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FINAL REPORT

RU-695

EARLY **LIFE** HISTORY OF PACIFIC HERRING  
IN AUKE BAY, ALASKA: RELATIONSHIPS OF  
GROWTH AND SURVIVAL TO ENVIRONMENTAL  
CONDITIONS

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## ABSTRACT

The primary objective of this study was to measure growth, fitness and survival of Pacific herring, Clupea harengus pallasii, larvae, and the concentrations of their prey and predators in Auke Bay, Alaska. The secondary objective was to assess the importance of food and predator concentrations to growth, fitness and survival of larvae so as to identify the factors which may contribute to year-class **success** or failure.

Five cohorts of herring were spawned in Auke Bay at an average rate of one every 19 d from April 18 to June 30. The eggs of the second and third cohort were found in the upper intertidal zone at the head of the Bay. Both spawnings were less than 250 m in length and had an average width of 5 m. They produced approximately  $9.8 \times 10^8$  and  $4.8 \times 10^8$  viable larvae, respectively.

Herring larvae feed primarily on the synchronously developing juvenile and adult stages of the dominant pelagic **copepods**, and secondarily on other small pelagic invertebrates including **mollusc veligers**, polychaete larvae and small fish eggs. Concentrations of prey of larval herring were calculated for 12 length classes of herring from zooplankton samples collected with a 165  $\mu\text{m}$  mesh net and from densities of copepod **nauplii** taken with a 24  $\mu\text{m}$  mesh net by members of the APPRISE project. Prey concentrations ranged from 20 to 171 mg dry weight\*  $\text{m}^{-3}$  over the May to July sampling season.

Three classes of invertebrate predators of herring larvae were identified: 10 species of jellyfish, hyperiid amphipods of the genus Parathemisto, and the chaetognath Sagitta elegans. Mean predator concentrations at date ranged from 0.9 to 34,027.7  $\text{mg}\cdot\text{m}^{-3}$ , with a geometric mean of 150.2  $\text{mg}\cdot\text{m}^{-3}$ . Jellyfish made up over 95% of the average concentration of predators at date.

Population growth rates in length of larval and juvenile herring were calculated from length-frequency analysis; they were essentially linear over

the larval stage and the early juvenile stage: **0.311**, 0.299, 0.312, and 0.386  $\text{mm}\cdot\text{d}^{-1}$  for cohorts 1, 2, 3 and 4, respectively. None of the rates were significantly different from each **other**, and all **fell** within the range reported for other populations of Pacific and Atlantic herring larvae.

Specific growth rates,  $G_w$ , of herring larvae ranging from 3.4 to 19.6  $\% \cdot \text{d}^{-1}$  were estimated from the width of the outermost ring of the **sagittal otoliths**. Nine percent of the variation in  $G_w$  was explained by a dome-shaped relationship between  $G_w$  and age of the larvae, and 4% of the variation was explained by a direct relationship between  $G_w$  and **In**-transformed mean prey concentration. There was no relationship between  $G_w$  and water temperature. Fitness of herring larvae was “measured with a **morphometric** condition factor, CF2. A direct relationship between CF2 and age explained 24% of the variation in CF2 and a dome-shaped relationship between CF2 and in-transformed prey concentration explained an additional 5% of the variation in CF2. The relatively weak correlation between  $G_w$  and CF2 and environmental factors was due to a lack of contrast in the environmental data; average temperatures of the upper 20 m of the water **column** fell within a narrow range of 7.2 to 8.2°C, and the range of prey concentration is one in which the growth response of herring larvae approaches saturation.

$G_w$  was 2.3  $\% \cdot \text{d}^{-1}$  higher, on average, than that predicted from an equation developed by Kiorboe and Munk (1986) from the growth of **laboratory-reared Atlantic** herring, *Clupea harengus harengus*, larvae. This suggests that Auke Bay herring larvae fed on high-density patches of prey that were not detected by plankton-net tows that integrated the upper 30 m of the water column. It also indicates that Kiorboe and Munk's (1986) equation may be applicable to natural ecosystems for the purpose of predicting minimum specific growth rates of herring larvae from prey concentrations.

The  $G_w$  and fitness data indicated that growth of herring larvae in Auke Bay was only weakly related to food concentrations, which suggests that if growth

and survival are directly related to **each** other, then survival must also have been weakly correlated with prey concentration, and, perhaps, more highly correlated with **non-trophic** agents of mortality such as predator concentration. This hypothesis was tested by comparing the rates of total mortality of cohorts 1, 2 and 3 with environmental factors.

Before estimating total mortality it was necessary to determine the rates of emigration of larvae out of the sampling area in Auke Bay. No significant **advection** or diffusion of herring larvae out of Auke Bay was measured and population models incorporating **advection** and diffusion explained less variation in density of herring larvae than simpler models that assumed a single loss rate. These results suggest that the larvae may have been retained within the Bay, but sampling outside of the Bay would have been required to confirm this hypothesis.

Total mortality,  $Z_t$ , of larvae was best described as decreasing with age,  $t$  (d), according to a Pareto-type function,  $Z_t = \beta t^{-1}$ , where  $\beta$  is a coefficient having values of 3.068, 0.785 and 2.660 for cohorts 1, 2 and 3, respectively. These rates were supplemented by calculating mortality rates for the period between hatching and the earliest date at which larvae were captured. Cohort 2 had an egg-larval mortality of 0.93 d<sup>-1</sup> for ages 0 to 1 d, whereas cohort 3 had a rate of 0.12 d<sup>-1</sup> for ages 0 to 20 d. Total mortality was most highly correlated with age of larvae, followed by body weight and spatial patchiness of the larvae. **It** was not significantly correlated with physical condition of the larvae or with the concentration of predators.

This study shows that growth and fitness of Auke Bay herring larvae in 1988 was not strongly dependent on prey concentration, a conclusion which does not support the critical period hypothesis of year-class formation. This study provides much less conclusive results concerning the causes of mortality. A direct link between survival and prey concentration is suggested by the coincidence of high mortality and **lower specific** growth rates and

morphological fitness in cohort 2, and by the absence of a correlation between mortality rate and predator concentration. However, mortality rates of cohorts 1, 2 and 3 are also correlated with factors related to the ability of larvae to evade predation: age, body size and spatial patchiness.

In order to better answer these questions, I recommend that future studies of the **early** life history of Pacific herring in Alaska focus on making more accurate measurements of growth, fitness and mortality, and on measuring the parameters of larger populations of herring larvae in order to test for the effects of density-dependence. This requires population **modelling** combined with hydrodynamic **modelling** in order to measure accurate rates of dispersal and mortality of the larvae, and the use of biochemical means for measuring recent growth rates of herring larvae.

## PREFACE

This Final Report was preceded by a Draft Report submitted in December 1988 and by an Abstract submitted to the Mineral Management Service Information Update Meeting held in Anchorage, Alaska, on February 6 to 7, 1989. The Final Report contains significant differences from the two previous documents. An article based on the **Final** Report is being prepared for publication in a peer-reviewed journal.

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## 1.0 INTRODUCTION

This is the final report of a study of the early life history of Pacific herring, Clupea harengus pallasii, in Auke Bay, Alaska. Stocks of Pacific herring in Alaska have fluctuated considerably in size due to exploitation and to variation in recruitment (Rounsefell 1930, Reid 1971, Fried and Weststad 1985). The proximate causes of the variation in recruitment are changes in the rate of egg production and in the survival rates of the egg, larval and juvenile stages; the ultimate causes are presumed to be the environmental factors that are responsible for these changes in population parameters. This study was designed to identify the environmental factors that are responsible for variation in survival of herring larvae in Auke Bay, Alaska. The primary objective was to measure the relationships between growth and survival of herring larvae and the concentrations of their prey and their predators and water temperature.

The question of how closely related are recruitment of Alaska herring and environmental factors is important because the development of the oil and gas reserves of Alaska's continental shelf has the potential to **reduce** the quality of inshore habitat and thereby reduce herring recruitment, or at least increase its variability. Pacific herring are expected to be vulnerable to changes in inshore habitat because they spawn in the intertidal zone and their larvae and juveniles feed and grow in estuaries and embayments.

The study was carried out in Auke Bay, Alaska, a semi-enclosed bay in southeast Alaska. Auke Bay was chosen because it is a spawning site for herring, and because it is the site for APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem), a multidisciplinary and multi-year study of the relationship between the phytoplankton spring bloom and the subsequent recruitment of commercially important species of fish and invertebrates in Auke Bay. APPRISE includes detailed measurements of the

physical environment, and the phytoplankton, zooplankton and larval fish communities of the pelagic zone. Some of these data were used in this study.

## 2.0 STUDY SITE

Auke Bay ( $58^{\circ}22'N$ ;  $134^{\circ}40'W$ ) is a small bay of 11.5 km<sup>2</sup> area located approximately 20 km north of Juneau (Figs. 1 and 2). The sides of the Bay are generally steep, falling to an average depth of 40 m over most of the Bay. Three major streams flow into the Bay: Auke Creek, Auke Nu Creek and **Waydelich** Creek and several minor streams including Bay Creek. Surface tides in Auke Bay are **semidiurnal** with diurnal inequality.

Shirley and **Coyle** (1986) summarized the research that has been conducted on the hydrography, current patterns and plant and animal communities of **Auke** Bay. Recent information on these components of the Auke Bay ecosystem has been collected as part of the on-going APPRISE research program (APPRISE Staff 1986, 1987, 1988, 1989). **Carlson** (1977, 1980) reports that Auke Bay is part of the home range of the Lynn Canal - Auke Bay herring stock, one of 5 separate herring stocks in southeast Alaska. **Iverson** (1972), Kirk (1973), Tetra Tec (1983) and Nebert (1989) have described current flow in Auke Bay as varying with season and tide pattern. During the summer the upper water layer of the stratified water column moves in a counter-clockwise gyre with current speeds up to 10 **cm·s<sup>-1</sup>**. Surface currents flow into the Bay **along** the north shore and **along** the southwest shore between **Spuhn Island** and the **Mendenhall** Peninsula and water flows out of the Bay between **Coghlan** and **Spuhn** Islands. With the decay of stratification of the water column in October, the counter-clockwise gyre is replaced by a complicated, tidally-forced, **two-** or three-cell circulation pattern.

Annual salinity and temperature cycles in Auke Bay from 1960 to 1968 were summarized by Bruce et al. (1977). The Auke Bay water column is unstratified from November to March with surface temperatures and salinities ranging from 3 to 5°C and 30 to 31 ppt, respectively. Stratification begins in April with rising air temperatures and fresh water input from snow melt and is complete by **July** at which time surface temperatures and salinities are approximately 14°C and 10 to 15 ppt, respectively. The **pycnocline** is at 20 m, **below** which

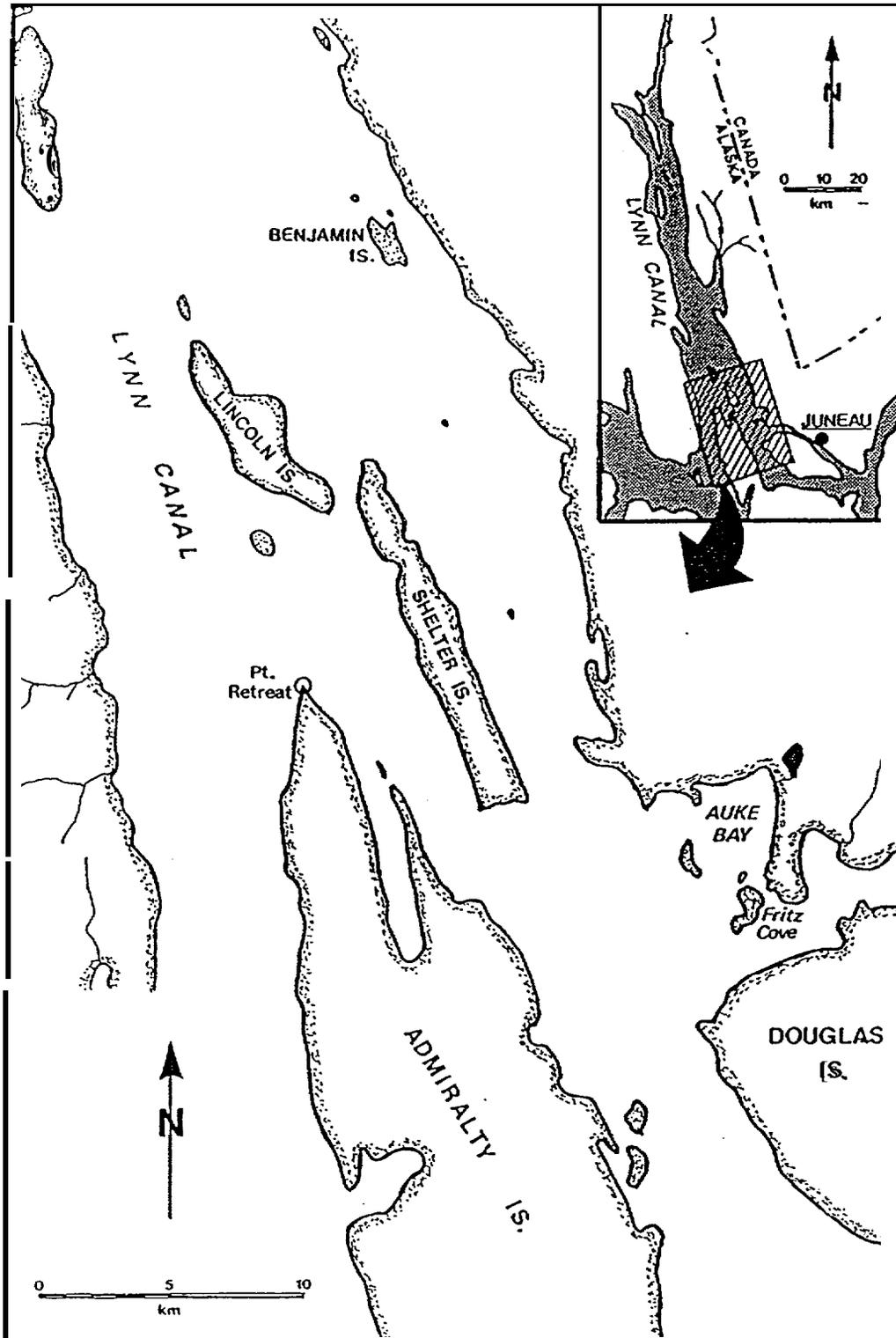
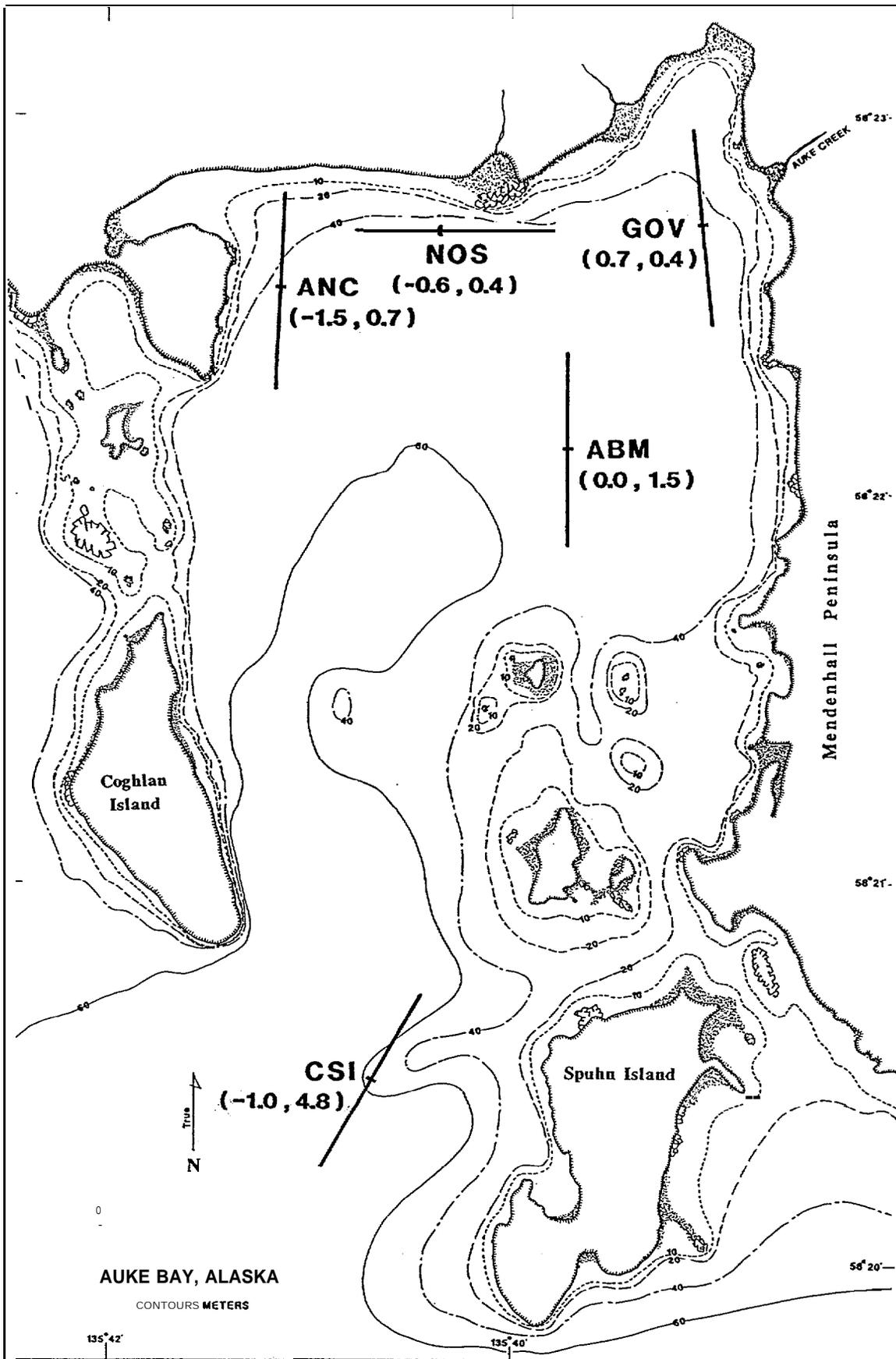


Figure 1 : MAP OF THE AUKE BAY- LYNN CANAL AREA



**Figure 2: MAP OF AUKE BAY SHOWING THE PLANKTON SAMPLING STATIONS AND THEIR X-Y COORDINATES**

temperatures and salinities are 5 to 8°C and 28 to 30 ppt, respectively. Storms and decreasing air temperatures destratify the water column in September and October.

### 3.0 MATERIALS AND METHODS

#### 3.1 Temperature and Salinity

Temperature and salinity profiles were measured by both the APPRISE team and **Envirocon** Pacific Ltd. (EPL), but the former data set was by far the most complete and was the primary data set used in this study. It was based on a CTD-meter with built-in memory that was lowered to a depth of 40 m, equilibrated for 1 rein, and then retrieved at a speed of approximately  $5 \text{ m}\cdot\text{min}^{-1}$ . Surface temperatures and salinities were also measured by personnel of the **Auke Bay Laboratory** (NOAA).

#### 3.2 Plankton Sampling

##### 3.2.1 Field Techniques

Five stations were sampled in Auke Bay: off the breakwater of the Government dock (**GOV**), North Station (**NOS**), Auke Nu Cove (**ANC**), Auke Bay Monitor (ABM), and mid-way between **Coghlan** and Spuhn Islands (**CSI**) (Fig. 2). Plankton samples were taken from May to July, 1988, with 3 m long bongo nets each having a mouth diameter of 0.6 m and a hard plastic cod end. A **General Oceanics** mechanical **flowmeter** was placed off center in one of the 2 nets in order to measure the volume of water filtered in a tow. Nets with mesh sizes of 333 and 505  $\mu\text{m}$  were used for capturing herring larvae, and nets with a mesh size of 165  $\mu\text{m}$  were used for capturing their **macrozooplankton** prey.

The nets were towed at approximately  $2 \text{ m}\cdot\text{s}^{-1}$  in a double oblique pattern from the surface to a maximum depth of 30 m and **back** to the surface. Contents of the **codends** were immediately preserved in either 5% formaldehyde and seawater for condition factor analysis or 37% isopropyl alcohol for **otolith** analysis. The latter samples were drained on a 165  $\mu\text{m}$  mesh screen and rinsed in freshwater before alcohol was added. Almost all of the plankton samples were taken during daylight between 900 and 2000 hours, but

at least one tow was taken at night between 2330 and 0130 hours every second sampling date, in order to correct the densities of herring larvae for evasion of the nets in daylight.

Densities of the main microzooplankton component of the diet of herring larvae, copepod nauplii, were taken from measurements made by members of the APPRISE project. This data was obtained from water bottle samples collected at 5 m depths from the surface to 30 m at 3 stations in Auke Bay once every 7 d from April 5 to June 21, 1988. The water from each bottle cast was filtered through a 24  $\mu\text{m}$  mesh, and the material retained on the mesh was preserved in 5% formaldehyde and seawater. The copepod nauplii in each sample were counted under a dissecting microscope, into 3 length classes: <150  $\mu\text{m}$ , 150-350  $\mu\text{m}$ , and >350  $\mu\text{m}$ .

### 3.2.2 Laboratory Analysis

#### 3.2.2.1 Herring Larvae

All fish larvae in the 333 and 505  $\mu\text{m}$  formalin and alcohol samples were sorted from the plankton samples under a dissecting microscope, but only the herring larvae underwent further processing. Only those larvae which were unmistakably herring were processed, and all borderline fish were classified as non-herring. Herring larvae that are fixed and preserved in alcohol decompose during storage and one of the first body parts to be lost is the double row of melanophores on the ventral surface that is the primary means for separating this species from eulachon, Thaleichthys pacificus, and sandlance, Ammodytes hexapterus, larvae. Decomposition was slowed by replacing the alcohol within 24 h of capture, by sorting fish larvae from the plankton as soon as possible, and by storing the larvae in large volumes of alcohol.

All herring were counted and measured for standard length (L or notochord length) to the nearest 0.1 mm with the vernier scale of a compound microscope. Up to 5 formalin-preserved larvae from each cohort in each

sample were randomly chosen for **morphometric** measurements. The cohorts were defined by their length ranges which were generally non-overlapping. Four **morphometric** characters were measured to the nearest 0.01 mm with an ocular micrometer: anal body depth (**ABD**), the dorsal-ventral depth at the anus, excluding the gut; pectoral body depth (**PBD**), measured at the pectoral girdle, including the gut; head width (**HW**), measured across the dorsal surface of the head, including the eyeballs; and eye diameter (**ED**), always measured along the antero-posterior axis of the eye. The larvae were then rinsed in fresh water, dried at 60°C for 24 h, stored in a desiccator for 24 h and weighed to the nearest 1  $\mu\text{g}$  on an **electrobalance** to obtain dry weight (**W**). The dimensions of the larvae were corrected for shrinkage or expansion caused by capture in towed nets using Gompertz models calibrated for Pacific herring larvae by **McGurk** (1985 b).

Preservation in alcohol without prior fixation in **formalin** renders fish larvae extremely fragile so it was not possible to measure their morphometry or their dry weight. Length was corrected for shrinkage due to net capture. **Otoliths** were removed from 6 fish from each sample for aging; the fish were chosen using **length** frequency plots so that at least one fish was taken from each of the 3 major cohorts present in the samples.

#### 3.2.2.2 Zooplankton

Each 165  $\mu\text{m}$  zooplankton sample was **split** several times and one **subsample** was completely identified and enumerated to the species level under a dissecting microscope. Length and width was measured for several specimens of each taxon in order to calculate dry weight from length-weight relationships taken from the scientific literature.

### 3.3 Prey Field of Herring

A definition of the diet of larval and **juvenile** herring in Auke Bay was first attempted from an analysis of their gut contents. About 25 larvae and 25

juveniles were picked at random out of the total set of formalin-preserved samples. The fish were chosen so that there was 1 for every 1 mm length bin over the 10 to 40 mm length range. The standard length of each fish was measured, the gut was opened under a dissecting microscope and all organisms found within were counted and identified. The lengths and widths of 30 organisms from each gut were then measured with an ocular micrometer. This information is listed in Appendix G and it was reviewed in Appendix J. It was supplemented by a review of the scientific literature on diet of Pacific herring larvae. This review is also in Appendix J.

In order to establish rules for the rigorous definition of the prey field, it was necessary to know the expected maximum and minimum lengths and widths of prey for each length interval of herring larvae. The maximum, mean and minimum lengths of prey from the southern British Columbia data shown in Table J1 of Appendix J were regressed on the mid-point of the herring length interval. Maximum and mean length of prey were highly correlated with herring length, but minimum length was not significantly correlated (Table J2 and Fig. J1). These results were supplemented by regressions of maximum, mean and minimum prey width on fish length reported by Checkley (1982) for feeding experiments with laboratory-reared Atlantic herring larvae exposed to natural zooplankton (Table J2).

Based on this analysis, I defined the prey field of herring larvae in Auke Bay as all taxa listed in Appendix I which have been found at least once before in a previous study of the diet of Pacific and Atlantic herring larvae, and which are smaller in length and width than the maximum lengths and widths predicted by the regression equations of Table J2. Comparisons were made first between the average prey length and expected maximum prey length because the relationships between prey length and predator length were established from data on Pacific herring. Organisms larger than the expected maximum length were rejected; the widths of the smaller, accepted organisms were then compared to the expected maximum width predicted from Checkley's

(1982) work on Atlantic herring larvae. Those that were below the maximum were finally accepted for the prey field. This procedure was done for each herring length interval using the expected maximum lengths and widths.

The final prey field includes all species of **calanoid copepods** of the appropriate size, all species of **harpacticoid copepods**, **cladocerans**, **mollusc veligers**, **polychaete** larvae and small fish eggs (Table J3). [It excludes monstrilloid (parasitic) copepods, all species of Cnidaria, barnacle nauplii and cypris, isopods, nemertean worms, the arrow worm Sagitta elegans, bryozoan cyphonautes, and echinopluteus and asteroid larvae because they have never been found in even trace amounts in the guts of herring larvae, and it excludes fish larvae and large fish eggs, several species of large **calanoid copepods**, the hyperiid amphipod Parathemisto, the tuniuate Oikopleura doica, crab and shrimp zoea and juveniles, and small adult **polychaete** worms because they are too long or too wide for herring larvae. **Ostracods** were not included because they were found in only one sample from Auke Bay.

This prey field does not include **copepod** eggs because neither this study nor APPRISE used techniques that could accurately measure **copepod** egg density. Copepod eggs are too small (10  $\mu\text{m}$  in diameter) and too easily broken to be sampled even with the water bottle system used by APPRISE. They are best sampled using techniques usually employed for phytoplankton enumeration (Dr. C. Low, Victoria, B. C., personal communication).

### 3.4 Prey Concentration

Prey density was derived by combining the densities of **zooplankton** defined as prey of herring larvae that were collected by EPL's 165  $\mu\text{m}$  mesh plankton nets with the densities of **copepod nauplii** collected as part of APPRISE.

Prey concentration ( $\text{mg dry weight}\cdot\text{m}^{-3}$ ) was calculated from prey density ( $\text{numbers}\cdot\text{m}^{-3}$ ) using dry weight-length and dry weight-width relationships reported in the literature. Concentrations of all stages of **copepods** and

cladocerans were calculated by first converting body width to wet weight using Pearre's (1980) equation for marine copepods

$$(1) \quad Y = 1.5598 X^{2.9776}$$

where Y = wet weight (mg) in formalin, and X = width (mm). Wet weight in formalin was then converted to live wet weight by assuming a 10% loss in weight during storage (Pearre 1980), and live wet weights were converted to live dry weights by assuming an 80% water content. Concentration of mollusc veligers was calculated from data on mean live dry weight and mean length for larvae of the oyster, Ostrea edulis, reared in culture from release to an age of 12 d by Holland and Spencer (1973). A regression of live dry weight on length was

$$(2) \quad Y = 0.5900 X^{3.6966}$$

n = 4; r<sup>2</sup> = 0.99; P < 0.01

where Y = mean live dry weight (mg), and X = mean length (mm). Concentrations of polychaete trochophores and small fish eggs were calculated by assuming a spherical volume [= 4/3 π r<sup>3</sup>, where r = radius (mm)], a specific gravity of 1 g·cm<sup>-3</sup>, and a water content of 80%, i.e.

$$(3) \quad Y = 0.2 \times 1 \text{ mg} \cdot \text{mm}^{-3} \times \frac{4}{3} \pi r^3 = 0.1047 X^3$$

where Y = live dry weight (mg), and X = length (mm).

### 3.5 Predator Concentration

Three classes of invertebrate predators were identified from the zooplankton collected in the 165 μm mesh tows and listed in Appendix I: gelatinous predators, which in this study consisted of at least 10 species of jellyfish (Cnidaria), the pelagic hyperiid amphipods Parathemisto spp., and the chaetognath Sagitta elegans. These organisms were chosen because they are

large enough to prey on young herring larvae and because examination of the gut contents of field-caught jellyfish (Stevenson 1962, Moller 1980b, Robinson 1988), and Parathemisto spp. (Sheader and Evans 1975, Yamashita et al. 1985), and laboratory predation experiments with jellyfish (Arai and Hay 1982, Bailey and Batty 1983, Bailey 1984, Purcell et al. 1987), with Parathemisto spp. (Yamashita et al. 1984), and with other species of hyperiid amphipod (Westerhagen and Rosenthal 1976), and with chaetognaths (Kuhlmann 1977) show that these organisms are predators of fish larvae.

Two species of carnivorous copepods which have been previously identified as potential predators on fish larvae: Tortanus discaudatus (Robinson 1988), and Centropages abdominalis (Turner et al. 1985), were not identified as such in this study because the specimens captured in Auke bay were too small to be significant predators on herring larvae. Theilacker and Lasker (1974) showed that euphausiid shrimps can feed on small fish larvae, and a large population of the euphausiid Thysanoessa raschii inhabits the near-bottom habitat of Auke Bay (Krieger 1987, Carls 1987). However, euphausiids were not considered in this study because they were never found in the 165  $\mu\text{m}$  mesh zooplankton samples.

Of the 57 jellyfish captured in the 165  $\mu\text{m}$  mesh tows, 23 (40%) were too damaged to be assigned a species or a bell diameter. Three rules were used to assign them to size classes: (1) if other jellyfish had been caught at the same dates and stations, then they were assigned to those size classes; (2) if no other jellyfish had been caught at that station on the same date, then they were assigned to the size classes of jellyfish captured at other stations on the same date; and (3) if no other jellyfish had been caught on that date, then they were assigned to size classes on the basis of the frequency distribution of size classes for the entire study period.

Densities of jellyfish were converted to concentrations by, first, correcting the measured bell diameter to live diameter by assuming a 7% shrinkage due to preservation and storage in 5% seawater formalin. This number was taken

from Larson's (1985) data on shrinkage of 8 species of jellyfish stored for 2 to 32 mo. The derivation of this number is described in section 1.0 of Appendix L. Second, live bell diameter was converted to dry weight using the equation

$$(4) \quad Y = 0.01 X^{2.65}$$
$$r^2 = 0.91, n = 215, P < 0.001, SE_b = 0.06$$

where Y = dry weight (mg) and X = live bell diameter (mm) derived from data on 7 species of jellyfish captured in Saanich Inlet, British Columbia, and reported by Larson (1985). The derivation of equation (4) is reviewed in section 2.0 of Appendix L.

Densities of Parathemisto were converted to concentrations by using the weight-length regression for Parathemisto guadichaudi that was reported by Williams and Robins (1979)

$$(5) \quad Y = 0.0064 X^{2.614}$$

where Y = live dry weight (mg), and X = length (mm). A weight-length regression for P. japonica that was reported by Yamashita et al. (1985) is very similar to equation (5). Densities of S. elegans were converted to concentrations using a dry weight-length equation reported by Sameoto (1971)

$$(6) \quad Y = 9.7 \times 10^{-4} X^{2.365}$$

where Y = dry weight (mg) and X = live length (mm).

Herring larvae become less vulnerable to capture by jellyfish, Parathemisto and S. elegans as they grow in size and develop proportionately higher swimming speeds. Bailey (1984) and Purcell et al. (1987) both reported decreases in capture success of herring larvae with increased length of herring larvae, but only Bailey (1984) reported sample sizes that were large

enough to calculate a significant regression between capture success and length

$$(7) \quad Y = 0.2397 \exp(-0.1721X)$$

$$r^2 = 0.83, n = 14, P < 0.01, SE_b = 0.0225$$

where  $Y$  = number of fish larvae eaten-h-l • (cross-sectional area of medusa)<sup>-1</sup>,  $X$  = mean length (mm) of fish larvae, and  $SE_b$  = standard error of the exponent. This equation was derived from data on 5 species of fish including Atlantic herring.

Equation (7) cannot be used directly to adjust predator concentrations for decreasing vulnerability of herring larvae to capture because predicted capture success is higher than would be expected in a natural ecosystem since Bailey's' (1984) experiments were conducted in containers of only 0.005 m<sup>3</sup> volume. de Lafontaine and Leggett (1987) recently reported a highly significant inverse relationship between predation mortality of fish larvae and the volume of the experimental enclosure. Predation mortality rates of the same magnitude as those measured in natural ecosystems can only be replicated in enclosure volumes of at least 3.2 m<sup>3</sup>. However, equation (7) can be used indirectly to adjust predator concentration by assuming that the effect of enclosure volume is to change the rate at which predators encounter prey, and not to affect the relationship between capture success and escape swimming speed. Then total predator concentration can be adjusted by the ratio of equation (7) at length  $L$  to equation (7) at length of hatch, i.e.

$$(8) \quad Y_t = X_t V_t = X_t \exp[-0.1721(L_t - 8.8)]$$

where  $Y_t$  = adjusted total predator concentration (mg•m<sup>-3</sup>) at age  $t$ ,  $V_t$  = index of vulnerability (range: 0 to 1),  $X_t$  = total predator concentration (mg•m<sup>-3</sup>) of at age  $t$ , and  $L$  = mean length (mm) of herring larvae at age  $t$ .

### 3.6 Spawn Surveys

Aerial surveys of the Auke Bay - Lynn Canal area were conducted by biologists of the Douglas office of the Alaska Department of Fish and Game (A **DFG**), every day or every second day from April 22 to May 15, 1988. They covered the shores of the mainland and the islands in Lynn Canal from Berners Bay to the southern end of Douglas Island. The surveyors searched for eggs on intertidal kelp, milt in the water, herring schools close to spawning beaches and bird and sea mammal activity. I conducted foot surveys of beaches in Auke Bay at least once a week from April 30 to June 19, 1988. At this time the shoreline of the Bay was searched with binoculars for flocks of seabirds feeding on spawn, and local residents of the Bay were interviewed at the three docks at the head of the Bay.

Herring spawn in Auke Bay was mapped with methods modified from the ADFG herring spawn survey protocol (e.g. **Blankenbeckler** 1987). Total length of spawn was measured by placing a rope marked in meter intervals along the upper limit of the spawn. Width of spawn was measured **along** transects established perpendicular to this rope at 1 to 10 m intervals. The distance between transects was reduced from the **ADFG** standard of 400 or 800 m to 1 to 10 m because the total lengths of the 2 spawnings that were mapped were less than 400 m long and because the spawn was distributed in patches with dimensions of only 1 to 30 m. A SCUBA survey was conducted to determine what proportion of the spawn was **subtidal**.

At each sampling date, samples of spawn were taken at 5 sites in order to estimate egg density and total egg number. The sites were chosen to represent the average spawn density estimated by eye over the nearby area. **All** of the vegetation and attached spawn were collected from within a 0.1 m' sample frame and immediately preserved in **Gilson's fluid** in water tight plastic bags.

In the laboratory the Gilson's fluid was decanted and the sample was placed in a fine mesh bag in a funnel until drops of fluid fell from the funnel at a rate of less than 1 rei<sup>n</sup>l. The wet **sample** was weighed **on** a balance and the type of vegetation was recorded. The mixture was then soaked in 5% formaldehyde and 28 ppt seawater for **24** h in order to assure a constant volumetric displacement. Each sample was drained, blotted dry on absorbent paper and its total volume measured as the amount of water it displaced in a large measuring vessel. The water was drained, the sample was **blotted** dry again and mixed thoroughly by hand and two **subsamples** of 5 ml volume each were removed and preserved in 5% formaldehyde and 28 ppt seawater. The number of eggs in each of the two **subsamples** was counted under a dissecting microscope. The number of **eggs·m<sup>-2</sup>** was the mean number of eggs·ml<sup>-1</sup> multiplied by the total volume of the sample and then multiplied by 10.

Hatching dates of cohorts 2 and 3 were forward-calculated from the known dates of spawning obtained from the spawn surveys using the average daily surface water temperatures of Auke Bay and **Alderdice** and **Velsen's** (1971) equation

$$(9) \quad Y = 0.7648 + 0.4367X + 0.0235X^2$$

where Y = development rate (%·d<sup>-1</sup>) and X = temperature ("C).

Spawning dates of cohorts 1, 4 and 5 were back-calculated from the known dates of hatching obtained from the growth models using surface water temperatures of Auke Bay and equation (9).

The percent of eggs that hatched into viable larvae was calculated from Alderdice and Velsen's (1971) equation

$$(10) \quad Y = 22.7560 + 1.5441X_1 + 13.8280X_2 - 0.0787X_1^2 - 0.9684X_2^2 + 0.1356X_1X_2$$

where Y = percent viable hatch,  $X_1$  = mean surface water temperature ("C) and  $X_2$  = mean surface salinity (ppt).

### 3.7 Juvenile Surveys

Juvenile herring were captured with dipnets as they schooled off the Auke Bay Government dock from August 14 to 25. One sample of juvenile herring was captured with a beach seine off the western beaches of **Spuhn Island** on August 15 by personnel of the Auke Bay Laboratory. Half of each sample was preserved in 5% formalin and half in 37% isopropyl alcohol.

Standard length of all fish in both **formalin-** and alcohol-preserved samples was measured to the nearest mm. No **morphometric** characters were measured because **McGurk's** (1985a) multi variate condition factor is applicable only to larvae less than 20 mm long. A subsample of 5 **formalin-preserved** fish were dried at 60°C for 24 h and weighed to the nearest 1  $\mu\text{g}$  on a balance.

### 3.8 **Otolith** Analysis

The two **sagittal otoliths** of an alcohol-preserved larva were removed with fine probes under a dissecting microscope and prepared for examination with techniques described by Neilson and Geen (1980) and **McGurk** (1984a). The **otoliths** were placed convex side down on a glass slide and embedded in clear plastic nail polish. The small **otoliths** of young larvae were examined without further treatment, but those of large larvae were ground to the midplane using "Imperial" brand lapping film (3 M Canada Inc.) in order to remove overburden that obscured the ring pattern. Particle sizes of 30 and 0.3  $\mu\text{m}$  were used in the initial grinding and final polishing steps, respectively. Grinding was done with a grinding jig described by **Neilson** and Geen (1980).

An Optical Pattern Recognition System (OPRS: Biosonics Inc., Seattle, Wash., U. S. A.) was used to count the number of rings, measure the radius of each otolith, and measure the width of the outer 4 rings. This system consists of a video camera attached to a compound microscope, a colour monitor and a desk-top computer with a hard-disc drive. OPRS used a frame grabber that digitized the video signal and re-displayed it on the monitor. A data acquisition program enhanced the ring pattern in the image by sharpening edges. Otolith radius was always measured along the longest axis of the otolith because herring otoliths become increasingly ovoid as they grow larger. Ring widths were measured at a minimum of 2 places on the otolith and the mean widths were used in all calculations.

### 3.9 Herring Length Frequency Analysis

Length frequency plots were the primary means for the classification of larvae and juveniles into cohorts. Plots were constructed for every sample that had at least 1 herring and for every sampling date that had at least 1 herring. In many samples the separate cohorts were clear and unmistakable and no further information was required to distinguish them. In other samples the length distributions were not clear because the mean lengths of the cohorts were close together or because the sample size was too low to allow reliable separation of cohorts by simple observation. In the former cases a computer program, NORMPC, was used to partition the data into cohorts. This program is a PC-version of a FORTRAN program documented by Tomlinson (1971) that partitions a length frequency into a number of normal sub-populations using a least-squares algorithm. Best results were obtained when external information was available to provide preliminary estimates of the number of cohorts, their hatching dates and their expected mean lengths and standard deviations. I followed an iterative approach to the problem: first, I calculated preliminary mean lengths and standard deviations for the samples that could be readily separated into cohorts by observation. Then, using hatching dates calculated from spawning dates using daily mean surface water temperatures in Auke Bay and expected average growth rates of Pacific

herring larvae from the literature (Stevenson 1962, McGurk 1987a), I assigned preliminary estimates of mean length to each cohort at each date and sampling site. These preliminary estimates were used as starting parameters for NO RMPC, which then calculated more accurate mean lengths, standard deviations and numbers for each cohort at each date and sampling site. These standard deviations were used to assign ranges of length appropriate for each cohort at each date, and the ranges were used to classify larvae in those samples that contained too few larvae to employ NORMPC. This procedure was repeated several times until I was confident that each larvae and juvenile had been accurately classified into its cohort. As a final check, lengths were plotted on date for each cohort and outliers, if present, were identified and reassigned.

### 3.10 Growth Models

Four models of growth were fit to the length-at-date data:

Linear:

$$(11) \quad L = 8.8 + b(t - t_0)$$

where  $L$  = length (mm) at Julian date  $t$ ,  $t_0$  = Julian date at hatch, and  $b$  = growth rate ( $\text{mm} \cdot \text{d}^{-1}$ );

Gompertz:

$$(12) \quad L = 8.8 \exp \left[ \frac{A_0 \exp\{1 - \exp[-a(t - t_0)]\}}{a} \right]$$

where  $A_0$  = rate of growth ( $\text{d}^{-1}$ ) at  $t_0$ , and  $a$  = rate ( $\text{d}^{-1}$ ) at which  $A_0$  decreases with Julian date;

von Bertalanffy:

$$(13) \quad L = \text{Linf}\{1 - \exp[-K(t - t_0)]\}$$

where Linf = length (mm) at infinite time, and K = growth coefficient (d<sup>-1</sup>); and

Logistic:

$$(14) \quad L = b1 + \frac{b2}{1 + \exp(-b3((t-t_0)-b4))}$$

where **b1** (mm), **b2** (mm), **b3** (d<sup>-1</sup>), and **b4** (d) are parameters.

These modified models were necessary because fitting a growth curve to length-at-date is the reverse of the conventional procedure where absolute age is usually known but initial size is not. In this case, the absolute age of the larvae was not known with as much certainty as the average length of yolk sac larvae. By fixing initial size at the average length of yolk sac larvae in Auke Bay (8.8 mm, Appendix C) a growth model could then estimate the Julian date at which **L=8.8** mm and so estimate the date 2.5 d after the hatching date of each cohort.

Specific rates of recent growth in dry weight were calculated from the widths of the 4 outermost rings of the **sagittal otoliths** as

$$(15) \quad G_w = \frac{1}{t} \ln \frac{W_1}{W_n} \times 100$$

where **G<sub>w</sub>** = specific rate of growth (% dry weight-d<sup>-1</sup>), **W<sub>1</sub>** = dry weight (µg) at capture, **W<sub>n</sub>** = dry weight (µg) before deposition of the **n<sup>th</sup>** otolith ring, and **t** = time (d) required to deposit 1 ring. Both **W<sub>1</sub>** and **W<sub>n</sub>** were calculated from length at capture and length before deposition of the **n<sup>th</sup>** ring, respectively, with a weight-length equation, and both lengths

were calculated from otolith radius using a regression of length on  $\ln(\text{otolith radius})$ . The calculated otolith radius before the  $n$ th ring was deposited was radius at capture minus the summed widths of  $n$  outer rings. The time period for which  $G_w$  as calculated was the reciprocal of the slope of the regression of ring number on date of capture for all cohorts combined.

### 3.11 Weight-Length Relations

Three allometric models were fit to the  $\ln$ -transformed weight-length data of each cohort and to the combined data of all cohorts: the standard linear or double-logarithmic model, a Gompertz-type model derived by Theilacker (1980) by eliminating time from 2 Gompertz equations describing growth in weight and length, and a logistic model.

#### Double-logarithmic:

$$(16) \quad \ln W = \ln(a) + b \ln L$$

where  $a$  ( $\mu\text{g}\cdot\text{mm}^{-1}$ ) and  $b$  are parameters;

Gompertz-type:

$$(17) \quad \ln W = b_1 - b_2(b_3 - \ln L)^{b_4}$$

where  $b_1$  = the natural logarithm of the asymptotic dry weight ( $\mu\text{g}$ ),  $b_3$  = the natural logarithm of the asymptotic length (mm),  $b_4$  = the ratio of the decay parameters in the Gompertz curves describing weight and length, and  $b_2$  has no obvious biological interpretation; and

Logistic:

$$(18) \quad \ln W = b_1 + \frac{b_2}{(1 + \exp(-b_3(\ln L - b_4)))}$$

where  $b_1(\mu\text{g})$ ,  $b_2$ ,  $b_3$  and  $b_4$  (mm) are parameters.

### 3.12 Condition Factors

The 4 **morphometric** characters were used with length and dry weight to calculate 2 condition factors: relative condition factor (**Ricker 1975**)

$$(19) \quad \text{CF1} = \frac{W}{\widehat{W}}$$

where  $\widehat{W}$  = weight ( $\mu\text{g}$ ) predicted from length using the weight-length equation for the combined data of all cohorts; and **McGurk's (1985a) multivariate condition factor** for Pacific herring larvae

$$(20) \quad \text{CF2} = 14.191 - 4.389\ln L + 2.184\ln ABD + 2.197\ln PBD \\ - 12.331\ln HW + 3.770\ln ED + 0.419\ln W.$$

CF2 classifies a Pacific herring larvae as feeding or starving primarily on the width of the head and, secondarily, on the depth of the body. Both variables shrink with starvation and expand with feeding. CF2 can only be calculated for non-yolk-sac larvae, and it classifies as starving fish that are both reversibly and irreversibly starving.  $\text{CF2} < 0$  identifies feeding larvae and  $\text{CF2} > 0$  identifies reversibly and irreversibly starving larvae. CF2 [called CV1 in **McGurk (1985a, 1986a)** and **CF** in **McGurk (1989)**] was shown by **Robinson (1988)** to be highly correlated ( $r^2=0.87$ ,  $P < 0.01$ ) with the ratio of RNA to DNA in the tissue of Pacific herring larvae, which confirms that CF2 is an accurate index of physical condition.

### 3.13 **Advection**, Diffusion and Patchiness

**Advection** of herring larvae was examined by first calculating the **centroid** or **center** of mass of each cohort in x-y coordinates for each age at which data from 3 stations was available, and then plotting the distance of each

successive centroid from the original one. The slope of the relationship between distance and time is an estimate of the **advection** rate. The x-y coordinate system for Auke Bay is shown in Fig. 2. The origin was set at the spawning beach of cohorts 2 and 3: the high tide level midway between Bay and **Waydelich** Creeks. The y-axis extended directly offshore on a direct north-south axis paralleling the western shore of the **Mendenhall** Peninsula. The x-axis roughly paralleled the north shore of the Bay. The coordinates of each sampling station were assumed to be the midpoints of the average **linear** distance travelled during a 10 min plankton tow.

The x-coordinate of a centroid for age t is

$$(21) \quad \bar{X}(t) = \frac{\sum_{i=1} N_{ti} x_i}{\sum_{i=1} N_{ti}}$$

where  $N_{ti}$  = density (**number·m<sup>-3</sup>**) of herring larvae at age t and position i and  $x_i$  = x-coordinate of position i. The y-coordinate of the centroid,  $\bar{Y}_t$ , was calculated similarly.

Diffusion of larvae from their hatch sites was calculated as the slope of the relationship between the spatial variance of the larvae

$$(22) \quad s_{xy}^2 = 2[s_x^2 + s_y^2]^{\frac{1}{2}}$$

and age. Spatial variance in the x-axis at age t was calculated as

$$(23) \quad s_{xt}^2 = \frac{\sum_{i=1} N_{ti} (X_i - X_t)^2}{\sum_{i=1} N_{ti}}$$

$s_{yt}^2$  was calculated similarly.  $S_{xy}$  was calculated only for dates at which 2 or more positive densities were measured.

$$(25) \quad N_t = N_0 \exp(-Zt)$$

where  $N_t$  = density (number  $\cdot m^{-3}$ ) at age  $t$  (d),  $N_0$  = density at hatch ( $t = 0$ ) and  $Z$  = loss rate ( $d^{-1}$ ) that is constant with age.  $Z$  is total mortality if losses due to **advection** or diffusion are assumed negligible.

The Pareto-type model was introduced by Hewitt et al. (1985). Like the linear model it has a single loss rate, but the rate changes exponentially with age instead of remaining constant.

$$(26) \quad N_t = N_0 \left( \frac{t}{t_0} \right)^{-\beta}$$

where  $N_0$  = density ( $m^{-3}$ ) at  $t_0$ ,  $\beta$  = mortality coefficient and  $t_0$  = the youngest age (d) in a data set. Mortality at any age can be calculated as  $Z_t = \beta t^{-1}$ .

**McGurk** (1989) describes the **advection-diffusion** models used in this report. They partition the variance in population density into that due to **advection**, diffusion and mortality, rather than to a single loss rate. The most complex of the set of **advection-diffusion** models is

$$(27) \quad N_{xyt} = \frac{C}{\sqrt{4K_x K_y t}} \exp \left[ \frac{-(x-x_0-ut)^2}{4K_x t} - \frac{(y-y_0-vt)^2}{4K_y t} - Zt \right]$$

where  $N_{xyt}$  = density (number  $\cdot km^{-3}$ ) at distances  $x$  and  $y$  (km) from the origin and age  $t$  (d),  $C$  = number of newly-hatched larvae per unit volume at  $t = 0$  d,  $H$  = depth (km) of the water layer in which larvae reside,  $K_x$  and  $K_y$  = coefficients of diffusion in the  $x$ - and  $y$ -axes ( $km^2 \cdot d^{-1}$ ),  $x_0$  and  $y_0$  = distances from origin to hatch site along the  $x$ - and  $y$ -axes (km),  $u$  and  $v$  = rates of **advection** along  $x$ - and  $y$ -axes ( $km \cdot d^{-1}$ ), and  $Z$  = total mortality ( $d^{-1}$ ) that is constant with age.

### 3.14.2 Egg-Larval Mortality

None of the herring larvae captured in this study were younger than 2 d old, therefore the daily egg-larval mortality,  $M_{el}$  ( $d^{-1}$ ), that occurred between hatching of the eggs and the first date at which measurements of mean larval density could be obtained was estimated by comparing the total number of larvae in Auke Bay at the earliest age,  $n_2$ , with the total number of viable larvae that hatched,  $n_1$ .  $M_{el}$  was assumed to be constant with time because the rate at which it changed with time could not be measured. Thus,

$$(28) \quad M_{el} = \frac{-1}{t} \ln \frac{n_2}{n_1}$$

where  $t$  = time (d) between date of hatching and date of first estimate of mean larval density.

The total number of larvae at time  $t$  was calculated as

$$(29) \quad n_2 = N_0 \cdot A \cdot H$$

where  $N_0$  = the density ( $m^{-3}$ ) of herring larvae in Auke Bay predicted by a population model for  $t_0$  the earliest age of the larval density data set,  $A$  = area ( $m^2$ ) of Auke Bay, and  $H$  = depth (m) of layer in which herring larvae resided. The assumptions of equation (29) are:

1. All larvae are retained in Auke Bay. This assumption is necessary because, as is reported in section 10.2, there was not enough spatial variation in larval density to identify the margins of the distribution of larvae. It is supported by the arguments that: (a) the advection and diffusion rates of herring larvae hatching into sheltered embayments like Auke Bay are an order of magnitude lower than those for cohorts that hatch into exposed offshore waters (see section 10. 1); (b) that Auke Bay possesses a counter-clockwise gyre of

surface currents that would tend to retain larvae in the Bay; and (c) that herring larvae may maintain themselves in Auke Bay by migrating vertically so as to take advantage of depth differences in current speed and direction (see section 10.1). This assumption is probably correct for cohorts in which the earliest age at which larval density was measured was only several d after hatching because the larvae were almost certainly still in Auke Bay at that age. The assumption would be less valid for cohorts with a longer time period between hatching and first measurement of larval density;

2. All larvae are retained within a vertical layer of depth H; and
3. There is no vertical or horizontal variation in the density of larvae within the Bay. These two assumptions are necessary because of the lack of data on the vertical distribution of herring larvae in Auke Bay and because no horizontal gradients of larval density were measured.

The total number of viable newly-hatched larvae was

$$(30) \quad n_1 = N_e \cdot a \cdot f_1 \cdot f_2$$

where  $N_e$  = mean density ( $m^{-2}$ ) of eggs on the spawning ground,  $a$  = total area ( $m^2$ ) of spawning ground,  $f_1$  = fraction of eggs that survived exposure and predation,  $f_2$  = fraction of surviving eggs that hatched viable larvae. The assumptions of equation (30) are:

1. All patches of eggs for each cohort were located and mapped. This is a reliable assumption for cohorts 2 and 3 because SCUBA survey showed that all spawning for these cohorts was restricted to the intertidal zone which was surveyed in **detail** by foot patrol;

2. There were no horizontal or vertical gradients of egg density on the spawning grounds. This assumption is appropriate because the highly patchy distribution of eggs meant that there were no significant correlations between the density of eggs and their position on the spawning beach; and
3. Egg mortality due to exposure and predation was uniform over the spawning ground. This assumption is supported by the argument that the spawning beds of cohorts 2 and 3 were too small (<250 m long) to have had “significant spatial differences in exposure or predation mortality.

Substituting equations (29) and (30) into equation (28) gives an expression for daily mortality during the egg-larval period in terms of the seven parameters defined above

$$(31) \quad M_{e1} = \frac{-1 \ln \left[ \frac{N_0 \cdot A \cdot H}{N_e \cdot a \cdot f_1 \cdot f_2} \right]}{t}$$

The effects on  $M_{e1}$  of variation in the assigned values of the seven parameters of equation (31) were examined by sensitivity analysis (section 10.3).

### 3.15 Statistical Analysis

All single linear regressions were predictive rather than functional regressions (Ricker 1973). Growth models, weight-length models and population models were fit to the data using non-linear regression. The **advection-diffusion** models were fit by first transforming them with natural logarithms because the transformed models provided more cases of convergence with lower residual sums of squares. The parameters of the population models were **also re-cast** in order to prevent exponential increases in their values that caused the non-linear regression program to cease functioning. For

example, the coefficients of diffusion were estimated as  $(4K)^{-1}$  rather than  $K$ .

Differences between cohorts of herring larvae in the relationships between otolith radius and fish length, and otolith ring number and age were tested using covariance analysis with dummy variables. For a linear regression of  $Y$  on  $X$  for  $n$  cohorts,  $n-1$  dummy variables were inserted to test for differences in intercepts and another  $n-1$  dummy variables were inserted to test for differences in slopes, e.g. for  $n=3$  cohorts

$$Y = b_0 + b_1X + b_2g_1 + b_3g_2 + b_4g_1X + b_5g_2X$$

where  $g_1$  = dummy variable with a value of 1 for cohort 1 and 0 for cohorts 2 and 3,  $g_2$  = dummy variable with a value of 0 for cohort 1, 1 for cohort 2 and 0 for cohort 3, and  $b_0$  to  $b_5$  = coefficients estimated by multiple linear regression. If  $b_2$  or  $b_3$  are significant ( $P < 0.05$ ), then there are significant differences between cohorts in their intercepts, and if  $b_4$  or  $b_5$  are significant, then there are significant differences between cohorts in their slopes.

Response surface techniques were used to describe the relations between responses (e.g. predator concentration, specific growth rate, condition factor), and variables (date, age, prey concentration, and temperature). This involved fitting a linear polynomial

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_1^2 + b_4X_2^2 + b_5X_1X_2$$

where  $Y$  = response,  $X_1$  and  $X_2$  are variables, and  $b_0$  to  $b_5$  = regression coefficients. Non-significant terms were rejected in a backwards stepping manner until a polynomial was found in which all terms were significant ( $P < 0.05$ ).

## 4.0 RESULTS - PHYSICAL AND BIOLOGICAL ENVIRONMENT

### 4.1 Temperature, Salinity and Water Density

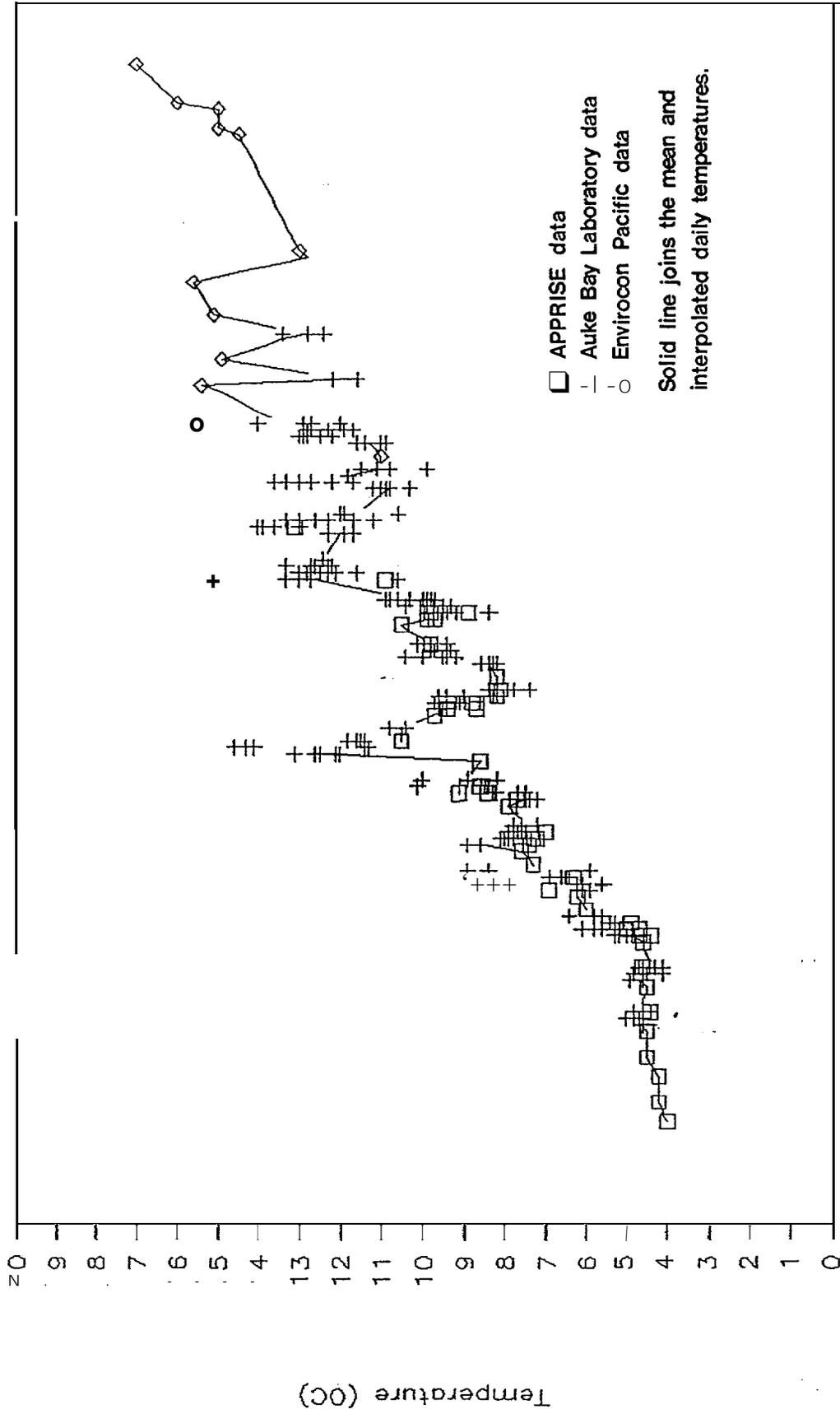
Mean water temperatures, salinities, and densities for the upper 20 m of Auke Bay Monitor (ABM) station collected by APPRISE are presented in Appendix N, profile data for temperature at ABM collected by EPL are presented in Appendix O, and surface temperatures and salinities collected by the Auke Bay Laboratory are presented in Appendix P.

The combined data on surface water temperature is plotted against date in Fig. 3. Surface temperature rose from a minimum of  $4.00^{\circ}\text{C}$  on March 14 to a maximum of  $17^{\circ}\text{C}$  on August 25, the rise being punctuated by transient maxima and minima, the most obvious of which was a period of rapidly increasing temperature from April 17 to May 14, followed by declining or stable temperatures from May 14 to June 6. These data were used to calculate incubation times of herring eggs laid in the intertidal zone of Auke Bay and in an analysis of the relationship between the dates of first spawning and mean water temperature in Auke Bay.

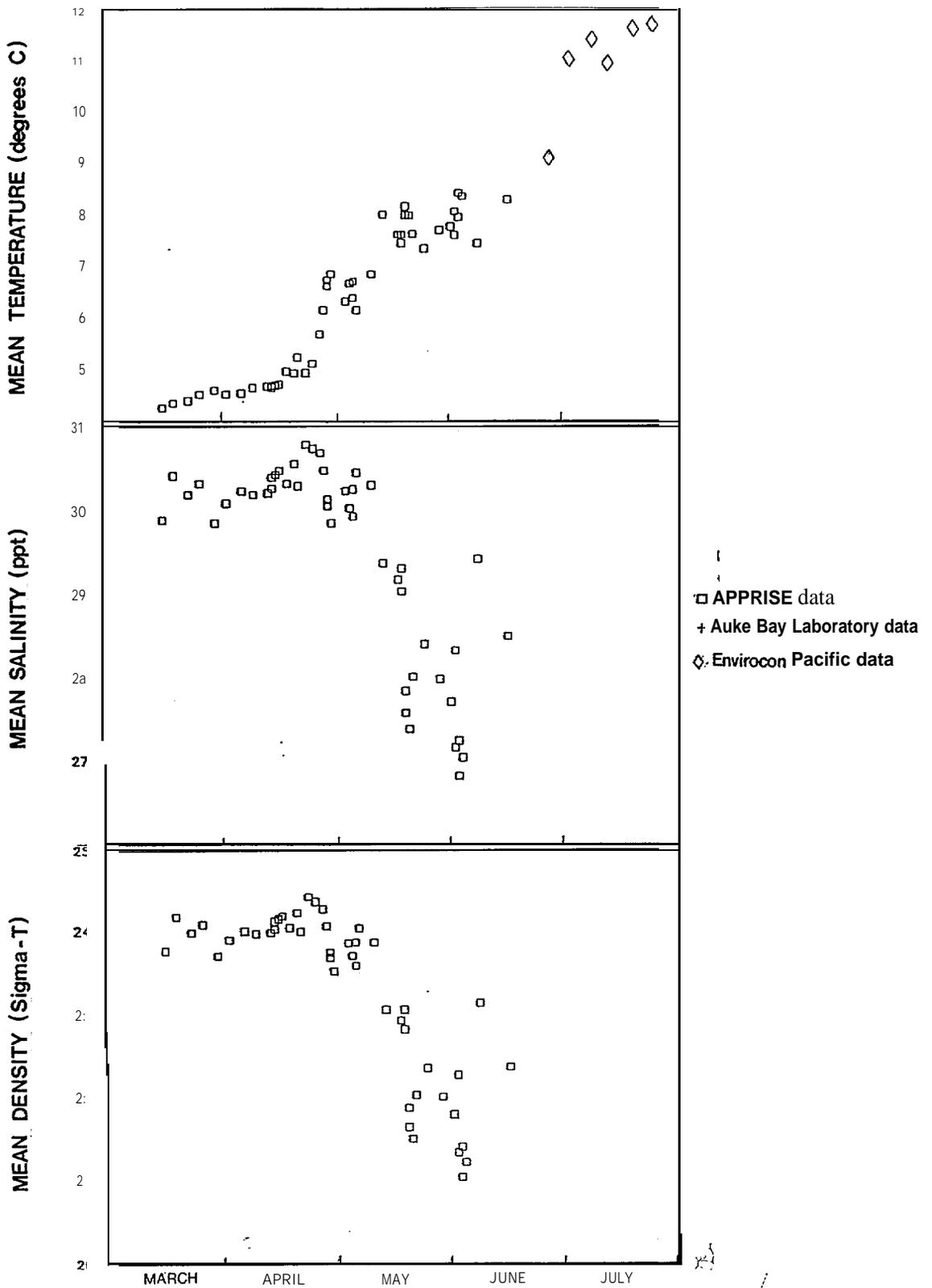
The same temporal pattern is more clearly evident in the mean temperature of the upper 20 m shown in Fig. 4. These data were used in analyses of the relationships between growth and condition and environmental variables. -

Mean salinity of the upper 20 m was constant at about 30.4 ppt from March 14 to May 7, and then it declined rapidly to a minimum of 26.82 ppt by June 1 in response to freshwater inflows from heavy rains (Fig. 4). Water density ( $\sigma\text{-t}$ ) followed a similar trajectory with date, being constant at about 24.0 from March 14 to May 7 and then declining rapidly to a minimum of 21.0 on June 1. The water column became progressively more stratified with date as are shown by profiles of density for the May 19 to June 14 period (Fig. 5).

**Figure 3: SURFACE WATER TEMPERATURES IN AUKE BAY IN 1988**

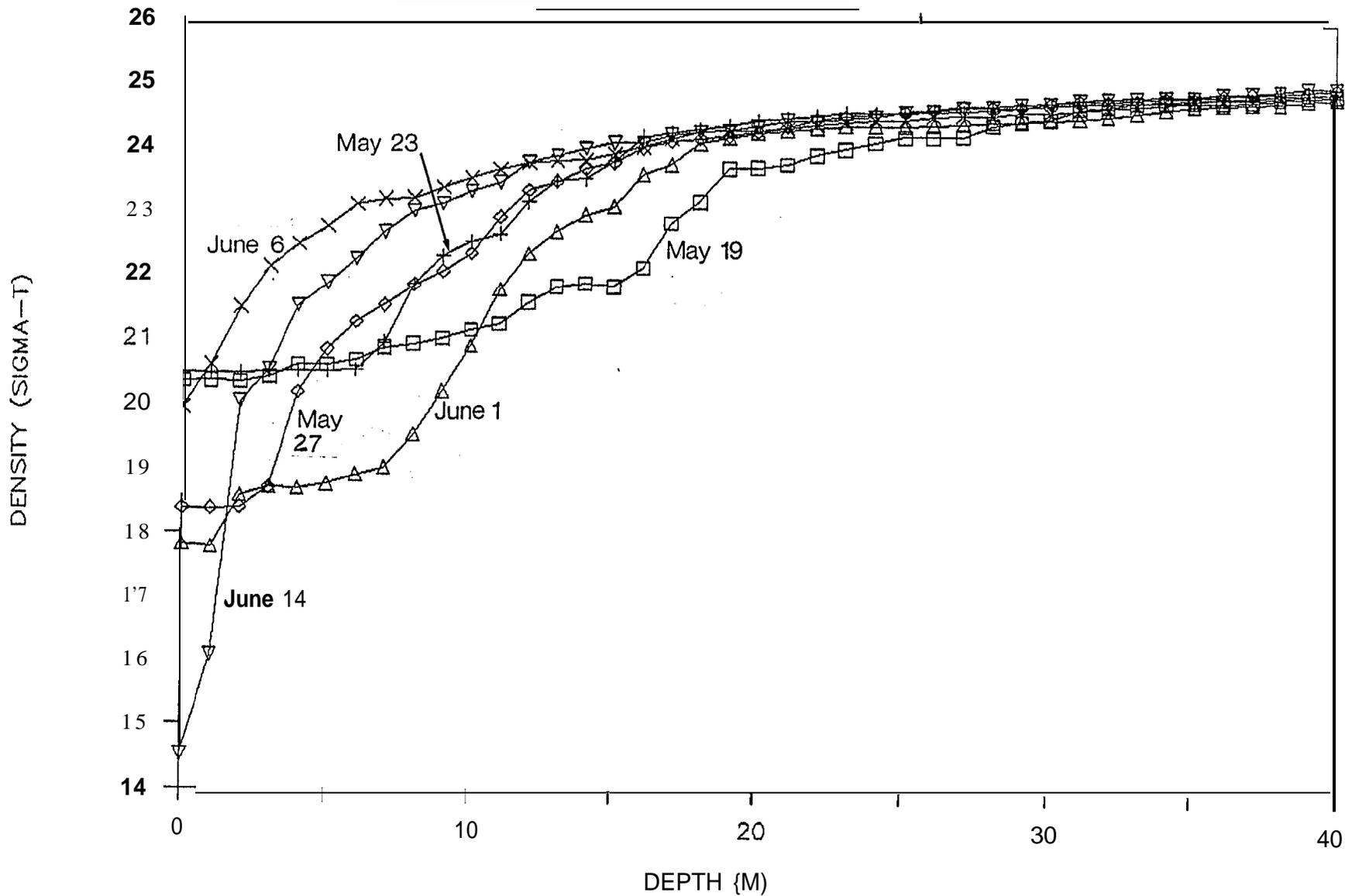


27-Feb 18-Mar 07-Apr 27-Apr 17-May 06-Jun 26-Jun 16-Jul 05-Aug 25-Aug



**Figure 4: MEAN TEMPERATURE , SALINITY AND DENSITY IN THE UPPER 20m OF THE WATER COLUMN**

**Figure 5: PROFILES OF WATER DENSITY ( $\sigma_t$ ) FOR THE UPPER 40m OF THE ABM STATION SHOWING INCREASING STRATIFICATION OF THE WATER COLUMN FROM MAY TO JUNE**



#### 4.2 Concentrations of Prey and Predators

Concentrations of the 19 components of the prey field of herring larvae are listed in Appendix K and plotted against date of capture in Fig. 6. **Mollusc veligers** and **copepod nauplii** had the highest average concentrations and **harpacticoid copepods** and **small fish eggs** had the lowest average concentrations. Prey concentrations were assigned to 6 separate length classes of herring larvae because the prey field changes with size of larvae (Appendix K, Fig. 7). The most striking feature of the mean prey concentrations is a U-shaped relationship with date; it decreased from a peak on May 27 to a minimum on June 10, and then increased to a second peak on June 20.

Concentrations of jellyfish, *Parathemiso* spp., and *Sagitta elegans* in Auke Bay are listed in Appendix M and plotted against date of capture in Fig. 8. Mean total concentrations of predators ranged from 0.9 to 34,027.7  $\text{mg}\cdot\text{m}^{-3}$  with a geometric mean concentration of 150.2  $\text{mg}\cdot\text{m}^{-3}$ . Jellyfish comprised an average of 97.6% (SE=5.3, n=15) of the total concentration of predators at all dates. Table 1 shows that, apart from several 100 mm diameter *Staurophora mertensi* captured in mid-July, the jellyfish captured in the 165  $\mu\text{m}$  mesh tows were relatively small; the modal preserved diameter was only 8 to 10 mm. Table 1 also shows that 36% of the total number of jellyfish were too badly damaged during capture to identify their species. These unidentified jellyfish consisted of fragments of large jellyfish, so the size distribution shown in Table 1 may underestimate the **actual** size distribution in Auke Bay.

Figs. 7 and 8 show that the concentrations of prey of herring larvae and the concentrations of their jellyfish predators were synchronous over the May 21 to June 25 time period. This suggests a functional response of jellyfish concentrations to concentrations of their **zooplankton** prey. Alternatively, the ratio of jellyfish to zooplankton concentrations may have been constant at all times and the variation in concentration of both components of the

**Figure 6: CONCENTRATIONS OF PREY OF HERRING LARVAE**

STATIONS : •1 - ABM

+ - ANC

◇ - CSI

△ - GOV

x - NOS

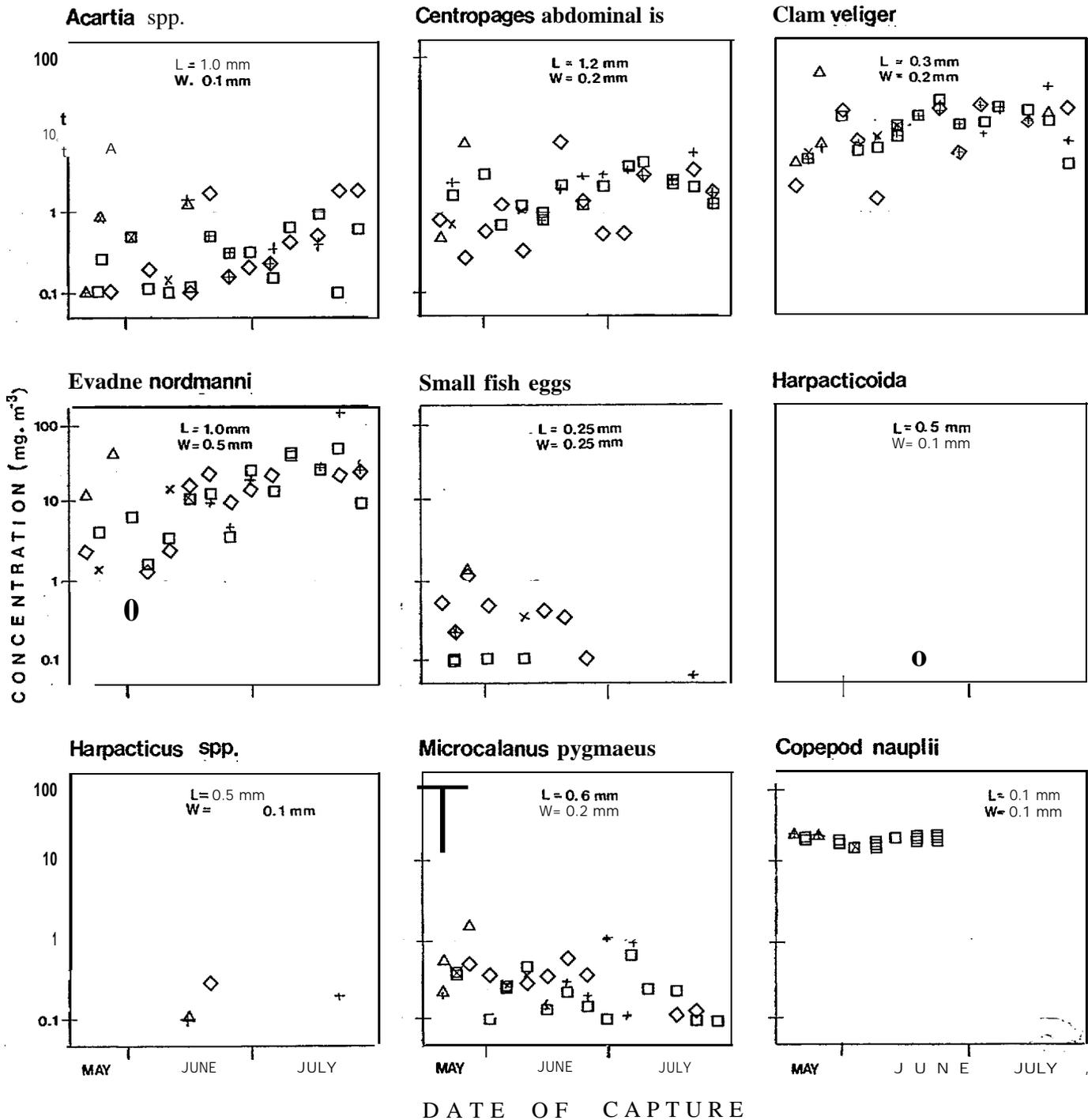
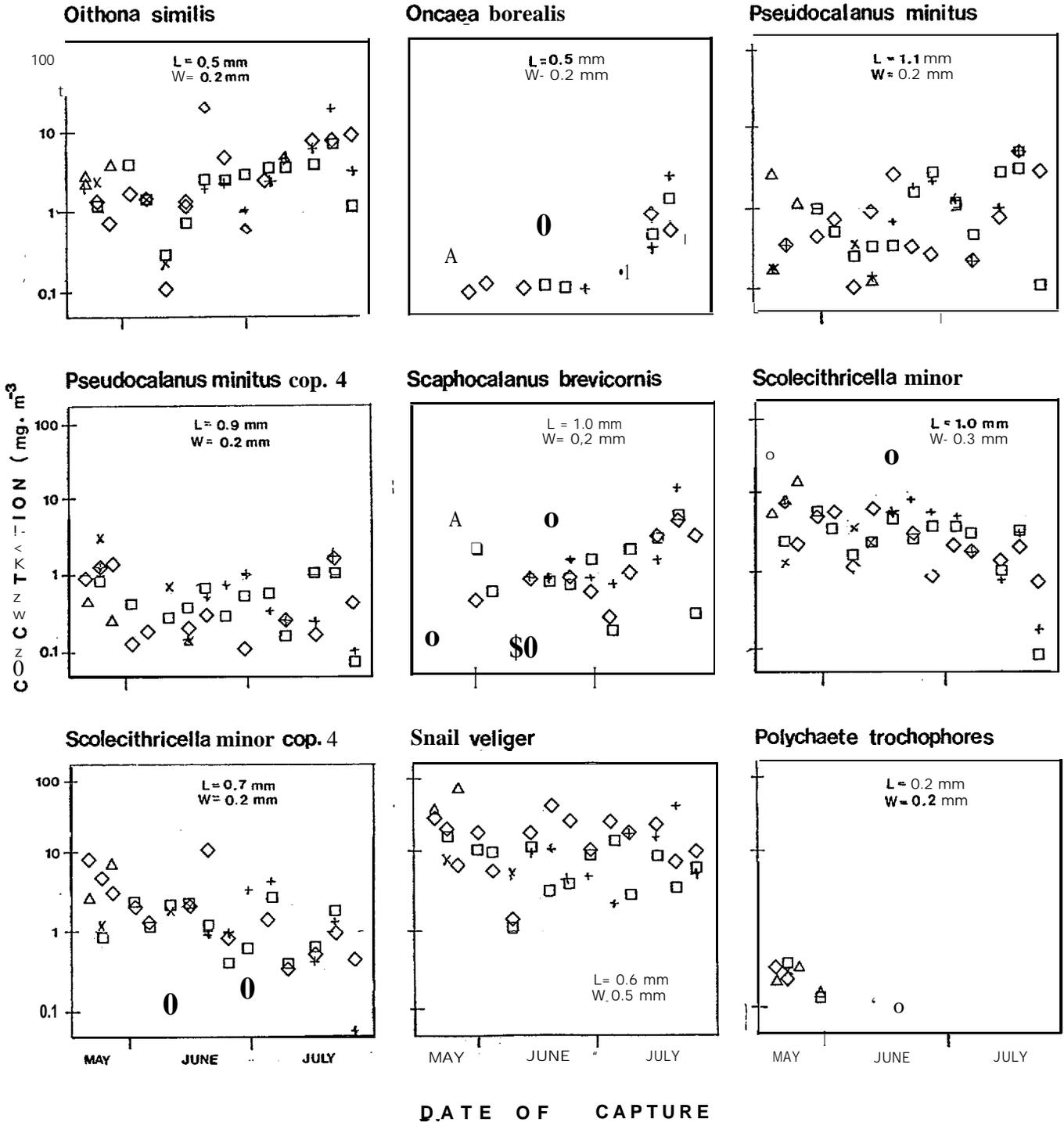


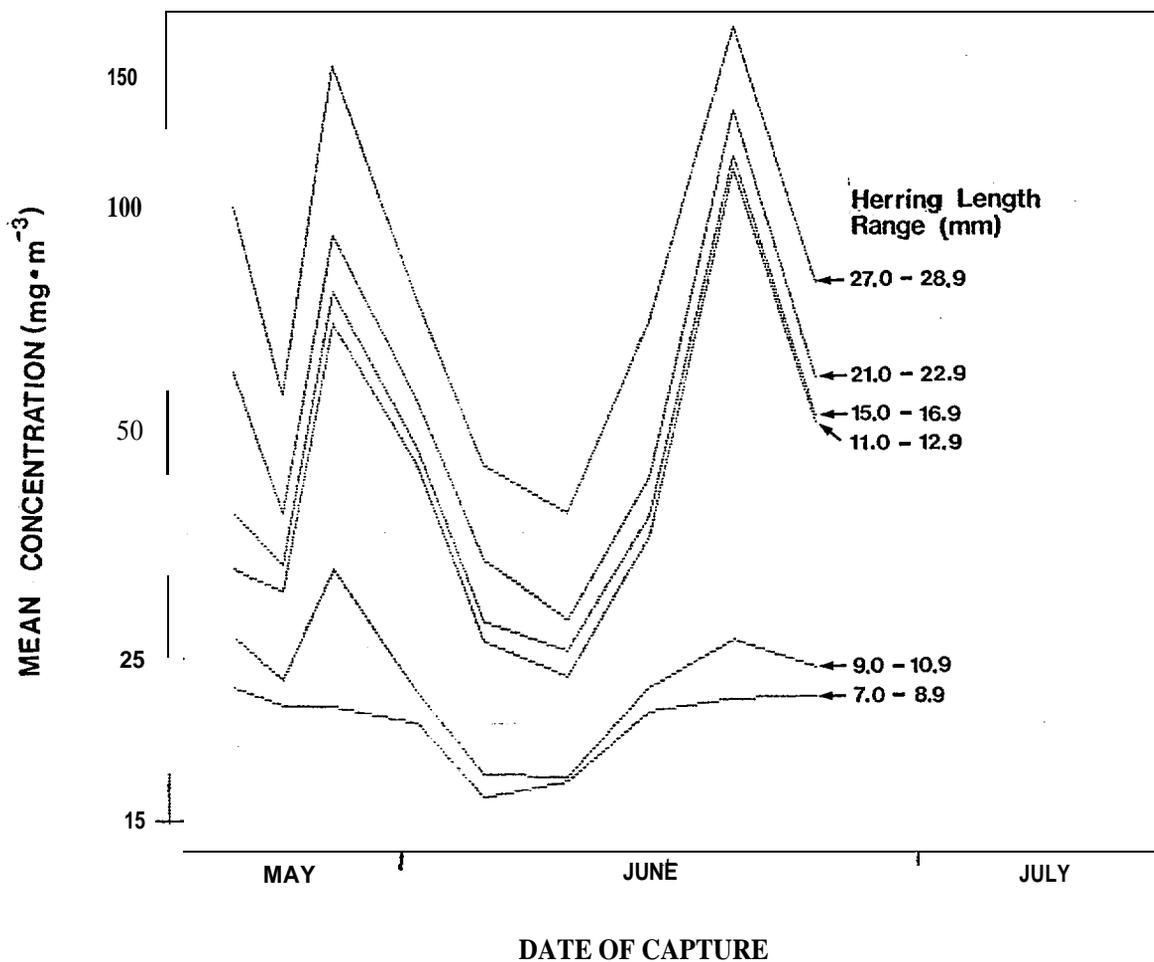
Figure 6 (cont.):

CONCENTRATIONS OF PREY OF HERRING LARVAE

STATIONS : □ ABM  
 + -ANc  
 o -CSI  
 A GOV  
 x -NOS



**Figure 7: MEAN CONCENTRATION OF PREY FOR 6 LENGTH CLASSES OF HERRING LARVAE**



**Figure 8: PLOTS OF CONCENTRATIONS OF PREDATORS OF HERRING LARVAE (symbols same as Fig. 6)**

**NOTE: Solid line is mean concentrations at date of jellyfish**

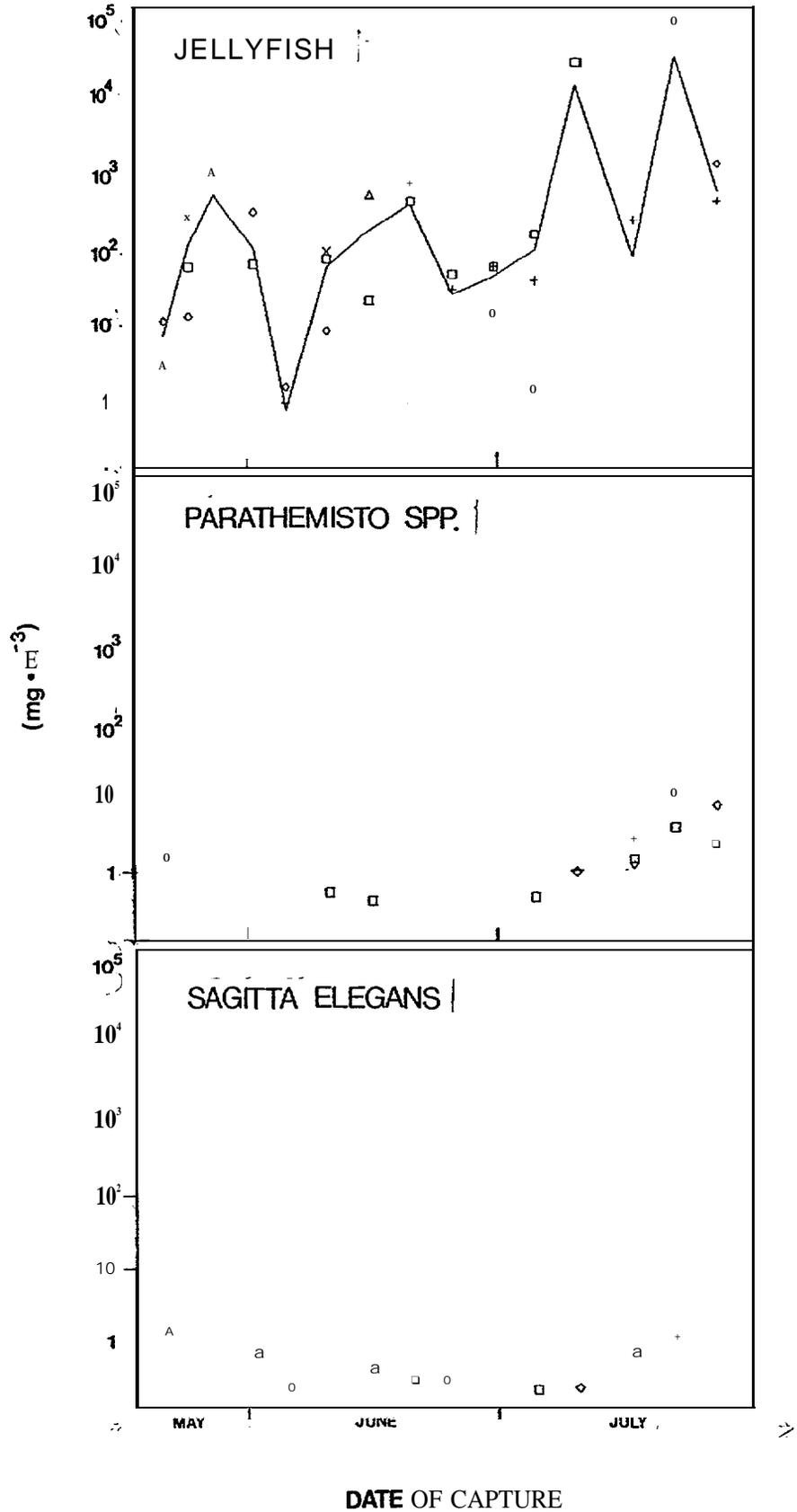


TABLE 1

Time and size distribution of jellyfish captured with 165  $\mu\text{m}$  mesh nets.

Species	Mean Bell Diameter (mm)	Number at Date															Total		
		May			June						July								
		21	24	27	1	5	10	15	20	25	30	5	6	10	17	22		27	
<u>Hybocodon prolifer</u>	3		1				1										2		
<u>Halitholus</u> spp.	3	1				1										1	3		
<u>Rathkea octopunctata</u>	3						1				1						2		
<u>Sarsia</u> spp.	8					1	2	1		3		1	1			1	10		
<u>Tiaropsis multicirrata</u>	10			1		1		2	1	1				1		1	8		
<u>Mitrocomella sinuosa</u>	12					1											2		
<u>Eperetmus typus</u>	15													1			1		
<u>Cyanea</u> spp.	16							1				1					3		
<u>Aequorea victoria</u>	20						1	1								2	4		
<u>Staurophora mertensi</u>	100											1			1		2		
Damaged medusae		2	5	1	1		3		5	1	1		1				21		
Total		3	7	2	2	1	7	4	1	0	2	5	1	3	2	2	1	6	58

Note: dashes indicate no data.

plankton was caused by the movements of different water masses into or out of the Bay. Response surface analysis was used in order to determine what proportion of the variation in jellyfish concentration was correlated with concentrations of prey for herring larvae (functional response) and what proportion was correlated with date (water movements or other external variables). Concentrations of prey and predators at individual sampling stations were used, rather than mean concentrations at date, in order to increase the size of the data set. For the same reason, total prey concentrations minus the mean concentration of **copepod nauplii** at date were used because this allowed the extension of the data set from June 25 to **July 27**. Only records with non-zero jellyfish concentrations were used in order to avoid using the  $\ln(X+1)$  transformation of jellyfish concentration. This meant the **elimination** of 11 of 40 records. The maximum amount of variation in jellyfish concentration was explained by the interaction of date and prey concentration

$$(32) \quad Y = -2.021 + 9.653 \times 10^{-3} X_1 X_2$$

$$r^2 = 0.28, n = 29, P = 0.003$$

where  $Y = \ln[\text{jellyfish concentration (mg}\cdot\text{m}^{-3})]$ ,  $X_1 = \text{Julian date}$ , and  $X_2 = \ln[\text{prey concentration (mg}\cdot\text{m}^{-3}) \text{ for the } 165 \mu\text{m mesh samples}]$ . This equation indicates that prey concentration and the unknown environmental factors subsumed by date were both responsible for significant proportions of the variation in jellyfish concentrations. Partial correlation coefficients of  $Y$  with  $X_1$  ( $r = 0.40$ ), and  $X_2$  ( $r = 0.32$ ) and  $X_1$  with  $X_2$  ( $r = 0.06$ ) indicate that date and prey concentration were equally important explanatory variables. The positive correlation coefficient for prey concentration supports the hypothesis that jellyfish aggregate at sites with relatively high concentrations of prey. Thus, habitat of herring larvae that contains high concentrations of prey also contains relatively high concentrations of predators.

## 5.0 DISCUSSION - PHYSICAL AND BIOLOGICAL ENVIRONMENT

The March to May period of 1988 was one of the warmest that has been recorded in Auke Bay during the past 14 years; Table 11 shows that for the five years (1975, 1976, **1986**, 1987 and 1988) in which herring larvae were studied in Auke Bay, the mean surface water temperatures over the March to May period in 1988 were, with the exception of the first 2 wk in April, generally 0.3 to 1.3°C higher than in previous years. These higher temperatures led to an early date at onset of the spring phytoplankton bloom (Ziemann et al. 1989). Mean concentrations of prey for young herring larvae, primarily copepod nauplii, were also high in the May to June period of 1988 relative to the previous three years (Paul and Coyle 1986, **1987**, 1988, 1989). However, there were significant differences in the concentration of prey for herring larvae of all length classes between late May and early and mid-June, 1988.

In summary, the habitat in Auke Bay was favorable for rapid growth of herring larvae. If the critical period hypothesis is correct, and survival of young fish larvae is directly related to successful feeding and high growth rates, then survival of herring larvae in Auke Bay in 1988 is predicted to be high relative to previous years. Also, survival of cohorts of herring that hatched during periods of high prey concentration in 1988 is predicted to be higher than that of cohorts that hatched during periods of low prey concentration in the same year. This study cannot test the first hypothesis because survival rates of herring larvae in previous years have yet to be calculated from APPRISE data. Instead, this study tests the critical period hypothesis by comparing growth and survival between separate cohorts of herring that hatched in 1988. This study also tests the hypothesis that survival of herring larvae is determined by predation as well as by food-limitation.

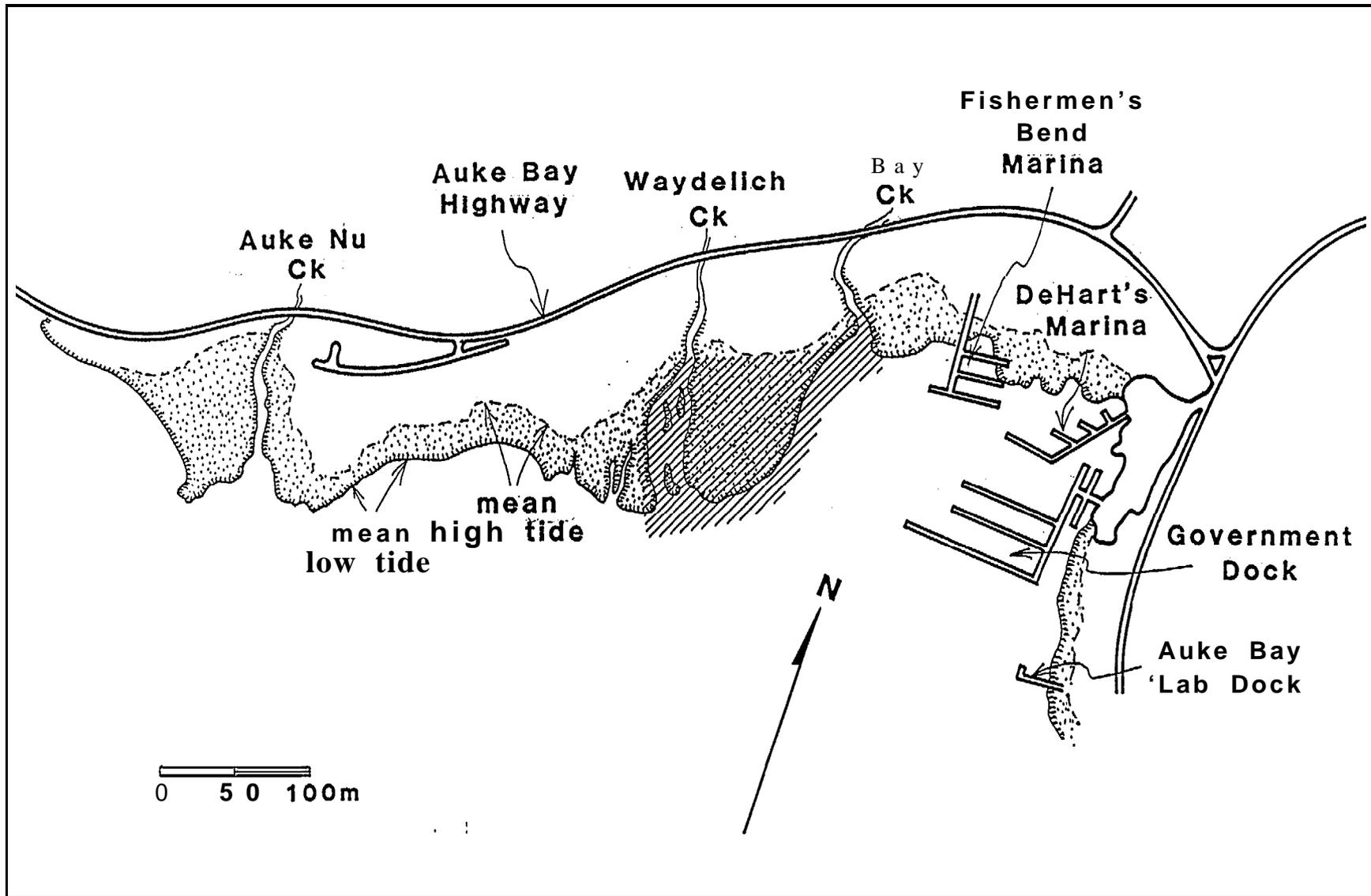
## 6.0 RESULTS - DISTRIBUTION AND SURVIVAL OF HERRING EGGS

### 6.1 Spawning Locations and Timing

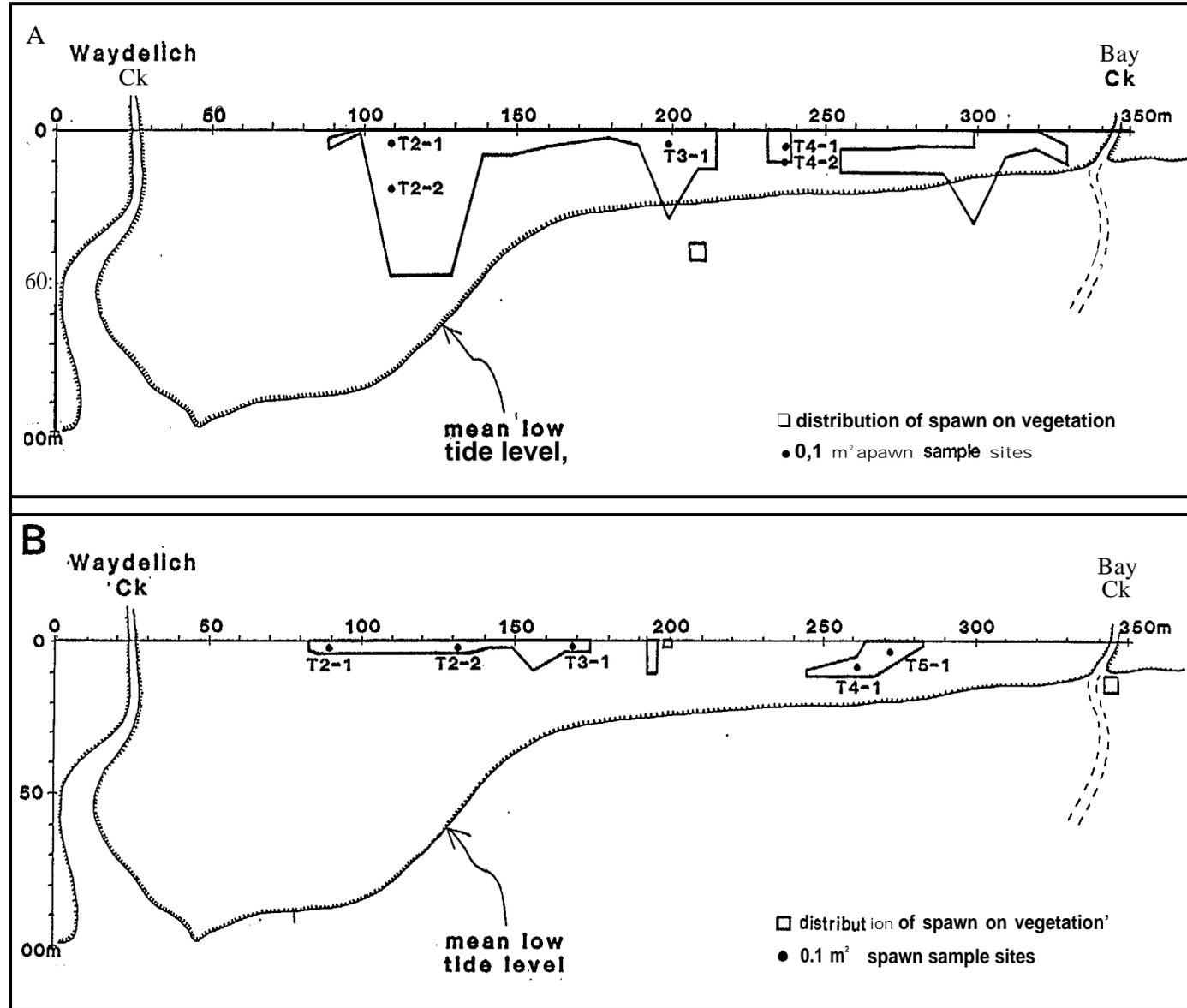
The major spawning of the Lynn Canal - Auke Bay herring stock occurred on April 30, 1988. Approximately 11.2 linear km of spawn was deposited on the shore from Bridget Cove 25 km north of Auke Bay to the mouth of Kowee Creek in Berners Bay (personal communication, D. **Ingledue, ADFG**, Douglas, Alaska). Over the next 10 d minor spawnings of herring were also observed on the shores of Benjamin Island, 10 km north of Auke Bay.

At least 5 separate spawnings of herring occurred in Auke Bay in 1988 producing 5 distinct cohorts of herring larvae. Only the eggs of cohorts 2 and 3 were observed and mapped on the beaches (Figs. 9 and 10). The eggs of the first, fourth and fifth cohort were not observed, but their dates of spawning and **hatching** were estimated by a combination of back-calculation of the growth rates of the herring larvae and of back-calculation of egg development rates from average surface water temperatures. The spawning and hatching dates of all 5 cohorts are summarized in Table 10.

The parents of the second cohort were first observed in **Auke Bay** on April 30 by ADFG aerial surveyors and by **local** fishermen and boat owners. The fish concentrated at the head of the Bay underneath Fishermen's Bend and **Dehart's** marinas and the Government docks. On May 5 to 7 these fish spawned in the intertidal zone of the beach between Bay and **Waydelich** Creeks, about 100 m west of Fishermen's Bend docks (Fig. 10A). Spawning was first observed early on the morning of May 5 in **Waydelich** Creek and on the beach immediately east of the Creek (personal communication, Mabel Burford, Auke Bay). Spawning was next observed on May 7 near Bay Creek at the other end of the spawning beach (personal communication, D. **Ingledue, ADFG**, Douglas, Alaska). Apparently spawning swept **along** the beach from the eastern end to the western end over the 2 d period. Several days afterward the spawners **left** Auke Bay because they were no longer observed under the docks and they were no longer caught in gill nets slung underneath the docks by **local** fishermen.



**Figure 9:** MAP OF NORTHERN SHORE OF AUKE BAY (hatched area of the intertidal zone indicates the location of spawning sites for cohort 2 and 3 herring)



**Figure 10: MAPS OF COHORT 2(A) AND 3(B) SPAWNING SITES IN THE INTERTIDAL ZONE OF THE NORTHERN SHORE OF AUKE BAY**

The parents of the third cohort were seen by local residents on May 29 underneath Fishermen's Bend dock. The actual spawning event was not observed, but it must have occurred shortly after May 29 because the spawn was reported on June 5 (personal communication, Mabel Burford, Auke Bay, Alaska). This spawn was also laid on the beach between Waydelich and Bay Creeks, on the same patches of intertidal vegetation that held the eggs of the second cohort (Fig. 10 B).

## 6.2 Egg Density and Number

The distribution of the eggs of the second and third cohorts on the beaches were mapped on May 18 and June 6, respectively. Eggs were laid on narrow strips of Fucus and Desmarestia within the upper 50 m of the intertidal zone. The strips covered a total length of about 250 m in each cohort. A SCUBA survey on May 18 found no eggs in the **subtidal** zone and no vegetation on which eggs could have been laid.

Density of cohort 2 eggs ranged from 80,400 to 994,500  $\text{m}^{-2}$  with a mean ( $\pm 1$  SD) of 508,100 ( $\pm 419,778$ ) (Table 2). Cohort 3 eggs were **almost** twice as dense, ranging from 182,800 to 3,166,900  $\text{m}^{-2}$  with a mean ( $\pm 1$  SD) of 1,088,880 ( $\pm 1,204,758$ )  $\text{m}^{-2}$ . However, the high variances of the densities meant that the two means were not significantly different ( $P > 0.05$ , Mann-Whitney U test) from each other. The high variances support the observation that egg deposition was highly patchy.

Cohort 2 eggs covered more than 4 times the area of cohort 3 eggs: 2949  $\text{m}^2$  compared to 662  $\text{m}^2$  (Table 3). Therefore, the estimated total number of cohort 2 eggs was twice as high as the estimated total number of cohort 3 eggs:  $1,498 \times 10^6$  and  $721 \times 10^6$ , respectively.

TABLE 2

Egg density of herring cohorts 2 and 3.

Date	Cohort	Sample Number	Meters from Origin	Meters from Upper Spawn Limit	Plant Type	Sample Wet Weight (g)	Sample Volume (ml)	Number of Eggs				Total Eggs in Sample	Total Egg Density (m <sup>-2</sup> )
								Subsample A	Subsample B	Mean	SD		
18 May 88	2	T2-1	110	5	<b>Fucus</b>	1031.9	750	746	581	663	117	99,450	994,500
18 May 88	2	T2-2	110	20	<b>Fucus</b>	411.2	100	428	375	402	<b>37</b>	8,040	80,400
18 May 88	<b>2</b>	<b>T3-1</b>	200	5	<b>Desmarestia</b>	662.9	350	415	313	364	<b>72</b>	25,480	254,800
18 May 88	2	T4-1	240	5	<b>Fucus</b>	448.5	450	<b>686</b>	<b>1,185</b>	<b>1,026</b>	224	92,340	923,400
18 May 88	2	T4-2	240	10	<b>Fucus</b>	234.5	150	1,028	888	958	99	28,740	<u>287,400</u>
												Mean	508,100
												SD	419,778
												n	5
06 June 88	3	<b>T2-1</b>	90	3	<b>Fucus</b>	658.1	550	<b>3,058</b>	2,700	2,879	253	316,690	3,166,900
06 June 88	3	T2-2	130	3	<b>Fucus/Desmarestia</b>	588.6	550	967	654	810	221	89,100	891,000
06 June 88	3	<b>T3-1</b>	170	3	<b>Desmarestia</b>	421.0	250	1,651	1,863	1,757	150	87,850	876,500
06 June 88	3	<b>T4-1</b>	260	8	<b>Fucus</b>	120.0	100	1,006	822	914	130	18,280	182,800
06 June 88	3	<b>T5-1</b>	270	5	<b>Fucus</b>	193.6	200	780	847	813	<b>47</b>	32,520	<u>325,200</u>
												Mean	1,088,880
												SD	1,204,758
												n	5

- Notes: 1. **Origin** is the intersection of upper limit of herring spawn with **Waydelich** Creek (Figs. 9 and 10).  
2. All **subsamples** of 5 ml volume.  
3. Number of **eggs** in sample = (volume of sample/5) x number of eggs in sub-sample.  
4. Each sample taken from area of 0.1 m<sup>2</sup>.  
5. Number of eggs m<sup>-2</sup> = number of eggs in **sample/0.1 m<sup>2</sup>**.

TABLE 3

**Estimated number and biomass of cohort 2 and 3 spawners and estimated number of newly-hatched larvae of cohorts 2 and 3.**

	<u>Cohort 2</u>	<u>Cohort 3</u>
Mean egg density (m <sup>-2</sup> )	508,100	1,088,880
Area of spawn (m <sup>2</sup> )	<u>2,949</u>	<u>662</u>
Number of eggs	1,498,386,900	720,838,560
Mean fecundity of female spawners	<u>25,000</u>	<u>25,000</u>
Number of female spawners	59,935	28,834
Ratio of male to female spawners	<u>1:1</u>	<u>1:1</u>
Number of male and female spawners	119,871	57,667
Average weight of spawning herring (g)	<u>110</u>	<u>110</u>
Biomass of spawners (kg)	13,186	6,343
Fraction of eggs lost during incubation	<u>0.25</u>	<u>0.25</u>
Number of newly-hatched larvae	1,123,790,175	540,628,920
Percent viable hatch	<u>87.1</u>	<u>89.3</u>
Number of viable larvae	978,821,242	482,781,626

Notes:

1. Mean egg density from Table 2.
2. Area of spawn from Figs. 10A and 10B.
3. Percent viable hatch from Alderdice and Velsen (1971)-

### 6.3 Development Rates and **Hatching** Dates

**Alderdice** and **Velsen's** (1971) equation [equation (9)] relating the daily development of Pacific herring eggs to water temperature was used to predict hatching dates of cohorts 2 and 3 from the surface water temperatures measured in Auke Bay (Tables 4 and 5). Mean temperatures were calculated for dates on **which** several separate measurements were available. Dates for which no temperatures were available were estimated by interpolation between neighboring dates. The eggs of **cohort** 2 are calculated to have hatched by May 19, 13 days after spawning on May 6 (Table 4), and the eggs of cohort 3 are estimated to have hatched by June 9, 11 days after an assumed spawning on May 29 (Table 5). These dates are increased or decreased by only 1 d if the lowest and highest temperatures at each date were used.

**TABLE 4**

Development rate of cohort 2 herring eggs.

<u>Date</u>	<u>Surface Water Temperature ("C)</u>			<u>Egg Development Rate (%·d<sup>-1</sup>)</u>			<u>Cumulative Egg Development (%)</u>		
	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>
06 May	9.0	8.2	10.0	6.599	5.926	7.482	6.599	5.926	7.482
07 May	8.8	8.8	8.8	6.428	6.428	6.428	13.027	12.354	13.910
08 May	8.7	8.7	8.7	6.343	6.343	6.343	19.369	18.696	20.252
09 May	8.6	8.6	8.6	6.258	6.258	6.258	25.628	24.955	26.511
10 May	12.5	12.0	13.1	9.895	9.389	10.518	35.523	34.344	37.029
11 May	13.3	11.3	14.3	10.730	8.700	11.815	46.253	43.044	48.844
12 May	11.4	10.5	<b>11.8</b>	8.797	7.941	9.190	55.050	50.985	58.034
13 May	10.5	10.5	<b>10.5</b>	7.941	7.941	7.941	62.991	58.926	65.975
14 May	10.6	10.4	10.4	8.034	7.848	8.222	71.026	66.775	74.198
15 May	10.1	10.1	10.1	7.573	7.573	7.573	78.598	74.347	81.770
16 May	9.7	0.7	9.7	7.213	7.212	7.212	85.810	81.559	88.982
17 May	9.4	8.7	9.6	6.946	6.343	7.123	92.757	87.902	96.105
18 May	9.3	8.7	9.7	6.859	6.343	7.212	99.615	94.245	103.317
19 May	8.7	8.2	9.6	6.343	5.926	7.123	105.958	100.171	110.440

Notes:

1. Development rate (%·d<sup>-1</sup>) = 0.7648 + 0.4367T + 0.0235T<sup>2</sup>.

TABLE 5

Development rate of cohort 3 herring eggs.

<u>Date</u>	<u>Surface Water Temperature (°C)</u>			<u>Egg Development Rate (%·d<sup>-1</sup>)</u>			<u>Cumulative Egg Development (%)</u>		
	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>
29 May	10.3	10.3	10.3	7.756	7.756	7.756	7.756	7.756	7.756
30 May	10.5	10.5	10.5	7.941	7.941	7.941	15.697	15.697	15.697
31 May	9.8	9.7	9.9	7.301	7.212	7.391	22.998	22.909	23.088
01 June	9.2	8.4	9.8	6.771	6.091	7.301	29.770	29.000	30.389
02 June	9.9	9.3	10.4	7.391	6.859	7.848	37.161	35.859	38.237
<b>03 June</b>	<b>10.2</b>	9.7	10.9	7.664	7.212	8.317	44.825	43.071	46.554
04 June	11.0	<b>11.0</b>	<b>11.0</b>	8.412	8.412	8.412	53.237	51.483	54.966
05 June	11.8	<b>11.8</b>	11.8	9.190	9.190	9.190	62.427	60.673	64.156
06 June	12.6	10.6	<b>15.1</b>	9.998	8.034	12.717	72.425	68.707	76.873
07 June	12.4	11.6	13.0	9.793	8.993	10.413	82.219	77.700	87.286
08 June	12.6	12.2	13.3	9.998	9.590	10.730	92.217	87.290	98.016
09 June	12.4	<b>12.4</b>	12.4	9.793	9.793	9.793	102.010	97.083	107.809
10 June	<b>12.3</b>	12.3	12.3	9.692	9.692	9.692	111.702	106.775	117.501

Notes:

$$1. \text{ Development rate } (\% \cdot \text{d}^{-1}) = 0.7648 + 0.4367T + 0.0235T^2.$$

## 7.0 DISCUSSION - **DISTRIBUTION** AND SURVIVAL OF HERRING EGGS

The Auke Bay herring spawnings of 1988 were 2 orders of magnitude **smaller** in length than those that occurred around Bridget Point. This follows a trend of decreasing spawning in Auke Bay over the last 30 years. Table 6 shows that from 1953 to 1960 the majority of the Auke Bay stock spawned in Auke Bay, but since 1972 spawning has shifted north of Eagle River and Auke Bay has received only trace amounts of spawn or no spawn at all. The northward shift in spawning location has coincided with a decline in stock size, and with an increase in boat traffic in Auke Bay.

The 1988 Auke Bay spawnings also differ from the Bridget Point **spawnings** in the type of spawning substrate. The intertidal zone at the head of **Auke Bay** is dominated by **Fucus** and **Desmarestia** and the **subtidal** zone is too muddy to support vegetation. Thus, herring spawn only in the intertidal zone. In contrast, **Blankenbeckler** and Larson (1987) report that in 1983, 58% of the spawnings north of Eagle River were laid in the **subtidal** zone and only 42% in the intertidal zone. The average width of spawn off the beaches ranged from 20.0 to 38.6 m (Table 7). They also reported that 73% of the Auke Bay-Lynn Canal eggs were laid on large brown kelps, e.g. **Laminaria**, 23% were laid on **Fucus** and 3% were laid on **Desmarestia**.

Mean densities of herring eggs laid in **Auke Bay** in 1988 were higher than the mean densities measured for **spawnings** north of Eagle River. **Blankenbeckler** and Larson (1982, **1985**, 1987) reported that the mean egg density of the Auke Bay-Lynn Canal stock in 1978, 1980 and 1983, measured for substrate that contained eggs, ranged from 117,000 to 874,238  $\text{m}^{-2}$  (Table 7).

The number of spawning cohort 2 and 3 females was calculated by dividing the total number of eggs deposited in Auke Bay by a mean fecundity per female. Mean fecundity of herring in southeast **Alaska** ranges from 9,450 to 53,865 and depends strongly on the age and length of the female (**Blankenbeckler** and Larson 1982: Table 9). Modal lengths of southeast Alaska herring range from **191** to 220 mm and the corresponding average fecundities range from 22,585 to

TABLE 6

Linear kilometers of spawn and estimated biomass of the spawning population for the Auke Bay-Lynn Canal herring stock.

<u>Year</u>	<u>Kilometers of Spawn</u>				<u>Biomass (10<sup>6</sup>kg)</u>			<u>Survey</u>
	<u>AB</u>	<u>NE</u>	<u>SE</u>	<u>Total</u>	<u>Acoustic</u>	<u>Visual</u>	<u>Spawn</u>	
1953				15.19				
1954				17.41				
1955	<b>13.33</b>			22.59				
1956	<b>18.52</b>			18.52				
1957	<b>23.89</b>	15.19		52.04				
1958	<b>24.45</b>			44.63				
1959	20.00			20.00				
1960	23.89			23.89		6.2		
1961				-				
1962								
1963								
1964								
1965								
1966								
1967								
1968								
1969						.. "		
1970				21.30				
1971								
1972	0.56	5.93	9.26	15.74	11.3			
1973	0.00	18.33	1.30	19.63	2.7			
1974	0.93	15.93	5.74	24.45	4.2			
1975	2.32	13.70	4.17	20.19	6.8			
1976	1.11	17.96	10.37	29.45	4.9			
1977	0.56	17.41	0.00	17.96	6.2			
1978	Trace	11.11	3.70	14.82	4.9		1.14	
1979	0.93	8.80	0.93	10.56	2.1	1.8		
1980	3.70	10.74	3.70	<b>18.15</b>	3.4	2.3	4.40	
1981	0.56	16.11	0.37	17.04	3.0	4.5		
1982	0.00	4.63	0.37	5.00	1.4	2.3		
1983	Trace	11.11	0.00	11.11	1.6		0.50	
<b>1984</b>	<b>Trace</b>	Trace	4.63	4.63		2.3	0.18	
1985	0.00	9.26	0.19	9.45	<b>2.1</b>	1.6		
1986	Trace	9.26	0.00	9.26				
1987	Trace	4.63	Trace	4.63		1.6		
1988	Trace	11.20		11.20			1.8	

## Notes:

1. Data from D. Ingledue (personal communication, Alaska Dept. Fish Game, Douglas, Alaska, USA)
2. AB = Auke Bay; NE = North of Eagle River; SE = South of Eagle River.
3. Dashes indicate no data.

TABLE 7

Spawn depth and width and average egg density for the portion of the **Auke** Bay - Lynn Canal herring stock that spawns north of Eagle River.

<u>Year</u>	<u>Incubation temp. (°C)</u>	<u>Spawn depth (m)</u>		<u>Avg. width of spawn (m)</u>	<u>Avg. spawn density (m<sup>-2</sup>)</u>	<u>Source</u>
		+				
1978	5-8	3.66	6.09	27.50	230,709	1
1980	5-8	3.04	7.61	38.63	874,238	1, 3
1983	7	2.13	9.14	20.00	117,000	2, 3
1984	8-9	0.61	11.58	---	---	4

---

Note:

1. 1 = **Blankenbeckler** and Larson (1982), 2 = **Blankenbeckler** and Larson (1985), 3 = **Blankenbeckler** and Larson (1987), 4 = **Blankenbeckler** (1987).
2. Dashes indicate no data.

29,415. Therefore, a mid-point fecundity of 25,000 was chosen for the calculations. This number is lower than the fecundity measured by **Blankenbeckler** and Larson (1982) for Lynn Canal spawners in 1978 (33,567) and 1980 (35,244), but higher than the fecundity measured by **Blankenbeckler** and Larson (1985) in 1983 (22,585). Using this number a total of 59,935 cohort 2 females and 28,834 cohort 3 spawners are calculated (Table 3). Assuming a sex ratio of 1:1, this is equivalent to 119,871 and 57,667 spawners, and assuming an average weight per spawner of 110 g, it is equivalent to spawning biomasses of 13,186 and 6,343 kg. These biomasses combined are approximately 1% of the biomass of the primary spawning north of Eagle River.

In order to estimate the number of viable larvae that hatched from these eggs it is necessary to know the mortality rate of herring eggs from predation, wave action and exposure. There is little consensus on the magnitude of predation mortality of herring eggs. Work done in the 1950's and 1960's in British Columbia (**Outram** 1958, **Taylor** 1964) and southeast Alaska (**Montgomery** 1958) produced loss rates ranging from 25% to 40%, but recent work on spawnings in southern British Columbia by **Haegeler** et al. (1981) suggests that the loss from predation and storms is actually closer to 10% because most spawnings in that region are subtidal and only a small fraction of the total egg complement becomes exposed to air as a result of normal tidal cycles. The current practice of ADFG herring biologists in southeast Alaska is to assume a 25% loss of eggs unless extraordinary concentrations of predatory birds are observed, in which case a loss of 50% is assumed (**Blankenbeckler** and Larson 1982). The eggs deposited in Auke Bay in 1988 were exposed to the greatest possible risk because they incubated in the upper intertidal zone and were exposed for several hours in each tidal cycle. However, predation was probably light because no more than 20 birds were observed feeding on cohort 2 and 3 eggs at any time. Wave damage was also light because there were no storms during the incubation period. Therefore, assuming a loss of 25% over the incubation period, the number of newly-hatched cohort 2 and 3 larvae that entered Auke Bay on May 19 and June 9 was estimated to be  $1,124 \times 10^6$  and  $541 \times 10^6$ , respectively (Table 3).

The percent of the hatching larvae that were viable can be estimated from the mean surface water temperatures and salinities over the incubation period using Alderdice and Velsen's (1971) model [equation (10)]. Mean ( $\pm$  1 SD, n) temperatures and salinities were 9.14 (0.72, 9) $^{\circ}$ C and 26.26 (1.42, 7) ppt over the May 6 to 19 incubation period, and 9.96 (0.63, 7) $^{\circ}$ C and 23.05 (1.55, 7) ppt over the May 29 to June 9 incubation period. These translate to viable hatches of 87.1% and 89.3% for eggs of cohort 2 and 3, respectively. Therefore, the number of viable larvae that hatched into Auke Bay was  $9.79 \times 10^8$  and  $4.83 \times 10^8$  for cohorts 2 and 3, respectively (Table 3). These estimates were used to calculate egg-larval mortality rates.

## 8.0 RESULTS - **GROWTH OF HERRING LARVAE AND JUVENILES**

### 8.1 **Number of Samples**

A total of 140 samples of plankton were collected from Auke Bay between May 15 to July 27 (Appendix A). This consisted of 43, 20 and 77 samples collected with the 165, 333 and 505  $\mu\text{m}$  mesh nets, respectively. The first 2 samples were taken on May 15 and subsequent samples were taken at intervals of 3 to 7 d until herring larvae were no longer captured by towed plankton nets. The last herring larvae was captured on July 27.

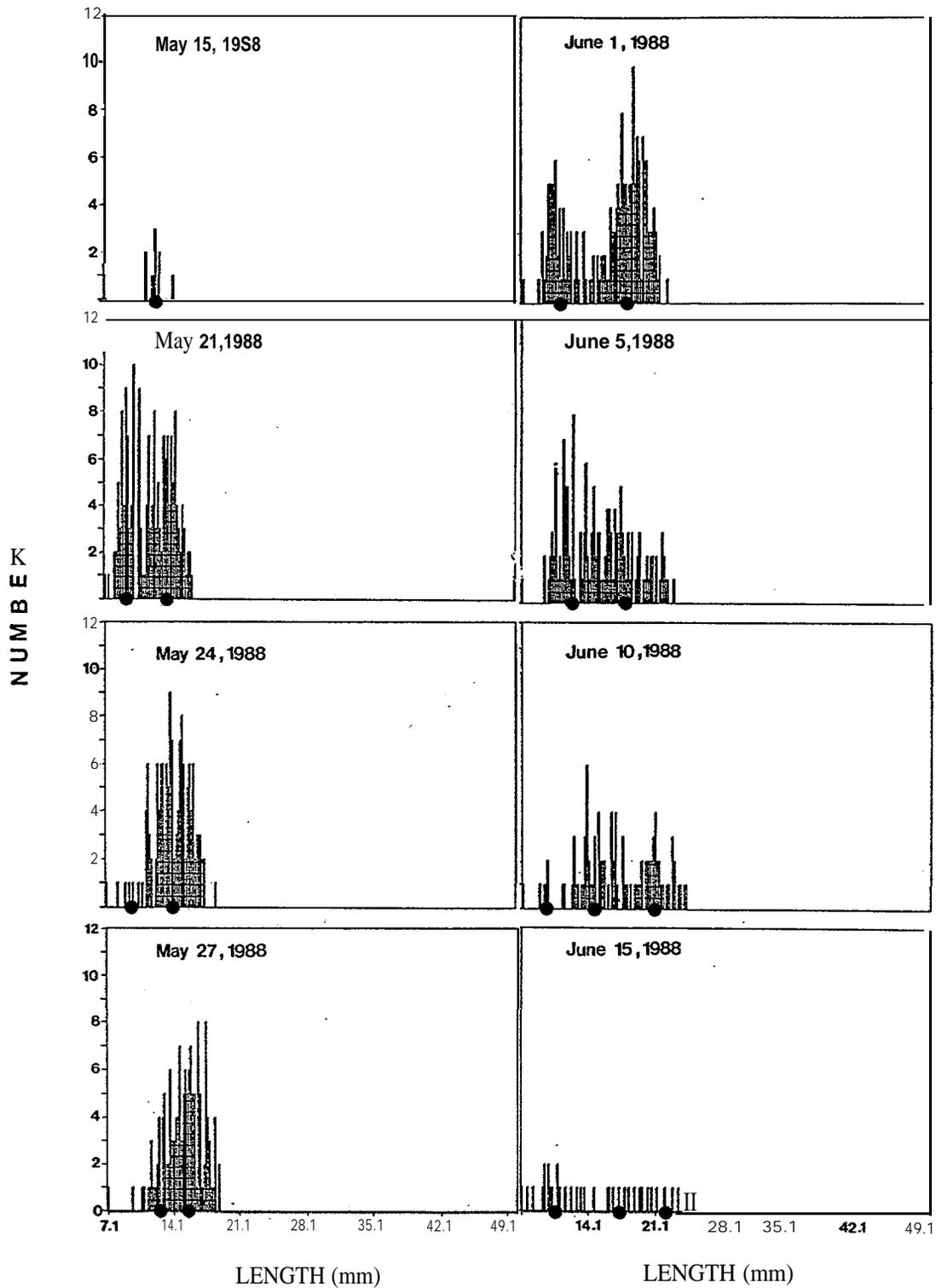
Nine samples of juvenile herring were taken in Auke Bay from August 14 to 25 (Appendix B). Eight of these samples were taken with a dipnet off the Government dock and 1 was taken by beach seining on the western shore of Spuhn Island by personnel of the Auke Bay Laboratory as part of their regular monthly sampling for salmonid fry. It was donated to this study by Alex Wertheimer (Auke Bay Laboratory, NOAA, Auke Bay). Collections of juveniles were taken as soon as they appeared in schools near the surface at the Government dock. I first observed them on August 14, but subsequent interviews indicated that they had appeared at the Auke Bay Laboratory dock 2 days earlier (personal communication, Bruce Wing, Auke Bay Laboratory, NOAA, Auke Bay). Attempts had been made since August 1 to capture juveniles with a purse seine set from the research vessel **Envirocon IV**, but no schools had been seen in Auke Bay until August 14. Juvenile sampling stopped after August 25 because the fish grew too large to catch them with a dipnet. The larger they grew, the deeper they swam and by August 25 they regularly swam below 1 m depth.

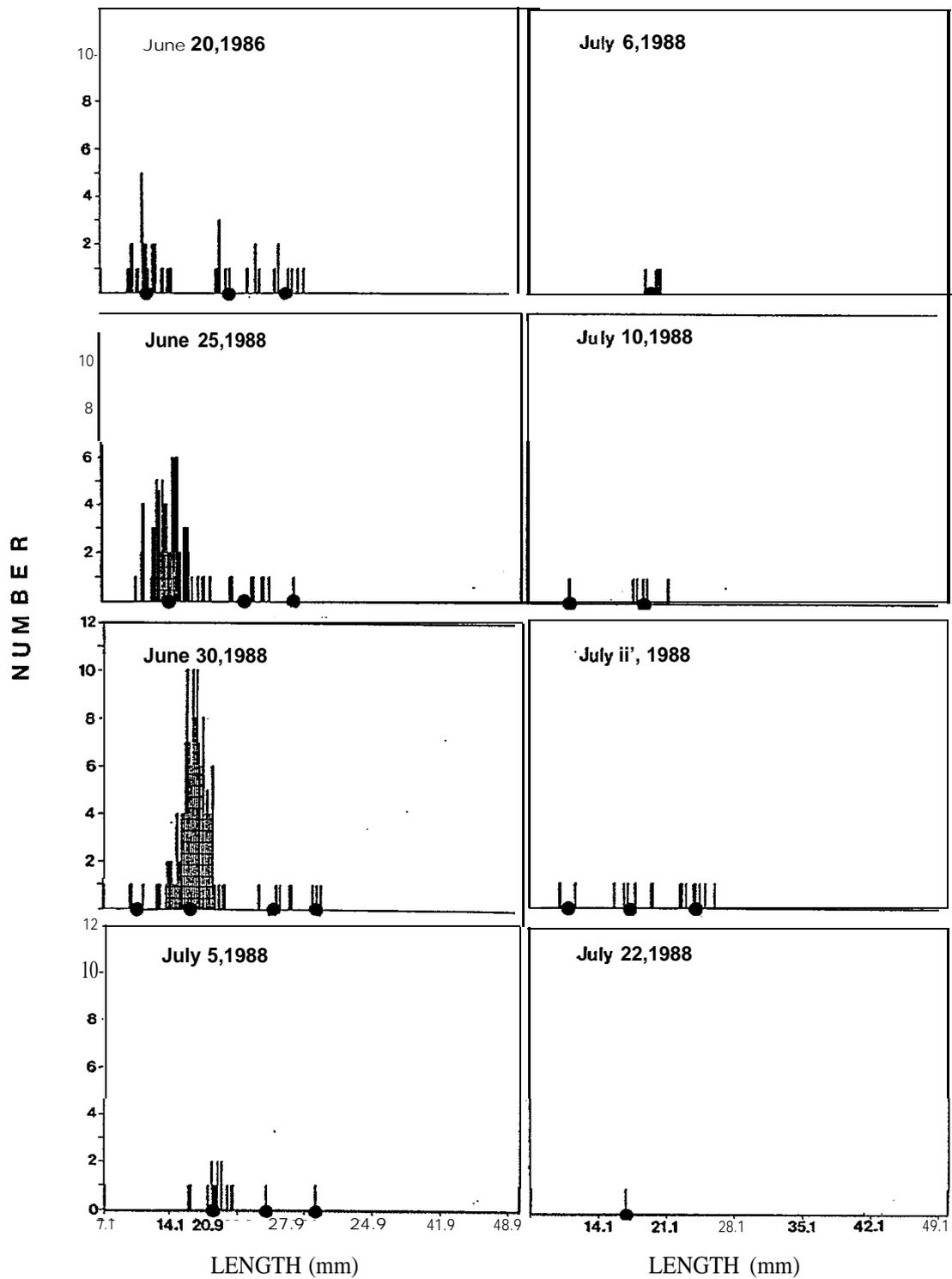
### 8.2 **Number and Timing of Cohorts**

The length frequency plots of the samples of larval and juvenile herring presented in Fig. 11 indicated that at least 5 cohorts hatched in Auke Bay in 1988. This is almost certainly the total number of cohorts in Auke Bay in

**Figure 11: LENGTH FREQUENCIES OF HERRING LARVAE AND JUVENILES**

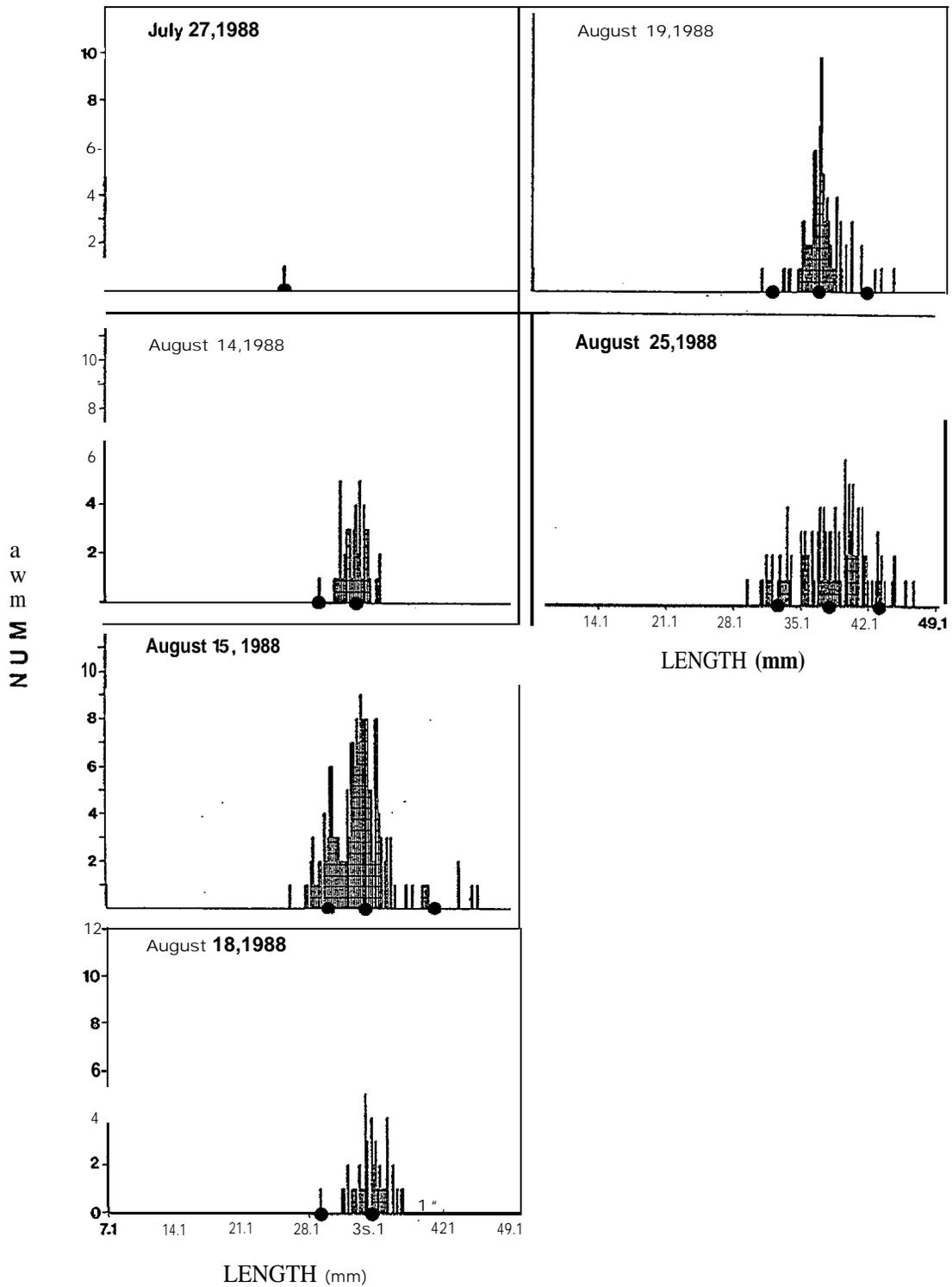
**NOTES:** -five cohorts of herring are evident as modes  
 - mean lengths are indicated by closed circles





**Figure 11 (cont.): LENGTH FREQUENCIES OF HERRING LARVAE AND JUVENILES**

**NOTES:** -five cohorts of herring are evident as modes  
 -mean lengths are indicated by dosed circles ;



**Figure 11(cont.):** LENGTH FREQUENCIES OF HERRING LARVAE AND JUVENILES

**NOTES:** -five cohorts of herring are evident as modes  
 - mean lengths are indicated by dosed circles

1988. It is unlikely that any other cohorts hatched before April because no large larvae were captured in the April plankton samples that were not clearly identified as cohort 1 larvae. It is unlikely that any other cohorts hatched in late July because spawnings at that late date are far outside the range associated with southeast Alaska: mid-January to June (Hay 1985). Only herring in Kotzebue Sound (Hay 1985) and in the Beaufort Sea (Ratynski 1983) are recorded as spawning in late July and August.

Spawning dates of cohorts 2 and 3 are known from ADFG aerial surveys and from personal communication with Auke Bay residents. Hatching dates of cohorts 2 and 3 were then forward-calculated from the spawning dates using average daily surface water temperatures in Auke Bay and Alderdice and Velsen's (1971) equation (Tables 4 and 5). The estimation of spawning and hatching dates of cohorts 1 and 4 proceeded in a reverse manner; hatching dates were back-calculated from the growth models presented in Fig. 12 and then spawning dates were back-calculated from hatching dates using average daily surface water temperatures and Alderdice and Velsen's (1971) equation (Tables 8 and 9). This procedure assumed that the average length of yolk sac larvae was the same for all 4 cohorts. The mean length ( $\pm 1$  SD, N) of yolk sac larvae listed in Appendix C was 8.8 ( $\pm 0.3$ , 20). Herring larvae take an average of 5 d to completely resorb the yolk at 6 to 10°C (McGurk 1984b). Therefore, it was assumed that the hatching dates were 2.5 d previous to the dates at which length was predicted to have been 8.8 mm.

Table 10 shows that the mean ( $\pm 1$ SD) period of time between spawning events in Auke Bay in 1988 was 19.0 ( $\pm 3.8$ ) d and that the mean ( $\pm 1$ SD) period of time between hatching events was 16.5 ( $\pm 4.6$ ) d. The difference between the two means is not statistically significant ( $P > 0.05$ , t-test). Table 10 also shows close agreements between the dates of spawning of cohorts 2 and 3 estimated from spawn surveys and the dates of spawning estimated from back-calculation from the hatching date predicted by the growth models. Close agreements also exist between the hatching dates of cohorts 2 and 3 forward-calculated from the spawning date, and the dates back-calculated from the growth models.

TABLE 8

**Development rate of cohort 1 herring eggs.**

<u>Date</u>	<u>Surface Water Temperature (°C)</u>			<u>Egg Development Rate (%·d<sup>-1</sup>)</u>			<u>Cumulative Egg Development (%)</u>		
	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>	<u>Mean</u>	<u>Low</u>	<u>High</u>
06 May	9.0	8.2	10.0	6.599	5.926	7.482	100.000	100.000	100.000
05 May	8.9	8.4	10.1	6.513	6.091	7.573	93.401	94.074	92.518
04 May	8.1	7.5	9.1	5.844	5.362	6.685	86.889	87.983	84.945
03 May	7.5	7.2	7.7	5.362	5.127	5.521	81.045	82.621	78.261
02 May	7.0	7.0	7.0	4.973	4.973	4.973	75.683	77.494	72.740
01 May	7.8	7.8	7.8	5.601	5.601	5.601	70.710	72.520	67.767
30 April	7.6	7.6	7.6	5.441	5.441	5.441	65.109	66.920	62.166
29 April	7.5	7.2	7.8	5.362	5.127	5.601	59.668	61.479	56.725
28 April	7.6	7.0	7.0	5.441	4.973	4.973	54.306	56.351	51.124
27 April	7.8	7.2	8.1	5.601	5.127	5.844	48.865	51.378	46.151
26 April	8.5	7.4	8.9	6.175	5.283	6.513	43.264	46.251	40.307
25 April	7.6	7.6	7.6	5.441	5.441	5.441	37.089	40.968	33.794
24 April	7.4	7.4	7.4	5.283	5.283	5.283	31.648	35.527	28.353
23 April	7.3	7.3	7.3	5.205	5.205	5.205	26.365	30.243	23.070
22 April	7.7	5.9	8.9	5.521	4.159	6.513	21.160	25.038	17.865
21 April	6.5	6.3	6.9	4.596	4.449	4.897	15.639	20.879	11.352
20 April	<b>7.0</b>	5.6	8.6	4.973	3.947	6.258	11.043	16.430	6.455
19 April	6.2	5.9	6.9	4.376	4.159	4.897	6.070	12.483	0.197
18 April	6.2	6.2	6.2	4.376	4.376	4.376	1.694	8.324	-4.700
17 April	6.1	6.1	6.1	4.303	4.303	4.303	-2.682	3.948	-9.076
16 April	6.0	<b>6.0</b>	6.0	4.231	4.231	4.231	-6.985	-0.355	-13.379

Notes:

1. Development rate (%·d<sup>-1</sup>) = 0.7648 + 0.4367T + **0.0235T<sup>2</sup>**.
2. Hatching date estimated as May 6 from back-calculation of **Gompertz** growth curve.

**TABLE 9**

Development rate of cohort 4 herring eggs.

<u>Date</u>	<u>Surface Water Temperature ("C)</u>			<u>Egg Development Rate (%·d<sup>-1</sup>)</u>			<u>Cumulative Egg Development (%)</u>		
	<u>Mean</u>	Low	<u>High</u>	<u>Mean</u>	Low	<u>High</u>	<u>Mean</u>	Low	<u>High</u>
25 June	11.0	11.0	11.0	8.412	8.412	8.412	100.000	<b>100.000</b>	100.000
24 June	11.0	11.0	11.0	<b>8.412</b>	8.412	8.412	91.588	91.588	91.588
23 June	11.0	9.9	11.5	8.412	7.391	8.895	83.176	<b>83.176</b>	83.176
22 June	11.8	11.8	11.8	9.190	9.190	9.190	74.764	75.785	74.218
21 June	12.7	11.7	13.6	10.101	9.091	11.050	65.574	66.595	65.091
20 June	10.8	10.3	11.2	8.222	7.756	8.604	55.473	57.504	54.041
<b>19 June</b>	11.0	11.0	11.0	8.412	8.412	8.412	47.251	49.748	45.437
18 June	11.2	11.2	11.2	8.604	8.604	8.604	38.839	41.336	37.025
17 June	11.4	11.4	11.4	8.797	8.797	8.797	30.235	32.732	28.421
16 June	11.5	10.6	12.0	8.895	8.034	9.389	21.438	23.935	19.624
15 June	12.4	11.7	13.3	9.793	9.091	10.730	12.543	15.900	10.235
14 June	13.5	13.0	14.0	10.943	10.413	11.485	2.760	6.809	-0.495
13 June	12.0	11.7	12.3	9.389	9.091	9.692	-8.193	-3.604	-11.979

Note:

1. Development rate (**%·d<sup>-1</sup>**) = 0.7648 + 0.4367\*T + **0.0235\*T<sup>2</sup>**.
2. Hatching date estimated as May 6 from back-calculation of Gompertz growth curve.

TABLE 10

Spawning and hatching dates of 4 cohorts of Auke Bay herring.

Cohort	Date of Spawning			Date of Hatching		
	Spawning Survey	Back-Calculation from Hatch Date	Interval Duration	Forward-Calculation from Spawning Date	Back-Calculation Growth Models	Interval Duration
1		April 18			May 6	
2	May 6	May 7	18.5	May 18	May 19	12.5
3	May 29	May 30	23.0	June 9	June 10	21.5
4		June 14	<u>15.5</u>		June 25	15.5
		Mean	19.0		Mean	16.5
		SD	3.8		SD	4.6
		N	3		N	3

Notes:

1. Hatching dates of cohorts 1 and 4 were back-calculated from Gompertz growth curves assuming length at 8.8 mm is equal to hatching date plus 2.5 days; spawning date back-calculated from hatching date and average daily surface water temperatures in Auke Bay using Alderdice and Velsen's (1971) incubation-temperature relation.
2. Hatching dates of cohorts 2 and 3 forward-calculated from spawning dates and average daily surface water temperatures in Auke Bay using Alderdice and Velsen's (1971) incubation-temperature relation; spawning dates estimated by observation by ADFG overhead flights and reports of Auke Bay residents.
3. Dashes indicate no data.

### 8.3 **Population** Growth in Length

Herring larvae were corrected for shrinkage due to capture using Gompertz models (**McGurk 1985 b**). No corrections to lengths were made for shrinkage due to fixation and preservation in **formalin** because formalin-preserved length is the standard to which all other lengths are adjusted. In the absence of experimental data on the effect of alcohol preservation on length of Pacific herring over the range of 9 to 45 mm, I compared mean lengths of pairs of **formalin-** and alcohol-preserved samples of herring larvae and juveniles of the same cohort captured on the same dates at the same stations within 4 h of each other. Forty six pairs of larval means and 7 pairs of juvenile means were taken from Appendix C and plotted against each other.

A linear regression of **alcohol-preserved** mean length of larvae on **formalin-** preserved mean length

$$(33) \quad Y = -0.133 + 1.044X$$
$$r^2 = 11.90, n = 53, SEb = 0.047, P < 0.001$$

was highly significant, but the slope was not significantly higher than **1.0 (P>0.05)**. Despite this finding, I believe that adjustment of **alcohol-** preserved larvae to the formalin-preserved standard is necessary because there are more points above the line of equality than there are below it, and most "authors who have examined the effect of alcohol on length of fish larvae in experimental conditions have found that it causes less shrinkage than formalin, e.g. **McGurk (1984a)**. Therefore, the regression was rearranged as

$$\text{Adjusted length} = (\text{measured length} + 0.133)/1.044$$

and all alcohol-preserved larvae had their lengths recalculated with this equation as is shown in Appendix C.

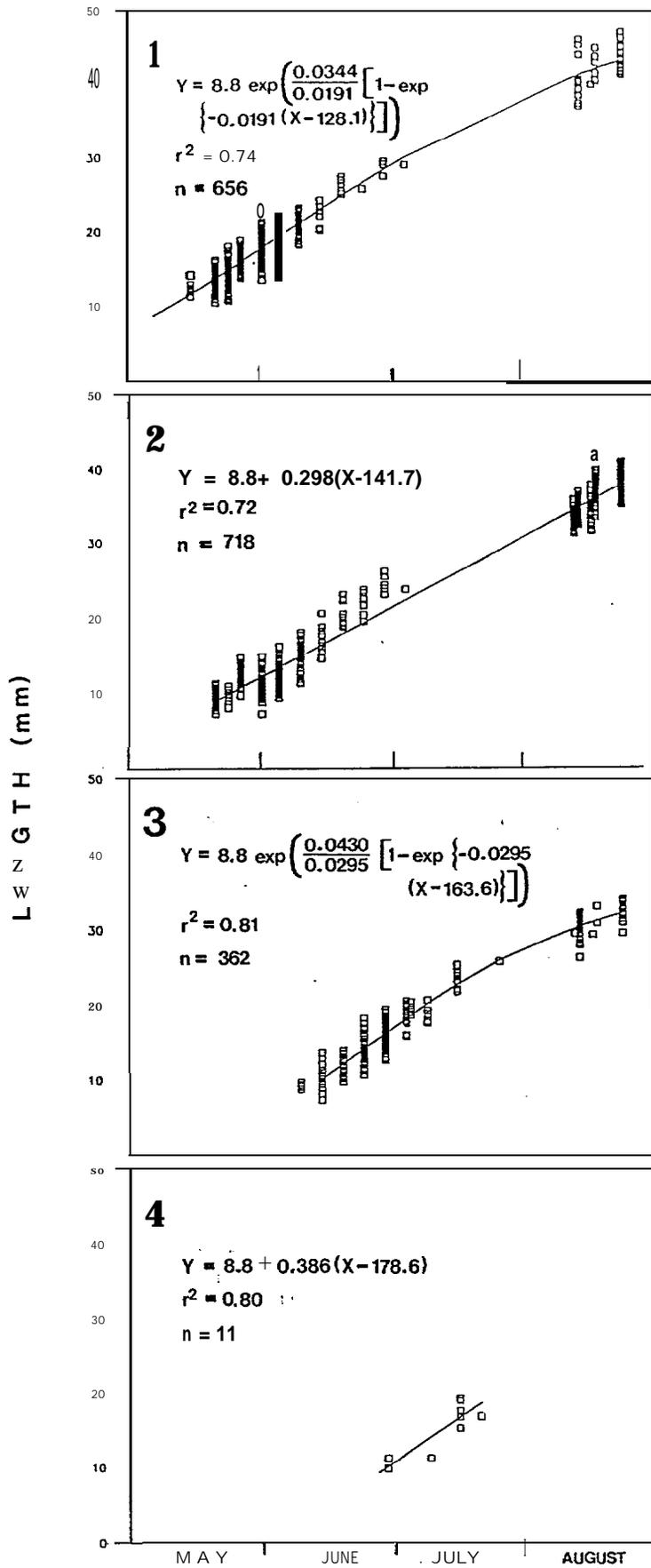
Modified models of growth in length were fit to the lengths-at-date of Appendix C for cohorts 1, 2, 3 and 4 (Fig. 12). There were too few cohort 5 data to fit any kind of growth model. All of the models were highly significant, but the von Bertalanffy and logistic models explained less variance than either the Gompertz or the linear model so they were not considered any further. The Gompertz model best fit the length data of cohorts 1 and 3 and the linear model best fit the length data of cohorts 2 and 4.

In order to compare growth between the 4 cohorts. I assumed that growth was essentially linear from hatch to metamorphosis in all 4 cohorts. Since length at  $t_0$  was set at 8.8 for all cohorts, the coefficient of growth of the linear model was used to make simple comparisons between the cohorts.

**Covariance** analysis with dummy variables showed that there were no significant differences in the coefficient between any of the cohorts. The average value for all herring larvae and juveniles in Auke Bay in 1988 was  $0.306 \text{ mm}\cdot\text{d}^{-1}$  (SE=0.003, N=1747).

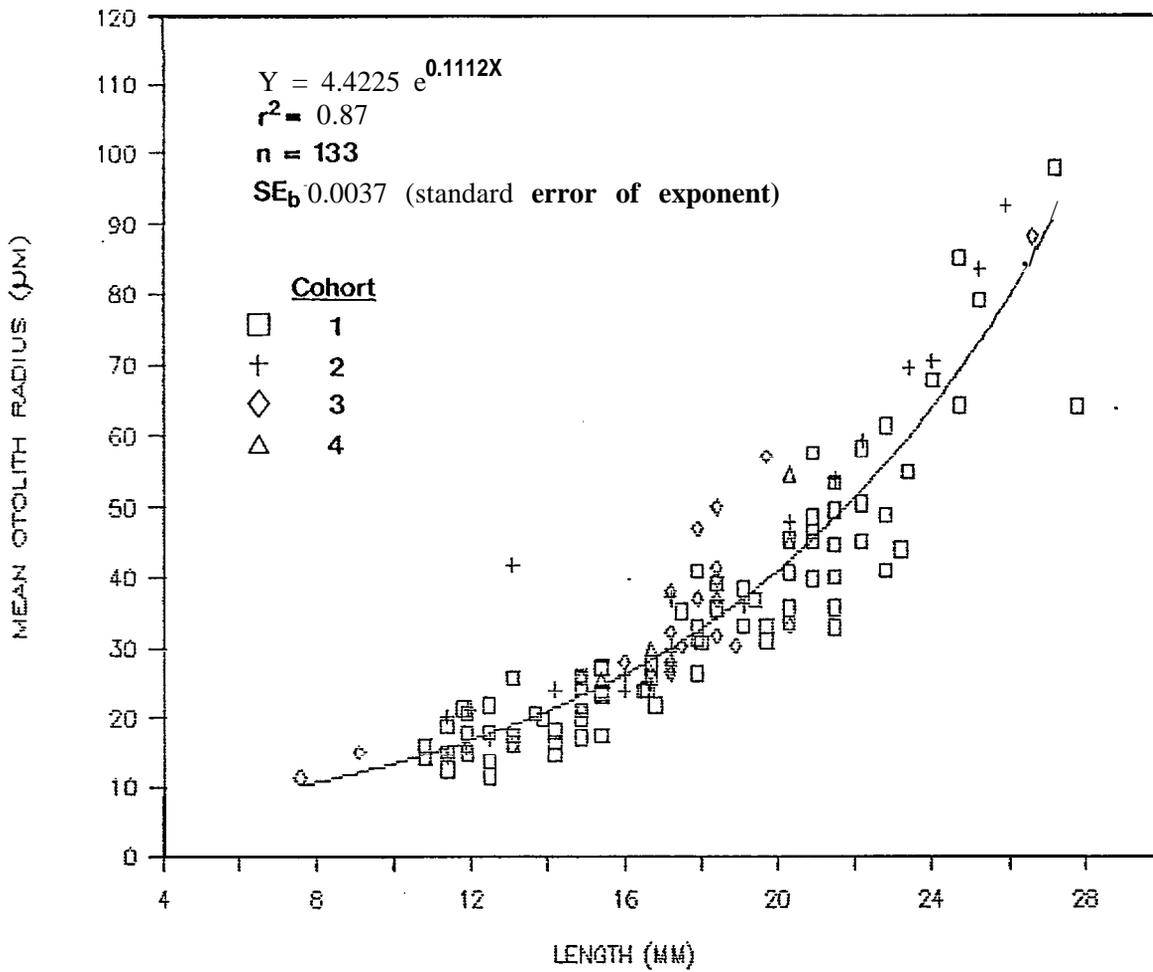
#### 8.4 **Otolith** Radius and **Ring** Number

The radii of the two **sagittal otoliths**, the number of rings in each **otolith**, and the widths of the outer four rings of **each** sagitta are listed in Appendix F. In order to calculate specific growth rates from the widths of the individual **otolith** rings it was necessary to develop a relationship between **otolith** radius and fish length. **Covariance** analysis with dummy variables showed that there were no significant differences between cohorts in their intercepts and slopes so a single linear regression of **ln(radius)** on fish length was calculated for the combined data of cohorts 1 to 4 (Fig. 13). This equation predicts that mean **otolith** radius is  $11.8 \mu\text{m}$  at a fish length of 8.8 mm, the average length of yolk sac larvae before the deposition of the first ring. Rearranging the equation gives



**Figure 12**  
**GROWTH IN LENGTH OF HERRING LARVAE AND JUVENILES OF COHORTS 1,2,3 AND 4**

NOTE  
Solid lines are Gompertz (cohorts 1 and 3) or linear (cohorts 2 and 4) growth models



**Figure 13: REGRESSION OF MEAN OTOLITH RADIUS ON LENGTH OF HERRING LARVAE**

$$(34) \quad Y = 8.9928 (\ln X - 1.4867)$$

where Y = fish **length** (mm) and X = **otolith** radius ( $\mu\text{m}$ ).

**Covariance** analysis with dummy variables was also used to examine differences between cohorts in the relationship between **otolith** number and age. Age was defined as the number of days between the hatching date (back-calculated from the population growth curves) and the date of capture. There were no differences between cohorts, so a single regression was calculated

$$(35) \quad Y = -2.96 + 0.84X$$
$$r^2 = 0.73, n = 128, P < 0.001, SE_b = 0.05$$

where Y = mean number of rings for a fish, X = age (d), and SE<sub>b</sub> = standard error of the ring deposition rate. The rate was not significantly ( $P > 0.05$ , t-test) different from 1.0. Equation (35) predicts that the first ring was completely deposited at an average age of 5 d after hatch. A comparison of the mean number of rings at date of capture and the number of rings predicted from equation (35) for cohorts 1 to 4 shows (Fig. 14) a close agreement between measured and predicted ring number.

### 8.5 **Weight-Length** Relations

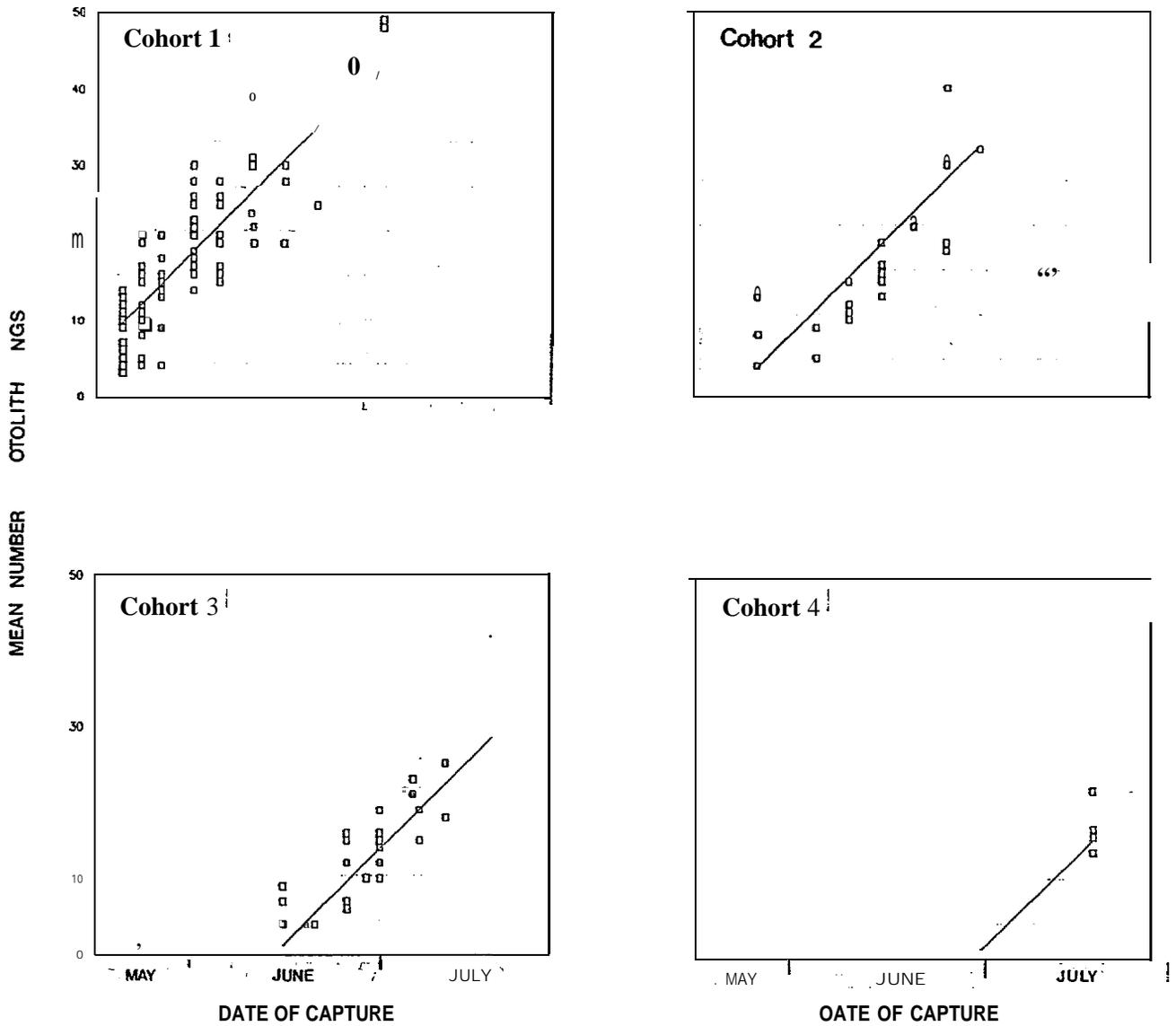
The logistic model provided the best fit to the weight-length data for cohorts 1 to 4 individually and for the combined data of cohorts 1 to 5. The 4 parameters of the logistic model are indistinguishable between cohorts, so only the fit to the combined data is shown in Fig. 15. This curve was used to calculate relative condition factor.

### 8.6 **Specific Growth Rates**

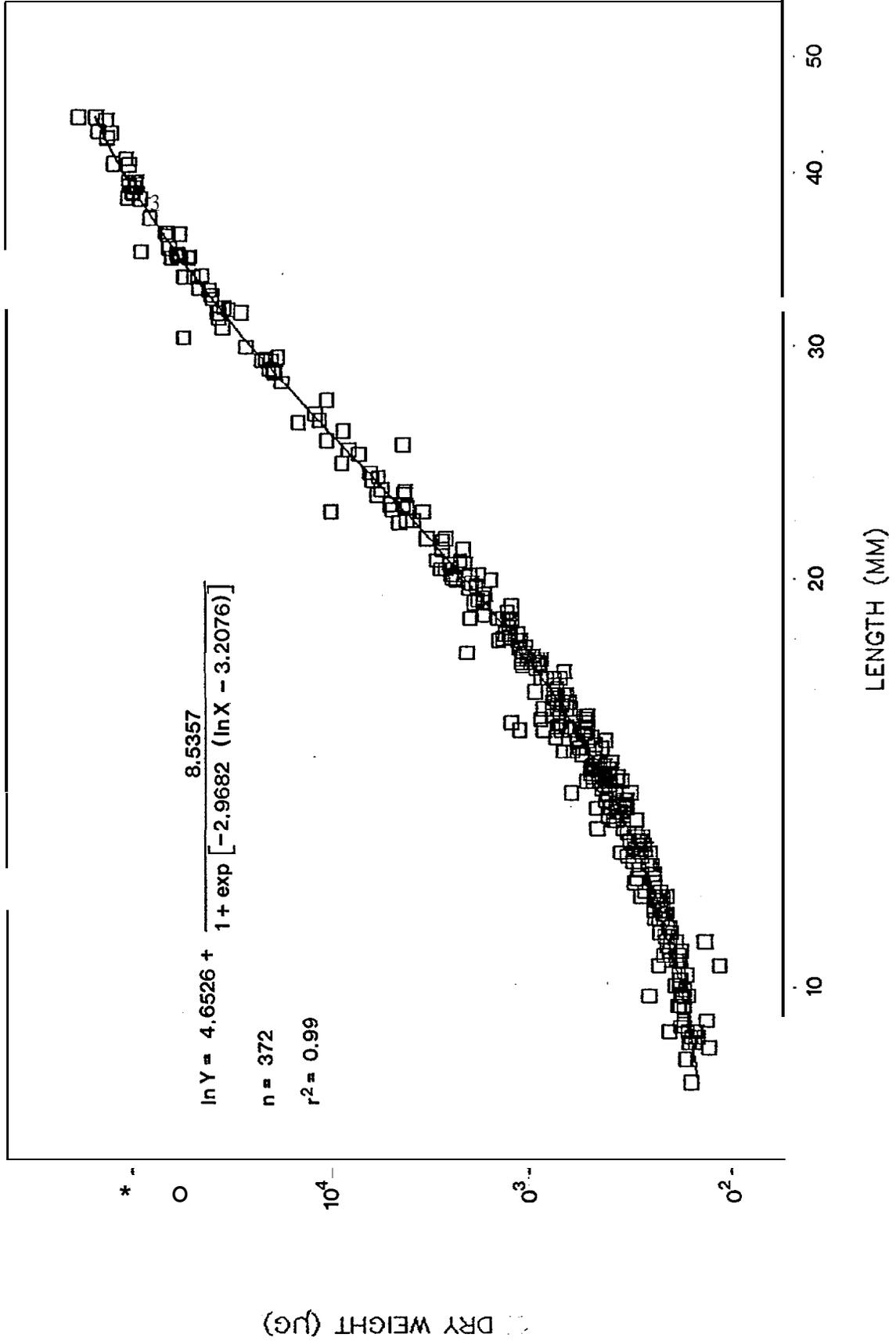
Specific growth rates calculated from the outermost rings in the **sagittal otoliths** are shown in Appendix F. They were **highly** correlated with each

**Figure 14: MEAN NUMBER OF OTOLITH RINGS PER FISH AT DATE OF CAPTURE**

NOTE: Solid lines are mean number of rings predicted from age of larvae using equation (3S)



**Figure 15: LOGISTIC REGRESSION OF DRY WEIGHT ON LENGTH OF HERRING LARVAE AND JUVENILES OF COHORTS 1,2,3,4 AND 5 COMBINED**



other ( $r=0.90$  to  $0.98$ ), so only the growth rates calculated from the **outermost ring**,  $G_w$ , are used in the following analyses. The dome-shaped relationships between  $G_w$  and date of capture for cohorts 1 and 3 in Fig. 16 suggests the presence of a dome-shaped relationship between  $G_w$  and age similar to that reported by Oiestad (1983, cited by Kiorboe and Munk 1986) for Atlantic herring larvae. However, the apparent absence of such a relationship in cohort 2 suggests the presence of a second factor, perhaps a relationship between  $G_w$  and prey concentration similar to that reported by Kiorboe and Munk (1986) for Atlantic herring larvae. Response surface analysis identified the following equation as explaining the maximum variance of  $G_w$  with all-significant ( $0.01 < P < 0.05$ ) coefficients

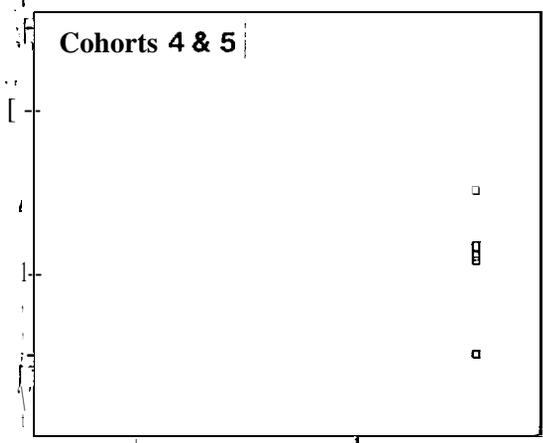
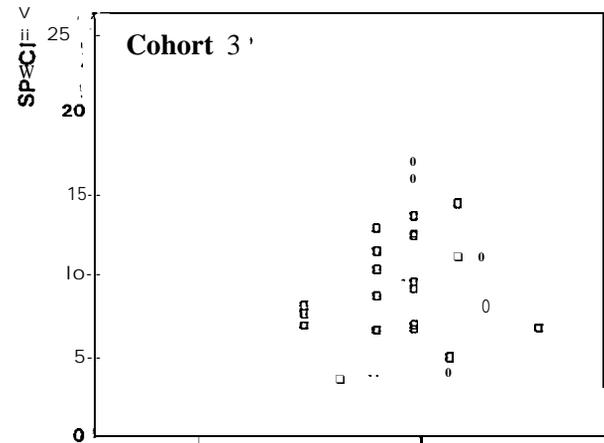
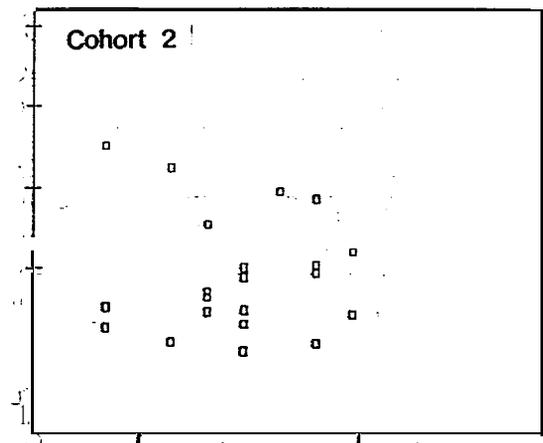
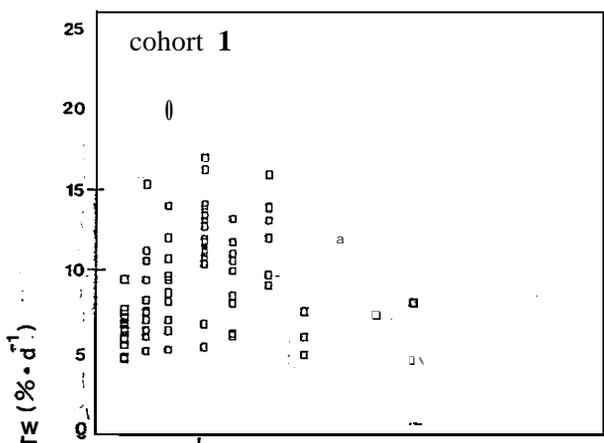
$$(36) \quad Y = -1.8231 + 0.3919X_1 - 0.0062X_1^2 + 1.5820X_2$$

$$r^2 = 0.13, n = 108, P = 0.003$$

where  $Y = G_w$  (%-d<sup>-1</sup>),  $X_1 =$  age (d) of larvae and  $X_2 = \ln[\text{mean prey concentration (mg dry weight} \cdot \text{m}^{-3}\text{)}]$ . Age and  $\text{age}^2$  explained 9% of the variance in  $G_w$  and  $\ln(\text{prey concentration})$  explained the remaining 4%. The residuals of this equation were not significantly ( $P > 0.05$ ) correlated with mean temperature of the upper 20 m of the water column. Equation (36) predicts that  $G_w$  is maximal at an age of 32 d.

The absence of a significant relationship between  $G_w$  and temperature, and the low level of variance in  $G_w$  explained by age and prey concentration, was due to a lack of contrast in the environmental data. Mean temperatures of the upper 20 m of the water column from May 21 to June 25 fell within a narrow range of only 7.2 to 8.2°C (Fig. 4), and although mean prey concentrations ranged from 20.7 to 171.8 mg dry weight  $\cdot$  m<sup>-3</sup>, the increase in  $G_w$  over this range of prey concentrations that is predicted from laboratory rearing studies is **only about 3%·d<sup>-1</sup>**. Fig. 17A compares  $G_w$  of Auke Bay herring larvae with that predicted by Kiorboe and Munk's (1986) regression model of  $G_w$  on  $\ln(\text{prey concentration})$  for Atlantic herring larvae; it is clear that  $G_w$  increases with prey concentration over the 20

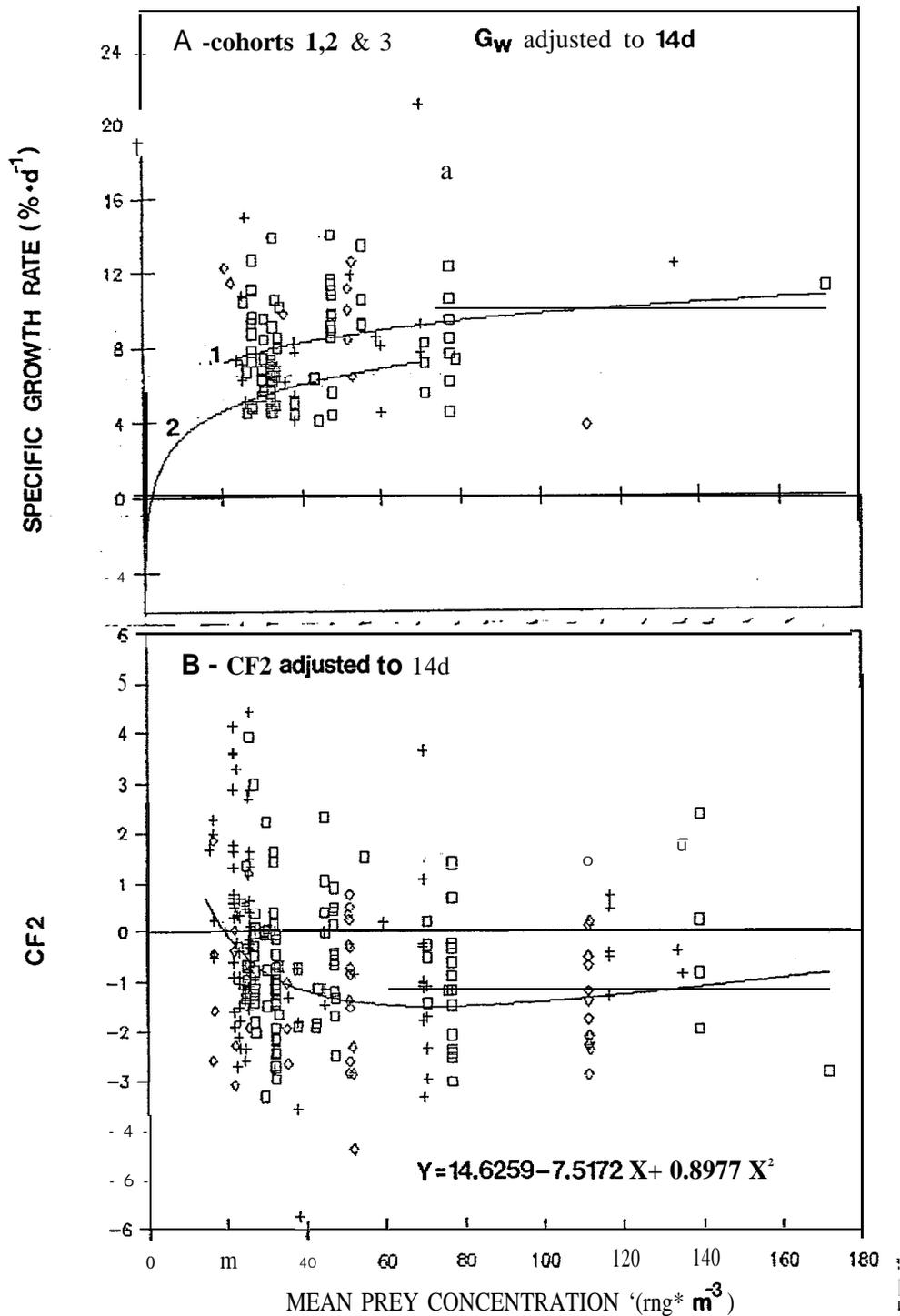
**Figure 16: SPECIFIC GROWTH RATE OF HERRING LARVAE  
CALCULATED FROM THE WIDTH OF THE OUTERMOST  
OTOLITH RING AT DATE OF CAPTURE**



DATE OF CAPTURE

DATE OF CAPTURE

Figure 17. (A) Specific growth rates of herring larvae of cohorts 1, 2, 3 and 4 as a function of mean prey concentration at date. Symbols as in Fig. 13. Growth rates were adjusted to those expected of a 14 d old larvae as explained in the text. Curve number 1 is specific growth rate predicted by equation (36) for a 14 d old larva. Curve number 2 is relationship reported by Kiorboe and Munk (1986) for laboratory-reared Atlantic herring larvae:  $Y = -1.36 + 2.00 \ln X$ . (B) morphometric condition factor CF2 as a function of mean prey concentration. CF2 values adjusted to those expected of a 14 d old larvae. Curve is CF2 predicted for a 14 d old larvae from equation (37).



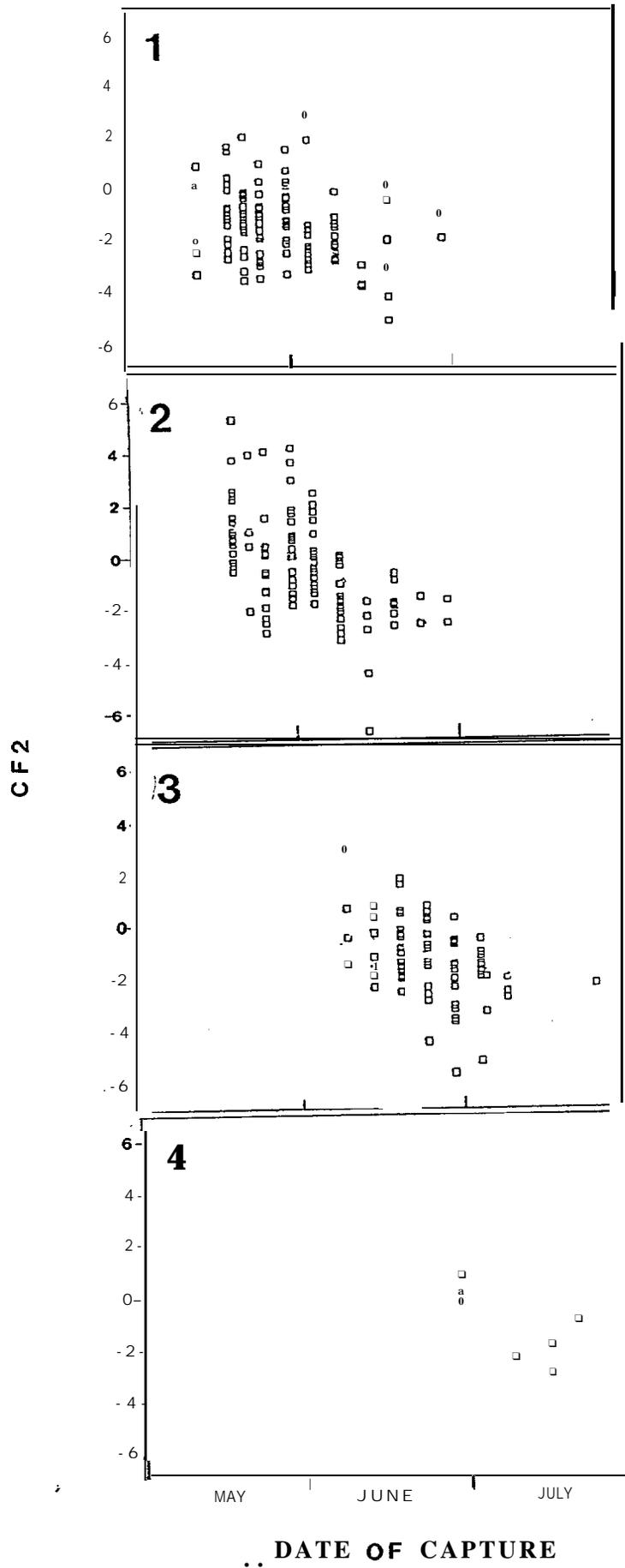
to  $170 \text{ mg} \cdot \text{m}^{-3}$  range at a much slower rate than it does over the 1 to  $20 \text{ mg} \cdot \text{m}^{-3}$  range.

[n order to compare growth rates of Auke Bay herring larvae with those predicted by Kiorboe and Munk (1986) it was necessary to adjust the former to those of a 14 d old larvae because Kiorboe and Munk's (1986) model was developed from 1 to 3 week old fish.  $G_w$  was adjusted by multiplying it by the ratio of  $G_w$  predicted for an age of 14 d and prey concentration ( $X_2$ ) by equation (36) to  $G_w$  predicted for age ( $X_1$ ) and prey concentration ( $X_2$ ) by equation (36). Over the prey concentration range of 20 to  $70 \text{ mg} \cdot \text{m}^{-3}$   $G_w$  of Auke Bay larvae was  $2.3\% \cdot \text{d}^{-1}$  higher on average, than that predicted by Kiorboe and Munk's (1986) model, which suggests that Auke Bay herring larvae may have been feeding on high density patches of prey that were not measured by plankton tows that integrated the upper 30 m of the water column.

## 8.7 Condition

The two condition factors are listed in Appendix E. Response surface analysis indicated that there were no significant correlations between CF1 and age,  $\ln(\text{mean prey concentration})$  and mean water temperature. Therefore, this condition factor was not examined further.

Unlike CF 1 there is substantial variation between cohorts in the trajectory of CF2 with date of capture (Fig. 18). The average condition of 0 to 10 d old larvae from cohort 2 was much lower (i.e. high CF2) than that measured for young larvae of cohorts 1 and 3. Since the mean date of hatch of cohort 2 (May 19) preceded the general decrease in concentration of prey that occurred between "May 27 and June 10, this observation suggests a direct relationship between CF2 and prey concentration. Another factor to be considered is age, because CF2 clearly decreases with age in all cohorts.



**Figure 18**

**CONDITION FACTOR**  
**CF2 ON DATE OF**  
**CAPTURE FOR HERRING**  
**LARVAE OF COHORTS**  
**1,2,3 AND 4**

Response surface analysis of age, prey concentration, and water temperature identified the following equation as explaining the maximum variance in CF2 with all significant (**0.001<P<0.01**) coefficients

$$(37) \quad Y = 15.6885 - 0.0759X_1 - 7.5172X_2 + 0.8977X_2^2$$

$$r^2 = 0.29, n = 261, P < 0.001$$

where  $Y = \text{CF2}$ ,  $X_1 = \text{age (d)}$ , and  $X_2 = \ln[\text{mean prey concentration (mg dry weight} \cdot \text{m}^{-3})]$ . Age accounted for 24% of the condition of CF2 and mean prey concentration **accounted** for the remaining 5% of the explained variation. CF2 was adjusted **to** an age of 14 d by adding to it the product of the coefficient for age of equation (37) and the difference between age and 19 d, i.e. **0.0759·(age-14)**. These adjusted **CF2's** are plotted against prey concentration in Fig. **17B**; **CF2** is predicted by equation (37) to enter the starving class at prey concentrations below **21.6 mg·m<sup>-3</sup>**.

## 9.0 DISCUSSION - GROWTH OF HERRING LARVAE AND JUVENILES

### 9.1 **Number** and Timing of Cohorts

The number of cohorts of Pacific herring identified in Auke Bay in 1988, 5, is the highest yet to be reported in one season at a single location. Jones (1978) reported only 2 cohorts per season in Auke Bay in 1975 and 1976, both Stevenson (1962) and McGurk (1987a, b) identified 3 separate cohorts per season of Pacific herring larvae in Barkley Sound, Vancouver Island, British Columbia, and Iizuka (1966) reported 2 cohorts per season in Akkeshi Bay, Hokkaido Island, Japan.

I attribute the difference in number of cohorts between this study and Jones' (1978) study to unknown biological factors, and not to problems related to sampling and data analysis. Jones (1978) sampled Auke Bay **with** plankton nets over the entire herring larvae season: from March 7 to August 28 in 1975 and from March to the end of July in 1976, so if there were more than 2 cohorts he would have captured them. Although he did not use length-frequency analysis to classify his larvae into cohorts, the standard deviations of the mean lengths of his larvae are similar to those calculated in this study, indicating that he classified his larvae at least as accurately as I did mine. Jones (1978) did not present his raw data in a form that would allow re-analysis using **NORMPC**.

Five cohorts of larvae per season are not **uncom** mon in Atlantic herring. Lambert (1984) reviewed the evidence concerning **larval** cohort succession in this species and reported that 6 to 12 cohorts of Atlantic herring larvae were identified in catches from St. Mary's Bay, Nova Scotia, over a 7 mo period, and 3 to 8. cohorts from St. **Georges'** Bay, Nova Scotia, over a 6 mo period.

Maximum density of herring larvae in Auke Bay in 1988 occurred at or before May 25 (Table 11), which is the earliest date for maximum density that has

TABLE 11

Approximate dates of maximum density of Auke Bay herring larvae in relation to mean surface water temperature. The **early** date for 1988 is associated with **higher** temperatures.

<u>Year</u>	Date of Maximum Density of Herring Larvae	<u>Mar. 1-14</u>			<u>Mar. 15-31</u>			<u>Apr. 1-14</u>			<u>Apr. 15-30</u>			<u>May 1-14</u>			<u>May 15-31</u>			<u>Reference</u>
		<u>Mean</u>	<u>SD</u>	<u>n</u>	<u>Mean</u>	<u>SD</u>	<u>n</u>	<u>Mean</u>	<u>SD</u>	<u>n</u>	<u>Mean</u>	<u>SD</u>	<u>n</u>	<u>Mean</u>	<u>SD</u>	<u>n</u>	<u>Mean</u>	<u>SD</u>	<u>n</u>	
1988	May 21	4.00	-	1	4.37	0.16	5	4.68	0.21	8	6.91	0.56	10	8.84	0.99	7	9.95	0.80	12	1
1987	June 2				4.05	0.24	4	5.53	0.12	3	5.39	0.49	6	7.60	0.86	3	8.34	0.76	4	2
1986	June 2				3.55	0.36	5	3.45	0.21	4	4.25	0.35	4	7.56	0.62	7	8.19	0.74	4	3
1976	June 1							2.90	0.80	2	5.30	1.60	3	5.20	0.10	2	6.50	0.50	2	4
1975	June 5							3.10	1.10	2	6.40	-	1	6.30	0.60	2	8.60	0.90	2	4

Note:

1. References: 1 = this study, 2 = Haldorson et al. (1988), 3 = Haldorson et al. (1987), 4 = Jones (1978).
2. Date of maximum density of herring larvae is an index of the date of first spawning.

ever been recorded in Auke Bay; it is at least 11 to 15 d earlier than the dates reported for 1975 and 1976 by Jones (1978), and 12 d earlier than the dates reported for 1986 and 1987 by Haldorson et al. (1987, 1988). This relatively early date of maximum density is associated with higher average surface water temperatures in April and May 1988 than in previous years, although there are no significant ( $P > 0.05$ ) correlations between dates of maximum density and mean temperatures for biweekly and monthly intervals from March 1 to May 31, probably because of low sample sizes. This observation is supported by Hay (1985), who reported highly significant inverse correlations between the mean time of spawning of Pacific herring in the Strait of Georgia and the mean surface water temperatures in March for the years 1951 to 1982. On average, an increase in mean March temperature of  $1^{\circ}\text{C}$  corresponded to a decrease in the mean date of spawning of 6 to 14 d in the Strait, a relationship that is similar to that observed in this study if one assumes that the date of first spawning and the date of maximum density of herring larvae are separated by a constant interval of time.

The mean ( $\pm 1\text{SD}$ ) spacing in time between **hatchings** of herring cohorts in Auke Bay, 16.5 ( $\pm 4.6$ ) d, is lower than the mean ( $\pm 1\text{SD}$ ) spacing in time between **hatchings** of Pacific herring in Barkley Sound, Vancouver Island, reported by McGurk (1987a), 19.3 ( $\pm 8.5$ ) d, and it is lower than the mean ( $\pm 1\text{SD}$ ) spacing in time between **hatchings** of Atlantic herring reported by Lambert (1984), 17.5 ( $\pm 6.5$ ) d. However, the mean ( $\pm 1\text{SD}$ ) spacing in time between spawnings of Auke Bay herring, 19.0 ( $\pm 3.8$ ), is comparable with the latter two averages.

## 9.2 Growth in Length

The 4 major results of the analysis of population growth of Auke Bay herring larvae and juveniles: (1) linearity of growth in length over the larval stage; (2) average growth rates of  $0.31 \text{ mm}\cdot\text{d}^{-1}$ ; (3) an increase in growth rate of larvae **hatching** later in the season; and (4) a decrease in growth rate of juveniles, have **all been** reported by previous authors for Pacific herring of Alaska, British Columbia, and Japan. Jones (1978) estimated

growth rates of Auke Bay herring larvae of  $0.35 \text{ mm}\cdot\text{d}^{-1}$  in 1975 and 0.30 and  $0.50 \text{ mm}\cdot\text{d}^{-1}$  in 1976. He also reported that the growth rate of juveniles in 1976 slowed to  $0.27 \text{ mm}\cdot\text{d}^{-1}$ . Stevenson (1962) reported a growth rate of  $0.30 \text{ mm}\cdot\text{d}^{-1}$  for a Barkley Sound, Vancouver Island, cohort hatching in March 1950 and a rate of  $0.41 \text{ mm}\cdot\text{d}^{-1}$  for a cohort hatching in mid-April 1950. Iizuka (1966) reported rates of 0.21 and  $0.32 \text{ mm}\cdot\text{d}^{-1}$  for herring larvae of Akkeshi Bay, Hokkaido Island, Japan. McGurk (1987a) reported linear rates of 0.36, 0.39, 0.40 and  $0.41 \text{ mm}\cdot\text{d}^{-1}$  for larvae of Barkley Sound in 1981 and 1982. McGurk (1984b) summarized the literature on growth in length and weight of both Pacific and Atlantic herring larvae and reported that the growth rates of Atlantic herring larvae are similar to those of Pacific herring larvae, ranging from 0.16 to  $0.43 \text{ mm}\cdot\text{d}^{-1}$ .

### 9.3 Specific Growth Rates

This study is the first to measure recent growth rates of herring larvae from widths of otolith rings. It reports that approximately 9% of the variation in specific growth rate is due to a dome-shaped relationship between growth rate and age and 4% is due to an increase in growth rate with increasing prey concentration. The remaining 87% of the variation is due to natural variation in growth rate between fish and to errors of measurement.

The conclusion that the otolith radius - fish length relationship is the same for all 4 cohorts supports the conclusion that population growth rates were similar for all four cohorts. Reznick et al. (1989) and Secor and Dean (1989) recently reported that slower growing fish have larger otoliths than equal-sized, rapidly growing fish. Although they worked with guppies, Poecilia reticulata, and young striped bass, Morone saxatilis, respectively, they argued that the relationship is probably common to most species of fish including Pacific herring.

Daily ring formation in the otoliths of larval and juvenile fish appears to be a universal phenomenon (Campana and Neilson 1985). It has been reported in

wild populations of Pacific herring larvae (McGurk 1987a) and in laboratory-reared populations of Atlantic herring larvae (Lough et al. 1982, Messieh et al. 1987). However, less-than-daily rates are also a common occurrence; they have been reported in populations of wild Pacific herring larvae by McGurk (1987a) and in laboratory-reared populations of Pacific herring larvae (McGurk 1984a) and Atlantic herring larvae (Geffen 1982, Lough et al. 1982, Campana et al. 1987). Two hypotheses have been advanced to explain this phenomenon: (1) the rate of ring deposition is directly related to the rate of growth of the fish and a threshold rate of growth must be exceeded before rings are deposited at a daily rate (Geffen 1982, McGurk 1984a); and (2) ring deposition is always daily, but rings deposited during periods of slow growth are too narrow to be resolved by light microscopy (Campana et al. 1987). These 2 hypotheses are not mutually exclusive and both have similar consequences for the practical application of otolith ring counts to ageing of herring larvae: the number of rings cannot be taken as an absolute index of age, but must be adjusted to take into account the apparent cohort-specific rate of ring formation. In this study an average rate of 0.84 d<sup>-1</sup> was measured and subsequently used to convert ring widths to specific growth rates. This rate of ring deposition is close to that which would be expected from the average linear rates of growth in length. Both Geffen (1982) and McGurk (1984a) reported equations relating ring deposition rates and growth rates; their equations indicate that growth rates of 0.31 to 0.37 mm·d<sup>-1</sup> should produce ring deposition rates of about 0.83 d<sup>-1</sup>, which is similar to the rate measured in this study.

#### 9.4 Condition

A comparison of the plots of CF2 on age given by McGurk (1986a: Fig. 1.12) for herring larvae of Bamfield Inlet, British Columbia, with the plots of CF2 on date of capture given in Fig. 18 of this report show similar ranges of CF2 values. The average CF2 of 3 separate cohorts of Bamfield inlet herring larvae ranged from about 2.0 at hatch to -1.5 to -2.0 at an age of 30 d, and the ranges of CF2 for individual larvae were 4.0 to -4.0. The great majority

of **CF2** values for the Auke Bay study also fall within these ranges. The major difference between the 2 studies is that all 3 **Bamfield** Inlet cohorts had positive average **CF2** values for the first 2 weeks after hatch, whereas only one of the 3 Auke Bay cohorts, cohort 2, followed such a trajectory. If we assume that **CF2** is measuring the same aspect of condition in both **Bamfield** inlet and Auke Bay herring larvae, then the condition of Auke Bay herring larvae was higher than that of **Bamfield** Inlet larvae, at least for cohorts 1 and 3.

#### 9.5 Relationships of Growth and Condition to Environmental Factors

Population growth rates, specific growth rates, and condition factors indicate that herring larvae of cohorts 1, 3, and 4 grew fast and were in good condition compared to other populations of Pacific and Atlantic herring larvae. This was due to prey concentrations that were consistently higher than the average concentration that **leads** to slow growth and irreversible starvation. In contrast, the specific growth rates and condition factors of cohort 2 larvae indicate that they experienced significantly higher **incidences** of reversible and irreversible starvation. This is presumably the result of **the** fact that cohort 2 larvae spent the first 2 weeks of their lives in a prey field of lower than average concentration.

This evidence offers partial support for the hypothesis that growth and condition of Pacific? herring is controlled by the concentration of prey. This qualified conclusion is necessary because the statistical correlations between specific growth rate and prey concentration, and between condition factor and prey concentration, are relatively weak, although they are statistically significant. The low correlations are due to a narrow range of environmental variability, and to the limited resolution of the techniques used to measure specific growth rate and physical condition.

If the critical period hypothesis is correct, and the primary agent of mortality of young herring larvae is irreversible starvation, then total

mortality of young larvae of cohort 2 is predicted to be higher than that of cohorts 1, 3 and 4. A corollary of the critical period hypothesis is that mortality due to predation is more important **than starvation in the dynamics** of **cohorts** 1, 3 and 4. These predictions are tested in section 10.0 by comparing total mortality of cohorts 1, 2 and 3 between each other and by searching for correlations between mortality, condition and predator concentration.

## 10.0 RESULTS - DISTRIBUTION AND SURVIVAL OF LARVAE

### 10.1 Cohort Densities

Numbers and densities of Pacific herring larvae captured in Auke Bay in 1988 are listed in Appendix D. Densities were calculated in 2 ways: directly from the number of herring larvae counted in each sample (Measured density), and corrected for the effect of net evasion (Corrected density). In this section, I examine the importance of 3 factors which may have biased estimates of larval density: (1) loss of alcohol-preserved larvae during storage of the unsorted plankton samples due to the decomposition of the larvae; (2) loss of larvae due to their extrusion through the meshes of the net; and (3) evasion of the towed plankton net by **larger** herring larvae..

In order to examine the first factor, 50 pairs of measured densities of formalin-preserved samples and alcohol-preserved samples taken **at** the same date and site were extracted from Appendix D. The ratios of the densities of formalin-preserved herring larvae to alcohol-preserved herring larvae of each pair were then transformed with natural logarithms in order to normalize the data (ln-transformation is used in all analyses of the density data in this study). The in-transformed ratios were not significantly connected with date of capture ( $P > 0.05$ ) or mean length of each pair of samples ( $P > 0.05$ ). Therefore, the type of preservative did not warrant any correction of herring larvae density.

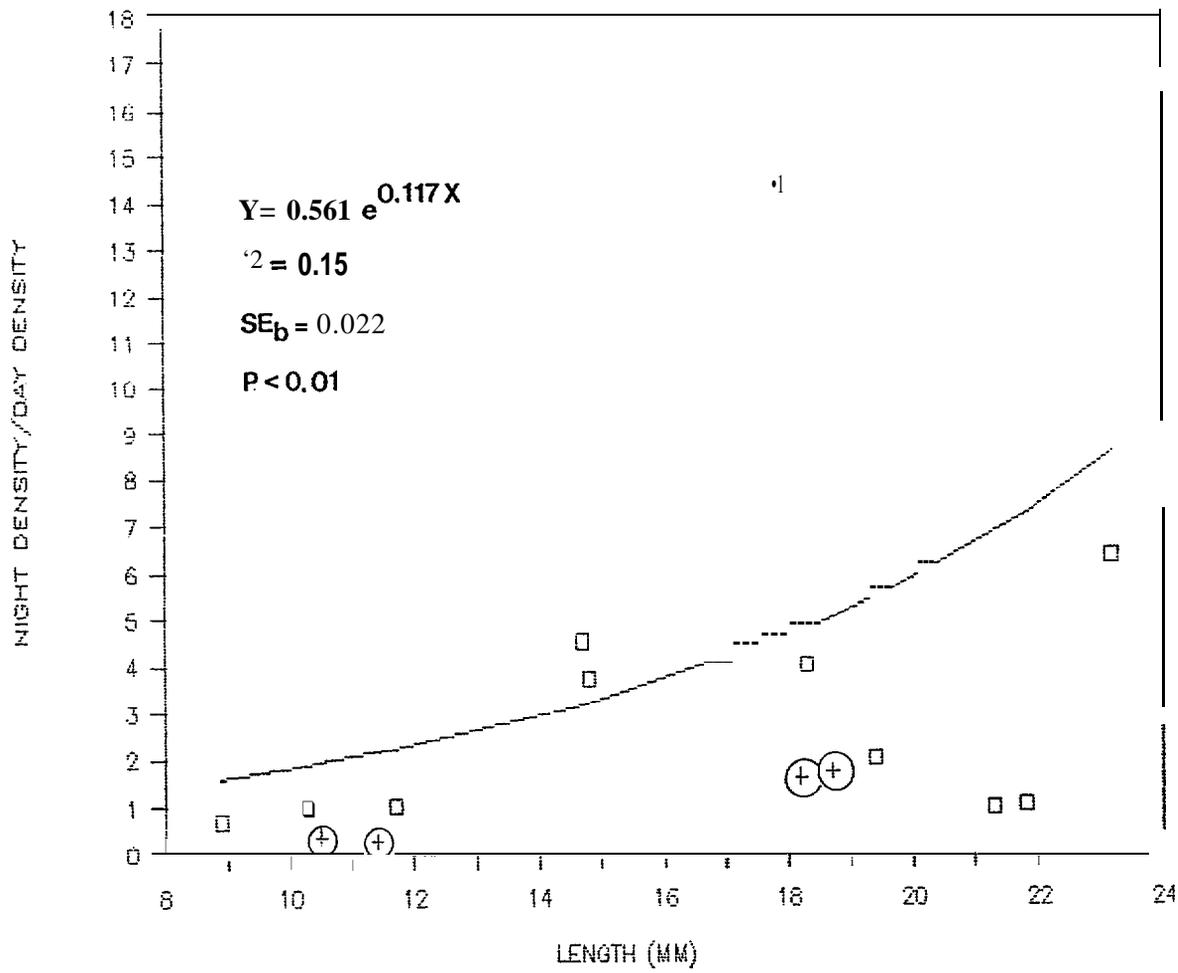
Plots of density of larvae against age for cohorts 3 and 4 (Fig. 22) suggest that extrusion of herring larvae through the 505  $\mu\text{m}$  mesh may have been a factor responsible for an underrepresentation of larvae younger than 15 d old. There is no data available to test the hypothesis that extrusion of young herring larvae occurs in 505  $\mu\text{m}$  mesh nets because there were no tows of the 333 and 505  $\mu\text{m}$  mesh nets taken **at** the same date and station. However, there are density estimates for 10 pairs of 165  $\mu\text{m}$  and 333  $\mu\text{m}$  mesh nets taken at the same date and site in Auke Bay in 1988 (Appendix D). Ratios of the 333

density to the 165 density were ln-transformed and plotted against mean length. The data showed no trend, indicating that extrusion is not a factor influencing the measured densities of herring larvae in the 165 and 333  $\mu\text{m}$  mesh catches.

**Evasion of towed plankton nets by fish larvae** has been shown to increase exponentially with length of larvae (Smith and Richardson 1977, Leak and Houde 1987, McGurk 1989). One method of correcting for this factor is to take advantage of the fact that evasion is **usually** lower during the night than during the day because the net is **less** visible to the larvae at night. The ratio of night to day densities at the same date and site can be used to adjust the densities measured by day tows. Six night tows were made in Auke bay in 1988 specifically for the purpose of generating a correction equation for net evasion. Separating the catches into cohorts gave 15 pairs of night/day densities (Appendix D). Plotted against mean length, the ratios clearly increase with length (Fig. 19). A linear regression of all of the ln-transformed ratio against length was significant ( $0.01 < P < 0.05$ ), but this regression could not be used to adjust catches for net evasion because it predicted a ratio less than 1.0 at mean lengths **below** 12.4 mm, which means that densities of larvae with mean lengths less than 12.4 mm would actually be decreased rather than increased as a result of correction for net evasion. This result is due to the inclusion of 2 very low ratios derived from a single night tow: sample number 46. Without these 2 ratios and 2 other ratios calculated from sample number 46, the regression of ratios on mean length predicted positive ratios at all lengths greater than 8.8 mm and so it was chosen as the most appropriate equation. Rearranged as

$$(38) \quad Y = Y_0 0.5608 \exp(0.1173X)$$

where  $Y$  = corrected density ( $\text{m}^{-3}$ ),  $Y_0$  = measured density ( $\text{m}^{-3}$ ), and  $X$  = mean length (mm), it was used to adjust all day densities for net evasion. The densities of sample number 46 were corrected with this equation because it was reclassified as a day catch. Night catches were not adjusted for net



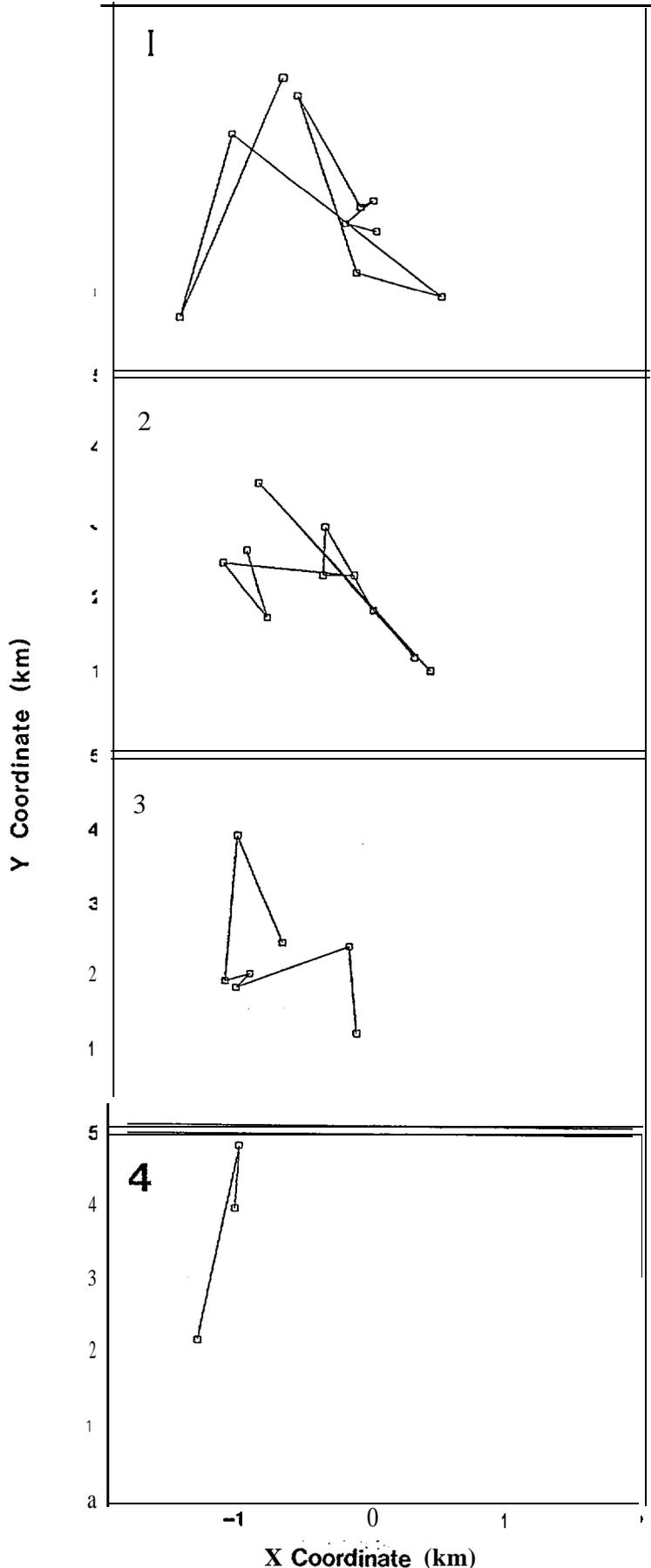
**Figure 19:** REGRESSION OF THE RATIO OF DENSITIES OF HERRING LARVAE CAUGHT AT NIGHT TO DENSITIES OF HERRING LARVAE CAUGHT DURING THE DAY ON MEAN LENGTH OF HERRING LARVAE (circled points were excluded from the regression)

evasion. Based on this equation, 63.5% of the available 8.8 mm long herring larvae, 30.7% of the available 15 mm long herring larvae and 5.3% of the available 30 mm long herring larvae were captured by day plankton net tows. These numbers are conservative compared to those calculated by other authors. For example, McGurk (1989) calculated that 68.6% of available 8.8 mm long herring larvae, 12% of available 15 mm long herring larvae and 0.2% of available 30 mm long herring larvae were captured in day tows of a 481  $\mu\text{m}$  mesh net in Barkley Sound, British Columbia. Leak and Houde (1987) calculated that 6.2% of available anchovy larvae, Stolephorus purpureus, 8.8 mm long and 0.3% of available anchovy larvae 15 mm long were captured in day tows of a 333  $\mu\text{m}$  mesh net in Hawaiian waters.

## 10.2 **Advection**, Diffusion and Patchiness

No significant ( $P > 0.05$ ) rates of **advection** were calculated from the change in position of the **centroids** of each cohort with date of capture because the **centroids** did not consistently move in one direction (Fig. 20). Instead, the **centroids** tended to remain between station ABM ( $y = 1.54$  km) and CSI ( $y = 4.84$  km) on the y-axis. No coefficients of diffusion were calculated because no correlations were found between **spatial** variance of larval density,  $S_{xy}^2$ , Julian date of capture, and age of larvae. These results indicate that herring larvae were retained in Auke Bay instead of being transported offshore. This conclusion was employed in the calculation of egg-larval mortality rates of cohorts 2 and 3, and as an assumption underlying the population models used to estimate total mortality of cohorts 1, 2 and 3.

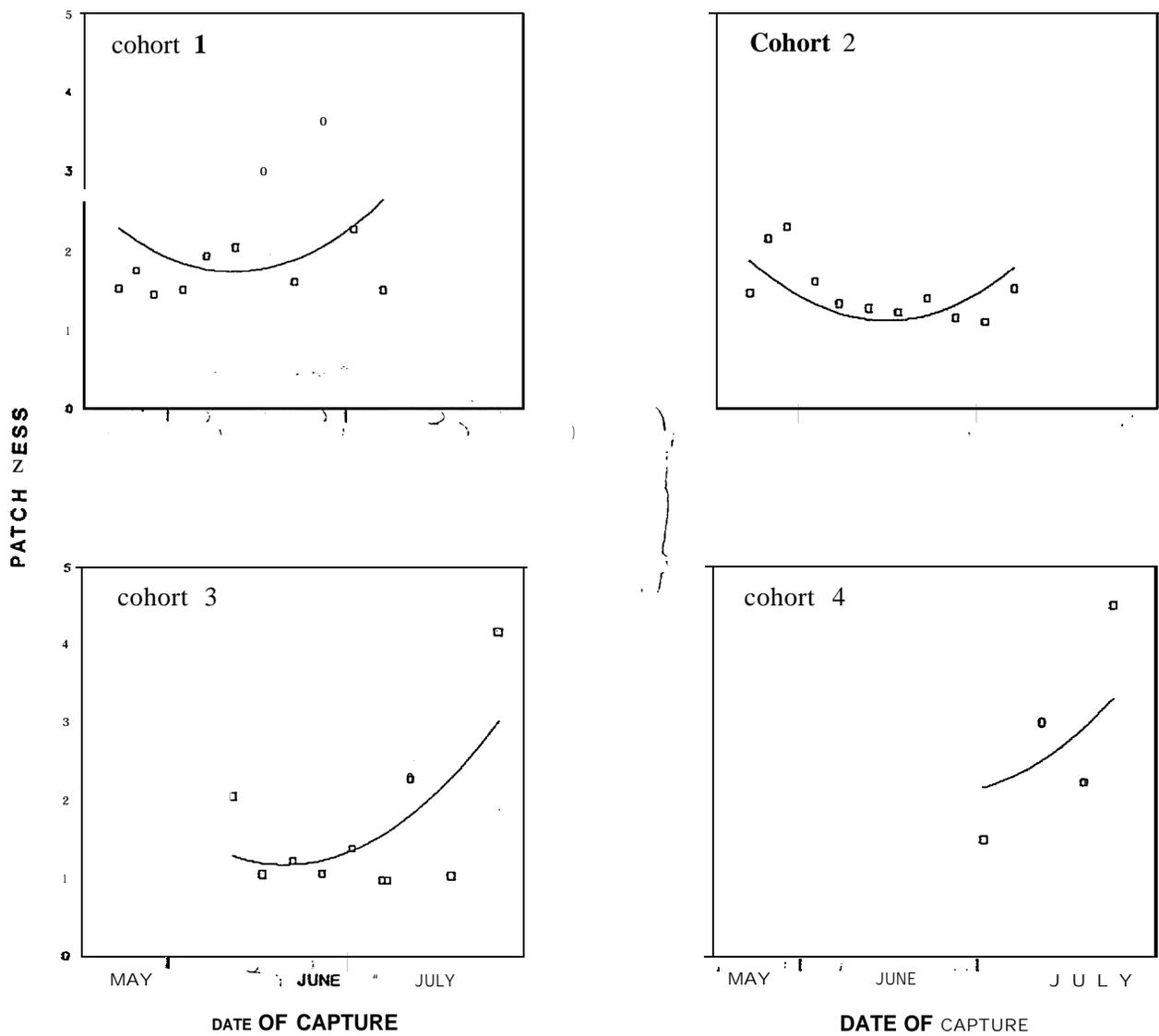
Examination of spatial patchiness at date for cohorts 1, 2, 3 and 4 shown in Fig. 21 suggested a positive relationship between patchiness and date of capture, as well as a curvilinear relationship between patchiness and age of larvae for each cohort. This was confirmed with response surface analysis; the equation that explained the maximum amount of variation in Lloyd's patchiness index with all-significant coefficients ( $P < 0.05$ ) was



**Figure 20**  
CENTROIDS OF COHORTS  
1,2,3 AND 4 AT EACH  
SAMPLING DATE AND  
X-Y COORDINATES  
(no offshore movement is  
apparent)

**Figure 21: SPATIAL PATCHINESS ON DATE OF CAPTURE FOR HERRING LARVAE OF COHORTS 1,2,3 AND 4**

**NOTE:** Solid lines are patchiness predicted from age of larvae and date of capture with equation (39)



$$(39) \quad Y = 58.2650 + 0.3620X_1 - 0.7226X_2 + 1.612 \times 10^{-3}X_1^2 + 2.29 \times 10^{-3}X_2^2 - 2.506 \times 10^{-3}X_1X_2$$

$$r^2 = 0.45, n = 36, P = 0.002$$

where  $Y$  = patchiness,  $X_1$  = age (d) of larvae, and  $X_2$  = Julian date of capture. A curvilinear relationship between patchiness and age was expected from previous studies of patchiness of fish eggs and larvae (Smith 1973, Hewitt 1981, McGurk 1987 b), but the significant effect of date suggests that one or more environmental factors that varied with date also affected spatial patchiness of herring larvae in Auke Bay.

The roles of 6 factors: mean temperature of the upper 20 m of the water column, mean total prey concentration, mean total predator concentration, adjusted mean predator concentration, and the average dry weight of the larvae, in controlling patchiness were examined by substituting them for date in an analysis similar to that of equation (39). All factors, including patchiness and age, were ln-transformed because it was assumed that they acted multiplicatively. Partial correlation analysis showed that ln(weight) ( $r=0.27$ ) and ln(adjusted predator concentration) ( $r=0.24$ ) had the highest correlation coefficients, with all other factors having coefficients ranging from 0.01 [ln(preys concentration)] to -0.14 [ln(temperature)]. Response surface analysis of the former 2 variables gave the following equation

$$(40) \quad Y = 5.76 \times 10^{-2} + 5.42 \times 10^{-3}X_1 + 1.18 \times 10^{-2}X_2^2$$

$$r^2 = 0.42, n = 35, P = 0.0002$$

where  $Y$  = ln(patchiness),  $X_1$  = ln[dry weight (ug)], and  $X_2$  = ln[adjusted mean predator concentration ( $\text{mg} \cdot \text{m}^{-3}$ )].

### 10.3 Mortality

A Pareto-type model provided the best fit to the density data of cohorts 1 and 2 (Fig. 22). None of the 3 population models gave an adequate description of the cohort 3 and 4 densities because they gave ecologically unreasonable parameter values: negative  $Z$  for the linear and Pareto models and extraordinarily high  $Z$  and negative  $K_x$  for the advection-diffusion model. I truncated the data set of cohort 3 so that it contained only the descending right-hand side of the catch curve, i.e. only densities that were 20 d or older, and re-analyzed this partial data set. This procedure is standard practice for the analysis of catches of fish the youngest and smallest members of which are too small to be fully catchable by the gear or “who live in a different habitat from the older and larger members of the population (Ricker 1975). The Pareto model explained the highest amount of variance of this partial data set.

Egg-larval mortality,  $M_{el}$ , was calculated from equation (31) to be 0.93 d<sup>-1</sup> over ages 0 to 1 d of cohort 2, and 0.12 d<sup>-1</sup> over ages 0 to 19 d of cohort 3 (Fig. 23). Sensitivity analyses of equation (28) were performed in order to assess the amount of error involved in these calculations. They involved changing each of the eight parameters separately in equation (31) by  $\pm 5\%$  and  $\pm 25\%$  and calculating the percent change in  $M_{el}$ . In both cohorts 2 and 3, a +5% to -5% and a +25% to -25% change in each of the parameters  $N_0$ ,  $A$  and  $H$  led to only a -2.5% and a -12.5% to +12.5% change in  $M_{el}$ , respectively. However, a +5% to -5% and a +25% to -25% change in  $t$  led to -4.8 to +5.3% and a -20.0 to +33.5% change in  $M_{el}$ , respectively. Therefore,  $M_{el}$  was most sensitive to  $t$ , the number of days between the mean date of hatching and the first date at which larval density could be estimated. Fortunately, this parameter was measured with relatively little error; both forward- and backward-calculation of the hatching date from the range of surface water temperatures did not alter the hatching date by more than 1 d (section 6.3). Thus a maximum probable error of  $\pm 30\%$  of  $M_{el}$  for both cohorts 2 and 3 is appropriate (Fig. 23).

**Figure 22: REGRESSIONS OF DENSITIES OF HERRING LARVAE ON DATE OF CAPTURE**

SOLID LINES ARE PARETO-TYPE POPULATION MODELS:  $N_t = N_0 \left( \frac{JD-a}{t_0} \right)^b$

where:  $N_t$  = density (  $m^{-3}$  ) at age  $t$ (d)

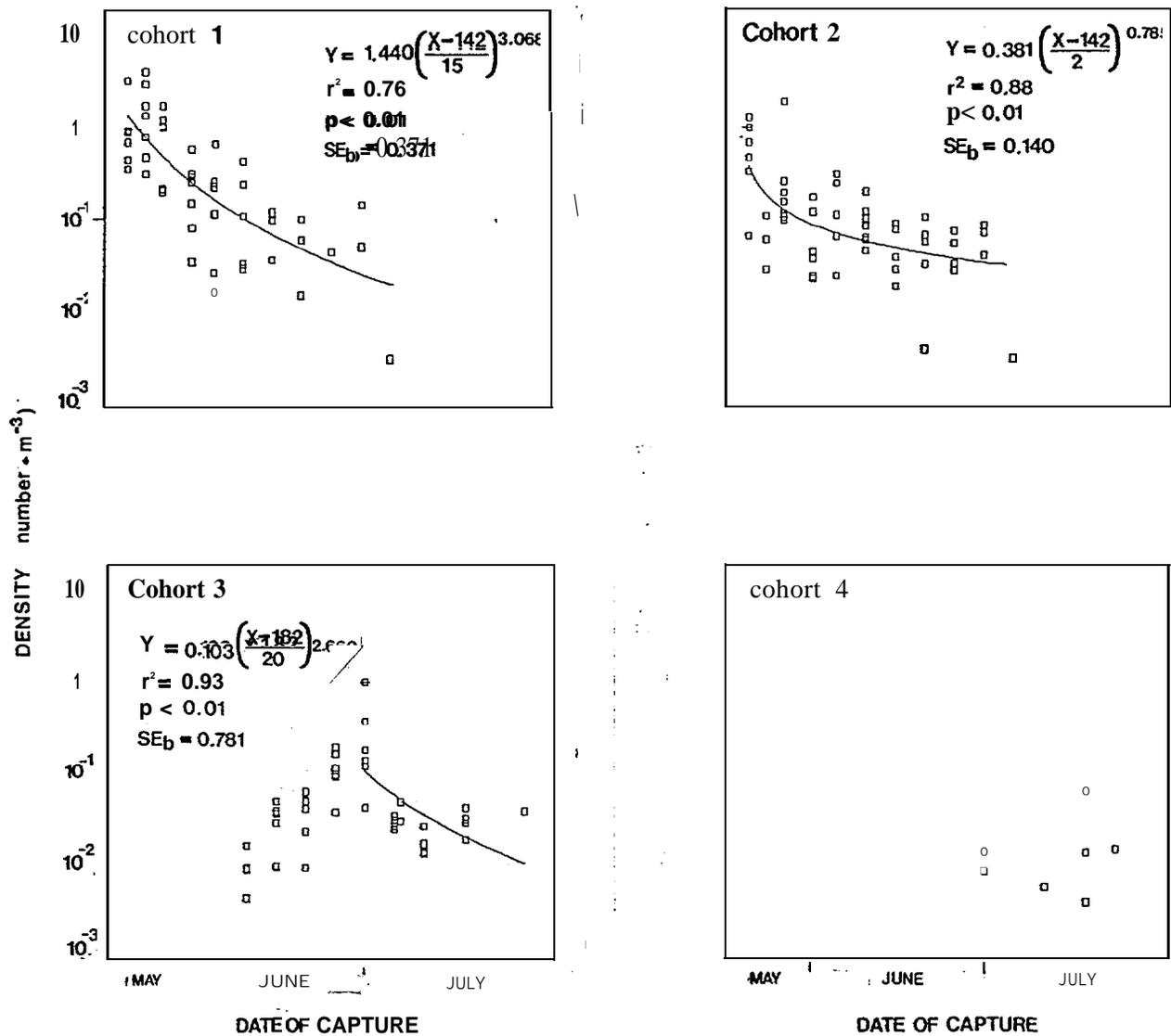
$N_0$  = density at age  $t_0$

JO = Julian date at capture

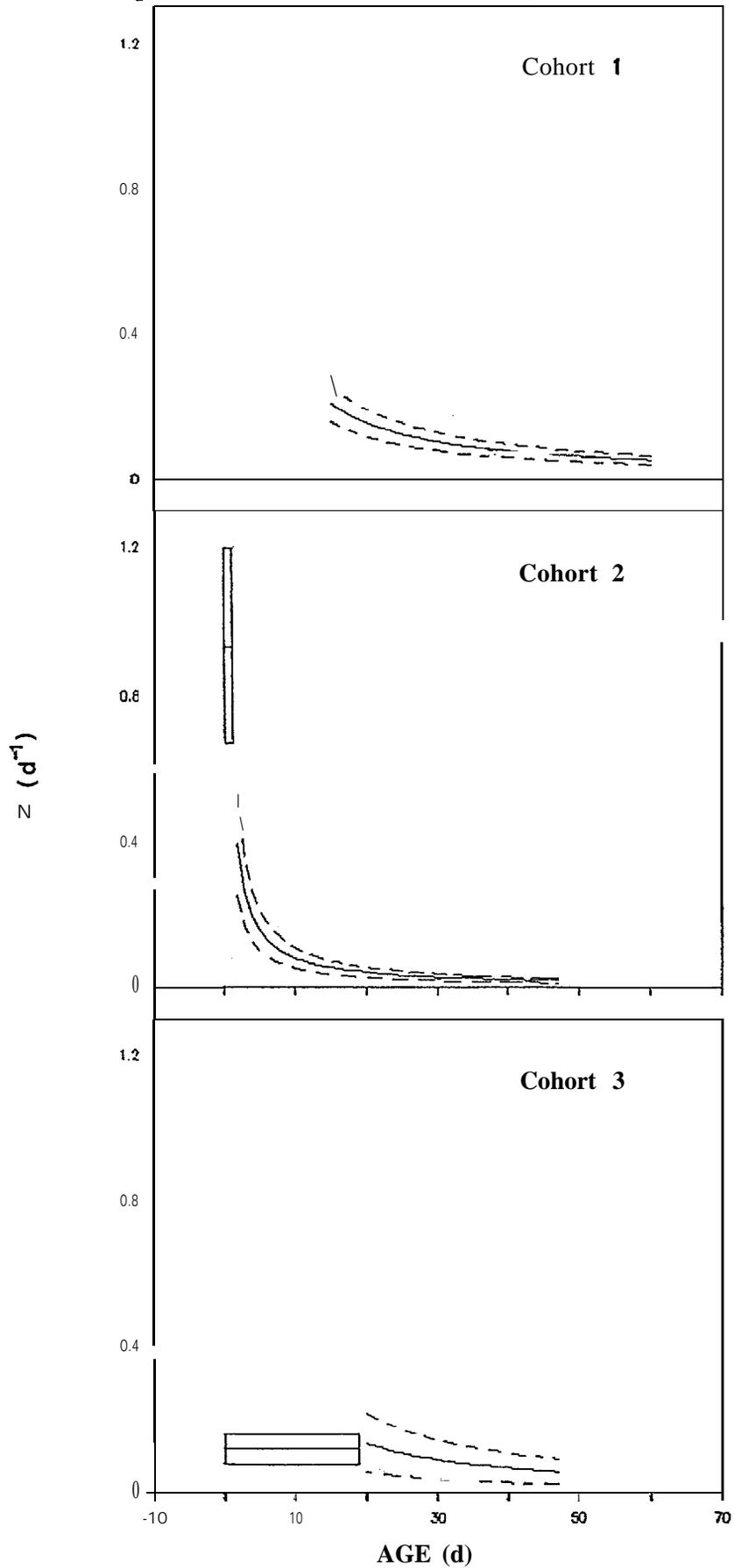
a = Julian date at hatch

b = youngest age in a data set

b = mortality coefficient



**Figure 23: TOTAL MORTALITY (solid lines) AND EGG-LARVAL MORTALITY (boxes enclose \*30% probable error). BROKEN LINES ARE 95% CONFIDENCE LIMITS OF TOTAL MORTALITY**



Two trends are clear in the plots of total mortality on age: first, the mortality of newly-hatched 0 to 10 d old larvae was about 6 times higher in cohort 2 than in cohort 3; and second, the mortality of cohort 2 larvae older than 10 d was half the magnitude of that in cohorts 1 and 3. Six factors: age (t) and mean dry weight (W) of the larvae, the mean total (P) and adjusted (P<sub>adj</sub>) concentrations of predators, mean CF2 condition, and spatial patchiness (p), were examined in order to assess their role in controlling mortality rate. All variables including Z were ln-transformed; 1 was added to age because of zeroes of O age, and 10 was added to CF2. Partial correlation analysis

	lnZ	<u>ln(t+1)</u>	lnW	lnP	<u>lnP<sub>adj</sub></u>	<u>ln(CF2+10)</u>	<u>lnp</u>
lnZ	<b>1.00</b>						
ln(t+1)	-0.39	1.00					
lnW	-0.11	0.43	1 . 0 0				
lnP	-0.03	0.10	0.21	1.00			
lnP <sub>adj</sub>	-0.14	-0.10	-0.32	0.94	1.00		
ln(CF2+10)	0.09	-0.37	-0.38	0.40	-0.24	1.00	
lnp	0.30	-0.11	0.34	<b>-0.04</b>	0.12	-0.03	1.00

showed that Z was most highly correlated with age, followed by patchiness, the adjusted concentration of predators, and weight of the larvae. Total concentration of predators and mean CF2 condition were weakly correlated with z. When all 6 variables were used in a multiple regression only age was selected as significant.

$$(41) \quad Z = 0.5273(\text{age}+1)^{-0.62}$$

$$r^2 = 0.54, n = 33, P < 0.001, \text{SEb} = 0.10$$

When age was excluded from the analysis, and only body weight of the larvae and their patchiness were included, as a test of the mortality-patchiness hypothesis (McGurk 1986 b), then response surface analysis identified the

following equation as explaining the most variation in  $\ln Z$  with all-significant coefficients.

$$(42) \quad Z = 0.9549 W^{-0.40} \quad p \ 0.81$$
$$r^2 = 0.46, \ n = 33, \ P = 0.0001, \ SE_w = 0.0819, \ SE_p = 0.3646$$

Equation (41) predicted higher  $Z$  at ages 0 and 1 for cohort 2 than was predicted by equation (42), but neither equation predicted the lower average  $Z$  in older larvae of cohort 2.

## 11.0 DISCUSSION - DISTRIBUTION AND SURVIVAL OF LARVAE

### 11.1 Advection and Diffusion

The absence of significant **advection** and diffusion of herring larvae out of Auke Bay supports the hypothesis that herring larvae were retained in Auke Bay. The retention area of the Auke Bay herring larvae was at least as large as Auke Bay because larvae were found between **Coghlan** and Spuhn Islands, but it may not have been very much larger than Auke Bay because many of the highest densities of herring larvae measured in Auke Bay were taken at ABM station in the middle of the Bay. This is not the distribution expected if larvae were being swept out of Auke Bay, but it is the pattern expected if the herring larvae were being retained within Auke Bay.

In order for the **centroid** of the Auke Bay spawnings to have remained within Auke Bay, i.e. to have traveled less than 5 km between hatching and the age of onset of schooling behaviour at 25 d (**Marliave** 1980, **McGurk** 1987 b), the average **advection** rate must have been less than or equal to  $5 \text{ km} \cdot (25 \text{ d})^{-1}$  or  $0.2 \text{ km} \cdot \text{d}^{-1}$ . This is similar to an **advection** rate of  $0.15 \text{ km} \cdot \text{d}^{-1}$  estimated by **McGurk** (1989) for Pacific herring larvae that hatched in **Bamfield** Inlet, British Columbia. Both Auke Bay and **Bamfield** Inlet are sheltered from strong offshore currents that could transport fish larvae large distances in short time periods, so it is not unreasonable to expect that Auke Bay herring larvae would have **advection** rates of similar magnitude to those of **Bamfield** Inlet herring larvae. The same reasoning predicts that herring larvae that hatch from open unsheltered coasts, or which hatch into offshore waters from eggs laid on the continental shelf, should be **advected** at rate much higher than  $0.2 \text{ km} \cdot \text{d}^{-1}$ . This is what has been observed for Atlantic herring larvae that have been studied in offshore waters, their **advection** rates are an order of magnitude higher than those measured in **Bamfield** inlet, ranging from 1 to  $3 \text{ km} \cdot \text{d}^{-1}$  on **Georges** Bank (**Wright and Lough** 1979, cited by **Munk et al.** 1986) to 3.4 to  $9 \text{ km} \cdot \text{d}^{-1}$  in the North Sea and off the west coast of Scotland (**Munk et al.** 1986, **Heath and**

MacLachlan 1987, Heath and Rankine 1988). However, not all patches of Atlantic herring larvae have been found in offshore waters of unidirectional current flow. Heath et al. (1987) reported the retention of a patch of Atlantic herring larvae for at least 2 wk in inshore waters of the Pentland Firth on the northern coast of Scotland due to the formation of a gyre in that area. Larvae in areas further offshore from the Firth were rapidly dispersed due to coastal currents.

The expected diffusion rates of herring larvae in Auke Bay can be calculated using a simple relationship between the radial velocity of dispersal of a cohort of herring larvae,  $v$  ( $\text{km}\cdot\text{d}^{-1}$ ), the coefficient of radial diffusion,  $K$  ( $\text{km}^2\cdot\text{d}^{-1}$ ), and the coefficient of mortality,  $Z$  ( $\text{d}^{-1}$ ). Okubo (1980) showed that for a population dispersing radially according to a one-dimensional form of equation (27), i.e.

$$(43) \quad N_{xt} = \frac{c}{4\pi HKt} \exp \left[ -\frac{x^2 + Zt}{4Kt} \right]$$

where  $N_{xt}$  is density ( $\text{km}^{-3}$ ) at position  $x$  (km) and time  $t$  (d), an isocline of constant density travels away from the centroid at a rate of

$$(44) \quad v = \frac{x}{t} = \pm 2K \left( \frac{1}{2t} - Z \right)^{\frac{1}{2}}$$

which rapidly converges to

$$(45) \quad v = \pm 2(KZ)^{\frac{1}{2}}$$

as  $t$  goes to infinity. This can be rearranged as

$$(46) \quad K = \frac{1}{Z} \left( \frac{v}{2} \right)^2$$

In this case,  $v$  is calculated on the assumption that most young larvae are retained in Auke Bay, i.e.  $v = 0.2 \text{ km} \cdot \text{d}^{-1}$ .  $Z$  is taken as the slope of a linear regression of  $\ln(\text{larval density})$  on age or date: 0.10 and 0.05  $\text{d}^{-1}$  for cohorts 1 and 2, respectively. Thus,  $K$  of Auke Bay herring is calculated from equation (46) to range from 0.1 to  $0.2 \text{ km}^2 \cdot \text{d}^{-1}$ . If the "retention area" is set at 10 km, instead of 5 km, then  $v = 0.4 \text{ km} \cdot \text{d}^{-1}$  and  $K$  is predicted to range from 0.4 to  $0.8 \text{ km}^2 \cdot \text{d}^{-1}$ . This range of diffusivities includes those reported by McGurk (1989) for Pacific herring larvae in Bamfield Inlet: 0.08 to  $0.48 \text{ km}^2 \cdot \text{d}^{-1}$ . These diffusivities are among the lowest measured for fish eggs and larvae, due probably to the enclosed nature of Bamfield Inlet that reduced wind- and wave-generated mixing of the upper water layer and due also to the relatively small area of Bamfield Inlet. Okubo (1971) has shown that the diffusivity of dye particles in the sea increases exponentially with scale as larger scale eddies are incorporated.

Since both Auke Bay and Bamfield Inlet are relatively small and sheltered embayments, it is not unreasonable to conclude that herring larvae that hatched into them have similar diffusivities. This reasoning predicts that herring larvae in offshore waters should have much higher diffusivities and this is indeed the case. Munk et al. (1986) reported horizontal diffusion coefficients of 18.41 and  $2.94 \text{ km}^2 \cdot \text{d}^{-1}$  for the long and short axes, respectively, of a patch of Atlantic herring larvae in the Buchan area of the North Sea, and Heath and MacLachlan (1987) reported horizontal diffusion coefficients ranging from 0.5 to  $10.0 \text{ km}^2 \cdot \text{d}^{-1}$  for a patch of Atlantic herring larvae off the western coast of the Outer Hebrides Islands.

In summary, the rates of advection and diffusion expected under the assumption that herring larvae were retained in Auke Bay are similar to those measured by McGurk (1989) for small cohorts of herring larvae that hatched in the protected waters of Bamfield Inlet. This analysis suggests that the retention area of Auke Bay herring was not much larger than the Bay itself. There are two possible mechanisms for retention of herring larvae in Auke Bay: a counter-clockwise gyre of surface currents, and diel vertical

migration of the larvae. Surface currents are important to the distribution of Pacific herring larvae **because the larvae aggregate** in the upper 20 m of the water column (Stevenson 1962, Robinson 1988). However, vertical migration of larvae in order to take advantage of different current speeds and directions at different depths has also been implicated as a retention mechanism in Atlantic herring in estuaries (**Fortier** and Leggett 1983) and off continental shelves (Stephenson and Power 1988). Both Stevenson (1962) and Robinson (1988) reported that Pacific herring larvae were aggregated in surface waters during daylight hours and sank lower in the water column during periods of darkness. This is a migration pattern similar to that exhibited by non-osmerid fish larvae in Auke Bay. **Haldorson et al.** (1988) reported that the larvae of six species of fish in Auke Bay actively migrated vertically in two distinct patterns: **eulachon** and **capelin** larvae rose to the surface at night and descended during the day, but all other species including walleye pollock, *Theragra chalcogramma*, rock sole, *Lepidopsetta bilineata*, flathead sole, *Hippoglossoides elassodon*, and northern smoothtongue, *Leuroglossus schmidtii*, sank at night and rose to the surface in the morning. Regardless of which type of migration pattern they exhibited, all six species returned to the depth strata, usually 5 to 15 m deep, with the highest concentration of copepod nauplii as soon as light intensity was high enough in the early morning to allow visual feeding. This evidence suggests that herring larvae in Auke Bay may have been exposed to different current speeds and directions as they moved through each diel cycle of vertical migration.

## 11.2 Mortality

This study is the first to describe total mortality of herring larvae as an age-dependent phenomenon. All previous reports have described the mortality of Pacific and Atlantic herring larvae as constant (**Das** 1968, **Dragesund** and **Nakken** 1971, 1973, **Graham and Chenoweth** 1973, **Lough et al.** 1981, **Henderson et al.** 1984, **Graham and Townsend** 1985, **Munk et al.** 1986, **Heath and MacLachlan** 1987, **McGurk** 1989).

The fact that cohort 2 hatched into a period of relatively low prey concentration, and that in the 0 to 10 d age period it had the lowest specific growth rates and CF2 condition and the highest total mortality, strongly suggests a link between prey concentration, growth and mortality. However, this linkage is not supported by a statistical analysis of mortality rate; the high egg-larval mortality rate of cohort 2 is not well explained by any variable except age.

## 12.0 GENERAL DISCUSSION

In this section I discuss the results of this study with special reference to the two hypotheses presented in the Introduction. First, I discuss the evidence supporting the hypothesis that was **tested** in this **study**: the idea that growth and fitness of larval herring is controlled by food production in their rearing area. Second, I briefly discuss the evidence supporting the two associated hypotheses underlying this study: the ideas that growth and fitness **limits** survival in larval herring, and that survival in the larval stage is the primary determinant of year-class success. Finally, I discuss the implications of this study for future research on the early life history of Pacific herring in Alaska.

### 12.1 Growth-food Production Hypothesis

The answer to the primary question of this **study**: what is the relationship between growth and fitness of herring larvae and environmental conditions in Auke Bay? Is that about 9% of the variation in specific growth rate is due to age and 4% is due to variation in prey concentration, and that 24% of the variation **in** condition factor is due to age and 5% to prey concentration. Prey concentration was not a major factor affecting growth and condition because it was relatively high over the sampling season.

An interesting result of this study is the fact that it confirms the validity of **Kiorboe and Munk's** (1986) relationship between specific growth rate and prey concentration. This suggests that experimental work on **laboratory**-reared herring larvae can be extended to natural ecosystems.

This study supports the results reported for studies of the condition of Atlantic herring larvae. In general, the relationship between condition and prey concentration is positive but weak, indicating that larvae are not food limited. **Blaxter** (1971) compared condition ( $WL^{-3}$ ) of Atlantic herring larvae from the **Firth** of Clyde with the biomass of zooplankton that was

retained on a 208  $\mu\text{m}$  silk mesh and which had been previously identified as prey from gut contents analysis. He reported that there was an inverse relation between condition and biomass, and concluded that this counter-intuitive result may have been caused in part by the unreliability of this simple index of condition and also by the difficulty of accurately measuring biomass of prey. Cohen and Lough (1983) measured the feeding rates (prey per gut), prey preferences, morphological condition (primarily body height/length ratios), and mortality of Atlantic herring larvae of the Georges Bank-Nantucket Shoals area. They reported that condition and feeding rate of larvae was greater in the 1976 season than in 1974 or 1975, and that mortality was lowest in 1976, which suggests a link between condition and mortality, but they did not find any significant correlations between condition, feeding rates or feeding preferences, and prey biomass or prey type as measured by 165  $\mu\text{m}$  and 333  $\mu\text{m}$  mesh nets. Townsend et al. (1986) reported that relative condition of Atlantic herring" larvae of the eastern Gulf of Maine was weakly correlated with concentrations of zooplankton as measured by 80 and 505  $\mu\text{m}$  mesh nets. Condition was highest in recently hatched larvae collected from the northeastern Gulf, it fell considerably in larvae collected from more southwestern waters, and then it rose slightly in larvae collected from the most southwestern point of the sampling area. The western area of the Gulf had higher concentrations of zooplankton, and as larvae were assumed to be transported in a southwesterly direction from their hatching sites, this pattern was interpreted as a positive response of larval condition to increased zooplankton densities.

## 12.2 Growth-mortality Hypothesis

The hypothesis that growth and fitness of fish larvae limits their survival is one of the 3 major assumptions justifying this study. The other 2 assumptions are a link between food production and growth, which has been discussed above, and a link between larval mortality and year-class success. Despite its crucial importance in the chain of logic that leads from growth of larvae to year-class strength, there is little empirical evidence to

support an inverse relationship between growth and mortality in wild populations. There is a direct positive correlation between growth and mortality between species, as Ware (1975) first demonstrated, but this relationship is most likely due to underlying negative relationships between population parameters and body weight. Petersen and Wroblewski (1984) and **McGurk (1986b)** have shown that mortality of fishes, including fish larvae, decreases with body weight to a power between 0.2 and 0.5, and growth rates of **all** organisms decrease with increasing body size because of the well-known inverse relationship between specific metabolic rate (rate per unit weight) and body size. This study shows that total mortality decreased with weight to the power of 0.40, and it offers partial support to the **mortality-patchiness** hypothesis by showing that mortality is weakly, but significantly, correlated with spatial patchiness of Pacific herring larvae.

There are few **intra-specific** comparisons of growth and mortality in larval fishes and none of them report an inverse correlation between growth and mortality. **McGurk (1984b)** compared pairs of growth and mortality estimates for wild populations of Pacific and Atlantic herring **larvae** and found no relationship. Graham and Townsend (1985) reported a correlation between growth and mortality of 7 cohorts of Atlantic herring larvae from coastal waters of Maine, but the correlation was positive.

There is **also** little empirical support for a relationship between physical condition and larval mortality. This study found no reliable evidence of a link between CF2 conditions and mortality of herring larvae in Auke Bay. This conclusion is similar to one reported by **McGurk (1989)**. He reported that the trajectory of CF2 condition with age was similar for 2 cohorts of Pacific herring larvae captured from **Bamfield Inlet**; but one cohort had a total mortality rate 3 times higher than the other, indicating that mortality was a multi-factor process and that factors other than starvation, presumably predation, dominated the population dynamics of at least 1 of the 2 cohorts.

Westernhagen and Rosenthal (1981) measured condition ( $W \cdot L^{-3}$ ) of Pacific herring larvae from Departure Bay, British Columbia, in 1974 and 1976, and concluded that there were significant differences between years in the number of poorly-conditioned fish: at any length the 1974 fish had better condition than the 1976 fish. However, Westernhagen and Rosenthal (1981) noted that recruitment of **adult** herring to the Strait of Georgia **stock** resulting from the 1974 year-class was only half that of the 1976 year-class, a result opposite to that expected from the condition factor data. **Chenoweth** (1970) reported that relative condition of Atlantic herring larvae **overwintering** in the Booth Bay area of the Maine coast from 1965 to 1968 was lowest in 1965, a winter in which mortality was unusually high. **Vilela** and **Zijlstra** (1971) reported the condition ( $W \cdot L^{-3}$ ) of Atlantic herring larvae from central and southern North Sea was not correlated with an index of recruitment to the adult stock 3 years later. The positive link between morphological condition, feeding rate and mortality of Atlantic herring larvae from **Georges Bank** reported by Cohen and Lough (1983) has been discussed above.

Hewitt et al. (1985) conducted a study similar **to** that reported by **McGurk** (1989), but dealing with the causes **of** death of northern anchovy, **Engraulis mordax**, larvae in the California Bight. They reported a similarly complex relationship between condition and mortality: predation was the major source of mortality in yolk **sac** larvae, but as yolk was absorbed and larvae began to feed, starvation became a significant source of mortality. As the larvae further developed, starvation rapidly declined and predation again became the dominant source of mortality.

In summary, it is self-evident that starving or slow-growing fish larvae will suffer higher mortality from disease, parasites and predators than well-fed and fast-growing larvae, but there is **little** reliable evidence to demonstrate the operation of this principle in wild populations of fish larvae. Instead, mortality appears to be a multi-factor process with starvation being only one of the factors.

Stevenson (1962) concluded that the principal cause of death of Pacific herring larvae that hatched from the northwestern shore of **Barkley Sound**, British Columbia, was their passive transport by inshore water currents to the open sea. **This was** based on the observation that the greatest concentration of newly-hatched larvae was found in inshore waters, and as they were carried seaward the numbers decreased at an approximately constant rate. Stevenson (1962) did not examine the factors directly causing death in offshore waters, but he suggested that death may be caused by the high salinity of the open sea.

**Alderdice** and Hourston (1985) reviewed the field and experimental evidence on the effects of salinity and temperature on survival of Pacific herring eggs and yolk sac larvae and concluded that the upper boundary of larval tolerance to salinity 'is 27.5 to 31.7 ppt, which is near the lower end of the range of salinities commonly encountered in offshore waters of British Columbia. They also examined the distribution of herring larvae in the Strait of Georgia, where surface salinities are generally 27 to 28.6 ppt and found that **larvae** from offshore areas of the Strait were actively feeding and growing. They concluded that the usual surface salinities and food supply in the open waters of the Strait were not a dominant influence on larval survival, and suggested that the disappearance of **larvae** in the **Strait as largely the** result of predation.

Predation is undoubtedly a major factor in the mortality of Pacific herring larvae; they are preyed upon by many species of fish (**Brodeur** et al. 1987), including adult and juvenile herring (Hourston and Haegele 1980, **Hourston** et al. 1981), and pelagic invertebrates (Stevenson 1962, Westernhagen and Rosenthal 1976, Arai and Hay 1982). Predation has been implicated as the most important agent of mortality in wild Atlantic herring larvae (**Moller** 1984).

### 12.3 Larval Mortality-recruitment Hypothesis

If the growth/condition-mortality relationship is an important component of the recruitment process, then its action must occur as **the** presence or absence of catastrophic mortality during the 2 to 3 week period after absorption of the yolk. This is **Hjort's** (1914) 'critical period' hypothesis, which has guided so much research in larval fish ecology this century. However, there is no unanimity in the scientific community on the validity of the critical period paradigm. Several reviews of the hypothesis have been conducted over the past 30 years, and none have found convincing evidence for the existence of catastrophic mortality during the first-feeding stage as reflected by a sharp break in a plot of population density with age (**Marr** 1956, May 1974, **Dahlberg** 1979). None of the catch curves reported for Pacific (**Stevenson** 1962, **Iizuka** 1966) or Atlantic (**Das** 1968, **Lough et al.** 1981, **Henderson et al.** 1984) herring larvae have the discontinuities that are expected from the critical period hypothesis. The catch curves reported **in** this study for Auke Bay herring larvae show that mortality decreases steadily with age, but the highest mortalities are predicted to occur during the yolk sac stage and not the first-feeding stage.

**Peterman et al.** (1988) reported the first test of **Hjort's** (1914) hypothesis for northern anchovy. They compared the abundance of anchovy at the egg, yolk-sac larval and 19-d old larval stage with the abundance of 1 year old recruits and found no significant relationships. Their review of the scientific literature on the reported correlations of fish egg and larval abundance with abundance of recruits produced diverse results; some stocks showed significant correlations and others did not. They noted that the closer the abundance samples were taken in time, the more likely a significant correlation is to exist.

In conclusion, this study has shown that herring larvae of Auke Bay grew at a high rate throughout the May to June, 1988, season because high densities of prey were available in the upper 30 m of the water column. This finding is

consistent with laboratory studies of the growth-prey density relationship of herring larvae. This study has also shown that mortality of herring larvae in Auke Bay varies between cohorts and changes rapidly with age, but that there are no clear links **between environmental conditions and** those changes in mortality.

The relevance of this kind of study to the problem of understanding the recruitment mechanisms of Pacific herring depends on a chain of logic whose basic assumptions are scientifically controversial. The questions involved in studying recruitment are so profound that their answers cannot realistically be expected for many decades. Therefore, even if the results of the study are accepted as establishing a link between growth and prey concentrations, so much else would remain to be done in order to relate growth to mortality and mortality to recruits that we must expect variation in year-class strength of Alaska herring to remain unexplained for a considerable time to come.

## 13.0 PLAN FOR BERING SEA STUDY

### 13.1 Objectives

I recommend that future studies of young herring in the Bering Sea focus on measuring the population dynamics of young herring, as well as measuring the interaction between growth and prey density. The following section explains the rationale underlying this recommendation.

The Auke Bay study has shown that growth of wild herring larvae is only weakly limited by food. Although this study is a successful first step, it is not certain that it **will** contribute substantially to our ability to predict year-class size from environmental conditions during the early life history stage if, as some researchers have argued, food supply is only one of a suite of factors that together control recruitment. It is entirely possible that **non-trophic** factors such as offshore dispersal or predation are just as important to survival as prey density. It may be more scientifically productive to shift the focus of future investigations from the growth-prey concentration question to questions of the roles of offshore dispersal and predation.

In conclusion, I recommend 3 significant differences in the basic study plan based on the Auke Bay experience. The Bering Sea study should **include:**

1. A strong component of **population modelling in order to obtain accurate estimates of mortality** and dispersal.

#### Rationale

If year class strength is established during the early life history stage of Pacific herring, then the primary factor responsible is mortality. Growth has a less direct influence on recruitment, but its magnitude may serve as an index of year-class success. Therefore, it is necessary to design future

studies so that they may accurately measure mortality rate and how it changes with age and size of herring.

Few species of commercial fish are more amenable to population **modelling** than Pacific herring. The eggs beds are discrete and easily located in the intertidal zone, thus the origin of each cohort of larvae can be identified and the dispersal of larvae way from the egg beds can be measured with more accuracy than is possible for species that spawn in the pelagic zone. Herring larvae and juveniles tend to remain in the **same** estuaries and coastal embayments in which they hatched, thus allowing a relatively accurate assessment of population size. The combination of accurate estimates of dispersal and a relatively small larval **retention zone** means that it is possible to calculate accurate and reliable estimates of larval mortality by subtracting dispersal from total loss rates.

Advection-diffusion **modelling** of populations of fish larvae is rapidly becoming the standard practice in early life history studies. Such models have recently been used to estimate dispersal and mortality of Atlantic herring larvae in the North Sea (Munk et al. 1986, Heath and **MacLachlan** 1987), Pacific herring larvae in **Barkley Sound, Vancouver Island (McGurk** 1989), plaice larvae in the North Sea (**Talbot** 1977), haddock eggs on Browns Bank, Nova Scotia (**Koslow** et al. 1985) and **capelin** larvae in Newfoundland (**Taggart** and Leggett 1987a, **1987b**).

2. A sampling protocol designed in advance of the sampling season in order to **satisfy** the data requirements of a population **model** designed in advance of the study.

### Rationale

A suitable population model should be designed in advance of the sampling season by experts in the field of statistical or computational **modelling** of dispersal processes in aquatic systems in consultation with biologists

experienced in sampling larval herring. Data requirements of the model **should** be used to plan the number of plankton stations and their locations, and the number of tows at each station.

It is a generally accepted principle that a sampling program designed in advance to answer specific questions will answer these questions more successfully than a sampling program onto which is applied an ad hoc analysis. Several versions of advection-diffusion models are available in the fisheries/oceanography literature. The choice of a model appropriate to herring larvae in the Bering Sea should be done by an expert in the field after a careful review of the subject.

Questions to be answered by this review include:

- (1) is an analytical model sufficient or **is** it necessary to build a hydrodynamic model of the study site?
  - (2) What is the simplest and most convenient method by which physical data on currents can be integrated with data on the distribution of herring larvae?
  - (3) must population rates, i.e. mortality, **advection**, and diffusion, be assumed to be constant with age or to change at a constant rate with age, as they were in the Auke Bay study, or can they be calculated as time-varying rates in order to follow **ontogenetic** and seasonal changes in population parameters?
3. The study should include **searches** for the locations and dates of the spawning sites and measurements of the abundance and survival of the **eggs**.

### Rationale

Three reasons support extending the program objectives to cover the distribution, abundance and dynamics of the egg stage:

- (1) egg mortality may play a role in year-class success because substantial natural mortality occurs during the egg stage and this mortality may be highly variable between spawning beaches and between years;
- (2) herring eggs are highly vulnerable to oil pollution of the intertidal zone; and
- (3) estimates of the location and density of newly-hatched larvae are a check on the validity of any model of larval population dynamics.

#### Optional Component of Study Plan

The study may include a program for collecting information on the feeding rates and prey types and sizes of herring larvae and juveniles, and how these variables change with size of herring and with season.

#### Rationale

Although the study of the food of herring larvae and juveniles collected in southern British Columbia waters provided a reasonably accurate template of the prey field of herring larvae in Auke Bay, it may not be an adequate template for herring larvae and juveniles feeding in the Bering Sea because of the differences in available types of prey between the 2 ecosystems. If this component is considered sufficiently important to warrant doing, then the study should (1) **employ** short duration (<60 s) plankton hauls to **shallow** depths (20 m) to reduce the probability of voiding of guts; and (2) include sufficient resources of time and manpower to allow the collection of at least several hundred non-zero guts.

### **13.2 Study Site**

This section presents 2 recommendations on the desirable characteristics of the study one.

1. **The study should be done in a region which has consistently received large amounts of spawn, defined as greater than 2.5 linear km of spawn, over the last decade.**

#### Rationale

Although it is certainly possible to conduct research on the **early** life stages of herring hatched from 'trace' spawnings, as the Auke Bay study has demonstrated, studies on larger spawnings are desirable for 2 reasons. First, large spawnings **will** ensure that there will be sufficient biological material. Second, the dynamics of populations hatched from large egg beds may be different from the dynamics of populations hatched from small beds because of density-dependent effects on growth, condition, dispersal and survival. The **importance** of density-dependence in the early life history of Pacific herring in Alaska may be assessed by comparing the population parameters of large cohorts hatched **in** the Bering Sea with the population parameters of the relatively small cohorts that hatched in Auke Bay in 1988. A spawning of 2.5 km long is recommended because it is an order of magnitude larger than the 2 spawnings that were observed directly **in** Auke Bay in 1988.

2. **The array of plankton sampling stations should extend a minimum of 10 km from the hatch sites in both of the 2 horizontal dimensions.**

#### Rationale

The Auke Bay study has shown that a transect extending 5 km from the hatch site is not long enough to define the retention area of **even** a 'trace' spawning. Locating the margins of the retention area is essential because it generates sufficient spatial contrast in population density to **allow the** accurate measurement of advective and diffusive transport of the larvae. This information on dispersal **can** be removed from the total rate of loss of larvae to give an accurate estimate of mortality. A minimum distance of 10 km along each side of an x-y grid is recommended **because** it is sufficient to

**cover** the dimensions of a patch of young larvae, but is small enough for **all** stations to be visited at **least** once within a 10 h period of daylight.

### 13.3 Technical Recommendations

This section presents brief discussions of 2 technical matters arising from the **Auke Bay** study that may be relevant to a future Bering Sea study.

#### 1. Net Extrusion

The problem of extrusion of small herring larvae through the meshes of plankton nets must be examined **in** order to accurately measure population density. I recommend conducting a series of paired tows of 165, 333 and 505  $\mu\text{m}$  plankton nets at the same sites at the same date at least 3 times over the sampling season. Comparison of the catches of the different mesh nets **would allow** correction of the measured densities for net extrusion.

#### 2. Density of **Microzooplankton**

The Auke Bay study showed that small water pumps with small diameter intake hoses do not produce reliable estimates of the densities of **microzooplankton**, primarily copepod **nauplii**, that are the main prey of first-feeding herring larvae. Although more powerful pumps may solve the evasion problem, a **simpler** course of action is to adopt the technique used by the APPRISE team: a large volume open and closing bottle which is dropped to the desired depth.

#### 3. Growth Rate

The validity of **otolith** ring analysis should be checked by" using a second and independent method of measuring recent growth rates. I recommend RNA/DNA analysis.

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