

POPULATION AND REPRODUCTIVE BIOLOGY OF THE SIX-RAYED
SEA STAR LEPTASTERIAS HEXACTIS
ON THE PROTECTED OUTER COAST

by

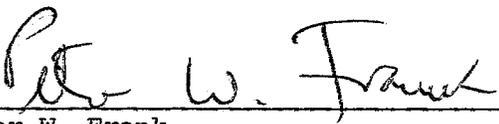
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TABLE OF CONTENTS

	<u>Page</u>
LIST OF TABLES.	vi
LIST OF FIGURES	viii
INTRODUCTION.	1
Statement of Purpose	5
Echinoderm Ecology and Reproductive Biology.	6
Reproduction in <u>Leptasterias hexactis</u>	8
GENERAL METHODS AND DESCRIPTION OF THE STUDY AREAS.	10
POPULATION BIOLOGY.	15
Population Study Methods and Materials	16
Results.	22
Discussion	63
FEEDING BIOLOGY	66
Asteroid Feeding Biology	66
Methods.	69
Results.	71
Discussion	106
REPRODUCTIVE BIOLOGY.	110
Method and Materials	111
Results.	115
Discussion	154
CONCLUDING DISCUSSION	161
APPENDIX.	173
BIBLIOGRAPHY.	177

LIST OF TABLES

TABLE	<u>Page</u>
1 The percentage of all adult and juvenile <u>Leptasterias</u> which occurred in each of the three morphological categories.	35
2 Information summary of <u>Leptasterias</u> density estimates for the three study populations	44
3 Summary of size-age class estimates for the three study populations	60
4 Mortality estimates for newly metamorphosed and 2 year old <u>Leptasterias</u>	62
5 Comparative prey species in <u>Leptasterias</u> ' diet for the three study populations	78
6 Prey species diversity indices calculated from the feeding data for the three study populations.	82
7 Analysis of comparative feeding study data: <u>Leptasterias</u> feeding on <u>Balanus glandula</u>	89
8 Mean caloric intake per feeding event and population ingestion rate for the three study areas.	90
9 Analysis of comparative feeding study data for sea stars in the three morphological categories	91
10 Overlap of <u>Leptasterias</u> ' and <u>Pisaster</u> 's diets in the Cape Arago-Sunset Rocky intertidal zone	104
11 Overlap of <u>Leptasterias</u> ' diets from Sunset Bay, Oregon and Lonesome Cove, San Juan Island, Washington.	105
12 Characteristics of <u>Leptasterias</u> ' embryos and larvae used to distinguish developmental age of brood	114
13 Comparison of male and female <u>Leptasterias</u> average wet weights	117

LIST OF TABLES continued

TABLE		<u>Page</u>
14	Comparison of peak male reproductive output for 1971.	123
15	Comparison of prebrooding females for number of mature eggs in their ovaries	123
16	Summary of 1971 brooding data recombined into eight larval developmental categories	140
17	Summary of 1971 brooding data combined into categories based on wet weight of the brooding female.	142
18	Comparison of brooding females from each study populations based on female wet weight.	143
19	Summary of data collected during the 1972 brooding season for 11 <u>Leptasterias</u> populations.	145

LIST OF FIGURES

FIGURE	<u>Page</u>
1 Map of Sunset Bay-Cape Arago Coastline	13
2 Growth of first year <u>Leptasterias</u> from the three study areas.	24
3 Weight change in starved <u>Leptasterias</u>	27
4 Weight change in <u>Leptasterias</u> fed on an indeterminate diet of the barnacle <u>Balanus glandula</u>	29
5 Weight change in <u>Leptasterias</u> fed on a maximum diet of the barnacle <u>Balanus glandula</u>	31
6 Percentages of all adult <u>Leptasterias</u> observed in the three study populations placed in the three morphological categories	37
7 Percentages of all juvenile <u>Leptasterias</u> observed in the three study populations placed in the three morphological categories	39
8 <u>Leptasterias</u> size frequency distributions in the Sunset Bay upper, middle and lower intertidal zones	48
9 <u>Leptasterias</u> size frequency distributions in the Middle Cove upper and lower intertidal zones.	50
10 Size frequency distributions showing the comparative population structure of the three study populations.	55
11 Weight frequency distributions of brooding females from the three study populations for the 1971, 1972 and 1973 brooding seasons	59
12 Annual feeding cycle of adult <u>Leptasterias</u>	74
13 Annual feeding cycle of juvenile <u>Leptasterias</u>	77

LIST OF FIGURES continued

FIGURE		<u>Page</u>
14	Total kilocalories contributed by principal prey species to the three study populations	87
15	Regression lines of total dry weight of prey on sea star size for the three morphological categories of <u>Leptasterias</u>	93
16	Gonad and storage organ indices for male <u>Leptasterias</u> from the three study populations	119
17	Gonad and storage organ indices for female <u>Leptasterias</u> from the three study populations.	121
18	Female storage organ indices vs. the number of weeks spent brooding	126
19	Percentage of adult <u>Leptasterias</u> found brooding during the 1971 brooding season	129
20	Number of females which began brooding during each week of the 1971 brooding season	131
21	Comparison of mean egg and embryo sizes for the three study populations during the 1971 brooding season.	134
22	Reproductive success of <u>Leptasterias</u> in the 1971 brooding season.	137
23	Initiation and termination of brooding in populations of <u>Leptasterias</u> for the 1972 brooding season	147
24	Size frequency distributions of eight <u>Leptasterias</u> populations sampled during the 1972 brooding season.	151

INTRODUCTION

The relationship between life history phenomena (such as reproductive strategy) and general evolutionary theory has been discussed only recently in the ecological literature. Murdoch (1970) points out that the population consequences of life history phenomena as they relate to fitness and natural selection were first discussed by Cole (1954). This was more than 20 years after the mathematical foundation of the theory of population genetics was summarized by Fisher (1930) in essentially its present-day form.

In his general theory of clutch size (in birds) Cody (1966) felt that the number of offspring would decrease as environmental stability and/or predator avoidance increased. Murphy (1968) disagreed and felt that uncertainty in survival, especially from zygote to first maturity, generated selective pressure for iteroparity. This may then entrain pressure for reduced energy allocation for reproduction (smaller clutch size) in order to insure longer life.

Hairston's et al. (1970) results contradicted Murphy's (1968) conclusion. They ascribed his results, i.e. the evolution of iteroparity, to the imposition of density-dependent reproduction on his model. They concluded from their own experiments that the widespread evolution of iteroparity is evidence of density-dependent population regulation.

Gadgil and Bossert (1970) conclude that populations living in more

stable environments with low incidence of catastrophic mortality would tend to encounter a relatively low availability of resources. In these populations they would expect to find low reproductive effort and life histories characterized by late maturation and longer life spans. These populations are said to demonstrate the "K-selected" reproductive strategy (MacArthur & Wilson, 1967). The "K" strategy is to maintain the highest density possible in a population at equilibrium, thus favoring genotypes which confer competitive ability, especially the capacity to seize and hold a piece of the environment and extract the energy produced by it (Wilson & Bossert, 1971).

Populations living in more variable environments with higher incidence of catastrophic mortalities would have higher quotas of resources available to them (Gadgil & Bossert, 1970). These populations would be expected to exhibit high reproductive effort and have their life histories characterized by early maturation and shorter life spans, i.e. the "r"-selected reproductive strategy (MacArthur & Wilson, 1967). The "r" strategy is to make full use of habitats which, because of their temporary nature, keep many populations at any given minute on the ascending portion of the logistics growth curve (Wilson & Bossert, 1971).

On a one-dimensional continuum between r and K the reproductive strategies exhibited by the two common asteroids of the Oregon rocky intertidal zone, Leptasterias and Pisaster, would appear to be far apart. The female Pisaster produces large numbers of energy-cheap ova which develop into long-lived planktotrophic larvae that are highly dispersible and capable of colonizing any suitable open habitat. The

female Leptasterias produces considerably fewer, more energy-expensive progeny and invests additional energy in brooding them. These larvae have very low dispersibility but are released as fully metamorphosed stars and are thus freed from the high level of mortality suffered by planktonic larvae (Thorson, 1950).

Vittor (1971) pointed out the synthetic nature of approaches which attempt to explain all life history strategies in terms of an r to K continuum. He felt that these terms should not be applied where the assumptions behind the concept of r and K selection are not met. The above comparison of Leptasterias and Pisaster is an example. The dominant selective factor which most influenced Leptasterias reproductive strategy of brooding was probably not a stable environment with low incidence of catastrophic mortality; but rather the unfavorable polar conditions including low surface salinities due to ice melt, poor planktonic food conditions, with a short summer productive period, and low temperature. It is felt that these conditions have selected against the production of planktotrophic larvae and explain why an estimated 95% of polar benthic invertebrate species produce some type of non pelagic larvae (Thorson, 1950; Pearse, 1969c).

Pianka (1970) summarized the controversy over r and K selection by stating that "certainly no organism is completely 'r-selected' or 'K-selected', but all must reach a compromise between the two extremes." MacArthur and Wilson (1967) anticipated much of this controversy and recognized in the preface of their book on island biogeography that their formulations would not long fit the "exacting results of future

empirical investigation." However they certainly accomplished their stated goal of "stimulating new forms of theoretical and empirical studies which will lead to a stronger general theory."

Frank (1968) discussed the relationship between life histories and community stability. He emphasized Cole's (1954) strong call for a more comprehensive theory to explain the ecological implications of life history features and stressed the need for adequate empirical data, especially from marine animals. Frank made the suggestion that the evolution of terrestrial communities initially was accomplished by the presence of longevous plants as a stabilizing effect. These long-lived plants tend to have indeterminate growth, many have asexual reproduction, and most have a relatively large "litter size" which tends to increase with plant size. In comparing terrestrial with marine communities he pointed out the lack of long-lived marine plants, but also the fact that short-lived, shallow, epibenthic plants are accompanied by animals with high fecundities and relatively long life spans, many of which have at least partially indeterminate growth. He indicates that these life history features apply for example to many coelenterates, molluscs and fishes, and perhaps echinoderms.

Recent long term studies on sea stars (Mauzey, 1966; Chia, 1964; Menge, 1970) are in accord with Frank's suggestion. These echinoderms appear to be long-lived (3-5+ years in Leptasterias: 6-10+ years in Pisaster) and are very fecund. However, much work is needed to clearly determine and evaluate the reproductive strategies of these animals and their consequences for the population and marine community in general.

Statement of Purpose

An organism's life history may be looked upon as the resultant of three biological processes: maintenance, growth, and reproduction (Gadgil & Bossert, 1970). Any population or organism has limited resources of energy and time at its disposal, and the three component processes of life history compete for these limited resources. This study is an investigation of the relationship between the population biology of an intertidal sea star and its reproductive strategy of brooding young. It was performed to determine how this species partitions the limited resources available to it among its life history processes, and the overall effect this has on population structure.

The investigation of the reproductive biology of a species on a population basis involves the study of many aspects of its natural history. The biology of Leptasterias has been considered on the organism level by Chia (1964, 1966a & b, 1968a & b), and the role of this sea star in the intertidal community has been described by Menge (1970, 1972a & b). These workers have investigated some aspects of Leptasterias reproductive biology in their studies. Therefore our work overlaps somewhat, and I have borrowed from their techniques. I have also benefited from ideas and results presented by these authors and from correspondence and discussion with them.

This paper is organized to follow the annual cycle of events in Leptasterias populations. It starts arbitrarily with the release of newly metamorphosed sea stars and follows the annual population cycles of growth, mortality, feeding and gonad preparation as they contribute

to the subsequent brooding and release of young and the beginning of another cycle.

Echinoderm Ecology and Reproductive Biology

Echinoderms have served as the subject of embryological investigations for many years. Consequently much is known about the reproductive processes and spawning periodicities of many species particularly those which occur in abundance near major marine institutions (Harvey, 1956). The majority of this work has been done with echinoids belonging to the genera Arbacia and Strongylocentrotus.

Recent workers with echinoderm reproduction have described oogenesis (Chia, 1968a in Leptasterias; Chatylene, 1969 in S. purpuratus), and the breeding cycle and gonad indices have been computed for many species (summarized by Boolootian, 1966). Since then the reproductive periodicities of several Indo-Pacific echinoids (Pearse, 1968, 1969a & b, 1970, 1972) and a New Zealand asteroid (Crump, 1971) have been investigated.

On a broader scale the relation of gut nutrient reserves to reproduction and nutrition in sea stars has been histochemically defined (Nimitz, 1971) and the mechanism of nutrient transfer demonstrated (Ferguson, 1969). Also the mechanism controlling sea star spawning was hypothesized by Kanatani and Shirai (1970). It involves the release of a gonad-stimulating substance (GSS) by the radial nerve (Chaet & McConnaughey, 1959) which acts on the ovary to produce an active substance (MIS, meiosis-inducing substance) responsible for oocyte maturation. After the oocytes mature, the sea stars spawn. Recent work

indicates the existence of such a GSS in echinoids as well (Cochran & Engelmann, 1972).

Despite this accumulated wealth of information on echinoderm reproduction there is still much truth in Nichols' (1964) statement concerning the lack of correlation between reproductive activities and ecological factors in echinoderms. The study of echinoderm ecology is a relatively new field which started on this coast in the 1950s. Again the majority of the early work was done with the ubiquitous echinoids, with the exception of Feder's (1956, 1958) work on Pisaster ochraceus. Since then Mauzey (1966) has studied the feeding habits and reproductive cycle of Pisaster, and Landenberger (1968, 1969) studied selective feeding and the effects of exposure to air in this species. Paine (1969, 1971) has explored the community shaping role of Pisaster and other asteroids.

Other ecological studies on asteroids include work on growth rates of Nepanthia belcheri (Kenny, 1969) and Luidia senegalensis (Halpern, 1970); and work on intensity of larval settling in Asterias forbesi (Loosanoff, 1964). Several studies of sea star feeding behavior include work on the escape responses of sea star prey (Feder, 1963; Mauzey et al., 1968) as well as an observation on general feeding behavior in a variety of subtidal sea stars (Hopkins & Crozier, 1966; Mauzey et al., 1968). The results of these and other pertinent studies on sea stars will be considered in the appropriate chapter below.

Most information about the species in question, Leptasterias hexactis, has been reported by Fu-Shiang Chia and Bruce Menge from the

University of Washington. Chia's work included a detailed description of oogenesis and larval embryology (1964, 1968a, 1968b) as well as a brief study of brooding behavior (1966a). Chia (1966b) also did a taxonomic study of the genus in which he combined the species L. aequalis and L. hexactis into the single species L. hexactis. Menge (1970, 1972a & b) recently completed a long-term study of this species in the San Juan Islands.

Reproduction in Leptasterias hexactis

The forcipulate asteroid, L. hexactis is found in the middle and lower intertidal zone and is distributed from British Columbia to Monterey Bay, California (Chia, 1966b). Most members of this genus brood their eggs, and several methods have been evolved for brooding within the genus (Hyman, 1955). Female L. hexactis accomplish this behavior by arching their arms orally, bringing them close together and forming a pouch into which they deposit their eggs via 12 orally located gonopores. The female attaches the tips of her arms to the undersurface of a rock and remains in this position for a period of 2 months (Chia, 1966a). After this period the young, which undergo direct development (Chia, 1968b), are released from the brood pouch onto the rock surface. The female then resumes the normal oral-surface-down position but continues to cover her young with her arms until they are able to feed on their own, several days later.

There are several other interesting aspects observed in the reproductive biology of L. hexactis. Menge (1970) and Chia (1968a) be-

lieve the female releases only enough eggs to fill the brood pouch, i.e. only that number which she can successfully manipulate, aerate, etc. and allow to develop completely. Menge (1970) felt that a female could handle the number of eggs approximately equal in volume to half the volume of the brood pouch, some of which were lost during development. Thus the female produces relatively few gametes when compared to non-brooding sea stars (Thorsen, 1946).

Allocation of energy is much different between male and female L. hexactis. The females produce a limited number of gametes but retain sufficient energy reserves to carry them through the 2 month brooding period as they do not feed during this time. The male L. hexactis produce large quantities of sperm and drastically deplete their energy reserves (see below). However after spawning the males are able to continue feeding, although they do so at a low rate.

Another interesting observation is that the larval sea stars will not develop to maturity outside the brood pouch. Any development that is observed is asynchronous with the timing of normal development, and the larvae rarely escape from the egg membrane. Larval development within the brood pouch is synchronous and direct (Chia, 1968a).

For the remainder of this dissertation Leptasterias hexactis will be the only species of this genus considered and will be referred to by the generic name Leptasterias.

GENERAL METHODS AND DESCRIPTION OF STUDY AREAS

In the study of asteroids it is customary to report their linear dimensions in terms of disc radius, designated "r" (Hyman, 1955) and the whole animal radius from the center of the disc to the tip of the arm, which is designated "R." Leptasterias is unlike most asteroids, having six rays instead of five, and this allows three axes from which a measure of total diameter can be made. Total sea star diameter, the equivalent to 2R in conventional terms, was the main measurement used in the field and was the mean value obtained from the three possible diameter measurements.

The tidal levels at each study site were obtained by observing the low point of the low tide, and marking its position. This was done on calm days and several different observations were made to offset the variability caused by wind and barometric pressure. From these reference points the vertical intertidal range was arbitrarily divided into three zones. The height of the level along the shore is given in feet above or below Mean Lower Low Water (MLLW). These are the lower intertidal zone, 0.0 feet and below, middle intertidal zone 0.0 to 2.5 feet and upper intertidal zone 2.5 feet to the upper boundary of Leptasterias. These zones are approximately the same as zones 4, 3, and 2 respectively of Ricketts et al. (1968). Leptasterias did not usually occur in zone 1, the highest intertidal zone.

The Study Areas

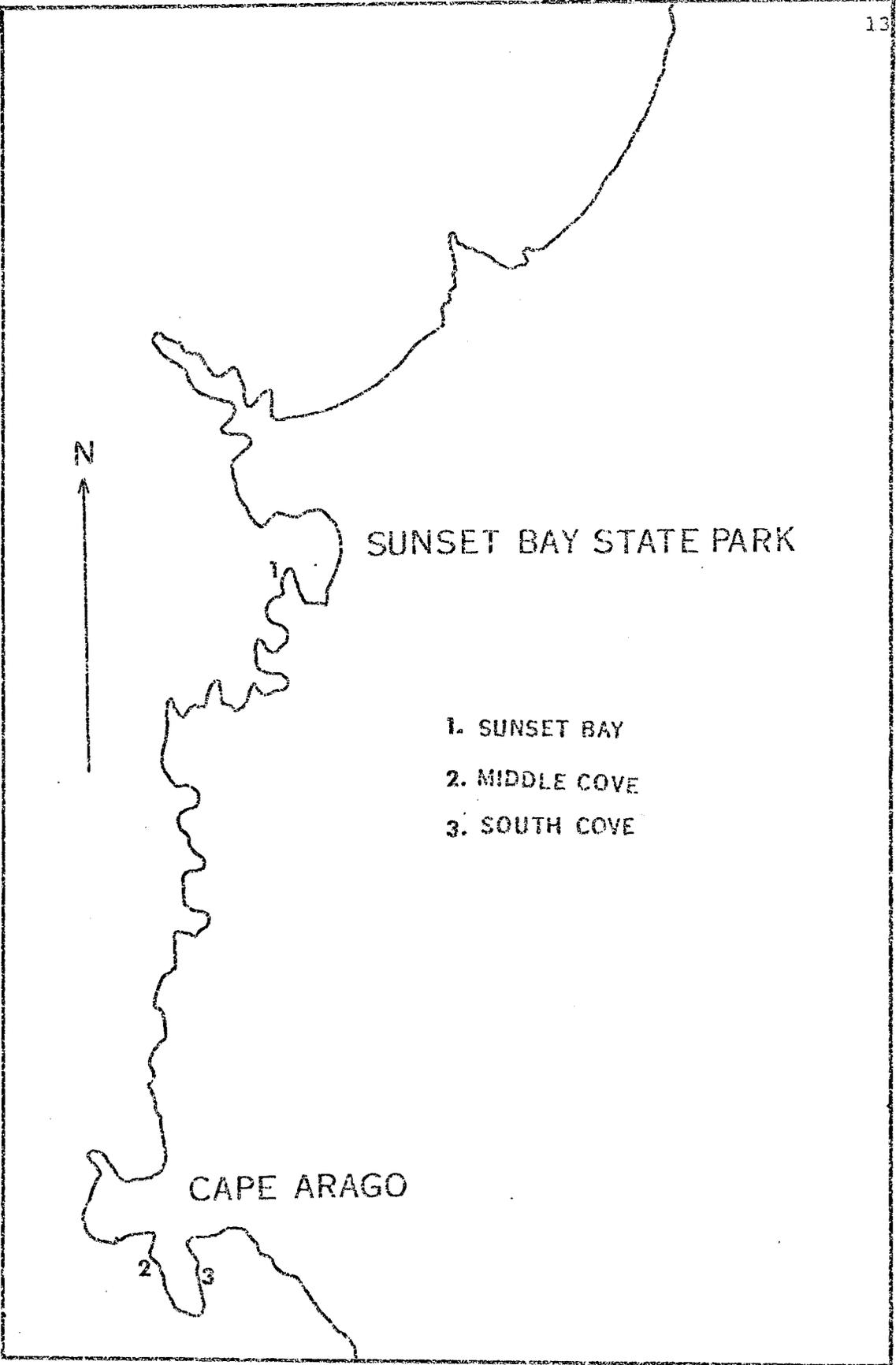
Three permanent study sites were established in the Cape-Arago Sunset Bay area; Sunset Bay, and Middle and South Coves, Cape Arago. These areas were selected because of their similar substratum, their year-round accessibility at low tide, and because of the densities and size frequency distributions of the resident Leptasterias populations.

The region from Cape Arago Lighthouse southward beyond Cape Arago State Park (Fig. 1) is comprised of steeply dipping interbedded sandstones, siltstones, and mudstones (Rottmann, 1970). It is characterized by a surf-cut bench and nearly vertical sea cliffs in various stages of formation and numerous small coves eroded along fault lines (Baldwin, 1966).

The Sunset Bay Leptasterias population was located on the south side of the bay on a relatively flat area with a boulder and cobble area at the north end. The sea stars were found within and adjacent to the boulder field described by Ebert (1966). The cobble area was at the base of a cliff and had a smaller area (20 by 30m) than the other two locations. This area is relatively protected from direct swells owing to outlying reefs and its geographic orientation.

The Leptasterias study area in Middle Cove was located approximately 100m from the base of the north-facing sea cliff and 10-20 m from the east-facing cliff. It was a mixed cobble-boulder area (63 by 21 m) on a relatively gradually sloping surf-cut bench. It was bounded on the south by large boulders and on the north by exposed bedrock and sand. The Leptasterias area was less protected from direct swells than

Fig. 1. Map outline of the Oregon coast in the vicinity of Sunset Bay and Cape Arago State parks. Location of three permanent study sites is indicated.



SUNSET BAY STATE PARK

- 1. SUNSET BAY
- 2. MIDDLE COVE
- 3. SOUTH COVE

CAPE ARAGO

2 3

was Sunset Bay, especially from west and southwesterly swells.

South Cove is directly exposed only to southerly swells and is more protected than Middle Cove. The northern base of the cove is a sandy beach and a relatively broad surf-cut bench is located at the base of the sea cliff on the west side. The sea stars were found within a cobble-boulder area (41 by 43 m) which extends from the sandy beach part way along the bench.

POPULATION BIOLOGY

Until recently the majority of life history investigations of sea stars was prompted by the damage they caused to commercial shellfish beds (Feder, 1970). These studies have shown that sea star growth depends mainly on temperature, the abundance and suitability of available food, and sea star size (Feder, 1970; Halpern, 1970).

In sea stars from temperate and the more northern waters growth is reduced and may stop entirely for several months during the coldest part of the year (Feder & Christensen, 1966; Halpern, 1970). When water temperatures get very low, many species cease feeding almost entirely (Feder & Christensen, 1966; Mauzey, 1966).

It is usually difficult to measure growth rates in populations of sea stars, as the growth rates can fluctuate greatly with varying conditions. All species studied so far are apparently capable of assimilating large quantities of food, if it is abundant and of the right kind (Feder & Christensen, 1966).

It is almost impossible to tell the age of a sea star from its size, because of these widely fluctuating growth rates. Trying to determine age groups on the basis of size frequency distributions will generally give fallacious results, especially for the larger animals as several year classes may overlap greatly in size (Ebert, 1968).

In this chapter I will present growth data for both young and adult

Leptasterias, describe the observed local variation in Leptasterias distribution and abundance, and review the factors contributing to these observed phenomena as discussed by Connell (1972) and others (Dayton, 1971; Ricketts et al., 1968) in recent review articles on the rocky intertidal community.

Population Study Methods and Materials

Growth Studies

The growth study of the newly released stars from the 1971 brooding season was followed in the field for a 1 year period. Monthly samples of 25-50 individuals were measured from each of the three study populations. The growth data obtained from this investigation were used in combination with size frequency data mentioned below to estimate age classes.

The 1 year laboratory study of growth in adult Leptasterias was performed at the University of Oregon using a cold constant-temperature room. During the 1971 brooding season 200 brooding female Leptasterias were collected from several Cape Arago-Sunset Bay populations. These animals were maintained in water tables at the Charleston marine station until 15 June 1971 when they were transferred to Eugene.

The experimental Leptasterias were divided into three groups of approximately equal size distribution. One group was dyed with neutral red and Nile blue A (Matheson Corp. Inc., Cincinnati, Ohio) respectively, using the method described by Feder (1955). Sea stars in the third group were left with their natural coloration.

All animals were damp dried with paper towelling and weighed to the nearest 0.1g on an Ohaus triple beam balance. In Leptasterias the madreporite is excentric and located in the inter-radii of two arms designated C and D by convention (Hyman, 1955). Using this notation the arm lengths of each Leptasterias were measured to the nearest millimeter. The resulting combination of color, weight, and variation in arm length allowed individual Leptasterias to be followed when placed together in small numbers.

Groups of eight Leptasterias were placed in 3 liter battery jars which contained flat sandstones taken from the sea stars' habitat. All sea water used was obtained from the Charleston marine station and filtered before use. All prey used in the feeding experiments were obtained from areas adjacent to the study sites.

Three replicates of eight Leptasterias were established at each of three feeding regimes. Individuals in the first regime were given all the food they could eat, the second was supplied with approximately half of what was given to the first, and members of the third regime were starved. These animals were maintained at a constant temperature (10°C) and a constant diurnal light regime (12 hour light/12 hour dark). The sea water was changed weekly and the battery jars were cleaned and prey replenished on approximately a bi-weekly basis. All sea stars were weighed monthly and measured every 3 months.

Maintenance Factor

The cobbles and small boulders in the areas inhabited by

Leptasterias undergo much movement by storm waves. The crushing and grinding action of the rolling stones can cause severe damage to the resident Leptasterias populations in terms of mortality and loss of limbs. To estimate the comparative impact this might have on the Leptasterias study populations an index of morphological condition was devised, and this was called the maintenance factor. Three categories were designated: normal, incomplete and regenerating, and beginning in May 1971 all sea stars observed in the field were classified according to one of these categories.

The normal category consists of sea stars which had all six arms intact and of approximately equal size and length. Those animals placed in the incomplete category have one or more arms regenerated to approximately half normal length or have recently lost portions of one or several arms. The regenerating class consist of animals which had lost one or more arms entirely, i.e. cut off at the disc margin, or, if regenerating one or more arms, the new limb(s) is only a few millimeters in length.

Density and Distribution

In the summer 1970 I arbitrarily chose Middle Cove of Cape Arago as a study site to familiarize myself with Leptasterias and its habits. The Middle Cove Leptasterias' cobble area was divided into a sampling grid and markers were placed at appropriate intervals to facilitate relocation at subsequent low tides. An arbitrary boundary, parallel to the shoreline, was established in the upper intertidal and grid points were

designated at 3 m intervals along it. Transects were then run parallel to this upper boundary every 3 m until the lowest intertidal was reached.

At each 3 m grid point along a transect a 0.5m^2 (0.7 by 0.7m) quadrat was taken. The placing of the quadrat at each station was determined using a random numbers table. Two place random numbers were preselected, converted to centimeters, and the quadrat placed at the corresponding distance along the transect line. The area within the quadrat was thoroughly searched down to bedrock substrate and the mean total diameter of all sea stars encountered was measured to the nearest half millimeter. An area of approximately 1500m^2 (63 by 21 m) was searched in this manner.

From my experience in summer 1970 it became apparent that proper estimation of Leptasterias density using transect techniques was very time consuming, and required fair weather and spring low tides. For these reasons only one large scale estimate of density was conducted for South Cove and Sunset Bay. During the summer 1971 at all three study sites, a series of transects was run parallel to the shoreline at several intertidal levels. The same transect methods described above were employed except the permanent grids were not established.

The cobble areas which Leptasterias inhabits are sometimes difficult to search. A quadrat might be placed over a large boulder or on a pile of rocks or on naked bedrock. To estimate the total surface area present within each quadrat was too time consuming to be profitable. All subsequent estimates of density combine areas that are not topo-

graphically homogeneous; however the stratified random placing of quadrats proportionally represents the substrate present and does provide a reasonable estimate of density.

The spatial dispersion of Leptasterias was determined at Middle Cove by the extensive sampling done there. The spatial dispersion of the Sunset Bay population was determined by sampling at the low, mid and upper tidal horizons. Each census took approximately 2½-3 hours. At least 100 animals were counted in each. All three were completed during two consecutive spring low tides. The spatial dispersion of the South Cove population was studied less thoroughly, and was interpreted from transects and general field observations. To determine the subtidal distribution of Leptasterias the subtidal zone immediately below the three study areas was investigated using SCUBA.

To observe movement within the intertidal zone a short term study was conducted in South Cove. A sample of 50 adults and 50 juveniles was collected on 15 June 1971 from throughout the South Cove intertidal zone and taken to the marine station at Charleston. The sea stars were dyed bright red with neutral red stain. These animals were returned the next day and released along a band in the lower mid-intertidal zone which ran parallel to the shore. The band was 20 m long and 2 m wide and large boulders at both ends of the band were cleared of algae and marked. The area was censused a month later to determine movement. The dye was persistent, as marked animals were recovered for several months after being released.

Population Structure and Dynamics

Initially the three main study populations were sampled on a seasonal basis to estimate population structure and dynamics. The sea stars were collected haphazardly and weighed to the nearest 0.1g on an Ohaus triple beam balance. The scale was protected by a water tight plywood case which was equipped with a hinged transparent door to allow readings to be made in the wind. After a year it was determined that the seasonal weight frequencies were of limited value. They were abandoned in favor of another technique.

For the sampling period from June to December 1971, size frequency distributions were taken in conjunction with the bi-weekly feeding observations. It was very difficult to see the young of the year and they were not included in the census. The remaining sea stars were grouped into 10 mm size categories, based on their total mean diameter. From January to April 1972 a more comprehensive series of size frequency distributions was taken. All sea stars encountered, including young of the year, were measured and grouped into 2 mm size classes.

These latter comprehensive size frequency distributions were analyzed to estimate age (size) classes using the probability paper techniques described by Harding (1949) and Cassie (1953). The former, less comprehensive size frequencies were used to estimate the relative number of sea stars within the calculated age (size) classes.

Results

Growth Studies

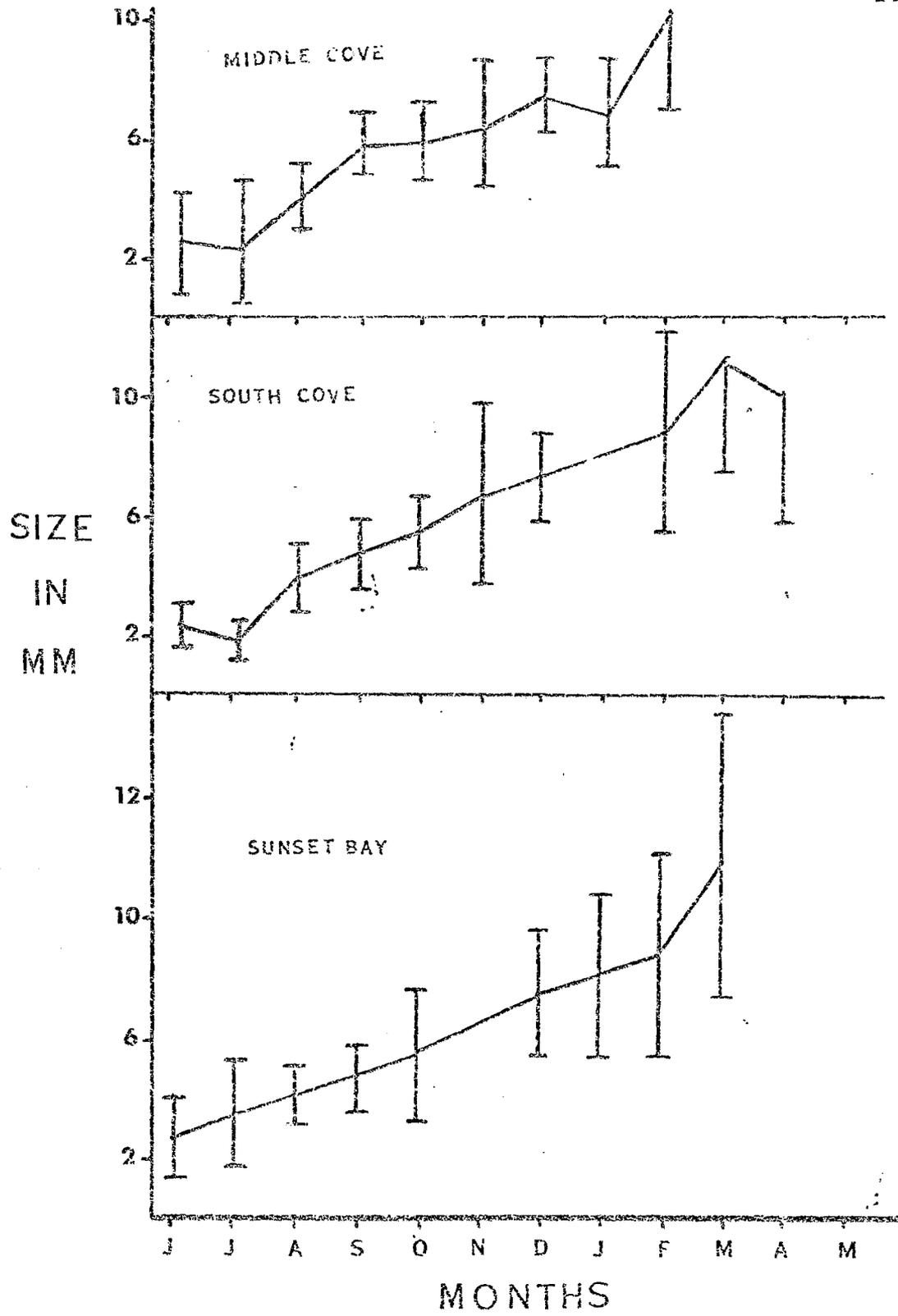
In 1971 the newly metamorphosed sea stars were released by the females in April through early May. At the time of release the young were 1.6 mm in diameter. This year class was followed on a monthly basis for 1 year. The monthly average size (Fig. 2) indicates a fairly steady increase in size throughout the year. The increase in the standard deviation with time suggests a disparity of growth among individuals as they become older.

The growth rate appears to be similar for all three study populations, with the young reaching an average size of 10.5 to 12.1 mm in the first year. This represents a seven fold increase in linear size in the young stars and is compared to an approximately 12 fold linear increase in size in newly settled Pisaster during their first year (Feder, 1970).

The growth of adult Leptasterias was measured in a laboratory experiment which was designed to study the relationship between feeding success and reproductive effort. Unfortunately the laboratory system proved inadequate to induce the female Leptasterias to brood. Although the stars gained weight, none released their eggs during the period the field populations were brooding. Active Leptasterias sperm was added to individual beakers containing single females, and still none could be induced to brood. Therefore the data are presented as a measure of Leptasterias' growth potential.

Because of the difficulty of weighing such small animals in the

Fig. 2. Growth of first year Leptasterias from the three study areas. Each point represents the mean diameter of a field sample of 25-50 sea stars. The vertical lines represent one standard deviation.



field the young stars were compared on a linear basis. In older stars the linear measurements are less accurate as they can vary over short periods (Feder, 1970). In order to avoid problems, both weight and linear measures were taken; the weight measurements proved to be more reliable and are used here.

Initially the maximum and intermediate feeding regimes were fed intertidal gastropods, Littorina spp. The sea stars ate these readily; however the littorines crawled up the sides of the battery jars and out of Leptasterias' reach. After 3 weeks the littorines were replaced by Balanus glandula. The barnacles were collected attached to a thin layer of sandstone substratum and were placed as food in the battery jars in this attached condition. The stars were checked daily and when those in the maximum feeding regime had consumed all their food, it was replenished. At the same time approximately half the amount of food given to the stars in the maximum feeding regime was given to those in the intermediate regime.

There was some initial mortality in all three feeding regimes. Mortality was greatest among the starved animals and there were many instances of cannibalism in this group. Because of this, it was necessary to provide the starved animals with a minimum amount of food. A low level of mortality continued through the 10 months the experiment was conducted, and was highest in the starved animals.

The per cent change in weight over the experiment is presented for the three feeding regimes in Figs. 3, 4, and 5. For comparison the stars were grouped in 2 g weight classes and separate curves plotted for

Fig. 3. Weight change in starved Leptasterias. Each symbol represents the mean per cent change in weight, based on the starting weight, of all animals within 2 gram weight classes. Symbol code: open circles = 0-2g; open squares = 2-4g; solid circles = 4-6g; triangles = 6-8g.

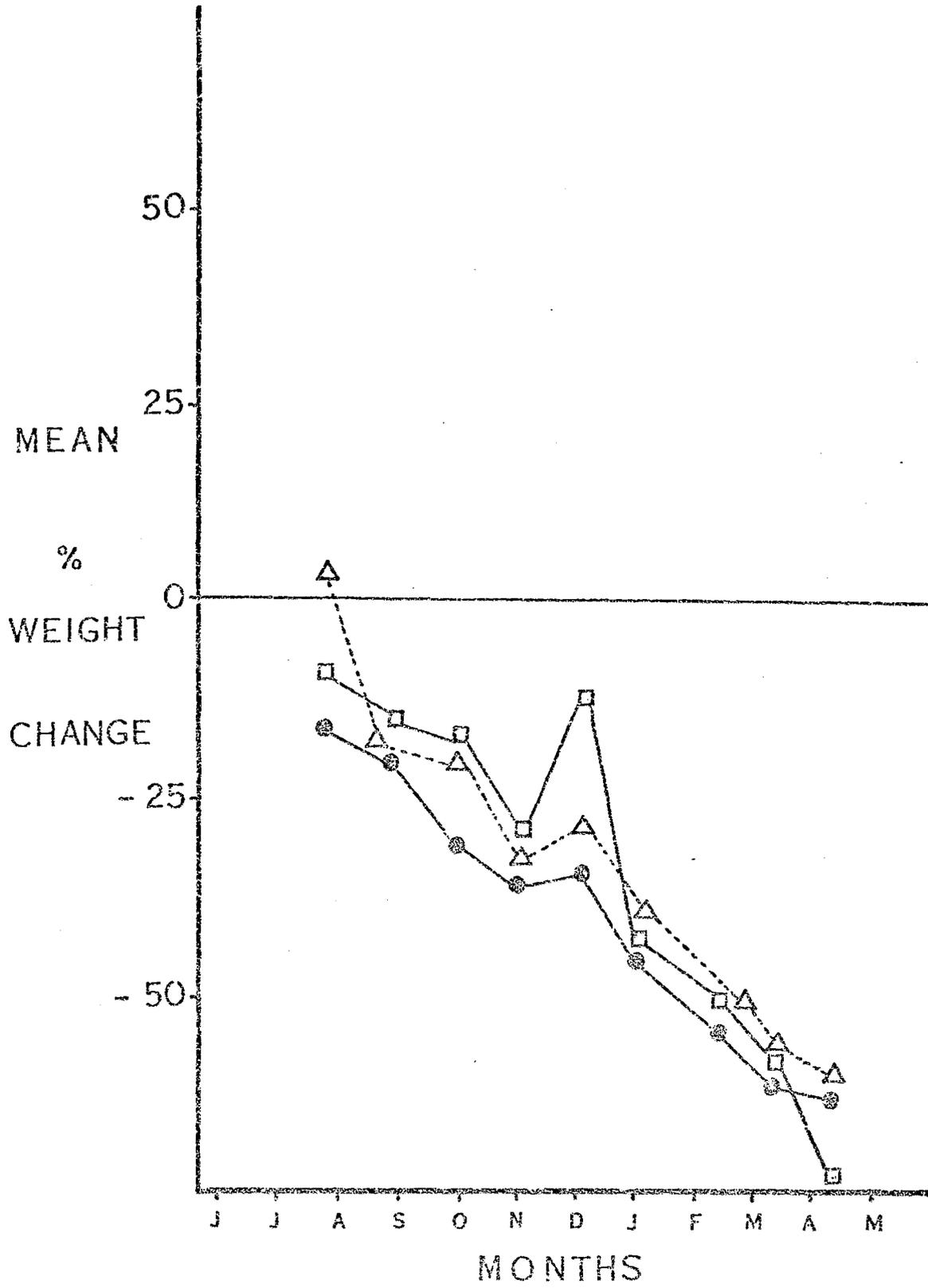


Fig. 4. Weight change in Leptasterias fed on an intermediate diet of the barnacle, Balanus glandula. Each symbol represents the mean per cent change in weight, based on the starting weight, of all animals within 2 gram weight classes. Symbols are the same as in Fig. 3.

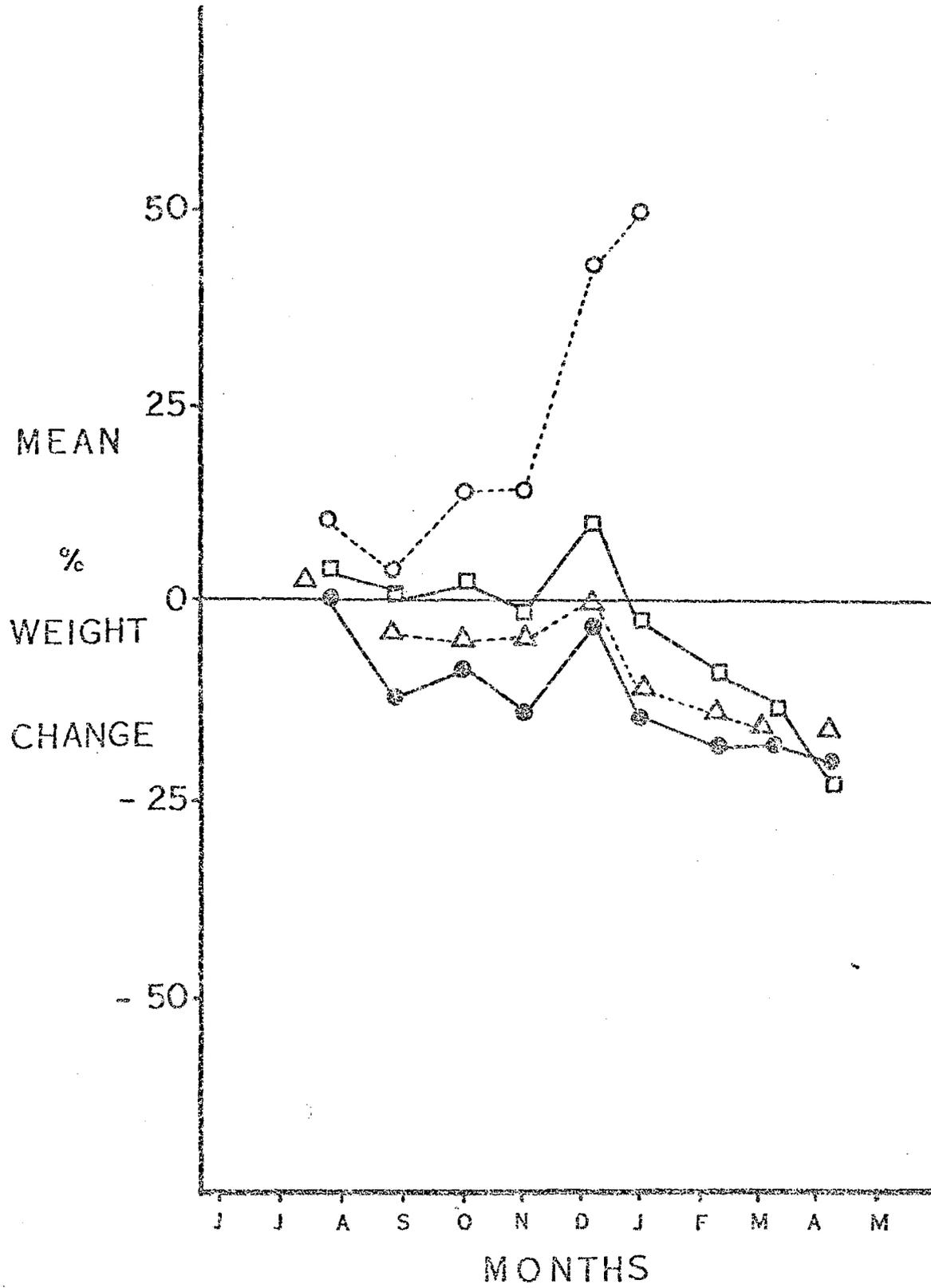
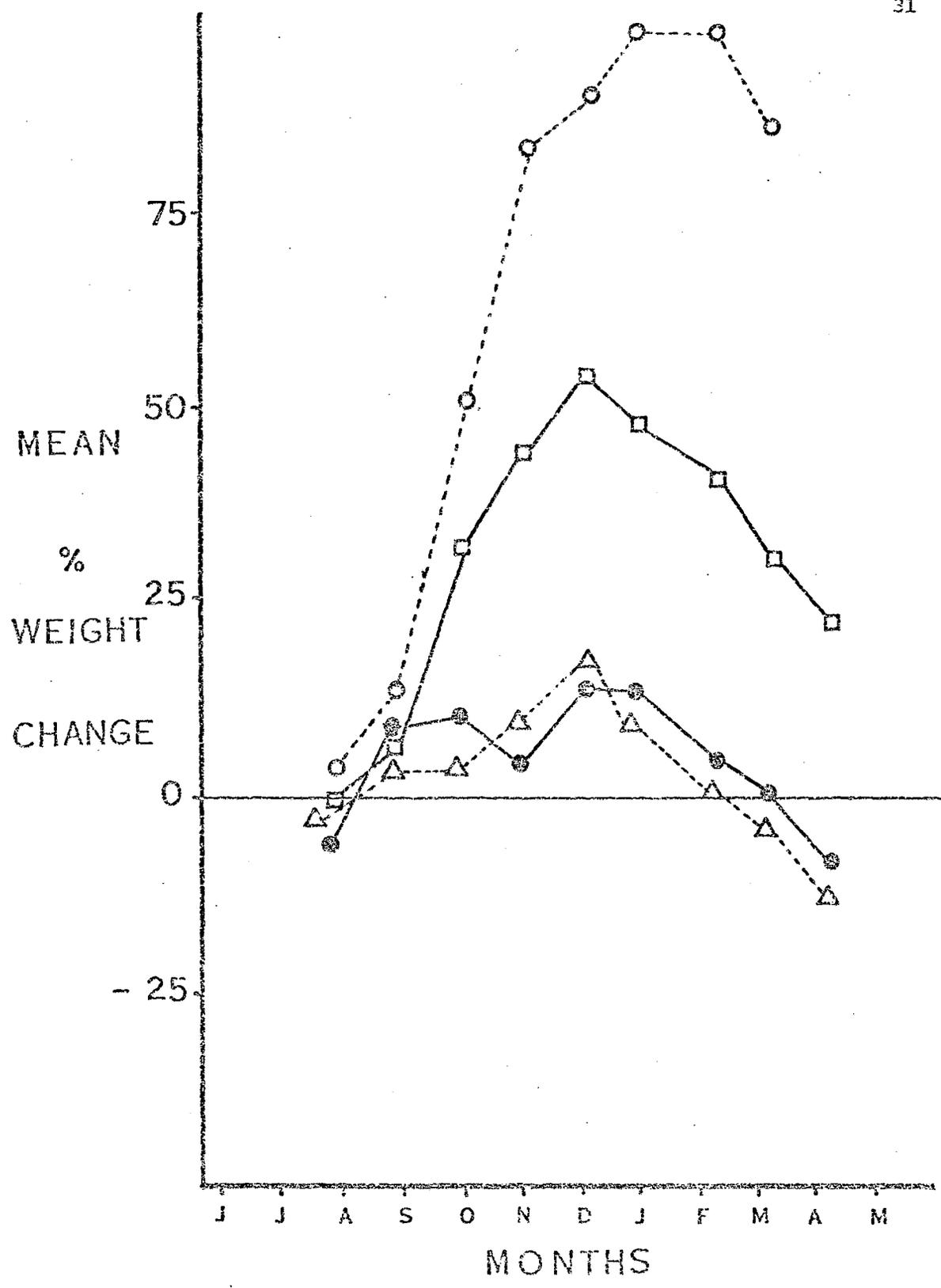


Fig. 5. Weight change in Leptasterias fed on a maximum diet of the barnacle, Balanus glandula. Each symbol represents the mean per cent change in weight, based on starting weight, of all animals within 2 gram weight classes. Symbols are the same as in Fig. 3.



each. The 0-2 g weight class is missing from the starved regime as all these small stars were cannibalized early in the experiment.

In all the growth curves an obvious increase in weight occurred between November and December. This corresponds to the period of maximum gonad and storage organ increase in size in preparation for the winter brooding. This increase was followed by loss of weight by all weight classes regardless of food availability. The animals in all three regimes stopped feeding through January and February and fed only sporadically through March.

This is the same feeding pattern observed in the field, and this does suggest some type of endogenous annual feeding cycle independent of light and water temperature. However, the sea water used in the experiment was obtained from within the Coos Bay estuary and became more dilute with increased winter runoff (Mrs. Jean Hanna, OIMB); therefore the decrease in feeding activity could have been an artifact of the reduced salinity. The experiment was terminated in mid-April, and the animals were returned to Cape Arago.

The starved sea stars (Fig. 3) lost weight on a relatively uniform basis. The smallest sea stars were least able to withstand starvation and became weak and then began to lose arms. They were cannibalized from the beginning by the larger sea stars. The most dramatic weight loss was seen in a star that went from 12.4 g to 3.5 g in 10 months. This animal remained in good morphological condition but shrank from 61 mm total diameter to 38.5 mm.

All weight classes in the maximum feeding regime (Fig. 5) gained

weight initially. After the peak in December all began to lose weight and the two largest weight classes went below their original weight. The 0-2g weight class showed the greatest percentage increase and the 2-4g weight class showed substantial gain in weight.

The sea stars in the intermediate feeding regime maintained approximately their initial weight until the December peak. After this all but the smallest weight class declined in weight. The 0-2g weight class did not follow this pattern but gained weight rapidly, and instead of declining after December, continued off the scale to 147% in March, 1972.

The pattern of weight change demonstrated by the stars in the intermediate feeding regime is thought to typify what occurs in the field. An adult female feeds during the summer and fall and obtains enough energy to mature her developing eggs and store reserves to maintain her through the 8 week brooding period. During the winter and early spring the sea stars do not feed and there is a corresponding loss in weight. After brooding season the stars replenish their reserve storage and any growth that occurs probably does so in the early summer before onset of reproduction.

The data also indicate that the smaller sea stars possess the greatest potential for increase in size and the least ability to withstand starvation. This species on the whole did not demonstrate the ability to withstand long term starvation as has been shown for Pisaster (Feder, 1970) and Astropecten irregularis (Christensen, 1970). The increase in size (147%) shown by the 0-2g weight class was overshadowed

by the growth of seven small Pisaster which were grown concurrently under identical conditions. These sea stars showed an average weight gain of 205% in the same time period.

The growth of Leptasterias is probably relatively uniform in the first (Fig. 2) and perhaps the second year in the three populations observed. After this time the growth potential of the maturing Leptasterias is differentially realized depending upon local conditions. This will be demonstrated below and in the later chapter on reproductive biology when the size of brooding Leptasterias females is compared.

Maintenance Factor

An arbitrary index of morphological condition, called the maintenance factor, was applied to all sea stars observed in the field from June 1971 to August 1972. The percentage of all adult and juvenile sea stars observed in each of the three categories is given in Table 1.

The morphological condition of the three populations correlates well with the degree of wave exposure each experiences. The Middle Cove population, which is most exposed, and had the greatest percentage of damaged individuals, both adults and juveniles. The Sunset Bay population, which is least exposed, had the lowest percentage, and the South Cove population was intermediate. In all three populations the juveniles had a higher percentage of injured animals than the adults, although this discrepancy became lower in the less exposed populations. These data suggest that the smaller (younger) sea stars are more susceptible to morphological damage from wave action especially in more

TABLE 1. The percentage of all adult and juvenile sea stars observed from June 1971 to August 1972 which occurred in each of three morphological categories.

Population	Morphological Category		
	Normal	Regenerating	Incomplete
Middle Cove			
Adults	58	15	27
Juveniles	44	33	23
South Cove			
Adults	62	13	25
Juveniles	55	25	20
Sunset Bay			
Adults	74	6	20
Juveniles	72	14	14

exposed areas. Another possible inference is that, whereas the morphological index data reflect damage from physical environmental factors they probably also give a relative index of mortality caused by these factors.

By collecting morphological data over a year's period it was hoped that an annual cycle of winter morphological damage and subsequent regeneration could be demonstrated. However, when the data are plotted over time (Figs. 6 & 7), no such pattern can be seen. What is apparent is the varying degree of morphological damage that can be inflicted during individual winters. The 1971 winter storms caused considerably less damage than did those of 1972. Although fewer censuses were taken and smaller numbers of sea stars observed in 1972, the data show a consistent trend which is probably genuine.

Fig. 6. Percentages of all adult Leptasterias observed in the three study populations which were placed in the three morphological categories. Symbol code: closed circles = normal sea stars; squares = sea stars with regenerating arms; triangles = sea stars with incomplete arms.

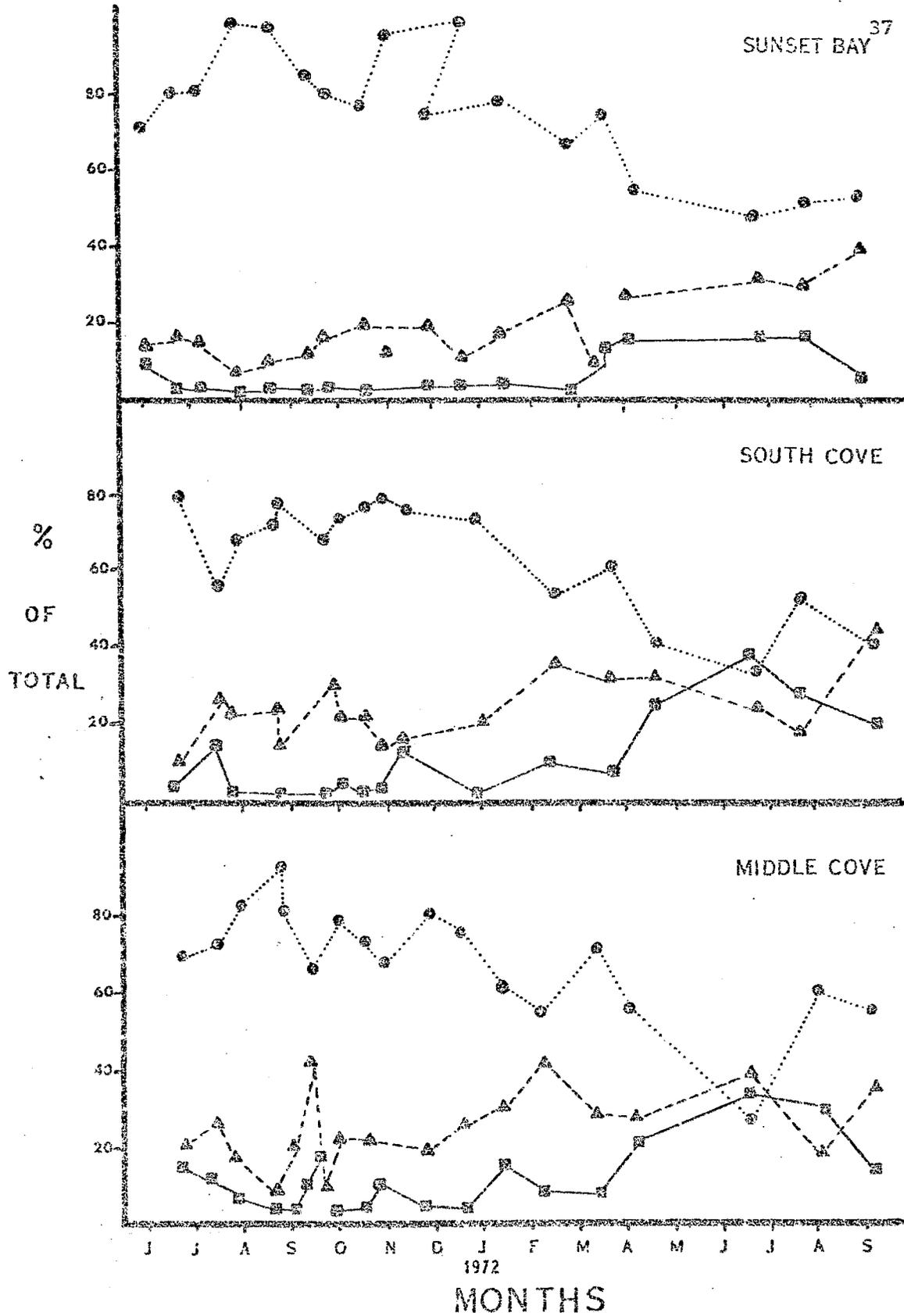
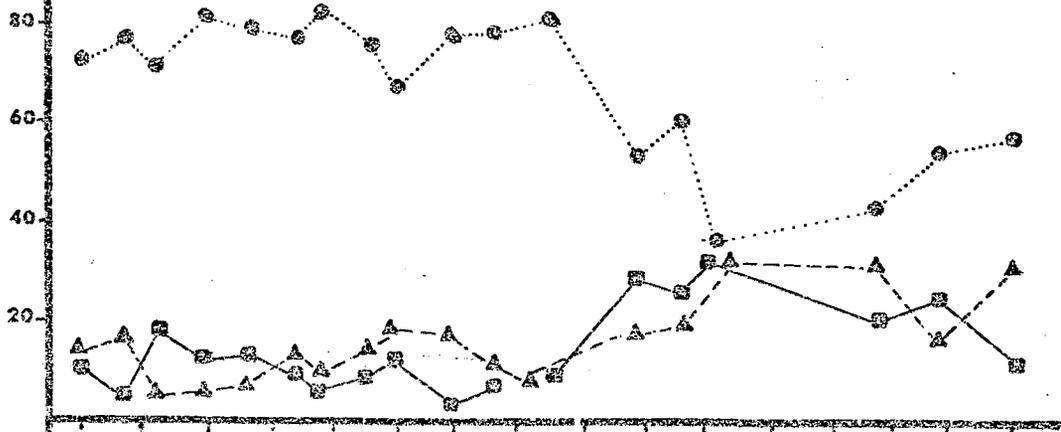
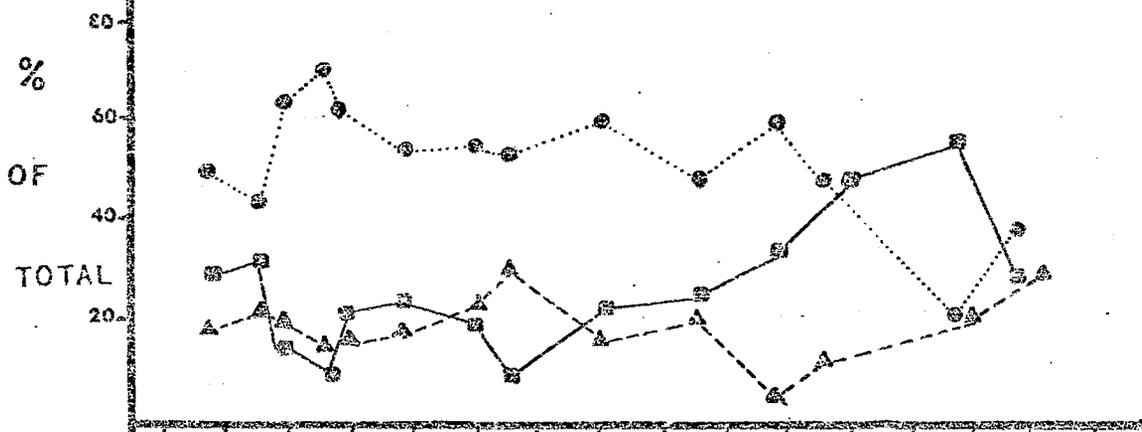


Fig. 7. Percentages of all juvenile Leptasterias observed in the three study populations which were placed in the three morphological categories. First year stars were not included in these estimates. Symbols are the same as those in Fig. 6.

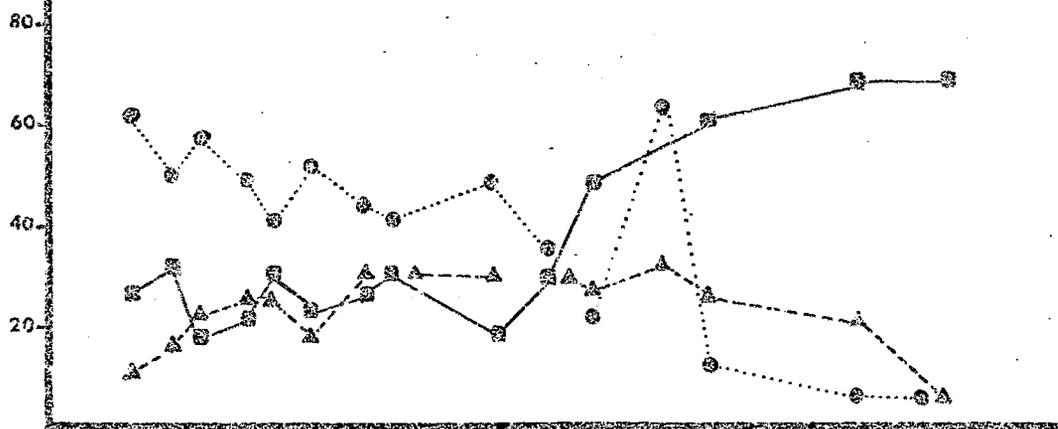
39
SUNSET BAY



SOUTH COVE



MIDDLE COVE



1972
MONTHS

Short term variation in the percentages of sea stars in the three categories were often more extreme than seasonal variation. The reason for this became apparent when individual censuses were made at discrete tidal levels. Sea stars in the high intertidal zone were in much better morphological condition than those in the lower intertidal zone. Therefore the intertidal area searched during a given census influenced the calculated maintenance factor index, and the area searched was ultimately influenced by the level of the low tide on the day of the census.

The maintenance factor values observed for Leptasterias were probably indices of the frequency of autotomy. Leptasterias will readily drop an arm when aggravated or trapped (pers. obs.) and several other stars are reported to autotomize (Swan, 1966). As was pointed out by Ricketts et al. (1968) "autotomy is of great survival value to animals that may be imprisoned by loose rocks overturned by wave action."

The suggested influence of the physical environment on Leptasterias as observed in the maintenance values does not rule out influence by biotic factors. The pattern of increased morphological damage in the lower intertidal zone could be the result of predation by an animal which is primarily subtidal in distribution. This possibility will be considered below when Leptasterias' mortality is reviewed.

Distribution and Density

In the Cape Arago-Sunset Bay areas investigated the horizontal distribution of Leptasterias was confined primarily to the mixed cobble

and boulder areas. When the adjacent areas consisted of sand and/or naked bedrock, no Leptasterias were found, and when the adjacent area contained very large boulders and upraised bedrock, few Leptasterias were encountered.

Other populations observed along the Oregon coast had somewhat different horizontal distributions. At Seal Rock very few Leptasterias were found in the cobble area where large numbers of small Pisaster occurred. The majority of this population of small Leptasterias was found in an undercut portion of Seal Rock adjacent to the cobble area, where they were wedged into small round depressions in the roof and side of the undercut.

Two other populations were observed at the Oregon coastal headlands, Cape Blanco and Yaquina Head. Unlike the friable sandstone found at Cape Arago, the underlying bedrock and cobble was made up of coarse basaltic agglomerates at Yaquina Head and tuffaceous indurated sandstone at Cape Blanco (Baldwin, 1964). In addition the intertidal zone topography was different. Instead of an even surf-cut bench, long narrow surge channels were cut perpendicular to the shoreline. In these channels local concentrations of cobble and flat pieces of loose bedrock occurred, and the majority of Leptasterias were found within these areas. Several other areas with very similar topography were thoroughly searched and no Leptasterias were found. These areas included Cape Perpetua, Strawberry Hill, and Boiler Bay.

Paine (pers. comm.) found many small Leptasterias in mussel beds on the Washington open coast, and I have encountered small Leptasterias

beneath the mussels in Middle Cove. These sea stars were 20-30 mm in diameter, and their sexual maturity was not determined. The mussel beds could possibly serve as nursery areas in the lower intertidal zone. The stars would be protected from desiccation and most predators would still have prey available to them. These stars were not studied further because to do so would require destruction of the mussel bed.

Chia (1966a) and Menge (1970) reported the vertical distribution for Leptasterias in the San Juan Islands. They found that Leptasterias occurred from a height of +2m to the lowest intertidal zone, and moved into the lower intertidal zone during the winter months to form mating aggregations. Mauzey (1966) reported a similar downward movement in winter for Pisaster.

On the open coast Feder (1970) reported that Pisaster did not demonstrate such a winter migration, and I have observed none for Leptasterias in the areas studied. The sea stars remained at approximately the same intertidal levels year round but did become more aggregated during the winter. However, this was probably a passive result of the winter storm conditions rather than an actual mating aggregation as proposed by Chia (1966a).

As was mentioned above, exposure to wave action is thought to be the chief cause of morphological damage and mortality. During the winter the sea stars move away from the smaller cobbles and under larger boulders and into crevices to escape from storms. These movements may have a vertical component, but the overall resultant movement is lateral. Moving down in the intertidal would only expose the stars to

more violent wave conditions. Because the larger boulders are limited in number a large aggregation of sea stars, both mature and immature, will accumulate beneath these boulders and remain there through the winter.

This clumping behavior is encountered throughout the year, not just in winter. In the calmer summer and fall months Leptasterias actively forage over the cobbles and boulders during high tides, but return to the undersurface of rocks during low tide exposure. Because this species is very susceptible to desiccation (Menge, 1970) it seeks out shaded areas that will remain moist. Such areas are limited in the intertidal zone, and the density data obtained during the summer months (Table 2), indicate a clumped distribution for all three study populations at the 0.5m^2 (0.7 by 0.7m) quadrat level.

The short term investigation of Leptasterias movement in the intertidal indicated this species ventures only short distances while foraging. A sample of 100 Leptasterias were dyed red and released along a band of cobbles and boulders 2m wide and 20m long in the middle South Cove intertidal zone. In a careful search of the same area one month later 19 dyed animals were found within or very close to the marked band of release, and no dyed animals were found in the adjoining areas. These recaptured sea stars appeared in good condition and several were actively feeding when found. During the next 4 months dyed individuals were encountered in haphazard feeding observations and had moved only a few meters from the original release area.

It is possible that the dyed sea stars may have moved great

TABLE 2. Information summary of density estimates for Sunset Bay, South Cove, and Middle Cove. The Index of Dispersion (variance to mean ratio) was calculated according to Sokal & Rohlf (1969). First year sea stars were not included in density estimates.

Population	Number Leptasterias Observed	Number of Quadrats	Intertidal Zones Densities/m ²				Index of Dispersion ¹
			Upper	Middle	Lower	Average	
Sunset Bay	294	29	11.7	29.6	23.6	20.3	8.16**
South Cove	83	42	3.6	5.5	2.3	3.9	2.53**
Middle Cove	70	70	2.6	2.5	1.0	2.0	1.42*

* indicates level of significance; ** = .01, * = .05.

¹The index of dispersion indicates a random distribution when it has a value of 1, and clumping when it exceeds 1.

distances laterally within the marked area, or that they moved away and returned to it. The small number of sea stars recaptured may indicate that the majority of dyed sea stars died or emigrated from the area entirely instead of being well concealed within it. This experiment should have been repeated at several tidal areas and followed more closely, but the time was not available.

However after observing Leptasterias in these three areas for 2½ years, their distribution became quite predictable, to the degree that individual sea stars were recognized and repeatedly found at the same location. It is possible that Leptasterias moves only short distances in the intertidal zone and that wave action and desiccation by exposure to air are the chief physical factors influencing these movements and the subsequent intertidal distribution of Leptasterias which will be considered next.

In the Cape Arago-Sunset Bay area Leptasterias occurred from a height of +2.5m down to the lowest intertidal. When the subtidal below the three study areas was searched no Leptasterias were found at South Cove or Middle Cove. At these two areas the surf bench gradually sloped into a series of sandstone reefs covered with short dense algae. The subtidal area was very steep at Sunset Bay dropping off rapidly to 6-8m at the edge of the intertidal. Several Leptasterias were encountered along this drop off, but they were in very low density compared to the intertidal zone directly above.

A summary of the intertidal zone density estimates made in the summers of 1970 at Middle Cove, and 1971 at South Cove and Sunset Bay,

is included in Table 2. In the South and Middle Cove study populations the lowest density of Leptasterias occurred in the lower intertidal zone. In Sunset Bay and South Cove the maximum density occurred in the mid intertidal zone, and at Middle Cove the upper and mid intertidal zones had approximately equal densities of Leptasterias.

The pattern of distribution of the Sunset Bay population is clearly seen in the results of three intertidal samples taken on 9 and 10 February 1972 (Fig. 8). The mid intertidal zone had the highest density (Table 2), the largest animals and greater numbers of small, first year stars. The upper and lower intertidal zone Leptasterias had approximately the same size distribution, but were very different in maintenance factor and density. The percentage of morphologically undamaged animals increased with height in the intertidal zone.

The pattern of morphological damage was also demonstrated in two samples taken at Middle Cove on 23 August 1972 (Fig. 9). The sea stars from the lower intertidal zone had encountered substantially greater morphological damage (31% Normal cf. to 70% for upper intertidal Leptasterias). Leptasterias from the upper intertidal zone were also larger than those from the lower intertidal zone.

No clear pattern of morphological damage was observed at South Cove. In general the animals in the lower mid-intertidal zone and those on the southern boundary of the study area suffered greatest morphological damage. Similarly these areas contained fewest young Leptasterias. I think this peculiar distribution is caused by the orientation of the South Cove intertidal zone, located on the west side of the cove (Fig. 1).

Fig. 8. Size frequency histograms giving the results of three intertidal zone samples conducted at Sunset Bay on 9 and 10 February 1972. Sea stars are grouped in 2mm size classes; i.e. size class 11 includes animals 11 and 12mm in total diameter. The percentages of adults and juveniles in the normal morphological category are indicated.

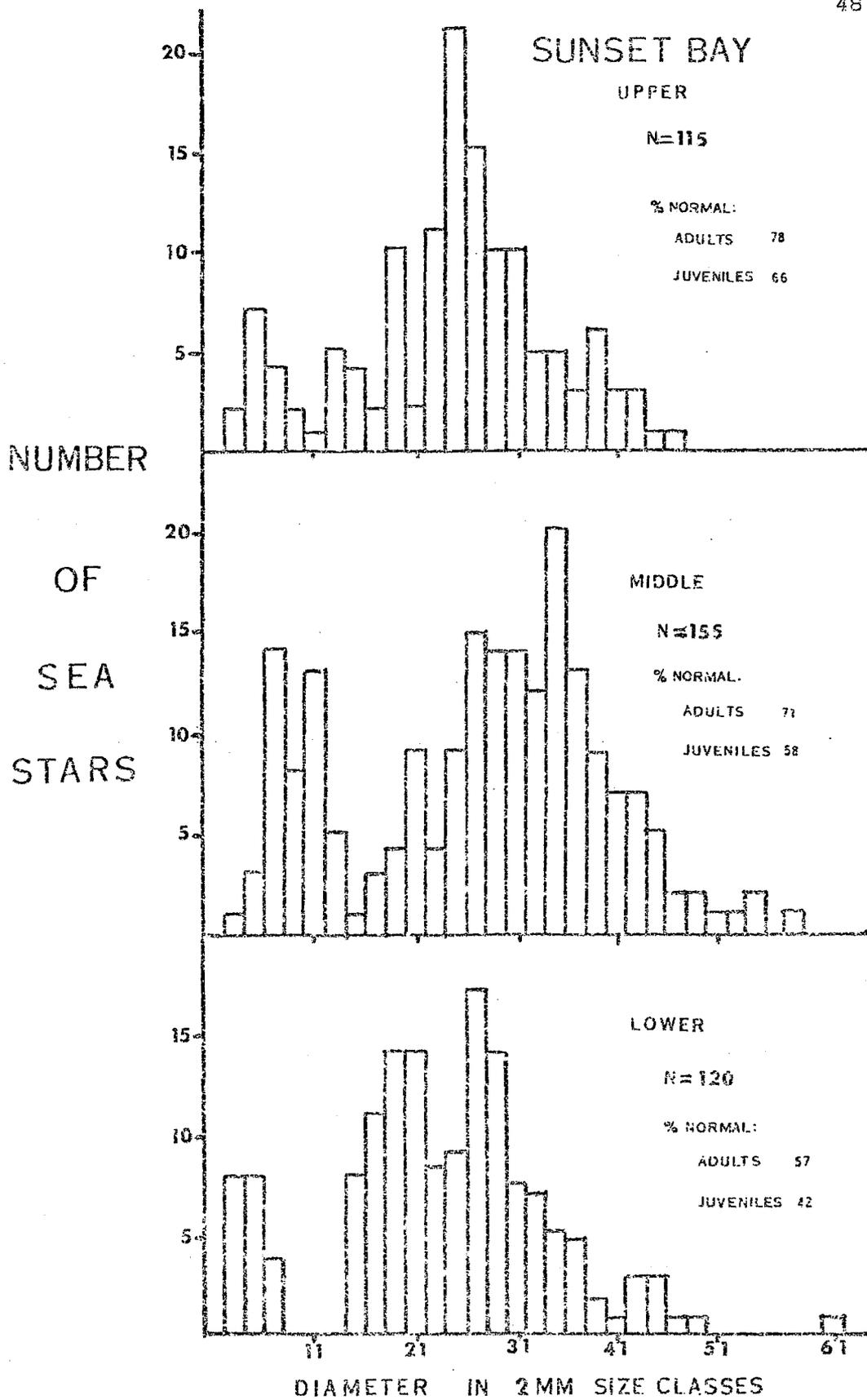
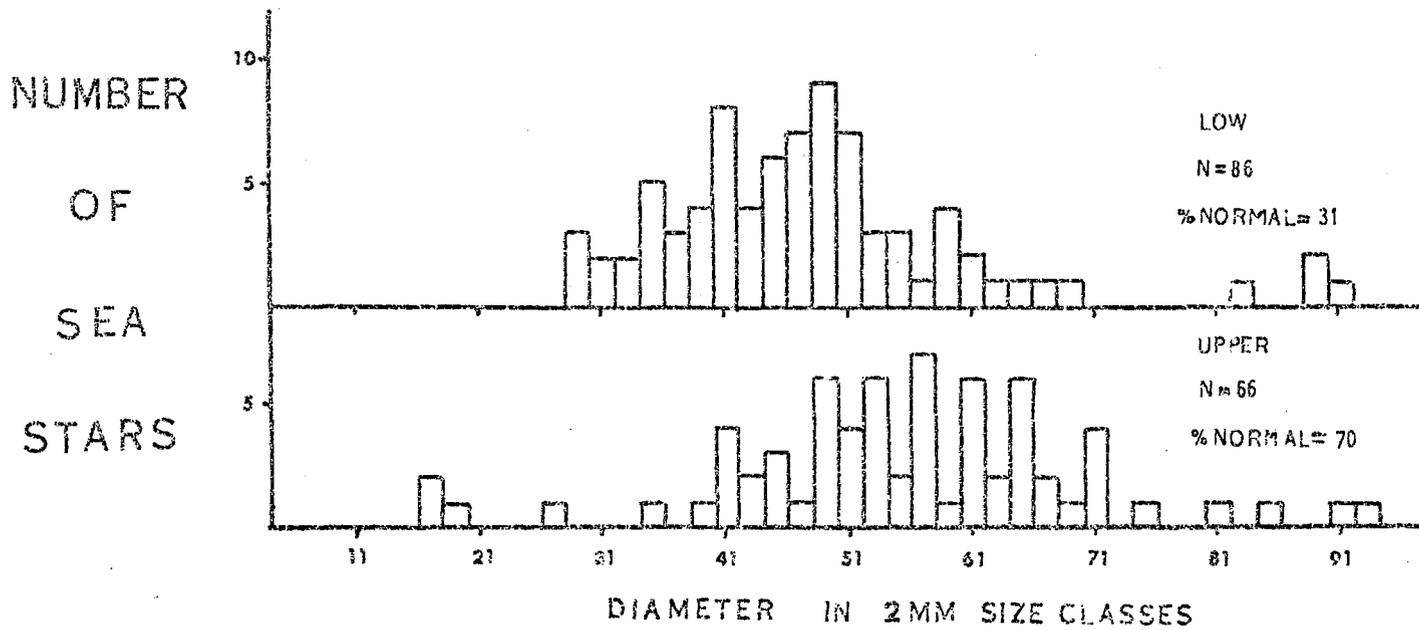


Fig. 9. Size frequency histograms giving the results of two intertidal zone samples conducted at Middle Cove on 23 August 1972. Sea stars are grouped in 2 mm size classes as in Fig. 8. The percentages of sea stars in the normal morphological category are indicated.

MIDDLE COVE 23 AUGUST 1972



At low tide the water line, relative to the rocky intertidal zone, extends north to south. However when the tide is in, the waves enter the intertidal in a south to north direction and are, in effect, crossing this area perpendicular to the low tide shoreline. Therefore the Leptasterias in South Cove are distributed along a desiccation gradient that runs primarily east to west, and a wave exposure gradient that runs primarily south to north.

For Leptasterias it appears that exposure to wave action decreases with increased intertidal height, while the possibility of desiccation increases. The interplay of these two factors is the dominating force accounting for the observed intertidal distribution of Leptasterias on the protected rocky outer coast, just as it is for the majority of intertidal animals found there (Ricketts et al., 1968; Connell, 1972; Dayton, 1971).

Population Structure and Dynamics

The same physical factors which influence Leptasterias' distribution are also thought to cause significant mortality. Wave exposure affects all sizes of Leptasterias but seems to cause more morphological damage to the small sea stars. At low tides during storms I have encountered adult Leptasterias that have been crushed flat by rolling rocks and boulders. Although no evidence exists, it is thought that many small Leptasterias are lost by being washed off rocks and out of the intertidal zone. Menge (1970) demonstrated Leptasterias' susceptibility to desiccation, especially during daylight low tides when the

wind is blowing and the sun is shining. He found that tolerance to desiccation increased with size, and desiccation probably is the cause of mortality of many of the first year stars, especially those released in the upper intertidal zone.

The observed lower limit of Leptasterias' vertical distribution is the lower intertidal zone. In this zone the young sea stars are least abundant and those sea stars that do occur here suffer the greatest morphological damage. The influence of physical environment on these observations has been discussed; however, they are thought to be influenced by a biological component as well.

During this study no common intertidal predators on Leptasterias were found and none have been observed in the field by other investigators (Menge, 1970; Chia, 1964). Leptasterias remains have not been identified in the stomach contents of any of the common intertidal fish investigated (Johnson, 1968, 1970). Predation by crabs and birds may occur. A gull was observed attacking an Evasterias troschelli and another was seen trying to swallow a Pisaster (P. Rudy, pers. comm.). However Leptasterias remains underneath the rocks during low tide and would not be readily accessible to bird predation. No intertidal crabs were observed feeding on Leptasterias and none of which I am aware are reported to do so (Hiatt, 1948; Knudsen, 1960).

Connell (1972) felt that the reason intertidal species live in a physiologically less congenial region at high levels is that they are forced to do so by interactions with competitors and natural enemies. That is, lower vertical limits are due primarily to biological causes.

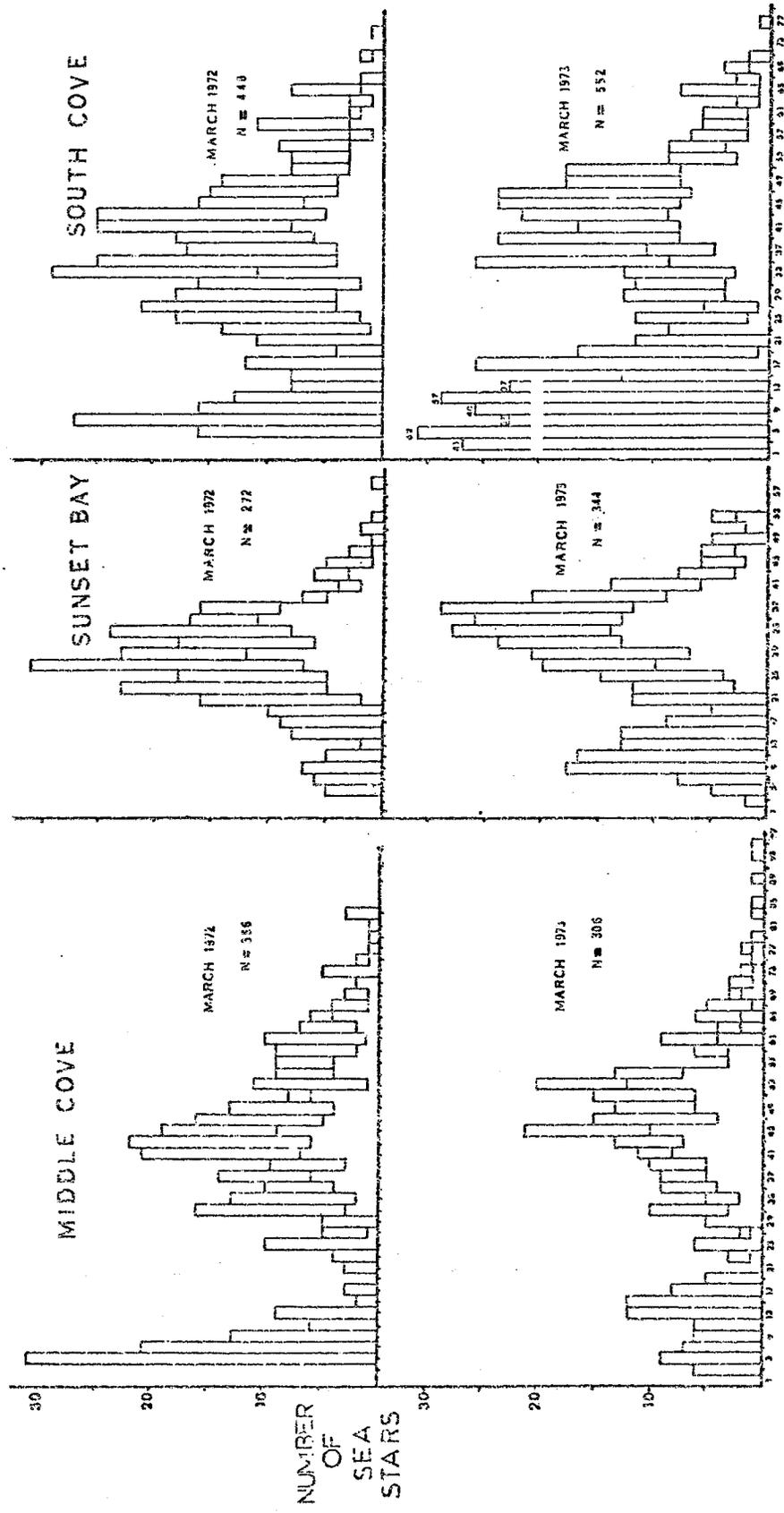
Birkeland (1971) found Leptasterias at 36-40m depths on Cobb Seamount 270 miles offshore of Washington. He felt this indicated the Leptasterias were not restricted to the intertidal zone by the demands of their own physiology and were probably prevented from exploiting the nearshore subtidal habitats by predators, competitors, or other animals.

Chia (1964) observed Leptasterias being fed upon by Solaster sp. Crossaster sp. and Pycnopodia helianthoides in the laboratory and Menge (1970) observed Solaster dawsoni and Dermasterias imbricata feeding on Leptasterias in the field. All of these asteroids have a predominantly subtidal distribution (Mauzey et al., 1968) and are potential predators and/or competitors with Leptasterias. In the Cape Arago-Sunset Bay subtidal I have observed all of these asteroids except Crossaster and their presence may play an important role in maintaining Leptasterias' vertical lower limit. Other primarily subtidal predators such as crabs or fish could also be partially responsible for Leptasterias' reduced success in the lower intertidal zone.

Dynamics

The three study populations varied in density (Table 2) and in size structure (Fig. 10). An attempt was made to monitor population dynamics by conducting seasonal measurement of weight frequency distribution. However these proved unsatisfactory as no clear pattern of population dynamics such as recruitment or growth was readily observable (Appendix 1). The variability encountered is probably due to several causes including the intertidal area searched, the wave conditions on the day

Fig. 10. Size frequency histograms showing the comparative population structure of the three study populations taken in March 1972 and 1973. Brooding females encountered during this period are represented in the clear unlined portion of the histogram.



DIAMETER IN 2MM SIZE CLASSES

before the observation, time of year, and variation in sampling behavior according to weather conditions. What is apparent from these weight distributions is that population structure remained relatively stable and that the size of the sea stars varied inversely with density.

Mortality and recruitment were estimated by combining a variety of data taken for the three populations over the 3 years of the study. Because of time limitations all these data were not taken during the same year.

From data that will be more thoroughly presented below in the chapter on reproductive biology, information on sex ratio, mean size of reproductive animals, and female reproductive effort and brooding success was obtained. The data on growth of the first year stars (Fig. 2) and on density (Table 2) presented earlier in this chapter, were also used. These data were combined with information derived from a comprehensive series of size frequency distributions taken in the field from January through April 1972 and more generalized estimates of size frequency made from May to December 1971. From this combination of data I believe a relatively accurate explanation of populations dynamics can be derived.

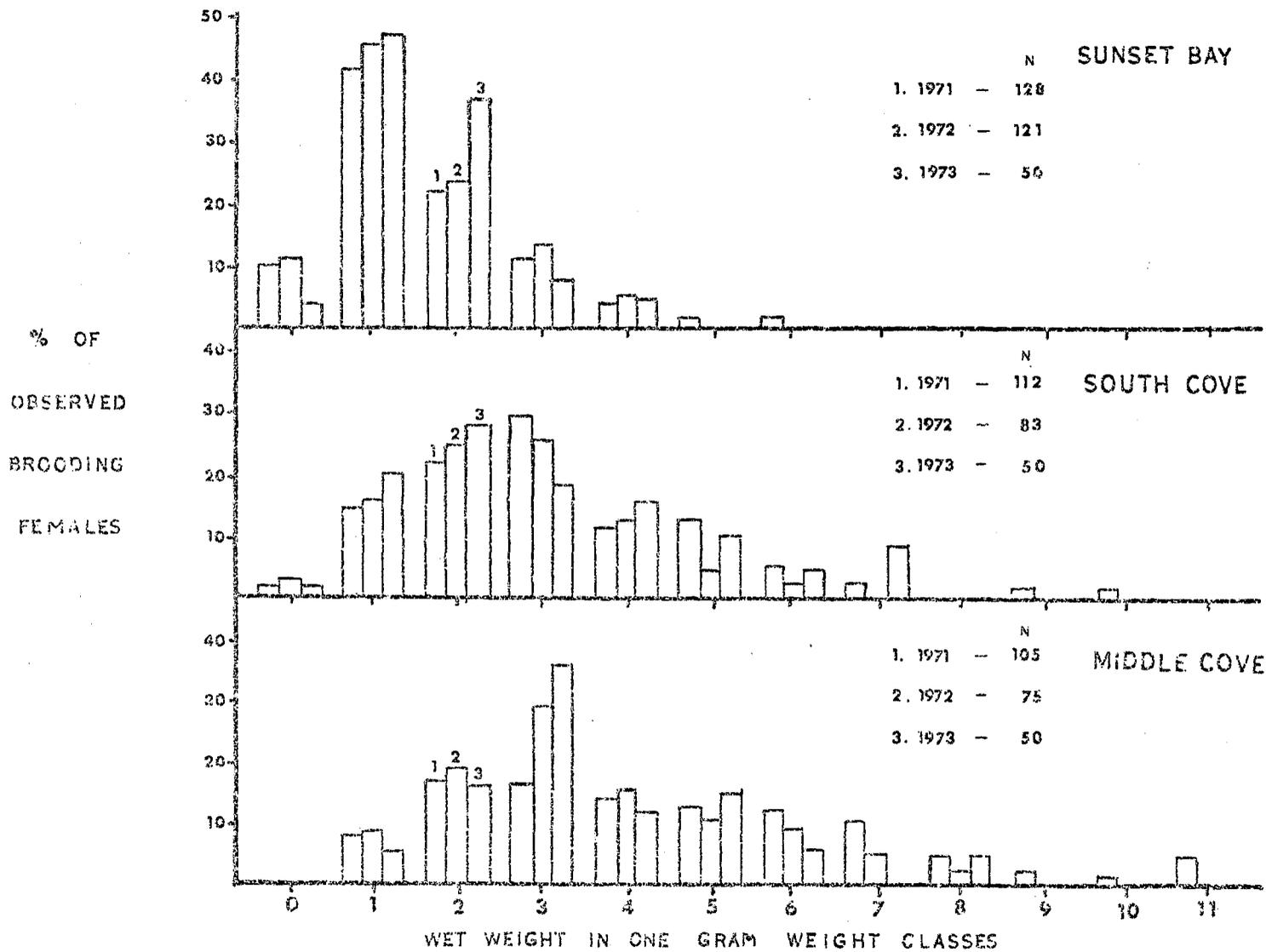
In the process of deriving this explanation several assumptions were made. The first is that female Leptasterias become sexually mature in their third year. Chia (1968a) has shown that the development of an oocyte from an oogonium to a ripe ovum requires about 2 years and that the gonads do not become functional until late in the first year. It was assumed therefore that females found brooding represented animals

that were in at least their third year. Secondly, it was assumed that reproductive effort was similar for a given size of female from a given population over the period of this study. Evidence supporting this assumption and a third that males and females are approximately the same size will be presented in a later chapter.

The final assumption is that the adult population size structure and density remained stable over the time of the investigation. This can be seen by comparing size frequency distributions made in March 1972 and 1973 (Fig. 10). This month is midway in the brooding season and the sizes of the brooding females are indicated. Both the adult size frequency and the distribution of brooding females are very similar for all three populations. When the brooding females observed during the 1971, 1972 and 1973 brooding seasons are compared (Fig. 11) for all three populations their similarity is again apparent. Also seen in this figure is that the Sunset Bay females become reproductively mature at smaller sizes than do the other two populations.

Forearmed with the knowledge of the size reached by first year stars (Fig. 2) and that the size of reproductive females represented at least the third year class (Fig. 10), the size frequency data for individual censuses, taken from January through April 1972, were plotted on probability paper. From these, age-size classes were distinguished using the methods of Harding (1949) and Cassie (1954). Because of their small size the first year class was probably underestimated and the older first year classes were inseparable owing to variable growth rates (Feder, 1970; Ebert, 1962). However the second year class was

Fig. 11. Weight frequency histograms of brooding females from the three study populations for the 1971, 1972, and 1973 brooding seasons. Sea stars are grouped in lg weight classes; "0" weight class includes all females weighing up to .99g, "1" = 1-1.99g, etc.



thought to have been sampled representatively and could be separated from both the first year and older sea stars using the probability paper method (Table 3). This therefore allowed a relatively accurate estimation of mortality up to 2 years, assuming constant annual births.

TABLE 3. Summary of size-age class estimates from the probability paper method of Cassie (1954) for the study populations. The 2+ year class includes all adult stars as no clear year classes could be defined.

Population	Year Class	Mean Size	N	Standard Deviation
Sunset Bay	0	7.5	84	3.52
	1	19.0	108	3.12
	2+	35.0	283	4.48
South Cove	0	8.0	92	2.90
	1	24.7	113	4.10
	2+	41.5	242	4.57
Middle Cove	0	8.5	12	3.09
	1	25.5	32	3.08
	2+	42.0	68	4.58

The size (diameter) estimates of age were then used to interpret the density data, for which the size of each star encountered had been recorded. Because the density of adult Leptasterias was known and because this was assumed to remain stable, the proportion of the number of adults encountered to the number of second year stars allowed a density value for these juveniles to be determined; i.e. if the adult Leptasterias occur in a density of $3/m^2$ and one juvenile is encountered for every three adults, a density of one juvenile/ m^2 is assumed.

From the data on reproductive biology of Leptasterias the number of young initially produced and later released after 8 weeks of brooding

was estimated by multiplying the average female size encountered in each population by the average number of eggs produced per gram and the average number of metamorphosed stars per gram in the brood pouch just before release. Leptasterias is known to occur in a sex ratio of 1:1, and all adult females produce broods. Therefore half the adults encountered in the density estimates were assumed to be potentially brooding females. Multiplying the number of eggs produced per female by the density of females give a value of the number of eggs produced per square meter, and a similar calculation will give the number of young released per square meter. These values can then be compared to the density estimates for second year juveniles and estimates of mortality obtained (Table 4).

Mortality encountered during brooding in 1971 ranged from 19-37% of the eggs produced. Of the young stars released at the end of brooding less than one-half of one per cent survived until they were 2 years old, regardless of the study area in which they occurred. Scanty data available from Middle Cove from fall 1970 indicates that 99.1% of the young stars did not survive the summer of 1970 and of those remaining 33% survived through the second year.

Owing to the nature of these data, the resulting estimates are to some degree suspect. Reproduction in 1970 could have been very low, although substantial numbers of brooding females were found in March 1970 at Middle Cove. The high mortality could be the result of an unduly severe winter in 1971-1972 as was reflected in the maintenance factor data (Figs. 6 & 7). However my estimates of second year

TABLE 4. Mortality estimates for newly metamorphosed and 2 year old Leptasterias from the three study populations. For explanation see the text.

Population	Mean ♀ Weight (g)	Mean Number Eggs Per ♀	Mean Number New Stars Released Per ♀	Brooding Mortality	Number New Stars Released/m ²	2nd Year Stars/m ²	2nd Year Mortality
Sunset Bay	2.2	203	145	28%	1079	4.5-6	99.6%
South Cove	3.8	337	274	19%	403	1-1.4	99.75%
Middle Cove	4.05	371	231	37%	204	.63-.8	99.7%

mortality agree very well with those of Menge (1970), and the same pattern of recruitment has been observed for several years. Therefore these mortality estimates are at least relatively consistent.

For an asteroid species, female Leptasterias produce a limited number of eggs which experience relatively high survivorship until release. The new young undergo high first year mortality and somewhat less mortality in their second year, so that each year only a few 2 year olds are recruited into the population and become reproductively mature. This continuous low level of recruitment and the consistent adult population structure suggest that Leptasterias is fairly long lived and enjoys a substantially lower mortality than do the young stars.

Discussion

The results of the growth studies correspond well with those of Menge (1970) in the San Juan Islands. He estimated the young stars reached a diameter of 10-14mm in the first year and found tremendous growth potential in Leptasterias with an unlimited supply of food. A major discrepancy in our results is the size at sexual maturity. Menge (1970) felt that Leptasterias became mature at from 2 to 4 years and found that the majority of Leptasterias weighing less than 2g were immature. I estimated that Leptasterias become mature in their third year but found that the Leptasterias become sexually mature at much smaller sizes, especially at Sunset Bay (vlg).

The differences in size of brooding females in the three study

populations is thought to indicate a difference in growth rate caused by local conditions. On the other hand, the relatively greater size reached by female Leptasterias both at Cape Arago and in the San Juan Islands could be due to later sexual maturity. However the former explanation is considered the most reasonable because of the demonstrated variable growth potential with food and the previously cited work on oocyte maturation (Chia, 1968a). Therefore it is thought that Leptasterias females become mature at the same age (probably in their third year) regardless of their size, and that growth rate is strongly influenced by local conditions.

In his recent paper on the rocky intertidal community Connell (1972) discussed the factors influencing vertical distribution. He argued that upper limits were most often determined by increased mortality from direct effects of extremes in the physical environment, general agreement is found by other workers (Dayton, 1971; Glynn et al., 1964).

Dayton (1971) considers the majority of reproducing populations in the intertidal zone to be most critically influenced by interactions among the component intertidal species, whereas Connell (1972) thinks biological interactions become limiting only where physical conditions are less harsh. Connell (1972) reported that populations exhibit variation in their age structures with changes in severity of physical factors. Populations which experience harsh physical conditions and those which live in more benign areas but are subjected to intense predation on the young are often composed of a single dominant class.

These are made up of animals that have experienced higher survivorship during a favorable year, in which physical conditions were more clement or predation was reduced. In the intermediate situation, where conditions are slightly less harsh or more predictable and predators are absent naturally, some young may survive every year and produce a population with a mixed age distribution.

The patterns of size (age) distribution observed in my studies of Leptasterias populations could all be intermediate cases as defined by Connell (1972) in which a few young are recruited yearly and adult mortality determines the subsequent mixed age population structure. However, differential success of year classes could also provide an explanation for the observed population age structures, which may be in flux rather than being stationary.

My observations could reflect only a short-term phenomenon which is a small part of the population dynamics of this species. I believe the brooding type of reproduction does allow a substantial number of young of the year to enter an area every year, and, although recruitment is low, new adults enter the population consistently on a yearly basis. Mortality is primarily due to physical causes, and in areas of low wave action adult mortality is low. The subsequent limits to individual growth are biological. In more exposed conditions mortality is greater, but the lower density releases the individual star to exploit the available resources more thoroughly and thus reach a larger size.

FEEDING BIOLOGY

Asteroid Feeding Biology

The majority of sea stars are carnivores that only occasionally act as scavengers (Feder & Christensen, 1966). Some species are known to exploit particulate food gathered with the aid of mucous sheets and flagellar currents, and others are suspected of at least supplementing their diet in this way (Anderson, 1966). Carey (1972) found changes in feeding type with increasing depth. The deep-sea asteroids feed on whatever is available and obtain food from the sediments as well as prey or animal remains; in the food-rich shallow waters of the inner continental shelf the asteroid fauna generally consists of specialized carnivores.

In the typical macrophagous sea star food is digested as it lies within, or enfolded by, the cardiac stomach. The folds of the stomach are closely applied to the food, and digestive enzymes are released only where there is direct contact between the stomach wall and the digestible tissue of the prey (Feder & Christensen, 1966). The digestive enzymes are produced only in the sac-like glandular pouches of the pyloric caecae and are carried to the cardiac stomach in the fluid of the perivisceral coelom (Anderson, 1966).

In addition to producing digestive enzymes the pyloric caecae also

serve as the chief organs of absorption and storage (Anderson, 1966; Nimitz, 1971). Nutrients are mobilized and transported to distant sites of utilization at all times, but especially in preparation for the breeding season as the gonads are built up at the expense of the reserve of the pyloric caecae. Ferguson (1968) has demonstrated the fluid of the perivisceral coelom as the likely vehicle for nutrient transport, as it bathes almost all the tissues except those of the outer surface. The manner in which epidermal cells of the sea stars receive nourishment is still not clearly determined. Some of the available data indicate that asteroids obtain a significant fraction of nourishment of at least their superficial cell layers by absorption of such things as sugars and amino acids from extremely dilute solutions in the sea (Anderson, 1966; Ferguson, 1963, 1969, and 1970).

Feeding Studies

The ecologically oriented field and laboratory studies of asteroid feeding were reviewed by Hyman (1955) and more recently by Feder and Christensen (1966). Since this last review a number of studies of asteroid feeding have appeared. Among these are the studies of coral-eating asteroid Acanthaster planci and its effect on the coral reef community (Chesher, 1969; Branham, et al., 1971; Porter, 1972; Goreau et al., 1972), and the laboratory and field feeding of Pisaster ochraceus (Mauzey, 1966; Paine, 1966, 1969; Landenberger, 1968; Feder, 1970) and P. giganteus (Rosenthal, 1971; Rosenthal and Chess, 1972).

Of the recent studies of asteroid feeding several exhibit an

ecologically more sophisticated approach to data interpretation and general application to current ecological theory. Christensen (1970) in his study of the sea star, Astropecten irregularis said "it is obvious that a proper interpretation of data obtained by stomach analysis cannot be given without a thorough background knowledge of the biology of the sea star as well as the organisms on which it subsists." He feels that gut contents per se were not a reliable "measure" of the quantitative composition of prey actually digested per time unit (A. M. Christensen, pers. comm.). The study of Mauzey, Birkeland, and Dayton (1968) which compared laboratory preference studies with field observations of ten Puget Sound asteroids, revealed that a wide variety of prey can occasionally be eaten, the diet may vary locally, and laboratory preference experiments must be checked with field data to discover which are the most important natural prey. They concluded that, in order to define the diet of any sea star, laboratory observations can neither be omitted nor relied upon exclusively, and that many observations from a number of locations throughout a year are necessary.

Careful studies by Paine (1969, 1971) have shown that a single asteroid predator can be very significant in determining the composition of an intertidal community. Paine (1969) points out that on the Pacific west coast Pisaster ochraceus and its main prey show considerable zoogeographic homogeneity (Ricketts et al., 1968) characteristic of the entire assemblage. Many species that characterize the association throughout its entire range can be shown to be affected either directly or indirectly by Pisaster (Feder, 1970; Paine, 1969).

Menge (1970, 1972a & b) has studied such an association between Pisaster and Leptasterias hexactis in the rocky intertidal region of the San Juan Archipelago. Menge (1970) feels that this area represents a suboptimal Pisaster habitat primarily because of the lower abundance of Pisaster's preferred prey, Mytilus californianus. Conversely he thinks that it is the "best" habitat for Leptasterias, since this sea star is abundant in the Archipelago but relatively rare on the open coast. In areas where Leptasterias and Pisaster co-occur Pisaster is dominant in that it somehow inhibits the food gathering of Leptasterias, thereby hindering growth (Menge, 1972b). Menge (1972b) argues that the specialization permitting coexistence in this case is apparently based on consumption of different sized prey.

Menge's work with the Leptasterias-Pisaster interaction is more thorough and the arguments more intricate than I have presented above. Similarly his work with Leptasterias' feeding is more detailed and derived than what I shall present here. I do not presume to suggest my study fulfills all the obviously necessary criteria suggested by Christensen (1970) and Mauzey et al. (1968); this was not my objective.

However comparisons are possible between my data and those of the studies mentioned. I feel they contribute to the overall understanding of the complex and variable interactions that allow species to exist over a range of habitats.

Methods

Feeding observations were made for the three main Leptasterias

populations on an approximately bi-weekly basis for a period of 20 months. The populations were sampled at lower low water and infrequently at higher low water on the same day. The sea stars generally do not forage when not under water but are known to continue feeding on prey captured during the previous high tide (Feder, 1970; Menge, 1970).

Each sea star was removed from the substratum and turned over; if the cardiac stomach was everted the sea star was counted as feeding. The prey found within the folds of the everted stomach or attached to the substrate directly beneath the sea star was recorded. Each prey species was identified at least to genus and, for some species, the size was also recorded. Each sea star observed was classified according to size (age) and morphological condition using the categories mentioned in the first chapter.

During the summer of 1972 each main Leptasterias population was sampled during the early morning spring low tides. Approximately 100 observations were made of Leptasterias feeding on its primary prey species the barnacle, Balanus glandula. Similar to other sea stars in the Family Asteridae (Feder & Christensen, 1966) Leptasterias uses force to remove this prey from the substratum, so all the barnacles were found within Leptasterias everted stomachs. The sea star's morphological condition and total diameter (2R) in millimeters were recorded, and the basal diameter of each prey barnacle was measured to the nearest half millimeter.

The barnacles' basal diameters were used to convert to dry weight values, using the regression equation calculated by Connell (1970) for

B. glandula. The total dry weight of all barnacles encountered in each feeding observation was calculated for comparison of the total dry weight of prey consumed per size class of Leptasterias in each population.

In order to determine the approximate contribution of each prey species to Leptasterias' total caloric diet Menge's (1970) regressions of prey size (diameter) on dry weight and the conversion factor of dry weight to kilocalories were used.

Estimates of the mean prey size and number were obtained for the main prey species, B. glandula by calculating the mean basal diameter and mean number of barnacles encountered per feeding observation for each population in the 1972 summer feeding study. Of the less frequently eaten prey only half were measured. The average prey size used to calculate caloric value was based on these measurements.

Throughout the study all species of sea stars encountered in the cobble areas common to Leptasterias were censused for feeding. Three species were observed, Pisaster ochraceus, Evasterias troschelli, and Henricia sp. but only P. ochraceus was abundant. The data obtained for P. ochraceus in the area of spatial overlap with Leptasterias will be presented and compared with those of Menge (1972b).

Results

The feeding data are in three parts. The first part will compare annual feeding cycles and prey selection among the three main study populations, as well as the diet of juveniles with that of the adults.

The second portion will present the results of the summer 1972 study in which the three populations are compared for feeding success as a function of sea star size. The final selection will compare my data from the open coast with those of Menge (1970, 1972a & b) for Leptasterias from the San Juan Archipelago.

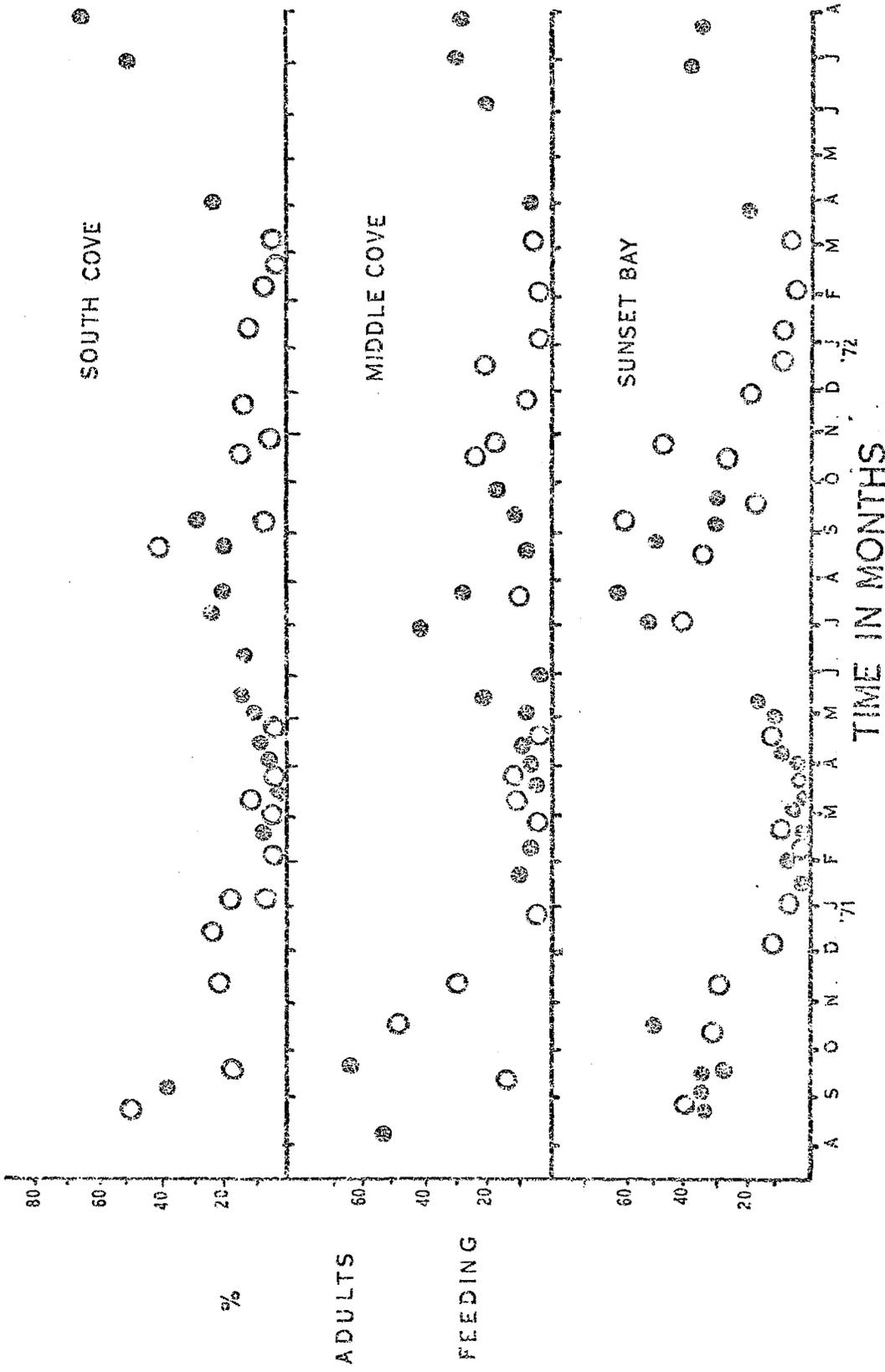
Annual Feeding Cycle

The adult feeding observations are summarized in Fig. 12, which shows the percentage of adults feeding on all prey over the study period. The graphical representation gives a fairly clear idea of the feeding pattern of adult Leptasterias on the open coast.

The graph shows that peak feeding activity occurs during the midsummer and continues until the onset of winter. Feeding during the winter months is reduced. It does not increase until late spring and then gradually increases to peak again in midsummer. This feeding pattern in adults complements the reproductive biology of Leptasterias (Chia, 1964), in that the adults store energy reserves in the pyloric caecae until midsummer when gametogenesis begins and the gonads increase in size until the winter reproductive period.

During the reproductive period the females brood the young for at least 8 weeks and do not feed. The males also become inactive and feed at a reduced rate. The graph (Fig. 12) is somewhat misleading in that the brooding females are included in the calculation of the percentage, and the actual values for males feeding during this period could be as great as twice the value given. However, these values would still fall

Fig. 12. Percentages of total adult Leptasterias observed that were feeding during feeding censuses at the three study areas. The open circles represent afternoon low tides, the solid dots represent morning low tides.



well below the maximum feeding rates seen during the summer.

When the artificially lowered winter feeding rate is kept in mind, comparison of the adult feeding pattern (Fig. 12) with that of the juveniles (Fig. 13) shows that both size (age) classes have a similar annual feeding schedule. The juveniles continue to feed through winter at a rate higher than that of adult males, but still below their peak feeding, which also occurs in midsummer.

Prey Selection

The feeding pattern of the adults and juveniles can be further compared by looking at the diet. Table 5 gives a summary of the relative numbers of prey species eaten by both adult and juvenile Leptasterias. In all three populations the adults included a greater number of prey species in their diets than did the juveniles. A much greater percentage of the juveniles rely on the barnacle, Balanus glandula, for their prey. For the three populations this percentage ranged from 84 to 91% of all juvenile sea stars observed feeding. When prey selection diversity indices are calculated (Table 6) this pattern is again demonstrated: in all populations the adults have higher indices than the juveniles. The lowest adult value, from the Sunset Bay population, is still greater than the highest juvenile value, from the South Cove population.

In all three populations there were greater percentages of juveniles feeding than of adults. This is chiefly due to the observed higher feeding rates in the winter months. The juvenile diet is

Fig. 13. Percentages of the total juvenile Leptasterias observed that were feeding during the feeding censuses at the three study areas. Symbols are the same as in Fig. 12.

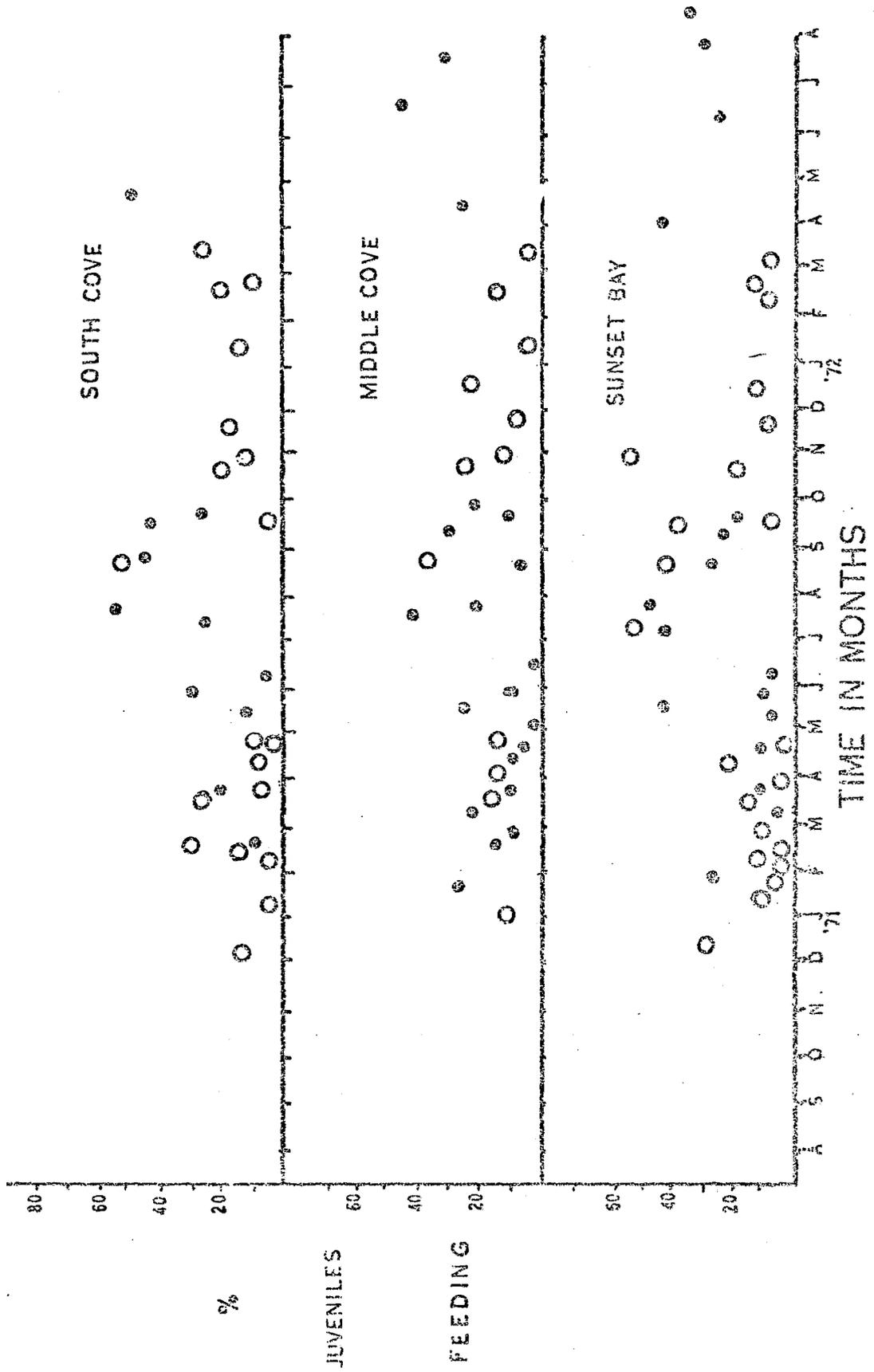


TABLE 5. Summary of the diet of Leptasterias as observed during feeding censuses by number and percentage.

- a. Sunset Bay
- b. Middle Cove, Cape Arago
- c. South Cove, Cape Arago

TABLE 5a. Prey Summary for Sunset Bay Leptasterias.

Species of Prey	Type of Predator			
	Adults		Juveniles	
	Number of Feeding Observations	%	Number of Feeding Observations	%
<u>Balanus glandula</u>	454	84.0	608	91.0
<u>B. cariosus</u>	6	1.0	2	0.3
<u>Hemigrapsus nudus</u>	2	0.3	1	0.1
<u>Petrolisthes cinctipes</u>	4	0.7	0	0
<u>Cirolana</u> sp.	0	0	2	0.3
<u>Idothea</u> sp.	3	0.6	0	0
<u>Pagurus</u> sp.	1	0.2	0	0
<u>Littorina scutulata</u>	33	6.0	20	3.0
<u>Tegula funebris</u>	0	0	0	0
<u>Acmaea scutum</u>	0	0	0	0
<u>A. digitalis</u>	5	0.9	1	0.1
<u>A. pelta</u>	5	0.9	0	0
<u>A.</u> sp.	3	0.6	5	0.7
<u>Calliostoma</u> sp.	0	0	1	0.1
<u>Thais emarginata</u>	3	0.6	0	0
<u>Mytilus</u> spp.	3	0.6	1	0.1
<u>Modiolus</u> sp.	4	0.7	0	0
<u>Tonicella lineata</u>	1	0.1	2	0.3
<u>Mopalia</u> spp.	0	0	0	0
<u>Spirorbis</u> sp.	16	3.0	28	4.0

TABLE 5b. Prey summary for Middle Cove Leptasterias.

Species of Prey	Type of Predator			
	Adults		Juveniles	
	Number of Feeding Observations	%	Number of Feeding Observations	%
<u>Balanus glandula</u>	183	69	129	90
<u>B. cariosus</u>	1	0.3	0	0
<u>Hemigrapsus nudus</u>	1	0.3	0	0
<u>Petrolisthes cinctipes</u>	4	1.4	0	0
<u>Cirolana</u> spp.	0	0	0	0
<u>Idothea</u> sp.	0	0	0	0
<u>Pagurus</u> sp.	0	0	0	0
<u>Littorina scutulata</u>	31	12	3	2
<u>Tegula funebra</u>	10	4	0	0
<u>Acmaea scutum</u>	4	1.4	0	0
<u>A. digitalis</u>	2	0.7	0	0
<u>A. pelta</u>	5	2	0	0
<u>A. sp.</u>	3	1	1	0.7
<u>Calliostoma</u> sp.	1	0.3	0	0
<u>Thais emarginata</u>	0	0	0	0
<u>Mytilus</u> spp.	0	0	0	0
<u>Modiolus</u> sp.	2	0.7	0	0
<u>Tonicella lineata</u>	2	0.7	0	0
<u>Mopalia</u> sp.	4	1.4	0	0
<u>Spirobis</u> sp.	12	4	10	6.6

TABLE 5c. Prey Summary for South Cove Leptasterias.

Species of Prey	Type of Predator			
	Adults		Juveniles	
	Number of Feeding Observations	%	Number of Feeding Observations	%
<u>Balanus glandula</u>	235	74	140	84
<u>B. cariosus</u>	1	3	0	0
<u>Hemigrapsus nudus</u>	4	1	0	0
<u>Petrolisthes cinctipes</u>	11	3	1	0.6
<u>Cirolana</u> sp.	0	0	0	0
<u>Idothea</u> sp.	0	0	0	0
<u>Pagurus</u> sp.	1	0.3	1	0.6
<u>Littorina scutulata</u>	27	9	10	6
<u>Tegula funebris</u>	8	2.5	0	0
<u>Acmaea scutum</u>	2	0.6	0	0
<u>A. digitalis</u>	1	0.3	1	0.6
<u>A. pelta</u>	6	2	1	0.6
<u>A.</u> sp.	0	0	0	0
<u>Calliostoma</u> sp.	1	0.3	0	0
<u>Thais emarginata</u>	2	0.6	0	0
<u>Mytilus</u> spp.	1	0.3	0	0
<u>Modiolus</u> sp.	0	0	0	0
<u>Tonicella lineata</u>	8	2.5	0	0
<u>Mopalia</u> spp.	4	1	2	1
<u>Spirorbis</u> sp.	17	5	7	4

TABLE 6. Prey species diversity indices calculated from the feeding data for the Sunset Bay, Middle Cove, and South Cove Leptasterias populations. Each observation of feeding was scored as a single event regardless of number of prey. For explanation of indices see Horn (1966) and Hurlbert (1971). Calculations use logarithms to the base e.

Population	Number of Observations	Number of Prey Species	H	H'	Hurlbert's V:H	Hurlbert's V':H
Sunset Bay						
Adults	545	14	0.76	0.80	0.31	0.26
Juveniles	671	11	0.43	0.45	0.18	0.15
South Cove						
Adults	328	14	1.12	1.18	0.44	0.39
Juveniles	166	10	0.64	0.71	0.30	0.20
Middle Cove						
Adults	266	14	1.16	1.24	0.46	0.40
Juveniles	143	4	0.36	0.39	0.29	0.22

characterized to a greater degree by small and/or non motile prey, and this will be considered below.

The diets of the juveniles and adults overlap markedly, particularly in the Sunset Bay population where sea star density is greatest ($20/m^2$) and the mean size is smallest. This great overlap in diet between size (age) classes can influence the intraspecific interactions in a given area. Members of the smallest size class, the young of the year, are also potential competitors for available food. Because of their small size no quantitative study of their feeding was made; however I do wish to present some pertinent field observations.

Chia (1966a) showed that the brooding female Leptasterias preferentially seeks the underside of a dark rough-surfaced rock on which to brood her young. In the three study areas 70% of the females observed with advanced broods were under rocks or boulders which had a large percentage of the surface covered with tube-secreting serpulid polychaete Spirorbis sp. The newly metamorphosed stars were released amongst the worm tubes and were observed to feed on the newly settled spirorbids almost exclusively until they reached a diameter of 8-10mm, which corresponds to approximately an age of 8 months (Fig. 2). As the young of the year grew larger their main prey shifted from spirorbids to recently settled barnacle spat and finally to small B. glandula (<1mm).

When the juvenile diets of the three populations are compared, the sea stars from Sunset Bay have the greatest number of prey species in their diet (11), but the South Cove animals have a higher prey diversity index ($H = 0.64$ cf. Sunset Bay $H = 0.43$). Middle Cove juveniles had the

lowest diversity index ($H = 0.36$) and the fewest prey species in the diet (4).

The greatest number of prey species observed for Sunset Bay juveniles is easily explained by the much greater number of observations ($N = 671$) that were made for this population. As mentioned earlier there is a much higher density at Sunset Bay, so many more sea stars were encountered during a low tide feeding census. Therefore, while the juveniles in this population showed the greatest dependency on B. glandula (91%), a greater number of rare species were encountered because of the large number of sea stars observed. A similar explanation can be made for the Middle Cove juvenile feeding data. The juvenile density was lowest at Middle Cove and therefore fewer juveniles were encountered during a low tide period. It is possible because of this lower number of feeding observations fewer rare species were encountered.

Adult Feeding

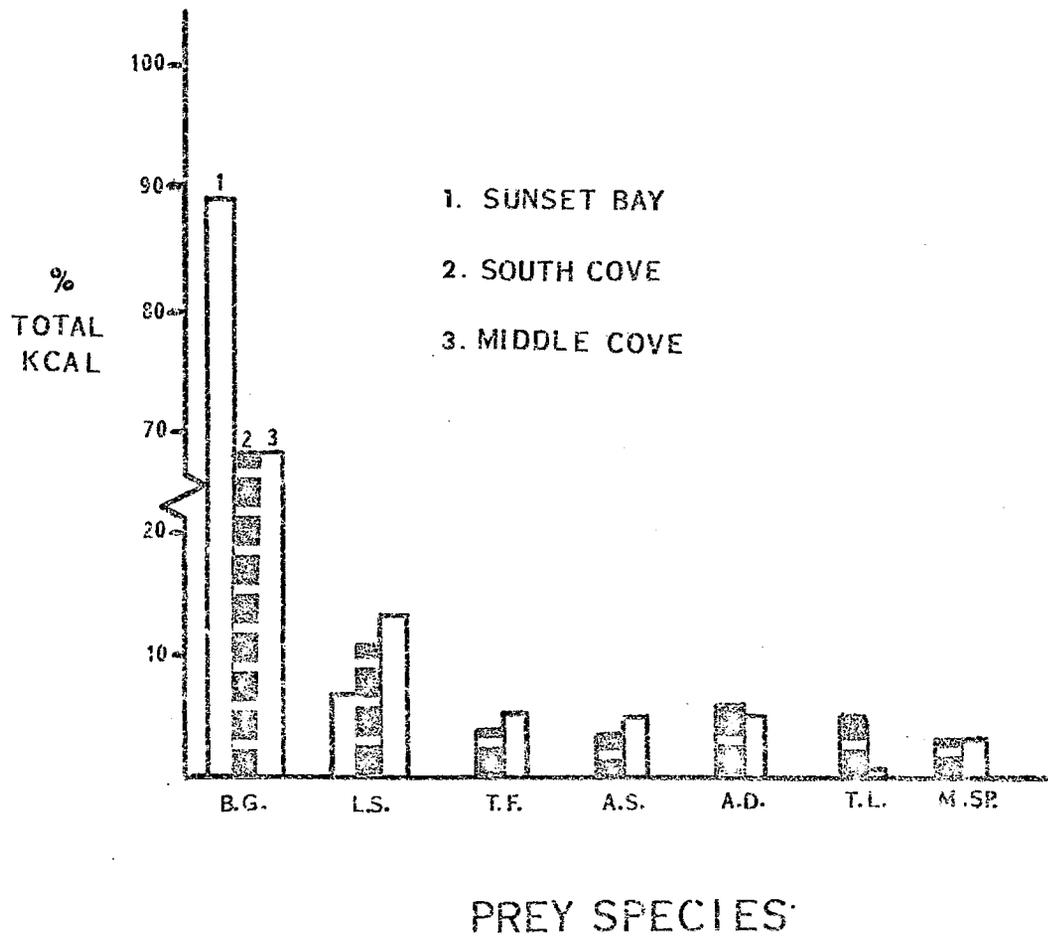
In the previous chapter a consistent order was pointed out among the three Leptasterias populations. The Middle Cove population had the largest mean size, greatest population maintenance cost and lowest density. The Sunset Bay population had the smallest mean size, lowest maintenance cost, and the highest density. The South Cove population was intermediate for all these values. The adult feeding data (Tables 6 & 7) follow this pattern: Sunset Bay sea stars had the lowest prey diversity and highest percentage of animals feeding; the Middle Cove population had the highest diversity of prey species and the lowest

percentage of sea stars feeding. The South Cove population was again intermediate for both values.

The low prey species diversity index obtained at Sunset Bay was due to the high percentage of adult animals which fed on B. glandula (84%) compared to South Cove (74%) and Middle Cove (69%). The relative importance of a prey species can further be assessed by its contribution to the caloric intake of a population (Fig. 14). B. glandula contributes 89% of the total caloric intake to the Sunset Bay population and 68% to both Middle Cove and South Cove populations. The second most important prey both calorically and numerically in all populations is Littorina scutulata. The remainder of prey species represented in Fig. 14 play significant roles (>1%) only in the Middle Cove and South Cove populations. All are mollusks and will be considered below. One common prey species not represented in Fig. 14 is the polychaete, Spirorbis sp., because I was not able to estimate its caloric content.

The prey selection data suggest that populations containing larger animals from less densely populated areas were able to secure a greater variety of prey. The sea stars from a crowded population of small sized individuals were feeding at a greater rate and on less diverse prey. Menge (1972b) suggested from his data that larger individual Leptasterias eat larger prey and that a larger sized predator added new species to its diet. Feder and Christensen (1966) felt certain that sea stars follow the general physiological rule that the rate of feeding, expressed as a percentage of their own body weight, declines as the sea star grows.

Fig. 14. Percentage of the total kilocalories contributed by principal prey species to the Sunset Bay, Middle Cove, and South Cove Leptasterias populations. The determination of kilocalories was made using Menge's (1970) conversion regressions of size to dry weight and dry weight to caloric content. (Code: B.g. - Balanus glandula; L.s. - Littorina scutulata; T.f. - Tegula funebris; A.s. - Acmaea scutum; A.p. - A. pelta; T.l. - Tonicella lineata; M. spp. - Mytilus species.)



Summer 1972 Feeding Study

In order to determine more clearly the differences in feeding among the three populations I designed a simple experiment that was completed during the summer of 1972. Three questions were asked: (1) what is the relationship between Leptasterias size and feeding success; (2) does this relationship vary between populations; and (3) are animals with morphological damage less successful feeders than intact animals of the same size? Each population was sampled during morning low tides until the first 100 sea stars, regardless of size, feeding on B. glandula were found. The animals and their prey were treated using the methods stated above.

Regressions of sea star size (diameter in millimeters) on total prey dry weight were calculated for the three populations. The correlation coefficients (r) were all significant ($P < .05$) and had positive slope. This suggests that a larger sea star does obtain larger prey, and is not surprising. The regressions were compared by analysis of covariance (Sokal & Rohlf, 1969) and no significant difference was found between them (Table 7).

The data indicate that the large sea stars enjoy superiority over the small in food capture abilities. To understand what effect this relationship has on overall population feeding success, an estimate for the mean caloric intake per Leptasterias feeding event can be calculated using the population feeding summaries (Table 8), by dividing the total kilocalories consumed by the number of feeding observations. When this is done, the Middle Cove value (9.0 calories/feeding observation) is

TABLE 7. Analysis of feeding study data (Fig. 15) gathered from Sunset Bay, South Cove, and Middle Cove. Comparison by regression and analysis of covariance (Sokal & Rohlf, 1969).

Number of Animals Examined			Significance of Difference	Regression Equation
Sunset Bay	Middle Cove	South Cove	among areas	
103	100	90	$F_{2,289} = 1.12, p > 0.3$	$y = .0991x - 1.75^a$

^ax = sea star total diameter (mm), y = dry weight of prey

almost twice that of Sunset Bay (4.6 calories) and South Cove is again intermediate (7.5 calories).

This difference can be decreased to some extent if we consider that the Sunset Bay population feeds at a greater rate than Middle Cove (23% cf. 16%). When the mean value for percentage of population feeding is multiplied by the mean calories consumed per Leptasterias feeding event a comparable ingestion rate is obtained (Table 3). From this comparison, although animals from the Middle Cove population spend the least amount of time feeding, they still obtain 45% more calories than members of the Sunset Bay population. Another interesting comparison is that the Middle Cove and South Cove sea stars have nearly identical ingestion rates. The degree of abstraction involved in these calculations makes them only rough estimates at best. However I believe they do describe the relative disparity in diets.

To answer the third question posed in this study, the data for the Middle Cove and South Cove populations, which were similar in size

TABLE 8. Percentage of adult and juvenile Leptasterias feeding from the three study populations and calculation of mean caloric intake per feeding event. Ingestion rate is the mean percentage feeding times the mean caloric intake.

Population	<u>Number Feeding</u> <u>Number Observed</u>	Mean % Feeding	Combined Mean %	<u>Total Kcal</u> <u>Ingested</u> <u>Total Number</u> <u>Observations</u>	Mean Caloric Intake	Population Ingestion Rate
Sunset Bay			22.7	6.1/1316	4.64	1.05
Adults	591/2979	21				
Juveniles	725/3095	24				
South Cove			19.0	3.8/502	7.5	1.43
Adults	329/1847	18				
Juveniles	173/878	21				
Middle Cove			16.5	3.9/433	8.95	1.47
Adults	281/2118	14				
Juveniles	152/857	21				

distribution, were combined and reseggregated according to the three morphological classes mentioned above (i.e. normal, incomplete, and regenerating). Regressions of sea star size on dry weight of prey (B. glandula) were calculated for each class (Fig. 15). All correlation coefficients were significant and the regressions were compared as before (Table 9).

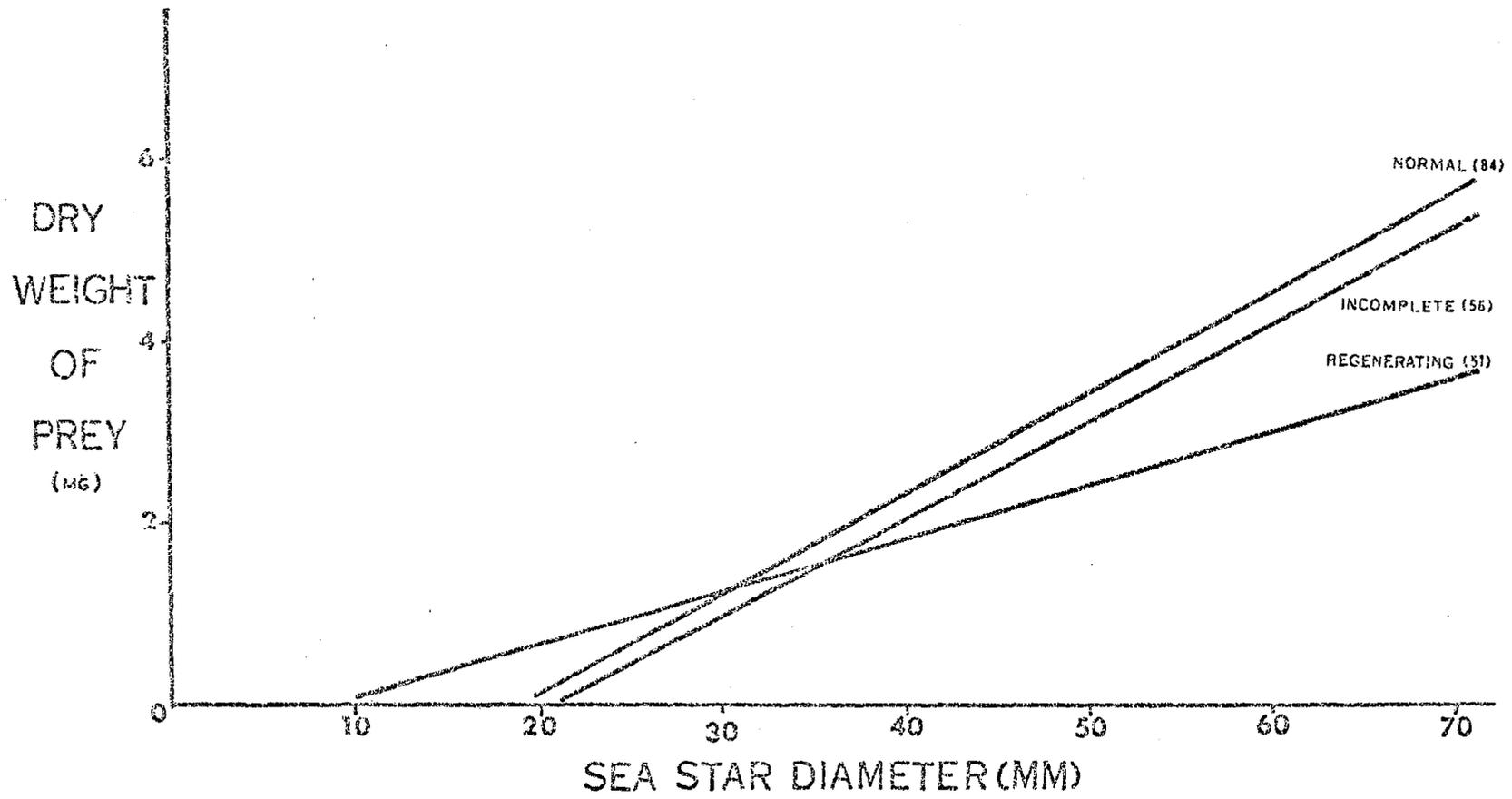
Although no significant differences were found among the morphological classes I believe a lowered potential for feeding success is suggested for sea stars that have lost one or more arms. The loss of an arm would obviously be a hindrance to a sea star especially since the main prey species is an attached sessile form which is generally pried off the substrate by use of the tube feet (Feder & Christensen, 1966).

TABLE 9. Analysis of feeding data from animals in three morphological classes: normal, incomplete, and regenerating. Animals were examined at Middle Cove and South Cove. Comparison by regression and analysis of covariance (Sokal & Rohlf, 1969).

Number of Animals Examined			Significance of Difference	Regression Equation
Normal	In- complete	Regener- ating	among classes	
85	55	51	$F_{2,184} = 1.45, p > 0.2$	$y = .1084x - 1.83^a$

^ax = sea star total diameter, y = total dry weight of prey

Fig. 15. Regression lines of total dry weight of prey on sea star size (diameter in millimeters). Each line represents a morphological category from the combined Middle Cove and South Cove data. Number of sea stars in each category is indicated.



Prey Species Characteristics

The main prey species, Balanus glandula, ranges from the Aleutian Islands to below Ensenada, Lower California, and is one of the most abundant animals on the Pacific coast (Ricketts et al., 1968). The biology of this species has been studied by Barnes and Barnes (1956) and more recently by Glynn (1965) and Connell (1970).

Connell (1970) found newly settled B. glandula at all shore levels on both sides of San Juan Island from June to early September. Settlement began in March and extended through October at Pacific Grove, California (Glynn, 1965). Observations from the Coos Bay area indicate settlement begins in late March and is heaviest from May through August with some settlement through October.

Few B. glandula settle below the intertidal level, probably because the cyprid larvae swim to the surface when they are ready to settle. Within the intertidal zone the barnacles settle and survive best at middle levels, although the breeding population is restricted to above the mean high low tide mark (Connell, 1970).

This stable breeding population reproduces in the summer and autumn, and because of this longer season of reproduction it is less vulnerable to chance weather catastrophes. As a result settlement is quite regular. The breeding population produces enough offspring to maintain itself and regularly colonize the lower intertidal zone. Because of its regular settlement throughout the intertidal zone B. glandula provides an extremely dependable food supply to several predators (Connell, 1970).

On San Juan Island Connell (1970) found that Thais spp. restricts B. glandula to the upper intertidal zone. No adults were found in the lower intertidal where Thais was able to eat them. In areas where no Thais were found adult B. glandula were abundant.

A similar situation was observed on the Oregon open coast. Inside Sunset Bay there are sections of sandstone reef completely surrounded by sand and heavily covered by large adult B. glandula. The sand restricts the access of B. glandula's main predators, Thais spp. and Leptasterias both of which have non pelagic larvae and cross the sand with difficulty. However in the cobble areas with Leptasterias large B. glandula are found only on the tops of large boulders where neither predator regularly forages.

During its first year B. glandula grows at a similar rate on both the open coast (Glynn, 1965) and in protected areas (Connell, 1970), reaching a basal diameter of 7mm. In the 300 observations of predation on B. glandula, in which the individual barnacles were measured, only 4 of 1055 specimens had a basal diameter 7mm or greater. Therefore, because L. hexactis can successfully feed on barnacles larger than 7mm (Menge, 1970; pers. obser.) and because the only readily accessible barnacles were smaller than this, it can be inferred that the majority of B. glandula in the cobble area are eaten before they reach sexual maturity at the age of 1 year and that Leptasterias contributes significantly to this predation.

A second balanoid barnacle, Balanus cariosus, was also eaten by Leptasterias but at a much lower rate. This species is not as common

as B. glandula in the Cape Arago area. It is reported to "assiduously avoid oceanic conditions, occurring only in deep crevices and under overhanging ledges in the low intertidal zone" (Ricketts et al., 1968). Menge (1970) reported Leptasterias had greater difficulty in removing B. cariosus than B. glandula. Connell (1970) found the settlement of B. cariosus on San Juan Island to be much more irregular than that of B. glandula.

The second most commonly observed prey in this study was the periwinkle, Littorina scutulata. This species, which is found all along the U.S. Pacific coast, inhabits the upper intertidal zone; its upper boundary is rarely more than a half meter above the height reached by the high tide (Ricketts et al., 1968). L. scutulata's lower boundary overlaps with the upper foraging range of Leptasterias, where my field notes indicate that L. scutulata is preyed upon more commonly than B. glandula. During storms many L. scutulata are washed into the middle lower intertidal (John Cubit, pers. comm.) and subsequently eaten by Leptasterias. L. scutulata is reported to exhibit an escape response to Leptasterias (Bullock, 1953), but Menge (1970) found this to be very weak and observed that the littorine was easily captured.

Like B. glandula, L. scutulata provides a regular, predictable source of food to Leptasterias. The upper portion of the population is relatively free from predation and provides a breeding population. The breeding population is able to maintain itself and provide a food source by regular seasonal spawning and subsequent settlement of pelagic larvae (Behrens, 1972; pers. comm.).

The small serpulid polychaetes, Spirorbis spp., are the main prey of the newly metamorphosed Leptasterias and are eaten at a lower rate by both juvenile and adult stars. Species of this genus are common to the entire Pacific coast and are typically found on small round boulders that are continually immersed in pools (Ricketts et al., 1968). These animals brood their young and are reported to release their larvae in February (Ricketts et al., 1968) although some species have a longer reproductive season (Peter Rothlisberg, Oregon State University, pers. comm.). The newly settled polychaetes are typically available to the newly metamorphosed sea stars which are released in April through early May.

The remaining prey species were preyed upon less frequently and will be considered in less detail. Several characteristics are common to some or all of these species. Almost all are common to the upper or middle intertidal and are distributed along the Pacific coast from Alaska to Baja California (Ricketts et al., 1968). Escape responses to Leptasterias have been demonstrated by many of the gastropods, including Tegula funebris, Acmaea scutum, A. pelta, and Calliostoma sp. (Pullock, 1953; Feder & Christensen, 1966). The porcelain crab, Petrolisthes cinctipes, is quick to autotomize walking legs or claws. Sea stars observed feeding on this species had only a leg or two in their grasp, never the whole crab. This observation is also true, to a lesser extent, for Hemigrapsus nudus which does not autotomize appendages as readily and was sometimes trapped by Leptasterias.

Some prey species find refuge in space, in that their intertidal

distribution is partially above or below that of Leptasterias. An upper refuge has already been mentioned for B. glandula and L. scutulata and is also found for Acmaea digitalis and Thais emarginata, two gastropod species which lack escape response to Leptasterias (Feder & Christensen, 1966). The chitons Tonicella lineata and Mopalia spp. have their lower distribution in the subtidal where Leptasterias is much less abundant (Menge, 1970).

Many of Leptasterias' prey species find a refuge in size. This generally small sea star is unable to attack successfully and feed on the larger individuals of many intertidal invertebrate species with which it normally comes in contact. Species which appear to have a refuge in size include Tegula funebris, Acmaea scutum, A. palta, Tonicella lineata, Mopalia spp. and Mytilus spp.

The effectiveness of this size refuge may be seen by referring back to the prey data summary (Table 5). This explains why the juvenile sea stars in all populations have low prey species diversity indices and fewer prey species in their diet. Animals from the Sunset Bay adult population, which is made up of small Leptasterias, were unable to capture any of the two largest gastropods, T. funebris or A. scutum; the other A. spp. captured by this population were generally quite small. The South Cove and especially the Middle Cove population with larger sea stars had greater success in capturing these species which were, on the average, much larger than those taken by Sunset Bay Leptasterias. The effect that a few of these large prey species (Table 5) can have on overall caloric intake can be seen in Fig. 14.

To complete this section on Leptasterias' prey species several of Menge's (1970, 1972a & b) observations are pertinent. In laboratory studies he found that Leptasterias selectively chose Littorina spp. over all other prey, and that B. glandula ranked very low in preference. Menge calculated the caloric yield of prey species consumed per gram of Leptasterias dry weight per hour spent feeding for the major prey species. In this series B. glandula had the lowest of measured values and Acmaea scutum was the highest in caloric yield. From his field studies, which were conducted during the day and night for both high and low tides, he found the percentage Leptasterias feeding at low tide was generally much lower than the percentage feeding at high tide. B. glandula were eaten less during day low tides than night low tides, and larger Leptasterias captured larger prey.

Based on Menge's observations, my feeding percentages are probably consistently low because they are all based on low tide observations; moreover the percentage of sea stars that were feeding on B. glandula may be higher than that observed.

Other general observations from my study of Leptasterias' feeding are: (1) the majority of prey eaten are non motile (sessile) and/or very small and are very predictable food sources; (2) all age classes of sea stars feed to some extent on B. glandula; this species, when eaten, is seldom more than 1 year of age; (3) the high density Sunset Bay population subsists almost exclusively on B. glandula and, although sea stars get fewer calories per feeding event than at either South Cove or Middle Cove, much greater stress on the prey population results; (4)

larger sea stars capture larger prey which are calorically more significant.

Comparison of Leptasterias Feeding Biology from San Juan Island
(Menge, 1970, 1972a & b) and Oregon's Protected Outer Coast

Any comparison made between the data from these studies must be prefaced with the fact that my sampling schedule was less comprehensive than Menge's.

Leptasterias followed the same annual feeding cycle on San Juan Island and the Oregon coast. All populations observed by Menge (1970) and myself had a similar peak in feeding during mid-summer and a decline during the winter reproductive period.

Menge (1970) sampled during both day and night low and high tides and was able to show distinct differences in diet between tides and between day and night feeding. He also observed changes in diet with season. Because my observations were made only during daylight low tides I did not observe any tidal differences, nor did I distinguish any differences in feeding between morning and afternoon low tides. However I did observe that consistently fewer Leptasterias were found feeding during storms, and that on equally calm days more sea stars would be feeding when it was damp and/or overcast rather than dry or sunny. Because of the relatively limited prey selection, no seasonal change in diet was observed. When a greater percentage of sea stars were found feeding, more species were included as prey.

The barnacle, B. glandula, was the numerically dominant prey species (35% of the number of prey eaten) eaten by the San Juan Leptasterias, yet it varied from 3 to 55% of the total diet between populations. In addition it ranked twelfth in overall caloric contribution to Leptasterias' diet. In the Oregon populations B. glandula contributed from 69 to 90% (Table 5) of the total diet and ranked first in caloric contribution in all three populations (Fig. 14).

Other prey species eaten by the two Leptasterias groups were generally the same but in obviously different proportions. The San Juan Leptasterias diet did not include Petrolisthes cinctipes, Hemigrapsus nudus or Mopalia spp. which co-occur with Leptasterias there, nor Tegula funebris, which does not. Littorina sitkana, Lacuna spp., Cyanoplax dentiens, and Thais canaliculata all were eaten by the San Juan Leptasterias but were relatively rare in the Cape Arago region. One chiton species, Katherina tunicata, which occurs in both areas was eaten only by the San Juan Leptasterias. However this species is distributed more widely in the San Juan intertidal (pers. obs.), than in my study area.

The diets of Menge's San Juan populations varied considerably from one another as well as from the Oregon populations. Menge (1972a) observed that the number of species in the diet was a function of the number of species available in an area and that available prey, in the broad sense, probably accounted for most of the differences between diets in different areas.

The San Juan Leptasterias populations had much greater variations

in size distributions, than those observed for Oregon. Menge (1972a) explained how these size differences could change the observed Leptasterias diet in that a larger size "would increase the number of prey species susceptible to successful attack which broadens the diet and changes the relative proportions of prey consumed."

Prey availability obviously influences size of individuals in a population. Menge (1972a) reasoned that the population at Lonesome Cove on San Juan Island had less food available in general, and most of it was small and energy poor, and thus the sea stars were small. One reason less food was available was because Pisaster ochraceus was present and competed with Leptasterias for food. Menge (1972a) felt that the "major environmental factor preventing increase in size in San Juan was apparently competition for food with Pisaster."

Menge (1972b) pointed out that these two sea stars overlap broadly with respect to food, space and time and compete for a limited food supply in the San Juan Islands. In a controlled experiment Menge (1970) removed all the Pisaster from one small island reef and placed them on a second; he left a third untouched as a control. The Leptasterias on the first reef, without the Pisaster, showed a significant increase in weight while the Leptasterias on the second reef, where the number of Pisaster was increased showed a significant decrease in weight. There was no significant change in weight on the third reef.

Sea star biomass densities (wet weight/m²) of Leptasterias and Pisaster were inversely correlated (Menge, 1972b). Menge felt that the sea stars compete for food and exist in competitive equilibrium throughout the San Juan Archipelago. He demonstrated this competitive inter-

action at Lonesome Cove where Leptasterias and Pisaster had an overlap of 71% in terms of numbers of prey in their diets. In order to determine the importance of the Leptasterias-Pisaster interaction for the observed Oregon populations I made a similar comparison.

I used the same index of overlap that Menge applied (Morisita, 1959, Horn, 1966). I compared the diet of all Leptasterias to that of all Pisaster observed for Sunset Bay, Middle Cove, and South Cove (Table 10). Because of the discrepancies in numbers of observations (2,000 vs. 84) I calculated the overlap using both raw numbers and percentages. I also compared the data given by Menge (1972b) for Lonesome Cove to my data for Sunset Bay (Table 5), as the two populations were very similar in size characteristics (pers. obs.).

The results show that Pisaster and Leptasterias overlap only 8% in terms of number of prey in their diets compared to 71% for Lonesome Cove. However, the Sunset Bay and Lonesome Cove Leptasterias populations show a 90% overlap in diet (Table 11). This indicates that similar sized Leptasterias select similar prey, and that small individual size of sea stars in a population can have more than one cause.

Menge (1972b) explained the coexistence of the two predators by "specialization" on different sized prey. The smaller Leptasterias are unable to capture large prey, whereas the larger Pisaster can. As mentioned earlier Menge felt that the San Juan Islands were a suboptimal environment for Pisaster, as its preferred prey species is not abundant there. My own observations indicate that Pisaster is much smaller on San Juan than those co-occurring with Leptasterias on the Oregon coast.

TABLE 10. Overlap of Leptasterias' and Pisaster's diets in the Cape Arago-Sunset Bay intertidal. The numbers of each prey eaten by all sea stars from Sunset Bay, Middle Cove, and South Cove are compared.

Prey Species	Pisaster		Leptasterias	
	Numbers	% of Total	Numbers	% of Total
<u>Tegula funebris</u>	62	74	18	9
<u>Balanus glandula</u>	4	5	1749	83
<u>B. cariosus</u>	4	5	12	0.57
<u>Mopalia spp.</u>	9	11	10	0.47
<u>Mytilus sp.</u>	2	2	5	0.24
<u>Modiolus sp.</u>	2	2	6	0.28
<u>Thais emarginata</u>	1	1	4	0.19
<u>Hemigrapsus nudus</u>	0	0	8	0.38
<u>Petrolisthes sp.</u>	0	0	20	0.95
<u>Pagurus spp.</u>	0	0	3	0.14
<u>Idothea sp.</u>	0	0	3	0.14
<u>Cirolana sp.</u>	0	0	2	0.09
<u>Littornia scutulata</u>	0	0	124	6.0
<u>Acmaea scutum</u>	0	0	11	0.5
<u>A. pelta</u>	0	0	17	0.8
<u>Calliostoma sp.</u>	0	0	3	0.14
<u>Tonicella lineata</u>	0	0	14	0.67
<u>Spirorbis sp.</u>	0	0	90	4.2

Using the overlap statistic of Morisita (1959):

$$C_{\lambda} = \frac{2\sum x_i y_i}{(\lambda_x + \lambda_y)XY} \quad \text{where } \lambda_x = \frac{\sum x_i (x_i - 1)}{x(x - 1)}$$

x_i = number of i th prey species eaten by predator X.

X = total number of prey eaten by predator X.

Using raw numbers: $C_{\lambda} = 3.7\%$

Using proportions: $C_{\lambda} = 7.8\%$

TABLE 11. Overlap of Leptasterias' diets from Sunset Bay, Oregon and Lonesome Cove, San Juan Island, Washington (Menge, 1972b). Comparison is made using the number of feeding observations (for Sunset Bay), and the number of prey species (in parentheses in the table) for Sunset Bay.

Prey Species	Leptasterias Population			
	Sunset Bay Numbers	% of Total	Lonesome Cove Numbers	% of Total
<u>Balanus glandula</u>	454 (1326)	87 (91)	305	61
<u>B. cariosus</u>	6 (20)	1	50	10
<u>Hemigrapsus nudus</u>	2	<1	-	-
<u>Petrolisthes</u> spp.	4	<1	-	-
<u>Idothea</u> sp.	3	<1	-	-
<u>Pagurus</u> sp.	1	<1	-	-
<u>Littorina</u> spp.	33 (50)	5 (3)	40	8
<u>Acmaea scutum</u>	-	-	30	6
<u>A. digitalis</u>	5	1	-	-
<u>A. paradigitalis</u>	-	-	30	6
<u>A. pelta</u>	5	1	20	4
<u>Thais emarginata</u>	3	<1	-	-
<u>Mytilus</u> sp.	3	<1	20	4
<u>Modiolus</u> sp.	4	<1	-	-
<u>Searlesia dira</u>	-	-	3	<1
<u>Cyanoplax</u> sp.	-	-	3	<1
<u>Cthalamus dalli</u>	-	-	3	<1
<u>Tonicalla lineata</u>	1	<1	3	<1

Using Sunset Bay data as number of feeding observations regardless of number of prey consumed: $C_{\lambda} = 93\%$

Using Sunset Bay data in terms of number of prey consumed: $C_{\lambda} = 90.5\%$

The lack of competition indicated by my data is relatively easy to explain. In the Leptasterias boulder-cobble areas, several species, including Pisaster, large sea anemones, mussels, and sea urchins, which are abundant on immediately adjacent solid substrate, are relatively vulnerable to crushing from the grinding action of the substratum during storms (Paine, 1969; pers. obs.) and avoid this area. Pisaster does frequent this area in the quieter waters of San Juan. This results in the observed competitive interaction (Menge, 1972b). Also the gastropod, Tegula funebris, a prey species regularly consumed by Pisaster (Paine, 1969) in absence of its preferred prey Mytilus (Feder, 1970), is missing (pers. obs.) from the San Juan areas investigated by Menge. This species is abundant in the cobble areas of the Oregon open coast and is often consumed by Pisaster in this region (Table 10).

Competition between Pisaster and Leptasterias on the open coast cannot be dismissed entirely. All investigators of the natural diet of Pisaster (Feder, 1959; Paine, 1966, 1969; Mauzey, 1966; Mauzey et al., 1968) indicate barnacles (5 species) as the numerically dominant prey (250%). Paine (1969) found that the barnacles were not preferred prey and not calorically the most important. Therefore conceivably interspecific competition could occur locally on the open coast where these species' distributions overlap.

Discussion

Many asteroid species seem to feed opportunistically, whereas other species evidently select their food from among a restricted group of

prey organisms (Feder & Christensen, 1966). Luidia sarsi for example shows a distinct preference for certain ophiuroid species, feeding at a very low rate when only "poor" food is available (Fenchell, 1965). There are great differences in food uptake in Astropecten irregularis when fed on different species of bivalves (Christensen, 1970).

The so-called generalists also show some prey preference as was mentioned for Pisaster (Paine, 1966, 1969; Feder, 1970) and Leptasterias (Menge, 1970). Menge (1972a) is probably correct however in saying that, for a given species, variable prey availability accounts for most of the differences between diets at different areas. However as he and Christensen (1970) point out, prey availability is contingent upon a number of biotic and physical factors.

Christensen (1970) found that Astropecten irregularis did not reach the same size in the Øresund as elsewhere because of its peculiar hydrographic conditions which fail to bring in the larvae of the preferred prey species. The competitive interaction between Pisaster and Leptasterias in the San Juan Islands inhibits Leptasterias feeding and growth. The resulting smaller predator size affect the prey available to this species (Menge, 1972b).

Physical environmental factors can have more direct effects on feeding. Populations of Pisaster eat much less in relatively unprotected intertidal areas than in areas better protected from wave action (Feder, 1970). During stormy periods the sea stars attach themselves firmly to the substrate and do not feed. This same response has been observed for Leptasterias and is thought to restrict its foraging ability

and thus the prey available to it.

Sea star size has been indicated as a factor in prey availability in that the larger sea stars are able successfully to attack the larger prey. Paine (1972, seminar at the University of Oregon) showed that, in Pisaster populations on the Washington open coast, mean individual size decreased as the population density increased. He felt that this had to do with the amount of food a Pisaster population is able to extract from an environment. Using this same reasoning one could explain the variation in size distributions seen in Oregon Leptasterias populations.

As was shown in the previous section, mortality in the smaller size classes is quite high and is probably contingent on physical rather than biological causes. Therefore adult animals reach a refuge in size, not unlike that described for Leptasterias prey species. Depending on the degree of post-maturity mortality few to many adults are available to exploit the prey population. Because of the indeterminate growth exhibited by Leptasterias, sea stars in low Leptasterias density populations can successfully feed and increase in size. Increased size allows the introduction of new prey species into the diet. The ultimate size a sea star could reach in a given area is dependent on many factors that are unique for a given population and an "optimal individual size" (Ebert, 1968) is eventually established for a population.

In less exposed areas with reduced physical stress mortality is reduced. The high predator density results in intraspecific competition for prey. The smaller sea stars eat therefore essentially the same prey as the adults. The final result is a population like that at Sunset

Bay.

Paine (1966, 1969) has demonstrated that Pisaster can exert great influence on the structure of the intertidal community. In its absence Leptasterias was also important in a community-shaping role in the San Juan Islands, especially as concerns herbivorous gastropods (Menge, 1972b). Leptasterias on the Oregon coast appears to have little influence on the intertidal community as its two main prey species, B. glandula and Littorina scutulata both have high turnover rates and retain breeding populations in high intertidal refuges.

REPRODUCTIVE BIOLOGY

Life history patterns of different organisms vary widely. Factors such as the time of first reproduction, number of reproductive efforts, type of development of young, clutch size, etc. all determine a pattern for a given species. This pattern is a reproductive strategy, and it is a function of environmental conditions.

In marine benthic invertebrates the chief environmental conditions to contend with are physical properties such as currents, water temperature, and salinity, and biotic properties such as availability of food for larvae and adults, time exposed to predation in the plankton, etc. The broad overlying themes of reproduction in benthic invertebrates have to do with the time spent as larvae and the mode of larval development (Thorson, 1946, 1950).

Thorson (1950) defines four basic types of larval development as: (1) non-pelagic brooded embryos that are nourished by yolk and emerge as juveniles; (2) lecithotrophic planktonic larvae which develop from large, yolky eggs, need no food and are able to spend a long time in the plankton; (3) planktotrophic larvae with a long pelagic life (2-3 months), which make up 70% of all marine invertebrates in recent seas; and (4) planktotrophic larvae with a short pelagic life which undergo little growth and development during the pelagic phase in which the time spent in the plankton varies from a few hours to a few days.

Particular reproductive strategies utilized by marine invertebrates characterize geographical areas. At the poles 95% of all species develop without a pelagic phase, while in the tropics 80-85% of species have long-lived planktotrophic larvae. The intermediate temperate areas have a mixture of types of larval development.

The Genus Leptasterias has a circumpolar distribution, and the majority of species produce non-pelagic brooded embryos and provide some type of parental care (Hyman, 1955). The brooding behavior of Leptasterias hexactis was reviewed in the Introduction. In this chapter the dynamics of Leptasterias' reproductive strategy of brooding will be presented in terms of the individual brooding female and the local population, and its significance will be discussed.

Methods and Materials

Leptasterias' annual reproductive cycle was followed by calculation of monthly storage organ (pyloric caecae) and gonad indices for the three main study populations. The indices consist of the ratio of the organ wet weight to the whole animal wet weight. The monthly sample of 8-12 adults usually consisted of the first adults encountered during the population census in the middle of the month. The animals were taken to the laboratory at Charleston where they were maintained in water tables until the indices were calculated, usually within 24 hours of collection. The sea stars were damp dried with paper towels, weighed and dissected; the gonads and storage organs were removed and weighed. These indices were computed for an 18 month period, September 1970 to

March 1972, and recorded two cycles of rapid gonadal increase and subsequent decrease with spawning.

In January 1971 just before the onset of brooding, samples of 20-30 sea stars were collected from several populations. The females in these samples were used to estimate the number of eggs produced by an individual female. These females were weighed, the ovaries were dissected out, and the number of mature ova found were counted.

During the 1971 brooding season, which lasted from early February through April, a weekly sampling schedule was followed. Each week the three main populations were sampled and the first 10 brooding females encountered were collected along with their broods. On alternate weeks the populations were censused to discover the per cent of adults brooding; this was done by searching the study area until at least 100 adult animals were found and their activity, i.e. brooding, feeding, etc. recorded.

The ten females collected each week from each population were placed in numbered glass containers with a small amount of sea water and transported back to the laboratory at Charleston. Here each female was damp dried and weighed with her brood in place in the brood pouch and then reweighed with the brood removed. In addition to the weight of the female, the diameter of the disc (r) and the radius (R) from the center of the disc to the tip of the arm were measured. From the weekly sample of ten females three or four were subsampled and used to calculate storage organ indices; the remaining females were maintained at Charleston until May 1971 when they were transported to Eugene for

laboratory growth experiments.

After the brood was taken from the female, it was placed in a numbered vial. Each brood was examined microscopically to determine its developmental stage and then preserved in formalin. The developmental sequence of Leptasterias as described by Chia (1968) was divided into eight developmental categories which correspond to the 8 weeks the embryos spent in the female's brood pouch (Table 12). Later the number of eggs or developing embryos were counted and a subsample of each brood was measured using an ocular micrometer. This two-dimensional measurement consisted of the total diameter of the unhatched egg and the fully metamorphosed stars; in the intermediate larval stage, the brachiolaria, the measurement was made at right angles to the brachiolarian axis, across the widest part of the larval body (Chia, 1968b).

In addition to the three main study populations other populations were sampled less frequently during the 1971 brooding season. The same sampling and measuring procedures were used for the females and their broods.

During the 1972 brooding season, which also commenced in early February and lasted into May, a different sampling schedule was followed. During this period the Middle Cove and South Cove populations were sampled three times and the Sunset Bay populations four times. Females were collected using the same sampling technique as in 1971, but larger samples were taken. The females and their broods were handled in the manner previously described for the 1971 brooding season. At the end of the 1972 brooding season the females were returned to their respective populations.

TABLE 12. Characteristics of Leptasterias embryos and larvae used to distinguish between the 8 weeks of development which is spent in the female's brood pouch.

Week	Developmental Characteristics
1	Newly spawned eggs to gastrula.
2	Formation of W and U shaped clefts which represent brachiolaria arms.
3	Embryo hatches from egg membrane to brachiolaria larvae, central sucker appears.
4	Five hydrocoel lobes, making the prospective adult form, appear on one side of brachiolaria.
5	Sixth hydrocoel lobes appears, three pair of tube feet on rays one through five, one pair on sixth.
6	Assumes adult shape; larval body is a thin, short stalk between rays one and six; eye spots on five terminal tube feet.
7	Mouth opens, all six rays have eye spots, marginal spines <3.
8	Three pair of marginal spines per ray, oral spines complete.

The 1972 field sampling techniques differed somewhat from those of the 1971 brooding season in that all sea stars encountered, including brooding females, were measured for their total diameter and were inspected for their morphological condition. Each sea star was examined and placed in one of three categories: (1) normal, if all arms and disc were intact; (2) incomplete, if a portion of one or several arms were missing, and (3) regenerating, if the sea star has lost an arm including part of the disc and was in the process of regenerating it.

In addition to the three main study populations, eight other

Leptasterias populations were sampled during the 1972 brooding season. These included populations along the Oregon coast located at Brookings, Cape Blanco, North Cove of Cape Arago, North Sunset Bay, and Yaquina Head. The three other populations were on San Juan Island in Puget Sound, Washington.

Each population was sampled as described for the main study populations. All the animals encountered were measured and checked for morphological condition. All brooding females were also measured and a sample of their brood removed to determine developmental stage. The time spent sampling each population and the number of sea stars encountered were used to calculate the relative abundance and to compare the populations. When, for a given population, the developmental stages of all broods sampled were determined, it was possible to estimate the onset and termination of brooding.

A limited amount of data was collected during the 1973 brooding season for the three study populations. Using the techniques described for 1972 each population was sampled until 100 brooding females had been encountered. Each female was measured and a few embryos were removed from her brood to determine the developmental stage. This was done as quickly as possible, and the female was replaced and allowed to continue brooding.

Results

The data on Leptasterias' reproduction will be presented as follows: The gonad and storage organ indices will be compared for the

three study populations and used to describe the annual reproductive pattern observed for this species. The data collected just before spawning will be analyzed for a comparison of reproductive effort between populations and within populations for two brooding seasons.

The brooding data then will be presented in terms of population reproductive effort and synchrony of brooding schedule. These data then will be recombined and analyzed in relation to the individual

Leptasterias female's size and the developmental stage of her brood.

In the final section, data from the three study populations will be combined with those for the other eight populations sampled in 1972 and used to describe the reproductive strategy of this species.

Gonad Indices

Male and female Leptasterias cannot be distinguished from one another externally; thus the sea stars used for gonad analysis were collected without knowledge of their sex except during the reproductive season when the females could be found brooding their eggs. By eliminating the sea stars collected during the brooding season an unbiased sample is provided from which determinations of sex ratio and comparison of male and female weight can be made. The average weight of male and female stars did not vary significantly ($p > 0.2$) within each population and the sex ratios did not depart significantly from unity (Table 13).

The monthly gonad and storage organ indices calculated for the males and females of the three study populations are presented in

TABLE 13. Comparison of male and female average wet weights. Animals were collected without knowledge to sex for gonad analysis.

Population	N	Average Weight	Significance of Difference (t values)
South Cove Cape Arago			
Males	62	5.17	-0.49 (n.s.)*
Females	61	5.02	
Middle Cove Cape Arago			
Males	62	5.48	-1.14 (n.s.)*
Females	59	5.08	
Sunset Bay			
Males	67	3.54	-1.282 (n.s.)*
Females	63	3.30	

*Not significantly different ($P > 0.2$)

Figs. 16 & 17. Comparison of the reproductive cycles for both sexes in all three populations reveals remarkable similarity. Eleven of the twelve peaks in gonad index occurred in January while five of the six peaks in the storage organ index occurred in August.

The sea stars spawn after the peak gonad size is reached and then both sexes have a period of gonad inactivity. The females initiate an earlier buildup of gonadal weight while the males start later and eventually produce three times the female weight of gonadal material before spawning. The eggs produced by the females are calorically more

Fig. 16. Gonad and storage organ indices for male Leptasterias from the three study populations from September, 1971 to February, 1972. Symbol code: triangles = gonad indices; circles = storage organ indices.

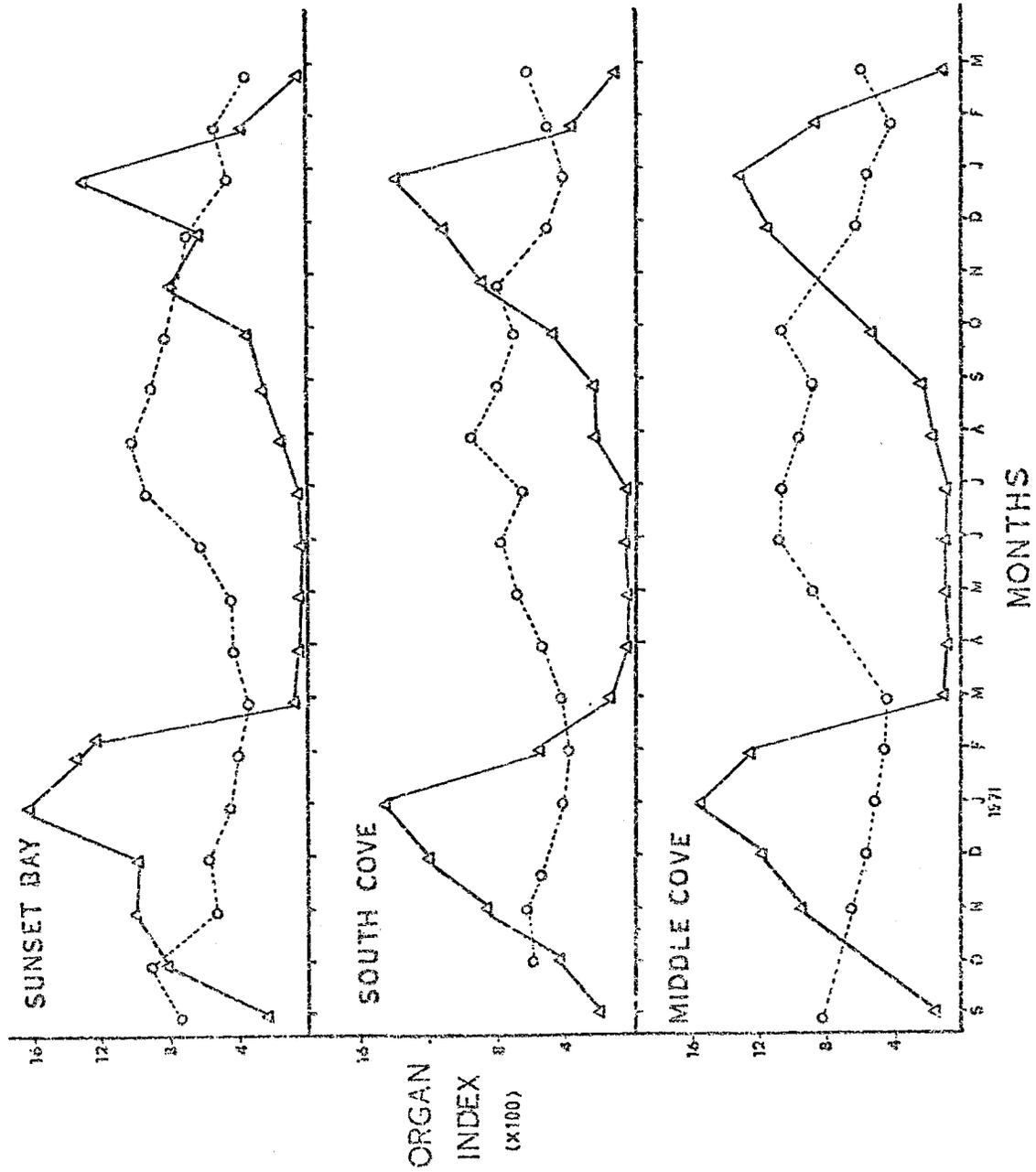
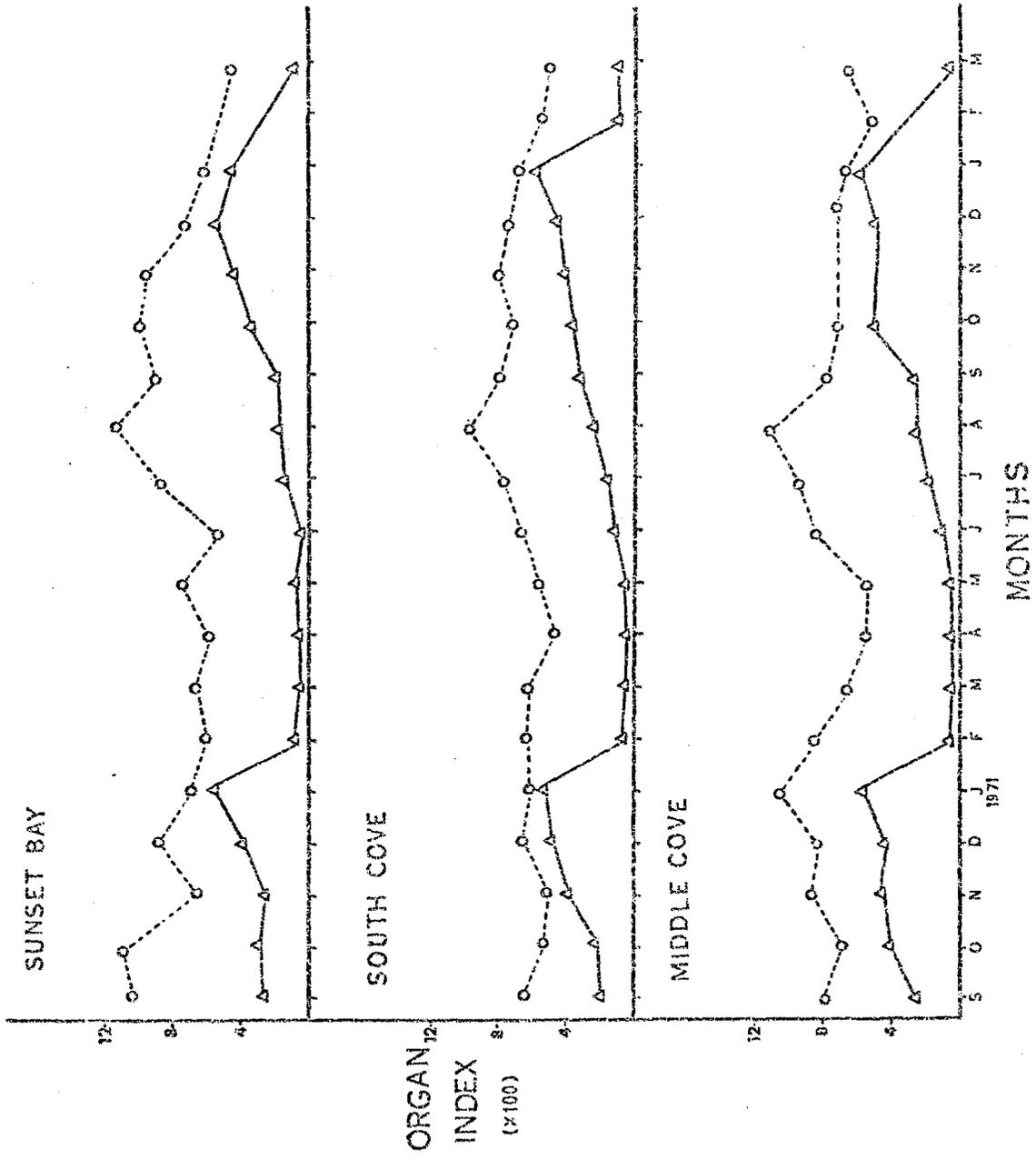


Fig. 17. Gonad and storage organ indices for female Leptasterias from the three study populations from September, 1971 to February, 1972.

Symbols are the same as in Fig. 16.



expensive than the male's sperm (6-6.5 Kilocalories/g for eggs; 4.7 Kilocalories/g for sperm; Menge, 1970). However, because the females produce less gonadal material than the males, they do not cause as severe a drain of their storage organ reserves during the period of rapid gametogenesis. Instead they utilize these reserves gradually during the brooding period. While the females do not feed during the brooding season, the males forage at a low rate and begin to replenish their storage organ reserves. With the onset of spring and through early summer both sexes feed, and the storage organs reach their peak and then decline as another cycle of gametogenesis commences.

Despite their differences in size structure all three study populations have similar peak gonad index values. This suggested a relatively linear relationship between sea star weight and reproductive effort. To test this the males collected in December 1970 and January 1971 were compared. Regressions of testes weight on sea star weight were compared and indicated significant differences between the populations (Table 14) although the regression coefficients were very similar. Coefficients of allometry (Allee et al., 1949) were calculated from the logarithms of testes weight and sea star weight using Bartlett's least squares method (Simpson et al., 1960). These values (Table 15) indicate a condition of positive allometry in which the geometric rate of increase in gonad weight is greater than that of body weight (Simpson et al., 1960). Comparison of male reproductive effort between 1971 and 1972 brooding seasons was not possible because of the small number of males sampled in 1972.

TABLE 14. Comparison of peak male reproductive output in 1971 for three study populations. Linear and exponential* regression equations of testes weight (y) on sea star weight (x).

Population	N	Regression Equations	Testes Weight on Sea Star Weight
Middle Cove Cape Arago	15	$y = .224x - .541$	$y = .046x^{1.61}$
Sunset Bay	23	$y = .235x - .227$	$y = .049x^{1.72}$
South Cove Cape Arago	10	$y = .22x - .397$	$y = .076x^{1.62}$

*The exponential regressions were calculated by linear regression of $\log x$ and $\log y$.

TABLE 15. Comparison of prebrooding females from four populations for number of mature eggs in their ovaries. Regressions of egg number on female weight were compared.

Population	N	Number Eggs gram body weight	Correlation Coefficients (r)	Combined* Regression Equation
North Sunset Bay	26	128	.85	
South Sunset Bay	13	103	.75	
Middle Cove	22	106	.87	**y = 113.1x - 29.77
South Cove	15	86	.76	

*No significant differences between regression equations ($p > 0.2$).

**y = number of eggs, x = weight of female in grams, r = 0.86,
S_{y,x} = 127.6

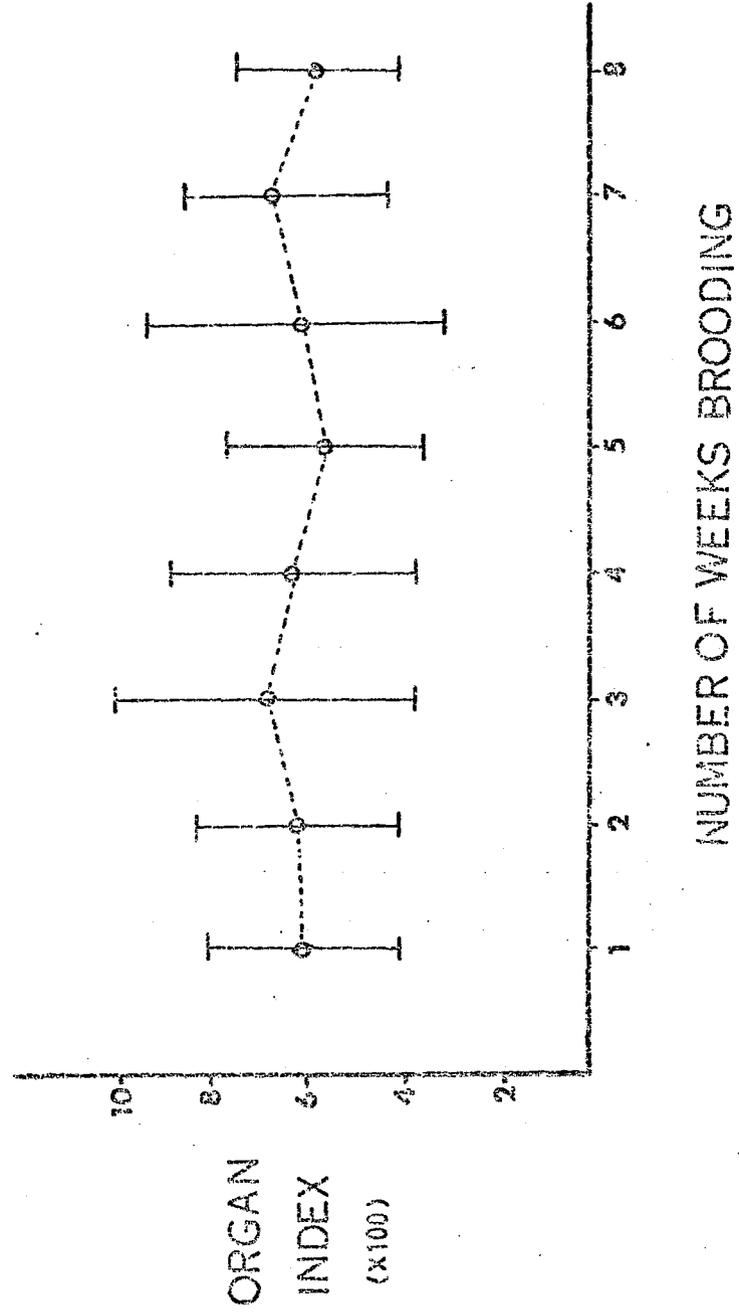
The females sampled in January 1971, to provide a prebrooding egg count were taken from the three main populations and from the north side of Sunset Bay. The weight of the eggs, estimated from brood weights, was subtracted from the prebrooding females' whole wet weight in order to compare them and brooding females for egg production and egg loss. Regressions were calculated of the number of ovarian eggs on corrected female wet weight. All the regressions were significant, and when compared no significant differences ($p > 0.2$) were found between the populations sampled (Table 15).

The relationship between egg number and female weight is roughly linear (Table 15). Scatter is great enough so that a fine analysis seems unjustified.

Since the prebrooding egg count indicated no significant difference in egg production for a given female size between populations, the gonad index for females in January before spawning was combined for the three study populations and 1971 and 1972 data were compared. The females did not vary significantly ($p > 0.2$) in reproductive effort for the 2 years, based on gonad indices.

Although the mean storage organ data follow a similar pattern for the three study populations, the few sea stars examined and the high degree of storage organ variability encountered rendered statistical comparison non significant. In 1971 storage organ indices were calculated for brooding females with broods in all stages of development in an effort to demonstrate the utilization of food reserves with time spent brooding. However no significant trend was observed (Fig. 18).

Fig. 18. Female storage organ indices vs. the number of weeks brooding. Each point represents the combined mean storage organ index (+2 S.D.) of all females examined with broods in each of the eight developmental stages.



All females fluctuated about a similar mean storage index value regardless of the stage of their brood.

Population Brooding Effort

The prebrooding egg count provided an approximation of egg production. The next question considered was what portion of the adult female population actually produced broods. Data from three sources support the view that in the three populations studied, nearly all the adult females produced broods during the 1971 brooding season.

In the dissection of 80 females for the January prebrooding egg count all the females had mature eggs in their ovaries; several had one or more rays completely lacking ovaries or with undeveloped ovaries, but all had the majority of ovaries filled with mature ova. Bi-weekly field sampling to determine the percentage of adults brooding showed a maximum near 50% (the maximum allowable with a 1:1 sex ratio) for the three main populations (Fig. 19). These observed maxima also occurred slightly after the peak of brooding initiation (Fig. 20). The final source of evidence comes from the gonad index data. Of all adult sea stars collected during the 1971 brooding season for calculation of gonad indices (N = 65) only two were females, and both of these had completely empty, spawned-out ovaries, similar to those of brooding females. It appears, therefore, that in the three populations most closely studied all adult females produced a brood.

A sample of eggs or embryos was taken from the brood of each brooding female collected in the 1971 and 1972 brooding study. The

Fig. 19. Percentage of adult Leptasterias found brooding during the 1971 brooding season. Each point represents the percentage of adults in the sample ($N \geq 100$) found with broods.

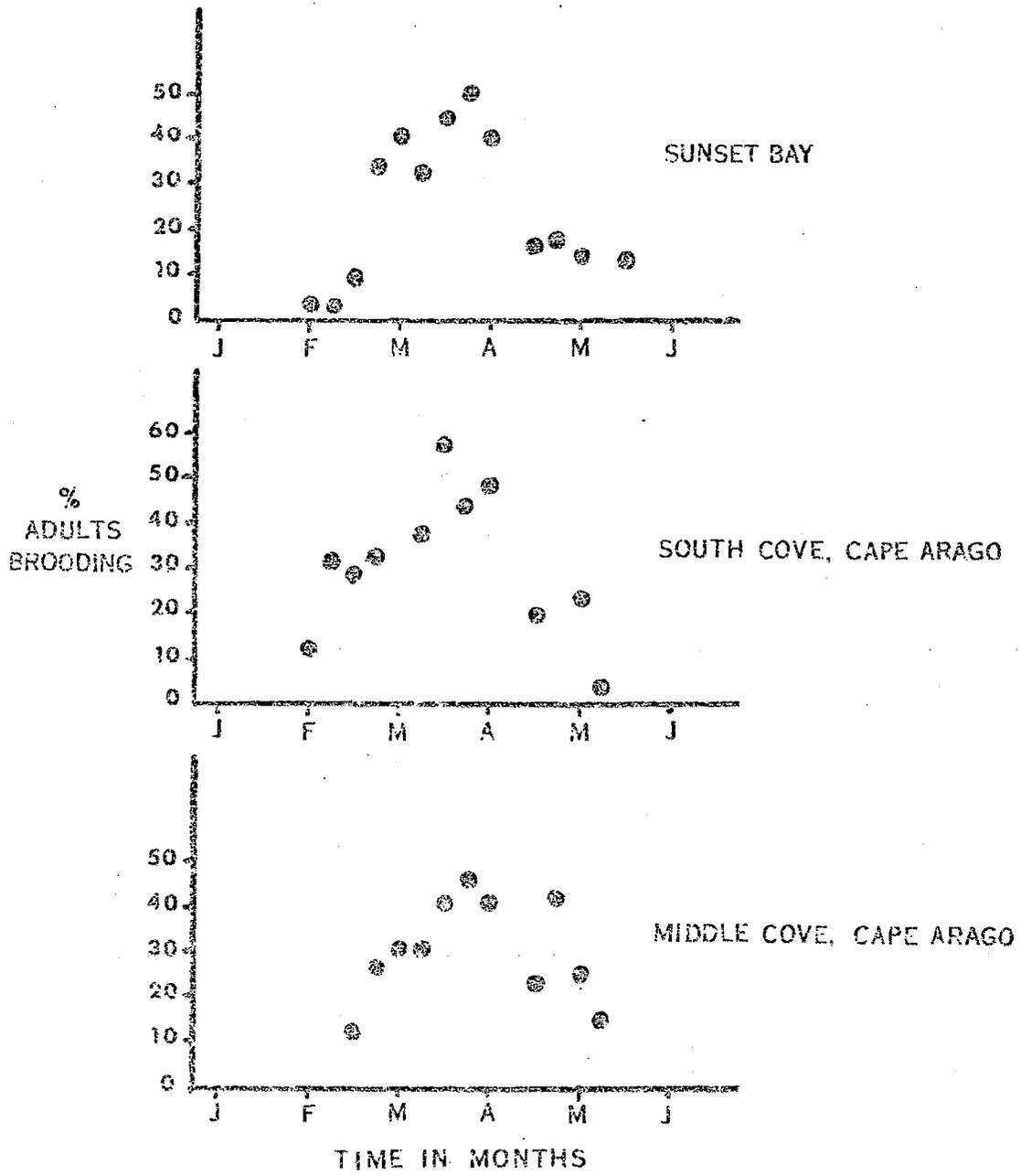
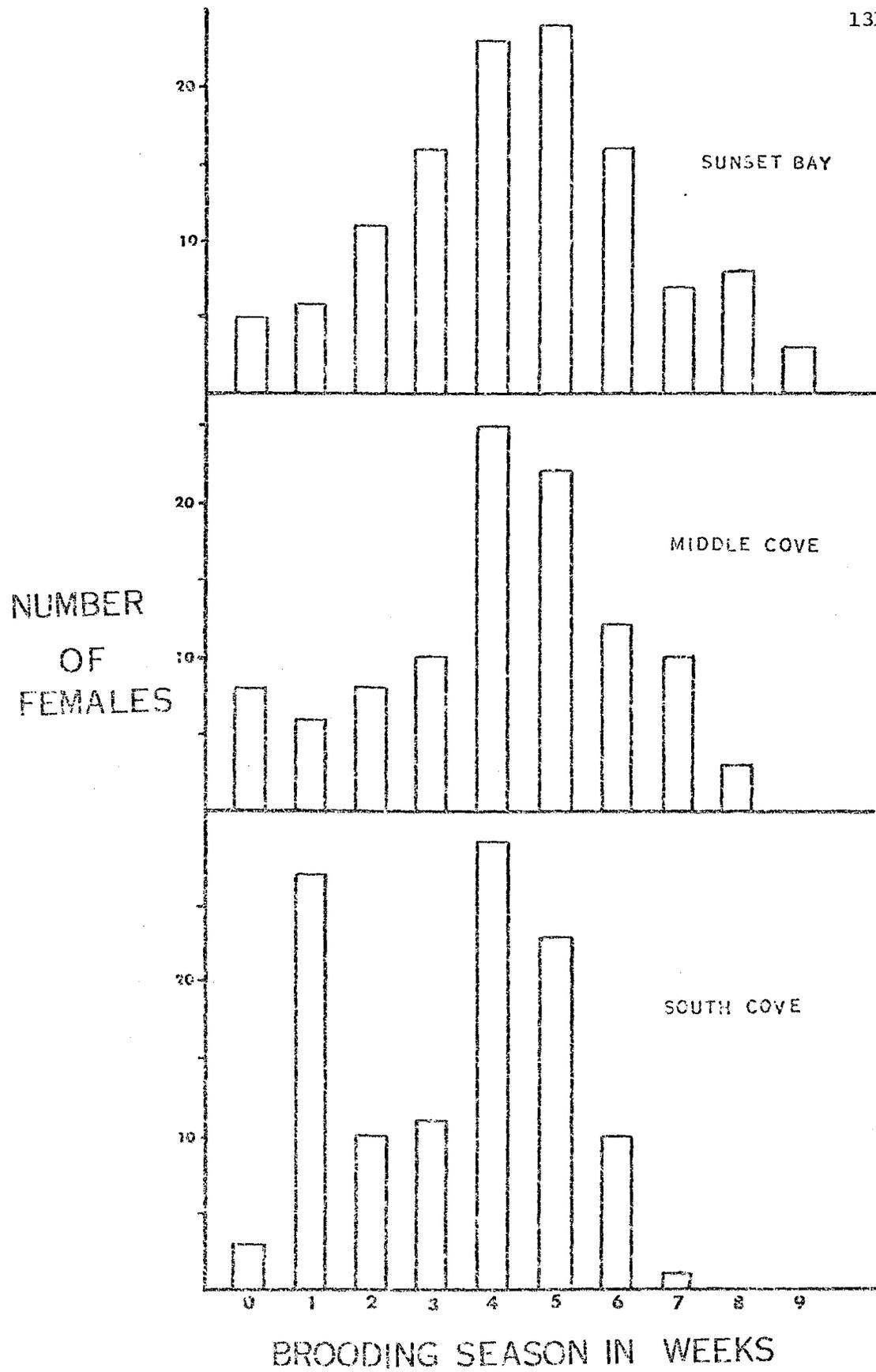


Fig. 20. The number of females which began brooding during each week of the 1971 brooding season. The time of brooding initiation was determined by the age of the embryos in the brood pouch when collected. In 1971 week zero was the first week in February.



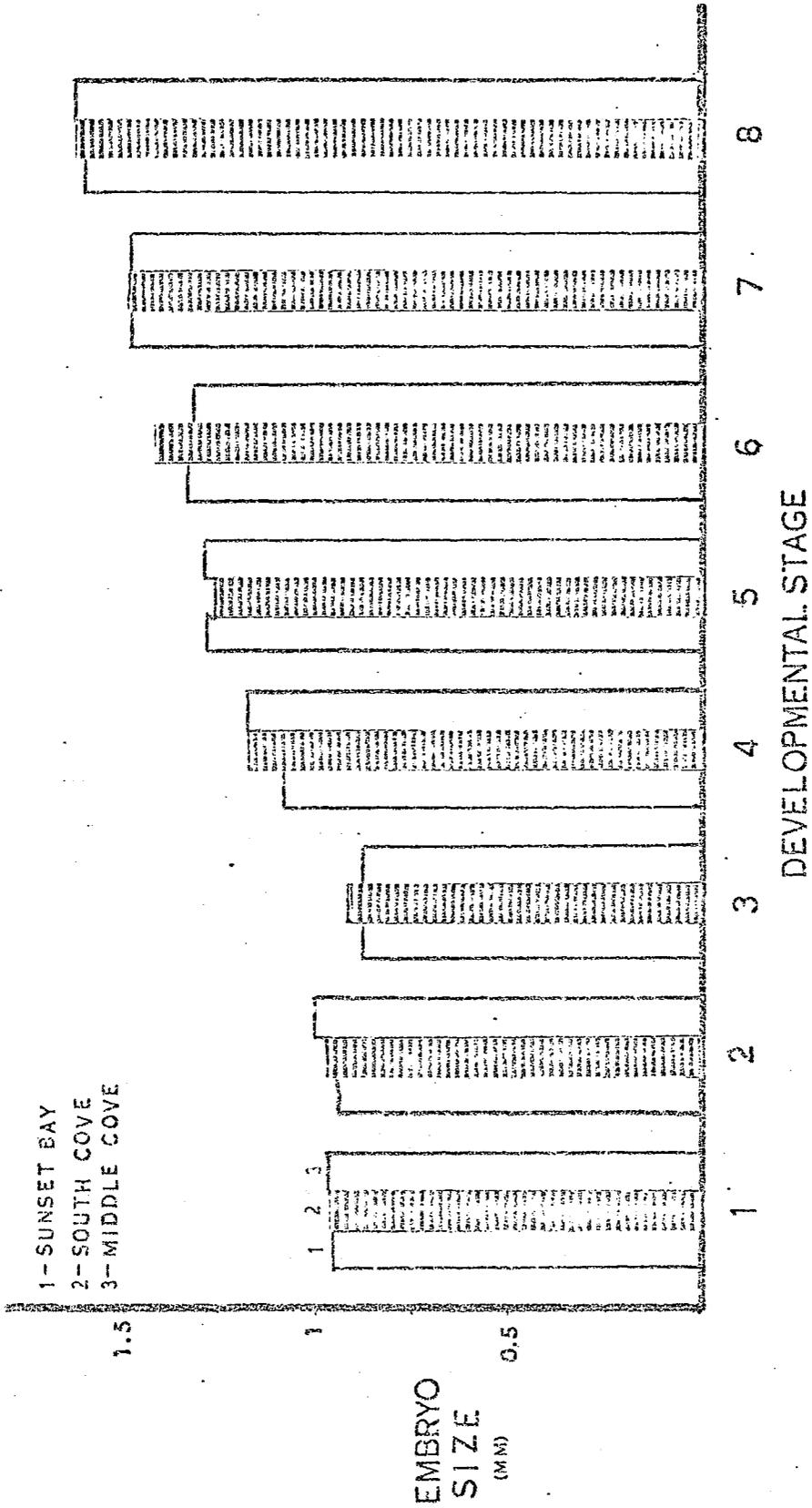
eggs were measured, and the mean size for each sample was used to calculate regressions of mean egg (or embryo) size on developmental stage for the three study populations. No significant difference ($p > .05$) in embryo size with stage was found between populations and within populations for the two brooding seasons (Fig. 21) which indicates egg size is relatively conservative in Leptasterias and that embryo number provides a good basis for comparison of reproductive effort and success between populations.

Brooding Success

Brooding success at the population level deals with the number of newly metamorphosed sea stars that are released after 8 weeks of brooding. The fact that these three populations vary in size structure, density, exposure to wave action, and several other respects has been pointed out. As a result one expects the Middle Cove population to be least successful. Whether it is least successful is not so interesting as is the degree of success it was able to achieve.

When the 8 week brooding season is considered, intuitively one expects the greatest chance of egg loss to occur during the period when the young are hatching out of their tough, protective egg membrane (Week 2-Week 3) and when they begin to metamorphose from the brachiolaria stage (Weeks 3 and 4) into the more motile star form (Weeks 5-8). In addition Chia (1969b) pointed out that newly laid eggs do not become sticky and adhere to one another until some time after laying; therefore this period also provides a chance for egg loss and

Fig. 21. Comparison of egg and embryo sizes for the three study populations during the 1971 brooding season. A mean size was calculated for each brood and an overall mean was calculated for each brood stage in each population.

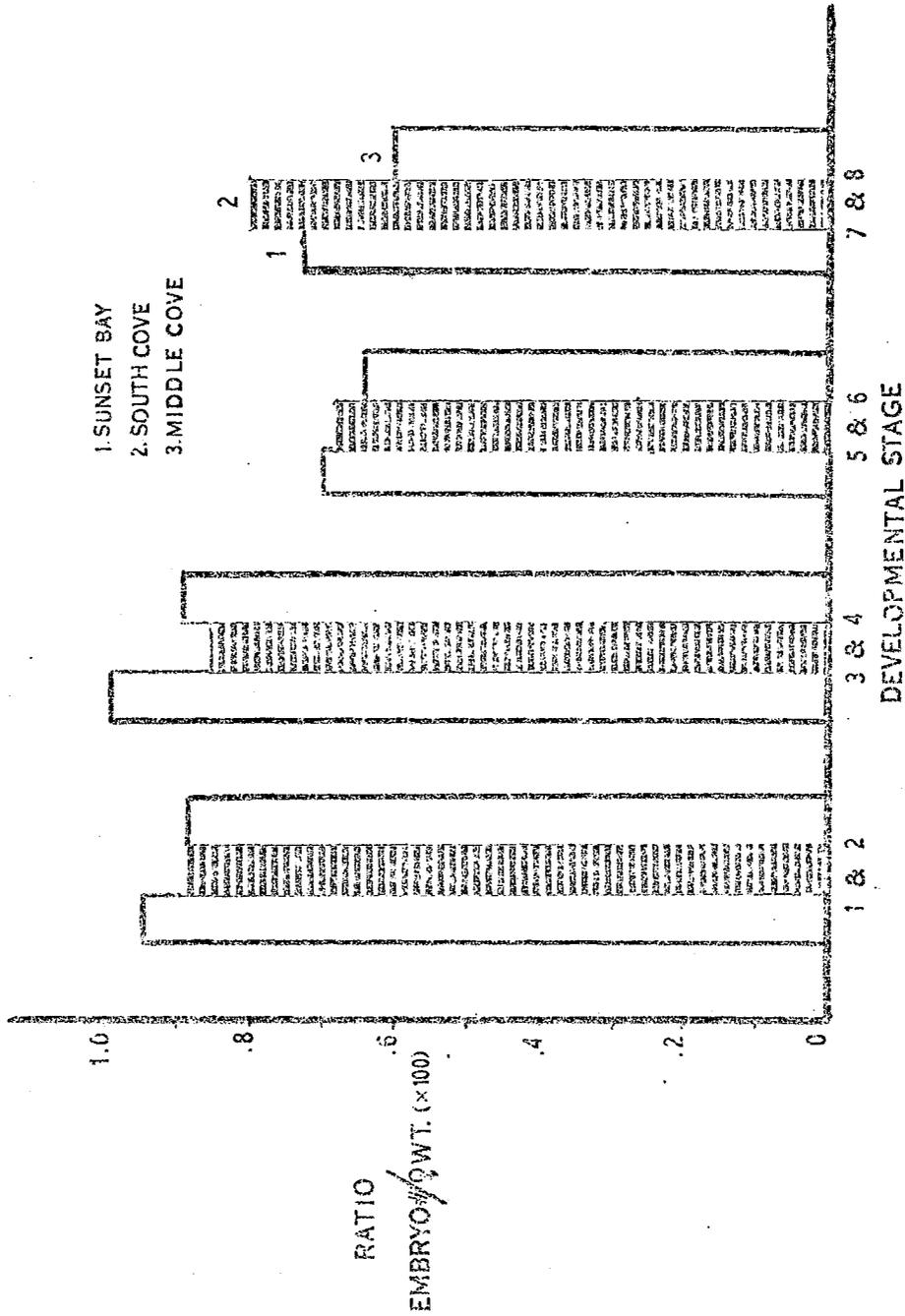


will be considered in more detail in a later section.

Comparison of the three study populations over the 1971 and 1972 brooding periods was accomplished by computing multiple regressions with egg number the dependent variable and female weight and developmental stage of the brood the independent variables. The multiple correlation coefficients were significant ($p < .01$) for all three populations in 1971 and the second independent variable, developmental stage of the brood, significantly reduced the variance of the dependent variable ($p < .10$); the 1972 brooding data were too variable to allow significant correlations. The three populations were used as treatments and the 1971 brooding data were compared using a multiple covariance analysis (Steel & Torrie, 1960) which indicated no significant difference between populations ($F_{2,338} = 1.025, p > 0.2$) in egg loss for females of the same size with broods in the same stage.

To overcome some of the variability in the data and to give a representative idea of comparative brooding success, the developmental sequence was divided into four 2 week periods and the mean ratio of embryo number to female weight was calculated for the 1971 data (Fig. 22). Even with this lumping of data the great variability of reproductive success is still evident. However, other points can be made. The data suggest that the embryos successfully hatch from the egg membranes with no detectable mortality. Chia (1966a) suggested the mother star aided her young in this process by mechanical manipulation of the brood. The drop in ratio values seen between stages 4-5, the period when the young stars' tube feet are becoming functional, suggests much of the

Fig. 22. Reproductive success of Leptasterias from the three main study populations for 1971. For each population the data are combined into classes consisting of two consecutive developmental stages and the mean number of eggs per gram of female weight for each class is given.



embryo waste is caused by the embryos themselves, once they become independently motile. The most impressive feature of this illustration is that, even with substantial egg loss and embryo wastage during the brooding period, the Middle Cove population was able to release over half the eggs produced as metamorphosed stars.

Brooding Synchrony

Brooding synchrony between populations was compared by assigning each brooding female collected a pair of numbers which corresponded to the week it was collected and the developmental stage of the embryos in the brood. The first week of brooding season was designated week zero, and subsequent weeks were numbered in order after this. The numbers one through eight were used to define the eight developmental categories which correspond to the 8 weeks the embryos spent in the mother's brood pouch. Therefore, by calculating the regression of developmental stage on the week sampled for each population, a series of regression equations can be used to compare synchrony between populations.

Regression lines were calculated and compared for both the 1971 and 1972 brooding seasons for the three main study populations. Brooding was observed to begin during the first week in February for both years at all three study sites. Comparison for both years between Middle and South Coves, Cape Arago showed no significant difference ($p > .05$) in the onset and pattern of initiation over the brooding season. The Sunset Bay population did show a significantly different ($p < 0.5$) pattern of brooding when compared to South Cove and Middle Cove during both 1971

and 1972. When the individual populations were compared separately for difference in brooding pattern between 1971 and 1972, all were found to differ significantly between the two brooding seasons. These results suggest that the timing of reproduction is based on relatively local cues which can vary between years.

The annual pattern of brooding synchrony among these three populations is seen more clearly when the 1971 data are transformed to show the week in the brooding season when each female observed began brooding (Fig. 20). All the female sea stars sampled in the Cape Arago populations initiated brooding within a 9 week period, and the peak period occurred during weeks 4 and 5. The Sunset Bay females also reached their brooding peak during weeks 4 and 5, but had a more even pattern of brooding initiation which was spread over a slightly longer period. However, despite the observed differences, the Leptasterias populations in the Cape Arago-Sunset Bay area exhibit a high degree of brooding synchrony on a yearly basis. The Middle Cove population has been observed for four brooding seasons and the South Cove and Sunset Bay populations for three. In each case brooding began in early February, peaked in late March and continued through April.

Combined Comparison of Brooding Characteristics

The three main study populations did not vary significantly in brooding success, and therefore they were combined for comparison on the basis of the developmental stage of the brood and female weight.

The data for the 343 females observed in 1971 was combined in

terms of the stage of their broods when collected. These data (Table 16) were then tested using each stage as an individual treatment. An analysis of covariance of egg number on female size indicated there were significant differences between stages in terms of egg loss.

TABLE 16. Summary of 1971 brooding data combined into eight developmental categories representing the stage of the females brood when collected. Stage 0 = values from females used in prebrooding egg count.

Stage	N	Number of Eggs g Female Weight	Average Embryo Size (mm)
0	50	100.2	-
1	74	81.4	.95
2	34	93.1	.97
3	71	90.8	.89
4	50	91.2	1.16
5	25	69.4	1.28
6	30	60.6	1.35
7	40	61.5	1.49
8	19	70.2	1.62

Stepwise comparison of the stages indicated that there was a significant difference ($p < .05$) between stage 0, ovarian eggs, and stage 1, the newly laid eggs; and between stage 0 and stage 2, the 2 week old eggs. This indicates there is some initial egg loss when the eggs are first released. The difference between stage 4 and stage 5 was not significant ($p > .10$) while the comparison between stage 4 and stage 6 yielded a significant difference ($p < .05$). As mentioned previously this

represents the period when the larvae are assuming the adult star shape. It is also the time when the female relinquishes her raised brooding position and becomes flattened against the rocky substratum although she still remains immobile and protects her brood. This combination of larval metamorphoses and female movement evidently contributes significantly to larval mortality.

On a population basis the mean size of the embryo was not significantly different for a given stage either between populations (Fig. 21) or between years within populations. However when mean embryo size is compared to female weight on a single stage basis there are significant positive correlations ($p < .05$) for stages 1 and 2. These indicate larger females tend to produce larger eggs. However no significant correlations were found after stage 2, although all correlation values were positive. This information suggests that the larger female stars, like the males, have a somewhat greater initial reproductive output per unit weight.

The brooding data were resegmented into 1g weight classes based on the weight of the brooding female. The weight classes were used as treatment groups, and a multiple regression analysis was run on the data. Egg number was used as the dependent variable and female weight and developmental stage of the brood as first and second independent variables respectively. The results were not significant and combining the data into 2g weight classes proved equally futile because of the high degree of variability encountered within weight classes. Therefore the data (Table 17) can only be interpreted on a limited basis.

TABLE 17. Summary of 1971 brooding data combined into categories based on the wet weight of the brooding female. The mean egg number is the average of all broods sampled in all eight developmental stages for each weight class.

Female Weight Class (g)	N	Mean Weight	Mean Egg Number Gram Female Weight
0-1	15	.90	89
1-2	76	1.47	88
2-3	73	2.49	92
3-4	73	3.44	83
4-5	34	4.37	88
5-6	28	5.48	75
6-7	17	6.56	71
7-8	11	7.70	60
8+	16	9.70	69

These weight class data suggest that the larger females are less successful than the smaller ones. When the whole brooding period is considered; the mean embryo number per gram female body, i.e. the number that are successfully brooded, drops off steeply after the 4g weight class (Table 17). However this is less clear when the brooding success with weight class is compared on a population basis (Table 18). The Sunset Bay females, which were generally smaller, had an even success rate for all weight classes. The Middle Cove females in the smallest weight classes did considerably better than did those in the heavier weight classes.

TABLE 18. Comparison of brooding females from each study population found in 1g weight classes. The mean egg number is the average of all broods sampled in all eight developmental stages for each weight class.

Female Weight Class g	Combined N	Egg number/Female weight (in grams)			
		Combined Average	Middle Cove	South Cove	Sunset Bay
0-1	15	89	-	-	89
1-2	76	88	79	86	91
2-3	73	92	91	91	90
3-4	73	83	75	90	80
4-5	34	88	94	82	87
5-6	28	75	59	83	-
6-7	17	71	72	71	-
7-8	11	60	60	-	-
8+	6	69	69	-	-

The conclusion that can be drawn from these data is that in an area of relatively high exposure to wave action the larger female Leptasterias seem less successful in brooding young to time of release.

Latitudinal Brooding Study

In the 1972 brooding season eight other Leptasterias populations were visited in addition to the three main study populations. Five of these populations are located on the Oregon coast and three on San Juan Island in Puget Sound. For each of these eight populations the relative abundance of sea stars was estimated by dividing the number seen by the time spent searching; a similar figure was calculated for the relative

abundance of first year stars (Table 19). Animals that were morphologically damaged were counted and the percentage of damaged stars in each population is given as a maintenance factor value. The number of females brooding was also counted and each brood sampled. After examining these brood samples for developmental stage, a mean stage (= time in brood pouch in weeks) was calculated, and both the initiation and termination of brooding was extrapolated for comparison between populations (Fig. 23).

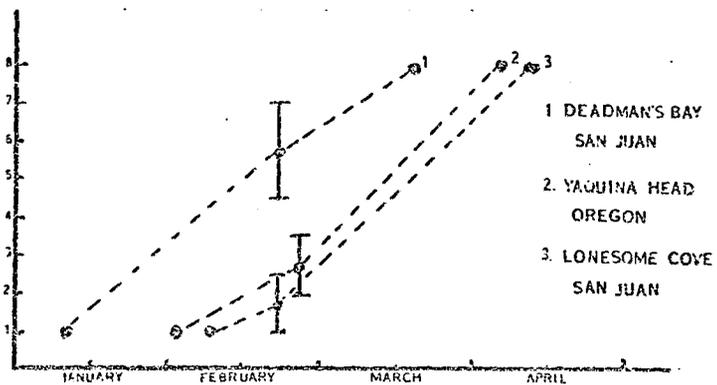
When the onset of egg laying is compared on a latitudinal basis, a general pattern is suggested with the northern populations starting earlier than those in the south. However the greatest discrepancy in brooding synchrony was not at the latitudinal extremes but between the San Juan Island populations. The Deadman's Bay population on the west side of the island was 4 weeks ahead of the two populations on the east side. This condition is typical of San Juan Island (Menge, 1970). A local pattern is again seen in the Cape Arago-Sunset Bay area with all five populations exhibiting essentially the same brooding schedule.

The three San Juan Island populations and the Yaquina Head population had low percentages of brooding adults (Table 19); however this is probably due to their being sampled during the first month of the brooding season. The remaining seven populations were sampled later and had considerably higher percentages. All except the Brookings population approached the theoretically possible 50 per cent of the adults brooding.

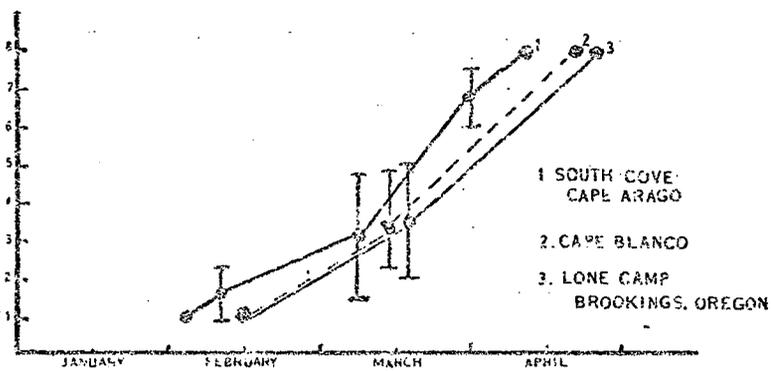
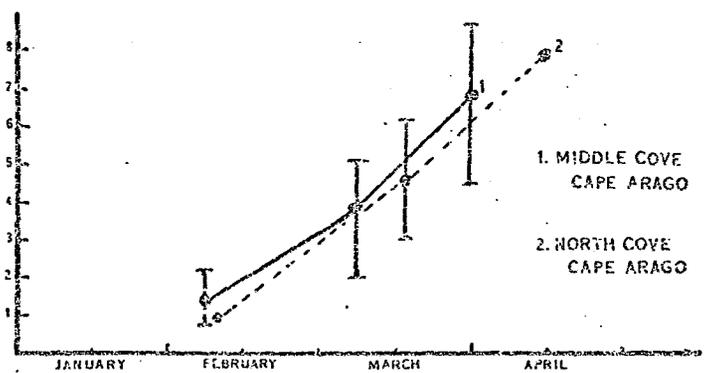
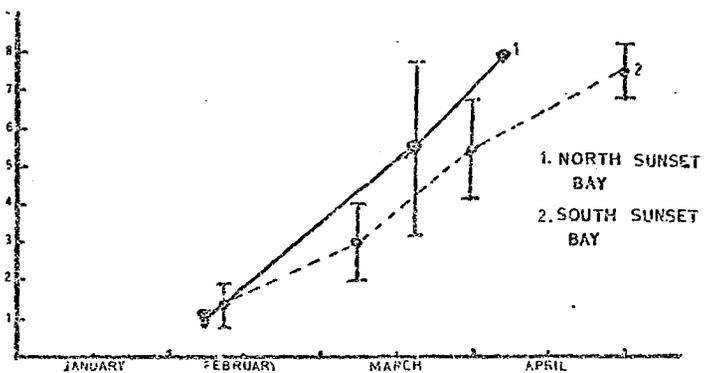
TABLE 19. Summary of data collected during 1972 brooding season. The asterisk (*) represents the three main study populations which were included for the sake of comparison. For explanation of values see text.

Population	1972 Date of Observation	N	Mean Size (mm)	Relative Abundance	First Year Star Relative Abundance	Maintenance Factor	Number Brooding Females	% Adults Brooding
Deadman's Bay San Juan	21 February	71	65.3	33.6	4.9	.26	12	24
Lonesome Cove Resort	20 February	120	41.5	43.6	10.2	.31	20	38
Lonesome Cove Far Point	20 February	131	36.4	87.0	18.8	.23	14	20
Yaquina Head	23-24 February	60	34.4	15.0	2.0	.47	11	39
North Sunset Bay	19 March	154	39.3	51.3	9.3	.53	50	48
*South Sunset Bay	31 March	218	29.3	90.0	21.0	.33	43	46
North Cove Cape Arago	17 March	245	35.4	89.1	35.4	.34	59	50
*Middle Cove Cape Arago	9 March	124	44.3	37.7	10.3	.49	33	45
*South Cove Cape Arago	10 March	121	40.1	59.0	16.7	.50	33	49
Cape Blanco	18 March	176	39.1	64.0	6.9	.33	50	45
Lone Ranch Brookings	16 March	73	39.1	32.4	2.6	.40	23	41

Fig. 23. Initiation and termination of brooding in populations of Leptasterias from locations along the Oregon coast and San Juan Island, Puget Sound for the 1972 brooding season. Points with vertical lines (= 2 S.D.) represent the mean developmental stage of the broods collected on the date sampled. Other points represent extrapolation to brooding initiation (stage 1) and brooding termination (stage 8).



DEVELOPMENTAL
STAGE



MONTHS

The remaining data collected during the 1972 brooding season are somewhat confusing, though there is some consistency. The two populations with the lowest relative abundances have equally low relative abundances of first year stars and generally high maintenance factor values which suggests these are marginal populations.

The three San Juan Island populations have very low maintenance factors indicating the calmer situation which generally persists in Puget Sound. The Deadman's Bay population is in the path of wave trains entering through the strait of San Juan de Fuca and the low maintenance factor value is probably a function of the extremely robust and large individuals which are resistant to morphological damage and characterize this population.

The relative calm conditions of Puget Sound allow Pisaster and Leptasterias to overlap significantly intertidally. As mentioned earlier, Menge (1972b) presented convincing evidence that when Leptasterias and Pisaster both co-occur in relatively high abundance there is competition for available resources. The end result is that the Leptasterias are kept at a small individual size and thus are unable to capture larger prey. The question arises what would the effect of this competitive interaction be on Leptasterias reproductive ability. Menge (1970) did not address himself to this question.

The Leptasterias population at Seal Rock, Oregon perhaps can provide an answer. This population, which was sampled during the 1971 brooding season, probably represents the extreme case of the Pisaster-Leptasterias interaction. Because of unusual current conditions or for

some other reason, large numbers of Pisaster had settled out of the plankton at Seal Rock for the past several years. There were many first and second year Pisaster in the boulder-cobble area typically inhabited by Leptasterias but avoided by adult Pisaster. Very few Leptasterias occurred with the small Pisaster but instead were in small depressions on the roof and side of an undercut at the base of Seal Rock adjacent to the boulder-cobble area.

These sea stars were small, and when several were examined for gonad development the males were found with active sperm but with testes much smaller than those observed for males in Cape Arago populations. Only one of four female examined had fully developed eggs in her ovaries, the remainder had very small eggs or none at all. Those females with broods were small, with a mean of 1.7g (range 0.5-3.8g, N = 24), but had a normal number of eggs for their body weight. However all the broods were in very early stages of development while the other coast populations observed had been brooding for 2 months. Perhaps therefore Pisaster can influence Leptasterias to the extent that population reproductive effort is reduced and the onset of brooding is delayed.

Menge (1972b) found that when Pisaster was removed from an area, the Leptasterias increased in mean individual size. What limits Leptasterias in the areas where Pisaster doesn't occur? The data collected during the 1972 brooding season (Table 19) lend some support to the earlier stated hypothesis that a population with a lower density, caused by juvenile mortality, will allow the surviving adults to exploit more readily the food resources which will result in larger sized individ-

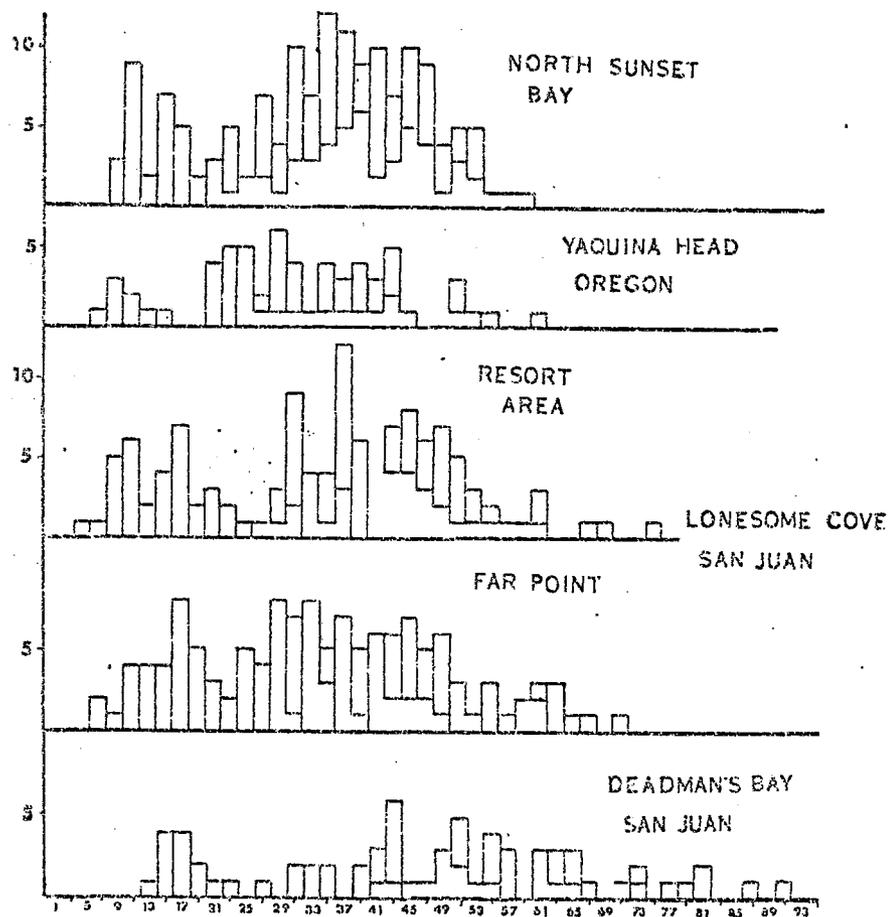
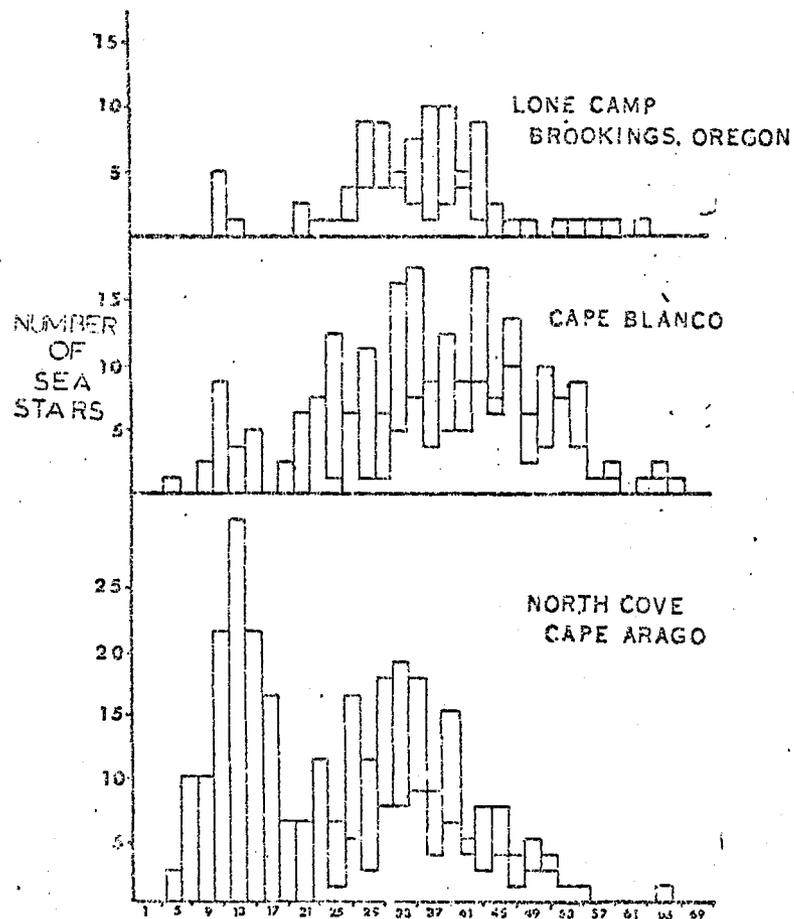
uals; more dense populations are held down in individual size because of the intraspecific interactions. The Cape Arago-Sunset Bay populations examined in this paper and those studied by Menge (1970) on the San Juan Islands (Fig. 24) are the best known and provide the best argument for the hypothesis.

The Deadman's Bay population on the west side of San Juan is subjected to relatively severe wave action. There are no Pisaster present and the Leptasterias reach a very large size. Another very similar population, which I was unable to census, is found at Cattle Point, also on the west side of San Juan Island (Menge, 1970). At Deadman's Bay Leptasterias density was low. The population structure and environmental conditions observed for this population were very similar to those at Middle Cove, Cape Arago.

The population at Lonesome Cove Far Point on San Juan Island is on the leeward side of the island and there are few Pisaster present as they were removed in a previous study (Mauzey, 1966). As can be seen (Table 19) this population is very similar to that at Sunset Bay in its characteristics, and both populations are similar to the North Cove, Cape Arago population, which is also in a relatively protected area with a low density of Pisaster. These populations all have a high Leptasterias density, low maintenance factors and small individual adult size.

The above populations perhaps represent the extremes of a continuum of population structure and the above stated hypothesis dealing with Leptasterias population structure in biologically and physically

Fig. 24. Size frequency histograms of the eight Leptasterias populations sampled during the 1972 brooding season. The clear areas (those size classes with no left hand margin) represent the brooding females observed.



DIAMETER IN 2MM SIZE CLASSES

controlled environments is artificial in that it describes these exceptional cases rather than the majority. The high degree of reproductive effort and success observed for these populations suggests they are enjoying relatively benign conditions. Those populations most severely limited by biological and physical factors such as the Yaquina Head, Brookings and Seal Rock populations should be consulted to complete the description of Leptasterias reproductive strategy and population structure. In these populations we find low densities with a small individual mean size and the females, although small, produce a full complement of eggs. Some individuals are not reproductively active; however the majority will attempt to reproduce, although they may have to delay the onset of reproduction.

The results of the study of Leptasterias brooding strategy can be summarized as follows:

1. Gonad and storage organ cycles illustrate a well-defined annual reproductive cycle with an inverse relationship between the two organs.
2. Male and female Leptasterias are distributed in a 1:1 sex ratio and do not differ significantly in wet weight.
3. There is a linear relationship between production of gonad material and sea star weight for both male and female Leptasterias.
4. In the populations closely studied almost all females produced broods. In less closely watched populations there is some indication that some females do not lay eggs every year.
5. Reproductive success is highly variable within and between

- populations.
6. During the brooding sequence there is significant loss of eggs during the time of egg laying and during the time of metamorphosis from brachiolaria larvae to the adult form.
 7. Large females from most exposed locations suffered the highest mortality of brooded young.
 8. Timing of reproduction appears to be contingent on local conditions although a general trend of earlier onset of brooding in more northerly populations was observed.
 9. Larger females produce somewhat larger eggs.

Discussion

The retention of young during their embryonic development in specifically adapted structures within or upon the body of the parent is common among echinoderms (Booolootian, 1966). Brooding behavior occurs in all three orders of the Asteroidea (Hyman, 1955). However, with the exception of the work done with Leptasterias (Chia, 1966a) most published accounts that deal with brooding behavior are primarily concerned with systematics (Booolootian, 1966).

Chia (1968) found that the developing oocyte undergoes a slow growth period which lasts about a year, then goes through a 6 month period of rapid growth and finally a "rest period" for about 5 months before it is spawned. Chia (1964) reported that maximum female gonad indices occurred in September in San Juan Island populations while in a later study Menge (1970) observed the maximum in October for the same

location. Both authors reported that brooding began in January and lasted through April on San Juan.

Chia (1968a) thought the "rest period" varied in that the gonad of all individuals reached a fully grown state at about the same time but spawned at different times, implying that spawning depends on the availability of proper stimulation from the environment. Menge (1970) believed that food was the critical factor; although the gonads were ripe in late summer, the animals would wait to build up energy reserves before spawning. The data collected in this study do not agree with the San Juan Island observations. The female Leptasterias in all three Cape Arago-Sunset Bay study populations continued to increase their gonad size until just before spawning. Additionally both male and female Leptasterias reached their peak storage organ indices in August and these declined steadily to the period beyond the brooding season when the stars again begin to feed actively.

This discrepancy may represent a real difference in the reproductive cycle between the two areas or may be an artifact of the small sample sizes taken in the San Juan Island studies (Chia, 1968a). The pattern of gonad buildup seen for Leptasterias in this study is typical of the other non-brooding sea stars that have been observed: gonad size increases continuously to just before spawning (Farmanfarmaian, et al., 1958 for Pisaster spp.; Czum, 1971 for Patiriella regularis). However a basic difference between these two reproductive types is that Leptasterias females produce approximately one third the gonadal material as the Leptasterias males whereas in non-brooding asteroids the female

often outproduces the male (Mauzey, 1966; Crump, 1971).

A further similarity for Leptasterias and non-brooding sea stars is the inverse relation between gonad and pyloric caecae (storage organ) indices. Farmanfarmaian et al. (1958) followed the reproductive cycles of several west coast sea stars. The pyloric caecae were largest when the gonads were shrunken and became reduced as the latter grew in size. Mauzey (1966) showed further that in Pisaster ochraceus this inverse relationship was related to seasonal patterns of feeding as was also suggested for Leptasterias in this study. There is again a difference between Leptasterias and the typical inverse relationship seen for non-brooding sea stars. The pattern for male Leptasterias is very similar to that of non-brooders, while the female reaches a higher maximum storage index and depletes it more gradually than the male, presumably because she must not only produce gametes but brood them for 2 months without feeding.

Chia (1966a) observed that the number of embryos produced by Leptasterias was correlated with size of female. In this study individual female output did not vary between three populations for 2 years and was closely correlated with female size. Menge (1970) reported a similar linear relationship for Leptasterias females up to 8-11g wet weight but larger animals did not follow this trend. Large Leptasterias are relatively uncommon and his observation was based on only a few animals.

When Menge (1970) overfed Leptasterias in an aquarium the sea stars grew rapidly. However the maximum gonad indices did not differ from

those from field populations, although the storage organ values were greater. In a similar experiment with the non-brooding sea star Patiriella regularis, Crump (1971) reported that both gonad and storage organ indices were considerably above the maximum seen for field populations. These observations indicate that reproductive output is consistent for female Leptasterias and the relationship of gonad size to body size remains constant in contrast to what occurs in non-brooding species.

In 1971 the data for the Cape Arago-Sunset Bay populations indicated that almost all adult female Leptasterias produced broods. The 1972 data also suggested a similar population reproductive effort for these populations. Menge (1970) reported that the incidence of reproduction rarely reached 50% in San Juan Island populations and that maximum incidence varied from year to year for the same areas. The population at Lonesome Cove Far Point was observed for several years and the stars there were increasing in number. However the mean size was decreasing and this actually affected population reproductive effort (Menge, 1970), i.e. few reproduced. The previously mentioned observations for Seal Rock also suggested that adverse conditions result in fewer adults reproducing.

Menge (1970) felt that energetic well-being of Leptasterias' populations seems to be the major factor behind temporal variations in the onset of brooding, maximum proportion of the population breeding and individual female brooding effort. He is probably correct in that available food energy does affect the maximum proportion of the popula-

tion brooding. However I do not think his data substantiate the claim of a difference in individual female reproductive effort with population, since his sample sizes are too small. Field observations suggest that in the extreme case of very severe physical or biological pressures the onset of brooding can be delayed. Menge (1970) did find differences in brooding onset between populations; however these remained consistent throughout his study. Similarly I found brooding onset to be very well synchronized in the Cape Arago-Sunset Bay region on a single year basis and predictable from one year to the next regardless of population structure.

Boolootian (1966) pointed out that no single abiotic factor exclusively influences the course of reproductive events in echinoderms. I would make the similar argument for a single biotic factor. Crump (1971) reported that the three populations of Patiriella he studied spawned during the same period although they varied greatly in reproductive potential. Similar observations have been made for many echinoderms including the asteroids Pisaster ochraceus and P. brevispinus (Farmanfarmanian et al., 1958; Mauzey, 1966), and the echinoids Strongylocentrotus purpuratus (Boolootian, 1966) and Dendraster excentricus (Niesen, 1969). Therefore, although the specific cues for onset of breeding have been established for a few species of echinoderms (Pearse, 1972) no general environmental mechanism, either physical or biological, is known.

The final question to be considered is why some animals brood while others produce planktotrophic larvae. Thorson's (1950) observed dis-

tribution of the brooding type of larval development with higher latitude is thought to be correlated with the short, seasonal phytoplankton blooms in the spring and the lack of sufficient planktonic food at great depths in this region (McConnaughey, 1970).

Benthic invertebrates which have planktotrophic larvae with a long life may be subject to great fluctuations from year to year in success of settlement, while those that have a non-pelagic or a shortened lecithotrophic development show only slight variations (Thorson, 1946). Thus, in terms of local population structure it is more equitable to produce larvae that remain stationary rather than those that may be swept away by current or perish because of insufficient planktonic food.

In the temperate latitudes conditions are less severe and temporally more predictable than those in the high arctic latitudes. This allows a planktotrophic larva to be relatively successful. However this strategy is costly in terms of larval wastage and often results in great fluctuations in local settlement success especially along coasts with strong longshore currents (Thorson, 1950, Efford, 1970).

Thorson (1946) describes species which can vary their mode of reproduction from a pelagic to a non-pelagic form or from a planktotrophic to a lecithotrophic development according to the surrounding conditions. One such species is the asteroid Henricia sanguinolenta, normally a brood protecting species, which will occasionally not protect the larvae. They will then float about suspended in the water; however there is no inherent difference between these larvae and those that are brooded.

Chia (1966a) has shown that brooding is necessary for the normal development of Leptasterias. None of the embryos survived without brooding. The main functions provided by brooding are protection, cleaning, maintenance of a uniform environment, and initiating the hatching process (Chia, 1966a).

By brooding, Leptasterias is able to provide a consistent source of recruitment to the local population. Although environmental conditions vary from year to year they are relatively predictable, and all members of the population are subjected to them. This results in generally stable populations well attuned to local conditions.

CONCLUDING DISCUSSION

This study proposed to answer the question of how Leptasterias apportion its limited resources of time and energy among the three life historical component processes: maintenance, growth and reproduction (Gadgil & Bossert, 1970). As these processes do "compete" for these resources it is difficult to separate and explain the action of one without involving one or both of the remaining processes.

Knowledge of the metabolic rates of Leptasterias during the periods of brooding and active foraging as well as the effect of temperature and size on metabolic rate would be desirable to understand more completely Leptasterias' life history. I did not undertake such an investigation during this study but I hope to do further research in this area.

In terms of reproductive strategy it has been said that no organism is completely "r-selected" or "K-selected," but all must reach a compromise (Pianka, 1970). The observed reproductive strategy of Leptasterias is in accord with this statement. The female Leptasterias produces a limited number of energy-expensive eggs. These are brooded for 2 months at additional cost to the female. Female Leptasterias become sexually mature in the third year, may live at least 5 years, and can produce two or more broods (see below). All of these features of Leptasterias' life history characterize a "K-selected" reproductive strategy (Gadgil & Bossert, 1970).

However the first commitment of adult Leptasterias is to reproduction. Normally all the females will produce a brood every year even at the expense of individual growth. If resources or physical limiting factors restrict populations in some way, all females may not produce a brood every year (see below), but all males will produce sperm and both sexes will sacrifice growth and remain small. An additional feature of Leptasterias' reproduction is that, although the young are brooded, there is high initial mortality and less than one per cent reach sexual maturity. Both features, high reproductive effort and high mortality of the young, are characteristic of the "r-selected" reproductive strategy (Gadgil & Bossert, 1970).

Without becoming involved with the theoretical controversy surrounding the evolution of different reproductive strategies (Vittor, 1970; Pianka, 1970; Hairston et al., 1970), Leptasterias' reproductive strategy of brooding can be evaluated on the empirical basis of its observed effectiveness. What I have suggested in this study is that by brooding and releasing the young, despite the high initial mortality, Leptasterias provides a steady annual corps of recruits. Once Leptasterias becomes established in an area, the consistent recruitment allows the population to maintain a relatively stable population. Therefore in terms of actual effectiveness on a local basis, Leptasterias' reproductive strategy approaches the theoretical goal of the "K-selected" reproductive strategy (MacArthur & Wilson, 1967).

The first year Leptasterias were shown to grow at a similar rate wherever observed, but thereafter growth varied with population. If my

assumption that sexual maturity occurs in the third year is correct, the small size of the reproducing females in some populations indicates that growth may be neglected in favor of reproduction. The annual patterns of feeding and reproduction indicate the source of this neglect. Both sexes appear to mobilize the major portion of their energy reserves, stored during the spring and summer period of active feeding, into the production of sperm in males, and into the production and brooding of eggs in the females. The period of active adult growth probably occurs only in the spring, and if resources are in some way limited, little growth is accomplished.

Small average size of individuals was observed in several types of Leptasterias populations sampled. Some populations had high densities of small individuals and low percentages of damaged stars. These populations appeared to be limited by intraspecific interactions. Other populations co-occured with high densities of Pisaster and the individual Leptasterias were kept small by interspecific competition (Menge, 1972b). A third type of population observed had low densities of small Leptasterias and high percentages of damaged animals; these populations were thought to be limited by physical environmental factors.

Almost all reproductive age females from those populations which were apparently controlled by intraspecific interactions were able to produce eggs and brood. In the populations encountering competition from Pisaster or exposed to pounding by waves not all females produce broods. However those females that did produce a brood had a similar number of eggs per unit body weight as the females which produced yearly

broods.

Chia's (1968a) observations that Leptasterias females take 2 years to mature their eggs may provide an explanation for these lower numbers of brooding females. Chia (1966a) pointed out that the brooding period was doubly taxing on a female Leptasterias in that not only must she brood her current clutch of eggs, but also the next year's eggs in her ovaries are going through a rapid growth phase. Both of these processes are placing demands on her stored reserves. It is possible that in females from stressed populations these ovarian eggs are not properly nourished during the brooding period and thus do not mature.

The result of this would be that all females would not produce a yearly brood but instead put "all their eggs in one basket" in alternate years. This strategy would explain the less than 50% of adults (i.e. all the females) brooding in a given year. This would also explain why several of the non-brooding females sampled at Seal Rock, Oregon were found with only small immature eggs in their ovaries when other females in the same population were brooding. However the lower number of brooding females seen in these populations could be explained by a lack of available energy. Some females may consistently fail to obtain sufficient resources to do more than maintain themselves and never produce a brood.

What is the cause of this small size in all of the above populations? Again the answer is available energy. Initially the star must obtain sufficient energy to maintain itself. If this is not available the star will lose weight and become more susceptible to loss of limbs.

Energy obtained beyond necessary maintenance levels goes into reproduction. Gametogenesis is a lengthy process starting in mid-summer and lasting through winter; a period of inactivity during which feeding activity is low follows. The period of active growth probably occurs during early summer when feeding activity is high and gametogenesis has not yet commenced.

Mauzey (1966) pointed out that the upper size limit of a sea star is probably not set by the maximum size a starfish of particular age can attain, but rather by an interaction with the size and abundance of prey in any particular area. Paine (1972, seminar U of O) found that individual size of Pisaster decreased with increased density. Similarly Leptasterias is held in check by interactions with its immediate environment. In areas of high sea star density an individual Leptasterias is less successful in consistently obtaining calorie-rich prey, and it is hampered by competition for a suitable space to avoid desiccation during low tide. This crowding is caused by other Leptasterias and by other invertebrates which seek crevices and under rock surfaces such as Tegula funebris and Acmaea scutum. This interaction is often seen, especially during summer low tides on clear days; Leptasterias of all sizes are crowded together on the undersurfaces of rocks and almost overlap one another.

Leptasterias is also inhibited by physical conditions. In areas of constant wave action the sea stars must clamp down on the rocks to avoid being washed away. This severely limits Leptasterias' foraging ability and limits the types of prey available to it. The sea star must feed on

the most readily available prey which is the barnacle Balanus glandula. By feeding consistently on these small, low-calorie prey Leptasterias obtains sufficient energy to maintain itself and perhaps reproduce; there is not often surplus energy available for growth, and Leptasterias remains small.

The measured "maintenance factor values," i.e. the proportions of damaged sea stars, were actually an indicator of the toll that the physical and biological environment was taking on a population. Those factors which induced high maintenance values did not appear to deter individual growth in some populations; while the reduced environmental stress suggested by low maintenance factors did not release individuals to grow larger in other populations. These latter populations had high densities of Leptasterias. These observations suggest that the pressure exerted by intraspecific crowding is high and has a measurable effect on the population.

In populations with low density and small individual size, high maintenance factor values could indicate an accumulated relative inability of individuals to sustain maintenance (and growth). In the laboratory growth experiments, regeneration time was relatively fast in overfed animals and retarded in starved Leptasterias.

Leptasterias is capable of both rapidly gaining and losing weight, as was demonstrated in the growth experiments. This indeterminate growth pattern makes it impossible to age a given individual, and hinders determination of the species' life span. Using the data for reproducing females and mortality of young stars up to 2 years old I calculated that

the average sized female in any of the three study populations would have to produce from two and a half to three broods to replace herself. This calculation was made with the assumption that there was no mortality after 2 years of age. Therefore if a female first reproduces at the end of her third year, she would live at least 4.5 years. However, there is some level of mortality for both adult and 2 year old Leptasterias, and the adult stars could live considerably longer than 5 years and produce more than three broods.

This relatively long life-span and the multiple reproductions proposed for Leptasterias is in agreement with its empirical description as a "K-selected" species. If Leptasterias lives this long is there any advantage to increasing in size? A linear relationship between sea star size and the size of prey was demonstrated. The larger the sea star, the larger the prey captured. As a star increases in size it is no longer limited to low-calorie yielding barnacles, but is capable of adding new calorie-rich prey to its diet and thus can grow rapidly.

Some populations I observed consisted of larger sized individuals at relatively low densities. Females from these populations followed the same approximately linear relationship of egg number to wet weight as did females from populations consisting of higher densities of smaller sized individuals. In addition there was some indication that these larger females produced larger eggs, a relatively unusual situation for an echinoderm (Booleotian, 1966).

When compared on a population basis the total number of eggs produced per square meter was much lower in the populations consisting of

larger sea stars. There was also some evidence that the larger females were less successful in brooding their eggs. Also in Leptasterias, like Pisaster, the volume and therefore the metabolic demands increase as the cube of linear dimension (Mauzey, 1966), while the increase in egg number is a linear function of weight. These observations suggest that larger individual size would be an advantage to the individual sea star but not to the population in terms of energy costs and reproductive output.

I do not wish to suggest that the above two types of populations, i.e. low-density with large individual size and high density with small individual size, are alternatives in a given area. I believe that they represent two separate population structures that have become established for separate sets of environmental conditions. The reproductive strategy of brooding allows Leptasterias to exist in a variety of environments and associations, and I believe a given population structure is predictable for a given environment.

In a relatively protected area, where Pisaster is low in number, I believe the resulting population structure of Leptasterias would be characterized by high sea star density and relatively small individual size. Limiting factors for this population would probably be available food and available suitable space. Large individual size would rarely be achieved, as it would require individuals to be consistently more successful in finding and capturing the rarer, more calorie-rich prey. The probability of this happening would be very low in a crowded situation and would decrease with increased density.

In an area that is geographically situated to avoid the onslaught of prevailing wave trains, but is susceptible to winter storms from other directions, the Leptasterias population would be characterized by low density and a large individual size. I found that the younger (smaller) sea stars were more susceptible to damage by physical factors and this results in significant mortality. Because fewer stars survive to become adults the density remains low and the individual adult star is freed from the limitation of resources caused by high density.

These sea stars are more successful in obtaining high-calorie prey and thus grow larger. The larger females produce a correspondingly larger number of eggs so that recruitment on an annual basis is still consistent, although reduced because of mortality. Therefore although this moderately exposed type of environment is less compatible, Leptasterias is still able to maintain a reasonably stable population. Populations in these habitats do not equal the carrying capacities of less exposed environments; but because of the prevailing environmental conditions the potential carrying capacity in these areas is probably significantly lowered.

In an area that is more exposed to the prevailing waves, the Leptasterias population is characterized by small individual size and a low density of sea stars. The more frequent exposure to wave action causes increased mortality in young Leptasterias and inhibits the ability of all sea stars to forage for food. Thus energy intake is reduced which effects mean individual size and reproductive effort. Some females do not produce broods and the males produce a smaller

volume of sperm. As a result fewer young are available annually as recruits to the adult population, and the sea star density remains low.

The above predictable outcomes for Leptasterias populations occur because, unlike sea urchins and other benthic invertebrates with long-lived planktotrophic larvae, Leptasterias young are not subjected to extra-local physical and biological factors that influence initial settlement. In Leptasterias populations all sea stars are subjected to the same set of environmental factors. There may be differential success in dealing with these factors among the individual age classes, but the resulting overall population structure will be well attuned to the local environment.

Leptasterias probably has little overall influence on the intertidal community on the protected outer coast, especially when compared to the larger, more voracious star Pisaster. Paine (1966, 1969) studied the community-shaping role of Pisaster and demonstrated how this star, because of its pattern of prey selection, influenced the species composition and abundance in the rocky intertidal community. Paine (1969) designated Pisaster a "keystone species."

Leptasterias does grow large in some situations and does have the ability to capture larger, motile prey. Thus it would seem to have similar potential to engage in a "keystone" role like Pisaster. However Leptasterias is not resistant to desiccation as is Pisaster and is therefore limited in the range it may forage. It must remain in the cobble-boulder areas where it can find a shaded, moist space to remain when the tide is out. Pisaster can forage over considerably more area

and, if left exposed during low tide, it is able to withstand desiccation for 6-8 hours without apparent damage (Feder, 1956).

This limited foraging range of Leptasterias combined with the fact that foraging time is often reduced because of wave action has perhaps led this sea star to preferentially select the barnacle, Balanus glandula as its major prey species. This species maintains a breeding population in a high intertidal zone refuge and regularly produces sufficient progeny to replace itself and colonize the whole intertidal zone (Connell, 1970). Probably because Balanus glandula is predictably available and widely distributed throughout the boulder-cobble area, less than 17% of the sea stars observed in this study were feeding on other prey.

The removal of barnacles from the substratum provides empty space for the settlement of new barnacles, other invertebrates or algae. Therefore Leptasterias' most influential role in the intertidal community may be the provision of space, a factor that is potentially limiting in the intertidal zone (Dayton, 1971).

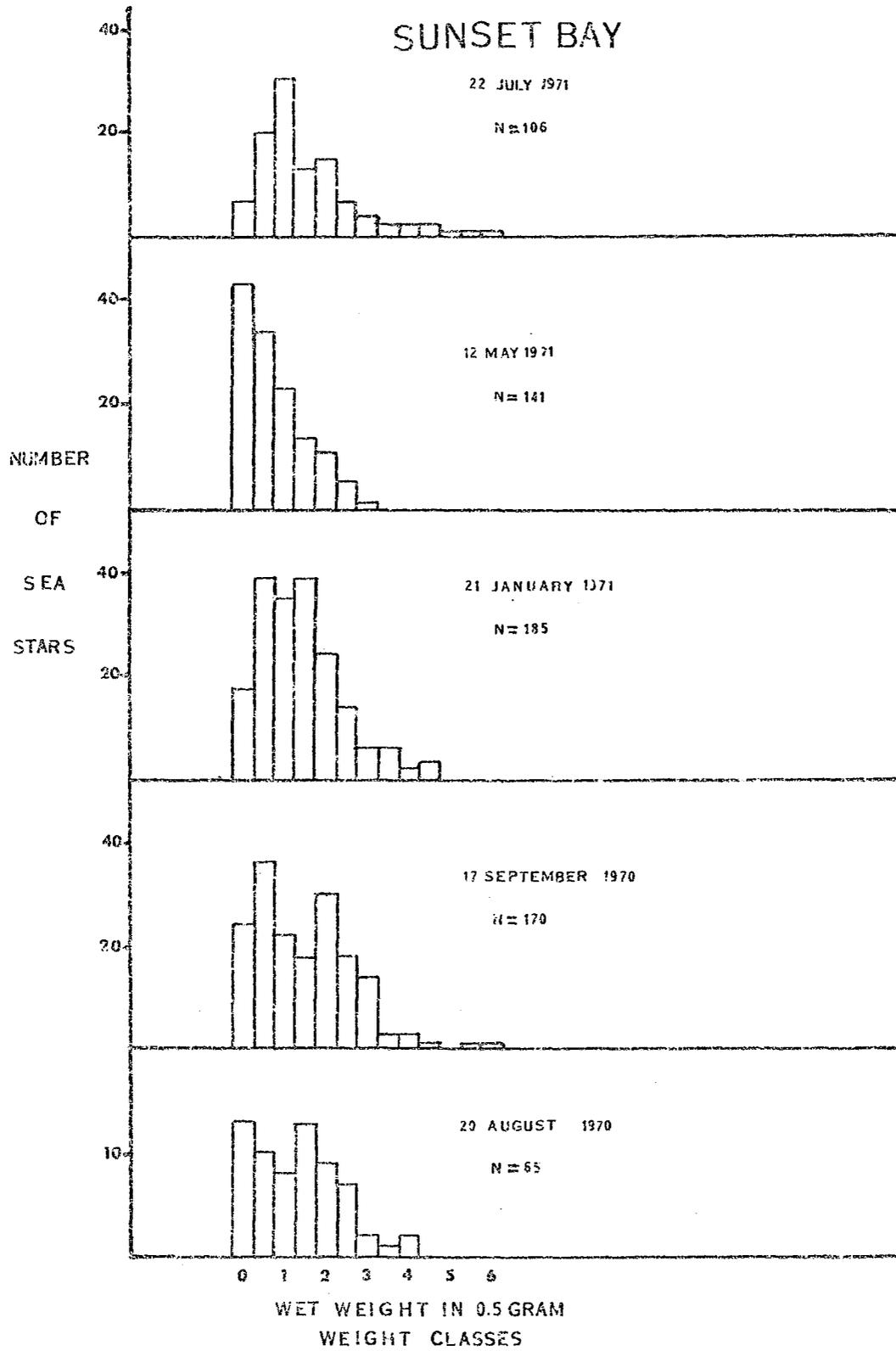
Pisaster is able to withstand long periods of exposure to air, even in direct sunlight (Feder, 1956). Leptasterias is highly susceptible to desiccation, is strongly photonegative (Menge, 1970) and seeks the undersurface of rocks during low tide. Pisaster's southern distribution extends into Baja California while Leptasterias' southern limit is Monterey, California (Menge, 1970). In Monterey, as is the general case to the north, the months August through October are the warmest, but during the summer heavy fogs and overcast conditions serve

to protect intertidal organisms from solar insolation (Feđer, 1970). South of Monterey, daytime summer low tides are often accompanied by clear, sunny weather. I believe Leptasterias' physiological inability to withstand these conditions is the chief factor limiting its southern distribution.

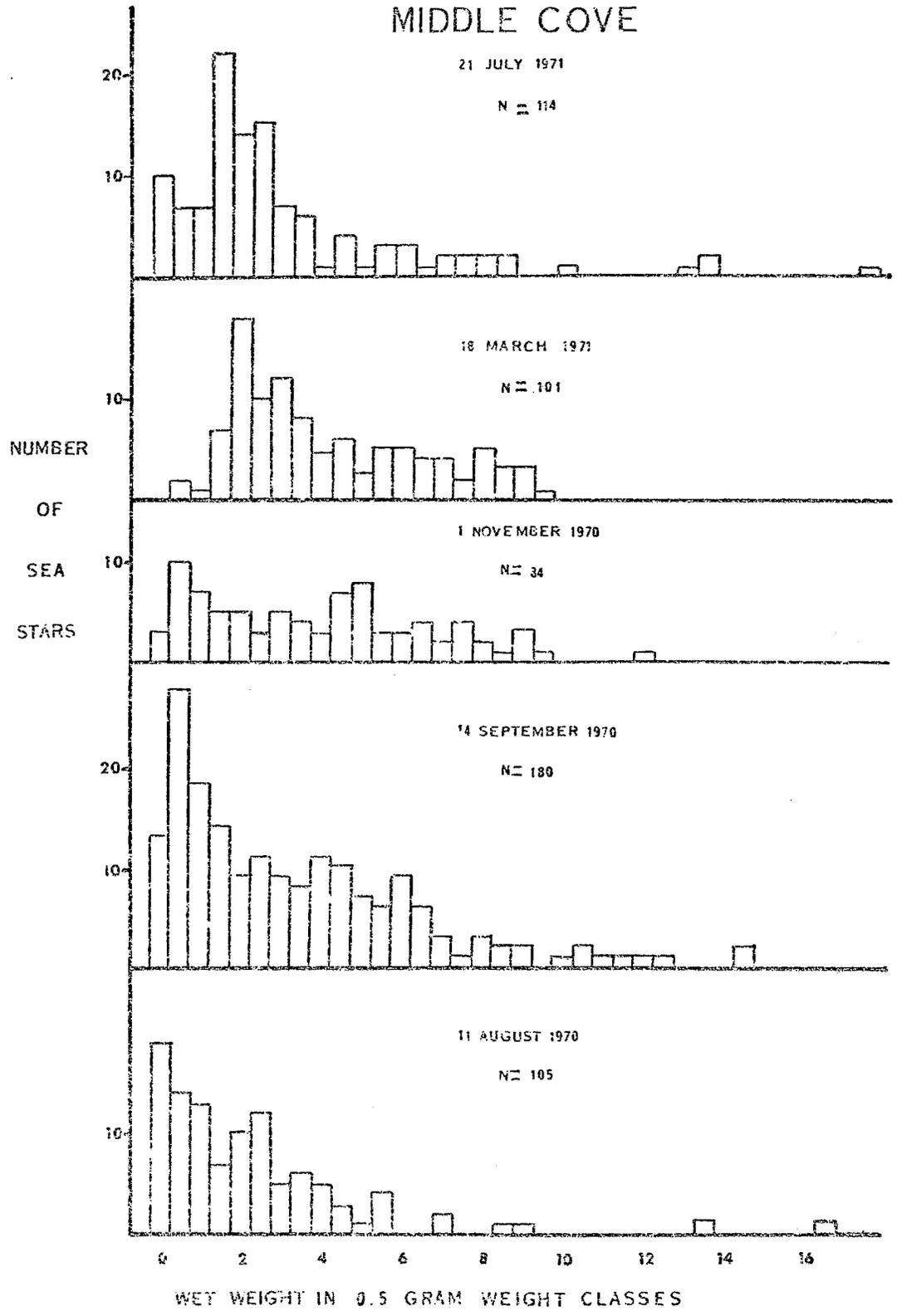
Leptasterias reproductive strategy of brooding allows this species to be successful on a local basis although its dispersal abilities are limited. Physiological limitations probably prevent Leptasterias from being a dominant predator in the intertidal zone and are probably important in limiting the range of its southern distribution.

APPENDIX

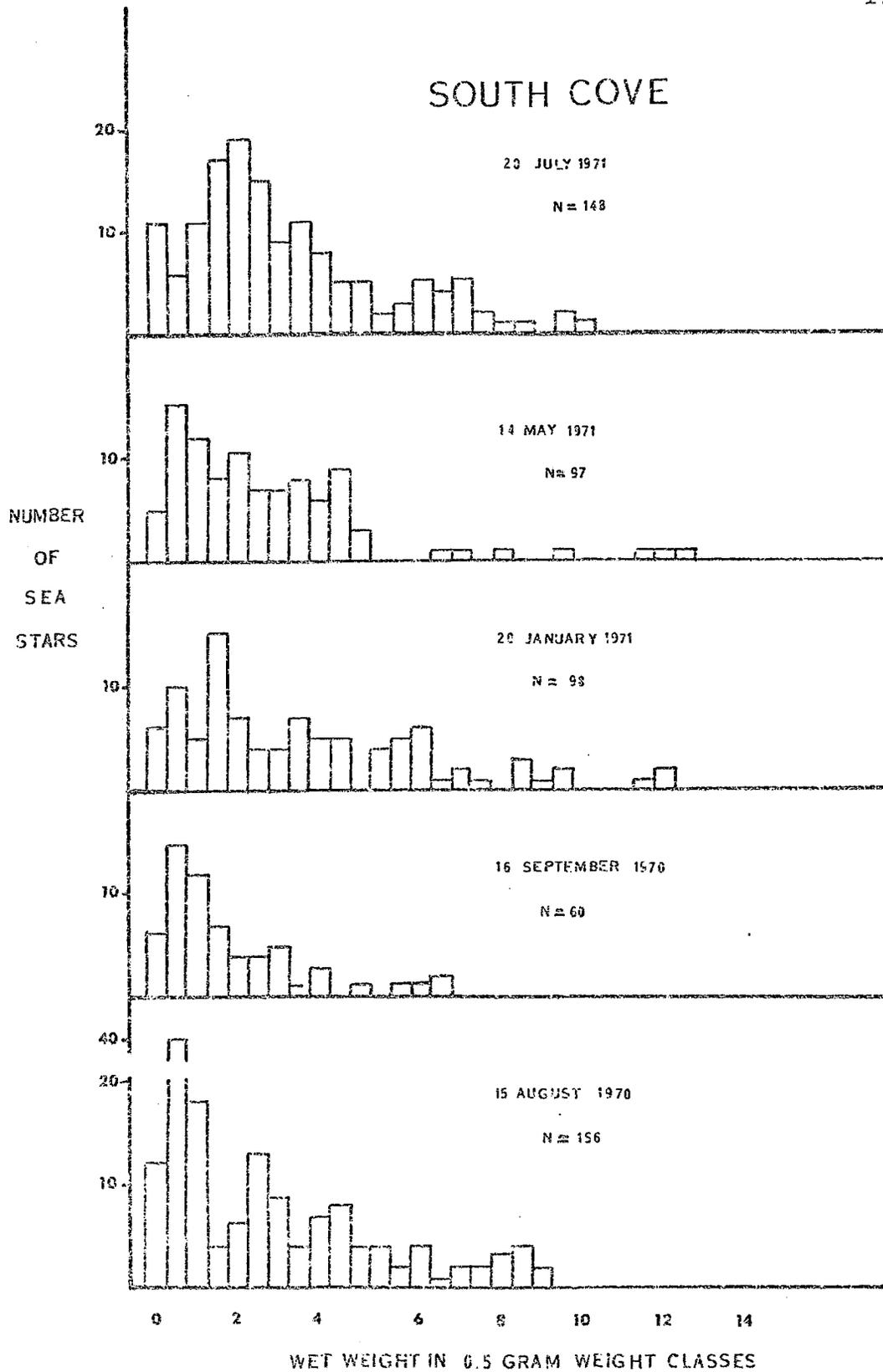
Weight frequency histograms of the three study populations. Sea stars are grouped in 0.5g weight classes; i.e. weight class 1 includes animals weighing 1.0 to 1.49g, etc.



MIDDLE COVE



SOUTH COVE



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