EARLY LIFE HISTORY CHARACTERISTICS OF PACIFIC HERRING, *CLUPEA HARENGUS PALLASI* VALENCIENNES 1847, IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA: HYDRODYNAMICS, DISPERSAL, AND ANALYSIS OF GROWTH RATES.

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ABSTRACT

Cohorts of larval Pacific herring, *Clupea harengus pallasi* Valenciennes 1847, were studied from hatch during the spring of 1985, 1986, and 1987 in the Strait of Georgia, British Columbia. The main objectives were to study the patterns in the larval dispersal process, to study a major spawning area for Pacific herring to determine whether this site may act as a nursery area for the resulting year-class, and to evaluate the current hypotheses concerning survival of the larval year-class for their applicability to Pacific herring.

Results indicated a significant proportion of larval herring which hatched in Lambert Channel quickly dispersed into Baynes Sound, probably through a combination of tidal movements and wind driven surface currents. Baynes Sound was shown to be much more stable than Lambert Channel due to strong stratification through freshwater input and protection from wind mixing by the surrounding land masses which may also have resulted in an earlier spring plankton bloom. Baynes Sound also had significantly higher densities of microzooplankton important to the early feeding herring larvae than Lambert Channel and outside waters. The suite of potential predators was also different between the two channels with Baynes Sound having more hydromedusae and Lambert Channel having more chaetognaths and polychaetes.

Analysis of larval growth rates using an RNA/DNA ratio technique on individuals from the yolk sac stage onwards indicated the larvae initially grew very slowly but, by postflexion were growing over 25 $\%\bullet d^{-1}$ in protein. Starvation did not appear to play an important role in mortality. The RNA/DNA ratio was demonstrated to be directly correlated with a morphometric condition factor for

Pacific herring larvae indicating it can also be used as a condition factor. There was a significant positive correlation between the mean protein growth rate measured with RNA/DNA ratios and the mean nauplii density. Feeding larvae in Baynes Sound were found to be growing faster than those in Lambert Channel suggesting Baynes Sound was being used as a nursery area. Analysis of otoliths suggested there was a significant increase in survival of larval herring having higher growth rates over as little as a 3-week period.

FRONTISPIECE

... "Scientific truth is the remotest of mistresses, she hides in strange places, she is attained by tortuous and laborious roads, but *she is always there!* Win to her and she will not fail you; she is yours and mankind's for ever. She is reality, the one reality I have found in this strange disorder of existence. She will not sulk with you nor misunderstand you nor cheat you of your reward upon some petty doubt. You cannot change her by advertisement or clamour, nor stifle her in vulgarities. Things grow under your hands when you serve her, things that are permanent as nothing else is permanent in the whole life of man. That, I think, is the peculiar satisfaction of science and its enduring reward... ".

H.G. Wells

from Tono-Bungay 1909 (p. 233)

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GENERAL INTRODUCTION

The ability of man to predict and/or control the population numbers of other organisms associated with him has been a tantalizing goal for centuries. Terrestrially this has developed into the practice of agriculture. In the marine environment, except for some successes in aquaculture, man is still essentially at the hunter/gatherer stage of development. Exploitation of fish has increased to the point where abundances of some of the stocks are no longer in excess in relation to man's need, therefore, the mechanisms for population control have become of interest.

Some of the attempts to formally predict future population densities in fisheries (Ricker, 1954; Beverton and Holt, 1957) used a direct spawner to recruit model. Gradually, however, researchers and fishery managers found these models did not always adequately describe their empirical data suggesting there must be other factors involved. Early in the twentieth century a Norwegian fisheries scientist, Johan Hjort (1914), observed that in the northern European fisheries there was a poor relationship between egg abundance and recruits to the fishery. He suggested that it was the larval stages and their subsequent interactions with their environment which might have been the determining stage in the recruitment process. The rationale was that since so many larvae are produced by the spawning adults, even a small change in the mortality rate would result in a large change in the final number of recruits. Hjort proposed two hypotheses from his treatise: (1) A critical period occurred during the initial "nourishment" of the larvae as they switched from endogenous to exogenous food sources and (2) drift of the larvae with the currents moves them into unfavorable areas with respect to growth.

The idea of a critical larval stage stimulated research on early life stages in a multitude of species and various proposed theories were advanced to explain larval survival. The Match-Mismatch Theory (Cushing, 1975) suggested the strength of the year-class was determined by the degree to which it was in phase with the spring plankton bloom. A poor match resulted in high mortality and vice versa. The Stability Hypothesis (Lasker, 1975) was postulated for northern anchovy and concerned wind mixing of the water column and the subsequent destruction of the high concentrations of phytoplankton due to stratification. The Larval Drift Hypothesis (e.g. Hjort, 1914; Nelson et al., 1977; Parrish et al., 1981; Sinclair et al., 1985) suggested physical events, such as Ekman drift, transport larvae away from favorable rearing areas. The Retention Area Hypothesis (Iles and Sinclair, 1982) proposed that larvae were spawned in oceanographically distinct areas which were relatively closed systems of a certain fixed size. It was the size and productivity of these areas which ultimately determined the upper limits of recruitment. The Predation Hypothesis (Moller, 1984; McGurk, 1985b) implied that it was predation on the larvae which determined the amount of mortality suffered by the year-class. Most of the above hypotheses were concerned with the influence of sufficient food concentrations for the larvae and the interaction of the physical environment with them. It should be noted here though that the premise of all these hypotheses is that recruitment to the fishery is determined in the larval stage. While this may be probable, it certainly has not been widely demonstrated (Peterman et al., 1988). This is primarily because the juvenile stages of most of the commercial species are hard to sample and therefore to study in order to verify that the mortality incurred during that stage is not decisive to the overall recruitment.

If early larval nutrition is important in the survival of the early life history stages of fish, adults should spawn in areas which promote growth and therefore

survival of the year-class. Spawning strategies of fish, based on larval fish densities over time, were examined in the northwestern Atlantic Ocean in a 4 year study known as MARMAP (Sherman et al., 1983; 1984). They tried to relate the spawning of species to physical mechanisms as well as biological production. They concluded:

> "... spawning strategies are adaptations of the spawning biomass to topographic and circulation features of the northeast shelf and the annual plankton production in each of the four subareas...".

To date, most studies on larval fish have used traditional sampling techniques to examine the growth and mortality characteristics of larvae. The larvae studied were often spawned in offshore areas necessitating a synoptic cruise program with large vessels in order to complete the study. For this study, Pacific herring, *Clupea harengus pallasi*, were chosen as a study animal primarily because of their spawning traits which allowed better testing of the recruitment hypotheses mentioned above. Pacific herring come in close to shore to spawn, generally in one major spawning wave at known times and locations. This allows a time series of samples to be easily collected daily. The region selected for study is one of the major spawning sites in the Strait of Georgia and the stock is recognized as a distinct entity by the Dept. Fisheries and Oceans Canada. Finally, the large numbers of spawners produce an abundance of larvae.

The overall goal of this study was to examine the post-spawning dynamics of Pacific herring larvae in an important spawning area for the apparent significance of any of the proposed larval survival mechanisms. The first field season (1985) was primarily exploratory in nature as I became familiar with the study area and the

techniques required to adequately sample the herring larvae. During that year, movement patterns of the herring larvae were discovered and it became evident the initial study area was too limited in area. Therefore sampling design was reassessed after the first season and changes were made in the size of the study area, other data to collect, and also in the methods for sampling the microzooplankton. These changes allowed for a better introduction of randomness into the sampling design. Therefore, the most detailed data sets resulted from the 1986 and 1987 field seasons.

This thesis has been divided into two chapters and only the data pertinent to the problem at hand are included for clarity of content. The first chapter deals with the relationship of the herring larvae with their environment and is divided into three separate parts. First, the study areas in the region were characterized physically with basic hydrographic measurements. Secondly, the study area was assessed for microzooplankton food resources important to the larvae during the period of study. Finally, the dispersal patterns of the emerging herring larvae were monitored as they moved away from the spawning grounds. Chapter 2 concerns the relative success the larvae experience over the duration of the study period. The operating assumption is that success, at the larval stage at least, is reflected by the growth rate of an animal as growth is the final result of the environmental factors operating on an individual. I have used a relatively new biochemical technique to measure the growth rates of individual larvae. In addition, a growth specific survival hypothesis is tested using data obtained from otolith microstructure.

Chapter 1. Early Life History Characteristics of Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia, British Columbia: I. Hydrodynamics and Dispersal.

I. INTRODUCTION

The role of the physical environment on the early life history stages of fish is now being recognized as an important component in the overall recruitment process. While Hjort (1914) postulated about the effects of currents on transporting larvae out of good feeding areas into poorer ones, it has only been recently that research has been conducted on some of the physical mechanisms. For example, Peterman and Bradford (1987) have related wind strength to the survival of northern anchovy year-classes while Sinclair et al. (1985) relate differences in survival of Pacific mackerel to El Nino events.

A relatively recent development has been the observation of possible oceanographic retention areas where larvae are retained in a particular geographical area due to the unique hydrographic properties of the region. These retention areas have been found to occur in the North Sea, the Irish Sea, the Gulf of Maine, and the St. Lawrence River estuary and are associated with physical processes such as gyres and frontal zones (Iles and Sinclair, 1982). Their theory suggests it is the physical size of the retention areas and their production that ultimately determines the upper limit to the size of the surviving year-class.

The movement of larvae into or away from favorable areas is suggested as playing a major role in the survival of the larval year-class (e.g. Hjort, 1914). Being

moved away from a favorable area could mean moving into one where there is unsuitable food in either type or amount or into areas where there is an abundance of predators. Coastal estuaries and embayments have been shown to be important nursery areas for the larvae and juveniles of many species of marine fishes (e.g. Joseph, 1973; Clarke, 1974; Lenanton, 1982). Atlantic herring larvae have been documented to drift from the spawning grounds to nursery grounds. In the Gulf of Maine, larvae that hatched offshore rapidly moved into the bays and estuaries along the coast and appeared to be retained there by means of estuarine circulation (Graham, 1972; 1982). Cushing (1986) indicated that herring larvae which were spawned near the coast of Britain drifted to their nursery grounds off the coast of Germany and Denmark. The mechanisms behind larval drift have been studied in a few cases and have been shown to occur through processes such as Ekman drift (Nelson et al., 1977) and estuarine circulation (Graham,1972; Henri et al., 1985).

There is an obvious evolutionary advantage for adults to spawn in areas and under certain conditions which tend to enhance the survival of their offspring. If the traits which which make an area suitable for spawning are relatively consistent in time and space, then spawning should regularly occur in these areas and would be adaptive. One of the major long-term spawning sites for Pacific herring (*Clupea harengus pallasi*) has been in the Denman Island area (Dept. Fisheries and Oceans Statistical Area 14). Egg survey data between 1951 and 1980 indicate that up to 80% of the total spawn in the St. of Georgia may be deposited in this area (Hourston et al., 1972; Hourston, 1981) and documented spawning records exist as least as far back as 1942 (Hourston, 1980). Therefore, this region may have features which are important to the early life history stages of Pacific herring.

II. OBJECTIVES

The objectives of this study were:

1. To map and compare the basic physical characteristics of the general sampling area.

2. To determine the important food groups relative to Pacific herring larvae in this region and compare the separate sampling areas with respect to potential prey densities.

3. To evaluate the areas for associated invertebrate predators.

4. To follow the dispersal patterns of the emerging herring larvae based on larval density changes away from the known spawning areas and compare the distribution patterns with the physical and biological characteristics of the study area.

III. MATERIALS AND METHODS

A. Study Site

Baynes Sound and Lambert Channel are situated on the western side of the Strait of Georgia, British Columbia with center channel midpoints of 49°32'N, 124°50'W and 49°31'N, 124°42'W respectively (Fig. 1.1). The region is classified as being in the northern Strait of Georgia and is characterized by weak and variable tidal currents with speeds of approximately 10 $cm \cdot s^{-1}$ (Thomson, 1981). Little is known of the tidal circulation in this area although there is some evidence of a residual counterclockwise circulation based on a drift bottle study (Thomson, 1981). Current meter observations in Lambert Channel also indicate there is a net tidal transport south of approximately 1 $km \cdot d^{-1}$ at 30 m (M. St. John, Dept. Oceanography, Univ. British Columbia, pers. comm.). On the ebb tide, tidal flows are in a southeasterly direction and also out of the northerly entrance to Baynes Sound over Comox Bar. The flow direction reverses on the flood tide.

Baynes Sound is separated from Lambert Channel by Denman Island and is approximately 40 m deep in the center of the channel. It has a northern opening to the Strait of Georgia over Comox Bar which has a depth of 3 m at low tide. The southerly entrance is through a narrow channel approximately 40 m in depth. There is freshwater input to Baynes Sound from the Comox River in the northern section as well as from several small creeks on the western side. Lambert Channel is situated between Denman and Hornby Islands and has a maximum depth of 60 m at center channel. For the purpose of this study, Lambert Channel has been defined to extend along the easterly side of Denman Island and south of Hornby Island. The

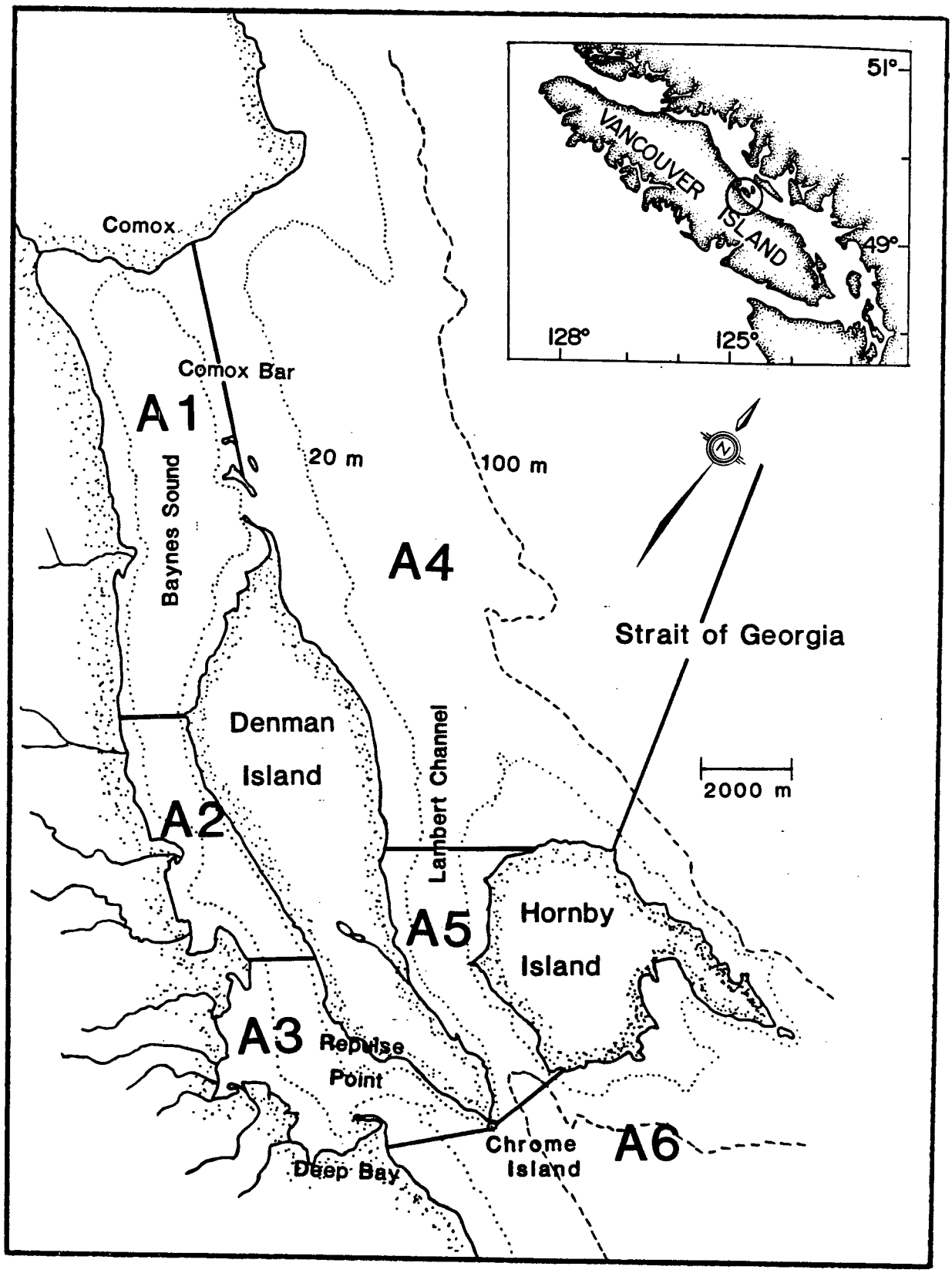


Figure 1.1. Diagram of study site showing the 6 defined sampling areas.

northerly section lies on a sloping ledge while the southerly portion is deeper and much steeper.

In 1985, three permanent transects were established on the east side of Denman Island to monitor the hatching herring larvae and three sampling stations in Baynes Sound (see below Section E for further details). It became apparent after the first year that the study site was too small. Therefore, in 1986 and 1987 the study site was divided into 6 different areas which were then further subdivided into 10 equally spaced transects perpendicular to shore. Transect 1 was the southernmost while transect 10 was the most northerly. This scheme naturally divided Baynes Sound and Lambert Channel into areas 1-3 and 4-6 respectively although not all areas were the same size (Fig. 1.1). Each transect was composed of three sampling stations. For transects within a channel, a station was located near each shore and one in center channel. The other transect stations on the offshore extending transects were sampled at approximately 50-100, 600 and 1800 m out from shore. A stratified random sampling protocol was adopted and two transects from each area were randomly selected during each sampling period.

B. Life History Synopsis

Pacific herring (*Clupea harengus pallasi*) usually begin to spawn in their third year when they have reached a standard length of 185 mm and a weight of 95 g. In British Columbia, they may spawn annually in February to March on inshore spawning grounds in the intertidal and shallow subtidal zones where females may lay up to 40,000 eggs each. Reproduction may occur up to 15 years of age. The adhesive spherical eggs are mainly attached to submerged vegetation and incubation takes approximately two weeks at 8 °C. The hatching larvae are transparent and

are approximately 8 mm long with a large yolk sac which is usually depleted in about 6 days. Metamorphosis from the larval to the juvenile form occurs about 10 weeks after hatching at a standard length of 25 to 30 mm. (see Hourston and Haegele, 1980 for review).

C. Sampling Vessels

In 1985, sampling was conducted with a 14 m commercial fishing boat equipped with a Loran C and radar for positioning purposes. Sampling of the herring larvae was conducted primarily at night in both Lambert Channel and Baynes Sound. Based on the results from 1985, I decided a greater range of areas required to be sampled as well as shallower depths and therefore, for 1986 and 1987, I switched to a 6 m open outboard vessel. This necessitated sampling during the daylight hours due to logistic constraints. During the last week of the sampling period in 1987, sampling was conducted from the MV Caligus, a 20 m vessel from the Dept. of Fisheries and Oceans Canada.

D. Physical Measurements

Wind data from March 1 to May 31 were obtained from daily observations made every three hours by staff at the Chrome Island light station at the extreme southern tip of Denman Island. This data record was part of the B.C. Shorestation Oceanographic Program run by the Institute of Ocean Sciences, Dept. Fisheries and Oceans. I arbitrarily chose three times per day (0335 h, 1235 h, and 2135 h) to estimate daily mean wind speeds and direction from the early morning, midday and late evening respectively. Wind directions were broken down into their two component vectors before averaging. Data were plotted in a stick diagram where the

length of the stick is proportional to the wind strength and the orientation is indicative of the wind direction.

Temperature/salinity (T/S) profiles were taken in the middle of each sampling area (transect 5, station 2) in both 1986 and 1987 using an Autolab^{TM} Model 602 portable temperature/salinity probe which was calibrated in the laboratory before the field season. Only one profile was obtained in 1985. The water column was sampled at depths of 0, 5, 10, 15, 20, 30, and 40 m. Surface water temperature was also measured with a glass thermometer and samples for salinity were taken from a surface bucket sample for correction of drift of the T/S probe over the sampling period. Sigma-t values (water densities) were calculated from the raw data using the formula described in "The Practical Salinity Scale" (Lewis, 1980). Daily surface temperatures at high tide were obtained from the staff at the Chrome Island light station.

Surface water movement was investigated in 1987 using a 3 m wide window-blind current drogue suspended at 3 m depth. This was deployed from a small boat and left for several hours to freely drift. Location was determined for the first 8 trials with a sighting compass by triangulation from three different sightings to the shore and with radar for the last two trials.

E. Phytoplankton Standing Stock

In 1985 four vertical profiles were taken with a large volume centrifugal pump (17 $l \cdot s^{-1}$ flow rate) in Baynes Sound to depths of 25 m to determine the depth of the chlorophyll *a* maximum and fluorescence measured with a Turner^{TM} flow-through fluorometer (Model 111). Output from the fluorometer was recorded

on a chart recorder. Fluorometer values were standardized by filtering 500 ml of seawater through a 4.7 cm Whatman^{TM} GF/C glass microfibre filter for each profile. The filters were then put in waxed paper envelopes, labelled, and frozen. Chlorophyll *a* values were determined in the laboratory using the fluorometric procedure outlined in Parsons et al. (1984).

In 1987, vertical profiles were taken in four different areas as described above (using a smaller diaphragm pump (0.6 $l \cdot s^{-1}$ flow rate) to depths of 15 m to determine the approximate depth of the chlorophyll maximum. Then a horizontal transect at the depth of the chlorophyll maximum was taken around Denman Island for comparison of Baynes Sound and Lambert Channel. Samples were standardized as described above for 1985.

F. Zooplankton Food Densities

1. Food Item Identification

In 1985, larval herring were captured using a night light and a lift net in area 1 to 5 from Day 84 to Day 121. Larvae were immediately picked off the net using forceps and individually preserved in vials with 5% formalin in seawater. Larvae in the last sampling periods (Day 121) were captured using bongo nets in brief tows (see below for further details on bongo net sampling). In the laboratory, 220 fish were examined for prey items in the digestive tract of the larvae using a dissecting microscope to view items through the wall of the gut. This technique was applicable to the herring larvae as the lift net did not damage them and they therefore remained clear after formalin preservation.

In 1986, larval herring were sampled over the study period in all 6 areas using brief oblique bongo net tows of less than 60 s to 20 m depth. The contents of the codend were immediately poured onto a 350 μm mesh screen, the larvae picked off with forceps, and placed into vials with 5% formalin in seawater. In the laboratory, larval guts were dissected out using fine needles. The contents were identified and measured with an ocular micrometer on a dissecting microscope. Two periods were chosen from Baynes Sound and Lambert Channel (Day 97 and Day 118) to represent the prey items being utilized by early and later feeding larvae. A total of 100 prey items were counted at each period in each channel. This equated to 100 fish being dissected for the first period and 32 fish for the second. Regurgitation or defecation was assumed not to be a problem as food items would probably not be selectively expelled.

2. Microplankton

In 1985 on Day 94, 18 uniformly spaced samples around Denman Island were taken in Baynes Sound and Lambert Channel using a bongo net with 54 μm dark green Nitex^{TM} mesh. Samples from the codends were preserved in 5% formalin in seawater. Volume of water filtered was determined with an Oceanics^{TM} digital flowmeter Model No. 2030 mounted in the mouth of the net. In the laboratory, three 5 ml aliquots were randomly taken from the total measured volume and counted for nauplii and copepods. Densities per m^3 were calculated and then converted to density per m^2 based on the depth of tow (e.g. number$\cdot m^{-2}$ = number$\cdot m^{-3}$ x depth).

In 1986 and 1987 during each sampling period, two transects were randomly chosen in each area and two samples taken on each transect; one near shore and the

other in the center of the channel or at the furthest offshore station. Samples were collected to 30 m or the bottom using a 30 m hose (2.0 cm inside diameter) attached to a diaphragm pump (250 $ml \cdot s^{-1}$ flow rate). The protocol involved twice lowering and raising the hose at a rate of 1 $m \cdot s^{-1}$ and pumping the resulting water through a 54 μm sieve to give a total of 1 l of water collected at each meter depth. The sample was preserved in 5% buffered formalin in seawater. In the laboratory, the entire sample was enumerated in a Bogorov tray under the following categories based on results from the gut contents analysis and the main groups of microzooplankters present: copepod eggs, nauplii, small copepods (< 1000 μm), large copepods (> 1000 μm), pteropods, bivalve veligers, bryozoan cyphonautes, decapod zoea, and the harpacticoid copepod *Microsetella* sp. Densities of the diatom *Thalassiosira eccentrica* were calculated by counting eight fields in the tray, determining the mean number per unit area and multiplying by the area of the tray.

G. Potential Zooplankton Predators

The densities of the predatory copepod, *Tortanus discaudatus*, were estimated in 1986 and 1987 in the 6 sampling areas from the microzooplankton samples taken with the diaphragm pump as described above. Densities of the hydomedusa, *Aequorea victoria*, the chaetognath, *Sagitta elegans*, and the polychaete, *Tomopteris septentrionalis*, were estimated from the bongo net samples for herring larvae (see below) in each of the study areas in Baynes Sound and Lambert Channel.

H. Larval Distribution and Dispersal

Sampling of larval herring in 1985 was mainly concentrated in Lambert Channel from Day 91 to 124 at three fixed transects perpendicular to the shore, equivalent to the 1986-1987 areas and transects of A5T4, A5T10, and A4T3. Each transect was composed of four stations at 100, 250, 500, and 1000 m from shore except No. 3, the northernmost, where the stations were 250, 500, 1000, and 2000 m offshore due to the shallow depths close to shore and the depth limitations of the sampling vessel. Baynes Sound was sampled from Day 90 to Day 120 at three fixed stations, equivalent to the 1986-1987 transects of A1T5S2, A2T6S2, and A3T4S2. In 1986 and 1987, two transects were randomly chosen in each study area and samples collected at all three stations.

The herring larvae were captured using 22 cm diameter bongo nets with 350 μm Nitex^{TM} mesh. Both frame and nets were black to reduce net avoidance by the larvae (LeBrasseur et al., 1967). Single cycle oblique tows (e.g. down and up) at a towing speed of 1.5 $m \cdot s^{-1}$ were done to 40 m or the bottom, whichever was shallower. Tows were done at night during 1985 and during daylight hours for 1986 and 1987. Tow times ranged from 30 s to 2-3 min. The nets were rinsed and the sample from each of the nets immediately preserved in 5% formalin in seawater. An Oceanics^{TM} digital flowmeter Model No. 2030 was mounted slightly off center in the mouth of the net to measure the amount of water filtered during the plankton tow.

Vertical distribution patterns for herring larvae were examined in 1985 by taking stepped oblique bongo net tows from 0 to 10 m, 0 to 20 m, and 0 to 30 m in

the same location at specified time intervals. Larval concentrations were converted to density (number$\cdot m^{-2}$) and the percentage of larvae at each depth interval calculated by subtraction. This was done for two time periods in 1985, Day 95 and Day 113. Horizontal distribution patterns of herring larvae with respect to the shore were evaluated by examining the larval densities along the transects over time. Dispersal patterns were determined by monitoring the change of larval densities (number$\cdot m^{-2}$) over time in each of the study areas.

I. Data Analysis

I used the SYSTAT^{TM} data package for a PC computer to analyze the data collected for this project. Parametric statistics were the tests of choice but, when the assumptions of normality or equality of variances did not hold and transformations could not correct the problem nonparametric methods were used. Sampling dates were converted into Calendar days to make data analysis easier. This format was used consistently throughout the thesis.

IV. RESULTS

A. Physical Studies

During Calendar Days 60 to 151 (March through May) the prevailing wind direction was from the south for all three years (Fig. 1.2). The wind was also the strongest from the south with mean speeds approaching 8.3 $m \cdot s^{-1}$ from the southeast quadrant and 6.4 $m \cdot s^{-1}$ from the southwest. Wind speeds generally tended to decrease over the season except for 1987.

The surface water temperatures from all three years were fairly similar in pattern starting at approximately 7.5 °C on Day 60 and increasing to 14 °C by Day 150 (Fig. 1.3). The first half of the study period showed less variation in surface temperature than the latter half. Mean values for temperature and salinity at several depth intervals indicated Baynes Sound differed from Lambert Channel mainly by having lower salinities in the surface waters and near the bottom at the 40 m interval (Table 1.1). This pattern was maintained through both 1986 and 1987. Mean temperature values showed no difference between the two channels except for the 30 and 40 m depth in 1987. Note the time periods of sampling for the two years were different in time duration.

The sigma-t values (water densities) calculated from the T/S profiles in 1986 from the different areas indicated there was strong stratification occurring in the two northern areas in Baynes Sound over the duration of the study. The stratification was not as intense in Area 3 and in Lambert Channel (Areas 4, 5, and 6), the water column appeared to be fairly well mixed from the surface to 40 m (Fig. 1.4). While sampling was not as intense in 1987 the same basic trends

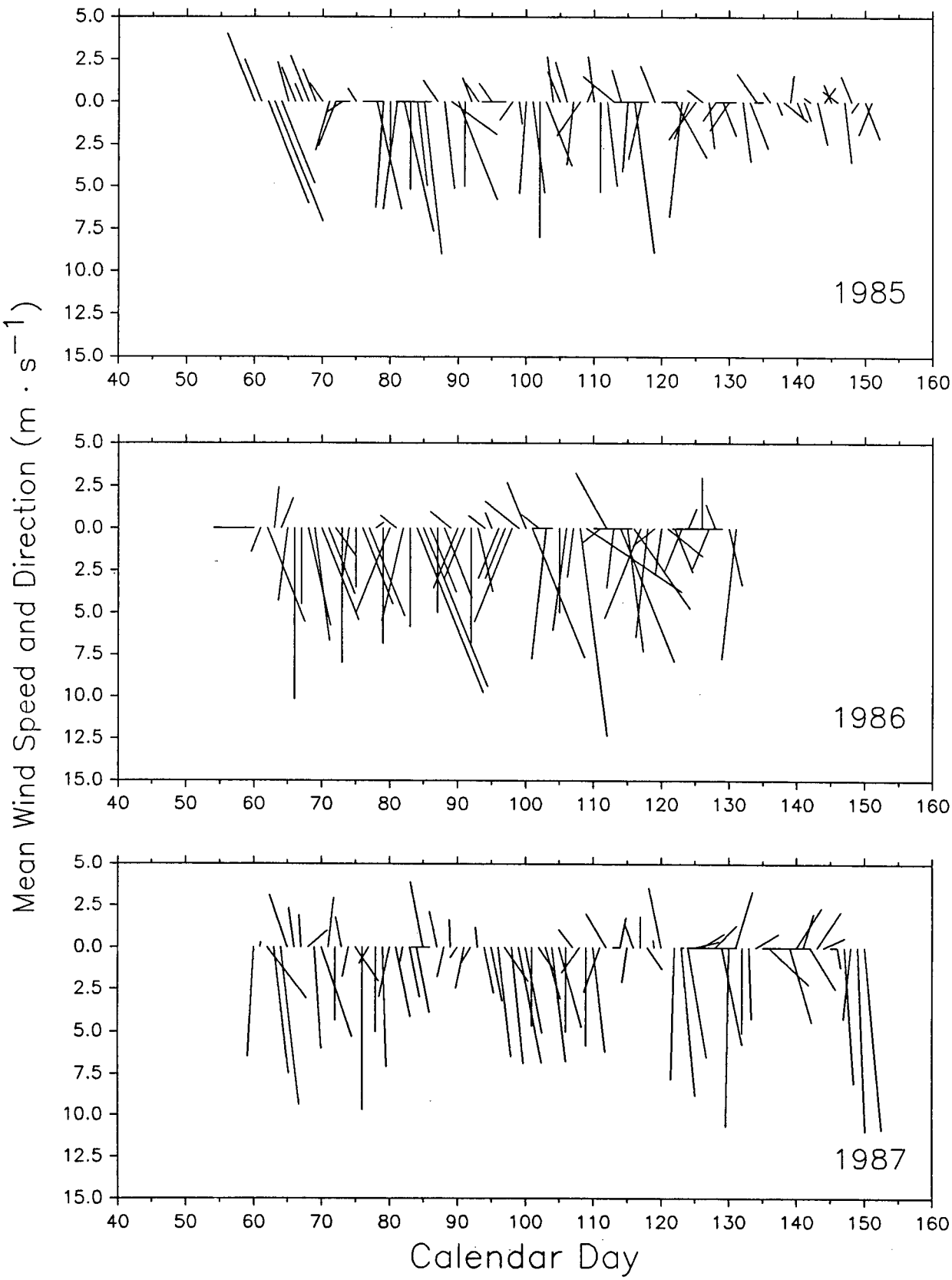


Figure 1.2. Wind vector stick plots for Calendar Days 60 to 150 from 1985 to 1987. Values are daily means from 3 times. Data from Chrome Island light station.

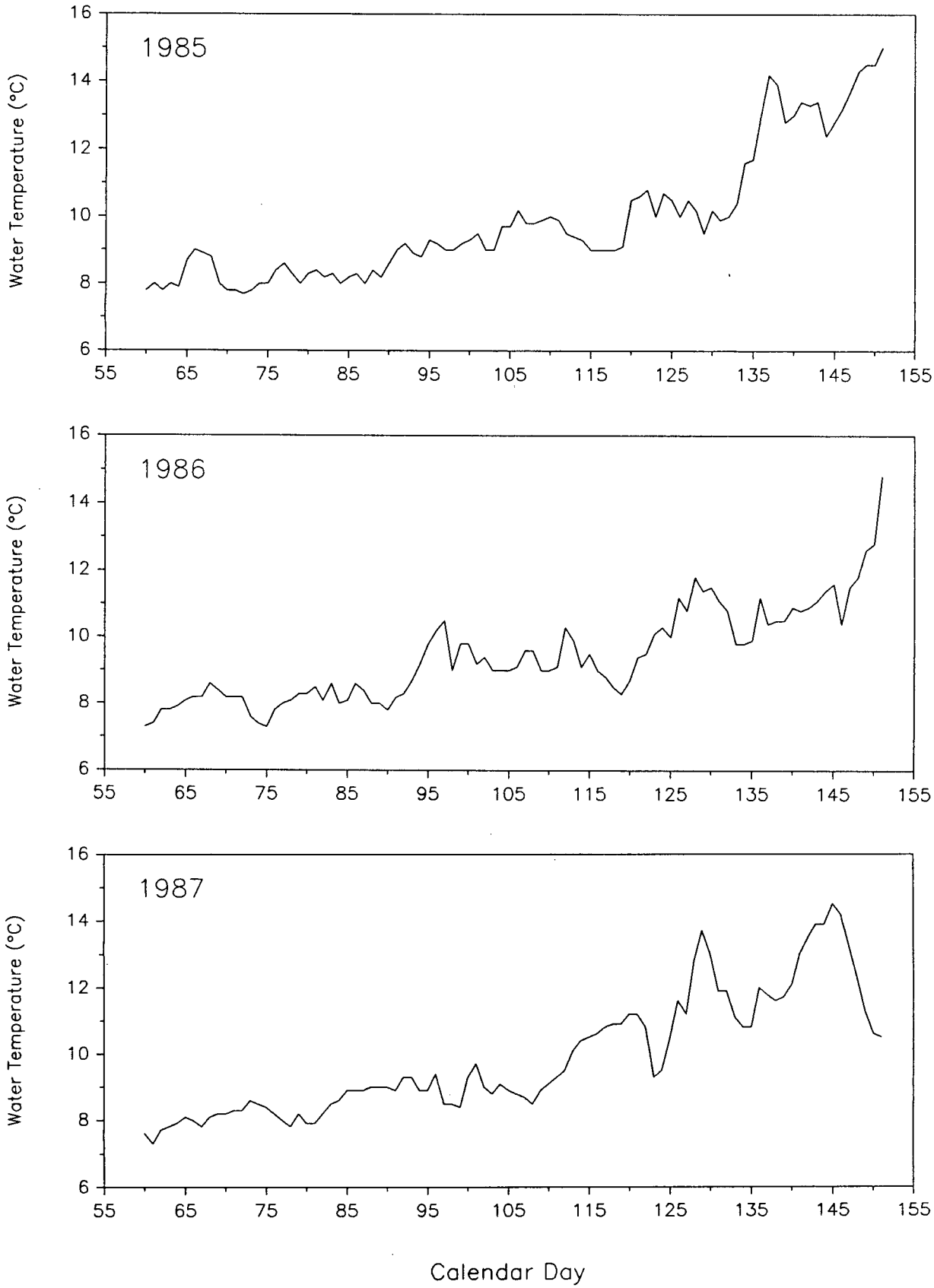


Figure 1.3. Daily water surface temperatures taken at high tide for Calendar Days 60 to 150 from 1985 to 1987. Data from Chrome Island light station.

Table 1.1. Mean temperature and salinity values from T/S profiles taken during 1986(Day 79-133) and 1987(Day 81-95) in Baynes Sound and Lambert Channel. Sample numbers: for 1986 - BS=23, LC=25; for 1987 - BS=6, LC=9. (+ = $p<0.05$ Student's t-test, * = $p < 0.05$, Mann-Whitney U test).

Depth	Temperature (°C)				Salinity (ppt)			
	Baynes		Lambert		Baynes		Lambert	
(m)	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
				1986				
0	9.54	1.39	9.44	1.02	26.69	1.66	28.29	0.54 *
1	9.31	1.15	8.93	0.84	27.08	1.32	28.31	0.44 *
5	8.67	0.69	8.58	0.68	28.40	0.39	28.53	0.49
10	8.36	0.50	8.37	0.55	28.77	0.25	28.80	0.46
20	8.11	0.37	8.15	0.46	29.09	0.27	29.17	0.42
30	8.00	0.30	8.04	0.36	29.27	0.19	29.34	0.33
40	7.97	0.26	8.01	0.31	29.37	0.17	29.52	0.22 *
				1987				
0	7.72	1.40	8.94	0.53	22.07	5.32	28.04	0.93 *
1	8.52	0.37	8.73	0.55	27.08	0.88	28.21	0.32 *
5	8.20	0.17	8.44	0.46	28.34	0.28	28.49	0.13
10	8.05	0.11	8.13	0.21	28.55	0.16	28.72	0.27
20	8.01	0.12	8.04	0.09	28.82	0.12	29.00	0.36
30	7.90	0.09	8.04	0.10 +	28.96	0.08	29.22	0.33
40	7.87	0.12	8.09	0.13 +	29.04	0.07	29.37	0.29 *

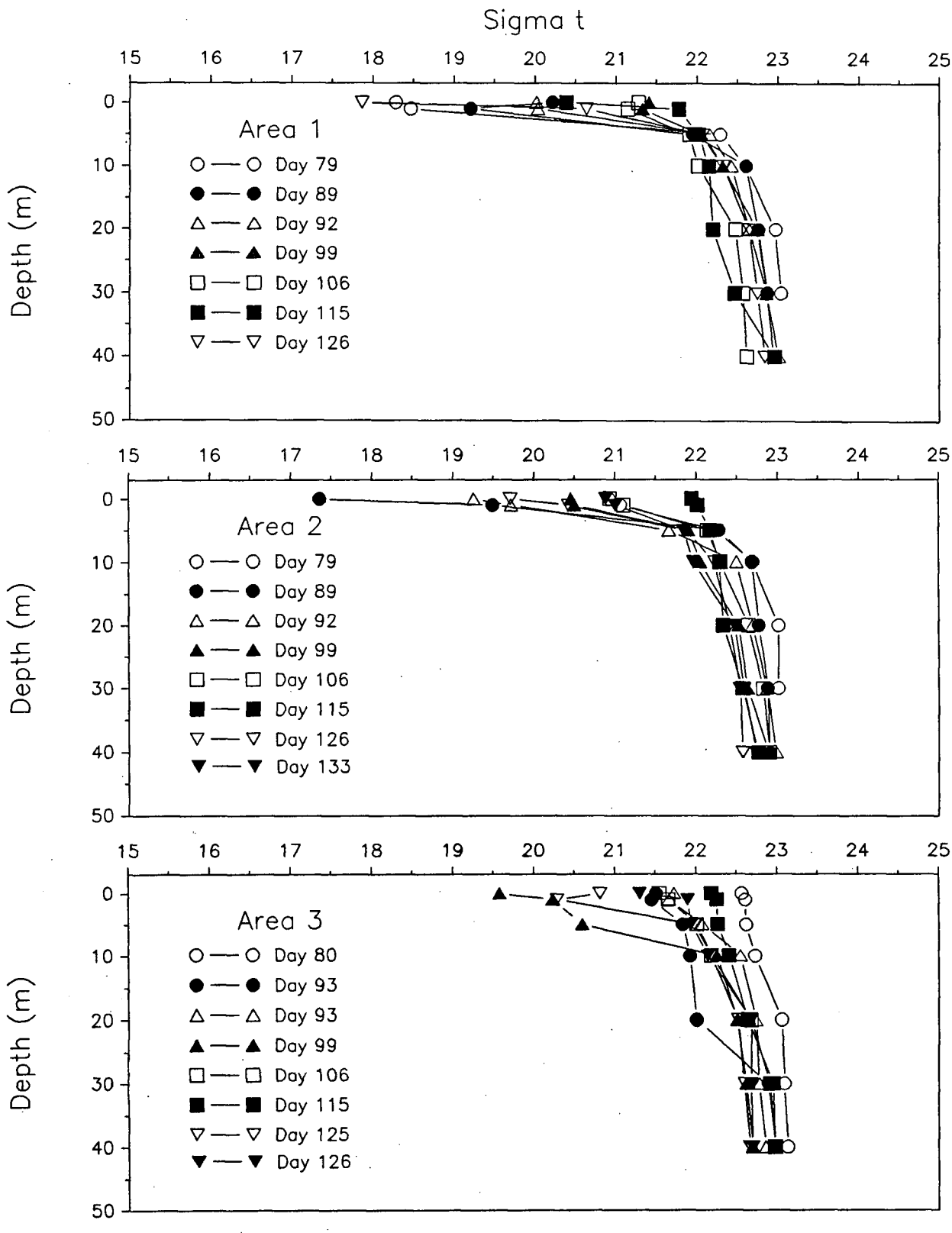


Figure 1.4. Sigma t profiles by sampling area over time for 1986.

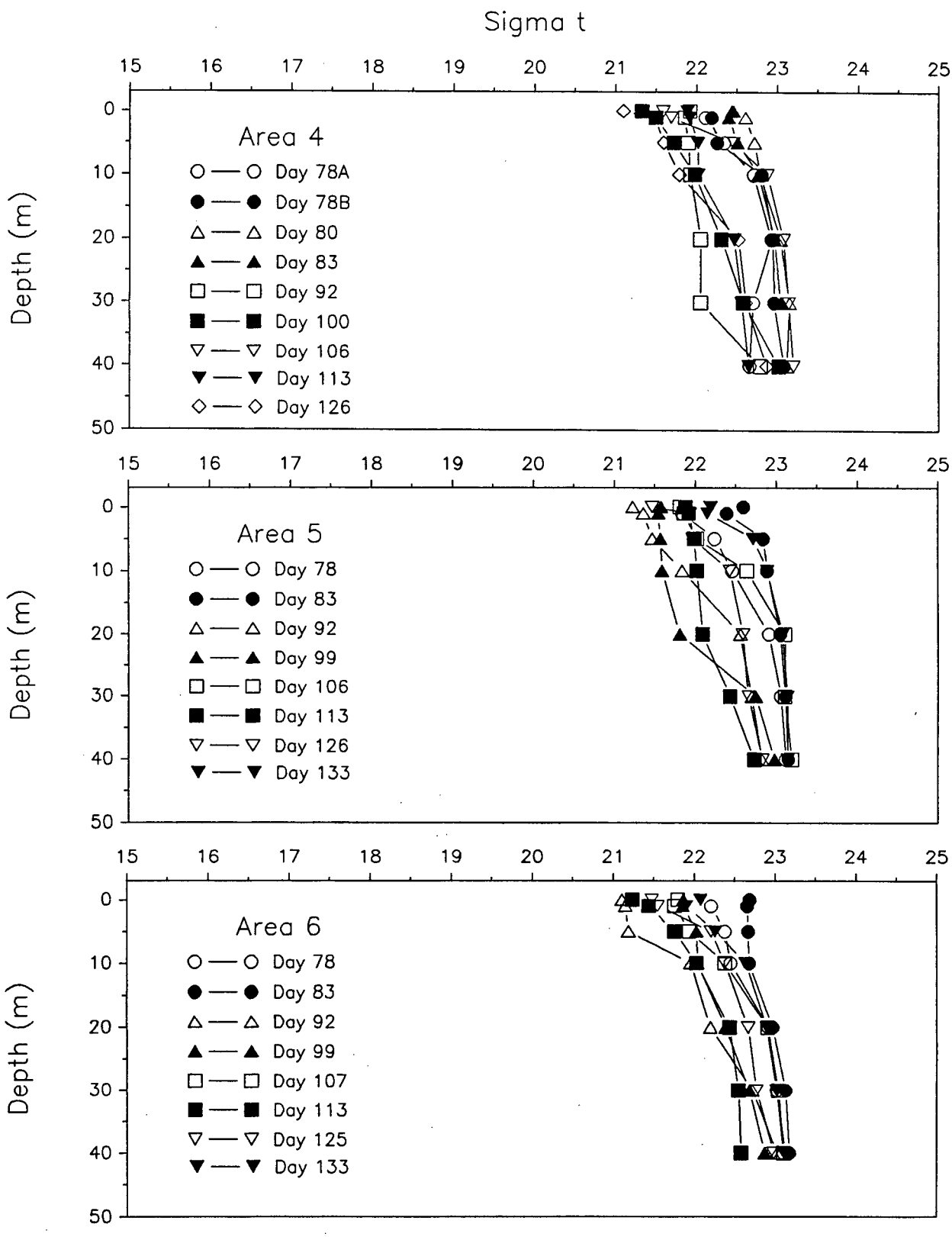


Figure 1.4. (continued).

appeared to be consistent between years (Fig. 1.5). Incidental samples taken in the deeper water outside the study areas in 1986 and 1987 showed the upper 40 to 50 m of the water column was relatively well mixed and closely resembled Area 6 (Robinson, unpub. data).

Speeds for the current drogue studies ranged from 40 to 854 $m \cdot h^{-1}$ (Table 1.2) (Fig. 1.6). The mean speed for trials done in Lambert Channel, excluding #5, was 325 ± 212 $m \cdot h^{-1}$ (x ± sd, n=3) while trials in Baynes Sound, excluding #2, was 199 ± 76 $m \cdot h^{-1}$ (x ± sd, n=5). The two trials were excluded because they were conducted in regions of extreme current influence. The resulting vectors of the current drogue tracks did not always follow the expected direction of tidal flow (e.g. northwest for flood tides and southeast for ebb tides). At the mouth of Baynes Sound, current drogue tracks exhibited a possible counterclockwise pattern. Trials #4, 5, and 6 showed movement patterns contrary to the expected tidal flows and were more in agreement with wind directions.

B. Phytoplankton Standing Stock

The vertical profiles for chlorophyll *a* in 1985 on Day 90 showed more chlorophyll *a* in area 2 than in area 3 (Fig. 1.7). Values ranged from approximately 1 to 3.5 $\mu g \cdot l^{-1}$ and there was generally a pattern of lower surface values, a maximum at 5-7 m and dropping back to lower concentrations at 15 m and below. By Day 121, in the north and south regions of area 3, the general pattern was the same as before but, the chlorophyll maximum in the northern section was quite high (8 $\mu g \cdot l^{-1}$) and much narrower than the one on transect 3. The profile from transect 3 showed a much sharper drop from the chlorophyll maximum to the lower values at 15 m.

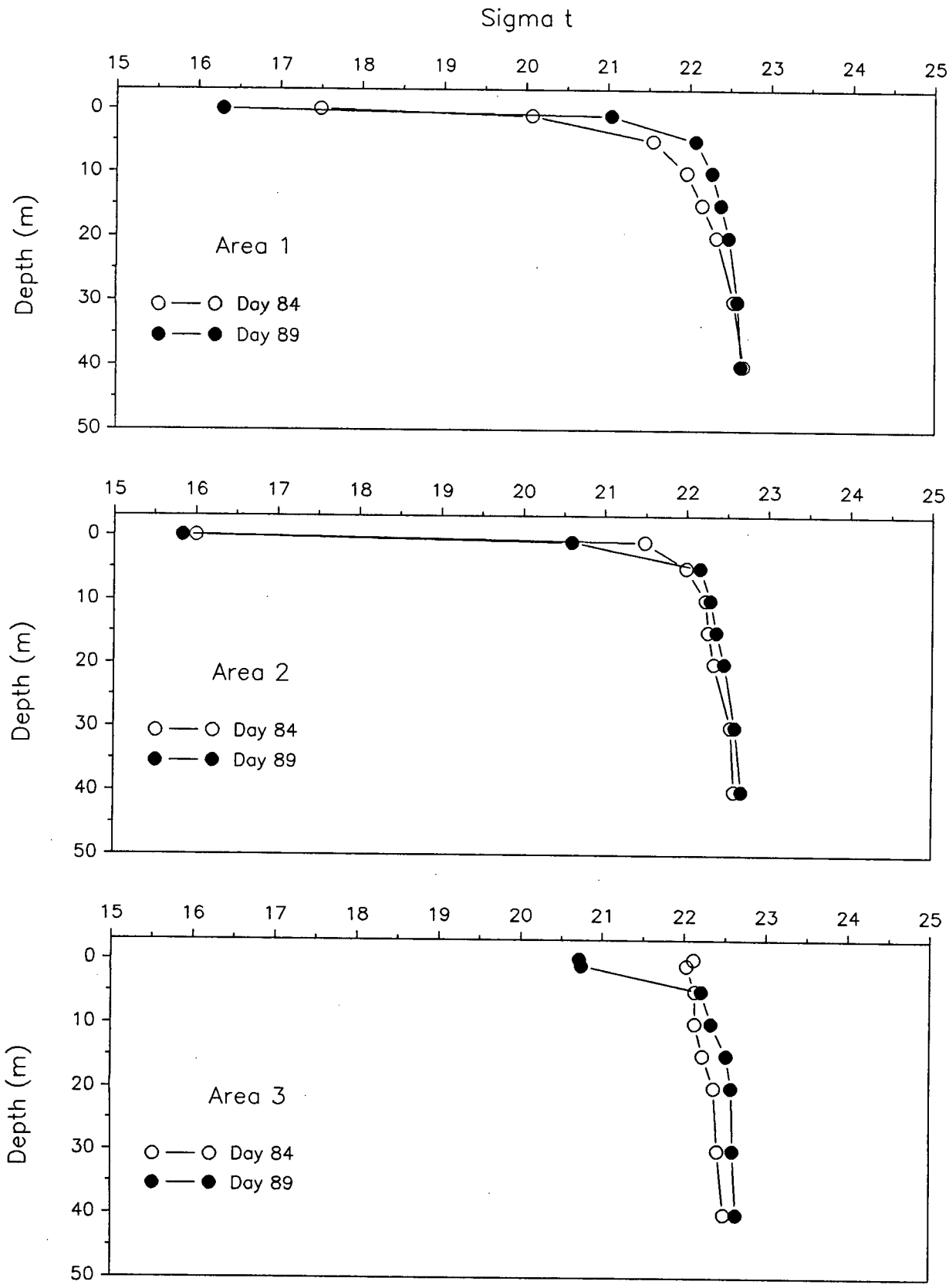


Figure 1.5. Sigma t profiles by sampling area over time for 1987.

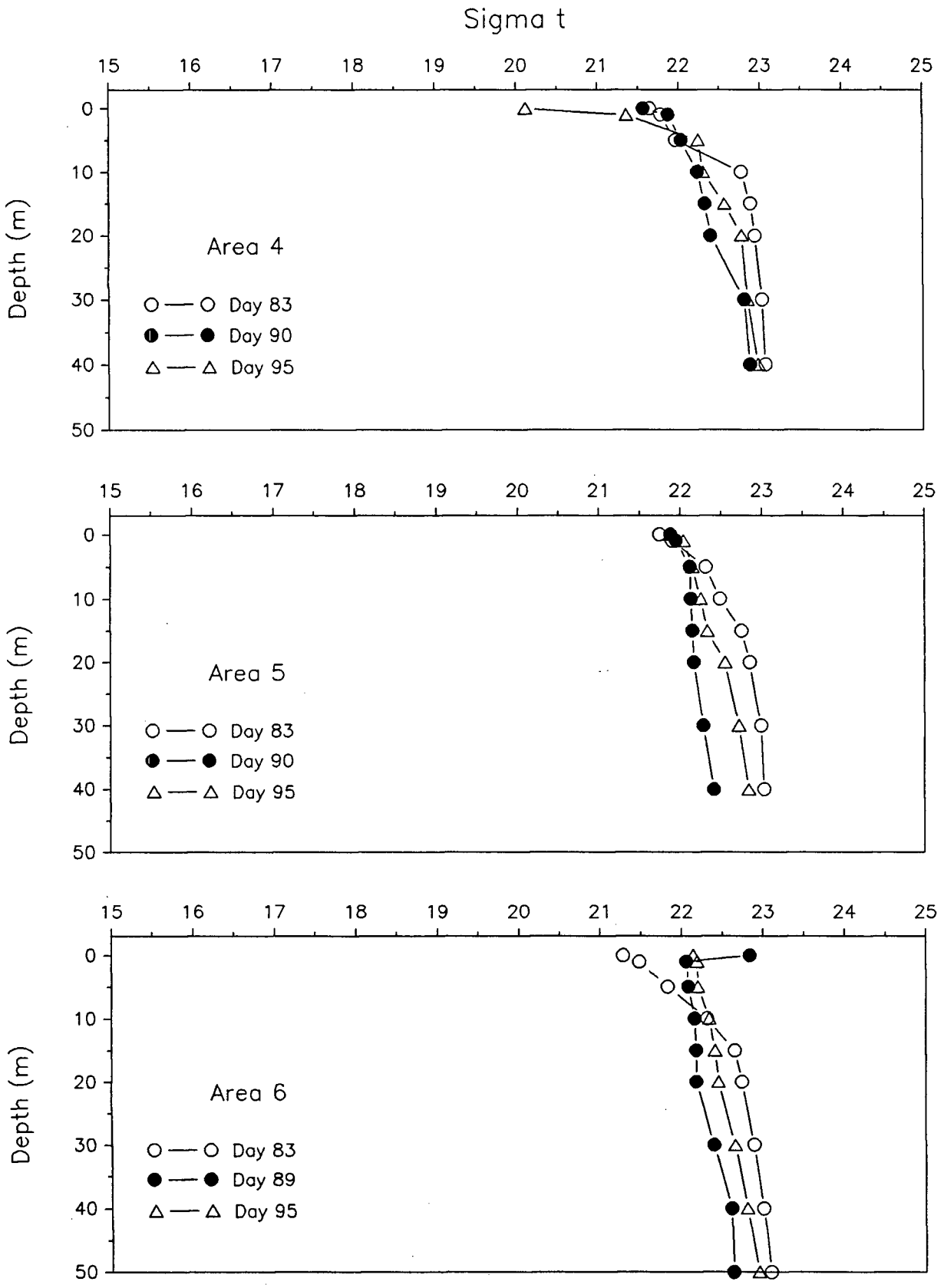


Figure 1.5. (continued).

Table 1.2. Results of current drogue work in Baynes Sound and Lambert Channel during 1987. For tides E=ebb, F=flood.

Day	Drogue Track	Area	Tide	Time	(h)	Dist. (m)	Drogue Dir.	Drogue Speed (m/h)	Wind Dir.	Wind Speed (m/s)
82	1	5	E	1046					NE	1.6
				1336	2.8	1145	NW	404.6	NE	1.6
				1708	3.5	2071	SE	586.7	SW	1.6
83	2	3	E	1011					NE	2.7
				1324	3.2	131	SE	40.7	NE	2.7
				1818	4.9	4184	SE	853.9	SE	2.2
84	3	3	E	935					SE	8.1
				1730	7.9	828	SW	104.5	SE	2.7
85	4	3	F+E	935					NW	10.8
				1737	8.0	2493	SE	310.5	NW	4.3
86	5	6	F+E	926					NW	5.4
				1712	7.8	4079	SE	525.0	W	6.5
87	6	5	F	1002					E	2.7
				1738	7.6	926	SE	121.8	W	4.3
88	7	3	E+F	622					SW	2.7
				1312	6.8	1296	W	189.8	SW	2.7
89	8	5	F	1028					NE	2.7
				1630	6.0	1127	NE	186.9	-	0.0
92	9	3	E	815					NW	1.1
				1735	9.3	2071	NW	222.0	SW	3.2
93	10	3	E	830					-	0.0
				1500	6.5	1080	SE	166.2	-	0.0

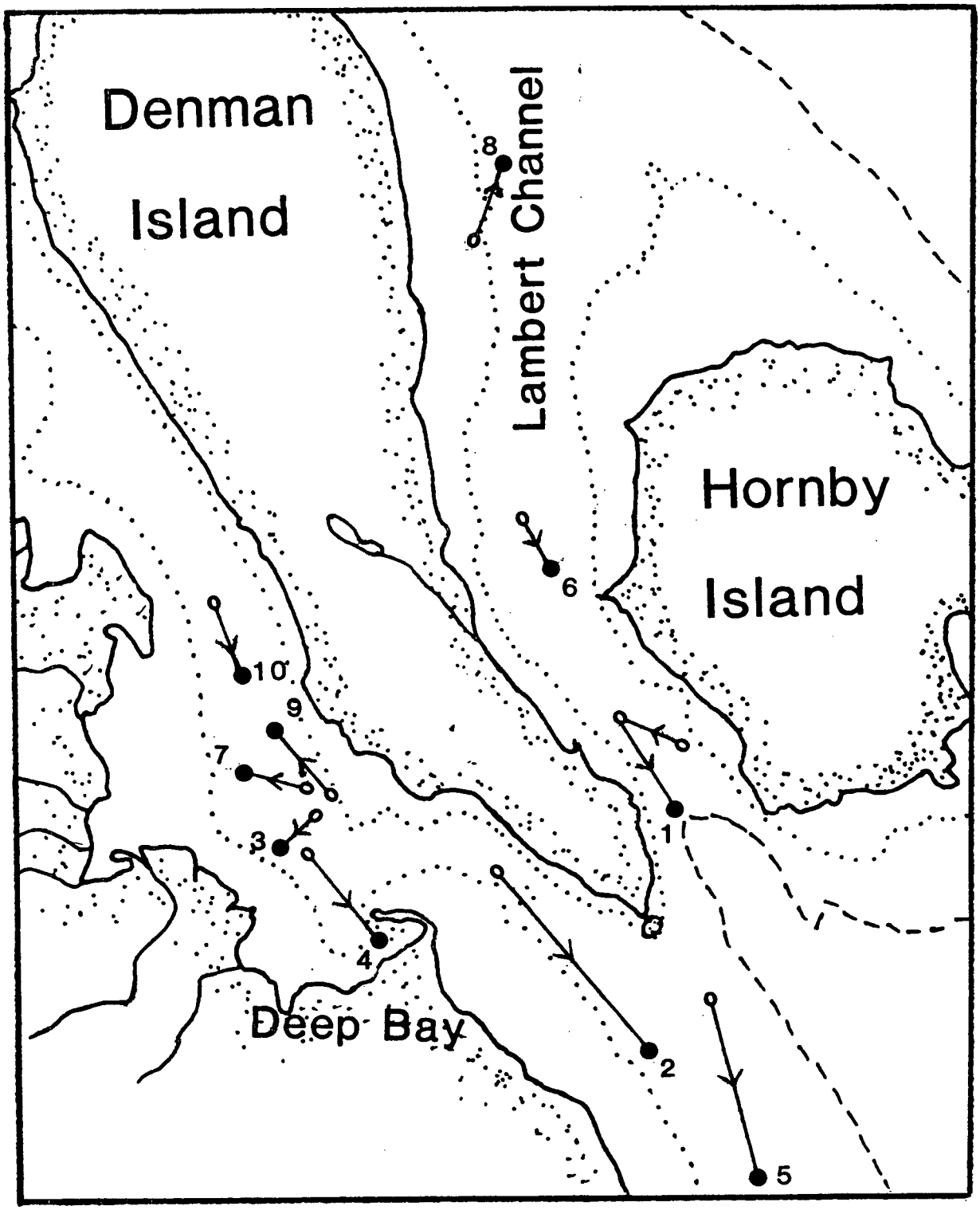


Figure 1.6. Diagramatic representation of the results of the current drogue studies conducted in 1987. Open circles indicate starting point, closed circles indicate finish, arrows indicate direction of movement.

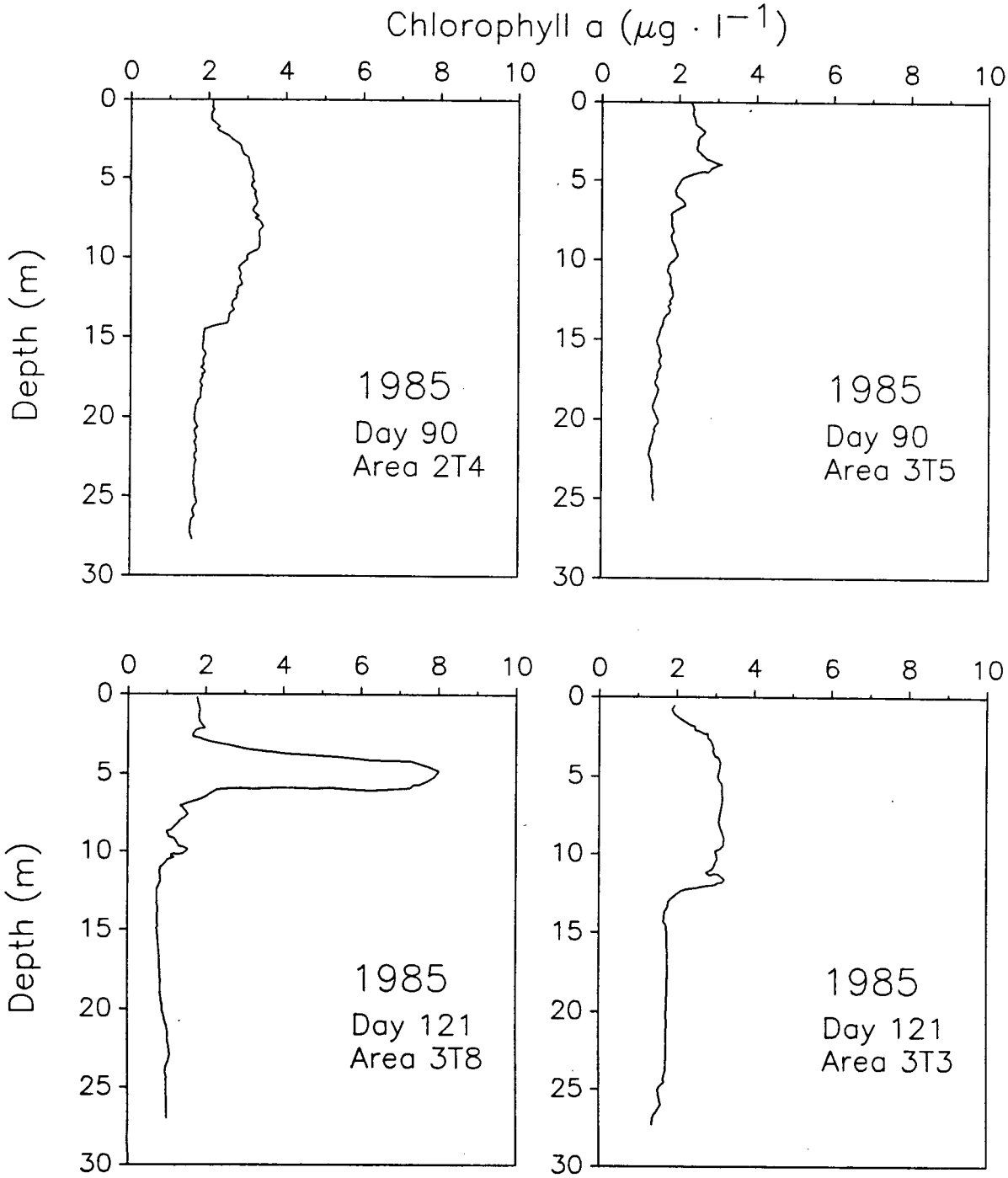


Figure 1.7. Chlorophyll *a* vertical profiles in 1985 and 1987 from various sampling areas and times.

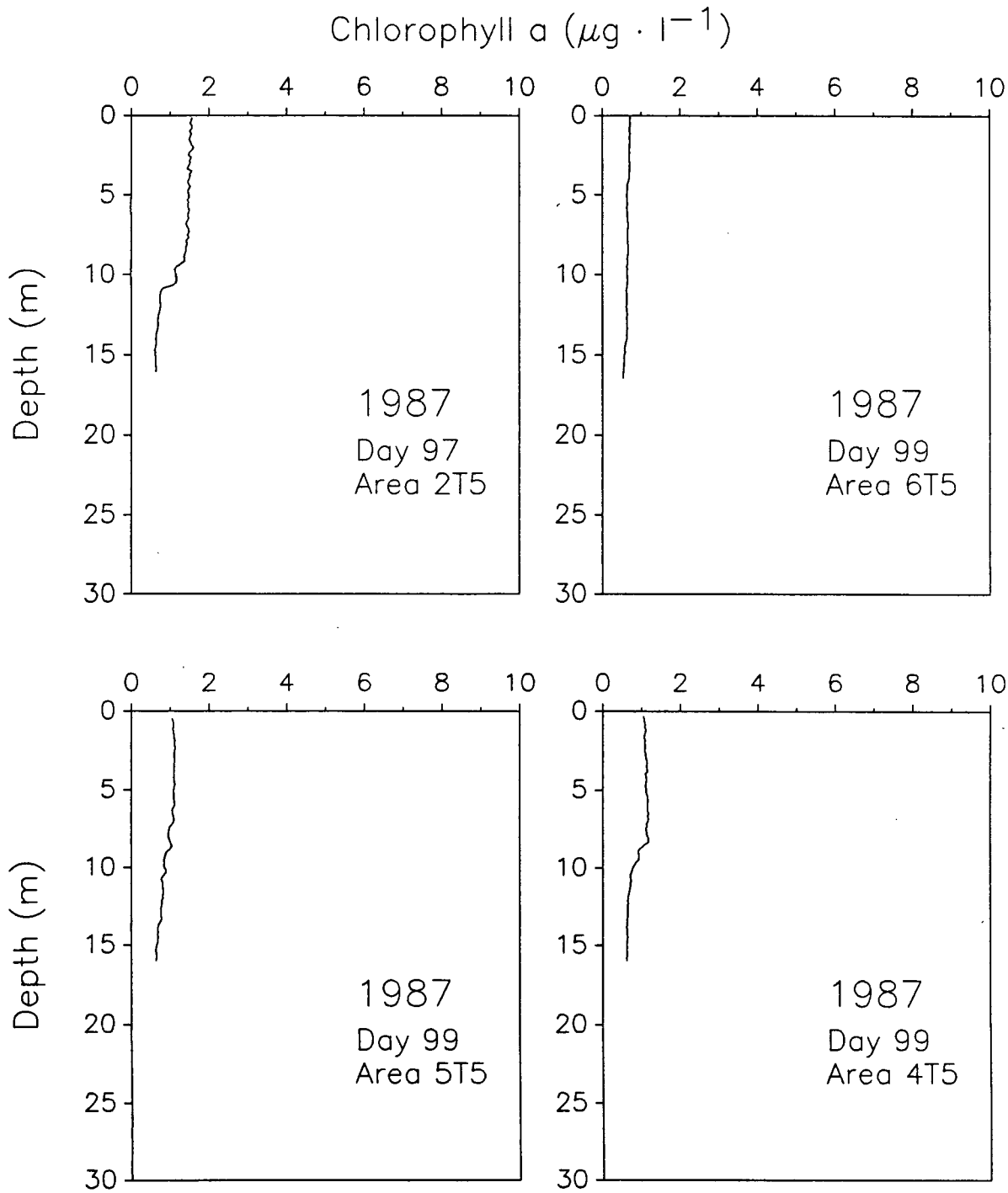


Figure 1.7. (continued).

In 1987, on Days 97 and 99, vertical profiles of chlorophyll *a* to a depth of 15 m showed lower values than those in 1985 but, for area 2 in Baynes Sound, the same profile pattern existed (Fig. 1.7). Values ranged from 0.5 to 1.6 $\mu g \cdot l^{-1}$. There was a gradation in the profiles from heterogeneous to homogeneous in the areas 2 to 6 respectively. Area 6 appeared to be completely mixed based on the uniform chlorophyll values down to 15 m. The overall chlorophyll maximum was estimated to be at 7 m. The horizontal profile taken at 7 m on Day 98 around Denman Island showed Baynes Sound had a higher chlorophyll *a* concentration than did Lambert Channel (Fig. 1.8). Chlorophyll *a* values at the estimated chlorophyll maximum ranged from 0.7 to 3.1 $\mu g \cdot l^{-1}$. Baynes Sound showed a section at the north end of Denman Island which had a distinctive peak in chlorophyll *a* concentration.

C. Zooplankton Food Densities

1. Food Item Identification

The larval gut content analysis from 1985 indicated the herring larvae were feeding primarily on three categories of prey items: copepod eggs, nauplii, and copepods (Fig. 1.9). Initially, eggs were the predominant food item but, gradually the proportion of nauplii and copepods increased after Day 114.

Similar patterns in food selection were found for larvae in 1986. The major groups of food identified were: copepod eggs, nauplii, copepods, bivalve veligers, diatoms, and unidentifiable material (Fig. 1.10). On Day 97, larval herring (10.1 ± 0.6 mm, standard length, x ± sd, n = 100) in both Baynes Sound and Lambert Channel were found to be feeding mostly on non-motile prey items such as copepod eggs, diatoms, and unidentifiable material, however, by Day 118 (3 weeks later), the

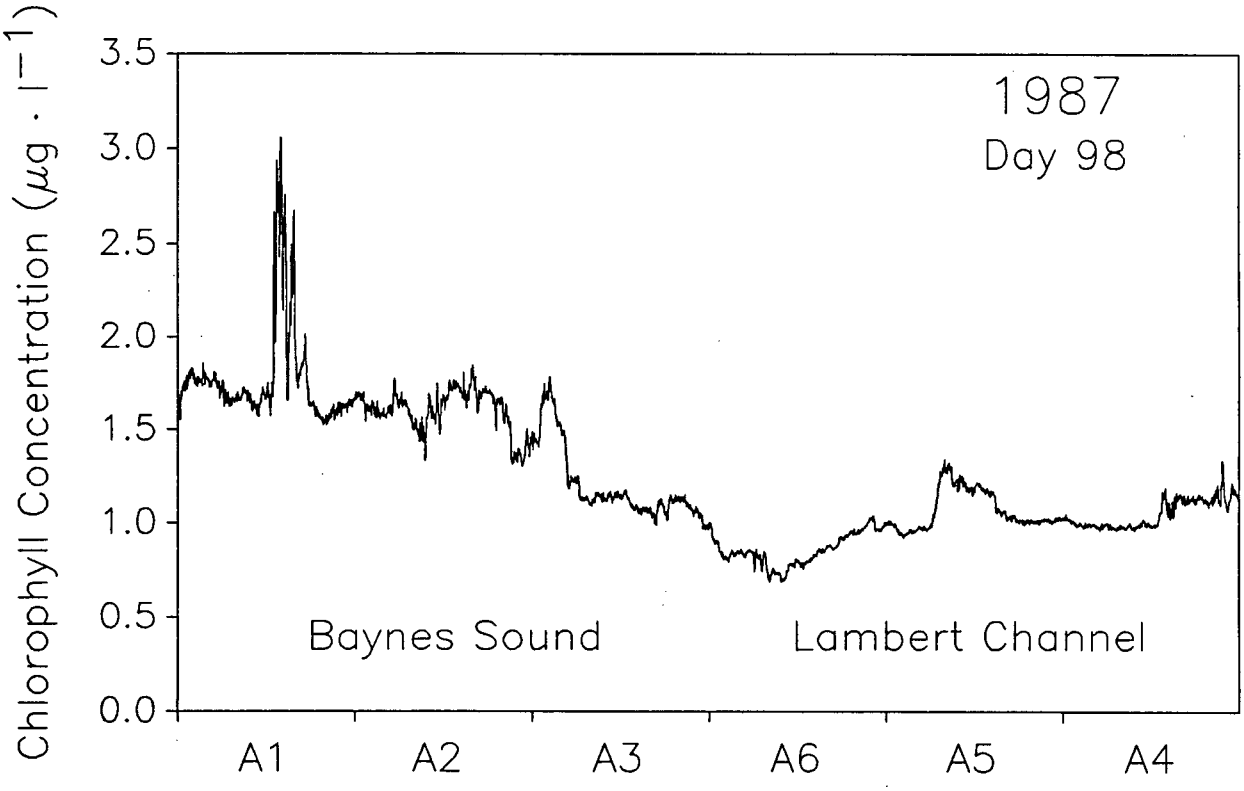


Figure 1.8. Chlorophyll *a* horizontal profile from 7 m encompassing Baynes Sound and Lambert Channel on Calendar Day 98 in 1987.

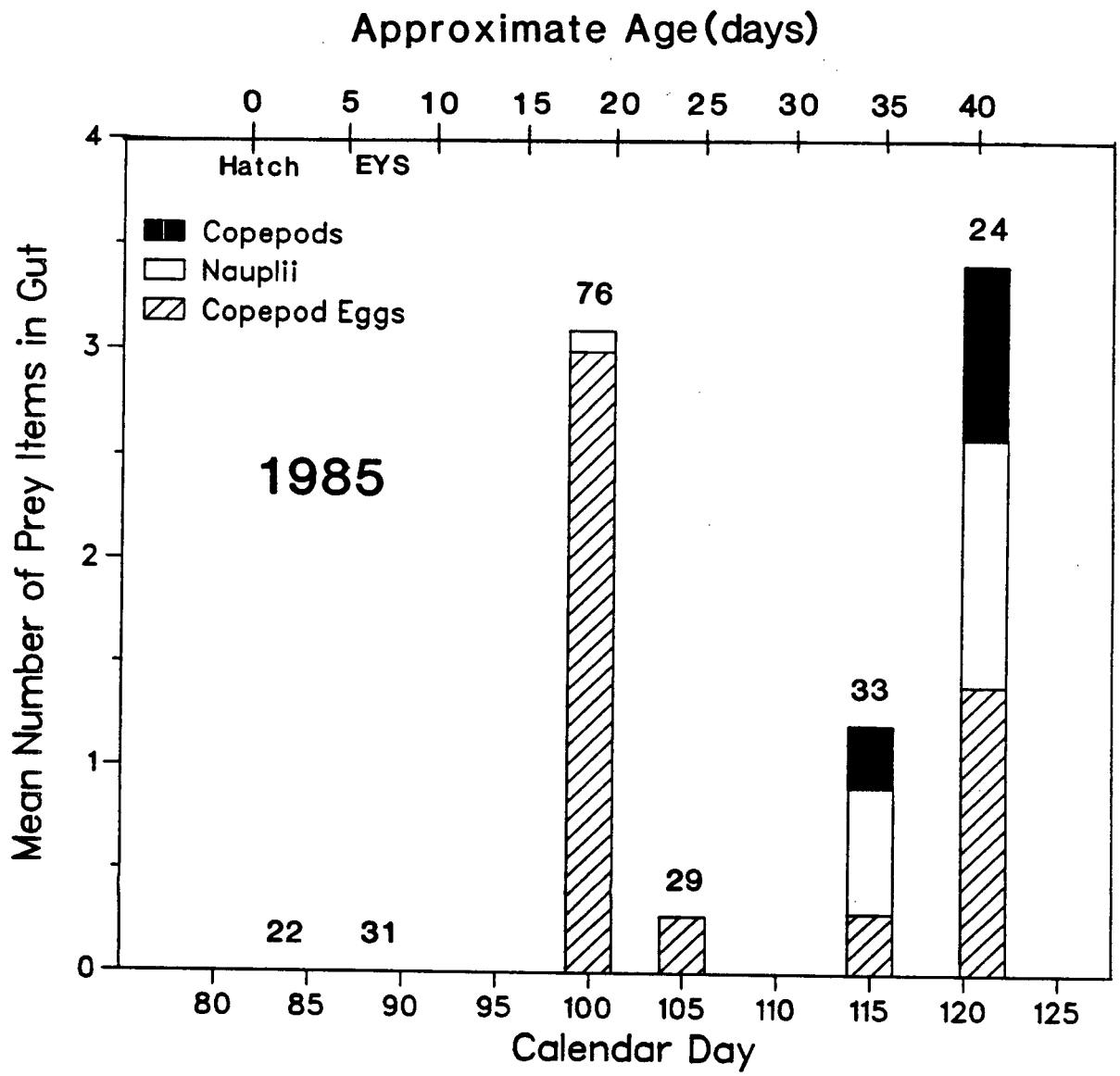


Figure 1.9. Mean number of prey items observed in the gut of larval herring in samples taken over time in 1985. Numbers over bars indicate the number of fish in samples. EYS = end of yolk sac.

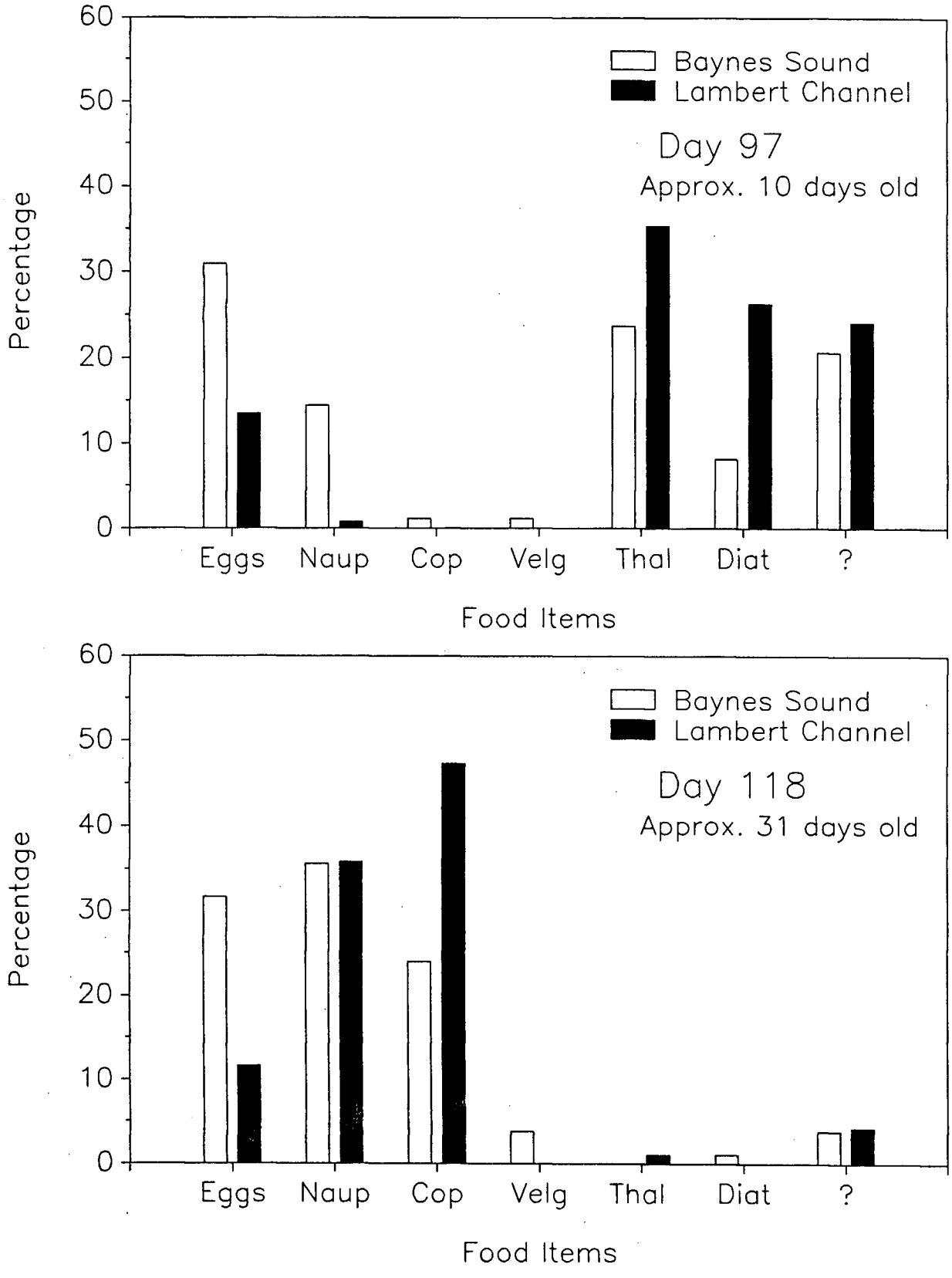


Figure 1.10. Percentage of occurrence in larval herring guts of seven major food groups from Calendar Days 97 and 118 during 1986 in Baynes Sound and Lambert Channel. Eggs = copepod eggs, Naup = nauplii, Cop = copepods, Velg = veligers, Thal = *Thalassiosira*, Diat = diatoms, ? = unknown.

larvae (16.6 ± 1.1 mm, standard length, x ± sd, n=32) had shifted mainly to nauplii and copepods.

The size range of prey items varied from about 60 to 620 μm in length with a mode at 80 μm for the first sampling period and from 60 to 1020 μm with two possible modes at 140 and 380 μm in the second (Fig. 1.11). Both periods exhibited a skewed right distribution of prey sizes indicating a concentration on the smaller sizes. The mean number of prey items per larvae from Day 97 was 2.2 ± 2.8 (x ± sd, n=100) and from Day 118 was 5.4 ± 4.3 (x ± sd, n=32).

2. Microplankton

The samples taken on Day 94 in 1985 indicated there were significantly higher food densities in Baynes Sound than in Lambert Channel ($p<0.01$ Mann-Whitney U test) (Fig. 1.12). Mean food densities for Baynes Sound was 502,521 ± 212,211 organisms$\cdot m^{-2}$ (x ± sd, n=10) and for Lambert Channel was 142,738 ± 39,886 organisms$\cdot m^{-2}$ (x ± sd, n=8). There was also a trend for areas 1 and 2 to have higher densities than area 3 in Baynes Sound. Copepods and nauplii seemed to have similar proportions.

The integrated time series of samples from 1986 and 1987 showed a pattern that was very similar to 1985. Again, Baynes Sound had higher food densities than Lambert Channel for both years ($p<0.01$ Student's t-test (1986), $p<0.01$ Mann-Whitney U test (1987)) (Fig. 1.13). Mean food densities in Baynes Sound and Lambert Channel for 1986 respectively were 453,424 ± 210,839 organisms$\cdot m^{-2}$ (x ± sd, n=59) and 333,589 ± 183,945 organisms$\cdot m^{-2}$ (x ± sd, n=56) and for 1987 were 917,458 ± 484,251 organisms$\cdot m^{-2}$ (x ± sd, n=24) and 459,000 ± 255,880 organisms$\cdot m^{-2}$ (x ± sd, n=24). The mean egg densities were generally lower than

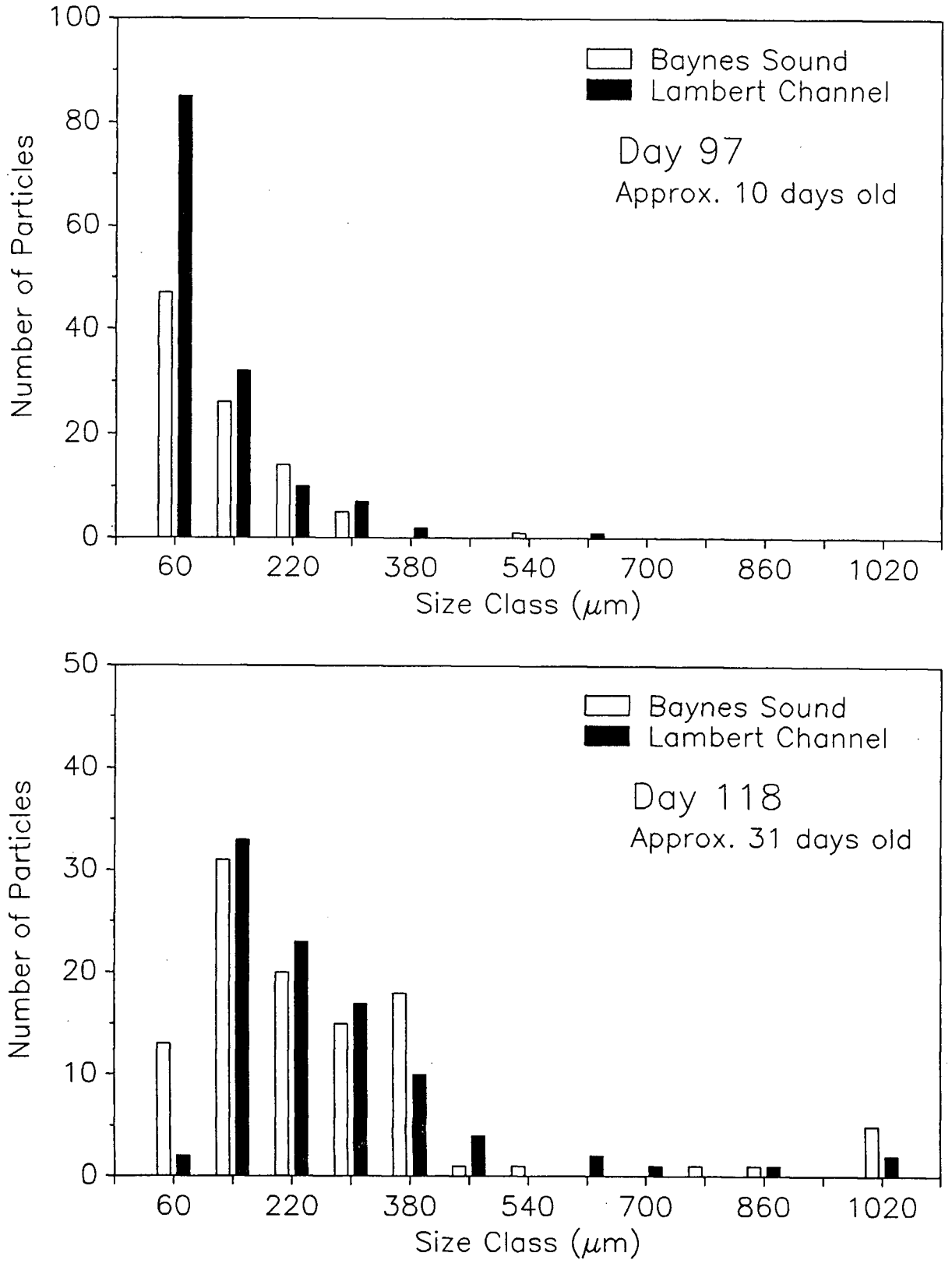


Figure 1.11. Frequency distribution of food particle sizes found in larval herring guts from Calendar Days 97 and 118 during 1986 from Baynes Sound and Lambert Channel.

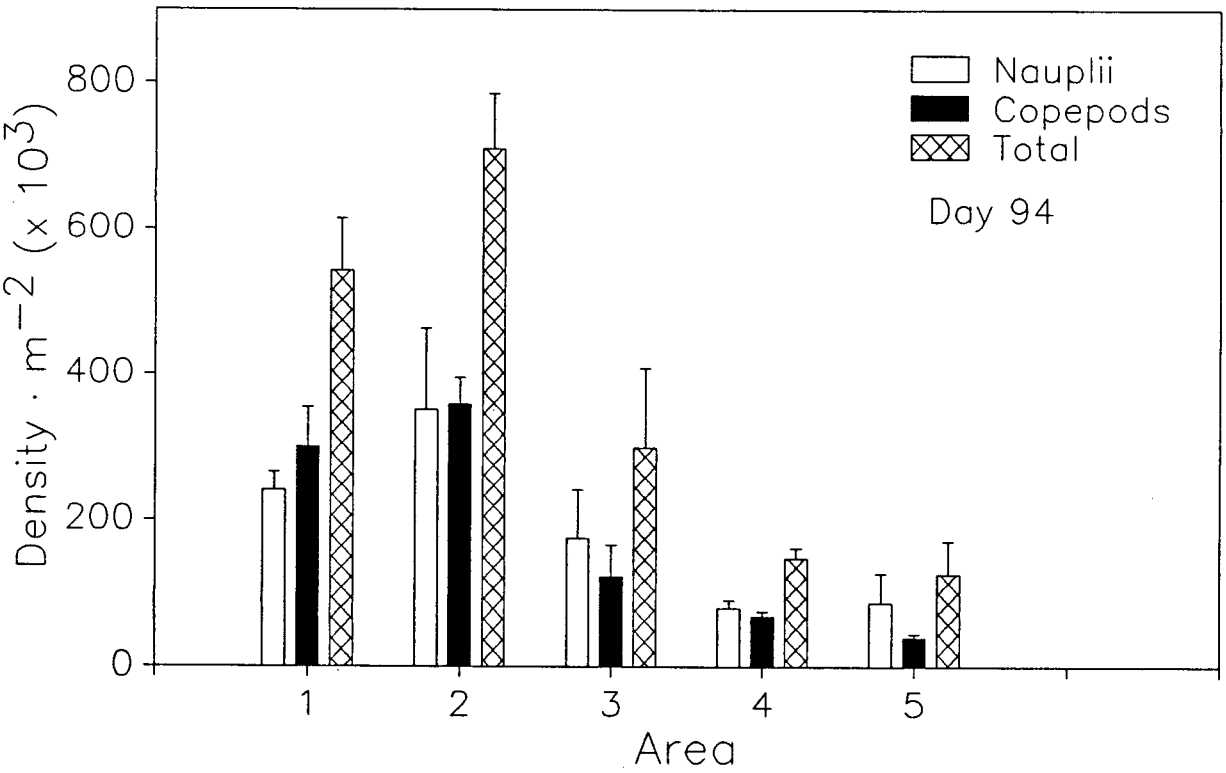


Figure 1.12. Summary of mean food densities for Pacific herring larvae by sampling area from Calendar Day 94 in 1985. Bars indicate 1 standard error of the mean.

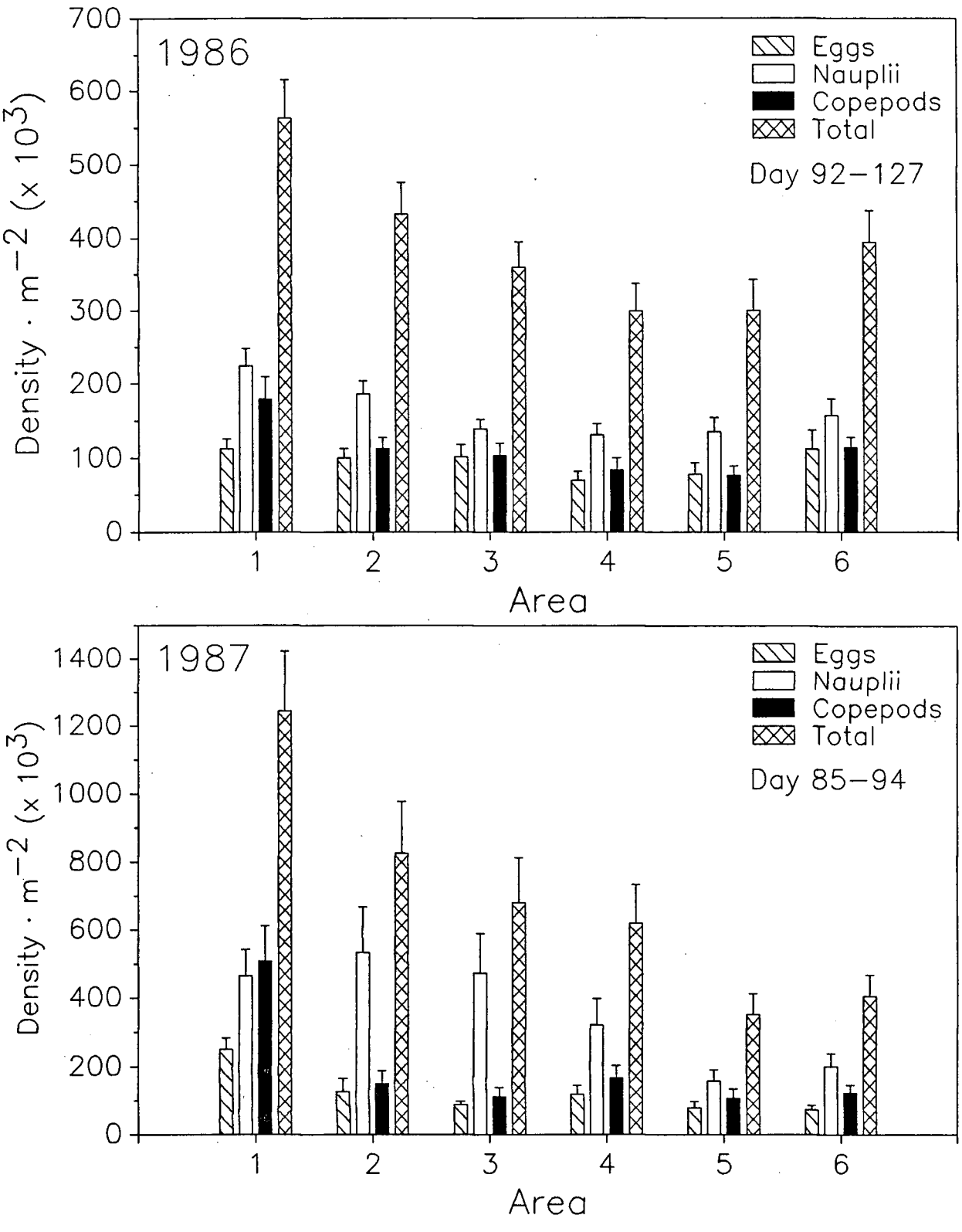


Figure 1.13. Summary of mean food densities for Pacific herring larvae by sampling area in 1986(Calendar Day 92 to 127) and 1987(Calendar Day 85 to 94). Bars indicate 1 standard error of the mean.

either the nauplii or the small copepods with the nauplii generally having the highest densities. Area 1 had the highest food densities over the two years and was significantly different from all the rest ($p < 0.05$ Tukey-Kramer test). None of the other areas were consistently different from all the rest ($p > 0.05$ Tukey-Kramer test).

The time series of mean food densities for 1986 in each of the areas showed a fluctuation in the densities (Fig. 1.14). This was apparent in most areas in both Baynes Sound and Lambert Channel. Sampling periods for 1985 or 1987 were of too short a duration to detect any similar trends.

There were no significant differences in pteropod or cyphonaut densities between Baynes Sound and Lambert Channel in 1986 or 1987 ($p > 0.05$ Mann-Whitney U test) but, Baynes Sound had higher densities of zoea ($p < 0.05$ Mann-Whitney U test) in both years (Table 1.3). In 1986 there was no significant difference in large copepod densities between Baynes Sound or Lambert Channel ($p > 0.05$ Student's t-test), however, there was a difference in 1987 ($p < 0.05$ Mann-Whitney U test). The reverse trend was found for *Microsetella* sp. with Baynes Sound having significantly higher densities than Lambert Channel in 1986 ($p < 0.05$ Mann-Whitney U test), but not in 1987 ($p > 0.05$ Student's t-test).

Thalassiosira eccentrica densities reached an early peak in 1986 around Day 100 in both Baynes Sound and Lambert Channel at densities of 1-2 $x10^8$ cells$\cdot m^2$, then quickly dropped off to 2-3 cells$\cdot m^{-2}$ by Day 125 (Fig. 1.15). In Baynes Sound, areas 1 and 2 had higher peak densities than area 3. In Lambert Channel, areas 5 and 6 had higher densities. The patterns of diatom bloom development were almost identical and synchronous for Baynes Sound and Lambert Channel.

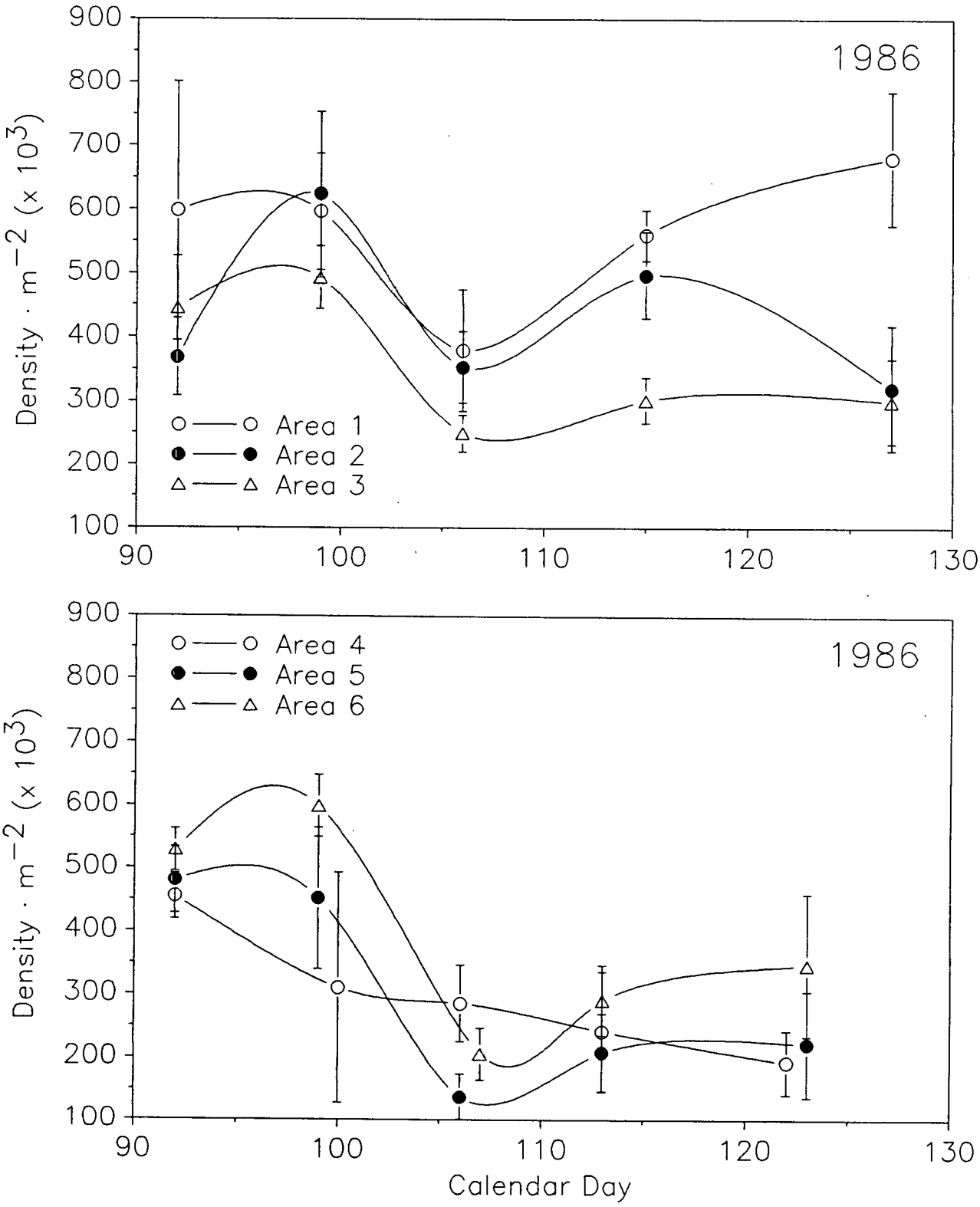


Figure 1.14. Mean food densities for Pacific herring larvae over time by sampling area for 1986. Bars indicate 1 standard error of the mean.

Table 1.3. Summary of incidental zooplankton densities ($\#\cdot m^{-2}$) ($x10^3$) taken with a diaphragm pump integrated over time from each of the areas for 1986 and 1987. (LgCop= copepods>1mm, Ptero=pteropods, Cyph=cyphonautes, Micro=*Microsetella* sp.)

Area	n	LgCop $\bar{x}$	LgCop sd	Ptero $\bar{x}$	Ptero sd	Cyph $\bar{x}$	Cyph sd	Micro $\bar{x}$	Micro sd	Zoea $\bar{x}$	Zoea sd
					1986						
1	20	12.1	11.1	8.5	4.7	16.2	12.9	1.6	1.8	7.2	8.6
2	20	11.9	12.4	6.2	4.6	17.5	10.7	1.0	2.0	2.6	2.2
3	19	6.3	6.4	3.9	2.8	12.3	10.5	3.3	4.5	4.8	7.3
Baynes	59	10.1	10.5	6.2	4.5	15.4	11.4	1.9	3.1	4.8	6.8
4	16	11.0	9.3	7.5	4.6	12.1	16.6	0.1	0.3	2.0	1.8
5	20	8.1	7.9	6.8	6.7	18.1	18.7	0.7	1.0	3.1	5.2
6	20	12.3	12.7	9.7	10.1	37.1	6.2	1.7	2.7	2.4	3.8
Lambert	56	10.4	10.2	8.0	7.6	23.2	24.0	0.9	1.8	2.5	4.0
					1987						
1	8	25.6	14.1	8.8	8.8	8.6	5.2	2.0	2.1	4.1	7.7
2	8	10.0	6.1	4.9	3.6	8.0	5.8	1.4	3.5	1.9	1.4
3	8	5.9	4.3	4.3	3.2	10.9	13.3	0.6	0.9	1.6	1.1
Baynes	24	13.8	12.4	6.0	5.9	9.2	8.6	1.3	2.4	2.5	4.5
4	8	6.8	6.0	3.6	2.3	9.5	9.4	0.3	0.7	1.0	0.5
5	8	2.9	4.6	4.9	3.7	8.9	8.7	2.0	3.0	0.1	0.4
6	8	3.3	1.7	4.1	2.7	27.1	20.5	0.9	1.4	0.6	0.9
Lambert	24	4.3	4.6	4.2	2.9	15.2	15.9	1.0	2.0	0.6	0.7

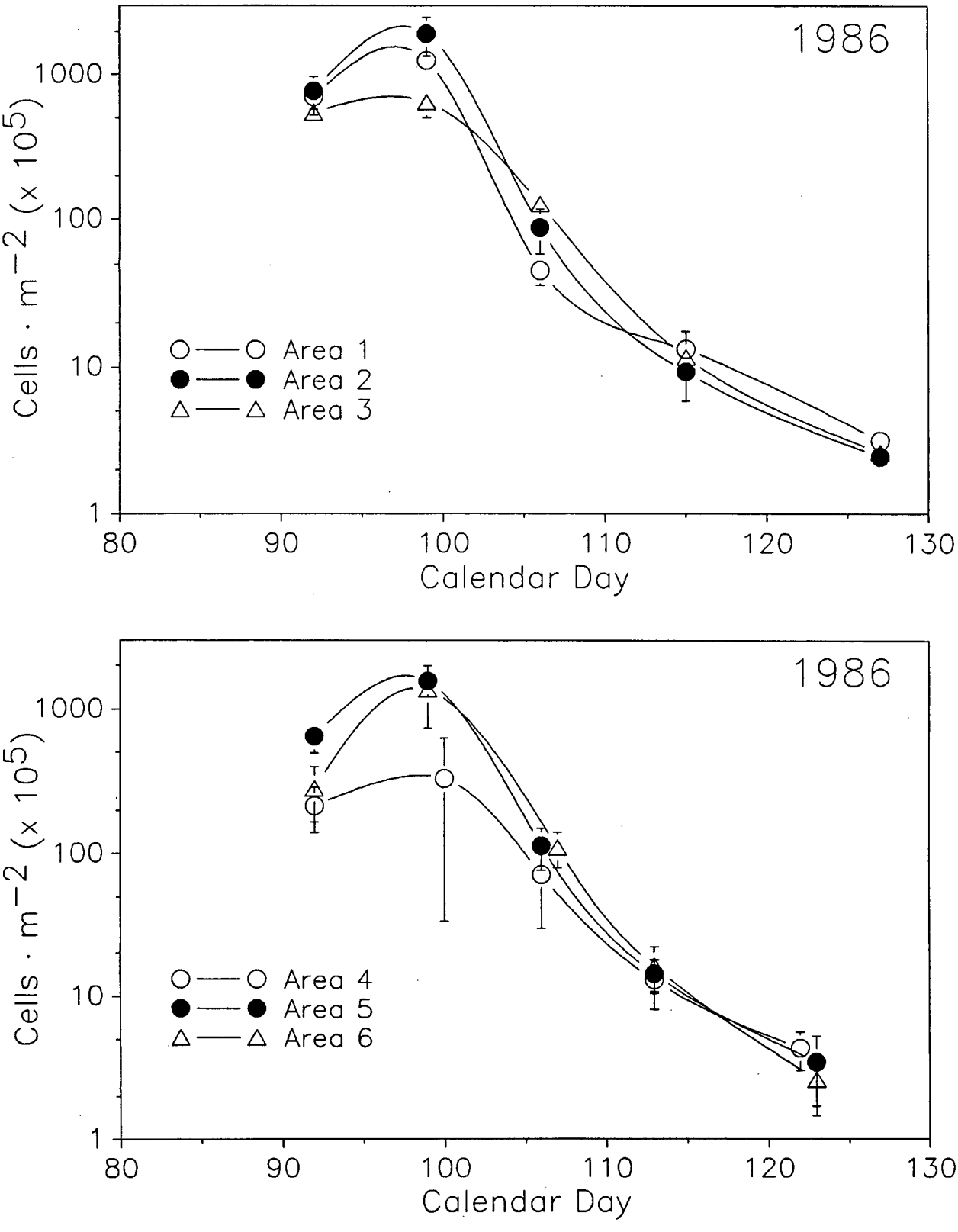


Figure 1.15. Mean densities of the diatom, *Thalassiosira eccentrica*, over time by sampling area for 1986. Bars indicate 1 standard error of the mean.

D. Potential Zooplankton Predators

The mean densities of *Tortanus discaudatus* in 1986 ranged from 1050 to 8050 copepods•m^{-2} while in 1987 densities ranged from 167 to 3375 copepods•m^{-2} (Fig. 1.16). Baynes Sound consistently had significantly more copepods than Lambert Channel ($p<0.01$ Mann-Whitney U test) and had a high to low density (copepods•m^{-2}) gradient from area 1 to 3. A time series of densities from areas in Baynes Sound showed densities increased slightly over time in area 1, decreased in area 2, and stayed at relatively uniform levels in area 3 (Fig. 1.16).

There were distinct differences between Baynes Sound and Lambert Channel for both years in the densities of the hydromedusa, *Aequorea victoria* ($p<0.01$ Mann-Whitney U test) (Fig. 1.17). Virtually all *A. victoria* were found in Baynes Sound in areas 1 and 2. Mean densities in Baynes Sound and Lambert Channel for 1986 respectively were 3.8 ± 8.6 ($\bar{x}$ ± sd, n=226) and 0.1 ± 0.5 individuals•m^{-2} ($\bar{x}$ ± sd, n=152) and for 1987 were 4.1 ± 7.4 ($\bar{x}$ ± sd, n=144) and 0.1 ± 0.6 ($\bar{x}$ ± sd, n=88) individuals•m^{-2}. Over time in 1986 in Baynes Sound, densities in area 1 increased while in area 2 densities decreased. Area 3 stayed at low levels throughout.

Lambert Channel had distinctly higher densities (individuals•m^{-2}) of the chaetognath, *Sagitta elegans*, than Baynes Sound ($p<0.01$ Mann-Whitney U test) (Fig. 1.17). Only area 3 showed any traces of the chaetognath but, it had lower densities than any other areas in Lambert Channel. Area 6 had the highest overall density.

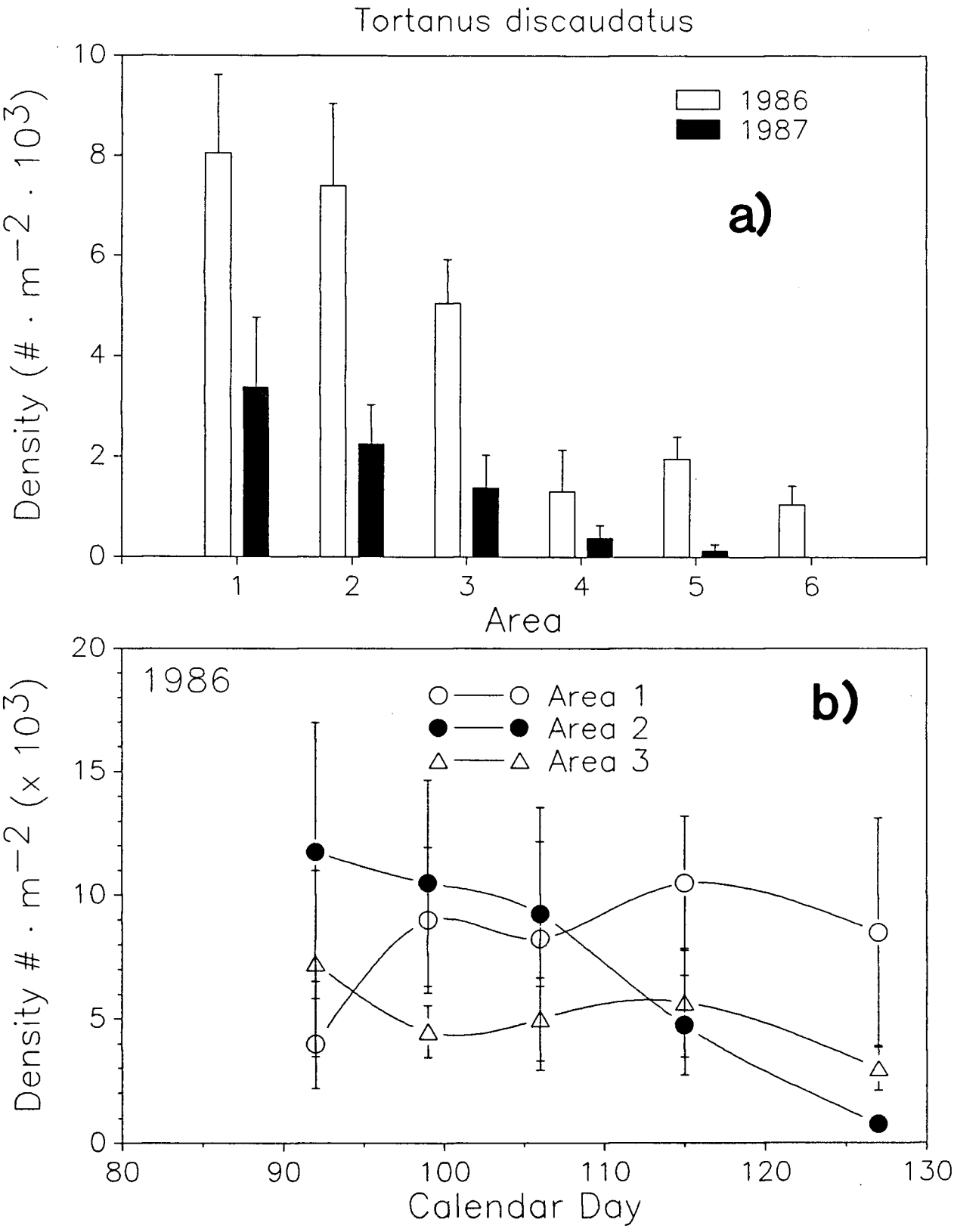


Figure 1.16. a) Mean densities of the copepod, *Tortanus discaudatus*, by sampling area for 1986 and 1987. b) Mean densities of *T. discaudatus* over time from Baynes Sound in 1986. Bars on both figures indicate 1 standard error of the mean.

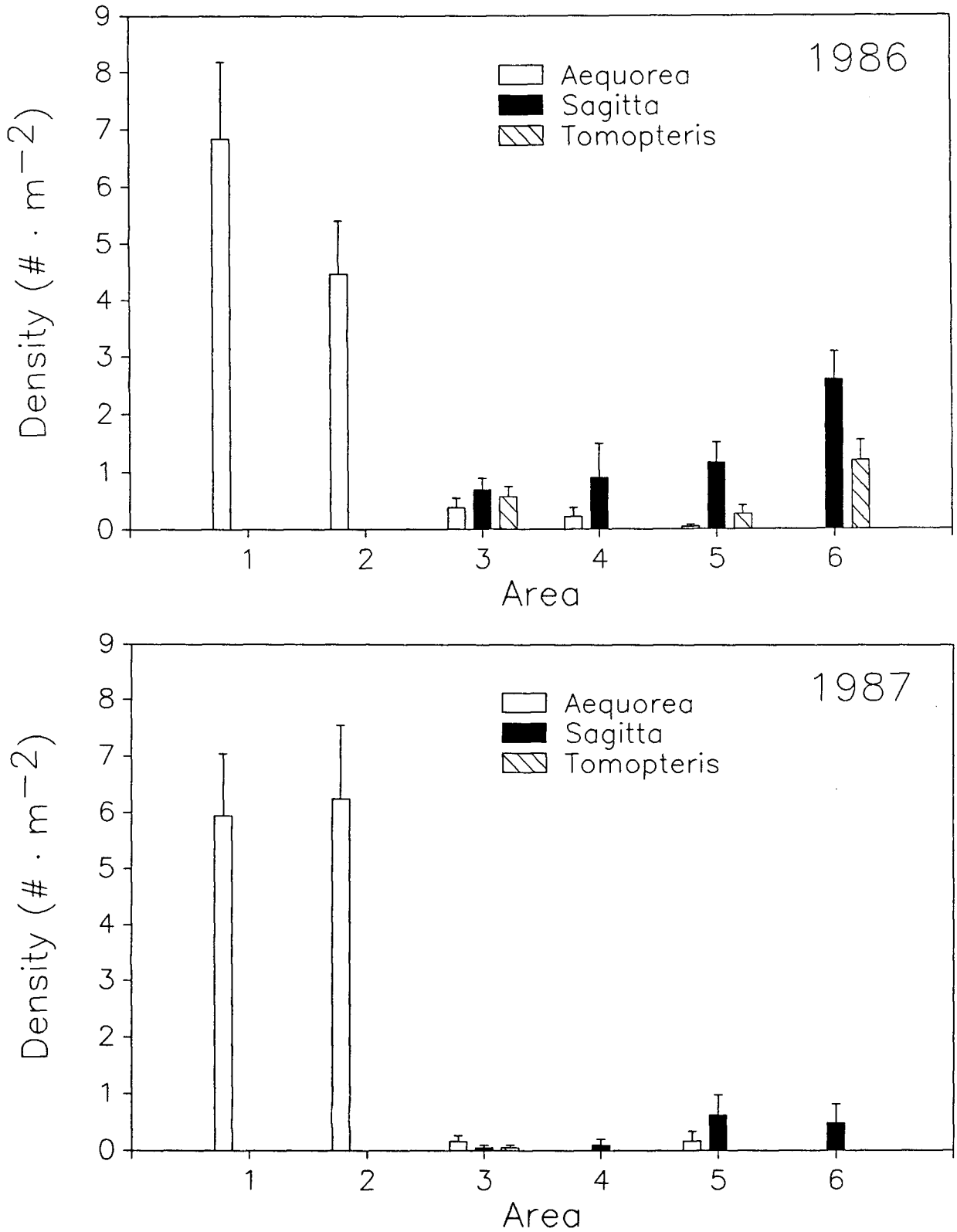


Figure 1.17. Mean densities of the hydromedusae, *Aequorea victoria*, the chaetognath, *Sagitta elegans*, and the polychaete, *Tomopteris septentrionalis*, by sampling area from 1986 and 1987. Bars indicate 1 standard error of the mean.

Lambert Channel had higher densities of the pelagic polychaete, *Tomopteris septentrionalis*, than Baynes Sound in 1986 ($p < 0.05$ Mann-Whitney U test) (Fig. 1.17). Area 6 tended to have the highest mean densities of all six sampling areas in 1986. Not enough specimens were captured in 1987 to do any comparative analysis.

E. Larval Distribution and Dispersal

The vertical distribution patterns of the herring larvae show most of the fish are found in the top 20 m of the water column from both Days 95 and 113 (Figs. 1.18, 1.19). There was a mean of 88.7% of the fish in the top 20 m of the water column on Day 95 and 77.8% on Day 113. The trends seem to suggest larvae are closer to the surface during the daylight hours and gradually sink lower in the water column during the periods of darkness. This characteristic is more pronounced in the older larvae from Day 113 although, the data are only from the later part of the day.

In the areas with extensive offshore regions (areas 4 and 6), horizontal distribution patterns of larvae show the larvae are close to shore when hatching, undergo dispersal into the deeper waters, but still maintain high levels close to shore in both 1985 and 1986 (Fig. 1.20). In channel areas (areas 1, 2, 3, and 5), the same general dispersal pattern existed with the larvae having high nearshore densities. There was a tendency of the eastern side of Baynes Sound to have higher densities than the west side.

The movement of herring larvae in all three years studied seemed to be away from the spawning grounds in Lambert Channel and into Baynes Sound, based on

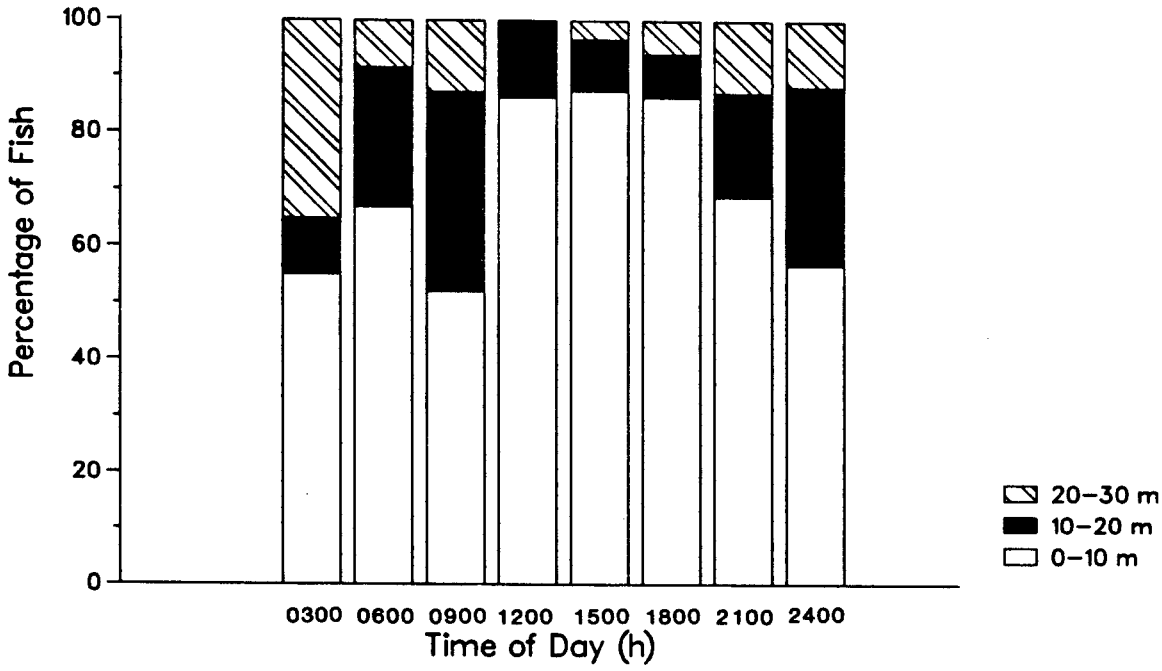


Figure 1.18. Percentage of herring larvae estimated in different levels of the water column every three hours over a 24 hour period from Calendar Day 95 in 1985.

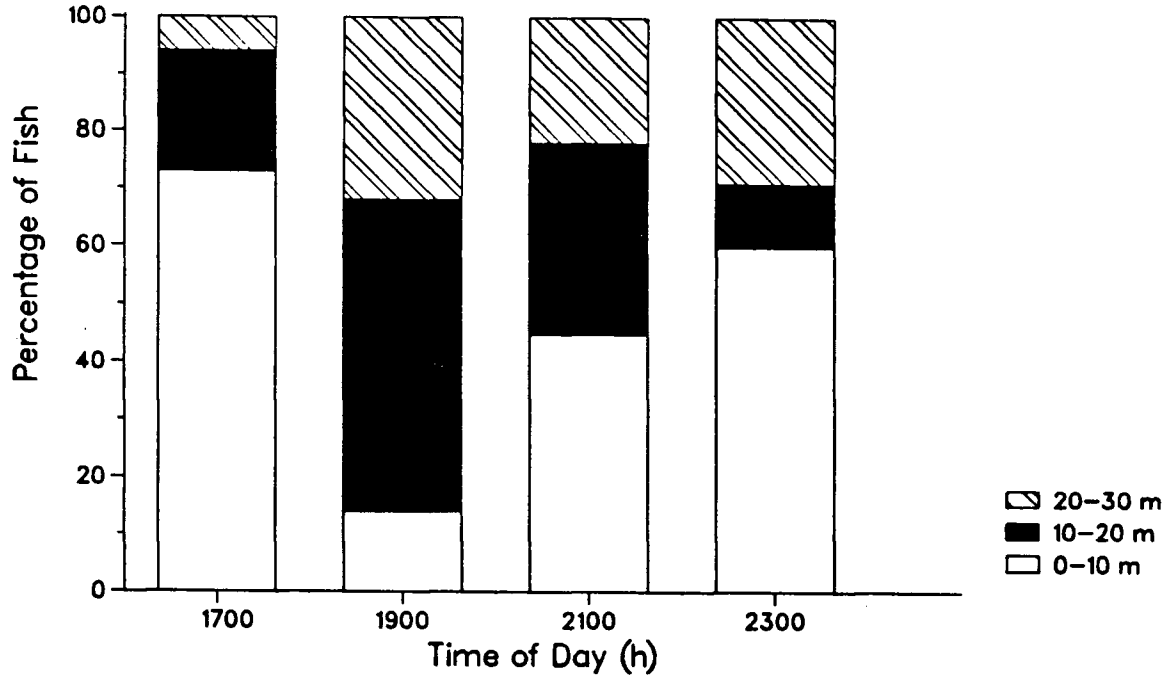


Figure 1.19. Percentage of herring larvae estimated in different levels of the water column every two hours over an 8 hour period from Calendar Day 113 in 1985.

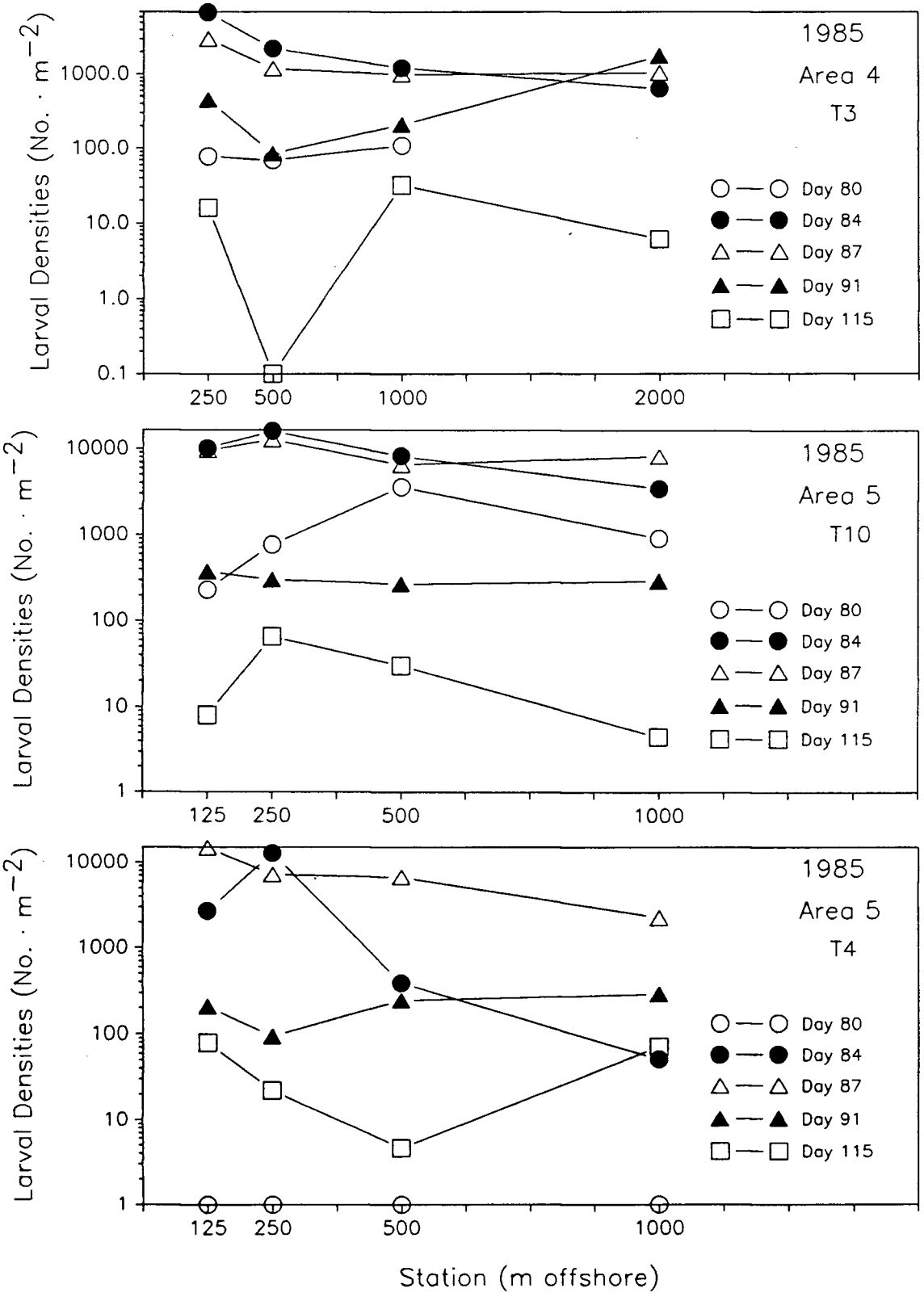


Figure 1.20a. Larval herring densities by transect station over time in 1985.

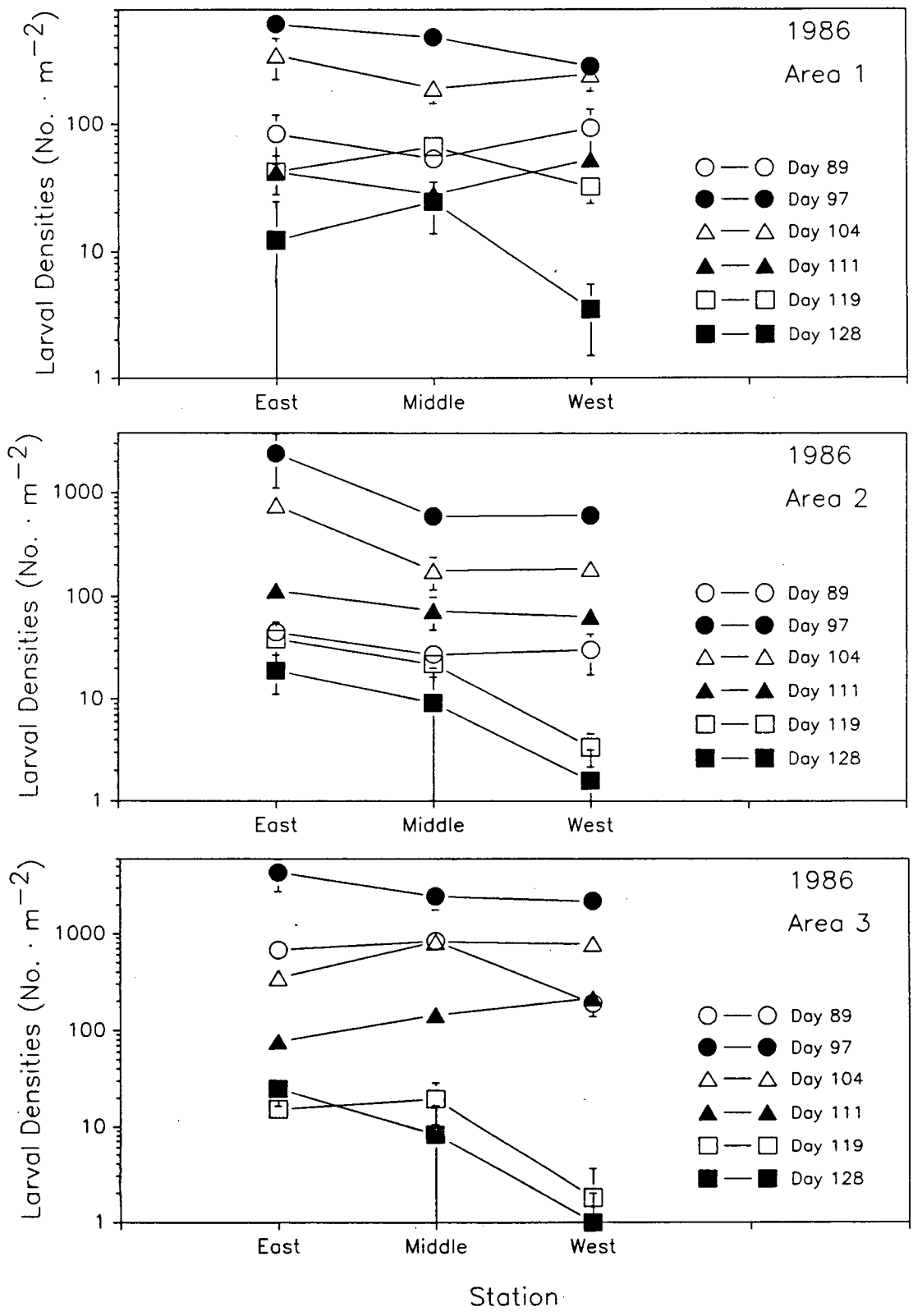


Figure 1.20b. Larval herring densities by area and transect station over time in 1986. Bars indicate 1 standard error of the mean.

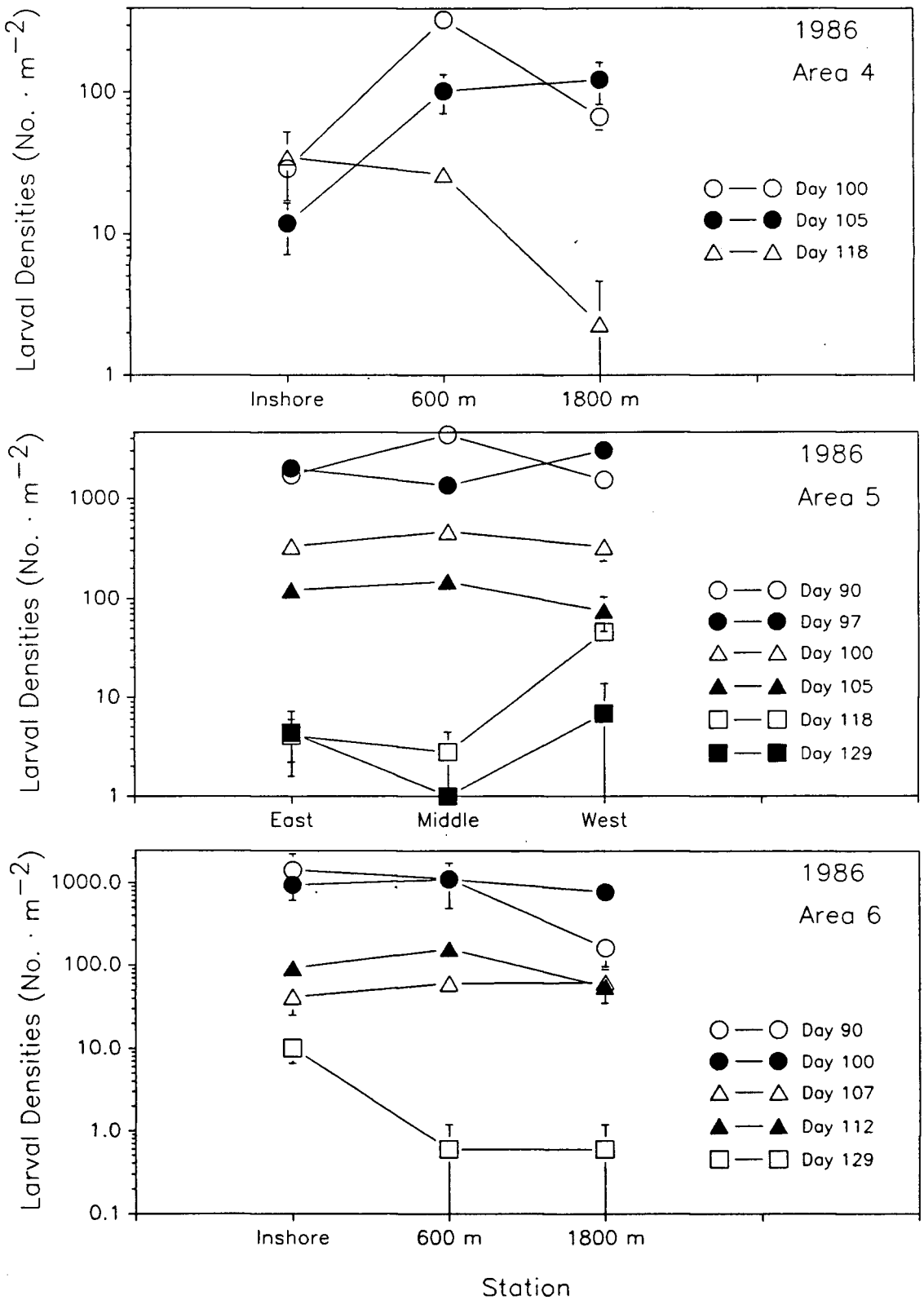


Figure 1.20b. (continued).

changes in larval densities. In 1985, early samples in Lambert Channel show a rapid increase in mean larval densities to a peak around Day 86 of over 4000 larvae$\cdot m^{-2}$ followed by a drop to about 400 larvae$\cdot m^{-2}$ by Day 91 (Fig. 1.21). After Day 91, there was a lower rate of decrease in the larval populations from 400 larvae$\cdot m^{-2}$ on Day 91 to about 10 larvae$\cdot m^{-2}$ by Day 123. Concurrently, by Day 90 in Baynes Sound, mean larval densities were higher than those in Lambert Channel and this trend continued from Day 90 to Day 109, after which the mean concentrations were roughly equivalent. In 1986 and 1987, similar patterns arose with Lambert Channel having initially higher densities of herring larvae than Baynes Sound and in 1986, Baynes Sound continually having higher mean densities of larvae than Lambert Channel throughout the study.

Larval densities over time in each of the study areas from years 1985 to 1987 showed similar patterns (Fig. 1.22). In Baynes Sound, Area 1 consistently had the lowest densities initially but gradually began to increase over areas 2 and 3. Area 3 usually had the highest initial densities. In Lambert Channel, densities were higher in area 5 but, gradually all three areas assumed similar values after the initial peak in hatching.

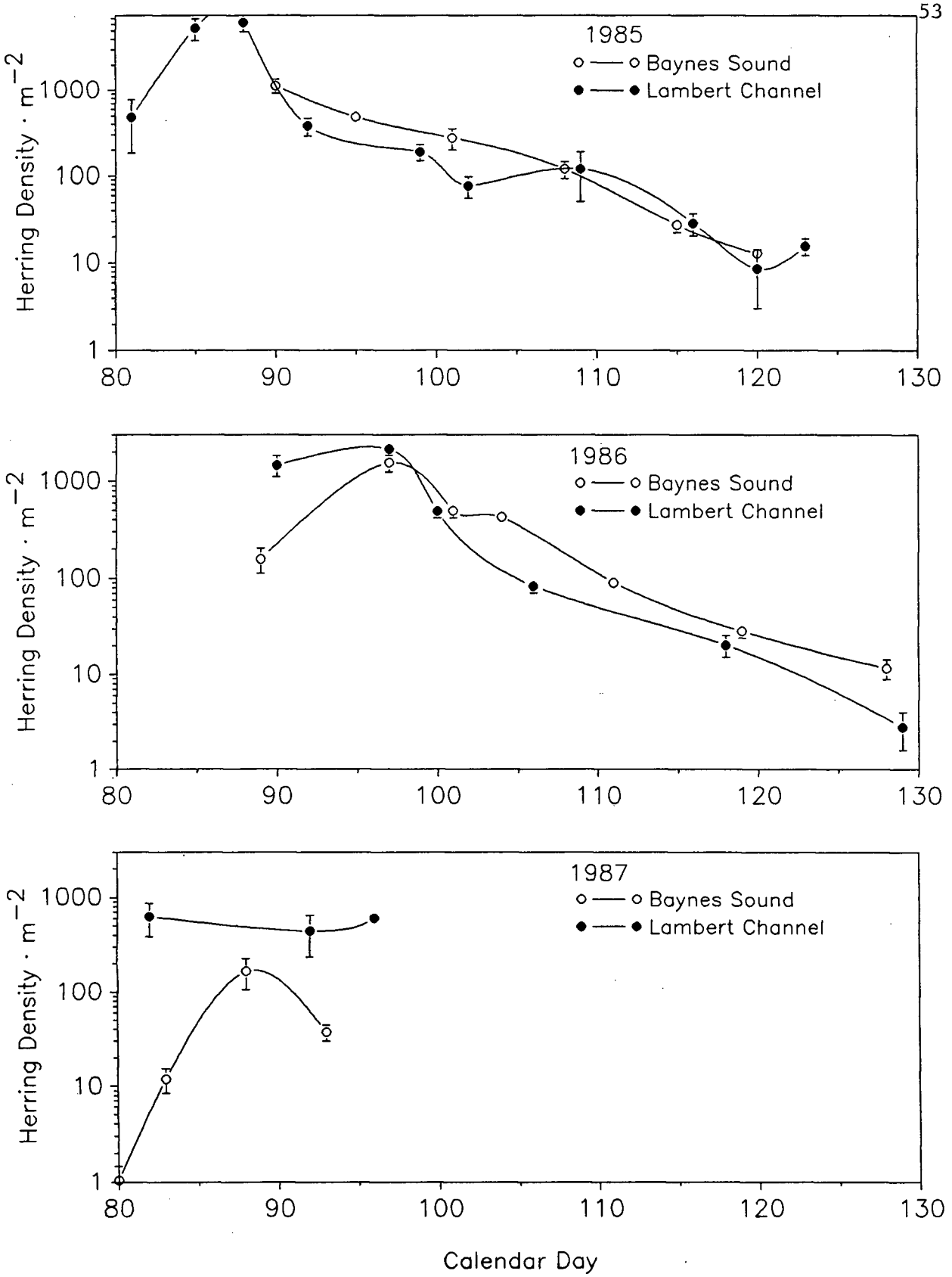


Figure 1.21. Summary of mean larval herring densities over time from Baynes Sound and Lambert Channel in 1985, 1986 and 1987. Bars indicate 1 standard error of the mean.

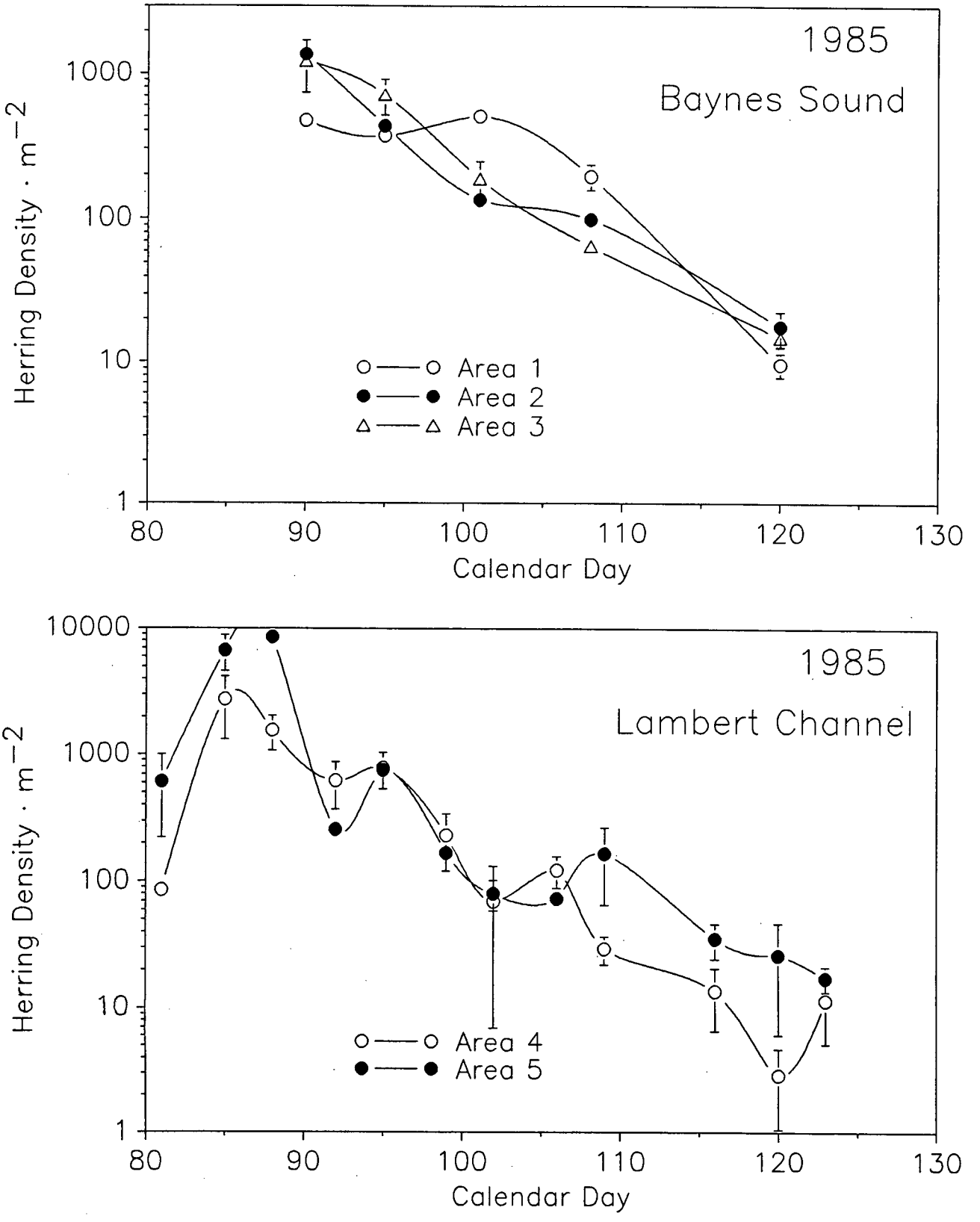


Figure 1.22. Mean larval herring densities over time by sampling area for the years 1985, 1986, and 1987. Bars indicate 1 standard error of the mean.

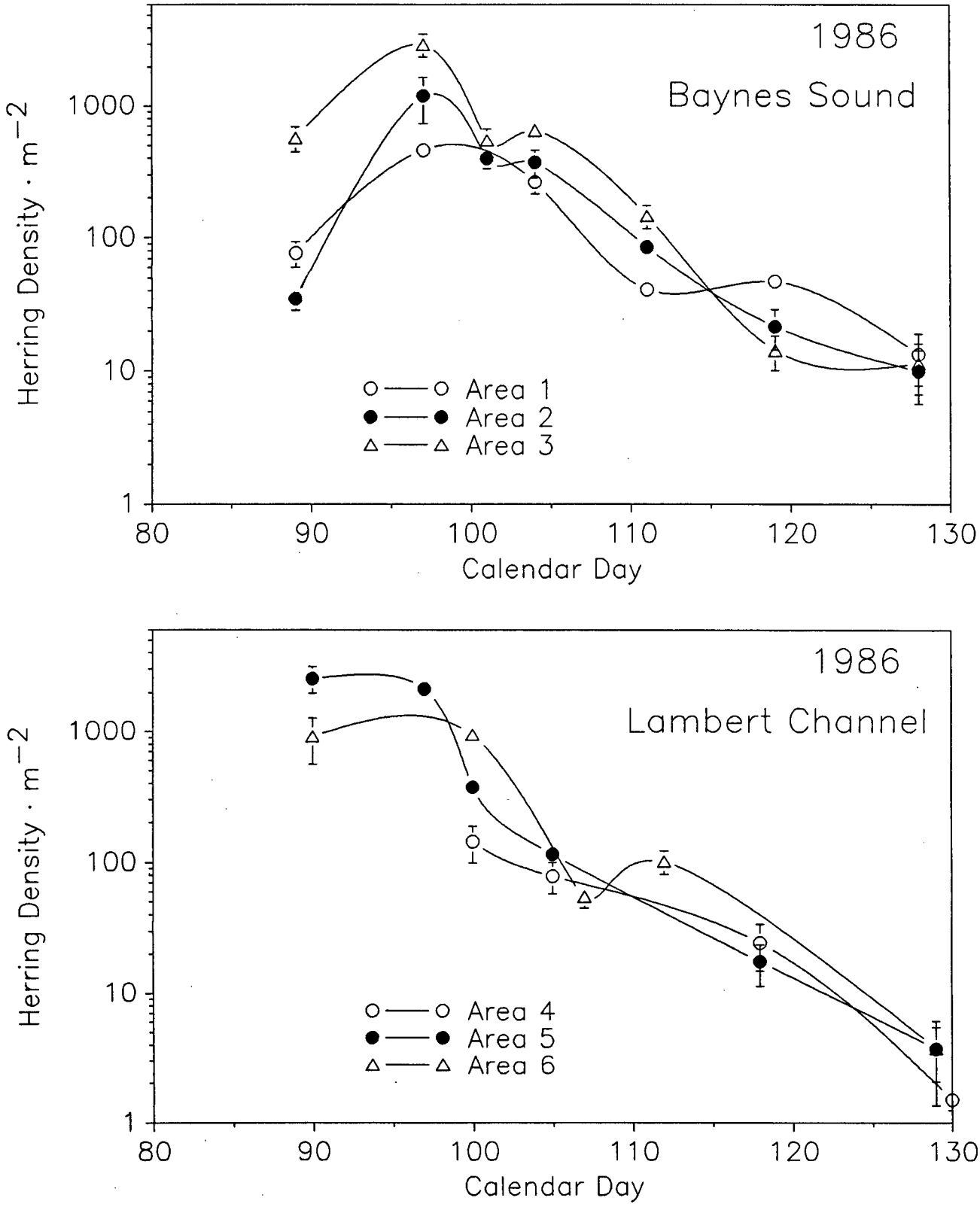


Figure 1.22. (continued).

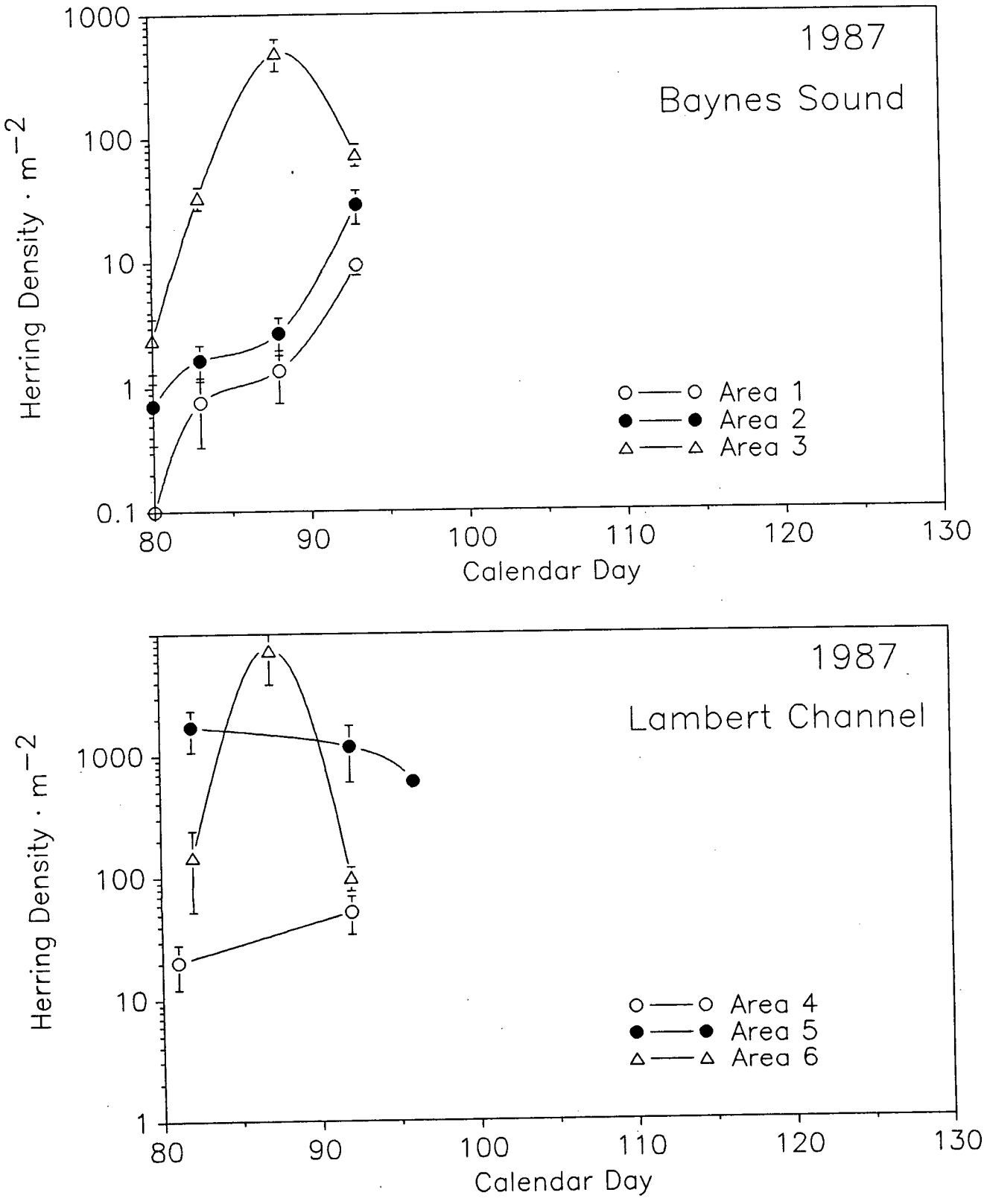


Figure 1.22. (continued).

V. DISCUSSION

A. Physical and Biological Characteristics

The physical measurements taken in the study area indicate Baynes Sound has certain physical characteristics which make it quite different from Lambert Channel and the surrounding outside waters. Stratification occurs early in the year, especially in areas 1 and 2, and is probably due to the freshwater input from the Comox River and the other small creeks at the north end of Baynes Sound. This is evident from the significantly lower salinities in the surface layer (Table 1.1) in both 1986 and 1987. The lower salinities in Baynes Sound at 40 m compared to Lambert Channel is probably due to the shallower depths found in Baynes Sound. Any estuarine flow occurring in Baynes Sound is probably south as there was no trace of the freshwater in area 4 based on the sigma-t profiles although turbulent mixing over Comox Bar could also have destroyed any trace of it. Over the duration of the study period, no significant amount of stratification was observed in the Lambert Channel areas suggesting wind mixing of the surface waters in all the outside areas was present. This mixing in the outside waters has implications for the timing of the onset of the spring plankton bloom. Vertical stability and light levels play an important part in the onset of the bloom (Riley, 1942; Sverdrup, 1953). It may also be possible that the flushing rates of the channels are important to the development of the bloom. Baynes Sound is more of a confined system than Lambert Channel due to Comox Bar at the northern end and the small restriction at the southern end. The introduction of phytoplankton-poor deep water from outside waters due to tides and wind mixing will decrease over the season and will probably decrease more quickly in Baynes Sound than Lambert Channel due to its properties of being semi-enclosed. Therefore, Baynes Sound may get an earlier bloom than Lambert

Channel and by extrapolation over the outside areas in the center of the strait. The differences in stability patterns in the study areas were also reflected in the few chlorophyll *a* profiles that were done. The areas in Lambert Channel showed lower densities of chlorophyll *a* and only very weak chlorophyll maxima were present, if at all. The horizontal profile on Day 98 in 1987 showed quite clearly Baynes Sound had higher levels than Lambert Channel. While the chlorophyll data by themselves are only a few snapshots in time, they do add support for the idea that stability in Baynes Sound allows for an earlier spring plankton bloom over Lambert Channel and outside areas.

The predominant southerly wind patterns with the strongest winds from the southeast suggests most wind drift of the surface water will be towards the northwest. The shallow water and subsequent bottom friction will tend to reduce tendencies toward an Ekman spiral to the right (Mitchum and Clarke, 1986). Therefore, any ichthyoplankton in the upper layers will be transported towards Vancouver Island and into Baynes Sound. Thomson (1981) estimates a transfer of about 3% of the wind velocity to the water in this area. With a mean daily wind speed of 8 $m \cdot s^{-1}$, this could translate into surface drift of over 20 $km \cdot d^{-1}$. The actual amount of transport is undoubtedly less as the momentum decreases with water depth but, it may still be enough to be significant.

Movement of the surface water mass with the wind was seen in some of the current drogue trials as the drogues appeared to move against the expected tidal flow and with the wind (e.g. track #'s 4, 5 and 9). This was the main purpose of the current drogue studies to document surface water movement counter to the prevailing tidal current. Generally, the flows of ebb tides in this region are southeast while flood tides are to the northeast. The net transport is southeast (M.

St. John, Dept. Oceanography, Univ. British Columbia, pers. comm.). There also appeared to be a possible eddy type circulation pattern in the southern mouth of Baynes Sound as the drogue tracks suggested a counterclockwise circulation during ebb tides although this conclusion is tenuous at best.

Before the different areas could be assessed for food resources relevant to Pacific herring larvae it was necessary to determine the type, size range and sequence of food items the larvae were utilizing (Frank, 1988). Results indicated the larvae initially concentrated on non-motile prey items such as the diatom, *Thalassiosira eccentrica*, and copepod eggs. Gradually, nauplii were taken and eventually larger copepodite stages up to a maximum of approximately 1 mm. These observations are supported by incidental larval herring feeding studies in the Strait of Georgia (Barraclough, 1967; Robinson et al., 1968; Robinson, 1969). They found almost identical types of prey items being taken and also the same size range of prey items (200 to 1100 μm for herring larvae 14 to 34 mm standard length). *Coscinodiscus* spp. (a closely related genus to *Thalassiosira eccentrica*) has been reported in previous studies to be fed on by cod larvae, *Gadus morhua*, (Nordeng and Bratlund, 1971; Last, 1978) but, the nutritional value (calories/individual) of a single diatom is quite low (Platt and Irwin, 1973). In addition, the silica based frustule of the diatom may be relative resistent to digestion. Therefore, I defined food relevant to herring larvae to consist of copepod eggs, nauplii, bivalve veligers, and small copepods and copepodite stages less than 1000 μm.

Using this definition to evaluate the study areas for their potential feeding benefits to herring larvae, Baynes Sound was shown to have overall higher prey densities than Lambert Channel. This trend was found for all three years, although the same length of time was not sampled in each. There was also a trend in Baynes

Sound where there was a high to low gradation from area 1 to area 3 in food densities. These patterns also suggest stratification and the inherent stability to the system it causes results in Baynes Sound being more productive earlier than Lambert Channel thereby producing greater food resources pertinent for herring larvae.

All of the plankton samples taken during this study could probably be defined as inshore. The lack of representative samples for the offshore deepwater region in the middle of the strait was because of time constraints imposed by the inshore sampling regime and also the limited capabilities of a small boat in open water. However, there is some information on offshore microzooplankton densities in this area and during the same time frame over a four year period from 1965 to 1968 (Bishop et al., 1966; Fulton et al., 1967; 1968; 1969) (Table 1.4). The mean (± sd) density of food items for herring larvae (copepod eggs, nauplii and small copepods) in the top 25 m over the four years was 186,875 ± 167,975 items$\cdot m^{-2}$ (x ± sd, n=26). If we assume this value is representative of the offshore food densities available to herring larvae, and compare it to the inshore plankton densities found in this study, the offshore food densities are only half that found in the inshore waters. This provides more insight into larval herring food densities as concentrations appear to decrease the further offshore one gets from Baynes Sound and seem to be directly correlated to the degree of stratification and stability of the area. The importance of stability may change over time however. As nutrient limitation begins to occur in the surface waters, other features may begin to become important in the maintenance of productivity of the area such as biological fronts (e.g. Parsons et al., 1981; 1983).

Table 1.4. Total microzooplankton densities in the middle of the Strait of Georgia at separate stations for 1965 to 1968. Total No. = eggs + nauplii + small copepods. Samples taken with bottles at various depths and data integrated from 0 to 25-30 m.

Date	Station	Total No. Microzoo/m^2 ($x10^3$)	Source
Mar 4/65	1	89 (0-30m)	Bishop et al., 1966.
Apr 8/65	1	115 (0-30m)	"
Mar 1/65	2	61 (0-30m)	"
Apr 5/65	2	69 (0-30m)	"
Mar 1/65	2'	51 (0-30m)	"
Apr 5/65	2'	38 (0-30m)	"
Mar 2/65	3	64 (0-30m)	"
Mar 12/65	3	59 (0-30m)	"
Apr 6/65	3	118 (0-30m)	"
	mean	74 ± 28	
Mar 24/66	1	328 (0-25m)	Fulton et al., 1967.
Apr 21/66	1	111 (0-25m)	"
Mar 22/66	2	77 (1-25m)	"
Mar 22/66	3	187 (1-25m)	"
	mean	176 ± 111	
Mar 2/67	1	362 (0-25m)	Fulton et al.,1968.
Mar 16/67	1	86 (0-25m)	"
Mar 31/67	1	705 (0-25m)	"
Apr 7/67	1	219 (0-30m)	"
Apr 13/67	1	199 (0-25m)	"
Apr 27/67	1	135 (0-25m)	"
Apr 5/67	2	491 (1-25m)	"
Apr 5/67	3	450 (1-25m)	"
	mean	331 ± 210	
Mar 6/68	1	167 (0-25m)	Fulton et al., 1969.
Mar 14/68	1	205 (0-25m)	"
Mar 20/68	1	317 (0-25m)	"
Mar 27/68	1	137 (0-25m)	"
Apr 8/68	1	117 (0-25m)	"
	mean	189 ± 79	
	overall mean	191 ± 162 (n=26)	

Stations:

1 - Middle of Strait off Nanaimo
2 - South of Hornby Island off Lesquiti I.
2'- East of Hornby Island in center channel
3 - North of Cape Lazo

Baynes Sound and Lambert Channel also differed substantially in their potential zooplankton predator complexes. Baynes Sound had higher densities of the carnivorous copepod, *Tortanus discaudatus*, than Lambert Channel in both 1986 and 1987. There is no reported evidence of this copepod being a predator on larval herring but, other predatory copepods such as *Labidocera* sp. (Lillelund and Lasker, 1971), *Euchaeta* sp. (Lillelund and Lasker, 1971; Yen, 1987), and *Centropages* sp. (Turner et al., 1985) have all been observed to feed on the early stages of larval fish in the laboratory. In one gut sample in 1985, I observed a *Tortanus* adult attached to the gut of a herring larvae. This observation in itself does not prove that this copepod is a predator of larval herring but, in view of the above information I decided to include it in the potential suite of predators. The densities of *Tortanus discaudatus* were directly correlated with the highest microzooplankton densities and thus showed a gradation from area 1 to area 3 in Baynes Sound. The densities of *T. discaudatus* may also be taken as an indirect indicator of potential larval herring food concentrations as it feeds heavily on similar types of prey items (Ambler and Frost, 1974; Mullin,1979).

Baynes Sound also had virtually all the hydromedusa, *Aequorea victoria*, with the largest concentrations in areas 1 and 2. This species has been shown to be an important predator on early stages of larval herring (Purcell et al., 1987) until the larvae are able to gain a size refuge from jellyfish predation (Bailey and Batty, 1984; Purcell et al., 1987). Lambert Channel had higher densities of the chaetognath, *Sagitta elegans*, and the polychaete, *Tomopteris septentrionalis*. These are typically deep water predators which probably explains why they are not found in any significant numbers in Baynes Sound. Both species have been shown to prey on larval herring (Lebour, 1923; Stevensen, 1962) and during 1987, I observed

chaetognaths feeding on the emerging herring larvae during the day in shallow water.

The different type of invertebrate predator complexes found in Baynes Sound and Lambert Channel suggest a pattern similar to the ecologically "safe site" scenario as suggested by Frank and Leggett (1982; 1985). In their study (1982) they found that capelin larvae (*Mallotus villosus*) as well as 11 other marine fish species including herring were spatially separated from their planktonic invertebrate predators due to separate water masses and this was argued as an adaptive feature of spawning. The same end result may occur as herring larvae that get moved into Baynes Sound may be separated from the "outside" predators of chaetognaths and polychaetes. While the larvae still have to contend with *Aquorea* predation, they may be able to outgrow the prey size range of this particular predator more quickly, especially as more food is present in Baynes Sound. It must be noted that these were the only potential invertebrate predators sampled. It may be other organisms may have a greater impact on larval herring with respect to predation but, my sampling methods were inadequate to sample them. For example, there were large populations of the euphausiid *Euphausia pacifica* in area 6 but because of their depth during the daylight hours they were below the maximum depth of bongo net tows. Euphausiids have been shown to feed on herring larvae (Bailey, 1984) as well as other fish larvae (Theilacker and Lasker, 1974).

B. Distribution and Dispersal

Pacific herring larvae initially appear to be concentrated in the upper surface waters throughout most of the day based on the vertical distribution studies. There

was some indication of a diel pattern of movement as the percentage of the larvae increased in the lower depths during the hours of darkness and this pattern appeared to increase and intensify as the larvae grew older. A diel movement of larval herring has also been observed in previous studies on Atlantic herring larvae although a larger vertical range was observed (e.g. Wood, 1971; Seliverstov, 1974). The important point of my results is they indicate the capture procedure utilized of taking plankton tows to a maximum depth of 40 m was accurately sampling the population at large and not missing a large proportion of the larval herring population which might reside below my net hauls during the day.

The horizontal pattern of larval herring densities with respect to the shore showed that larvae dispersed away from the spawning beds nearshore into the deeper offshore waters. However, there were always a significant density of herring larvae (larvae$\cdot m^{-2}$) close to the shore. This observation agrees with results from Powles et al. (1984). The fact the nearshore densities were close to or greater than the offshore samples indicate that densities (larvae$\cdot m^{-3}$) in the shallow inshore waters must be somewhat higher. The mechanism causing this nearshore distribution pattern is unknown at the present time. It may be a function of behavioural patterns of the herring larvae (e.g. Henri et al., 1985) or it may simply be a result of the physical phenomenon of the "no slip" condition close to the shore (Vogel, 1981). This condition occurs at the outer boundary of a flow where current velocities approach zero due to frictional forces exerted by the bottom or sides of a container. Whatever the cause, it has direct implications for larval fish surveys in that larval herring surveys conducted too far offshore will tend to underestimate the population with the result of overestimating mortality rates.

The density estimates in each of the study areas over time gives an indication of the movement patterns of the herring larvae. Direct observations during this study and records of spawning from the Dept. of Fisheries and Oceans indicate virtually all the spawning of the adult Pacific herring occurs in Lambert Channel and none in Baynes Sound. This is an important point as in 1985 and 1986 Baynes Sound generally had higher densities than Lambert Channel about two weeks after the major hatch of the larvae and maintained higher densities throughout most of the study period, especially in 1986 (Fig. 1.22). This indicates the larval herring are moving into Baynes Sound from Lambert Channel and also implies that Baynes Sound has higher immigration, lower emigration, lower mortality rates, or a combination of the above. Based on results from herring egg surveys in the area (Schweigert and Haegele, 1988a; 1988b; Haegele and Schweigert, 1987) and estimating the number of herring larvae in Baynes Sound from peak densities, I calculated at least 9%, 3% and 1% of the potential larvae hatching drifted into Baynes Sound after hatching in the years 1985 to 1987 respectively. When Baynes Sound is examined by area over time, area 3 had initially the highest densities of larvae over areas 1 and 2 in all three years. This indicates the larvae are mainly entering Baynes Sound from the southern entrance.

The mechanism of movement of the larvae is probably a passive one as the swimming abilities of herring larvae at this stage of their development are weak (Batty, 1984). The most likely explanation for this movement into Baynes Sound is through wind drift caused from the strong southeast winds which predominate at this time in conjunction with the water movement created by the tides. During Day 85-95 in 1987 when larvae were hatching, wind speed was weak and direction variable (Fig. 1.2). Samples for larval herring densities in Baynes Sound showed lower values than Lambert Channel and there did not appear to be the influx of

larvae over time seen in the two previous years. On this side of the strait, there is generally a net southward transport of water based on the tidal movements and therefore, the larvae are transported into area 6 where the winds push them into Baynes Sound. Once in Baynes Sound, the protection from the wind drift provided by the surrounding land masses, the shallower water and higher friction forces near the shore, and the stratification of the water column all probably assist in maintaining the larvae in this channel.

Chapter 2. Early Life History Characteristics of Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia, British Columbia: II. Analysis of Growth Rates.

I. INTRODUCTION

Hjort's (1914) first hypothesis suggested recruitment to a year-class of fish was determined in the very earliest larval stages and a critical period occurred during the switch from endogenous feeding on the yolksac to exogenous feeding on plankton where starvation induced mortality was high. Despite a profusion of studies designed to test this hypothesis, no firm conclusion has been reached (for review see May 1974; Rothschild, 1986). One of the major problems has been sampling a rapidly dispersing larval fish population with enough resolution to detect a sharp change in the mortality rate over the short period of time in the feeding transition phase. Because of the resolution problem, research has been conducted to establish whether larvae are indeed starving in the field. This has been done for herring, *Clupea harengus,* (e.g. Hempel and Blaxter, 1963; Chenoweth, 1970; Ehrlich et al., 1976; McGurk, 1985a), cod, *Gadus morhua,* (e.g. Koslow et al., 1985; Neilson et al., 1986), plaice, *Pleuronectes platessa,* (e.g. Shelbourne, 1957; Ehrlich et al., 1976), northern anchovy, *Engraulis mordax,* (O'Connell, 1976; 1980) and jack mackerel, *Trachurus symmetricus,* (Theilacker, 1978; 1986).

Three basic methods have been used to diagnose nutritional condition in larval fish: morphometric, histological and chemical. Morphometric indices have been the most extensively used and range from various types of ratios (e.g. Fulton's Condition Factor (weight/length^3) (Fulton, 1902; Hempel and Blaxter, 1963) to

multivariate analyses of various somatic measurements (McGurk, 1985a; Theilacker, 1986). A problem associated with this technique is the error introduced through morphometric changes (e.g. shrinkage) by net capture (Theilacker, 1980, Hay, 1981), preservation (Theilacker, 1980; Hay, 1981; 1982; 1984), growth stanzas (Balon, 1984), and individual variability of larvae due to differing egg sizes with differing amounts of yolk (Blaxter and Hempel, 1963). Another drawback is the relatively coarse resolution in time required as a significant weight or size change has to occur before it can be reliably detected.

Histological methods have been used effectively on jack mackerel (Theilacker, 1978; 1986), northern anchovy (O'Connell, 1980), herring (Ehrlich et al., 1976), and plaice (Ehrlich et al., 1976). These studies then used subjective criteria in addition to various ratios or multivariate analyses to categorize a larva as to nutritional condition. A drawback to this method is the preparation and handling time needed to prepare and analyze the samples.

While each technique has certain attributes and advantages, the chemical condition factors are probably the most sensitive as changes in the fish would occur first at the cellular level, then the tissue level and finally at the organism level. Some studies report significant differences in certain chemical constituents in as little as two to four days (Ehrlich, 1974; Buckley, 1981). A chemical method used to measure the state of growth and nutritional condition in larval fish is the ratio of ribonucleic acid (RNA) to deoxyribonucleic acid (DNA). Use of this ratio is based on the premise that while the DNA per cell is approximately constant, the amount of RNA in the cell is directly proportional to the amount of protein synthesis occurring. Several studies have shown there is a linear relationship between the rate of protein synthesis and the RNA/DNA ratio (e.g. Haines, 1973; Buckley,

1979; 1980; 1982; 1984). Buckley (1984) found if the RNA/DNA ratio was combined with data on water temperatures, 92% of the variance in the protein growth rate could be explained. This technique is particularly appropriate for studying the short-term growth of larval herring as well as other larvae. Ehrlich (1974) has shown herring larvae produce predominantly protein and some carbohydrate instead of triglycerides during their early growth stages (up to 20 mm). The resolution of this method then allows one to follow changes in growth rates on a fine time scale.

The concepts of growth and mortality in organisms have often been thought to be closely interrelated. The rationale is that in small organisms, such as fish larvae, faster growth will allow the larvae to outgrow the prey fields of some of their predators (Cushing, 1975; Hunter, 1981). When empirical studies are done on a single species the results are not as clear. For wild populations of Atlantic herring larvae , Graham and Townsend (1985) found over a three year period a significant positive correlation between growth rate and mortality. McGurk (1984a) compiled data from several studies on both Atlantic and Pacific herring larvae and found no significant correlation between growth rate and mortality for wild populations. Smith (1985) suggested there was an inverse relationship between growth and mortality for larval anchovy. When rates of growth and mortality are compared among species, there is generally a positive correlation between them (Ware, 1975).

The major problem associated with examining the relationship between growth and mortality with traditional methods is the amount of work needed to generate a single data point with sufficient accuracy for a rapidly dispersing population. The logistic sampling limitations of this approach then allow only a few points to be generated each year and a relatively long period will elapse before any

significant relationship can be determined. Another approach is therefore needed to examine this problem.

Lee (1912) published a study which indicated that backcalculated lengths of fish from scale readings were often underestimated due to increased mortality on the larger fish of the cohort. This has become known as Rosa Lee's Phenomenon (for review see Ricker, 1969; 1975). Other structures in fish also show ring structures proportional to the growth of the fish such as otoliths and fin rays. Otoliths in some larval fish have been shown to have concentric rings in daily increments (e.g. Barkman and Bengtson, 1987; Jenkins, 1987). Daily rings in larval herring have been suggested (Townsend and Graham, 1981; Jones,1985) but, may depend on the growth rate and size of the fish (McGurk, 1984b; Campana et al., 1987).

Therefore, Rosa Lee's Phenomenon could be used to test whether there was any relationship between growth and mortality on two samples of fish over time from the same population. Specifically, the mean ring width for a specified time interval could be compared between two samples. If the mean ring width differed, that would be evidence for selective mortality with growth. This type of analysis has been used for larval bluefin tuna, *Thunnus thynnus* (Brothers et al.,1983) and in larval and juvenile yellow perch, *Perca flavescens* (Post and Prankevicius, 1987). Both studies suggested enhanced survival of faster growing members of the cohort.

II. OBJECTIVES

The objectives of this chapter were:

1. To evaluate the ontogenetic development of growth rates of a developing cohort of larval Pacific herring.

2. To assess whether RNA/DNA ratios can be used as condition factors for larval fish.

3. To compare the growth rates of herring larvae between Baynes Sound and Lambert Channel.

4. To evaluate Hjort's 1st hypothesis about starvation of first feeding larvae.

5. To assess whether higher growth rates imply higher survival rate for herring larvae in this area.

III. MATERIALS AND METHODS

A. RNA/DNA Ratios

1. Field Study

To follow the instantaneous protein growth rates via the RNA/DNA ratios of the herring larvae, samples were taken over time with bongo nets at the middle transect (T5) in each area using 30 to 60 s oblique tows. A subsample of captured larvae (n = 6 to 23 depending on the densities available) were individually placed in numbered 1.5 ml plastic microcentrifuge vials containing 1 ml of 20 μm filtered seawater. These were immediately frozen and stored in liquid nitrogen for later analysis. The larvae were alive when frozen and the whole capture and preserving procedure took less than 10 min. Larval lengths were corrected for shrinkage in the liquid nitrogen before analysis of the data. A second subsample of the captured herring larvae was taken and preserved in 5% formalin in seawater for later morphometric analysis. A third subsample was preserved in 80% ethanol for otoliths (see below).

2. Starvation Controls

A control study was done to compare the larval herring RNA/DNA ratios observed in the field study to those from larvae known to be starved. In 1986, eyed eggs from natural spawn of Pacific herring were collected from Denman Island (Fig. 1.1) and held in aerated seawater at 8°C until hatching. Larvae were then transferred to aerated 70 l containers filled with 20 μm filtered seawater. A mesh size of 20 μm was selected as it is the lower size limit between microzooplankton and nanoplankton (Omori and Ikeda, 1984). Temperature was regulated with an external water bath to reflect temperature patterns found in the field. The salinity

was constant at 29.0 ppt. At approximately three day intervals subsamples (n = 6 to 15) of the larval population were taken and treated as above for later analysis of RNA/DNA ratios.

3. Laboratory Analysis

To measure the small concentrations of nucleic acids found in larval herring I used the LePecq and Paoletti (1966) fluorometric procedure, modified by Karsten and Wollenberger (1972,1977). This technique is based on the enhanced fluorescence of nucleic acids after introduction of the dye ethidium bromide (2,7-diamino-10-ethyl-9-phenyl-phenanthidinium bromide) and is sensitive to small amounts of nucleic acids at concentrations down to 0.05 $\mu g \cdot ml^{-1}$ for DNA and 0.1 $\mu g \cdot ml^{-1}$ for RNA. Prasad et al. (1972) have shown that results from this technique are comparable with those from the traditional modified Schmidt-Thanhauser method used by Buckley (1984). For this study, an individual larva was thawed, measured for standard length to the nearest 0.2 mm using an ocular micrometer with a dissecting microscope, and staged morphologically according to Doyle (1977). There were three basic stages used in this study, each with three substages. Stage 1 was yolk-sac larvae, stage 2 was preflexion post-yolk-sac larvae and stage 3 was postflexion larvae. The larva was then placed in 3 ml of ice-cold phosphate buffered saline and homogenized and sonicated with a Polytron tissue grinder at 24,000 rpm for two 10 s treatments. Two replicates of 0.5 ml aliquots were taken and processed for determination of DNA and two for the total nucleic acids (Fig. 2.1). Fluorescence of the sample was measured with a FOCI Ratio Fluorometer-2 (Farrand Optical Company Limited) on sample mode.

Two modifications were made in the Karsten and Wollenberger technique. Incubation time was increased from 20 to 30 min and the RNase concentration was

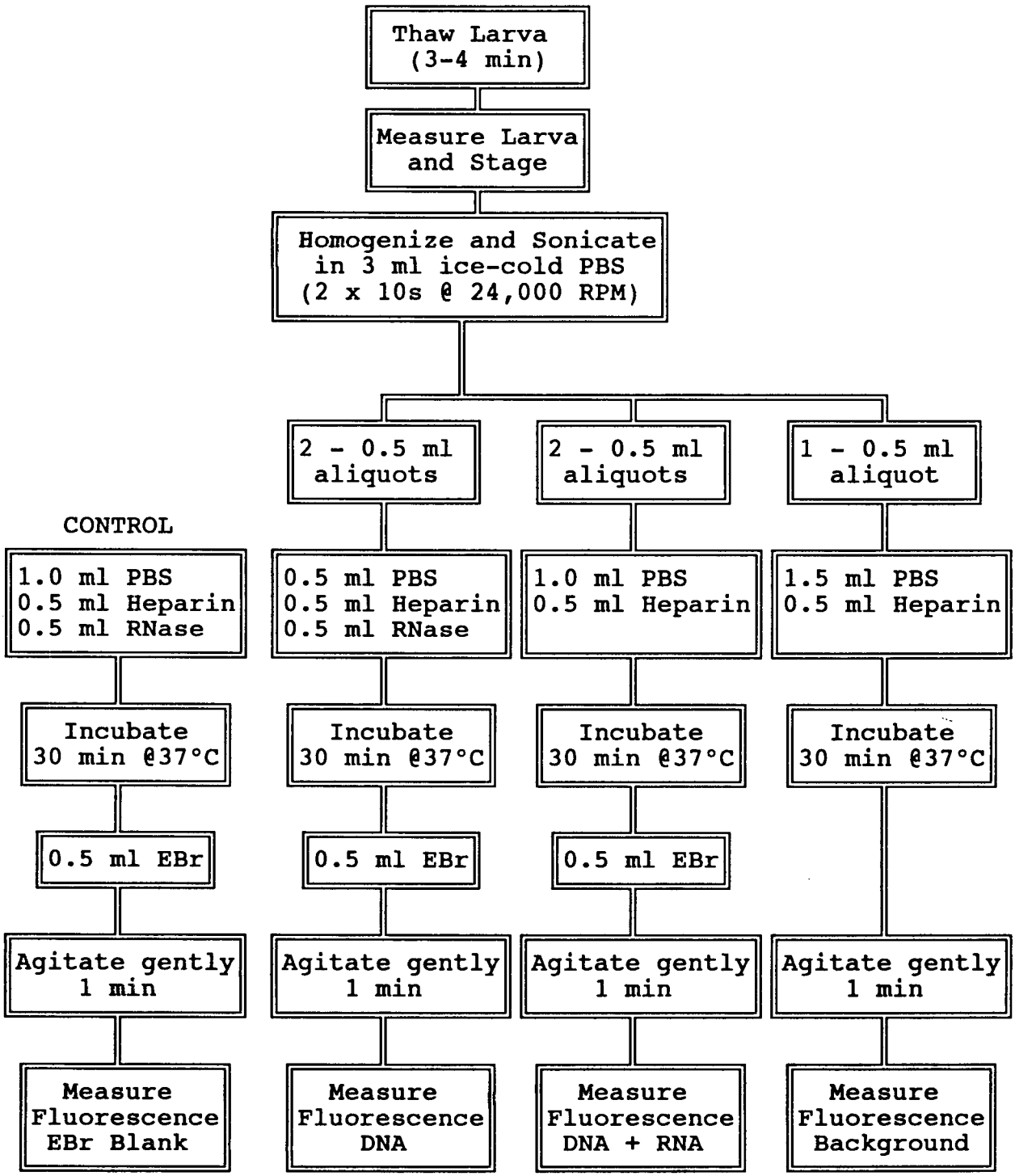


Figure 2.1. Schematic flowchart of the analytical scheme used to analyze the nucleic acid concentrations in Pacific herring larvae.

increased from 50 to 100 $\mu g \cdot ml^{-1}$ for added assurance that essentially all the RNA would be hydrolyzed by the enzyme. Standard curves were done for both DNA and RNA. Processing time of the samples by two persons was one fish every 5 min after the initial time lag of 30 min due to the incubation period. Samples were randomly chosen each day from the liquid nitrogen storage tanks so systematic errors would not affect a particular size group.

A standard curve of DNA concentration vs fluorescence was produced using known dilutions of DNA (Type III, Sigma Chemical Co.) at 0.05, 0.1, 0.25, 0.5 1, 2, 3, and 4 $\mu g \cdot ml^{-1}$ and were analyzed using the Karsten and Wollenberger technique (1972, 1977). Three replicates were done at each concentration. For the RNA (Type IV, Sigma Chemical Co.) concentration vs fluorescence standard curve, the RNA solution had to be corrected for DNA contamination before analysis using an alkali hydrolysis. Concentrations of 0.25, 1, 5, and 19 $\mu g \cdot ml^{-1}$ were analyzed as described above for DNA.

To calculate a known condition factor (CV1) for Pacific herring larvae, subsamples of larvae preserved in formalin were measured for standard length, anal body depth, pectoral body depth, head width and eye diameter using an ocular micrometer on a dissecting microscope according to the protocol specified by McGurk (1985). The larvae were then dried at 80°C for 3 days and weighed to the nearest microgram on a Mettler M3 microbalance. The condition factor for a larva was calculated as:

(1) $CV1 = 14.191 - 4.389 (\log SL) + 2.184 (\log ABD) + 2.197 (\log PBD) - 12.331 (\log HW) + 3.770 (\log ED) + 2.197 (\log DW)$

where SL is standard length (mm), ABD is anal body depth (mm), PBD is pectoral body depth (mm), HW is head width (mm), ED is eye diameter (mm), and DW is dry weight (mg).

4. Net Selection

In 1987, sampling was conducted to determine whether there was any selection of the net for larvae with lower RNA/DNA ratios. If net avoidance was occurring, then the RNA/DNA ratio should increase at night as the net avoidance of the larvae reduces. Three replicate oblique bongo net samples to 40 m were taken in area 5 (T6S2) on Day 96 at 0900 h and 2100 h. The captured larvae were placed in vials as described above and frozen and stored in liquid nitrogen until they were analyzed in the laboratory. Samples were processed using the Karsten and Wollenberger method (described above).

5. Critical Ratio

Buckley (1984) examined the relationship between the instantaneous protein growth rate (the dependent variable), the RNA/DNA ratio (the independent variable) and water temperature. The relationship was linear ($r^2 = 0.92$) and was given as:

$$G_{pi} = 0.93 \cdot T + 4.75 \cdot RNA/DNA - 18.18 \quad (2)$$

where G_{pi} is the protein growth rate (percent per day), T is water temperature (°C) and RNA/DNA is the RNA/DNA ratio. Buckley's study involved temperature ranges from 2 to 20°C and eight species of marine fish larvae including Atlantic herring (*Clupea harengus harengus*).

Equation (1) can be further manipulated by setting G_{pi} equal to zero and then rearranging to give:

(3) $$RNA/DNA = R_{crit} = (18.18 - 0.93 \cdot T) / 4.75$$

where R_{crit} is what I call the critical ratio and the other variables are the same as above. The critical ratio is the theoretical RNA/DNA ratio where there is no net protein growth in a larval fish at a specified temperature.

B. Otoliths and Survival

Larvae were captured in 1986 using bongo nets as described above. The larval subsamples in 1986 for otoliths were taken from the bongo net tows for RNA/DNA ratios as described above and the larvae preserved in 80% ethanol. In the laboratory, the larvae were measured and staged and the left and right sagittal otoliths dissected out using fine dissecting needles. The otoliths were mounted on slides and a drop of immersion oil was placed on each otolith. Samples were analyzed from two distinct periods, Calendar Day 107 and Calendar Day 128 and were from Lambert Channel. The otolith was examined under a compound microscope at 1500 times magnification, the diameter and radius measured with an ocular micrometer, and the radiating rings traced from the primordia to the edge of the otolith along a reference line using a drawing tube. The resulting traces were measured using a digitizing board connected to a PC computer.

Ring widths were compared between the two sample periods for the first seven increments. Distances from the primordia was made equal as early rings in the later second sample were somewhat obscured by overlaying layers.

IV. RESULTS

A. RNA/DNA Ratios

1. Nucleic Acid Standards

There was a very high degree of correlation between the nucleic acid concentrations and the fluorescence (Fig. 2.2). The slope for the RNA standard curve was only 23% that of the DNA standard curve. There was a very low amount of variance between the replication used in the laboratory analysis of the aliquots of the nucleic acids. The mean percentage difference for the DNA replicates for 1986 was 0.62 ± 0.70 (n = 731) and for 1987 was 0.42 ± 0.51 (n = 484). For the total nucleic acids, the mean percentage difference for 1986 was 0.68 ± 0.81 (n = 731) and for 1987 was 0.43 ± 0.49 (n = 484).

2. Starvation Controls

For the herring larvae starved from hatching in 1986, there was a significant increase in the mean RNA/DNA ratio over the first four days from 1.82 to 3.37 ($p < 0.001$, Student's t-test) after which there was a decreasing trend in the mean ratio reaching 0.50 by the time the last larvae had died (Fig. 2.3). Marked on the figure is the observed end of yolk sac stage (EYS) and the point-of-no-return (PNR) calculated from McGurk (1984a) for Pacific herring at these temperatures. At the calculated PNR of 11 days, the mean ratio was 2.06.

The mean standard length of the population increased for 8 days after which it slowly decreased leveling out around day 14 at approximately 8.5 mm. The reduction in length occurred as the RNA/DNA ratio reached the critical ratio of 2. Variation in the standard length between sampling periods was generally less than that observed in the RNA/DNA ratios.

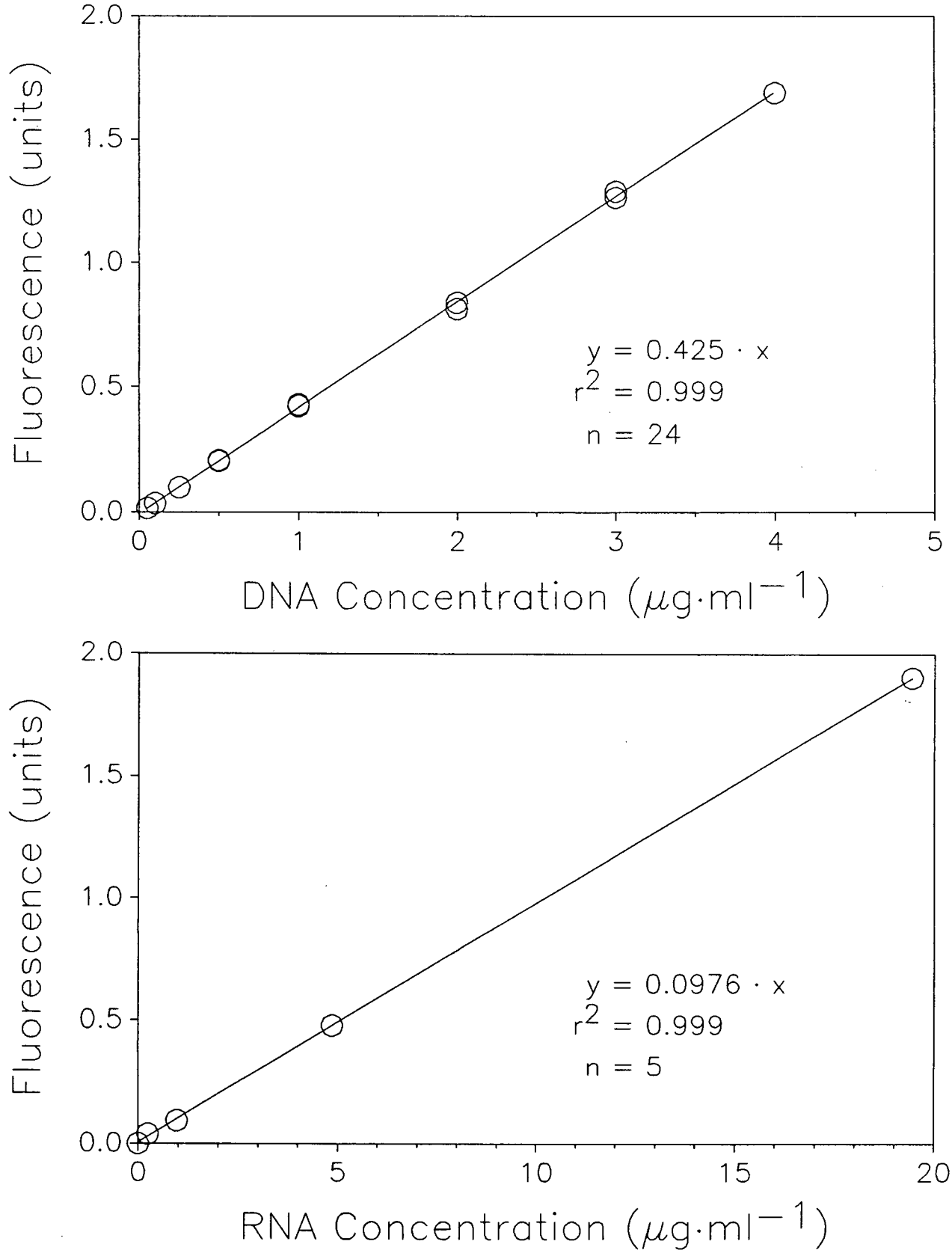


Figure 2.2. Plot of the relationship between nucleic acid concentration and the relative fluorescence for DNA and RNA.

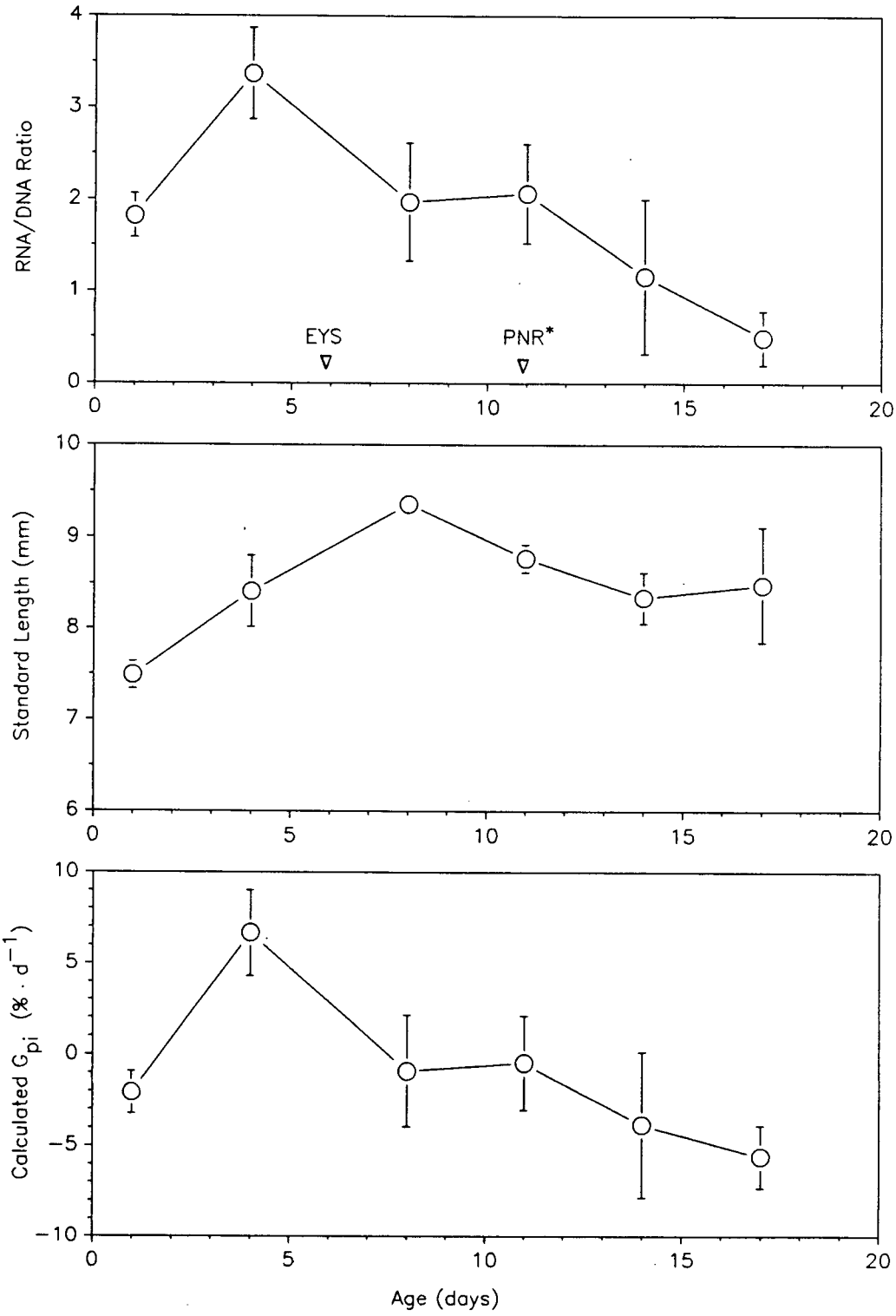


Figure 2.3. Progression of the RNA/DNA ratio, standard length, and calculated protein growth rate of starved Pacific herring larvae over time in the starvation control tank. Bars indicate 1 standard error of the mean. EYS = end of yolk sac; PNR = calculated point-of-no-return (McGurk, 1984).

The protein growth rates calculated from equation (1) show the same pattern as the RNA/DNA ratios due to the direct relationship between them. The mean values ranged from -5.6 to 6.7% protein increase per day while individual growth rates ranged from -10.0 to 17.3%.d^{-1}.

3. Net Selection

There were no significant differences in the mean RNA/DNA ratios or the standard lengths between the 0900 h and 2100 h samples ($p > 0.05$, Mann-Whitney U test) (Table 2.1).

4. Functional Relationships

There was a close relationship between the standard length of the post yolk-sac herring larvae and the dry weight for 1986 ($r^2 = 0.97$, $n = 400$) (Fig. 2.4). The relationship was curvilinear and could not be made linear through the normal logarithmic transformations. Therefore, I used a polynomial to fit the curve. The yolk-sac larvae appeared to grow mostly in length as their weight increased very slowly ($r^2 = 0.047$, $n = 153$). The equation of best fit for the post yolk-sac larvae was:

$$(4) \qquad Wt = -1.87 + 0.56L - 0.052L^2 + 0.0016L^3$$

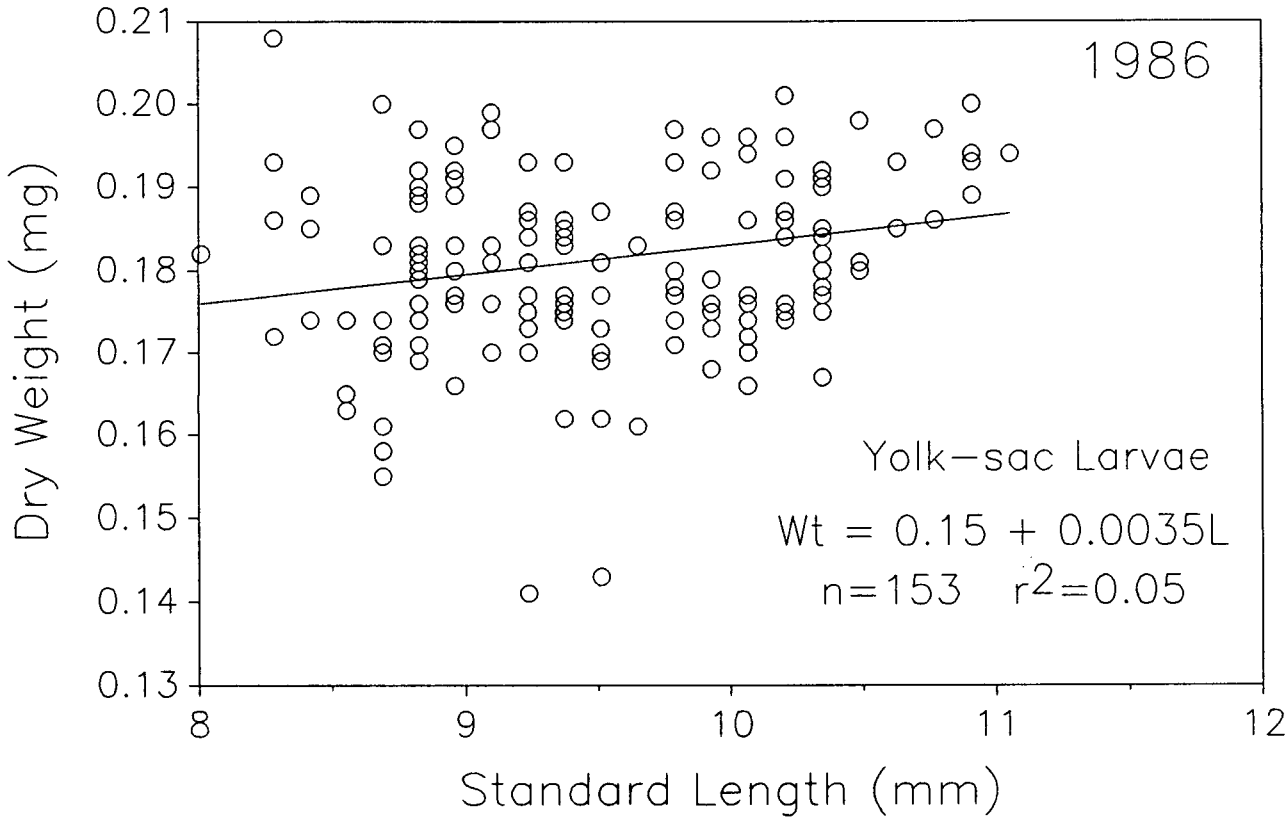
where Wt is dry weight (mg), and L is standard length (mm).

5. Field Study

There was a roughly linear increasing trend of the RNA/DNA ratio with standard length for both 1986 and 1987 (Fig. 2.5). Variation in the ratio decreased with increasing size of the larvae. The RNA/DNA ratio ranged from 0 to approximately 12. In 1986, approximately 44% of the variation in the RNA/DNA

Table 2.1. Comparison of RNA-DNA ratios and standard lengths between groups of fish captured during the daylight hours vs those caught at night on Day 96 in Area 5.

Time	n	RNA-DNA ratio $\bar{x}$	RNA-DNA ratio SD	Standard Length(mm) $\bar{x}$	Standard Length(mm) SD
0900	28	2.97	1.01	9.06	1.22
2100	24	2.66	0.69	8.45	0.64



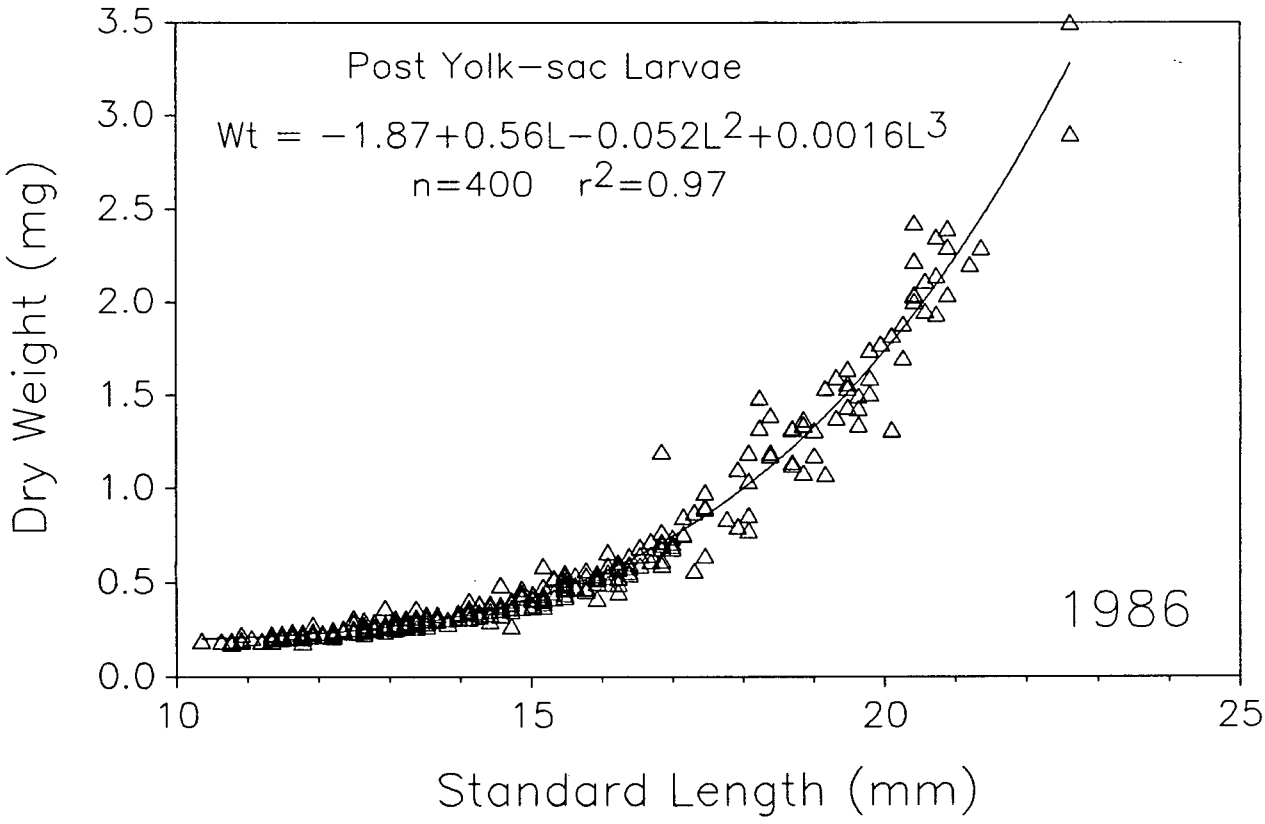


Figure 2.4. Functional relationship between dry weight and standard length for yolk-sac and post yolk-sac Pacific herring larvae in 1986.

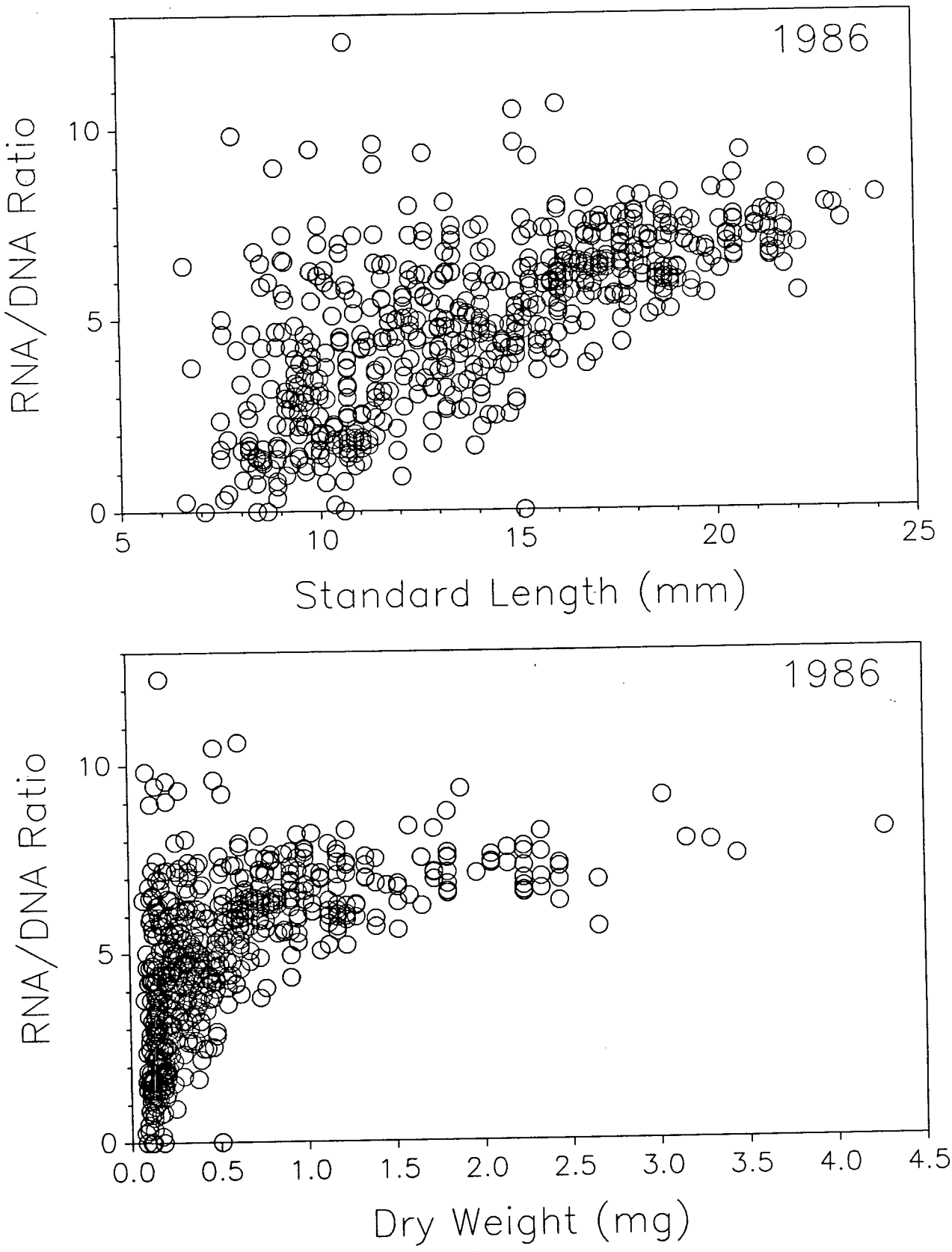


Figure 2.5. The relationship of standard length and dry weight with the RNA/DNA ratio in Pacific herring larvae from 1986.

ratio could be explained by the standard length. When the dry weight was predicted from the standard length using equations (4) and (5) and plotted against the RNA/DNA ratio, a logarithmic trend was found where it appeared the RNA/DNA ratio started to approach an asymptote at a weight above 2 mg at a RNA/DNA ratio of 8 (Fig. 2.5).

The mean RNA/DNA ratios for each morphological stage (Doyle, 1977) tended to increase except for stage 2a (the stage at which first feeding occurs) in 1986 in both Baynes Sound and Lambert Channel where there was a drop in the mean although it was not significant (Table 2.2). This same pattern was not found in 1987. The mean ratios ranged from about 2.5 for stage 1a to about 7 for stage 3c. Stages in Baynes Sound and Lambert Channel seemed to have similar RNA/DNA ratios. Larval herring in 1987 had lower ratios than similar stages from 1986. The RNA concentration in the fish increased much more quickly by stage than did DNA, in what appeared to be an exponential type of pattern (Fig. 2.6).

The percentage of larvae below the calculated critical ratio by morphological stage in both Baynes Sound and Lambert Channel for 1986 and 1987 decreased with each successive stage (Table 2.3). Early stages had fairly high percentages under the critical ratio but, by stage 2b, there were no larvae under the critical ratio.

During 1986, the RNA/DNA ratio increased over time in a curvilinear fashion with a decrease in the ratio around Day 105 which appeared in both Baynes Sound and Lambert Channel. Baynes Sound showed less variation than Lambert Channel and all three areas (1-3) seemed to track fairly closely. The mean RNA/DNA ratio tended to increase over time from approximately 2 at Calendar day 90 to 7 by Calendar day 126 (Fig. 2.7). During the first half of the study period,

Table 2.2. Summary of mean standard lengths(mm) and RNA/DNA ratios of Pacific herring larvae captured in Baynes Sound and Lambert Channel by morphological stages (Doyle, 1977) for the years 1985 to 1987. St.=Stage

	Baynes Sound					Lambert Channel				
		Length(mm)		Ratio			Length(mm)		Ratio	
St.	n	$\bar{x}$	SD	$\bar{x}$	SD	n	$\bar{x}$	SD	$\bar{x}$	SD
					1985					
1a	0	-	-	-	-	0	-	-	-	-
1b	6	8.67	0.36	-	-	15	9.11	0.33	-	-
1c	31	9.57	0.51	-	-	29	9.95	0.43	-	-
2a	30	10.57	0.40	-	-	13	10.99	0.36	-	-
2b	35	11.89	0.69	-	-	22	12.56	0.71	-	-
2c	22	13.73	0.67	-	-	29	14.93	1.21	-	-
3a	0	-	-	-	-	18	18.15	0.98	-	-
3b	0	-	-	-	-	17	19.58	0.75	-	-
3c	0	-	-	-	-	0	-	-	-	-
					1986					
1a	8	7.99	0.77	3.33	3.16	28	8.56	0.87	2.25	1.49
1b	28	10.16	0.78	3.18	1.98	25	9.43	0.72	3.21	2.10
1c	22	10.68	0.92	4.73	2.77	7	10.65	0.79	4.95	0.85
2a	38	12.21	1.02	4.28	1.80	32	11.54	1.21	3.65	1.75
2b	28	13.29	1.31	4.78	1.56	22	13.11	1.06	4.67	1.23
2c	44	15.28	1.49	5.15	1.42	26	14.97	1.26	5.42	1.30
3a	36	16.75	1.23	6.07	1.12	18	16.75	1.53	5.57	1.86
3b	37	18.22	1.13	6.70	0.81	20	17.33	1.88	6.59	1.42
3c	32	20.35	1.51	7.15	0.99	11	19.41	3.13	7.65	1.13
					1987					
1a	0	-	-	-	-	28	8.77	0.57	2.42	0.88
1b	0	-	-	-	-	95	9.32	0.62	2.76	1.08
1c	34	10.41	0.94	2.87	1.41	141	10.33	0.75	2.74	0.86
2a	10	11.82	0.82	3.57	0.80	26	11.60	1.12	3.17	0.88
2b	10	12.92	0.91	4.11	1.16	9	12.31	1.95	3.70	0.86
2c	0	-	-	-	-	0	-	-	-	-
3a	0	-	-	-	-	0	-	-	-	-
3b	0	-	-	-	-	0	-	-	-	-
3c	0	-	-	-	-	0	-	-	-	-

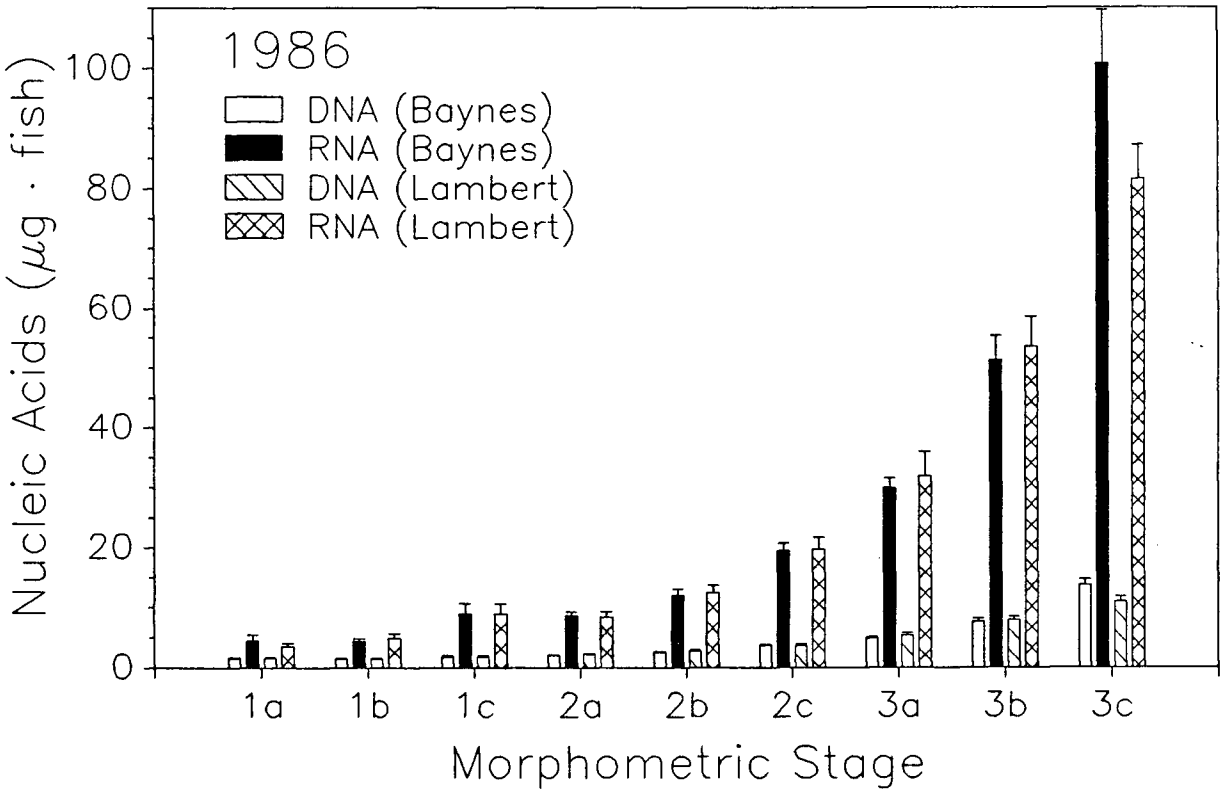


Figure 2.6. The nucleic acid concentrations of herring larvae by morphological stage (Doyle, 1977) for 1986. Bars indicate 1 standard error of the mean.

Table 2.3. Percentage of Pacific herring larvae having RNA-DNA ratios below the critical ratio($\%R_{crit}$) by morphological stages(Doyle, 1977) for 1986 and 1987. -- = no observation.

	1986				1987			
	Baynes		Lambert		Baynes		Lambert	
Stage	n	$\%R_{crit}$	n	$\%R_{crit}$	n	$\%R_{crit}$	n	$\%R_{crit}$
1a	8	50.0	27	59.3	0	--	28	39.3
1b	28	35.7	25	52.0	0	--	95	21.1
1c	22	22.7	7	0.0	34	23.5	141	17.7
2a	38	15.8	32	28.1	10	0.0	26	3.9
2b	28	0.0	22	0.0	10	0.0	9	0.0
2c	44	0.0	26	0.0	0	--	0	--
3a	36	0.0	18	5.6	0	--	0	--
3b	37	0.0	20	0.0	0	--	0	--
3c	32	0.0	11	0.0	0	--	0	--

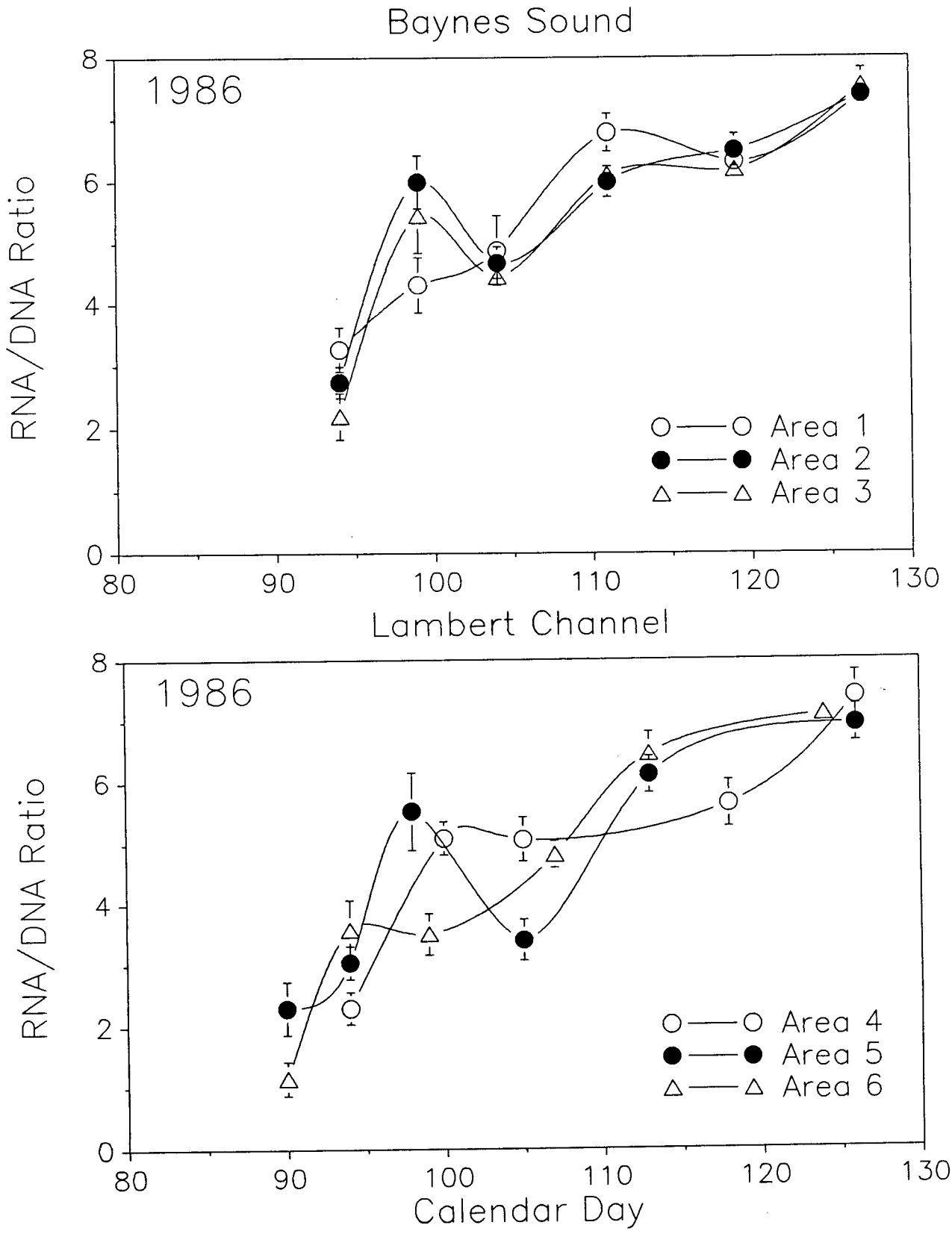


Figure 2.7. Progression of the mean RNA/DNA ratio of field caught Pacific herring larvae over time from the 6 sampling areas in 1986. Bars indicate 1 standard error of the mean.

from Day 90 to Day 108, the variance in the RNA/DNA ratio was significantly higher ($p < 0.001$, F-test) than it was in the latter half from Day 109 to Day 126. In 1987, the lack of larvae in Baynes Sound during the early sampling periods made any determination of a pattern impossible although the values scaled similarly. Lambert Channel did not show such a rapid rise in the RNA/DNA ratio as that observed in 1986 (Fig. 2.8).

To compare the growth rates (via the RNA/DNA ratios) and the standard lengths of the herring larvae from Baynes Sound and Lambert Channel, the study period was divided into two periods; an early period containing the yolk sac larvae plus stage 2a (Calendar Day 92 - 104) and a later feeding period from Calendar Day 104-Day 128 (Table 2.4). For the first time period in 1986, there was no difference in the mean RNA/DNA ratio values between Baynes Sound and Lambert Channel ($p > 0.05$, Mann Whitney U test) although the mean standard length of larvae was greater in Baynes Sound ($p < 0.01$, Mann Whitney U test). For the second period, the mean RNA/DNA ratio for Baynes Sound was significantly higher than that for Lambert Channel ($p < 0.01$, Mann Whitney U test). The mean standard lengths were also significantly higher in Baynes Sound ($p < 0.01$, Mann Whitney U test). In 1987, the early feeding period showed that Baynes Sound had higher mean values for both RNA/DNA ratios and standard length ($p < 0.01$, Mann Whitney U test) than Lambert Channel.

In 1986, there was a fairly rapid decrease over time in the percentage of herring larvae below the critical ratio in both Baynes Sound and Lambert Channel and by about Calendar Day 105-107 there were no larvae exhibiting a loss in growth (Table 2.5). The samples from Baynes Sound and Lambert Channel in 1987 did not

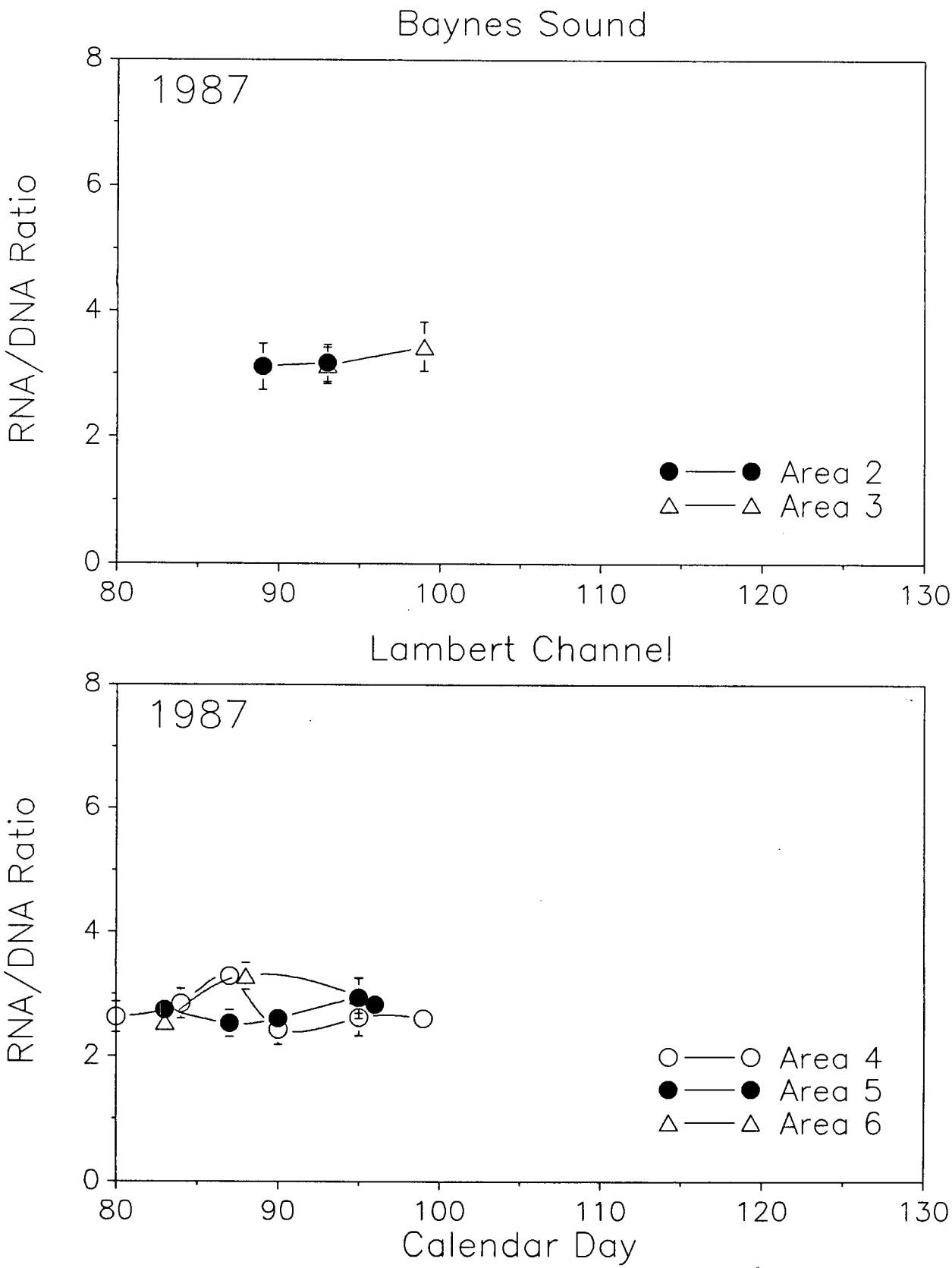


Figure 2.8. Progression of the mean RNA/DNA ratio of field caught Pacific herring larvae over time from 5 of the 6 sampling areas in 1987. Bars indicate 1 standard error of the mean.

Table 2.4. Comparison of RNA/DNA ratios and standard lengths between Baynes Sound and Lambert Channel for two time periods.

Channel	n	RNA/DNA ratio $\bar{x}$	RNA/DNA ratio SD	Standard Length(mm) $\bar{x}$	Standard Length(mm) SD
		1986			
		Calendar Day 92 - 103			
Baynes	127	3.82	2.24	10.87	1.64
Lambert	101	3.69	1.88	10.23	1.66
		Calendar Day 104 - 128			
Baynes	208	6.09	1.42	17.01	2.59
Lambert	125	5.72	1.71	15.98	2.95
		1987			
		Calendar Day 88 - 105			
Baynes	50	3.25	1.31	11.25	1.31
Lambert	141	2.79	0.87	10.58	1.14

Table 2.5. Percentage of Pacific herring larvae having RNA/DNA ratios below the critical ratio($\%R_{crit}$) during the sampling periods in Baynes Sound and Lambert Channel for 1986 and 1987. -- = no observation.

Baynes Sound			Lambert Channel		
Day	n	$\%R_{crit}$	Day	n	$\%R_{crit}$
			1986		
--	--	--	90	23	60.9
94	60	48.3	94	46	43.5
99	49	2.0	98-100	45	11.1
104	43	0.0	105-107	52	5.8
111	55	0.0	113	30	0.0
119	60	0.0	118	6	0.0
127	38	0.0	124-126	28	0.0
			1987		
--	--	--	80	17	23.5
--	--	--	83-84	87	26.4
--	--	--	87-88	52	11.5
89	15	26.7	90	28	28.6
93	18	5.6	95-96	81	23.5
99	17	29.4	99	14	21.4

show a clear trend over time but, indicated there were approximately 20 to 30% of the larvae below the critical ratio most of the time.

Initially, the shape of the frequency distributions of the RNA/DNA ratios for Baynes Sound and Lambert Channel in both 1986 and 1987 were skewed right but, gradually assumed a more normal distribution over time (Fig. 2.9). Because of logistic sampling problems, some sampling periods in Lambert Channel had to be combined in order to show all three areas. In 1986, the mode moved right over time and the range of values initially increased then decreased. Modes were also evident in 1987 especially in Lambert Channel but, there was no obvious progression in the modes over the time studied.

The RNA/DNA ratio was correlated with McGurk's (1985) condition factor (CV1) to test the applicability of the ratio as a larval herring condition index. There was a good correlation ($r = -0.87$, $n = 29$, $p < 0.01$) between CV1 and the RNA/DNA ratio (Fig. 2.10).

There were no significant correlations between the mean RNA/DNA ratio and any of the mean food group densities (number$\cdot m^{-2}$) for the yolk-sac and very early feeding herring larvae in 1986 or 1987 (Table 2.6). However, for the feeding larvae in 1986, there was a significant correlation between the mean larval RNA/DNA ratio and the mean nauplii densities as well as the total food densities. There were no significant correlations between the RNA/DNA ratio and copepod egg densities or small copepods (< 1 mm) ($p > 0.05$).

Linear growth rates of the herring larvae based on progression of the modes of the length-frequency histograms ranged from 0.27 to 0.36 mm$\cdot d^{-1}$ (Table 2.7).

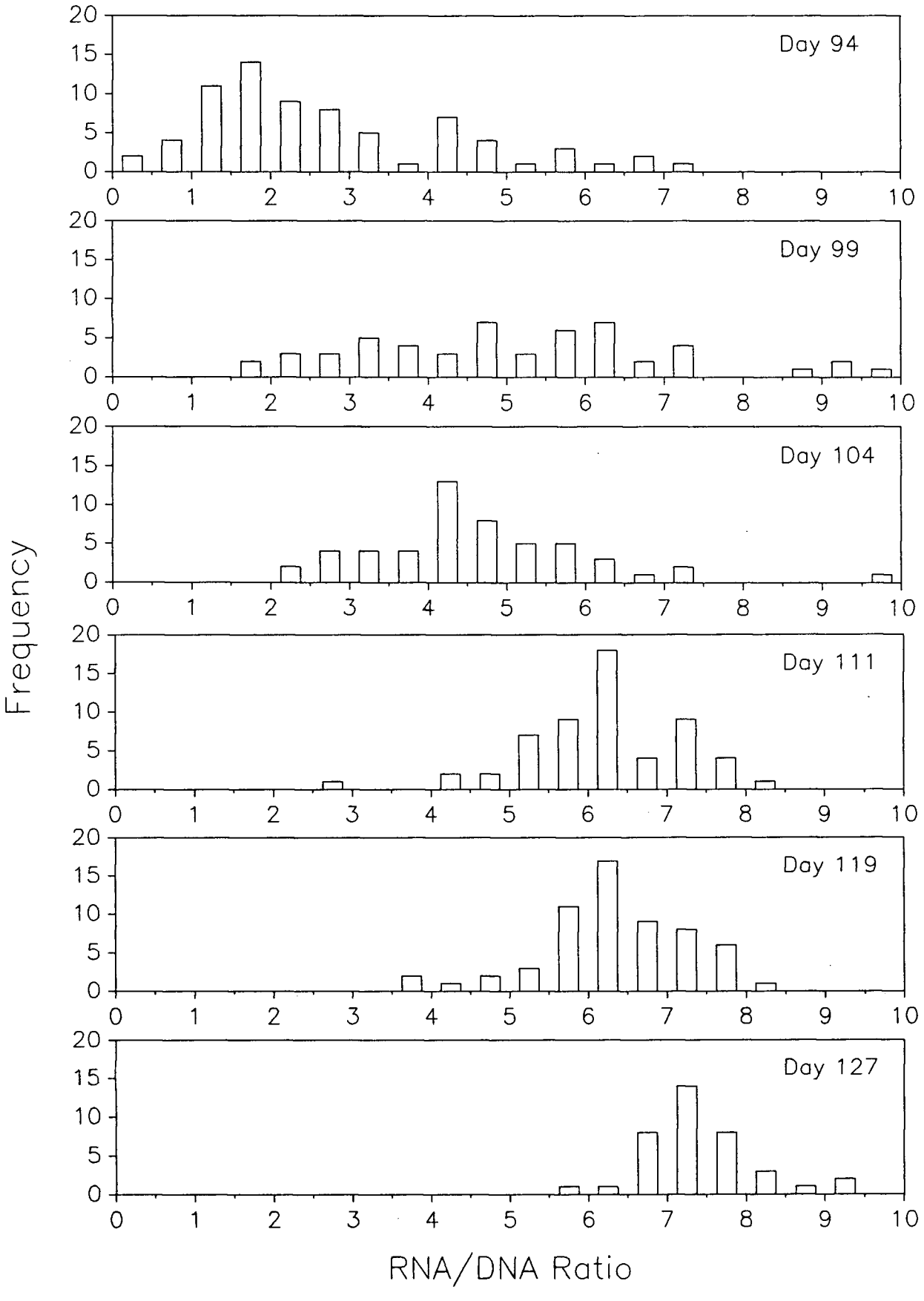


Figure 2.9a. Frequency distributions of the RNA/DNA ratios over time in Baynes Sound during 1986.

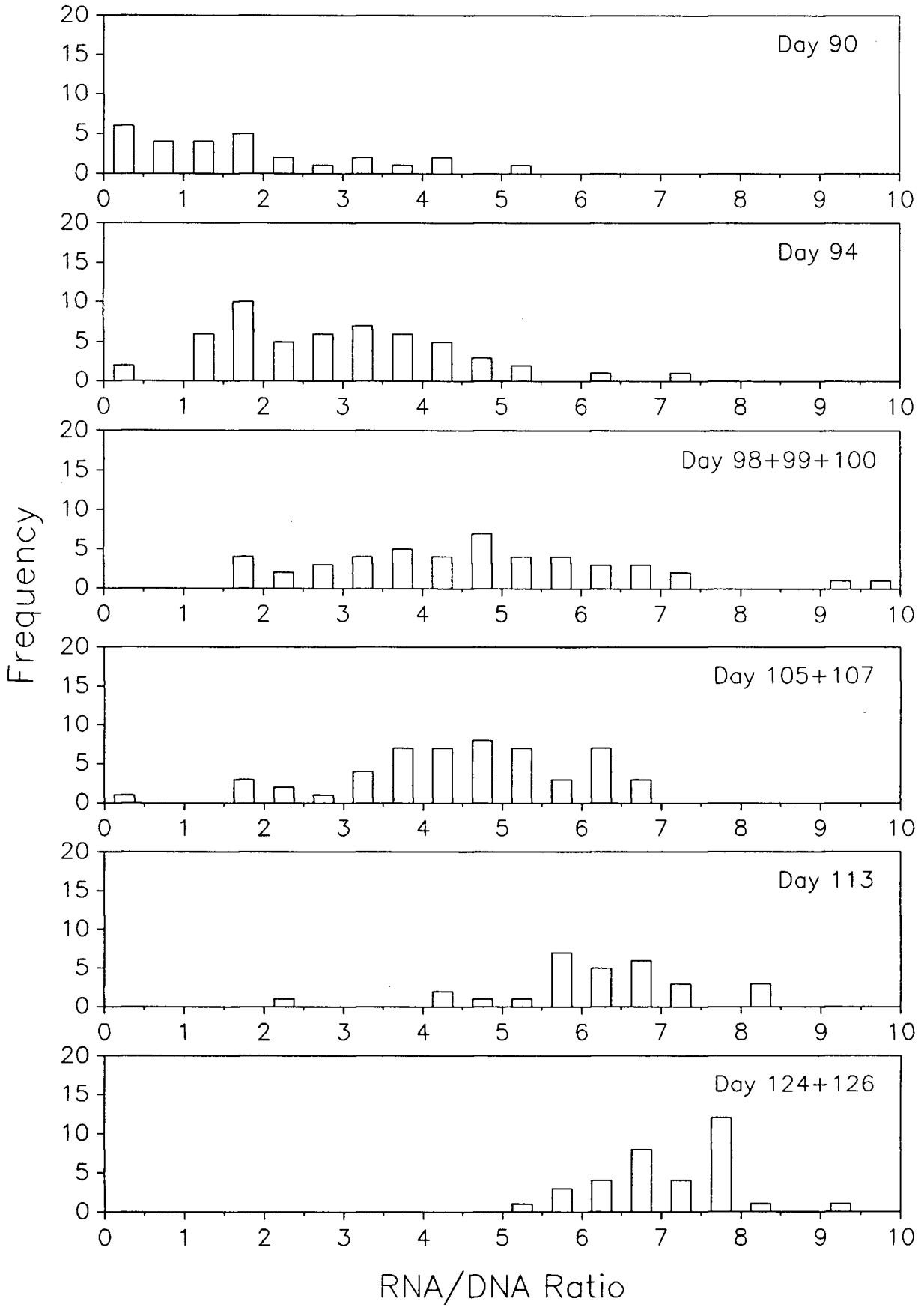


Figure 2.9b. Frequency distributions of the RNA/DNA ratios over time in Lambert Channel during 1986.

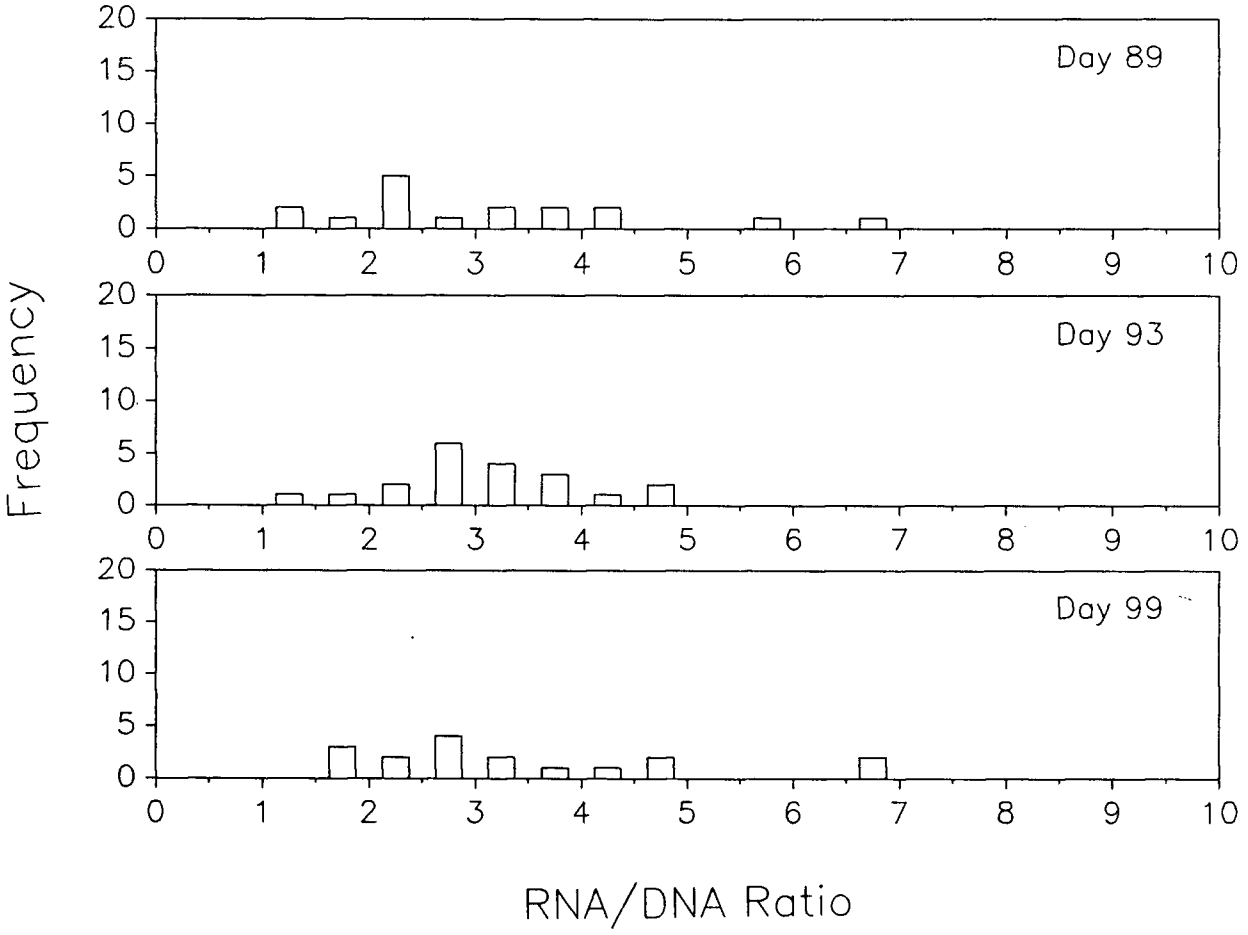


Figure 2.9c. Frequency distributions of the RNA/DNA ratios over time in Baynes Sound during 1987.

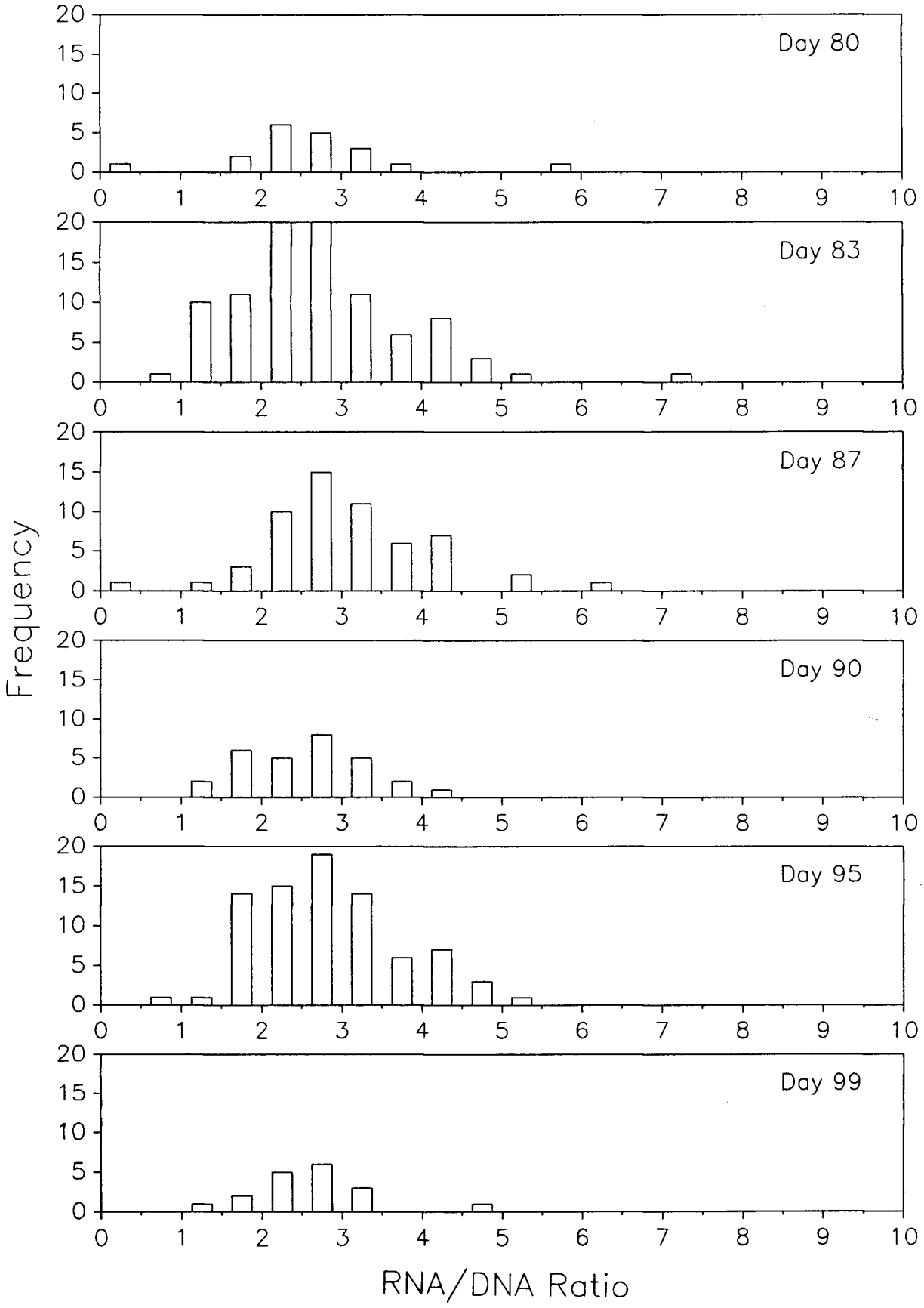


Figure 2.9d. Frequency distributions of the RNA/DNA ratios over time in Lambert Channel during 1987.

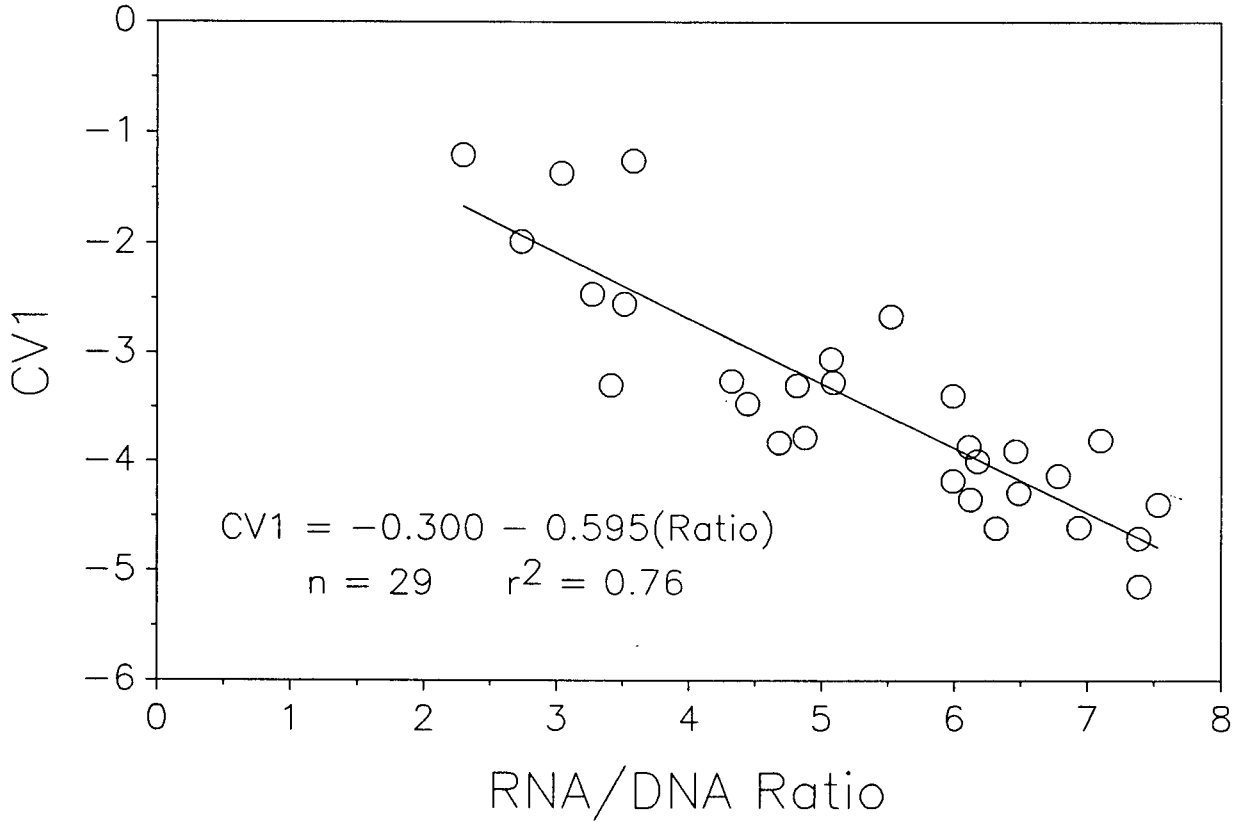


Figure 2.10. Relationship between the RNA/DNA ratio and the morphological condition factor, CV1.

Table 2.6. Correlation coefficients (r) between the mean RNA/DNA ratio and mean densities of the major food groups for the the six sampling areas in Baynes Sound and Lambert Channel over time during 1986 and 1987. Small copepods are defined as copepods smaller than 1 mm in length. (* = $p<0.05$, ** = $p<0.01$)

Year	Time Interval	n	Copepod Eggs	Nauplii	Small Copepods	Total Food
1986	Day 92-100	13	0.38	0.31	0.33	0.16
	Day 106-127	19	0.18	0.71**	0.36	0.48*
1987	Day 86- 94	8	0.08	0.04	0.38	0.09

Table 2.7. Summary of the mode progression analyses of the length-frequency histograms (Appendix 1) from Pacific herring larvae captured in Baynes Sound and Lambert Channel from 1985, 1986 and 1987.

Year	Channel	n	Growth Rate ($mm \cdot d^{-1}$)	r^2
1985	Baynes	4	0.29	0.99
	Lambert	9	0.34	0.98
1986	Baynes	6	0.27	0.98
	Lambert	6	0.31	0.99
1987	Baynes	3	0.35	0.99
	Lambert	4	0.36	0.99

The histograms are shown separately in Appendix 1. While Lambert Channel had slightly higher linear growth rates than Baynes Sound, analysis of the slopes indicated there were no significant differences ($p > 0.05$, F test).

B. Otoliths,Growth and Survival

The radius of the first ring from the primordia in the Day 128 sample was equal to the third ring in the Day 107 sample. Therefore, ring increments 3 to 9 of Day 107 were compared with increments 1 to 7 of Day 128. There was a significant increase in the mean ring width for the first seven increments between the two sampling dates of Day 107 and Day 128 ($p < 0.001$, z-test) (Table 2.8). The distribution of ring widths were normally distributed after logarithmic transformation. There was a low positive correlation between an increment width and the one preceeding it for the first sample ($r^2 = 0.17$, $p < 0.05$, $n = 139$) and no significant correlation for the second ($r^2 = 0.02$, $p > 0.05$, $n = 125$) (Fig. 2.11).

Table 2.8. Seven day mean of otolith ring increment width (μm) from Pacific herring larvae in Lambert Channel 1986. (** = $p<0.01$, z test).

	Calendar Day 107	Calendar Day 128
n	140	126
$\bar{x}$	0.76	0.88**
s	0.23	0.24
min.	0.27	0.43
max.	1.72	1.71

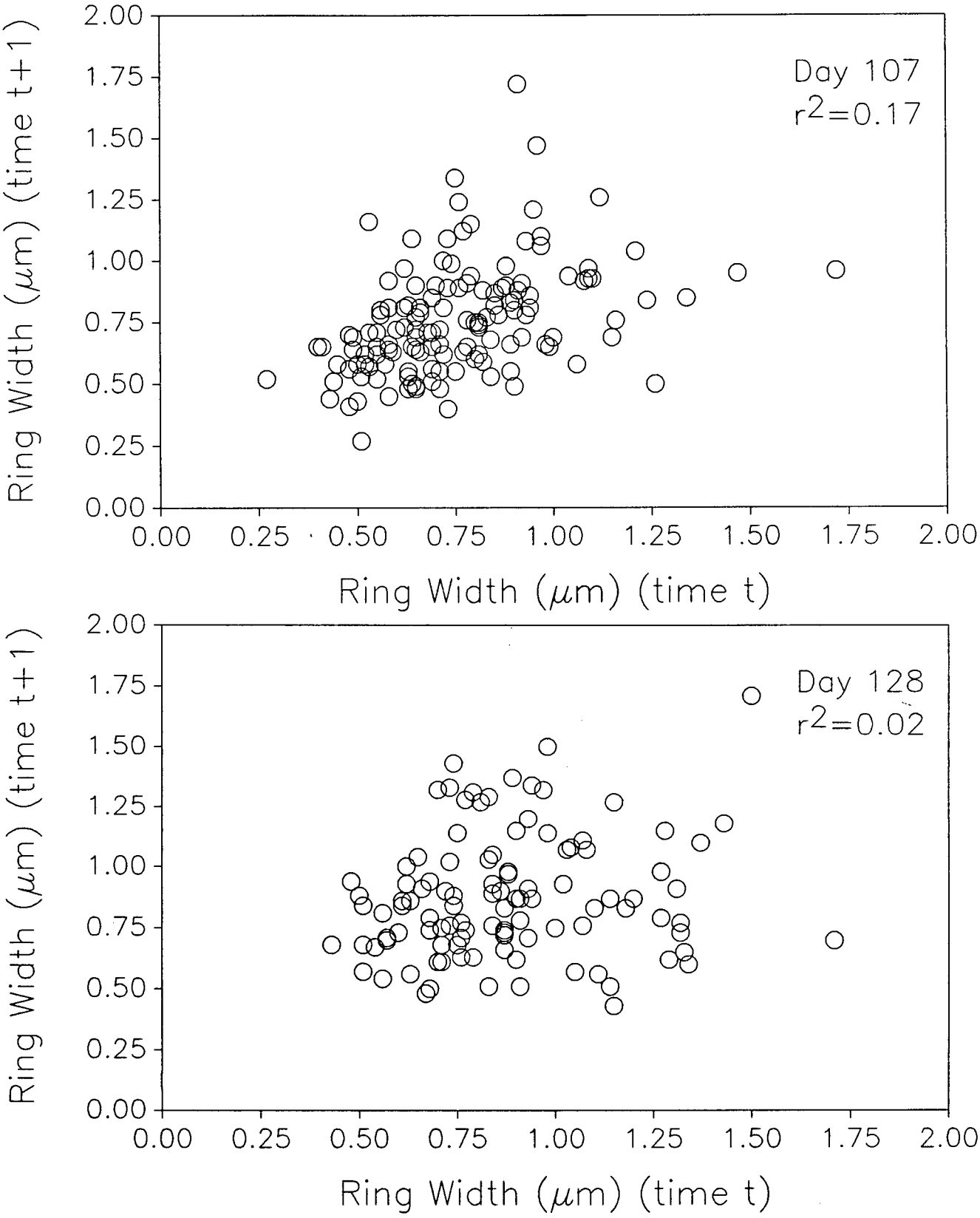


Figure 2.11. Relationship between an otolith ring increment width in Pacific herring larvae and the one preceeding it for the two time periods Calendar Day 107 and Calendar Day 128 in 1986.

V. DISCUSSION

A. Technique

The RNA and DNA values generated in this study are in agreement with previous values published for larval fish as well as for other organisms and tissues (Tarr, 1958; Bulow, 1970; Karsten and Wollenberger,1972; 1977; Buckley, 1980; Wright and Hetzel, 1985; Clemmessen, 1987). To my knowledge, this study is the first to look at the RNA/DNA ratios of individual fish larvae smaller than 800 μg dry weight. This increased sensitivity was gained by using a fluorometric technique for analysis of the nucleic acids. I feel the speed, simplicity, precision, and versatility of this technique for measuring growth and condition in larval fish emphasizes the usefulness of incorporating the technique into sampling designs for other larval fish studies. Limitations of the technique being used as a condition factor arise when the specimen being analyzed begins to synthesize other compounds, such as lipids or carbohydrates, as storage products. For larval herring, Ehrlich (1974) has shown they produce mainly protein up to approximately 20 mm therefore this method is quite applicable. This approach is also unique in the fact that an estimate of the protein growth rate of individuals in the population can be obtained from a single point sample in time.

B. Starvation Controls

The calculated protein growth rates (percent per day) of the larvae quickly dropped to zero after exhaustion of their yolk sac although, the frequency at which the larvae were sampled was not high enough to demonstrate this unequivocally. The drop to zero of the growth rate was then followed by a reduction in length as

the effects of inadequate nutrition presumably began to occur (Fig. 2.3). This pattern of shrinkage in standard length was similar to that found by Blaxter and Hempel (1963) for starved Atlantic herring larvae. The RNA/DNA ratio values and the initial increasing then decreasing pattern of the ratio was very similar to that found by Clemmesen (1987) for Atlantic herring larvae, however, the drop in the ratios of her fish appeared to happen about day 4. It was also found by Buckley (1980) on winter flounder (*Pseudopleuronectes americanus*) where the drop occurred after exhaustion of the yolk sac at age 5 days at 8 °C. The difference with Clemmessen's study may be due to the higher rearing temperatures she used (14.9 °C) or lower yolk reserves in the larvae. The duration of the yolk sac stage in this study was comparable to several other studies on captive larval Pacific herring (e.g. Schnack, 1981; McGurk, 1984).

Before Day 8 the coefficient of variation (standard deviation x 100/mean) of the RNA/DNA ratio was approximately 50%, however, from Day 8 onwards the coefficient of variation ranged from 79 to 191% suggesting the herring larvae were experiencing starvation effects. Blaxter and Hempel (1963) defined the point where a larva, deprived of food, is unable to feed even if suitable food becomes available, as the point-of-no-return (PNR). For water temperatures used in this study, McGurk (1984a) calculated it took starved Pacific herring larvae 11 days to reach the PNR. This value is comparable to findings on Atlantic herring larvae (Blaxter and Hempel, 1963; Blaxter and Ehrlich, 1974). In this study, the mean RNA/DNA ratio at 11 days (from McGurk, 1984a) was 2.06, almost identical to the calculated critical ratio (2.03) derived from Buckley (1984). Clemmesen (1987) starved Atlantic herring larvae at different ages up to day 50 and found the RNA/DNA ratios seem to fall to approximately the same levels observed in this study. A similar pattern was found for larval striped bass although the experiment only lasted for 14

days (Wright and Martin, 1985). Therefore it appears the critical ratio and the calculated PNR both have RNA/DNA ratios approximately equal to 2. This idea would be interesting to investigate in a future project.

C. Field Study

Due to the daylight, ichthyoplankton tows and the net size used, I recognize some net avoidance of larger larvae undoubtedly occurred especially at the very largest sizes. If weaker or smaller larvae were selected for, the observed growth rates would be underestimates of the population and this study would represent a worse case scenario. However, results from the day versus night RNA/DNA ratios of captured larvae on Day 96 in 1987 indicated there was no selection of slower growing larvae during daylight hours when net avoidance would be expected to increase. In addition, the linear growth rates of the captured larvae ($mm \cdot d^{-1}$) compared favorably with other studies on Pacific herring larvae (Stevenson, 1962; Schnack, 1981; McGurk, 1987). Therefore, I feel most of the samples were representative of the population. The one dominant mode and the almost imperceptible second mode in the length frequency plots (Appendix 1) indicated this study is representative of the growth and condition of the year-classes produced from this area. I have ignored the "daily" cohorts produced by the first spawning wave and assumed they are all one cohort. The existence of a single dominant cohort is also supported by observations (D. Chalmers, Dept. Fisheries and Oceans, pers. comm.) on the spawning dates and estimated amounts in this region (Haegele and Schweigert, 1987; Schweigert and Haegele, 1988a; 1988b) (Fig. 2.12). Spawning was observed to occur at various locations over a period of 5 days in 1985, 10 days in 1986, and 14 days in 1987 with peaks at Calendar days 69, 73, and 69

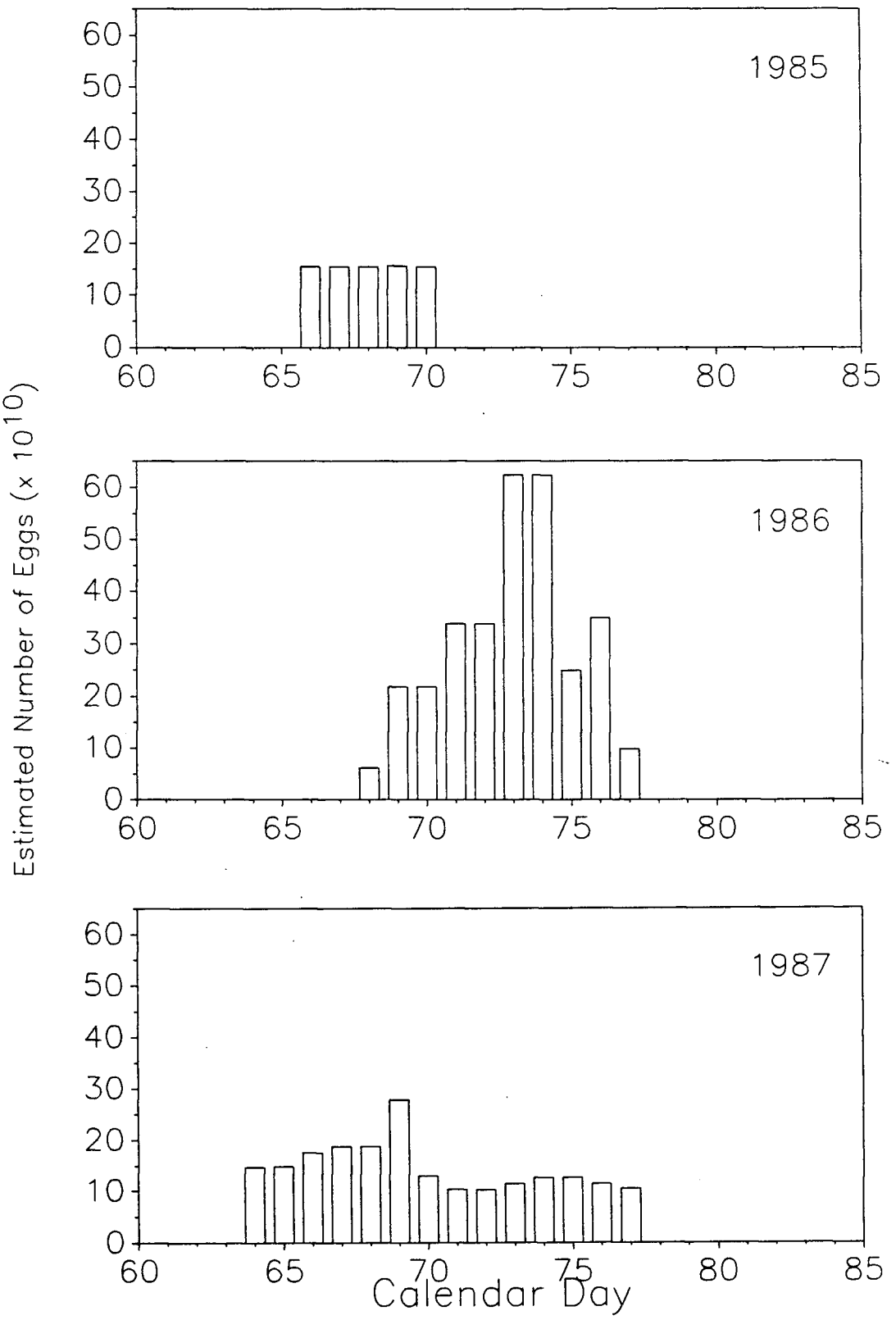


Figure 2.12. Spawning estimates and times for Pacific herring in the Denman and Hornby Island region from 1985, 1986 and 1987. Data from Haegele and Schweigert, 1987; Schweigert and Haegele, 1988a; 1988b; D. Chalmers, Dept. Fisheries and Oceans, pers. comm.

respectively. The peak in hatching in 1986 suggests that the larvae found in Baynes Sound and Lambert Channel are probably the same approximate ages.

The larval herring did not show the traditional linear allometric log-log relationship between weight and length found for most fish. This curvilinear trend was also found by McGurk (1985b) for Pacific herring larvae and may be due to the larvae going through different growth stanzas as their bodies undergo drastic transformations before they complete metamorphosis into a juvenile. The yolk-sac larvae showed a very slow increase in weight with length as they utilized the energy resources in their yolk but, the weight increase implies they must also be supplementing it with some external food. This is probably occuring in the later yolk-sac stages. Predicted values of dry weight from standard length for the post yolk-sac larvae scaled very closely to values given by McGurk (1985a).

The relationship between size and RNA/DNA ratio seems to reach an asymptote at a ratio of approximately 7.5 equating to a protein growth rate of 25.4 %/day at a water temperature of 8.5 °C. The assumed asymptote is approached at a dry weight of about 1 mg or about 18 mm. If we use the mean linear growth rates calculated from the size frequency histograms (Table 2.7) and apply them to the change in size from 8 to 18 mm, this may mean the larvae encounter possible surface to volume metabolic restrictions by about age 30 to 35 days.

Using Doyle's (1977) morphological staging system to categorize the larvae was useful in that it allowed a finer definition of when the larvae started feeding. Pacific herring larvae appear to fit the defined patterns described by Doyle up to stage 3c. After stage 3 the pattern seems to break down as the myomere segmentation (muscle bundles) appears different for Pacific herring than it does for

Atlantic herring larvae (Robinson, pers. obs.). The view of the larvae experiencing problems in the switch to exogenous feeding is supported by the mean ratios for the morphological stages in 1986 where there is a consistent increase in the ratios at each successive stage except for stage 2a (the onset of exogenous feeding) (Table 2.2). This same drop was not observed in 1987 however the RNA/DNA ratios were lower also for each stage. Any starvation problems experienced by the larvae seem to be over by stage 2b as there were no larvae found below the critical ratio. If the difference in mean standard length is calculated (using the minimum value for stage 1c and the maximum values for stage 2b) and divided by the mean linear growth rate ($mm \cdot d^{-1}$) from the size frequency histograms, it will take the larvae approximately 10 days to grow through stage 2a. This will be the window of direct starvation.

Although the trend was not consistent, the mean RNA/DNA ratios of the larval herring generally tended to increase over time (Fig. 2.7). This implies, during the first 36 days of life, the herring larvae in the field are not growing at a simple exponential rate because the RNA/DNA ratio, which is directly related to the instantaneous protein growth rate, increases with time.

In 1986, the main hatch of larvae was estimated to start about Calendar Day 88 (inclement weather prohibited sampling from Calendar Day 87 to 89) and probably continued for 6 or 7 days. If I assume the hatch began on Calendar Day 88 and the duration of the yolk sac stage was 6 days (McGurk, 1984a; this study), then the compulsory switch to exogenous feeding would start around Calendar Day 94. All areas, in both Baynes Sound and Lambert Channel, showed a levelling off or a decrease in the RNA/DNA ratio in the Calendar Day 95 to Calendar Day 102 period after a previous period of rapid increase (Fig. 2.7) suggesting the larvae

underwent a period of increased nutritional difficulties. In 1987, the switch to exogenous feeding was estimated to occur about Calendar Day 86 and extend for about 12 days based on the spawning records. While the trend was not as clear, there were drops in the mean RNA/DNA ratio in the areas in Lambert Channel.

In 1986, as the mean RNA/DNA ratio in each area continued to increase, it appeared by about Calendar Day 105 the larvae were at a stage where their growth increased well above the critical ratio and showed no signs of the earlier fluctuations. There were also no larvae found below the critical ratio after this date (Table 2.5). This again suggests if starvation is a significant factor in regulating population numbers in this cohort of larval herring, it will have to act primarily in a window of about 11 days. Herring would be affected from the end of the yolk sac stage on about Calendar Day 94 (assuming a yolk sac stage of 6 days) to about Calendar Day 105. This value for the window of starvation is very close to the duration estimated for the morphological stage 2a. If the fish were unable to capture food, then the window of the PNR would be 6 days from Calendar Days 99 to 105. A similar trend for larval Pacific herring, showing a brief initial period where larvae were diagnosed as starving, was found by McGurk (1985a) using a multivariate condition factor (CV1). This view of a larval escape from food restrictions, with respect to starvation, after a brief time period is supported by a study on jack mackerel, *Trachurus symmetricus* (Hewitt et al., 1985). They found starvation was an important source of mortality rate only during a window of about 7 days during the first feeding stage. Ware and Lambert (1985) also found mortality in Atlantic mackerel (*Scomber scombrus*) rapidly increased during the first feeding stages, then decreased a few days later.

This study supports some of the traditional views of the early life history feeding dynamics of herring. I found evidence that larvae undergo some brief problems switching to a planktivorous diet and this occurs during a small time window following exhaustion of the yolk sac. This is consistent with Hjort's original first hypothesis. However, for this cohort, I can find no evidence to indicate a "critical period" is present where a large increase in mortality occurs due to starvation during the switch to exogenous feeding. The mean RNA/DNA ratios during the estimated starvation window (Calendar Days 94 to 105) are significantly greater ($p < 0.05$, Student's t-test) than the critical ratio and the percentage of larvae below the critical ratio (Table 2.5) during this period is small and declines quickly. This does not mean of course that a "critical period" could not exist at another time when some sort of catastrophe occurred. It only implies one was not found in the time frame which I examined.

When the mean RNA/DNA ratios from the field are compared to the critical ratio one can see there is a relatively rapid increase from values near the critical ratio on Calendar Day 90 to approximately 5 by day 100. It appears then, early yolk sac larvae (around day 90) grow very slowly or lose weight as the mean RNA/DNA ratios are so close to the critical ratio. These early low values for the RNA/DNA ratio were also found by Clemmesen (1987) who found initial ratios of approximately 2.2. This characteristic may also be due perhaps to the production of biochemical compounds other than protein. It is possible the increase in the ratio is overestimated as slower growing larvae may experience higher mortality rates. The RNA/DNA ratios I found in the field are higher than those reported by Fukuda et al. (1986) for Pacific herring larvae, Clemmesen (1987) for Atlantic herring larvae, and Wright and Martin (1985) for larval striped bass fed in the laboratory, but the differences may be due to population differences or the fact fish larvae are

notoriously difficult to raise normally in captivity. Although there are very few studies on RNA/DNA ratios in the field, the values obtained in this study were comparable to other studies of fish larvae on Atlantic cod and haddock (Buckley and Lough, 1987).

The excellent correlation between the morphological condition CV1 derived by McGurk (1985a) for Pacific herring larvae and the RNA/DNA ratio indicates that the RNA/DNA ratio can be used as a condition factor (Fig. 2.10). McGurk calibrated his CV1 condition factor to laboratory starved animals and went to great lengths to ensure all measurements were orthogonal. His technique though would not be applicable to another species without undergoing the same calibration process. This study shows there is a good relationship between relative body measurements and the rate of protein growth of the animal and so the RNA/DNA ratio technique should be able to be used on any species without any extra effort on the part of the researcher.

There was a significant difference in 1986 between Baynes Sound and Lambert Channel in the mean growth rates of the feeding stages of the herring larvae while no difference was found for the pre-feeding stages. This difference in the growth rates between the two channels is probably due to the higher food densities found in Baynes Sound discussed in Chapter 1. The positive correlation between the RNA/DNA ratio and nauplii density suggests that for the size range studied in this project nauplii are the most important factor in the early growth of the herring larvae. The relatively high correlation coefficient (r) of nauplii density vs RNA/DNA ratio for the feeding larvae is probably making the r for the total food density vs RNA/DNA ratio significant. If the nauplii densities are converted to number$\cdot l^{-1}$ in this study, mean values for areas 1 to 6 ranged from 6 to 9.3

nauplii$\cdot l^{-1}$. These densities are from integrated samples taken from the surface to the bottom or 30 m whichever was less. Therefore, they are probably underestimates of the densities larvae would encounter as the effect of patchiness would tend to increase densities at certain levels. Early laboratory estimates using *Artemia salina* suggested that densities of 100-170 nauplii$\cdot l^{-1}$ were required for the survival of herring larvae (Werner and Blaxter, 1980, Schnack, 1981) however later studies have indicated the food densities need only be in the 9 nauplii$\cdot l^{-1}$ range for survival (Gamble et al., 1981) and that herring larvae may become satiated at densities of 30 nauplii$\cdot l^{-1}$ (Kiorboe and Munk, 1985). These prey density requirements for survival have also been found for larval capelin (Frank and Leggett, 1986). The results from this study are generally close to these reported values.

The early skewed right RNA/DNA ratio distributions and wide range (Fig. 2.9) suggest, due to the extended hatching of the cohort of larval herring, the observed protein growth rates may partly be caused by larvae of slightly different ages. It may also be a function of a few larvae learning to feed and supplementing the energy from their yolk sac reserve. As the mode moves right from Calendar Day 90 to Calendar Day 124 for 1986 the percentage in the low RNA/DNA ratio categories reduce. From Calendar Day 94 on there is a suggestion of bimodality in the distributions which could indicate a group has learned to feed well and has a head start on the rest of the cohort. More detailed samples are needed to determine whether or not this apparent feature is real. As the mode progresses to the right over time, the RNA/DNA ratio distribution in Lambert Channel becomes more truncated, and is similar to that found for field-caught populations of sand lance and haddock (Buckley, 1984, Buckley and Lough, 1987). The distribution on Calendar Day 124+126 shows there are no larvae below the critical ratio of about 2

which means they have either been lost (due to predation or starvation), or their feeding abilities have increased so they can easily meet their basic nutritional requirements.

D. Otoliths and Survival

The rejection of the null hypothesis that there was no difference between the mean ring widths for the first 7 days suggests there is growth dependent mortality occurring in larval herring over as little as a three week period. The samples were taken from Lambert Channel after Day 105 and therefore according to the above growth analysis these are the survivors from the switch to exogenous feeding. Predation should then be the major source of mortality. This indirect assessment of mortality assumes the population sampled at Time 2 is the same as at Time 1 but, due to the discreteness of this stock and the apparent continuity of the samples throughout the sampling period this assumption I feel has been met. The technique does not require the rings examined to be daily increments as conditions for the laying down of the rings should be identical for both periods. Net evasion is not a factor in this study as it will increase with size and only tend to emphasize the difference. This growth dependent mortality has also been suggested for larval tuna (Brothers et al., 1983) and for yellow perch (Post and Prankevicius, 1987). The results of this study indicate that this is a case of reversed Rosa Lee's Phenomena. Enhanced growth of a larva in Lambert Channel appears to reduce the mortality rate acting upon it by probably allowing it to outgrow some of their predator's prey size ranges as speculated by Cushing (1975) and Hunter (1981).

GENERAL DISCUSSION

The principal findings of this study indicated Baynes Sound was hydrographically different from Lambert Channel and outside by being more stable and by having higher densities(number$\cdot m^{-2}$) of microzooplankton important to larval Pacific herring. Circulation patterns appear to transport larvae into Baynes Sound from Lambert Channel where they gradually form higher densities than those found in Lambert Channel. Protein growth rates as measured with RNA/DNA ratios are higher in Baynes Sound than Lambert Channel and an otolith microstructure study suggested that higher growth rates enhanced survival.

The results of this study support the assertion by Sherman et al. (1984) that the spawning stategies of fish are linked to the annual plankton production cycle and circulation patterns in the area. It appears for the year-class of larval herring produced in this major spawning region there is a close relationship between the physical and the biological processes. My view of the dynamics in the early life history process is as follows. Adult herring spawn in the inshore region of Denman and Hornby Islands in the spring just before the spring plankton bloom when the predominant direction of the wind is from the south. Through a combination of surface wind drift and tides, a portion of the hatching herring larvae in Lambert Channel are advected into Baynes Sound where the water conditions are more stable due to stratification by freshwater input from the Comox River and assorted streams and from a lack of wind mixing resulting from the protection of the surrounding land masses. This stabilization may lead to an earlier spring phytoplankton bloom which the microzooplankton, important to the early feeding herring larvae, can begin to exploit. The stability and other characteristics of

Baynes Sound may also be responsible for the difference in the predator complexes found between Baynes Sound and Lambert Channel (the latter being more representative of the Strait of Georgia). The higher food densities result in higher growth rates for feeding herring in Baynes Sound than in Lambert Channel. This then results in lower mortalities due to the reduction in time that a larvae will spend in a particular predator's prey field.

There are two theories on why Atlantic herring spawn when they do. Cushing (1975) suggests the spawning herring are trying to match the emergence of the larvae with the onset of the plankton bloom. Sinclair and Tremblay (1984) refute this and suggest the herring spawn at certain times so that the larvae have enough time to grow to a size which will enable them to complete metamorphosis within a seasonal envelope. In the case of Pacific herring, there may also be another factor involved. If predation on larvae by planktonic predators is a major source of mortality but the larvae are able to outgrow some of their predators size ranges, then an earlier start to the spring plankton production cycle will allow the larvae to outgrow their predators sooner. This may be important because densities of predators such as chaetognaths and ctenophores tend to increase during the summer(Alvarino, 1965; Larson, 1986). The timing of spawning then may partly be a method to reduce predation and therefore earlier spring plankton blooms will be a benefit to the survival of the larvae.

There was no information from this study on the fate of the larvae that were dispersed out of the study site into deep water areas. Therefore, no absolute statements can be made concerning the benefits accrued by larvae that remain inshore. However, if growth rates are linked to mortality rates and growth is a function of food density (up to a certain point) then, the high to low gradient of food

densities found from inshore to offshore would suggest mortality is higher offshore. The fact that herring spawn very close to and in the intertidal zone suggests there must be some selective advantage of starting the larvae off close to shore. There are also other benefits of remaining inshore for the larval herring. Schooling begins just prior to metamorphosis (Rosenthal, 1968; Marliave, 1980) and if the larvae are widely dispersed by the circulation patterns in the Strait of Georgia, this may present a problem. Juvenile herring schools tend to be found inshore in sheltered bays and around islands (Hourston, 1959), therefore schools would have to traverse back inshore if one assumes that they are able to form in the offshore regions.

One of the objectives of this study was to examine the applicability of the proposed hypotheses of larval survival and recruitment mentioned in the general introduction. As is the case for most differing theories on the same topic, all tend to apply at some time under certain conditions. Not enough data are available to evaluate the relative frequency of each. Cushing's (1975) theory on the match-mismatch of the larval herring hatch with the occurrence of the spring plankton bloom appears to generally agree with the observations but, due to differences in the stability of the areas, the initiation of the bloom may be drawn out over an extended period in different areas and therefore an exact match in time may not be critical. It will depend on how important site specificity is. This also ties in somewhat with Lasker's (1975) stability hypothesis. Certainly, increased stability appears to be positively correlated with higher food densities (number$\cdot m^{-2}$) but, movement of larvae into Baynes Sound, a type of larval drift (*sensu* Hjort, 1914), seems to be enhanced by wind drift which in itself causes instability through wind mixing. Whether or not the area around Baynes Sound can be called a retention area is unclear. Larvae seem to be maintained in Baynes Sound through either immigration, low emigration or low mortality. However, in keeping with the

concept of Iles and Sinclair (1982) where the size of the retention area defines the upper limit to the stock size, Baynes Sound may be too small an area for such a title. Baynes Sound seems to fit the definition of a nursery area though as food densities are higher, there are different potential predators, growth is higher and the larvae seem to be maintained in there. The Strait of Georgia with its restricted openings at the north and south ends might be regarded as a retention area if one exists at all. There was no strong evidence in this study of a critical period where a large proportion of the larvae died during the onset of feeding as suggested by Hjort (1914) or even over an extended period of time. This observation implies that predation was the main source of mortality for larval herring in the inshore region. The otolith study extends this reasoning and suggests this mortality affected the slower growing individuals thus linking the physical and the biological components of the environmental system. McGurk (1985b) also came to the same conclusion that predation and not starvation was the major source of mortality for larval herring.

To my knowledge, this is the first time a detailed analysis of growth has been done on individual herring larvae in a field situation. The results indicated that for the inshore population, starvation probably does not play a major role and if it does happen, it will take place within a time window of about 10 to 11 days at 8-9 °C. This explains why this stage is hard to detect with synoptic net sampling as the numbers of dispersing larvae are too difficult to accurately estimate. The RNA/DNA ratio was also found to be significantly correlated with McGurk's (1985a) CV1 condition factor, probably the best morphometric condition factor available for Pacific herring larvae. This suggests the RNA/DNA ratio is a good estimator of condition. It does not need to be calibrated therefore it may be a better measure to use for multispecies comparisons.

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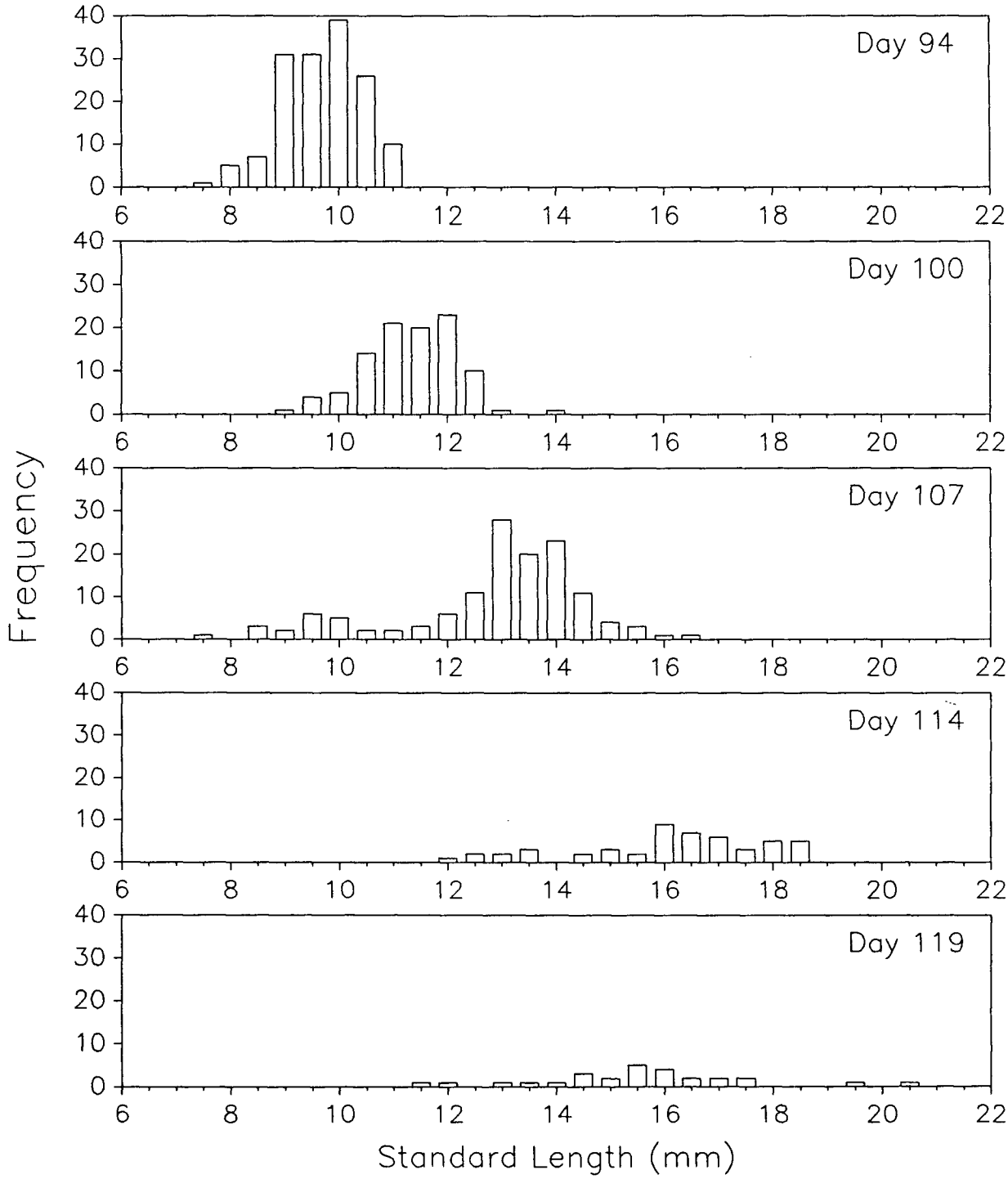
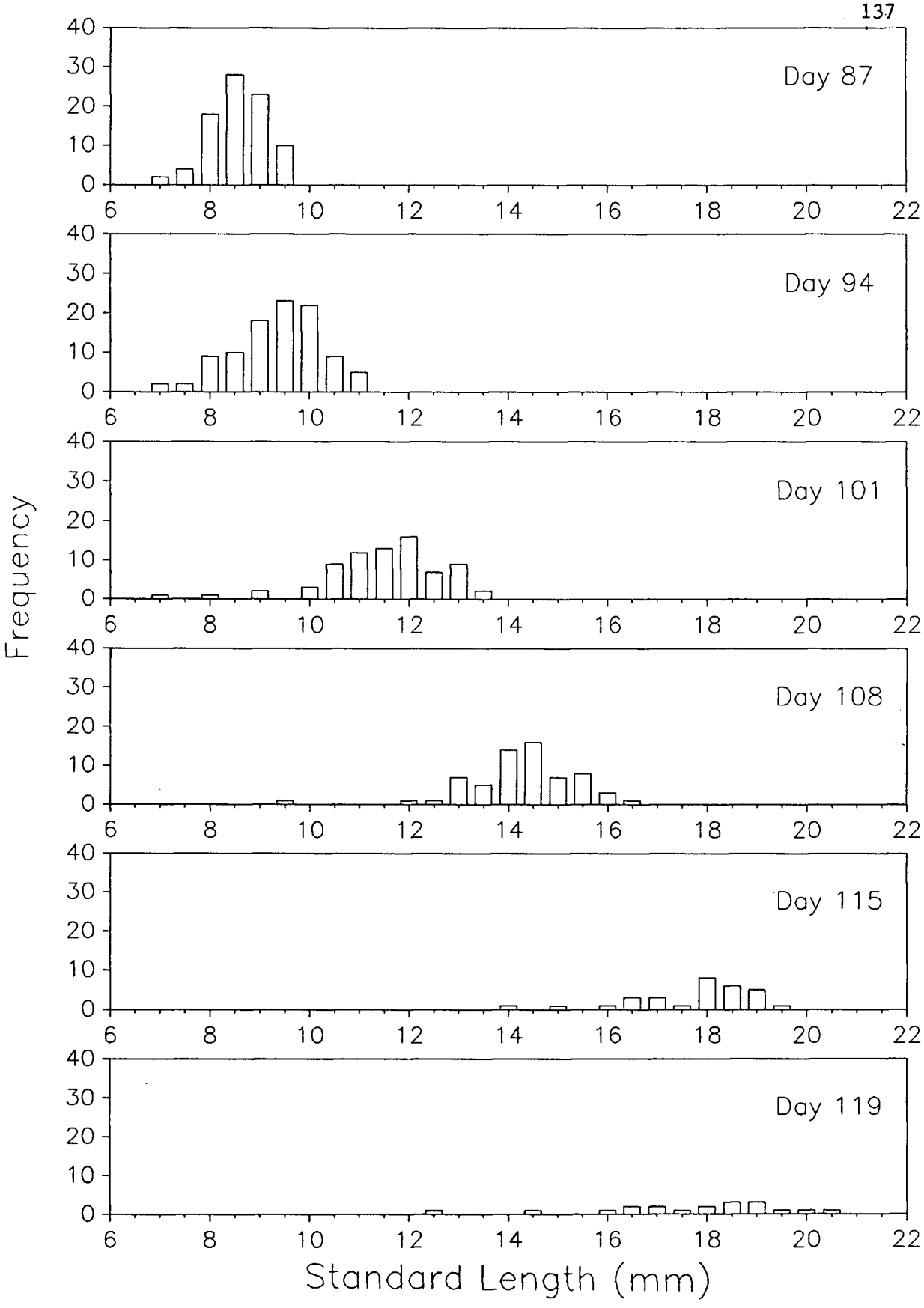
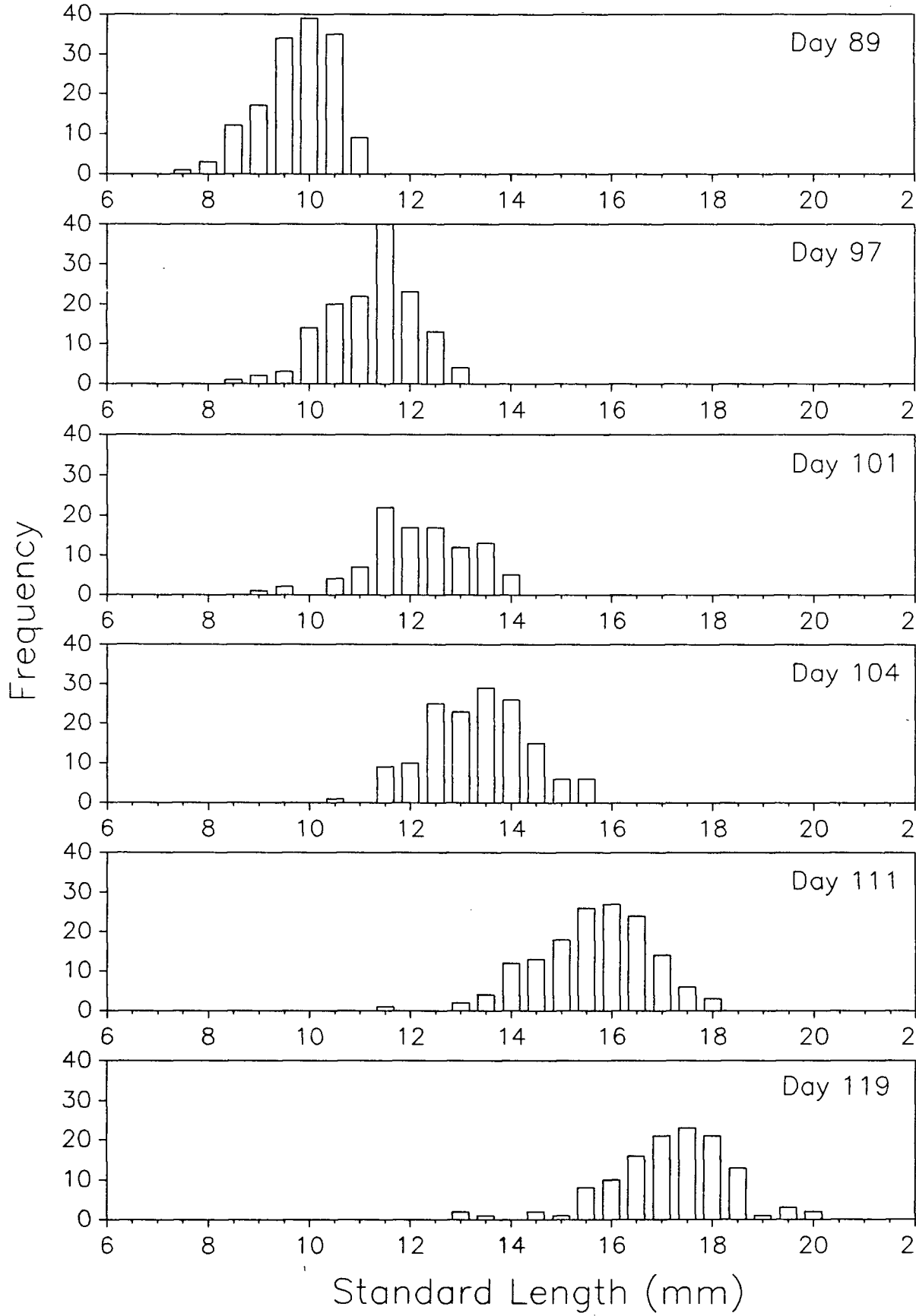


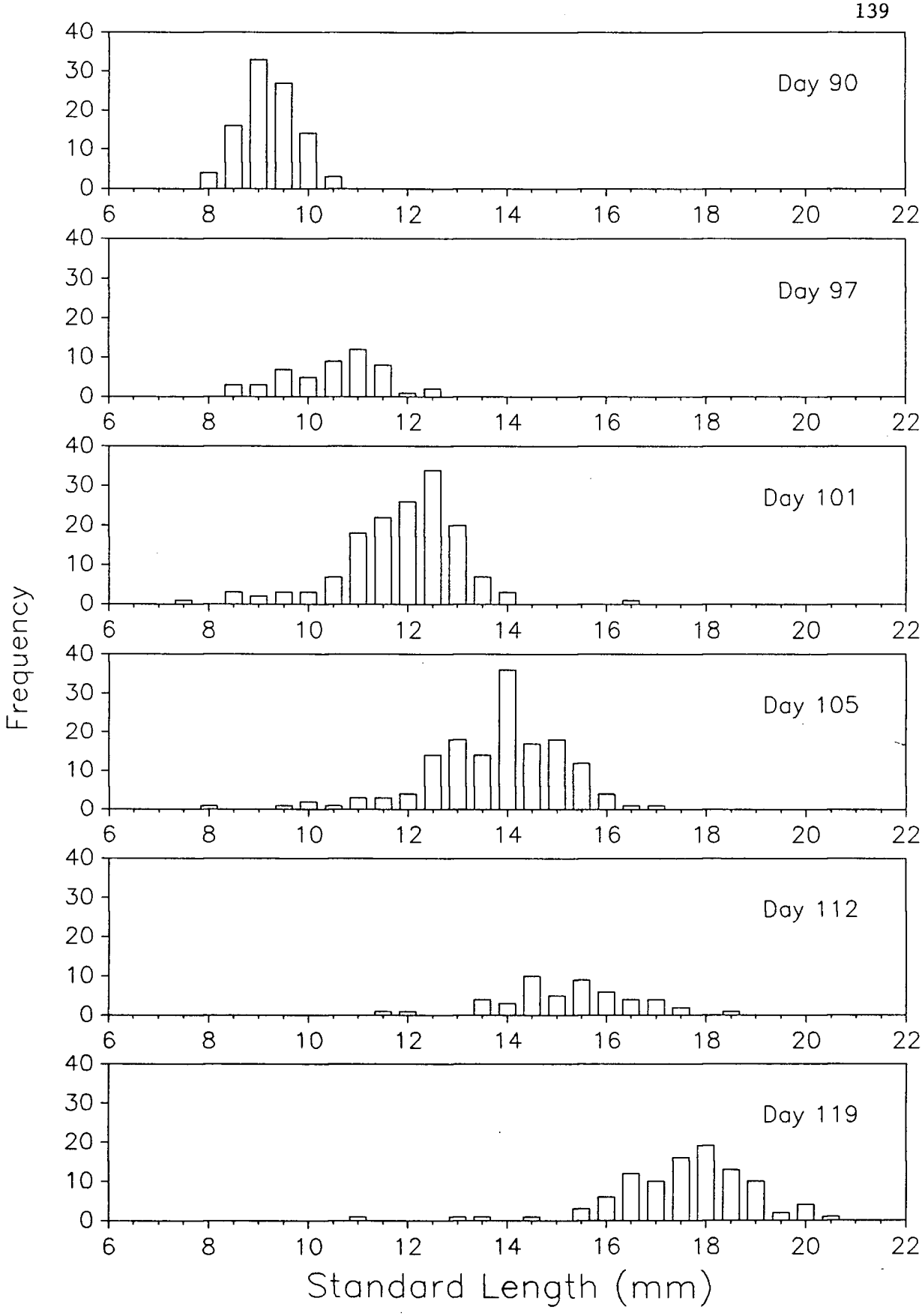
Appendix 1a. Size-frequency histograms for Pacific herring larvae in Baynes Sound 1985.



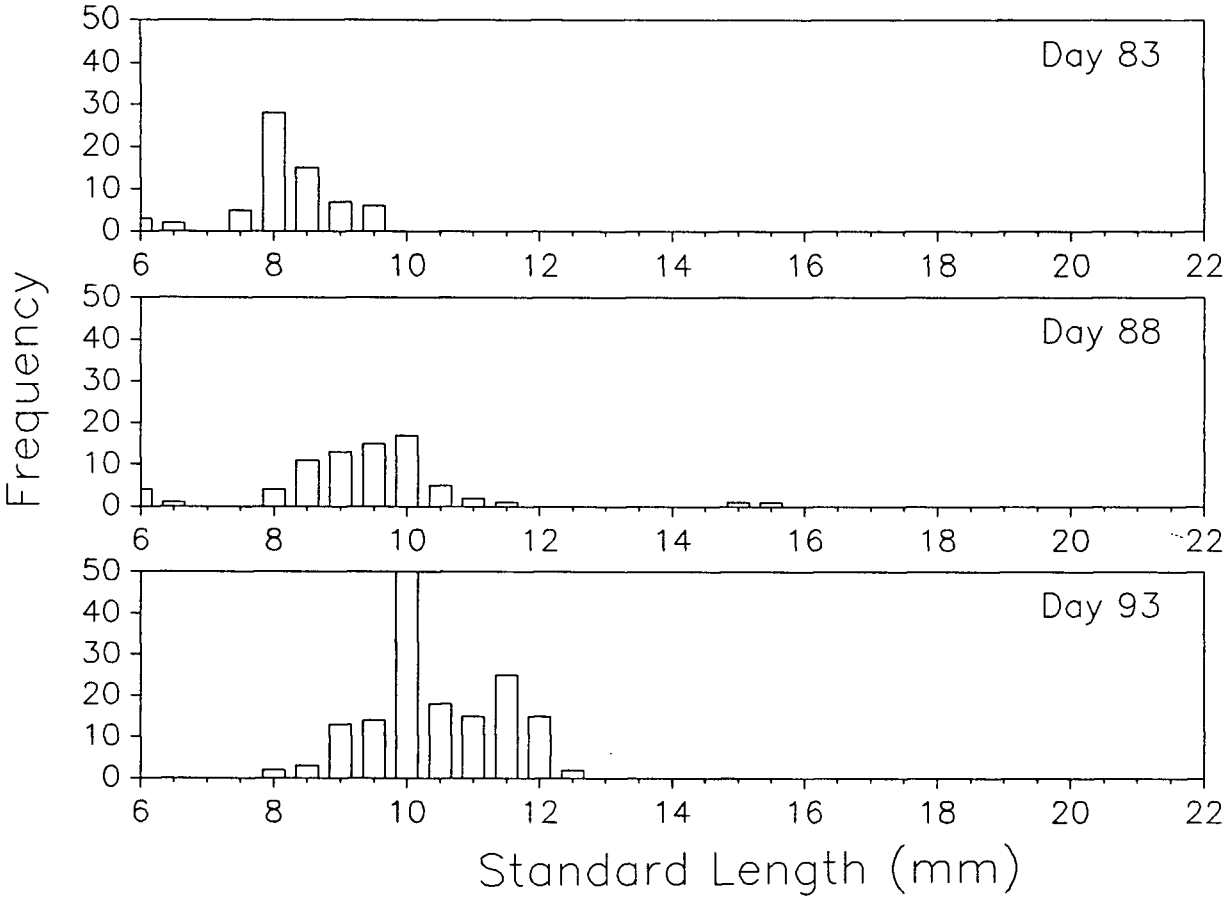
Appendix 1b. Size-frequency histograms for Pacific herring larvae in Lambert Channel 1985.



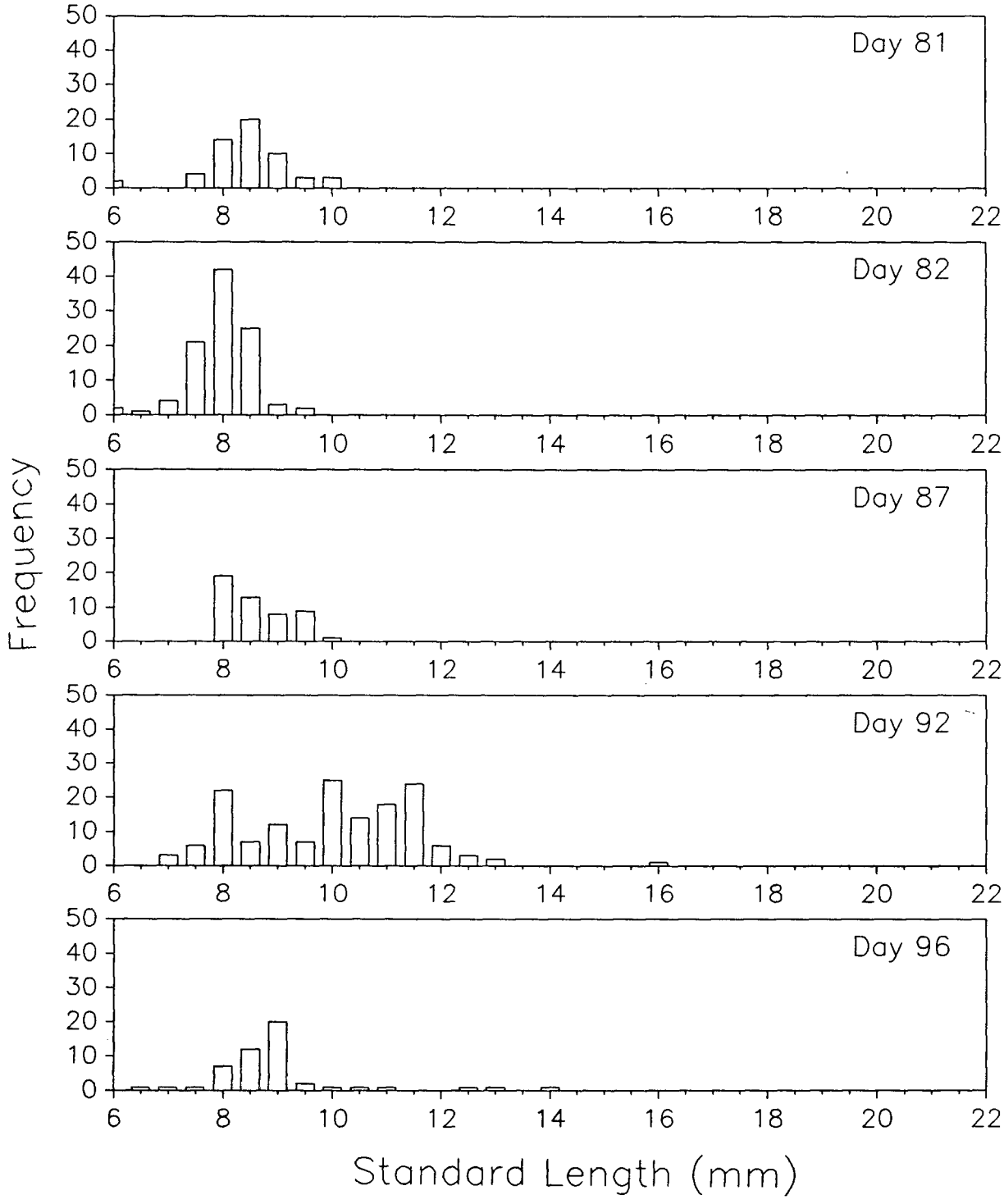
Appendix 1c. Size-frequency histograms for Pacific herring larvae in Baynes Sound 1986.



Appendix 1d. Size-frequency histograms for Pacific herring larvae in Lambert Channel 1986.



Appendix 1e. Size-frequency histograms for Pacific herring larvae in Baynes Sound 1987.



Appendix 1f. Size-frequency histograms for Pacific herring larvae in Lambert Channel 1987.