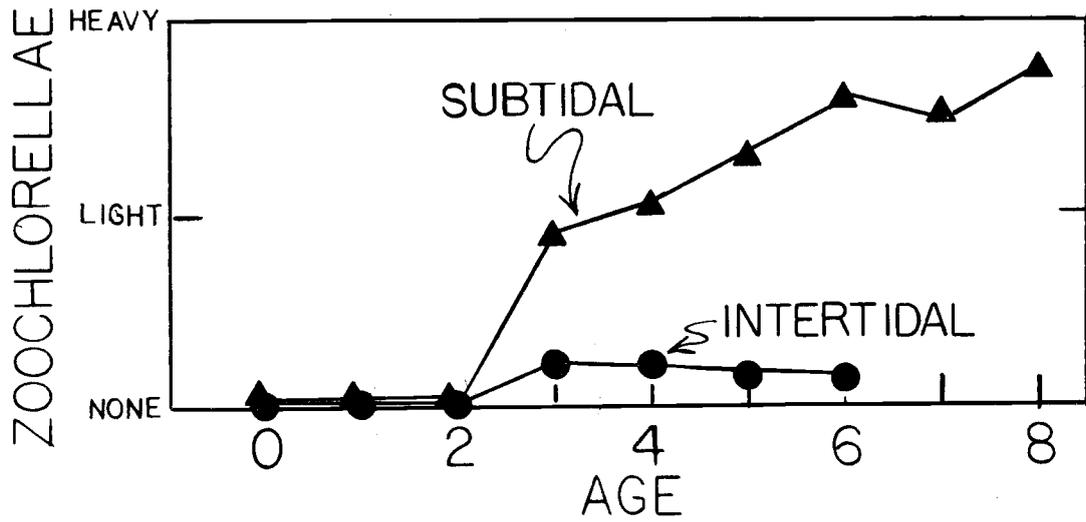


Figure 16. Mean degrees of infection of zoochlorellae in cockles from the intertidal and subtidal environments, Netarts Bay.

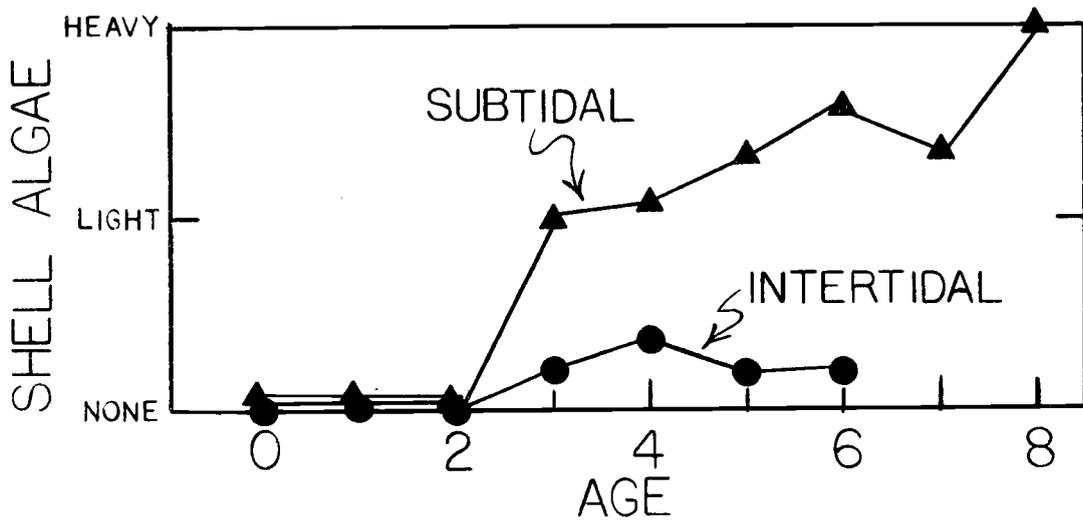


Figure 17. Mean degrees of epiphytic algae on shells of cockles from the intertidal and subtidal environments, Netarts Bay.

### Tide Level and Shell Algae

Epiphytic red and green algae grow symbiotically on shells of subtidal populations (Figure 17). In the intertidal most shells are clean. The heaviest growth of shell algae as well as occasional barnacles occurs on the oldest shells.

### Growth Data from Specific Sites

The age distribution of each population sampled in Netarts Bay varies from the others (Figure 18). The average differences in growth rates of individuals from each population seem to increase after two years of age (Figure 19).

Cockles from Tillamook Bay (ODFW, 1975-1976) show similarities in growth to the Netarts Bay cockles. The curves from three Tillamook locations are very similar (Figure 20), and best match the heights of Subtidal I and II from Netarts Bay.

Zero and one year old animals are close in height from all the sample sites in Netarts, Tillamook, and Oregon Aquafoods fish ponds (ODFW, 1975-1976).

The collections taken from the subtidal of Tillamook Bay have most of the animals below four years old, which is different from the Netarts subtidal collection. It shows there are abundant juveniles in the subtidal areas, which can be sampled better with a

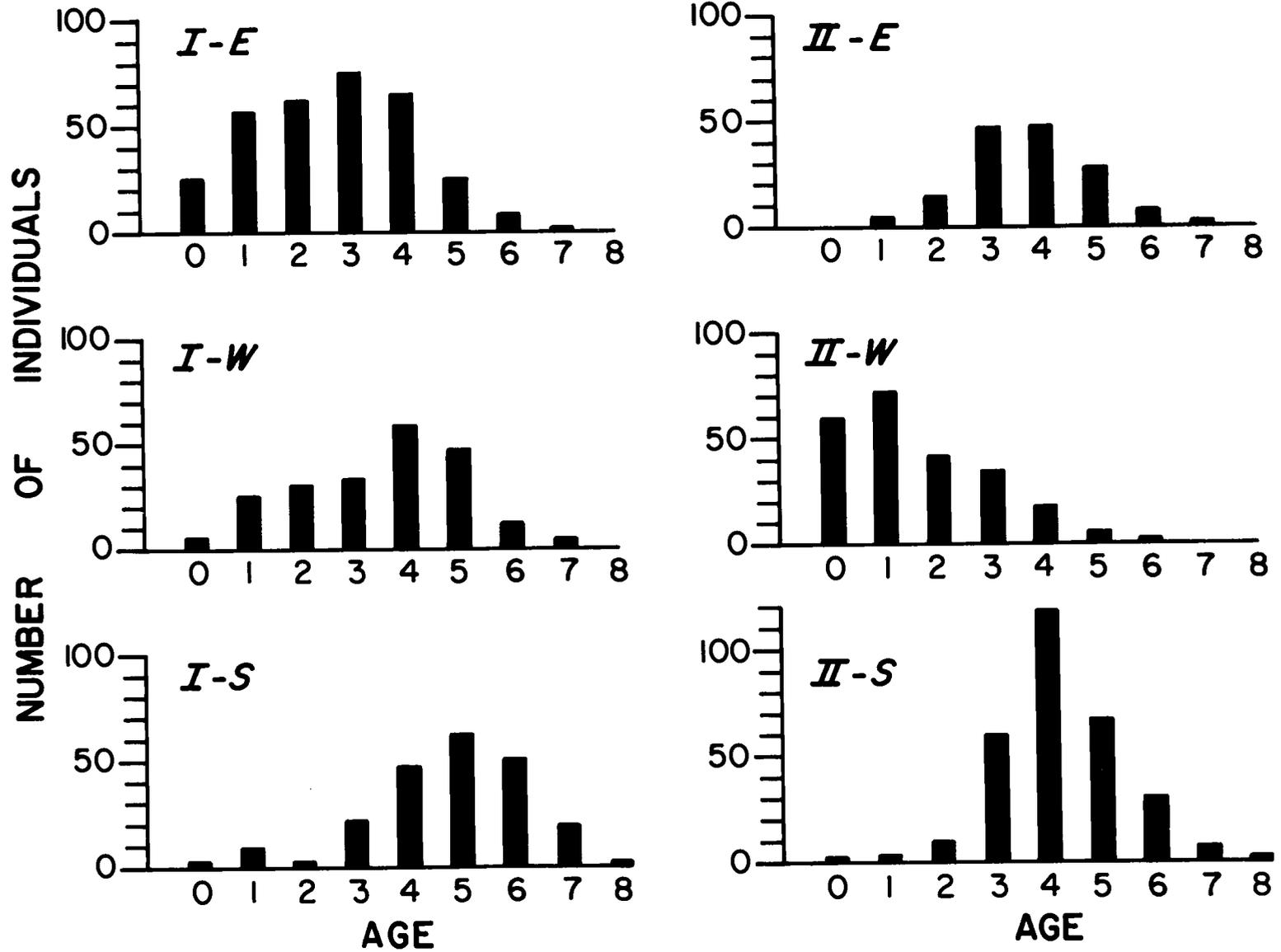


Figure 18. Age-frequency histograms of *C. nuttallii* from the six sampling sites, Netarts Bay.

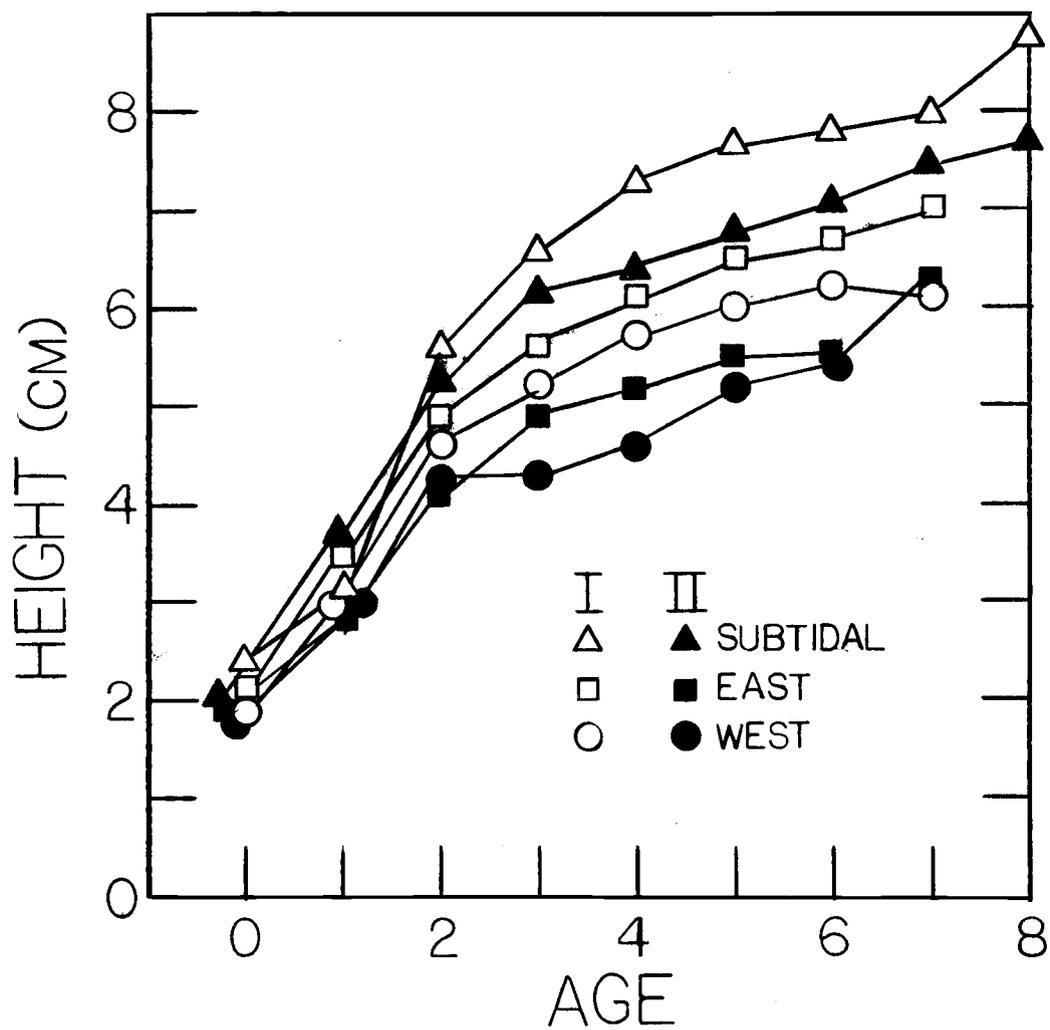
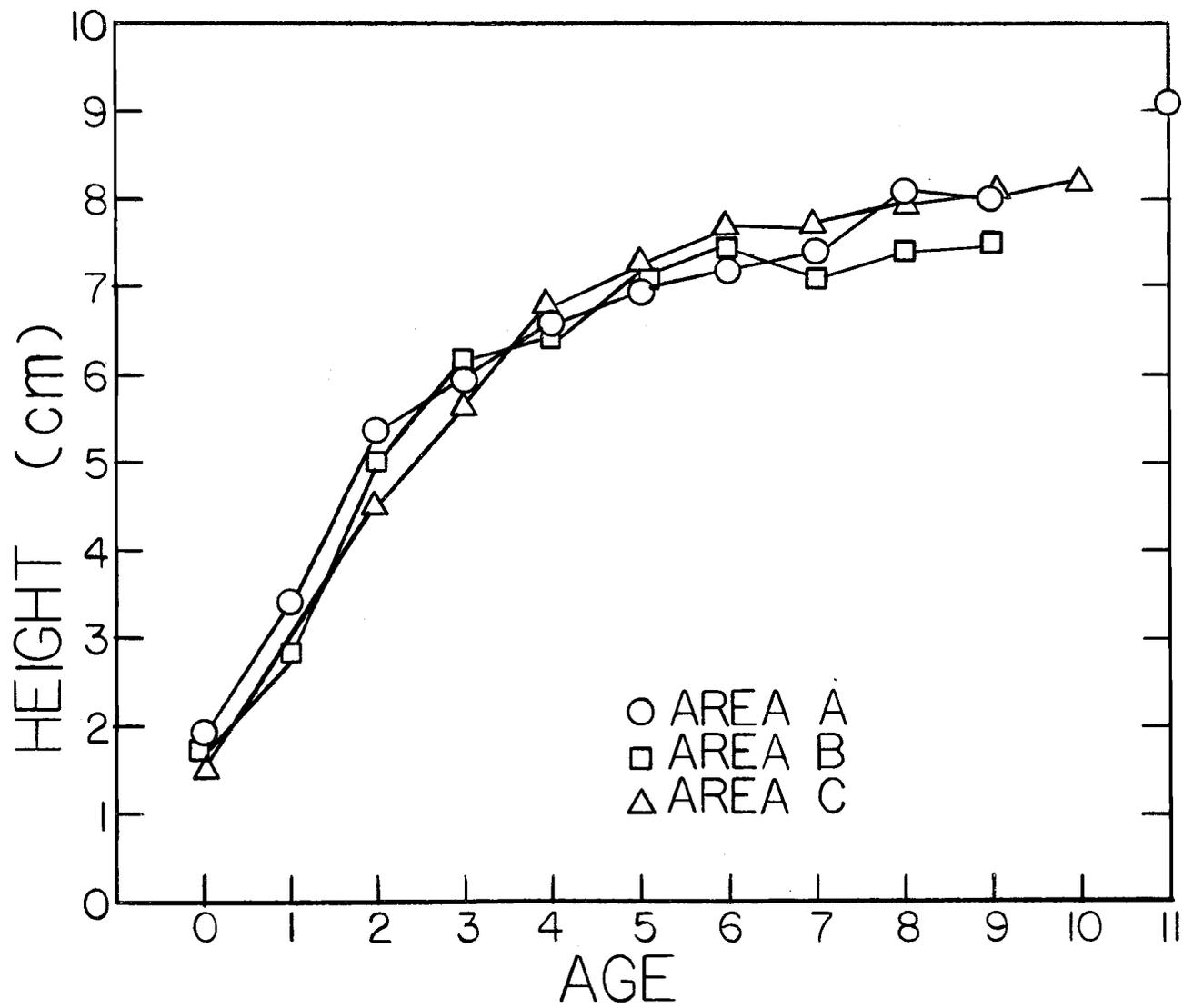


Figure 19. Absolute growth of shell heights in the six sampling sites, Netarts Bay.

Figure 20. Absolute growth of shell heights in three subtidal sites, Tillamook Bay.



suction dredge than by hand (Figure 21).

#### Shell Tagging Data

Cockles which had been tagged and planted on October 4, 1975 were retrieved in two collections on May 4, 1976 and June 15, 1976. Of 65 tagged at intertidal site I-East, 10 were found in the first collection and 15 were found in the second (Table 4). At Subtidal II none of the tagged cockles were retrieved, and had apparently been moved by the currents. During the months of winter, there was severe erosion of sand at I-East. The auger spike, which marked their location, showed a quarter of a meter of removed sediment after several storms in November. Sand was redeposited in the same location in the Spring. The 38 percent retrieval of tagged cockles from the same area in which they were planted was an unexpectedly high return, suggesting that there is not much migration of cockles from intertidal areas.

Each shell revealed a check exactly at the dimensions it had when it was originally measured in October. Overall, the animals which were recovered after seven months, grew about 10 percent, and those recovered after eight months grew about 16 percent. The younger animals showed the greatest growth during the period. The average growth of all the individuals retrieved was greater than the average of a year's growth of two, three, or four year old cockles

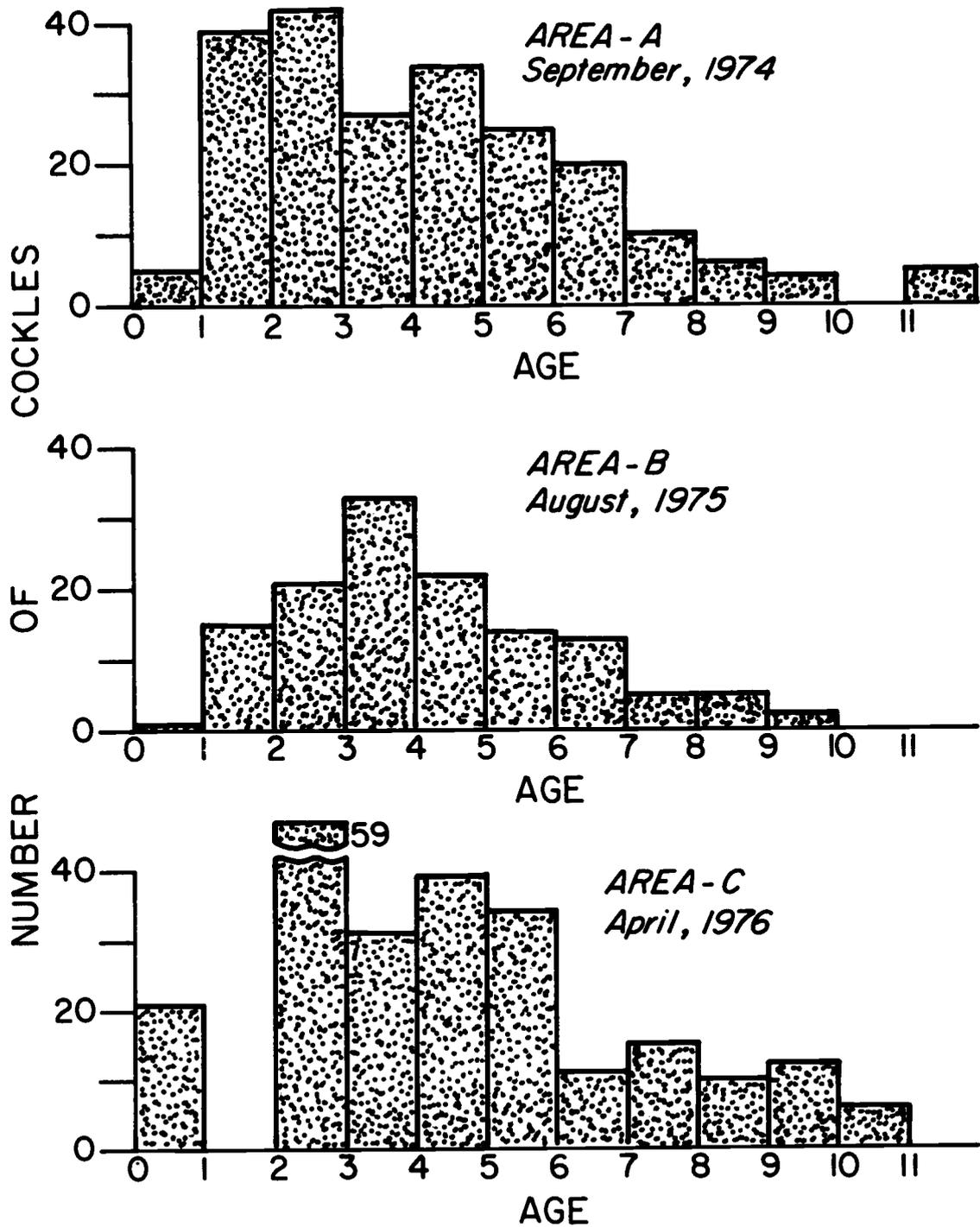


Figure 21. Age-frequency histograms of *C. nuttallii* from three subtidal sites, Tillamook Bay.



from I-East.

### Abiotic Data

#### Hydrology

The temperature and salinity data from this study separates into winter and summer seasons (Table 1). The salinities at Station I and Station II are both above 30 parts per thousand during the summer and below 30 parts per thousand during the winter. Station II salinities are consistently lower than those at Station I.

The temperature data can be divided into two seasons also. The water temperature reads below 12 degrees C during the winter months of this study. Station II has higher temperatures than Station I, downbay, in most cases. Two winter temperatures are slightly higher at Station I than Station II.

The data all come from isolated measurements and do not represent monthly means of temperature or salinity. From Glanzman et al. (1971) there are hydrological data on a station (D.E.Q. #6) in Netarts Bay which is located between the two stations of this study. Isolated salinity and temperature measurements, which were taken over wide intervals from 1960 through 1969, show great variations in temperature and salinity for any particular month from year to year. The tidal flushing of the bay is so great that

daily insolation or rainfall can immediately and drastically affect the temperature and salinity.

#### Intertidal Sample Site Elevations

Three of the four intertidal sample sites are virtually of the same elevation above mean lower low water in Netarts Bay, and the fourth is higher than the rest (Figure 22). Intertidal I-East, II-East, and II-West all have mean heights between .54 and .63 feet above MLLW, and sample site I-West is 1.21 feet above. The four beaches are very level. The heights are in reference to the tide station at the Oregon State University Marine Science Center at South Beach, Oregon. The height of MLLW there is -4.16 feet below mean sea level.

Beaches 0.5 above Newport MLLW would be theoretically exposed an average of 2.06 hours per day, and beaches 1.5 feet would be uncovered 3.76 hours per day over the year (Larsen and Hancock, 1977). The maximum theoretical difference between average exposure times of the beaches would be less than two hours. These calculations do not take into account the choking effect of the estuary and the lag time between up and downbay in the tidal cycle. The difference in the times of high tide between the public boat docks and Whiskey Creek is between 10 and 92 minutes (Glanzman et al., 1971). The lag time for an ebbing tide to reach low slack is between

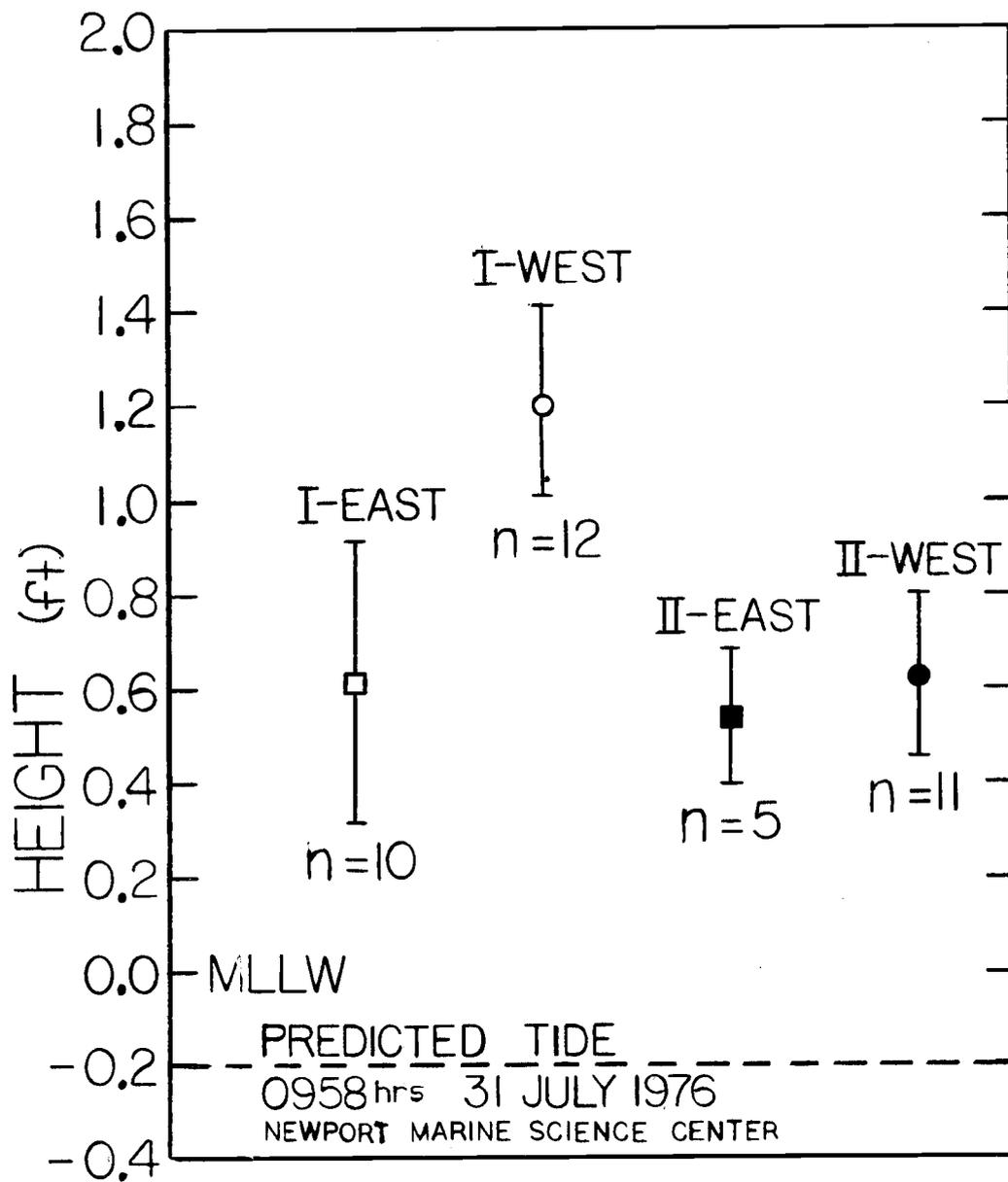


Figure 22. Heights of the four intertidal sites above mean lower low water, Netarts Bay.

43 and 77 minutes between these two locations. Calculations of the average amount of exposure each day also neglect to consider the varying proportions of day to night exposure throughout the year.

Observations during this study suggested that Station II was at least an hour later than Station I in reaching low slack tide, during the spring tides on which we sampled. Both East sample sites were covered well before their corresponding West sites, which was explainable by their close proximity to the main channel. Another factor which further retarded the influence of rising tides on the West flats were the great beds of Zostera marina.

#### Sediment Parameters

Sediment cores were significantly different in their water and volatile solids content using analysis of variance F-tests at the 99 percent confidence level. A contrast of means showed most significant differences between means from subtidal and intertidal site groups. The only other significant contrast in means was between East and West sample sites. The sample sites could be ranked in three groups, from lowest to highest percentages of water and organics in the sediment: 1) Subtidal, 2) East, and 3) West.

Glanzman et al. (1971) took sediment samples from transects that coincide with Station I and II, and found that sediment sizes decreased toward the head of the bay. Larger sediment sizes exist

where strong currents are present. Their stations 15D, 20D, and 16D were similar to Subtidal I, Subtidal II, and I-East, respectively, and all had large mean grain sizes. Their station 17E was equivalent to II-West and the mean particle size of this site was smaller, but much more uniform.

Shabica et al. (1976) examined the sediments of the bay and their station near II-West contained the highest organic carbon in the bay. Their data confirmed that Station I sites had in general larger diameter grain sizes than Station II, intertidal II-West had the smallest mean particle sizes, and the channel sites had low percentages of organic carbon and large mean grain size.

#### Associated Benthos

Shabica et al. (1976) did cluster analysis of the common invertebrate species collected from 69 stations in the bay, and grouped all their stations within six clusters representing benthic communities. Subtidal I was in one of their clusters, intertidal I-West and II-West both had invertebrate communities that fit into a different cluster, and sample site II-East was isolated from the rest.

The Japanese oyster drill, Ocenebra japonica, introduced with the oyster Crassostrea gigas, was found during the cockle study exclusively at sample site II-West. Many juvenile cockles had been preyed upon by this species, as evidenced by the bored holes in

their shells, and the frequent attachment of one or more Ocenebra  
to uncovered Clinocardium nuttallii.

## IV. DISCUSSION

The results of this study clearly indicate that C. nuttallii populations in Netarts Bay differ in their age structure, growth patterns, and timing and degree of gonad development at different locations in the bay. The six sample sites in the study represent a range of tidal habitats in this estuary. A number of questions arise from examining these data:

1) How is the physical environment of each population related to its growth?

2) Are the differences in size distribution among populations due to differences in growth rates or age structures or some combination of both of these two?

3) How stable are the populations in terms of recruitment and mortality?

4) What are the effects of exploitation, predation, and 'migration' upon population age structure?

5) Does the cockle population spawn synchronously, and how is age related to reproduction?

6) Is there a difference in gamete contribution among the sites?

If it is assumed that the cockles of Netarts Bay are part of a single interbreeding population, the observed differences in the

cockles at the sample sites are due to environmental influences. Cockles, like the majority of estuarine benthic macrofauna, broadcast a large number of eggs, which experience a great mortality in the water column. Thorson (1950) has argued that it is selectively advantageous for a species with this mode of reproduction to have large breeding populations to insure fertilization. The mixing processes of Netarts Bay provide a means of transporting gametes and larvae for large distances within and outside the bay. Therefore, it is suggested that the characteristics of the cockles at each site is a reflection of the interaction of the physiology and behavior of the cockle with the environment rather than a genetic difference.

#### Physical Environment and Growth Rates

The most striking result of this study is that all six sample sites follow the same rank order in almost all measured parameters of cockle population and environmental data (Table 3). Sample sites can be separated into three pairs: 1) Subtidal at Station I and II, 2) Intertidal East at I and II, and 3) Intertidal West at I and II based on percentages of ripe individuals during spawning season, shell size and weight parameters, and sediment parameters. The separation suggests a consistent effect of the environment upon the growth and reproductive capabilities of Clinocardium nuttallii. Percentages of water and volatile solids in the sediment, current

velocities, mean grain size, amount of deposition, and anerobic conditions separate the stations into the same groups.

Duration of submergence of the cockle populations is the most obvious difference between sites. The two subtidal sites are distinct from the others in every category. Since the intertidal beaches can be lumped together in terms of time of submergence, their population differences must be attributed to other factors.

The major benefit of continuous submergence upon growth is the increased time available for feeding (Kristensen, 1957). A secondary benefit is escape from extremes of temperature, salinity, and dessication. An added advantage in the subtidal environment such as the channels of Netarts Bay is that swift currents carry an abundance of phytoplankton past the filtering cockles, but do not allow detritus or fine sediments to clog siphons. Swift currents of the subtidal are evidenced by the low pore water and low organic content of the sediments as well as large grain size.

Roa (1953) has shown for Mytilus edulis and M. californianus that shell weights are heavier in relation to body weights from animals taken subtidally. He suggested that shell weight is dependent upon the amount of contact the animals have with calcium dissolved in the water, and that food material in the water is not necessarily a prerequisite for shell growth. Crassostrea virginica has been found to have a higher ratio of shell weight/dry body weight

from the subtidal than from the intertidal (Dame, 1972), which supports the idea that shell growth is somewhat independent from tissue growth, and is greater in a submerged environment.

Calcium, a conservative constituent of seawater, varies directly with the salinity of coastal water. Small contributions of fresh water from the local watershed and Columbia River plume and of high salinity water from coastal upwelling dictate slightly different seasonal patterns of salinity in coastal waters near Netarts Bay (Park, Osterberg, Forster, 1972). Seasonal salinity-calcium concentrations in the Bay can be correlated somewhat with shell growth, but cannot be as well correlated as food supply with shell growth, because salinity maxima tend to occur in the late summer and fall.

In this study, both gonad development and shell growth were concentrated in the Spring months, corresponding to coastal surface phytoplankton blooms, which peak in May and are depleted by June (Anderson, 1972). Fifteen tagged cockles at I-East grew more in the period from October, 1975 to June, 1976 than the average shell growth for an entire year at that same site. Kristensen (1957) also found that major growth of C. edule occurs in the Spring and essentially ends by July. The exception to the summer cessation of growth is in zero year spat which grow until winter conditions set in.

The formation of aragonite, which composes the two inner layers

of shell of C. nuttallii (Mitchell, 1935), is favored by increased temperatures (Wilbur, 1964). Although general temperature increases in Netarts Bay do correspond with the season of shell growth, the temperature maximum extends well past growth peaks.

Variation in relative growth within populations appears to be greater in weights than in size. Brown, Seed, and O'Conner (1976) attribute the larger variation in tissue and shell weights of C. edule to the instability of the intertidal environment with respect to availability of food. For Clinocardium there is no difference between subtidal and intertidal relationships in the shape of the shell (Figures 13 and 14). However, the allometric relationship between shell weight and height differs between these two environments (Figure 15), which supports Brown et al. in their conclusions.

The environmental factors are sufficiently different between Station I and II to account for the larger mean shell sizes and weights from Station I (downbay). Generally, the upbay Station (II) experiences warmer and fresher water than the downbay station. Decreased CO<sub>2</sub> solubility and calcium concentration upbay inhibit shell growth, but slower circulation and reduced tidal prism are probably more important. Productivity has been measured (Glanzman et al., 1971), but no significant variation was measured anywhere in the bay. Slower circulation, made apparent at Station II by smaller particle sizes, may carry less total food to the area and allow

greater amounts of suspended sediment to be inhaled through cockle siphons. These circumstances may explain the particular absence of ripe individuals from the intertidal sites at Station II.

These same factors explain greater growth at East intertidal sites compared to West intertidal sites, both up- and downbay. There is no apparent differences in beach heights, except for I-West, which is slightly higher (Figure 21). The East sites tend to become submerged sooner, because of their proximity to the channel, which may give these beaches the general advantages for growth of the subtidal, while eel grass beds in both West sites may retard current speed and circulation. Although the West areas are very high in suspended organic matter, it is mostly in the form of detritus from eel grass production (Shabica et al., 1976). Too much organics hampers filter feeding cockles, which actively select phytoplankton from inhaled material (Verwey, 1952).

Filter feeding bivalves in Netarts Bay are probably greatly dependent upon coastal primary production. Verwey (1952) calculated that cockle and mussel populations in the Dutch Wadden Sea consume a great deal more energy than the Wadden Sea can produce annually without the input of the North Sea. Though estuaries have higher rates of production than the open sea, the tidal flux, 75 percent of the bay volume in Netarts Bay, imports much greater amounts of plankton and organic material during any time period. McMurray

(1977) found that phytoplankton production in an estuary with a large tidal prism is largely controlled by nearshore population dynamics. For the six sites in Netarts Bay, those with the most contact with the tidal currents are the sites which produced the largest cockles.

#### Distribution of Symbiosis

Zoochlorellae has a very interesting distribution in Netarts Bay cockles with respect to sample sites and age distribution. Hartman (1972), who collected only from the intertidal in Yaquina Bay, found this symbiosis to increase with age to 35 percent of animals above four years. In Netarts Bay, only a few intertidal individuals were found with zoochlorellae even among the oldest, while the subtidal sites produced more than 50 percent of its adults with zoochlorellae even among the oldest, while the subtidal sites produced more than 50 percent of its adults with zoochlorellae. This algae may benefit growth and survival of older submerged C. nuttallii, in the way the relationship provides nutritive benefit to tridacnids (Yonge, 1975). The incidence of shell algae, which parallels that of zoochlorellae, also differs between subtidal and intertidal. These relationships suggest that in Netarts Bay there is no gradient between the subtidal and intertidal environments but a sharp distinction, which is physically defined by steep channel banks.

### Age Distribution

The age distribution of each population within the bay is related to biotic factors of recruitment, predation, exploitation, and natural mortality. It is also a function of mobility of the individuals in the population. Kristensen (1957) described the dynamics of Cerastoderma edule as an endless compromise between niches suitable for setting as spat versus those suitable for optimum growth. Beaches exposed to strong currents make poor recruitment beds. Baggerman (1953) demonstrated that initial spatfall of C. edule is only temporary, and that spat may be transported by currents after metamorphosis until they reach a size from 1,800-2,000 microns or about four weeks old. The Cerastoderma spat tend to accumulate in places with weak currents as a result of transport and not setting behavior. Although no setting data were taken during this study, the age distributions show high percentages of juveniles at intertidal sites compared to those at subtidal sites (Figure 18). Intertidal II-West and I-East have especially high percentages of zero, one-, and two-year cockles, which may reflect slower current speeds at these sites than in the channel.

The strength of currents in transporting cockles may be demonstrated by the results of retrieving tagged cockles. Intertidal I-East had a 38 percent return, after a winter in which sediment was

removed from that site by storms, while the Subtidal II tagged individuals had apparently been moved, because none were ever found.

The greatest percentage of tagged cockles which were retrieved at I-East was of those younger than four years.

'Migration' from areas of settlement with weak currents to areas of strong currents has been suggested as a behavior of adult cockles, which would explain their age distribution (Kristensen, 1957). The mechanism he proposed is that older cockles may dig back in the substrate too slowly, when exposed, and thus be washed into a channel or other high exposure area. Netarts Bay data support this idea because the lack of older cockles in the intertidal is even more pronounced than the lack of juvenile cockles in the subtidal (Figure 18). Clam-dredge samples from Tillamook Bay taken by the ODFW show some juvenile cockles of zero through two years, which suggests a bias from hand picking of Netarts subtidal samples, but subtidal populations from both bays have large numbers of specimens over five years old. It is clear that the subtidal environment favors the growth rate of cockles, but it also favors a significantly older distribution of ages.

Mortality influences age distribution as do settlement and migration. Exposure to extreme heat and cold can cause mass fatalities. Orton (1937) documented large numbers of C. edule completely uncovered and gaping on intertidal flats during summer

heat waves. This was witnessed at Netarts on several warm days, especially at West sites on Zostera beds, where temperature of the sediment surface was measured up to 25 degrees C. Mass mortalities of greater proportion resulting from freezing of intertidal beaches have also been recorded (Kristensen, 1957). The older cockles are the first to go in such extremes, thus contributing to the lack of adults in the intertidal.

Major predators of C. edule have been found to differ from the intertidal to the subtidal (Kristensen, 1957), and predation pressure on cockles appears to differ among the sample sites at Netarts Bay also. Plaice, Plueronectes platessa, is a devoted connoisseur of C. edule in the subtidal, and is selective toward small size, but is not a significant predator of cockles in the intertidal. This relationship may exist in Netarts Bay between pleuronectid fishes, particularly English sole (Parophrys vetulus), and C. nuttallii, although Netarts is more important as a habitat for maturing juvenile flatfish, which tend to feed in the sandy bottoms of channels toward the mouth (Shabica et al., 1976). On the intertidal, gulls and oystercatchers are known predators of C. edule. On several occasions in Netarts Bay, we observed glaucous-winged gulls, Larus glaucescens, prey upon Clinocardium by lifting them up and dropping them to the ground in flight. Larger cockles would make better prey for this type of food gathering, because a heavier shell would fall with

greater momentum, and break more easily than a light shell. Other birds may crush small shells with their beaks or swallow them whole. If predators cause significant mortality in Netarts Bay, they could influence age distribution toward the pattern that was recorded.

Clinocardium nuttallii is the major prey species of the Japanese oyster drill, Ocenebra japonica, which is found exclusively at II-West in Netarts on what Squire (1972) called "drill island." This site was the most densely populated with cockles and had the most juveniles of any sample site, suggesting it has been a good location for larval setting, but not for growth or survival of C. nuttallii. The impact of O. japonica predation upon the cockle population at II-West is not known, but it is a unique impact to that location in the bay.

Exploitation of the intertidal populations by human sport diggers is another impact unequally applied to the sites. "Clammers" are concentrated in the northern half of the bay during low tides, while upbay sites are seldom visited. At Station I, particularly I-West, diggers reach densities more than 60 per square kilometer (Shabica et al., 1976). The diggers, who could collect up to 36 clams per day each,<sup>1</sup> are definitely a force in removing older larger cockles from the intertidal. An incidental effect of heavy human use of the bay at low tide is a shift of a large proportion of the bird population

-----  
<sup>1</sup> This bag limit has been reduced in 1977 by the ODFW to 20 clams per day.

to the southern half of the bay, which they normally do not occupy (Shabica et al., 1976).

It is suggested that the overall effect of predation and exploitation must not be too great, because the age distribution of the sample sites does not necessarily reflect the pressures specific to them. Site I-West has the greatest digging pressures, yet has a dominance of older specimens, and in fact ranks third in mean age behind the subtidal sites. Intertidal I-East is without a large adult portion of its population, yet was not observed to be heavily preyed upon, while II-West has even greater abundance of juveniles in an area especially susceptible to oyster drills.

It seems that recruitment, natural mortality, and 'migration' caused by physical factors in the environment are the most influential in determining age structures of populations within the bay. Predation and exploitation seem to be secondary forces, especially in the intertidal, because age structures of those populations do not reflect the pressures specific to them. Differences in age structure between specific sites correlate better to physical factors. The dynamics of populations in the rocky intertidal environment may be similar for C. nuttallii populations in an estuarine environment. The populations in the upper rocky intertidal are dominated by physical factors, which cause the major mortality and inhibit growth, while predators are the major influence of

population structure in the lower intertidal (Dayton, 1972). The intertidal environment at Netarts is physically stressful enough to limit age structure and growth of cockles. What is not known is the amount of recruitment in the subtidal or the extent of predation there. If predation in the subtidal is specific to juveniles, and natural mortality in the intertidal is specific to adults, then the subtidal environment can be designated as a 'refugia' of the adult population.

#### Population Density

One other consideration is the effect of population density upon growth, mortality, and recruitment. In general, an inverse relationship has been found between the stock of C. edule and the number of successful recruits (Hancock, 1970). The relationship is based upon intraspecific competition for food and space of settled spat with older age groups, especially with the cohort from the previous year. In dense beds a source of mortality can even be inhalation of larvae by adults. The level of recruitment is not found to be dependent upon the number of spawners in the population, as the mortality after settlement of spat seems to be the most important factor. The density of the European cockle, Cardium edule, can be as much as 2,200 individuals per square meter (Kristensen, 1957), which is many times greater than the density of Clinocardium nuttallii (ODFW, personal communication). The density of cockle beds in Netarts

Bay may not be as an important factor in determining yearly recruitment as it is on European tidal flats.

### Reproduction and Synchronous Spawning

Clinocardium nuttallii has been classified as functionally hermaphroditic, defined by male and female gonads developing simultaneously side by side in each animal. Coe (1943) noted that the condition of functional hermaphroditism is often preceded by a juvenile period of maleness or femaleness. He also mentioned the functionally hermaphroditic species to have protandric spawning behavior, that is discharging male gametes separately before female gametes.

From this study it is not possible to reconcile the question of whether self-fertilization is possible or usual for C. nuttallii. Internal self-fertilization seems unlikely, because the maturation of unfertilized eggs in most molluscs occurs only up to the metaphase of the first meiotic division, and then is inhibited at that stage until a sperm enters (Raven, 1949). It is more likely that the largest and most mature female gametes observed are still secondary oocytes, and that meiotic divisions and maturation into ootids and ova have not been completed. Spermatocytes undergo two meiotic divisions and mature into spermatids and spermatozoa within the follicles.

There is some evidence from the male to female follicles ratio

(Figure 7) that C. nuttallii may discharge male gametes before female gametes, but there is no evidence that a phase of singular maleness or femaleness precedes hermaphroditism in juveniles. Tridacnid species are called protandric functional hermaphrodites, because only spermatozoa are produced in the gonads of young animals (Wada, 1952), and self-fertilization is very unlikely because simultaneous spawning never occurs in Tridacnidae (Wada, 1954). The close taxonomic relationship of Tridacnidae to Clinocardium has been noted, and it is suggested here that their reproductive behavior may be similar.

The results do show a dominance in the number of ripe male gonad above the number of ripe female gonads at every site (Table 2). One possible way this dominance may be explained, if not a histological artifact, is that male follicles may ripen and partially spawn more than once over the long spawning period, because of their shorter time of development. Another possibility is that some environmental conditions within the bay; e. g., time of submergence, may cause an uneven amount of production of male and female gametes. Oyster populations have responded to internal and external environmental conditions by changing the proportions of sexes (Coe, 1943; Galtsoff, 1964). Environmental conditions favoring growth tend also to favor female development. Elvin (1974) found a correlation between formation of mature oocytes in Mytilus

californianus and food availability, and noted that resorption is the predominant fate of egg material. Cockles, which experience conditions limiting to growth, may respond by halting oocyte development, while male gonads may continue to ripen.

Environmental factors which determine the long-term expression of growth at the sample sites also work in the short term to affect different rates of gonadal development. The early spring ripening of gonads coincides with the spring shell growth spurt, but ripe gonads continued to occur through late summer. The percentage of ripe individuals from each site during the spawning period reflects the ranking of the sites in terms of growth conditions, as shown by absolute growth plots (Figure 19). The subtidal sites and intertidal I-East produced the greatest percentages of individuals with ripe male and female gonads, and the three remaining sites were far behind, especially in the production of female gonads (Table 3). Only six specimens with ripe female gonads were collected from II-West.

Synchronism in ripening and spawning is a significant aspect of cockle fecundity when comparing local populations. There must be some selective advantage favoring synchronous development, because all sites except II-West had eighty percent or more of one sex or the other ripe in a sample at some time during the study, and sites Subtidal II, Subtidal I, II-East, and I-East all showed synchronous ripeness of both sexes in at least one sample (Table 2). Besides

synchronism within sites, there is also synchronism between sites. There is a simultaneous ripening of female follicles at all sites in Station II in May, 1976 and Station I in July of that year (Figure 9). The synchronism of Station II sites ripening before Station I sites could perhaps be explained by the slightly, but consistently warmer temperatures observed at Station II.

Temperature is considered a key influence in triggering spawning (Fretter and Graham, 1964). In the one instance when C. nuttallii spawned in the laboratory, it followed a series of alternating warm and cold baths (Butler, 1968). This may explain the stimulus for spawning in the intertidal, but does not suffice for the subtidal. The synchronous development of intertidal and subtidal populations must be accounted for. There is a temperature contrast between winter and spring 1976 (Table 1), which may be linked with initial simultaneous gonadal ripening, after which cockles may spawn individually throughout the spring and summer. It has been very difficult to induce spawning of the basket-cockle in the laboratory, because even when conditioned, they do not spawn all at once, but at a very sporadic and slow rate (Breese, personal communication).

This behavior makes sense in the context of functional hermaphroditism, as there is not the same pressure to spawn as a population as there is in a dioecious species. A dioecious species, which sheds gametes externally, usually spawns synchronously as a

population in order to maximize potential fertilization (Thorson, 1950). Hermaphroditism is thought of as an adaptation of a species, which has some difficulty in reproducing, and is more common among fresh-water and terrestrial molluscs than marine species (Fretter and Graham, 1964). Clinocardium and Tridacna may have adapted this method of reproduction, because their populations are not very dense. It is suggested, however, that cross-fertilization does occur within these species, because synchronous ripening within and between populations has been shown in this study, protandric spawning has been observed in tridacnid species and suggested in this study, and a high measure of genetic variation has been found in Tridacna maxima (Valentine et al., 1973). Synchronism of gonadal development is a partial adaptation of Clinocardium nuttallii to increase chances of cross-fertilization, but there is not as strong an advantage to synchronously spawn as in other bivalves.

The high percentages of ripe juvenile specimens compared to the general age distribution of individuals (Figure 10), is related to the synchronous development of gonads. That two-year cockles are the age class with the highest proportion of ripe gonads, male and female, suggests that either youngest cockles are the most reproductively active, or that they are ripe over the longest period of time. The former is contradicted by data from the subtidal sites, which have the oldest populations and high percentages of ripeness.

However, even the subtidal samples have the highest percentages of ripe gonads at their youngest year classes, which are three and four. The phenomenon may be related to the length of the spawning period and the synchronism of spawning. If the youngest cockles develop randomly out of synchronism with the established populations, chances would increase of collecting ripe young cockles over the entire spawning season. Thus, the synchronism of ripening and decline is most sharply defined in populations with the most adults, while the sites with the most juveniles, show gonads in the same conditions for several months (Figures 9 and 18). In the latter case, the I-East gonadal index hovered about ripeness, while II-West never produced a ripe sample. This would lead to the conclusion that C. nuttallii reaches sexual maturity in two years, and becomes more synchronous in gonadal development with its local population with increasing age.

Finally it is important to discuss the possibility that certain areas of Netarts Bay are more important than others in contributing spat. Kristensen (1957) calculated that the density of C. edule beds is the most important factor in determining the population which produces the most ova. He found that individuals of the same length develop the same number of ova, even though they may have unequal growth rates. It appears that C. nuttallii of equal length do not necessarily spawn the same quantities of gametes. There seems to

be a large variation among populations in the percentages of individuals whose gonads ever reach a ripe stage, and if synchronism of development increases chances of fertilization, it could be a significant factor reducing or increasing the number of spat produced from each site. There can also be qualitative differences in gametes, such as spawned oocytes deficient in glycogen or proteins (Elvin, 1974).

The subtidal environment at Netarts Bay is most likely producing the most fecund individuals, and the most synchronous gonadal development within site populations. On the other hand the intertidal region of the bay is several times the area of the channels, and probably more densely populated. Weighing superior individual fecundity against overwhelming numbers leaves the discussion of which area produces more gametes inconclusive, and may be immaterial since it has been suggested that number of larvae in the water is a less important factor in establishing future breeding stocks than survival success of spat and juveniles. It should be noted, however, that the subtidal area may be a significant seed area in the bay in such years when extremely harsh environmental conditions may render the intertidal populations impotent. Subtidal populations may also be important as a source of abundant meroplankton to be incorporated in the general food web of the estuary.

## SUMMARY

- 1) Samples were taken of Clinocardium nuttallii for a year from six intertidal and subtidal sites in Netarts Bay, Oregon, for the purpose of histological examination of gonads and growth studies. Each site was found to have individual environmental and population characteristics. Shell growth was correlated to the amount of contact with seawater through tidal submergence, as subtidal sites had the highest rates of growth. Food availability was probably the most important factor influencing growth, which was greatest in the Spring months.
- 2) Sample site populations each have distinct growth rates and age distributions. Juveniles are found predominantly in the intertidal, while adults are in the subtidal. Zoochloellae symbiosis is found almost exclusively in subtidal adults.
- 3) The intertidal sites may be more suitable for recruitment, while the subtidal may have advantages for survival and growth. Survival of settled spat may be more important for the success of recruitment than the amount of gametes produced. Greater natural mortality among older cockles in the intertidal is probably due to extremes in the physical environment.

- 4) Exploitation and predation appear to be minor influences upon the age distribution, but do tend to reduce the number of intertidal adults and subtidal juveniles. There is a 'migration' of older cockles from the intertidal to the subtidal due to a weakened ability to remain buried in the substrate.
- 5) The sexual differentiation of C. nuttallii is functional hermaphroditism. Gametogenesis begins in January and ripe gonads are found from March through September. There is synchronism of development within sample sites and among sites, but spawning may be more individualistic. Nuttall's cockle may have protandric development and spawning behavior similar to the tridacnid clams.
- 6) The subtidal produces the most fecund populations, but the intertidal population outnumbered the subtidal by several times. The subtidal may be a valuable seed area during years when environmental conditions render the intertidal population impotent, and a valuable source of meroplankton to be incorporated in the food web of the estuary.

## BIBLIOGRAPHY

- Anderson, G. C. 1972. Aspects of marine phytoplankton studies near the Columbia River, with special reference to a subsurface chlorophyll maximum, In The Columbia River estuary and adjacent ocean waters. Bioenvironmental studies, A. T. Pruter and D. L. Alverson, eds. University of Wash. Press, Seattle and London. p. 219-240.
- Baggerman, B. 1953. Spatfall and transport of Cardium edule L. Arch. Neer. Zool. 10(3):315-342.
- Boyden, C. R. 1971. A comparative study of the reproductive cycle of the cockles Cerastoderma edule and C. glaucum. J. Mar. Biol. Assoc. U. K. 51:605-622.
- Brown, R. A., R. Seed, and R. J. O'Connor. 1976. A comparison of relative growth in Cerastoderma (= Cardium) edule, Modiolus modiolus, and Mytilus edulis (Mollusca: Bivalvia). J. Zool. Lond. 179:297-315.
- Butler, J. A., R. E. Milleman, and N. E. Stewart. 1968. Effects of insecticide Sevin on survival and growth of the cockle clam Clinocardium nuttallii. J. Fish. Res. Bd. Canada 25(8):1621-1635.
- Carriker, M. R. 1961. Interrelation of functional morphology, behavior and autecology of the bivalve Mercenaria mercenaria. J. Elisha Mitchell Sci. Soc. 77:168-241.
- Coe, W. R. 1943. Sexual differentiation in molluscs. I. Pelecypoda. Quart. Rev. Biol. 18(2):154-164.
- Coe, W. R. 1947. Nutrition, growth, and sexuality of the pismo clam (Tivela stultorum). J. of Exp. Zool. 104(1):1-25.
- Coe, W. R. and H. J. Turner. 1938. Development of the gonads and gametes in the soft shell clam (Mya arenaria). J. Morph. 62(1):91-111.
- Cole, H. A. 1956. A preliminary study of growth-rate of cockles (Cardium edule L.) in relation to commercial exploitation. J. du Conseil Exp. de la mer. 22:77-90.

- Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. 40(1):49-77.
- Conrad, T. A. 1837. Descriptions of new shells from upper California, collected by Thomas Nuttall, Esq. J. Acad. Natur. Sci. Phila. 7:227-268.
- Creek, G. A. 1960. The development of the lamellibranch Cardium edule L. Proc. Zool. Soc. Lond. 135:243-260.
- Dame, R. F. 1972. Comparison of various allometric relationships in intertidal and subtidal American osysters. Fish. Bull. 70(4):1121-1126.
- Davenport, H. 1960. Histological and histochemical technics. W. B. Saunders Company, Phila. 401 p.
- Dayton, P. K. 1972. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41(4):351-389.
- Edmonson, C. H. 1919. Cardium corbis a monoecious bivalve. Science 49:402.
- Edmonson, C. H. 1920. Edible Mollusca of the Oregon Coast. Occasional Papers of the Bernice Pauahi Bishop Museum, Honolulu 7(9):178-201, 6 Figs.
- Eisma, D. 1965. Shell characteristics of Cardium edule L. as indicators of salinity. Neth. J. Sea. Res. 2(4):493-540.
- Elvin, D. W. 1974. Oogenesis in Mytilus californianus. Ph. D. Thesis. Corvallis, Oregon State University. 171 p.
- Evans, J. W. 1972. Tidal growth in the cockle Clinocardium nuttallii. Science 176:416-417.
- Fraser, C. McL. 1931. Notes on the ecology of the cockle, Cardium corbis, Martyn. Trans. Roy. Soc. Canada (Sec. 5) 25:59-72.
- Fretter, V. and A. Graham. 1964. Reproduction, In Physiology of mollusca, K. M. Wilbur and C. M. Yonge, eds. Academic Press, N. Y. p. 127-164.

- Galtsoff, P. S. 1964. The American oyster, Crassostrea virginica Gmelin. Fish. Bull. of the Fish and Wildlife Service, Vol. 64.
- Gonor, J. J. 1972. Gonad growth in the sea urchin, Strongylocentrotus purpuratus (Stimpson) (Echinodermata: Echinoidea) and the assumptions of gonad index methods. J. Exp. Mar. Biol. Ecol. 10:89-103.
- Guthrie, D., C. Avery, and K. Avery. 1974. Statistical interactive programming system (SIPS). Users reference manual. Technical Report No. 36. Dept. of Statistics, Oregon State University. 111 p.
- Hancock, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates, In Fish stocks and recruitment. (proceedings of a symposium held in Aarhus 7-10 July 1970), B. B. Parrish, ed. p. 114-125.
- Hartman, H. C. 1972. A green algal symbiont in Clinocardium nuttallii. Ph.D. Thesis. Corvallis, Oregon State University. 55 p.
- Holland, D. A. and K. K. Chew. 1974. Reproductive cycle of the manila clam (Venerupis japonica), from Hood Canal, Washington. Proc. Natl. Shellfish Assoc. 64:53-58.
- Johnstone, J. 1899. Cardium. Memoirs of Liverpool Marine Biological Committee, Vol. 2. 95 p.
- Keck, R., D. Maurer, and R. Malouf. 1974. Factors influencing the setting behavior of larval hard clams, Mercenaria mercenaria. Proceed. Nat. Shellfish Assoc. 64:59-66.
- Keen, A. M. 1936. A new pelecypod genus of the family cardiidae. San Diego Soc. of Nat. Hist. Trans. 8(17):119-120.
- Keen, A. M. 1936. Revision of cardiid pelecypods. Proc. Geol. Soc. Amer. for 1936. p. 385.
- Keen, A. M. 1938. West American caridae. Proc. Geol. Soc. Amer. for 1937, 294-295.
- Keen, A. M. 1963. Marine molluscan genera of Western North America. An illustrated key. Standard University Press, California, 126 p.

- Kreger, D. 1940. On the ecology of Cardium edule L. Arch. Neer. Zool. 4:157-200.
- Kristensen, I. 1957. Differences in density and growth in a cockle population in the Dutch Wadden sea. Arch. Neer. Zool. 12: 351-453.
- Larsen, I. and D. Hancock. 1977. Tidal exposure periods in reference to Marine Science Center tidal data, Newport, Oregon. School of Oceanography. Oregon State University, Corvallis, Oregon, unpublished.
- Machell, J. R. and J. D. DeMartini. 1971. An annual reproductive cycle of the gaper clam, Tresus capax (Gould), in south Humbolt Bay, California. Calif. Fish and Game 57(4):274-282.
- Marriage, L. D. 1958. Bay clams of Oregon. Educational Bull. No. 2 Fish Commission of Oregon. 47 p.
- Martyn, T. 1782. Le Conchyliologiste universel, dessine et peint d' apres nature et arrange selon le Systeme de l'Auteur. (Angl. et Gaul.) Lond. 1782. 2 Vol. fol. Biogr. Un Suppl. 73, p. 267.
- McCloy, J., J. M. Dodd, H. C. Davies, F. B. J. Edmonds, and J. H. Orton. 1937. Rate of growth of totally submerged Cardium edule. Nature 138:800-801.
- McMurray, G. 1977. Species-specific phytoplankton production rates during a spring diatom bloom in Yaquina Bay, Oregon. Ph.D. Thesis. Corvallis, Oregon State University. 216 p.
- Mitchell, H. D. 1935. The microscopic structure of the shell and ligament of Cardium (Cerastoderma) corbis Martyn. J. Morphology 58:211-220.
- Montgomery, R. 1957. Determination of glycogen. Arch. of Biochem. and Biophys. 67:378-386.
- Orton, J. H. 1926. On the rate of growth of Cardium eduli. Part I. Experimental observations. J. Mar. Biol. Assoc. N. S., 14(1):239-279, 11 Figs.
- Orton, J. H. 1933. Summer mortality of cockles on some Lancashire and Cheshire Dee beds in 1933. Nature 132:314-315.

- Park, P. K., C. L. Osterberg, and W. O. Forster. 1972. Chemical budget of the Columbia River, In The Columbia River estuary and adjacent ocean waters, A. T. Pruter and D. L. Alverson, eds. University of Wash. Press, Seattle and London. p. 123-134.
- Quayle, D. B. and N. Bourne. 1972. The clam fisheries of British Columbia. Fish Res. Bd. of Canada Bulletin 179. 70 p.
- Rao, K. P. 1953. Shell weight as a function of intertidal height in a littoral population of pelecypods. *Experientia* 9(12):465-466.
- Raven, C. P. 1949. Morphogenesis: The analysis of Molluscan development. Pergamon Press, New York. 270 p.
- Reid, P. 1968. The distribution of digestive enzymes in lamelli-branchiate bivalves. *Comp. Biochem. Physiol.* 24:727-744.
- Reid, R. G. 1969. Seasonal observations on diet, and stored glycogen, and lipids in the horse clam, Tresus capax (Gould, 1850) *Veliger* 11(4):378-381.
- Ropes, J. W. 1968. Reproductive cycle of the surf clam, Spisula solidissima, in offshore New Jersey. *Biol. Bull.* 135:349-365.
- Ropes, J. W. and A. P. Stickney. 1965. Reproductive cycle of Mya arenaria in New England. *Biol. Bull.* 128:315-327.
- Rowe, K. E. 1975. 1975 news.notes for SIPS users. Statistical Computing Report 162. Dept. of Statistics, Oregon State University. 28 p.
- Sanders, H. L. 1968. Marine benthic diversity: A comparative study. *The American Naturalist* 102(925):243-280.
- Shabica, S., A. Amandi, B. Bartlett, C. Coombs, H. Frolander, L. Grothaus, K. Howe, C. Kornet, L. McCallum, C. Munson, T. Seal, H. Stout, and D. Wilson. 1976. The natural resources and human utilization of Netarts Bay, Oregon. Oregon State University. Corvallis, Oregon. 247 p.
- Silvey, G. E. 1968. Interganglionic regulation of heartbeat in the cockle Clinocardium nuttallii. *Comp. Biochem. Physiol.* 25:257-269.

- Slotta, L. S., D. A. Bella, D. R. Hancock, J. E. McCauley, C. K. Sollitt, J. M. Stander, K. J. Williamson. 1974. An examination of some physical and biological impacts of dredging in estuaries. Interim progress report. Oregon State University, Corvallis, Oregon 173 p.
- Smoker, J. V. 1976. A mendelian study of Crassostrea gigas. M.S. Thesis. Corvallis, Oregon State University. 49 p.
- Snedecor, G. W. and W. G. Cochran. 1968. Statistical methods. The Iowa State University Press, Ames, Iowa, U.S.A. 593 p.
- Squire, D. R. 1972. The Japanese oyster drill, Ocenebra japonica in Netarts Bay, Oregon. M.S. Thesis. Corvallis, Oregon State University. 65 p.
- Taylor, C. C. 1960. Temperature, growth and mortality - The Pacific cockle. J. du Conseil 26(1):117-124.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Reviews 25:1-45.
- Valentine, J. W., D. Hedgecock, G. S. Zumwalt, F. J. Ayala. 1973. Mass extinctions and genetic polymorphism in the "Killer Clam," Tridacna. Geol. Soc. of Amer. Bull. 84: 3411-3414.
- Verwey, J. 1952. On the ecology and distribution of cockle and mussel in the Dutch Wadden Sea, their role in sedimentation and the source of their food supply. Arch. Neer. Zool. 10:171-239.
- Viles, F. and L. Silverman. 1949. Determination of starch and cellulose with anthrone. Analytical Chem. 21:950-953.
- Wada, S. K. 1952. Protandric functional hermaphroditism in tridacnid clams. Oceanogr. Magazine (Tokyo) 4(1):23-30.
- Wada, S. K. 1954. Spawning in the tridacnid clams. Japanese Jour. Zool. 11:273-285.
- Westenhouse, R. G. 1968. Developments in the methodology for glycogen determination in oysters. Nat. Shellfish Assoc. Proceed. 58:88-92.

- Weymouth, F. W. 1923. Life history and growth of the pismo clam. Fish. Bull. No. 7, Cal. Fish and Game Comm., Sacramento. 120 p.
- Weymouth, F. W. 1925. Growth and age at maturity of the Pacific razor clam Siliqua patula (Dixon). Bull. U. S. Bur. of Fisheries 41:201-236, 27 Figs.
- Weymouth, F. W. and H. C. McMillin. 1931. The relative growth and mortality of the Pacific razor clam (Siliqua patula, Dixon) and their bearing on the commercial fishery. Bull. U. S. Bur. of Fisheries 46:543-567.
- Weymouth, F. W. and S. H. Thompson. 1931. The age and growth of the Pacific cockle (Cardium corbis Martyn). Bull. U. S. Bur. Fish. 46:633-641.
- Wilbur, K. M. 1964. Shell formation and regeneration, In Physiology of mollusca, K. M. Wilbur and C. M. Yonge, eds. Academic Press, N. Y. p. 243-282.
- Wilbur, K. M. and G. Owen. 1964. Growth, In Physiology of mollusca, K. M. Wilbur and C. M. Yonge, eds. Academic Press, N. Y. p. 211-242.
- Winckworth, R. 1929. Notes on nomenclature. Proc. Mal. Soc. London 18(5):228-229.
- Yonge, C. M. 1975. Giant clams. Scientific American 232(4): 96-105.