POPULATION BIOLOGY OF
BAY ANCHOVY IN
MID-CHESAPEAKE BAY

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PREFACE

Maryland Sea Grant supported the research on bay anchovy ecology in mid-Chesapeake Bay. Both field and laboratory approaches were followed from 1986 through 1988 to characterize the population. Vital rates, reproductive parameters, recruitment patterns, energetics, trophic relationships, chemical composition and effects of hypoxia on early life stages were studied. We believe that results of our research include significant contributions to knowledge of bay anchovy, the most abundant fish in Chesapeake Bay and other east coast estuaries.

The report is presented in nine chapters. Authorship varies among chapters. Four of the chapters have drawn heavily on thesis research. Chapter 3 contains the Master's thesis results of Timothy A. Newberger. Chapters 6, 7 and 8 contain results of Master's thesis research of Ana V. Vazquez.

The Abstract briefly describes the project and presents general conclusions of the research. An expanded Summary follows the Abstract and presents the most important results. Each chapter is a detailed report of an aspect of the research. Figures and Tables are numbered consecutively through the report. The single References section contains all literature cited in the report.

ABSTRACT

Ecology of bay anchovy (Anchoa mitchilli), the most common fish in Chesapeake Bay, was studied in the field and laboratory from 1986-1988. Trawling surveys in mid-Chesapeake Bay provided samples to estimate seasonal relative abundances and were the basis for estimating population age structure, growth rates, mortality rates, reproductive parameters, recruitment patterns and trophic relationships. Hydrographic conditions were examined and zooplankton abundances estimated in the frontal zone off the Patuxent River mouth, the focus of the Bay research. Laboratory energetics experiments at three diet levels and three temperatures gave estimates of food consumption, assimilation efficiencies, metabolic demands, growth efficiencies and chemical composition of bay anchovy. Tolerances of eggs and yolk-sac larvae to hypoxic waters also were tested.

Bay anchovy up to 86 mm fork length (FL) and age 3+ were collected. The population was dominated by age 0+ recruits in late summer and fall of 1986 and 1987, and by age 1+ individuals prior to the recruitment period. Females were more common (53.7%) than males (46.3%) in collections. Relative abundance of bay anchovy in the study area was nearly five times higher in 1986 than in 1987. Growth rates were rapid and sustained throughout the short lifespan. A von Bertalanffy growth model fit to back-calculated lengths at annuli and fall marks on otoliths gave $L_\infty = 139.65$ mm, $K = 0.21$, and $t_0 = -1.16$ yr. Annual mortality rates from catch-curve analysis, ranged from 89-95%. Males and females matured at 40-45 mm FL, primarily at age 1. Most females apparently spawned from mid-May to mid-August, releasing from 500 to 2,000 eggs each night during the peak spawning month (July). More than 92% of egg production was by age 1 anchovy in 1986 and 1987. Hatch-dates of recruits, determined from otolith daily increment counts, indicated peak hatches in mid-July in 1986 and late June - early July in 1987. Mean young-of-the-year growth rates, including larval stage growth, for individuals at 40-110 days posthatch averaged 0.47 mm d^{-1} in each year.

Bay anchovy offered three diet levels of Artemia nauplii at 19, 23, and $27^{o}C$ grew from 0.75 to 4.49% daily. Consumption ranged from 6.8 to 28.0% of body weight. Assimilation efficiencies ranged from 34.2 to 87.8% and were >80% at the lowest diet level (10% body weight) for each temperature. Gross growth efficiencies ranged from 14.4 to 38.3% and were highest at low ration-temperature and high ration-temperature combinations. Oxygen uptakes increased as anchovy grew but weight-specific oxygen uptakes declined as anchovy weight increased. Caloric energy budgets were developed for the nine temperature-diet level combinations. In the Bay, anchovy fed most from dawn to mid-morning and least from midnight to predawn. The diet was mostly copepods, other plankton and detritus. Based upon weight-specific stomach contents and gut evacuation rates, daily rations were estimated to range from 9.0 to 16.2% of body weight in a $19\text{-}27^{o}C$ temperature range. Proximate analysis gave the following constituents: moisture 70.0-77.4%; ash 9.4-14.5%; protein 56.1-75.3%; lipid 11.2-33.7%. The chemical composition of bay anchovy that were fed Artemia nauplii in the laboratory changed from that characteristic of wild anchovy. Total lipids increased and fatty acid profiles began to resemble those of the Artemia.

Eggs of bay anchovy were less tolerant of low oxygen conditions than were yolk-sac larvae. Estimated LC_{50} was 2.8 mg O_2 L^{-1} for eggs and 1.6 mg O_2 L^{-1} for yolk-sac larvae. Survival of eggs and larvae was affected significantly when oxygen concentrations fell below 3.0 and 2.5 mg L^{-1}, respectively.

SUMMARY

A three-year project on bay anchovy *Anchoa mitchilli* ecology in mid-Chesapeake Bay was carried out in the frontal zone near the mouth of the Patuxent River. Major objectives included (1) determining population structure and vital rate parameters, (2) examining trophic relationships and energetics, and (3) estimating oxygen tolerances of eggs and yolk-sac larvae under hypoxic conditions similar to those that occur in the Bay. Trawl surveys were carried out beginning in July 1986 and continuing through November 1987. Laboratory energetics studies and oxygen tolerance experiments were completed in 1988. Field studies included descriptive hydrography and zooplankton collections in conjunction with the trawling effort.

Relative abundance of bay anchovy was nearly five times higher in the study area during 1986 than in 1987, primarily because the recruitment level of age 0+ anchovy in late summer 1986 exceeded that in 1987. Relative abundance was highest in both years during September, when catches were dominated by age 0+ recruits. Examination of two Baywide abundance indices suggested that ten-fold or greater differences in abundance of bay anchovy have occurred during the past 30 years.

Female bay anchovy were more abundant than males in most months. The mean sex ratio in catches was 1.16 female:male (i.e. 53.7% female). Female and male length-weight relationships did not differ significantly. Length-weight relationships and condition factors did vary seasonally. Bay anchovy were in the best condition during summer and poorest condition in winter-spring.

Otolith examination analysis indicated that annuli were present. Ages of bay anchovy ranged from age 0+ to age 3+. The largest anchovy collected during the study was 86 mm fork length (FL) although a 95 mm FL individual was collected subsequently. Few (<1%) bay anchovy live to age 3. The population is dominated by age 0+ and 1+ individuals. The population consisted of approximately 85% age 0+ recruits in late summer of 1986 and 1987.

Von Bertalanffy growth models and a Gompertz growth model were fit to size-at-age data. The best model, which was based on back-calculated lengths (or weights) at annuli and fall marks, indicated that asymptotic length L_∞ = 139.65 mm FL, K = 0.21 and $t_0 = -1.16$ yr. From this von Bertalanffy model, predicted fork lengths-at-age are: Age 1 = 50.9 mm; Age 2 = 67.7 mm; Age 3 = 81.4 mm. No bay anchovy as large as the predicted asymptotic length were collected. The relatively low K and high L_∞ values indicate that bay anchovy grows fast throughout a short lifespan and that near-maximum lengths are seldom attained because of its high mortality rate.

Annual mortality rates, based on declining abundances of older age-groups in catches, termed catch-curve estimates, ranged from 89-95%. Three "empirical" mortality-estimating methods also were applied and gave annual rates of 27-76%, values considerably lower than the catch-curve estimates. The catch-curve estimates are believed to be the better estimates of mortality.

Recruitment of bay anchovy 15-30 mm FL was first observed in mid to late July of 1986 and 1987. Significant recruitment occurred earlier in 1987 (mid-

July) than in 1986 (early August).

Male and female bay anchovy matured at 40-45 mm FL, primarily at age 1. There was no evidence based upon ovary examination and gonosomatic index to indicate that age 0+ recruits spawned in 1986 or 1987. The spawning season, as indicated by ovary and testis weights and ova developmental stages, extended from mid-May to mid-August. Females are serial, batch spawners. Virtually all females spawned each night during July, the peak spawning month. Female batch fecundities ranged from 500 to 2,000 and were closely related to body size. More than 92% of estimated egg production in 1986 and 1987 was by age 1 females.

Daily increments in otoliths of young-of-the-year bay anchovy indicated that hatch dates of surviving recruits were primarily in June and July of both 1986 and 1987. Peak hatch dates in 1987 were in late June - early July, approximately two weeks earlier than in 1986. Mean water temperature, a factor believed to regulate spawning, reached 27°C earlier in 1987 and ultimately reached peaks >2°C higher in 1987 than in 1986.

Estimated young-of-the-year growth rates for bay anchovy at 40-110 days posthatch ranged from 0.20 to 0.47 mm d^{-1}. Methods that included the larval stage in the growth rate estimate (von Bertalanffy model, otolith daily increment method), gave rates of 0.46-0.47 mm d^{-1} in both 1986 and 1987. Methods that did not include growth of premetamorphic stages (modal length progression, one of the regression estimates of standard length on otolith daily increments) generally gave lower rates of 0.20 to 0.46 mm d^{-1}. Zooplankton, the principal food of bay anchovy in the study area, did not differ significantly in abundance between 1986 and 1987 during the July-October period when most anchovy reproduction, growth and recruitment occurred.

In the laboratory, when *Artemia* nauplii diet levels of 10, 20 and 40% of bay anchovy body weight were offered to juvenile anchovies in combination with temperatures of 19, 23 or 27°C, mean consumption rates ranged from 6.8 to 28.0% of anchovy body weight. Consumption was lowest at 19°C and highest at 27°C at each diet level. Weight-specific daily growth coefficients increased significantly with increasing diet levels and temperatures. Daily percentage weight gains ranged from 1.50 to 2.32% at 19°C, from 0.75 to 2.50% at 23°C and from 1.17 to 4.49% at 27°C.

Oxygen consumption increased significantly as weight of anchovy and temperature increased. Mean weight-specific oxygen uptakes ranged from 0.272 $mgO_2/g/h$ at 19°C to 0.439 $mgO_2/g/h$ at 27°C. The weight exponents of oxygen uptake vs anchovy weight regressions ranged from 0.65 at 19°C to 0.73 at 23°C and did not differ significantly among temperatures. The Q_{10} was 2.247, indicating a nearly two-fold expected increase in weight-specific oxygen uptake for a temperature increase from 19° to 27°C.

Caloric energy budgets indicated that assimilation efficiency ranged from 34 to 88% and decreased as diet level increased. Assimilation efficiencies were high (>80%) only at the 10% diet level at each temperature. Despite low assimilation efficiencies, anchovy grew rapidly at high diet levels. Gross growth efficiency ranged from 14.1 to 38.8% and was highest at the 19°C, 10% diet level and the 27°C, 40% diet level. Net growth efficiency, which increased as diet level increased at each temperature, ranged from 18.5% to 59.0%.

The percent of ingested energy allocated to metabolism declined as diet level increased. The metabolic energy, as a fraction of physiologically useful energy, was highest at 23°C and lowest at 19°C. The percent of ingested energy that was excreted increased as diet level increased at each temperature. The highest caloric expenditures for excretion occurred at the lowest temperature (19°C). Maintenance rations, estimated from routine metabolic rates, were 2.62, 4.92 and 7.31% of body weight at 19°, 23° and 27°C, respectively.

Stomach contents of field-collected bay anchovy from a 24-h series in both 1986 and 1987 indicated that copepods, the predominant food, were present in 92% of the stomachs. The other major foods were tintinnids, detritus and diatoms and, less frequently, cladocerans, bivalves, ostracods and polychaetes. Food items found infrequently included barnacle nauplii, amphipods, mysids and crab zoeae. Tremadode parasites occurred in 19% of the stomachs.

There was a distinct feeding periodicity. The major feeding activity occurred from dawn to mid-morning. Minimal feeding occurred from early evening until predawn.

Mean weight-specific stomach contents ($\bar{S}$) of bay anchovy ranged from 0.21 to 3.54% of body weight. The $\bar{S}$ for daylight samples ranged from 1.61% at 17:00 to 3.54% at 09:20. During the night $\bar{S}$ varied from 0.21% at 03:48 to 1.42% at 20:52. There was a strong positive correlation between anchovy length and weight-specific stomach contents. The power functions which described those relationships can be used to predict mean stomach contents for bay anchovy of specific lengths.

The instantaneous stomach evacuation rates (h^{-1}) were estimated in the laboratory and increased significantly with temperature. They were 1.32, 2.26 and 2.50 at 19, 23 and 27°C, respectively. The corresponding estimated 95% digestion times were 2.26, 1.33 and 1.20 hr.

The estimated daily rations, based upon weight-specific stomach contents and stomach evacuation rates, were 9.0, 13.1 and 16.2% of body weight (dry weight basis) at 19, 23 and 27°C, respectively. During summer, bay anchovy in Chesapeake Bay can be expected to consume from 10-20% of their body weight daily. The laboratory energetics experiments had indicated that weight-specific growth rates of juveniles were 1-2% per day when ration was in the 10-16% range, suggesting that similar growth rates could be achieved in the Bay.

Chemical composition of bay anchovy varied in relation to diet level and temperature. Overall ranges of body constituents for wild and experimental anchovy were: moisture, 70.0-77.4%; ash, 9.4-14.5%; protein, 56.1-75.3% and lipid, 11.2-33.7%.

Temperature did not affect the amount of protein, lipid or the condition indices of bay anchovy. Protein, moisture and ash content decreased as diet level increased at each temperature while lipid content, condition indices and

the C/N ratio increased. Lipid content of bay anchovy increased under all laboratory feeding conditions. Temperature had no significant effect on the individual fatty acid profiles, but increases in ration elevated the amount of monounsaturated and depressed the amount of polyunsaturated fatty acids. Anchovy before the feeding experiments had fatty acid profiles like those of wild anchovy, with high amounts of 20:5 and 22:6 polyunsaturated fatty acids that are characteristic of zooplankton and planktivorous fish. After a feeding experiment, fatty acid profiles were transformed and began to resemble the profiles of *Artemia*. The *Artemia*-fed anchovy had depressed levels of 20:5 and 22:6 fatty acids and elevated levels of $18{:}1^{\wedge 9}$ and 18:2.

Oxygen levels below 3.0 mg L^{-1} and 2.5 mg L^{-1} may impact bay anchovy eggs and yolk-sac larvae, respectively. The LC_{50} for eggs was 2.8 mg O_2 L^{-1}. Many eggs that were incubated at <3.0 mg O_2 L^{-1} were alive but did not hatch. The LC_{50} for yolk-sac larvae was 1.6 mg O_2 L^{-1}, indicating that yolk-sac larvae are more tolerant of hypoxic conditions than are eggs.

CHAPTER 1. BACKGROUND, RATIONALE AND OBJECTIVES

E.D. Houde and E.J. Chesney

The bay anchovy (Anchoa mitchilli) is a small, schooling pelagic species in the Chesapeake Bay. Hildebrand and Schroeder (1928) recognized it as the single most abundant fish in the Bay and noted its importance as food for predatory fishes. In recent years it has continued to be the dominant species collected in Chesapeake Bay surveys (Horwitz 1987) and in other mid-Atlantic estuaries (Vouglitois *et al*. 1987). Bay anchovy is common wherever it occurs, its range extending from the Gulf of Maine to the Yucatan coast (Bigelow and Schroeder 1953; Hoese and Moore 1977, Byrne 1982; Morton 1989). Although usually recorded as the single most abundant species in fish surveys along the entire Atlantic and Gulf coast, its biology has been little studied, perhaps because of its small size (<110 mm length) and because it is not harvested by man.

Because of its dominance in the Chesapeake Bay and other coastal/estuarine systems, the bay anchovy is a key contributor to the food of large predatory fishes which are important in both commercial and recreational fisheries. Bay anchovy is recorded as a major food of many Atlantic and Gulf coast fishes (e.g. Bigelow and Schroeder 1953; Merriner 1975; Chao and Musick 1977; Sheridan, Trimm and Baker 1984). Bay anchovy also must play an important role in converting plankton production into usable forage biomass for predators (Baird and Ulanowicz, in press) such as weakfish, summer flounder, striped bass and bluefish in Chesapeake Bay. Because bay anchovy is abundant, forages in large schools, and is dependent in all of its life stages on zooplankton as food (Hildebrand and Schroeder 1928; Detwyler and Houde 1970; Carr and Adams 1973; Homer and Boynton 1978; Livingston 1982; Houde and Lovdal 1984), it may be a significant consumer of zooplankton production. This aspect of bay anchovy ecology is not well understood, although it has important implications for plankton productivity, fish production and environmental health in the Chesapeake Bay.

The potential importance and dominance of bay anchovy in Atlantic coastal/estuarine ecosystems perhaps is best appreciated from results of ichthyoplankton surveys. Its eggs and larvae generally dominate catches, accounting for 60-99% of the ichthyoplankton (Dovel 1971, 1981; Wood *et al*. 1979; Flores-Coto *et al*. 1983; Olney 1983; Houde and Lovdal 1984). Pearson (1941) noted that larval bay anchovy was the dominant fish larva in lower Chesapeake Bay; more recent surveys (Dovel 1971; Wood *et al*. 1979; Olney 1983; Dalton 1987) have confirmed its continuing dominant role. Dovel (1971) found that bay anchovy spawned throughout the entire salinity gradient of Chesapeake Bay and Olney (1983) noted that the reproductive period is protracted, continuing at least from May through August.

Goal and Objectives

An overall goal of the project was to increase knowledge of the population dynamics and energetics of bay anchovy and, where possible, to determine how environmental factors influence its ecology. We chose to confine our field study to the area near the mouth of the Patuxent River and the adjacent frontal zone in the Chesapeake Bay. Laboratory research on feeding, energetics, and oxygen tolerances was carried out at the Chesapeake Biological Laboratory. The following objectives were successfully attained:

1. Determine the monthly age/size structure of the anchovy population near the Patuxent River and related biological characteristics (e.g. abundance, growth rate, size at maturity, spawning, mortality, hatch-date frequencies, recruitment patterns).

2. Describe the characteristics of the frontal zone near the Patuxent River mouth, including seasonal hydrographic conditions and zooplankton abundances.

3. Estimate the fecundity, spawning frequency and daily egg output of individual female bay anchovy.

4. Establish laboratory populations of adult bay anchovy to produce eggs for oxygen tolerance experiments and to be used in energetics experiments.

5. Determine foods and estimate ingestion, growth, and metabolism of bay anchovy in the laboratory and in the Bay. Develop energy budgets.

6. Determine the proximate chemical composition of bay anchovy and carry out a specific analysis of fatty acids in bay anchovy. This objective was added during the third year of the study.

7. Estimate the minimum oxygen tolerances of eggs and yolk-sac larvae of bay anchovy.

Some of the original project objectives were not achieved or were achieved only to a limited extent. The seemingly straightforward objective to analyze bluefish stomachs as a means to evaluate the importance of bay anchovy in its diet failed because bluefish regurgitated most stomach contents during collection. We were unable to evaluate the minimum oxygen tolerance of adult bay anchovy. Determination of bay anchovy distribution and abundance in relation to the tidal front near the mouth of the Patuxent River was only partly achieved, in large part because few anchovy were caught during a field experiment specifically designed to fulfill this objective.

Approaches

Field and laboratory approaches were followed, and are described in detail in Methods sections of following chapters. In the field surveys, repeated trawl collections of bay anchovy were made in 1986 and 1987 to obtain abundance data, and to estimate population vital rate and reproductive parameters. Birth-date frequencies of newly-recruited, young-of-the-year anchovy also were determined from the 1986-87 field collections. Anchovy collections were accompanied by hydrographic measurements and zooplankton abundance determinations. Results based on field data are reported in Chapters 2, 3, 4, 5 and 7.

Laboratory energetics studies in 1988 were completed using juvenile bay anchovy collected by trawl and brought to the laboratory, where they were reared on specified rations and at specified temperatures. Energy budgets, growth rates, rations, assimilation efficiencies and growth efficiencies were obtained. Results are reported in Chapter 6.

Chemical composition of bay anchovy, based on "wild" anchovy and on individuals reared in the laboratory were determined during 1988. Proximate analyses and fatty acid analyses were carried out and are reported in Chapter 8.

Oxygen tolerances of eggs and yolk-sac larvae were estimated in respiration chambers. In 1988, eggs and larvae were obtained from a laboratory population of adults that were induced to spawn via temperature and photoperiod controls. Results are reported in Chapter 9.

CHAPTER 2. THE BIOLOGICAL AND PHYSICAL SETTING

E.D. Houde, E.J. Chesney, C.E. Zastrow and T.A. Newberger

INTRODUCTION

Bay anchovy is distributed throughout the tidal waters of the Chesapeake Bay (Dovel 1971) and is known to have a wide tolerance of salinity and temperature throughout its broad geographic range (Morton 1989). Dovel (1971) and others subsequently have suggested that seasonal changes in distribution occur, and that major spawning occurs in the subestuarine rivers of the Chesapeake Bay, resulting in complex tidally-driven transport patterns of larvae that presumably affect distributions and ultimately recruitment success of bay anchovy. Catch data indicate that adult anchovy are abundant year-round in the Bay proper (Horwitz 1987). Spawning is intense in the open waters of the Bay (Olney 1983; Dalton 1987; Houde, unpublished data), demonstrating that the species is ubiquitous in the Bay and that earlier interpretations that stressed the importance of subestuarine distributions and spawning may have overstated the case.

Bay anchovy schools often are visible on the surface of the Bay on calm days from June to September. The distribution of schools has not been documented but they are not uniform. Most visible schools in mid-Chesapeake Bay are seen along the flanks of the Bay. On some days schools seem to be particularly abundant in the frontal area at the mouth of the Patuxent River, the study area selected for this research.

We had hypothesized that bay anchovy would be most abundant in the tidal front offshore of the Patuxent River mouth (Figure 1), based on visual sightings and the possibility that plankton organisms which serve as anchovy food would be concentrated in the convergent zone. It was difficult to strongly support the hypothesized relationship (Newberger et al., Chapter 2) because of the variability in occurrences and catches of anchovy. Nevertheless, the Patuxent River mouth and frontal region served as a convenient study area in which to survey anchovy abundance and to provide samples for a detailed assessment of its population biology, including studies on energetics and trophic relationships.

METHODS

Anchovy trawl collections were made in 1986 and 1987 along a transect of stations (Figure 1). Hydrography (temperature and salinity) was described on each collection date at each station. Zooplankton from pump samples was collected at some stations on all anchovy sampling dates. The most consistent and intensive collection efforts were made at Station 7, at the outer edge of the area where the tidal front usually was visible. Newberger et al. (Chapter 3) provide details of methods and results of the anchovy collection efforts. Here, we summarize information on hydrographic conditions and zooplankton abundances in 1986 and 1987 during the collecting period.

Temperature and salinities were recorded at 1-m depth intervals, using a Beckman RS5-3 Thermistor/Salinometer in 1986 and a YSI Model 33 meter in 1987. Dissolved oxygens were not measured although, in retrospect, it would have been desirable to have obtained oxygen data. It is possible from changing

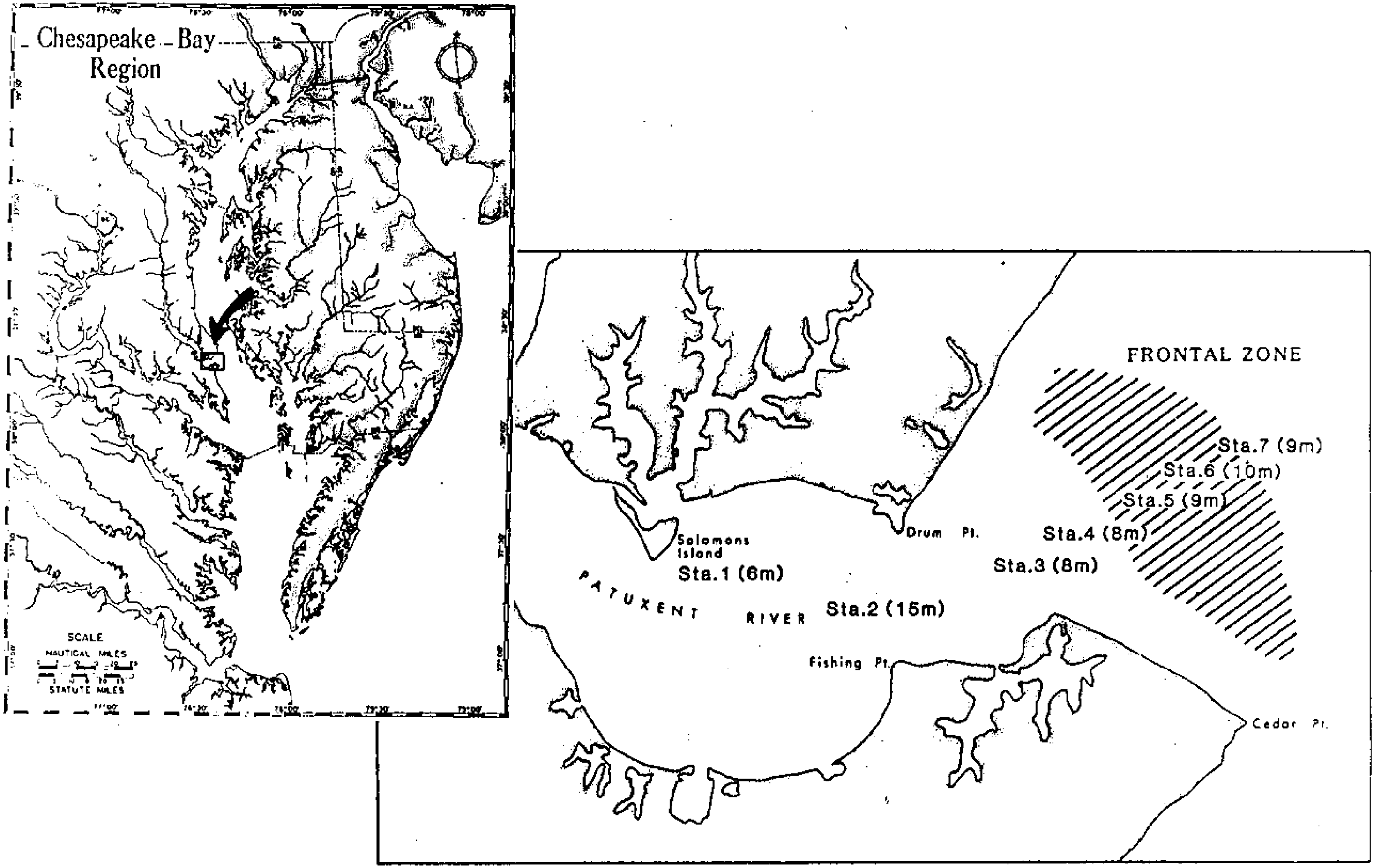

Figure 1. The mouth of the Patuxent River and frontal area offshore that were the 1986-1987 study area for the bay anchovy ecology research. Stations at which bay anchovy trawl collections were made and hydrographic conditions measured are indicated.

characteristics of the pycnocline and bottom salinities to infer probable low oxygen events during summer months.

Zooplankton was pumped from the surface, from the pycnocline (or mid-depth) and from 1-m above the bottom. A centrifugal pump fitted with a 51-mm hose was submerged to sampling depth. Pumping rate was 50-70 liters per min. Duplicate samples of 100 liters from each depth were pumped onto a 53-μm screen and preserved in 5% buffered formalin. Only the samples from Station 7 were analyzed and are reported. In the laboratory, plankton samples were brought to a standard volume and 4 ml aliquots were counted to obtain estimates of density, reported as numbers per liter. Here, we report for each collection date only mean water column densities of adult copepods, copepod nauplii, and total zooplankton. Taxa-specific data are available on adult copepods and cladocera and could be analyzed in the future.

In 1986 we routinely operated a Lowrance 170 kHz chart-recording, depth sounder from the outboard-powered boat that we used to trawl for anchovies. We made no attempt to analyze the chart recordings but we present examples to illustrate how such echograms could be used to quantify or index bay anchovy abundance and patchiness in the Chesapeake Bay. Acoustic methods have been proposed for future bay anchovy biomass assessments (Houde and Brandt 1989--Maryland Sea Grant Proposal).

RESULTS

Temperature

Seasonal surface temperatures at Station 7 peaked during late July in 1986 and in early August 1987. Temperatures ≥27°C occurred 10-15 days earlier in 1987 and the peak of 29.8°C in 1987 was 1.5°C higher than the peak temperature in 1986 (Figure 2). Surface and bottom temperatures >27°C were sustained for a longer period in 1987 than in 1986.

Monthly mean surface temperatures for the Station 7 data in July through October indicate that 1987 was a particularly warm summer (Table 1a) compared to 1986 or to a long-term average compiled by NOAA from surface temperatures at Solomons, Maryland (Kelly 1988).

Salinity

Seasonal increases in surface salinity were observed at Station 7. Both surface and near-bottom salinities were higher in 1986 than for corresponding dates in 1987 (Figure 3). Surface salinities from July to November ranged from 14.1 to 18.8 ppt in 1986 and from 12.9 to 14.9 ppt in 1987. Salinities near-bottom were more variable from week to week than were surface salinities. Weekly bottom salinities at Station 7 varied by as much as 5.5 ppt during the July to November period of 1986 but varied by a maximum of 1.1 ppt in 1987 for those months. Bottom salinities sometimes varied by ≥4 ppt from week to week during April to June 1987, but no corresponding data for the same period were available in 1986.

Mean surface salinities at Station 7 in July - October 1986 and in July - August 1987 were above the long-term mean for Solomons, Maryland (Table 1b). September and October 1987 surface salinities at Station 7 were lower than the

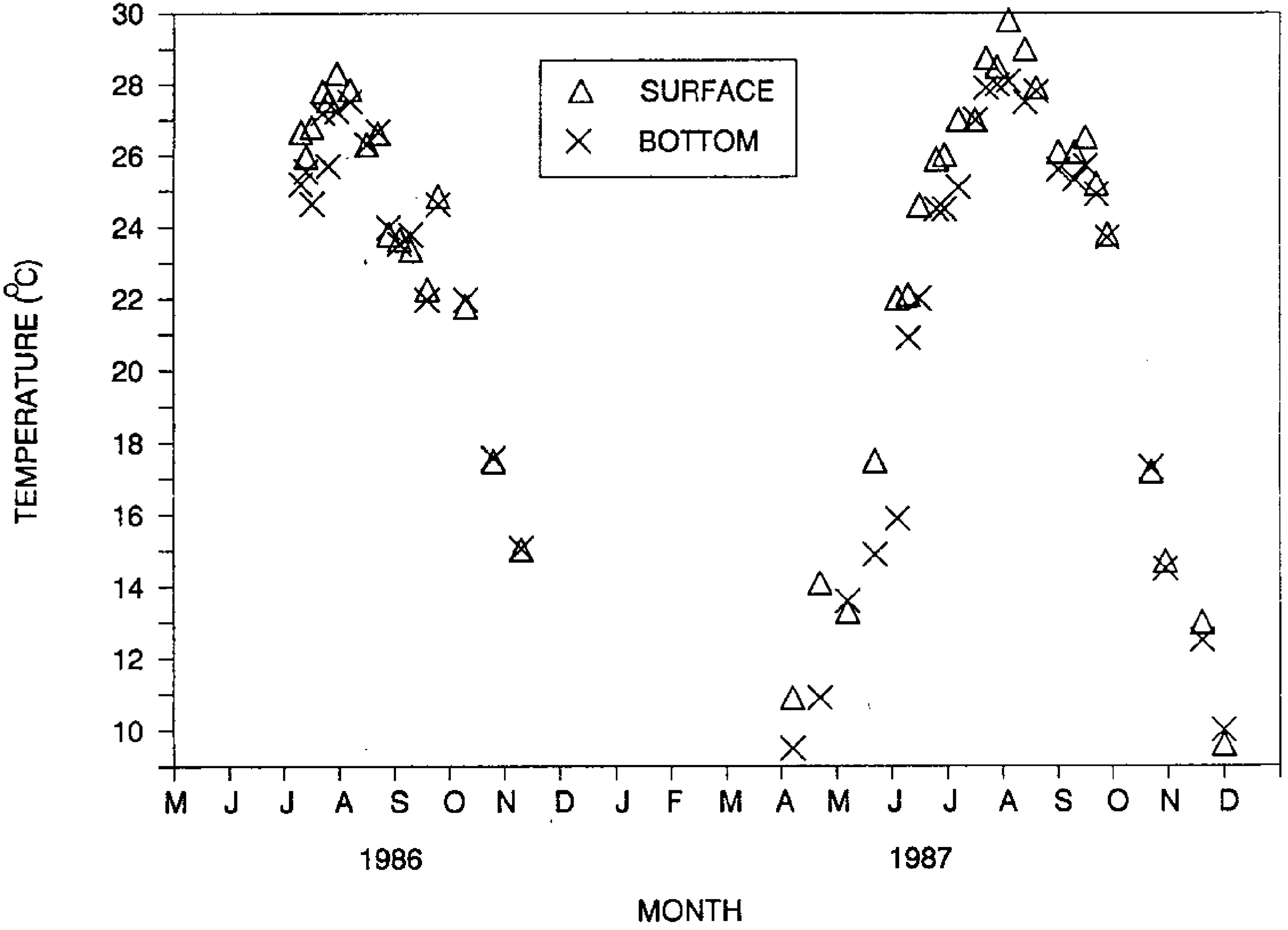

Figure 2. Surface and bottom temperatures at Station 7 during the 1986-1987 bay anchovy field program.

Table 1a. Mean surface temperatures for July through October 1986 and 1987 at Station 7 compared to the long-term mean for Solomons, Maryland (Kelly 1988). July through October was selected because these are the months when most growth, reproduction and recruitment of bay anchovy occur.

	July	August	September	October
1986	27.2	26.2	23.5	19.6
1987	27.8	28.9	26.0	18.6
Long-term $\bar{x}$	26.7	26.7	24.3	18.7

Table 1b. Mean surface salinities for July through October 1986 and 1987 at Station 7 compared to the long-term mean for Solomons, Maryland (Kelly 1988). July through October was selected because these are the months when most growth, reproduction and recruitment of bay anchovy occur.

	July	August	September	October
1986	15.3	17.0	17.4	18.6
1987	13.5	14.3	14.5	14.5
Long-term $\bar{X}$	12.6	13.5	14.8	16.0

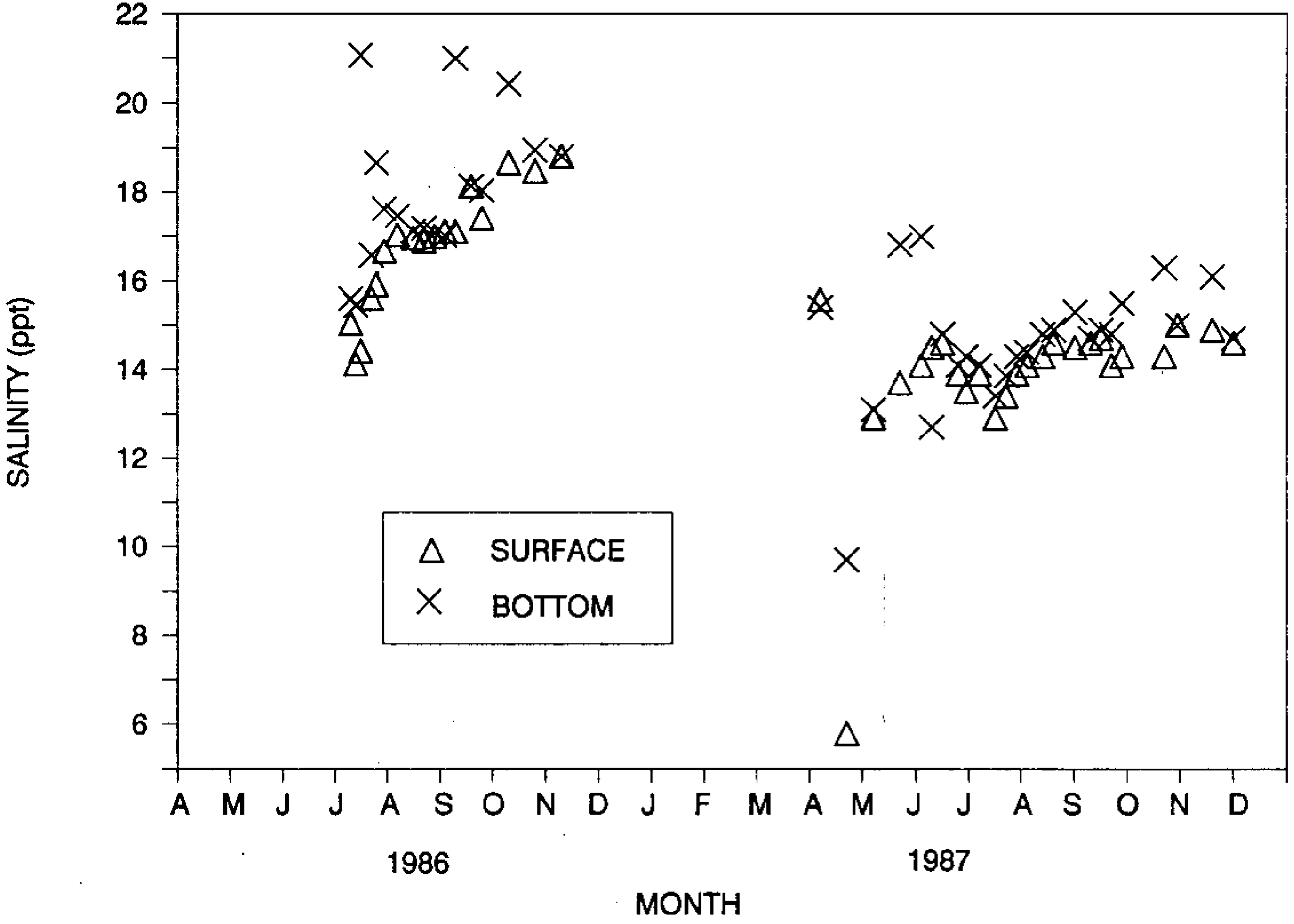

Figure 3. Surface and bottom salinities at Station 7 during the 1986-1987 bay anchovy field program.

long-term mean (Kelly 1988).

The Frontal Region

The bottom topography and examples of depth-contoured temperature - salinity profiles along the sampling transect (Figure 1) are illustrated in Figures 4 and 5. These examples illustrate the stratified summer conditions in the frontal region that were observed during the study. A moderate to well-developed pycnocline usually was present. Bottom salinities sometimes changed significantly within a few-day period (Figures 4 and 5), especially in 1986, indicating occasional transport into the study area of high-salinity and presumably low-oxygen bottom waters.

The frontal area often was visible and characterized by a debris-laden slick in the shaded region indicated in Figure 1. The slick occasionally extended as far shoreward as Station 3 but usually was bounded by the area between Stations 4 and 7. The slick, when visible, was most prominent on ebbing tides. It formed an arc across the frontal zone and sometimes extended several kilometers to the south.

On some days the contoured profiles along the sampling transect illustrated the structure associated with the front. The isotherms and isopycnals domed in the frontal area (Figures 4 and 5). Relatively saline water was displaced toward the surface at the front. The feature apparently resulted from ebbing Patuxent River water converging with the offshore Bay water and bottom topography effects. The deep depression in the Patuxent River mouth between Stations 2 and 3 shallows quickly near Station 3 before deepening again bayward of it (Figures 1 and 4). Doming of the isotherms and isopycnals occurs at the ridge and just bayward of it between Stations 3 and 5 (Figures 4 and 5), suggesting that ebbing Patuxent River water is steered toward surface in the frontal zone by the bottom topography.

Zooplankton

Zooplankton was abundant in 1986 and 1987 at Station 7, the primary station where anchovies were sampled. Densities of copepods, copepod nauplii and total zooplankton retained on the 53-µm screen for the weekly collections are given in Figure 6. For comparable periods (July - October), mean copepodite and copepod densities were nearly identical at 42.9 and 43.8 per liter in 1986 and 1987, respectively (Table 2). Most of the adult copepods during these months were *Acartia tonsa* and *Oithona* sp. For the July - October period, copepod nauplii mean densities were 120.9 and 196.6 per liter in 1986 and 1987, respectively (Table 2), and total zooplankton mean densities were 166.6 and 241.9 per liter in 1986 and 1987. The densities of the three zooplankton categories did not differ significantly between years in the July - October period (Mann-Whitney Test, $P > .50$ for adult copepods and $P > .10$ for nauplii and total zooplankton).

There were seasonal changes in copepod densities that can be seen in 1987 when sampling extended from April through September (Figure 6). Copepod densities were low from April to early June, increased after mid-June, and declined in September. Patterns of copepod nauplii densities are not so clear, although they also apparently were most abundant from late June through

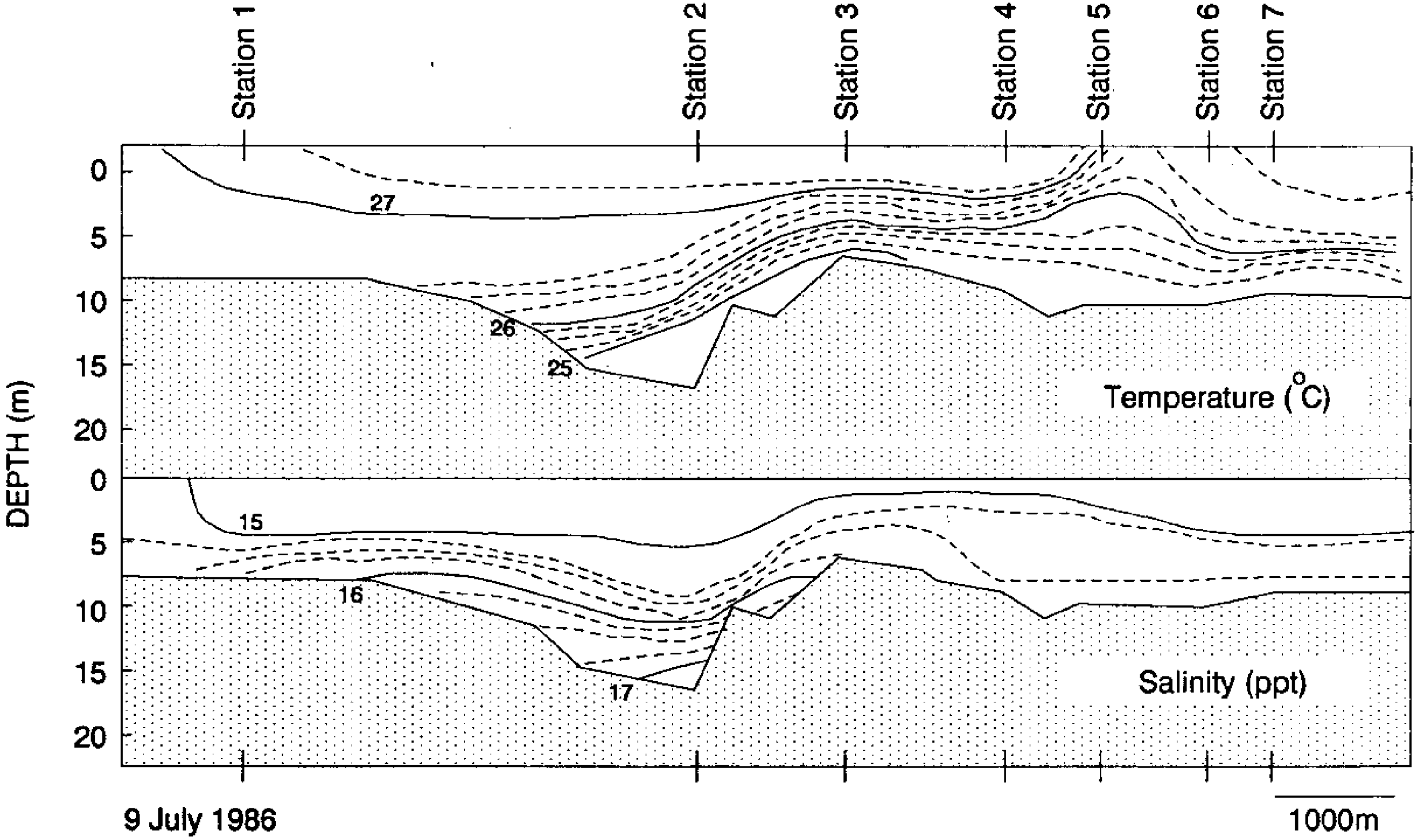

Figure 4. Contoured temperature and salinity profiles in the frontal zone near the Patuxent River mouth (Figure 1) on 9 July 1986.

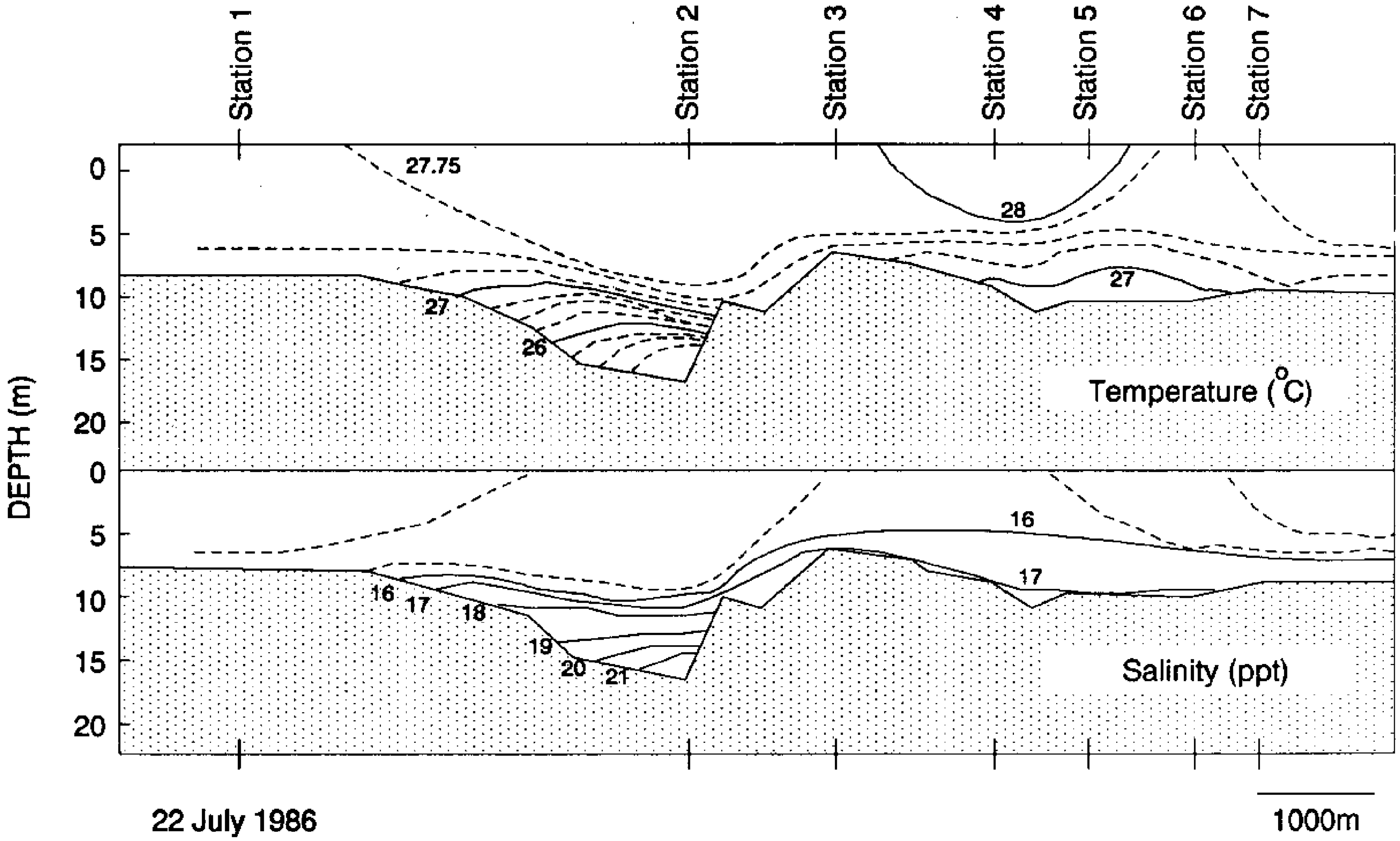

Figure 5. Contoured temperature and salinity profiles in the frontal zone near the Patuxent River mouth (Figure 1) on 22 July 1986.

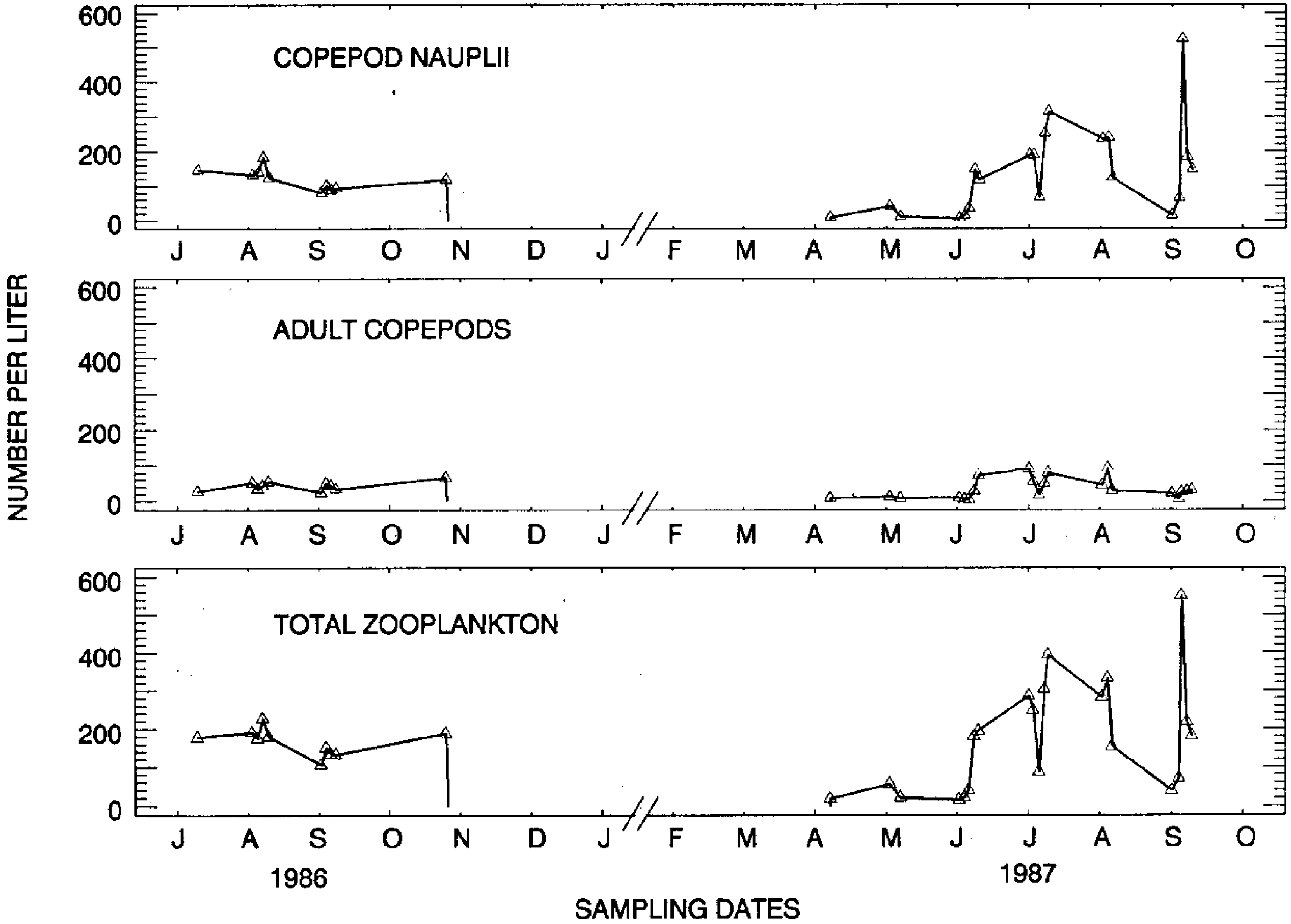

Figure 6. Abundances (number per liter) of total zooplankton, copepod nauplii, and copepodites/copepods at Station 7, 1986-1987. No samples were collected from November 1986 through March 1987.

Table 2. Zooplankton mean densities at Station 7, the standard anchovy trawl station, located at the bayward edge of the frontal zone near the Patuxent River (Figu 1). (s = standard deviation; c.v. = coefficient of variation).

Year		Category								
		Copepodites & Copepods			Copepod Nauplii			Total Zooplankton		
	n	$\bar{X}$	s	c.v.	$\bar{X}$	s	c.v.	$\bar{X}$	s	c.v.
1986 (July-Oct)	10	42.9	13.2	0.31	120.9	31.3	0.26	166.6	35.2	0.21
1987 (Apr-Sept)	22	33.4	28.5	0.85	146.3	129.0	0.88	181.8	145.9	0.80
1987 (July-Sept)	13	43.8	28.5	0.65	196.6	129.7	0.66	241.9	141.5	0.59

August. Variability in zooplankton densities among sampling dates, as expressed by the coefficient of variation ($^s/\bar{x}$), was 2-3 times higher in 1987 than in 1986 for each of the categories (Table 2).

Echograms

Echo traces from the 170 kHz sounder were a good indicator of bay anchovy schools and also of patchiness in distribution within the sampling area. Traces that were obtained indicated that anchovy were a primary source of marks recorded by the sounder (Figure 7). No attempt was made to quantify the echo traces. But, there was an obvious relationship between density of traces in the water column and anchovy 10-min trawl catches. In the example provided (Figure 7), the echogram with the light traces was associated with a catch of 3 anchovies while that with the heavy traces had an associated catch of 1,331 anchovies.

The sounder recordings also demonstrated the strong patchiness of bay anchovy that sometimes was present in the study area. The two traces (Figure 7) were made on 21 August 1986, within 20 min and 0.5 nautical mile of each other.

DISCUSSION

Temperatures in the study area during summer, when bay anchovy food consumption, growth, and reproductive activity are maximum, were higher in 1987 than in 1986. Monthly mean surface temperatures in summer 1986 differed by only 0.5 to 0.8°C from the long-term means for summer temperatures near Solomons (Kelly 1988). The 1987 surface temperatures were from 1 to 2°C higher than the long-term mean surface temperatures. Furthermore, temperatures peaked 10-15 days earlier in 1987 than in 1986, which may have accelerated the bay anchovy reproductive season and subsequent recruitment of age 0+ anchovy. Newberger et al. (Chapter 3) collected significant numbers of young-of-the-year anchovy in mid- to late July 1987, two weeks earlier than in 1986. A birth-date analysis on age 0+ bay anchovy from late August to October collections indicated that peak hatch dates in 1987 occurred in the period 25 June-10 July, approximately 15-20 days earlier than in 1986 (Morin and Houde, Chapter 5).

Surface and water column salinities were approximately 2-3 ppt higher during summer 1986 than in 1987. Because bay anchovy are well adapted to tolerate wide salinity ranges (Morton 1989) and occur throughout the Chesapeake Bay (Hildebrand and Schroeder 1928; Dovel 1971), the observed annual differences in salinity may have had little effect on anchovy occurrence and population dynamics.

Salinities within 1 m of bottom were more variable among weekly sampling periods from July to November 1986 than for the corresponding period of 1987. Summer months' variability in near-bottom salinities is caused in part by occasional cross-Bay intrusions of high-salinity water from the deep trough of the Bay during wind-forced pycnocline tilting (Malone et al. 1986). The consequences of such intrusions to bay anchovy biology are unknown, but if such intrusions of high salinity, and presumably hypoxic, water are frequent, anchovy distribution and possibly dynamics may be affected. Weekly salinity

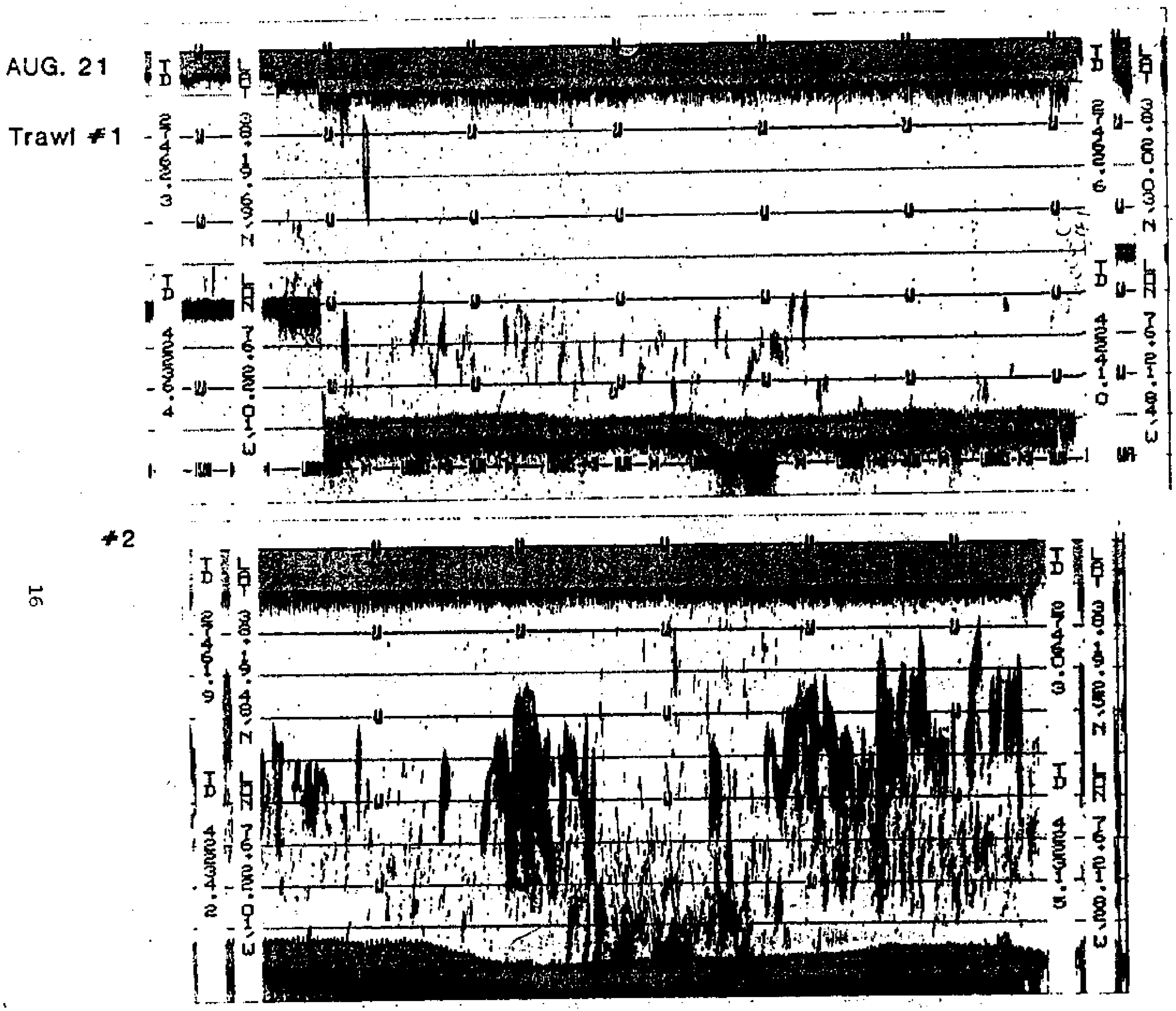

Figure 7. Echograms from a 170 kHz sounder made on 21 August 1986 near Station 7 (Figure 1). The heavy marks on the lower trace are believed to represent bay anchovy schools. Trawl catches coincident with the traces were 3 (upper trace) and 1,331 (lower trace). Bottom depth is approximately 9 m.

differences as great as 5.5 ppt in the bottom 10-15% of the water column on the sampling transect occurred in 1986, indicating more dynamic physical exchange between waters of the study area and deep Bay in that year than in 1987, when weekly salinity differences from July - September never exceeded 1.1 ppt. If the 1986 salinity fluctuations near the seabed of the study area resemble those that occurred more widely in the Bay, there was no apparent negative consequence for 1986 recruitment success in bay anchovy. Recruitment of age 0+ bay anchovy in 1986, based on trawl catch-per-unit-effort in the study area, was several times higher in 1986 than in 1987 (Newberger et al. Chapter 3).

The frontal zone in which the study was carried out is a dynamic area influenced by river discharge, tidal effects and bottom topography that may affect anchovy abundance and occurrence. A deep basin in the river mouth, a ridgelike sill immediately bayward of the basin, and a gradually deepening profile bayward of the sill characterize the area. This topography and the location of the study area between Cove Point to the north and Cedar Point to the south are believed to provide conditions suitable for development of a tidal convergence bayward of the river mouth. Variability in bay anchovy trawl catch-per-unit-effort made it impossible to demonstrate that abundance was enhanced in the zone of convergence, but catches generally increased in an offshore direction, with mean CPUE highest in the area where the front often was visible (Newberger et al., Chapter 3). A specific 4-day frontal zone study in August 1987 was designed and carried out to assess the possible role of the frontal zone in aggregating bay anchovy (Newberger et al., Chapter 3). Unfortunately, few anchovy were collected during that experiment, making it impossible to quantify relationships between the convergent zone and anchovy ecology.

There were no obvious differences in zooplankton abundances between 1986 and 1987 in the study area that might explain the greater mean anchovy abundances (Newberger et al., Chapter 3). None of the three major categories - copepods, copepod nauplii, or total zooplankton - were judged to be significantly different in mean densities between years during July-October, the primary period of reproduction, larval growth, and recruitment of age 0+ anchovy. Densities of copepod nauplii, a major food of bay anchovy larvae, were similar to those observed in Biscayne Bay, Florida in studies on bay anchovy larval ecology (Houde and Lovdal 1984; Leak 1984). Copepods, the most common food item in juvenile and adult bay anchovy stomachs during this study (Vazquez and Houde, Chapter 7), were abundant in the study area from July to November in each year.

Although mean densities of zooplankton were similar in each year, the day-to-day variability in densities within the study area was more than twice as high in 1987 as in 1986. It is not known what influence, if any, this variability might have had on the relatively low abundances and low recruitment of bay anchovy that was observed in the study area during 1987, although extensive fluctuations in copepod nauplii abundances might have been a factor affecting survival and growth of anchovy larvae.

Mean densities of copepods near Calvert Cliffs, a site 15 km north of the bay anchovy study site and also on the western side of the Chesapeake Bay, ranged from 11.8 to 36.8 per liter for July to September periods from 1976 to

1980 (data summarized from Olson 1987). The Calvert Cliff copepod densities are lower than those estimated near the mouth of the Patuxent River in 1986 and 1987. The five-year mean for Calvert Cliffs ($\bar{x}$= 22.1 per liter) is approximately one-half that for the two years near the Patuxent River mouth ($\bar{x}$ = 43.4 per liter). Copepod nauplii densities at Calvert Cliffs (5.4 to 68.9 per liter) were very much lower than those at Patuxent River (120.9 and 196.6 per liter) but the 73-µm mesh in the Calvert Cliffs study probably allowed most nauplii to escape. Densities of copepods near the Patuxent River anchovy study area might be higher than at other sites on the western side of the Bay, but this possibility cannot be substantiated without synoptic studies to compare the areas.

CHAPTER 3. RELATIVE ABUNDANCE, AGE, GROWTH AND MORTALITY OF BAY ANCHOVY (*ANCHOA MITCHILLI*) IN THE MID-CHESAPEAKE BAY

T.A. Newberger, E.D. Houde and E.J. Chesney

INTRODUCTION

The bay anchovy, *Anchoa mitchilli*, (family Engraulidae) is abundant and important as forage for several commercially important fishes in the Chesapeake Bay. Anchovy is eaten by weakfish, striped bass, bluefish and summer flounder (Homer and Boynton 1978; Merriner 1975; Richards 1976; Schaeffer 1970). It is believed to be the most abundant fish in the Chesapeake Bay and perhaps in the entire coastal western north Atlantic (Hildebrand and Schroeder 1928). Bay anchovy is widely distributed and abundant throughout its range over the continental shelf and in coastal bays and estuaries from the Gulf of Maine to the coast of Brazil (Hildebrand 1963). It also is found in coastal regions of the Gulf of Mexico from Florida to the Yucatan peninsula (Hoese and Moore 1977). Bay anchovy is a small planktivorous fish that generally does not exceed 110 mm total length (Hildebrand and Schroeder 1928). Nevertheless, this very abundant species is believed to be a major link in the food chain through its role in the conversion of planktonic biomass into available forage for larger piscivorous fishes (Hildebrand and Schroeder 1928; Baird and Ulanowicz 1990). There are no commercial fisheries for bay anchovy.

Despite its important role in the ecology of the Chesapeake Bay, there is little knowledge of bay anchovy population biology. Studies on this species in the Chesapeake Bay mainly have focused on the egg and larval stages, although some research has examined aspects of adult bay anchovy ecology. Homer and Boynton (1978) analyzed stomachs of fishes from the Calvert Cliffs region of the Chesapeake Bay and demonstrated that bay anchovy is a significant component of the diets of many piscivorous species. Horwitz (1987) summarized catch data from the Calvert Cliffs region of the Chesapeake Bay. Olney (1983) reported that bay anchovy spawning in the lower Chesapeake Bay occurred between May and August and that its eggs and larvae accounted for 96 and 88 percent, respectively, of the total number of fish eggs and larvae collected. Dalton (1987) studied the abundance and distribution of bay anchovy eggs and larvae between 1971 and 1978 in the mid-Chesapeake Bay. She found that egg production varied among years, but that during summer bay anchovy comprised 99 and 67%, respectively, of all fish eggs and larvae collected.

Studies of adult bay anchovy ecology in regions other than the Chesapeake Bay are primarily from Delaware Bay and Barnegat Bay, New Jersey. Stevenson (1958) addressed several aspects of bay anchovy ecology in Delaware Bay including relative abundance, distribution, reproductive biology, and feeding. However, he could not develop a technique to successfully age bay anchovy and thus could not accurately estimate adult growth and mortality rates. PSEG (1984) compiled and synthesized information on bay anchovy, including aspects of both adult and early life stages. However, their growth model and size-at-age data did not adequately describe observed size-at-age of bay anchovy from the Chesapeake Bay. Vouglitois *et al*. (1987) documented and discussed the seasonal abundance and distribution of bay anchovy in Barnegat Bay.

An age and growth analysis is an integral component of any population dynamics study. Estimates of growth rates, size-at-age, life span, abundance-at-age, and age-at-maturity are products of an age and growth study. All are dependent upon accurate aging of individuals in the population. Determining the age structure of a population allows the relative abundances of annual cohorts to be estimated and recruitment variability to be inferred. By following the decline in abundances of cohorts with time, total mortality (which in an unfished population equals natural mortality), can be estimated. Similarly, increases in size and weight of individuals in specific cohorts can provide growth rate estimates. The parameters of growth models are dependent upon size-at-age data. Determination of growth rate is essential in yield models that are used to assess populations and to estimate sustainable yields to man or to other predators (Gulland 1983).

Objectives of this study were to develop an effective method to age bay anchovy; to determine size-at-age and length-weight relationships; to estimate growth and mortality rates; to determine population age structure and maximum age; to fit a growth model to the size-at-age data; and to examine temporal and spatial relative abundance and its variability in the mid-Chesapeake Bay.

METHODS

Field Collections

Sampling was conducted from July 1986 to December 1987 from 7-m (1986) and 8-m (1987) outboard powered boats. Each vessel was equipped with a fish finder and Loran C. In addition, a 170 kHz recording sounder was used in 1986. In 1986, samples were collected weekly from July to September and twice monthly from October through November. In 1987, samples were collected in each month except January. Sampling in 1987 was weekly from May to September, monthly in December and February and twice monthly in remaining months. Except on one date, anchovies were collected only at Station 7 in 1986, but on a transect of five stations in 1987 (Figure 8, Stations 1,2,3,5,7). Because anchovies were rare at the transect stations during winter (February and March), trawl-tows were made at a mid-Bay site east of the regular trawling stations in approximately 30 m of water during those two months.

Anchovy sampling was standardized to 10 minutes of mid-depth trawling at 2-3 knots using a 4.9 m semi-balloon otter trawl with 3 mm stretched-mesh codend liner. Duplicate tows were made at station 7 on each sampling date. A single tow was made on each sampling date at the remaining 1987 trawling stations. All anchovies were immediately fixed in 10% buffered formalin. Water temperature, salinity, and conductivity also were recorded at each station at 1-m depth intervals. Zooplankton was collected at Station 7 in each year by pumping 100 liters of water from three discrete depths (surface, 5 m, and near bottom) through a 53-µm mesh net. In 1986, acoustic records of nekton and large planktonic organisms were collected during the trawl tows with a 170 kHz Lowrance recording fish finder. Additional anchovy, zooplankton and hydrographic data samples were collected every 6 hr during two 24-hr series at Station 7 that were completed on 29-30 June 1986 and on 30 June-1 July 1987.

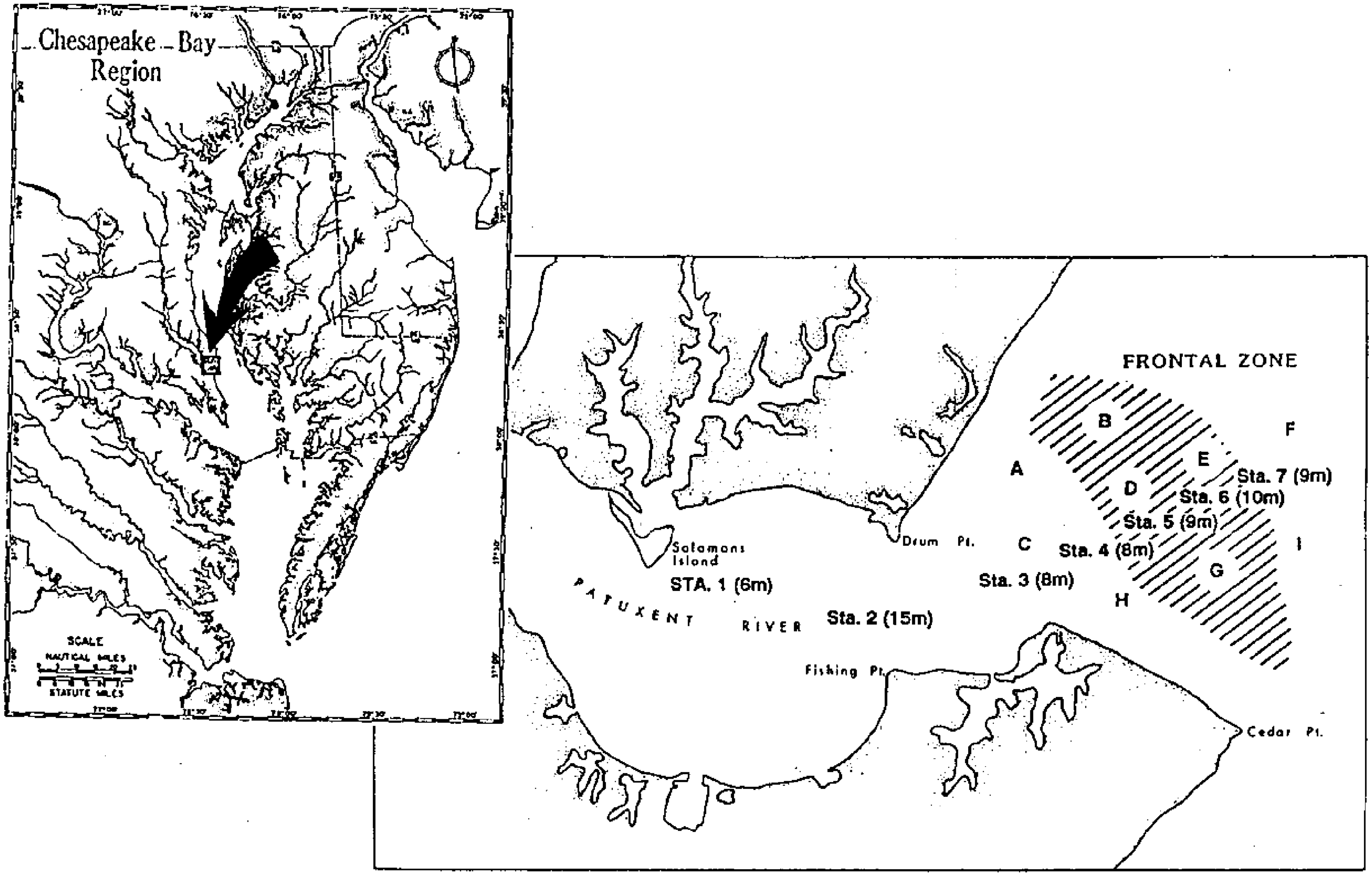

Figure 8. Bay anchovy sampling area in the mouth of the Patuxent River and adjacent frontal zone. Sampling stations and depths of the seven transect stations (stations 1-7) and "frontal zone" stations (stations A-I) are illustrated.

In 1987 intensive sampling was conducted for five days at a grid of stations in the Patuxent River mouth (Figure 8, Stations A-I) to study anchovy distribution relative to a tidal front (see Houde et al., Chapter 2). Some anchovies used in the aging analysis were collected in spring 1986 in the Patuxent River at the mouth of Saint Leonard's Creek, several km upriver from the study's usual transect stations.

Laboratory Procedures

The anchovy samples were drained and rinsed with water after two days in 10% formalin. The fish were soaked for at least two hr in water before storing in 70% ethanol. The total wet-weight of the catch was measured with a top-loading balance to the nearest 1.0 g. The number of anchovies was counted if the catch was <300 fish. For larger catches, three samples of 50 anchovies were weighed to estimate the mean anchovy weight. The total number of fish in the collection was estimated by dividing the total catch weight by the estimated mean anchovy weight.

Length, weight, and sex were determined for up to 100 anchovies selected randomly from the standard station (Figure 8, Station 7) catches on each sampling date. Lengths of an additional 100 randomly selected fish also were measured. When the standard station catches were small (<50 anchovies), other stations' catches were substituted. For samples with <100 fish, all fish were weighed, measured and sexed. Length was measured as fork-length (the distance between the tip of the snout and the medial rays of the tail) to the nearest 1.0 mm and weight was obtained as wet weight to the nearest 0.01 g. Sex was determined by dissection and gonad examination at 35-75X magnification. Ovaries were recognized by their rounded appearance, soft texture, and sometimes the presence of large yolked oocytes. Testes were flatter, had sharp edges, a firm texture and no large visible cells (Stevenson 1958). Winter-collected anchovies and young-of-the-year anchovies were more difficult to sex and often required gonad examination under higher magnification. Generally, fish of ≥25 mm fork length could be sexed confidently.

Initially, otoliths were not removed at the time that length, weight, and sex were determined. In each month of collection, ten to 15 sagittae were extracted from anchovies in each of three anchovy length intervals; large (>65 mm), medium (45-65 mm) and small (<45 mm). Saggitae are the largest of the three otolith pairs and, in bay anchovy, were the only otoliths that exhibited annual increments at 35-75X magnification. It became apparent that if otoliths were not removed from a fish within one month after fixation and preservation, degradation ensued, despite the effort of rinsing the formalin from the fish. Degraded otoliths appeared chalky and were difficult or impossible to read. Therefore, beginning with 1987 collections, otoliths were extracted within two weeks of sample preservation.

Additionally, a more exhaustive otolith sampling procedure was employed in 1987. Five otolith pairs from each five mm size-class of anchovy were extracted from randomly-sampled fish. Otoliths were extracted from fish other than those in the two random samples of 100 only if there were insufficient numbers of anchovies within a five mm length-class to obtain five otolith pairs. This sampling procedure ensured that all length classes represented in each collection were sampled for otoliths and that the most abundant length classes were not oversampled. Because of this procedure, aged individuals were not a random sample of the anchovy lengths represented in the collections.

More than 1,000 otolith pairs were obtained from the anchovies. Otoliths were extracted with fine forceps under 10-20X magnification and then cleaned in 70% ethanol. A small artist's brush was used to tease clinging membranes from otoliths. The brush also was the best tool to handle and manipulate otoliths with minimal risk of breaking them. After drying on a blotter, all otoliths were stored dry in a plastic tray with drilled holes aligned in rows and columns. Each otolith pair in a tray was identified uniquely by its column and row number. Data recorded for each otolith pair included date of capture, time of capture, station number, fork length, weight, sex, and otolith sample number.

Several methods were tested to prepare otoliths for reading and measurements. Larger otoliths, usually from older fish, were often too thick to observe annuli without further processing. However, approximately 75% of extracted otoliths could be read by placing them in water or 10% ethanol in a black tray and examining them at 35-75X with reflected light. A polarizing filter placed between the otolith and the objective lens greatly improved readability. Clearing methods, which involved immersing otoliths in cedar wood oil, clove oil, or 3:2 glycerin:ethanol (Bagenal and Tesch 1978) for periods ranging from several hours to two weeks, did not improve readability.

Several otolith grinding methods were tried (Jearld 1983). Otoliths were mounted on glass slides with epoxy resin and ground to the focus (Figure 9) with 600 grit wet-dry carborundum paper and polished with 0.3-µm alumina compound. Although this method improved the readability of some otoliths, results were not consistent. A second method involved grinding and polishing unmounted otoliths with 600 grit carborundum paper and alumina compound, respectively. The advantage of this method was that otoliths could be ground on both sides, resulting in thin sections. Preparation time was reasonable and readability often was greatly improved.

Because sagittae of fish may grow asymmetrically, especially in older individuals when increments often are deposited only on the interior (sulcal) face (Brothers 1987), otolith transverse sections (Figure 9) were prepared for some otoliths to allow potentially obscured annual marks (annuli) to be observed. Thin transverse sections from 12 of the largest bay anchovy otoliths were prepared using an Isomet saw so that ages estimated by two otolith preparation methods could be compared. The Isomet saw has two thin, motor-driven circular diamond blades that are separated by a thin spacer (the thickness of the spacer determines the thickness of the otolith section). The sections were mounted on glass slides and polished with 0.3-µm alumina compound before being examined at 40X with transmitted polarized light. Otolith thin sections usually were easier to read than were the same otoliths observed whole. However, care must be taken to insure that transverse sections include the otolith focus (Figure 9) to prevent loss of annuli and age underestimation. Sectioned otoliths were read from a different plane than were whole otoliths and thus they could not be used to generate back-calculated fork lengths from an otolith radius - fork-length relationship that had been derived from whole otolith measurements. For sectioned otoliths, back-calcu-

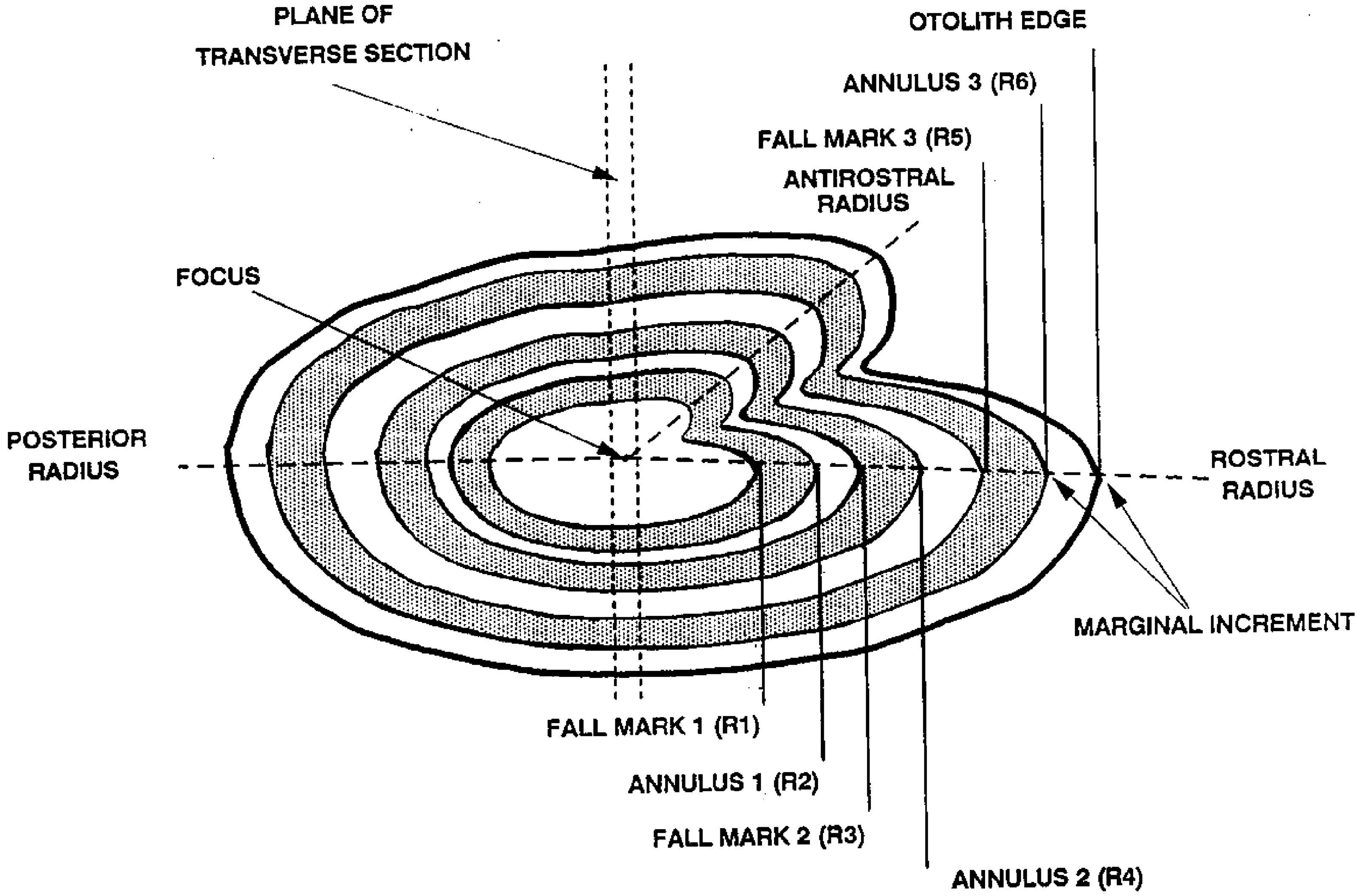

Figure 9. Diagram of an otolith from an age 3+ anchovy indicating the focus, annuli, fall marks, rostral radius, antirostral radius and posterior radius. The plane of an otolith transverse section also is indicated.

lation measurements either were made before sectioning or were made from the unsectioned otolith of the pair. If an Isomet saw had been readily available throughout the study, sectioning would have been the preferred procedure for larger otoliths that were difficult to read.

Some otoliths also were prepared for reading under a scanning electron microscope (SEM). This process involved mounting otoliths in acrylic resin, grinding to the focus, polishing with 0.3-µm alumina compound and etching with 10% acetic acid. The grinding, polishing, and etching often required repeating until a satisfactory image could be generated. Due to the labor required and inconsistent results, routine SEM examination of otoliths for annuli was not practical.

Scales from 25 anchovies were examined to age the fish and to compare ages so obtained with those estimated from their otoliths. Scales were removed from near the base of the anal fin or behind the operculum and scrubbed with an artist's brush to remove membranes and surface pigments. The scales were mounted between two glass slides and examined under a compound microscope at 40X with transmitted light. Because relatively few scales remained attached to anchovies that had been captured and preserved, and because many scales were regenerates, scale analysis was not practical for routine aging purposes.

Otolith Data Collection

In addition to aging fish by counting otolith annuli, otolith measurements were made to establish an otolith size - body size relationship to allow back-calculation of estimated length at age (Bagenal and Tesch 1978) and to validate annual increment (annulus) deposition (Beamish and McFarlane 1983). An annulus was defined as the interface between an opaque and hyaline zone where the opaque zone was more centrally located (proximal) compared to the hyaline zone (Fitch 1951). We defined the fall mark as the interface between a hyaline and opaque zone where the hyaline zone was proximal to the opaque zone. This interface was clearly visible in bay anchovy otoliths but was not as distinct as were annuli. The fall mark apparently was laid down over a relatively longer period (mid-September to mid-October) compared to an annulus.

To determine the otolith radius that was best related to fork length, 60 otoliths were measured from the focus to margin along three different radii. These were defined as the rostral radius, the posterior radius and the antirostral radius (Figure 9). Linear regressions of fork length on each otolith radius indicated that the rostral radius provided the best relationship. Annuli and fall marks along the rostral radius were more distinct. Furthermore, measurement error was reduced because the otolith is longest along that axis.

Both sagittae from each fish were examined to determine age but only the right sagitta was measured. Two separate otolith readings were obtained to confirm age, but otolith measurements were not repeated. The otolith focus was located by rotating a polarizing filter between the otolith and the objective lens of the stereomicroscope. An hour-glass shaped region of scattered light was observed that would rotate as the filter was rotated, with the narrow region of the scatter lying directly over the otolith focus. Measurements from the focus to each annulus, fall mark, and otolith edge (Figure 9) were obtained with a microscope ocular dial micrometer at 37.5 or 75X .

An otolith was rejected from the analysis based on one or more of the following criteria: 1) nonreadablility due to preservative-induced otolith degradation; 2) conflicting age estimates between replicate readings; and 3) presence of false annuli. False annuli were identified by their very narrow hyaline and opaque zones compared to adjacent annuli and often were not visible completely around the otolith (Collins and Spratt 1969). Of 1,025 otolith pairs that were examined, 16% were rejected in the aging analysis. Otoliths rejected for aging were used in the otolith size-body size relationship if the rejection was not because of otolith degradation.

Data Management

Three major data bases were constructed: catch-per-unit-effort, otolith data and size frequency data. Catch-per-unit-effort files included the following data for each tow: date of capture, time of capture, station number, catch in numbers and catch in weight. The otolith data base included the following data for individual fish from which otoliths were extracted: date of capture, time of capture, station number, fork length, weight, sex, otolith code number, age, otolith measurements R1 - RT (Figure 9) and magnification at which measurements were taken. The size frequency data base included the following information on randomly selected anchovies from the catches: date of capture, time of capture, station number, fork length, weight, sex and otolith code number. Sex, weight and otolith code number were not determined for every anchovy in the size frequency data base.

Analyses

Catch data (number per 10 min trawl tow) were summarized as mean catch-per-unit-effort (CPUE) by month, year and station although all statistical analyses were performed on the Log_{10} -transformed catch data. Possible differences in mean $\mathrm{Log}_{10}(\mathrm{CPUE} + 1)$ between years, months and stations were tested with analysis of variance (factorial model with interaction). A 30-yr anchovy abundance index, constructed from the Chesapeake Bay Tributaries Juvenile Index data base provided by the Maryland Department of Natural Resources, was compared to a 13-yr trawl abundance index from the Calvert Cliffs region of the Chesapeake Bay (Horwitz 1987). Possible correlation between the DNR and the Calvert Cliffs abundance data was examined using the non-parametric Kendalls' Tau procedure.

Sex ratios in the catches were summarized by month. Observed numbers of males and females were tested against an hypothesized 1:1 ratio by a chi square homogeneity test.

The length-weight relationship was described by the power equation:

$$W = a\,L^{b}.$$

Taking logarithms (base e) gave the linear relationship:

$$\mathrm{Log_e(Weight)} = \mathrm{Log_e}(a) + b\ \mathrm{Log_e(Length)},$$

where a is the y-intercept and b is the slope (Bagenal and Tesch 1978). The slopes were compared to determine if the allometric relationship varied between sexes or seasons (Analysis of Covariance). Fulton's condition factor (Ricker 1975) was calculated from the length-weight data. The relationship is:

$$K = (W/L^3)C$$

where K is the condition factor, W is weight, L is length and C is an arbitrary constant ($C = 10^6$ in this study). Possible condition differences between seasons and sexes were examined (Analysis of Variance).

A marginal increment analysis was used to validate annual otolith increment deposition (Bagenal and Tesch 1978, Beamish and McFarlane 1983). An otolith marginal increment is the distance from the most recent annulus to the otolith edge (Figure 9). If there is a true annulus, the marginal increments should be minimal at only time each year, just after annulus formation.

The relationship between otolith size and fork-length was described by a third order polynomial that was fit to the combined male and female otolith radius and fork length data. A combined sexes model was chosen after testing for possible differences between sexes in the otolith size to fork length relationship (ANCOVA) found no differences.

The otolith - fork-length relationship was used to back-calculate anchovy fork lengths from otolith measurements at annuli and at fall marks. Fall marks occurred in anchovy otoliths from late September to early October. The mean at fall mark "three" is not representative of a complete otolith growth interval because the oldest fish were collected during the summer just prior to fall mark formation. The mean length at annulus "three" included two approximated values in its calculation because the age and otolith measurements for these two anchovies were determined from cross-sections of their otoliths rather than from the whole otoliths. The approximations were made by subtracting the marginal increment observed in the cross sectioned otoliths from the total radius measurement of the whole unsectioned otolith. Because the most recent annual growth increment is very small in an age 3+ anchovy, the estimated measurements should closely approximate the measurements had they been determined from whole otoliths.

To account for age variation within a year-class that is associated with a prolonged recruitment period caused by the protracted spawning season and differing capture dates, otolith "ages" were adjusted to estimate true age in years. The age adjustment procedure was based on knowledge of the peak spawning period (Dalton 1987) and time of otolith annulus formation (this study). Assigning a mean hatch date of 15 July, a mean date of annulus deposition of 15 May and knowing the date of capture, fractions of years were either added or subtracted from the otolith age depending on the date of capture. For example, an age 2 anchovy collected on 15 June would be one month less than two years old.

Growth

The von Bertalanffy growth function (VBGF) was fit to length-at-age data. The model is:

$$L_t = L_\infty\ (1 - e^{-k(t-t_0)}),$$

where L_∞ is the average maximum theoretical length that a fish could attain if it were to continue to grow as described by the model, k is the coefficient that describes the rate at which length approaches the maximum theoretical length, and t_0 is the age at which the fish would have been zero length had it always grown as described by the model (Ricker 1975). Models were fit to the mean back-calculated lengths-at-age, and to the lengths-at-adjusted age (ages adjusted to fractions of years as described above).

Instantaneous seasonal (summer and winter) growth rates were calculated from the mean back-calculated lengths-at-age where:

$$\text{instantaneous growth} = \log_e L_2 - \log_e L_1.$$

The summer season was defined as the time between otolith annulus formation and fall mark formation. Winter was defined as the time between otolith fall mark formation and annulus formation.

Growth-in-weight also was described by the von Bertalanffy model. This form of the von Bertalanffy model is:

$$W_t = W_\infty\ (1 - \exp(-k(t - t_0))^b,$$

where b is the exponent of the length-weight relationship. The growth-in-weight form of the VBGF is useful when estimating biomass fluctuations (production) in fish populations (Ricker 1975). The parameters of the weight form of the VBGF were derived from the length form of this model and from the parameters of the length-weight relationship.

The Gompertz model also was fit to the mean back-calculated weight-at-age data. The model is:

$$W_t = W_0\ (\mathrm{EXP}\ (G\ (1 - \mathrm{EXP}\ (-gt))))$$

where W_0 is the weight at time $t = 0$; G is the instantaneous rate of growth when $t = 0$ and weight = W_0; and g is the instantaneous rate of decrease of the instantaneous growth rate (Ricker 1975). The Gompertz growth model is effective in describing sigmoidal growth in fish (Moreau 1987).

Abundance-at-Age and Mortality

To estimate abundance-at-age from catch-per-unit-effort, a sample length distribution of otolith-aged anchovies was adjusted proportionally to the length distributions of random samples of anchovies from the catches. This adjustment required randomly excluding some data from otolith-aged anchovy to achieve proportionality between the length frequencies of otolith-aged and randomly-selected anchovy. This procedure was applied to catches grouped by two week intervals and fork lengths grouped by 5 mm intervals.

To develop an age-length key the length-frequency and otolith aging data were used to compute mean fork lengths at age, their standard deviations, and 0.95 confidence intervals about the mean fork length at each age (Zar 1974). Anchovies of lengths within the 0.95 confidence interval of a single age-group were assigned that age. Anchovies with fork lengths that fell within the 0.95 confidence intervals of two age classes, were in a "region of doubt". A Z-statistic was computed for each doubtful fork length to assign a probability for each of the two age-classes to which it could be assigned. The proportion of the normal distribution corresponding to each Z-statistic was read from statistical tables. These proportions (i.e probabilities) were used to assign anchovies of fork lengths within a region of doubt to one of the two possible age classes. The number of fish-at-age were then summed for the random samples grouped by two-week collection intervals. Relative abundance-at-age was estimated by proportionally assigning the random sample abundance-at-age estimates to the catches of the corresponding two-week intervals.

Mortality estimates were generated from the relative abundances-at-age by catch curve analysis (Ricker 1975). The relationship between abundance and age was assumed to follow a negative exponential relationship. A catch curve is the plot of the $\log_e$-transformed abundances on age. The slope of this regression is the annual instantaneous total mortality rate (Z) which, in an unfished population, is the instantaneous natural mortality rate (Robson and Chapman 1961). Annual percent mortality is derived from the instantaneous rate by the relationship:

$$\text{annual percent mortality} = (1 - e^{-Z})100 \text{ (Ricker 1975).}$$

Three empirical methods also were applied to obtain independent estimates of mortality to compare with the catch curve estimates. These methods required the use of empirically derived algorithms. Pauly (1979) derived a relationship to estimate natural mortality from the von Bertalanffy growth model parameters and mean environmental temperatures for 175 fish species and stocks. The relationship is:

$$\mathrm{Log}_{10}(M) = -0.0066 - 0.279\ \mathrm{Log}_{10}(L_\infty) + 0.6543\ \mathrm{Log}_{10}(K) + 0.4634\ \mathrm{Log}_{10}(T),$$

where M = annual instantaneous natural mortality rate, L_∞ and K are parameters from the VBGF, and T is the mean environmental temperature. The mean environmental temperature used for bay anchovy was computed from monthly average water temperatures from 1983-1987 that were collected at the Chesapeake Biological Laboratory.

Ssentongo and Larkin (1973) derived a relationship between total mortality, mean age and age at first capture, or mean length and length at first capture, of captured fish. Their age-based relationship for fish that spawn at discrete annual intervals was derived from the equation of exponential decay, $N_t=N_0e^{-Z}(t-t_c)$. The relationship is:

$$Z = \log_e(((t-t_c + 1)/(t - t_c))*(n/(n + 1)))$$

where t is the mean age of captured fish, t_c is age at first capture and n is the number of fish captured.

Hoenig's (1983) relationship between total mortality rate and fish longevity, which was derived from data on approximately 75 unexploited or nearly unexploited fish stocks also was used. The model is:

$$\log_e Z = 1.46 - 1.01 * \log_e(t_{max}),$$

where t_{max} = maximum observed age.

RESULTS

A total of 31,325 bay anchovies weighing 27 kilograms were collected from 317, 10 min standardized trawl tows during the two-year study. The catch-per-unit-effort (CPUE) data for both years and all transect stations are summarized in Table 3. The observed standard station CPUE was higher in 1986 than in 1987 (Figure 10). Highest observed catches at the standard station were made in September of each year. The combined-stations CPUE also indicated greater abundances in 1986 than in 1987 (Figure 11), with peak catches observed in September 1986 and March 1987. The mean catch-per-unit-effort (CPUE) across both years and from all stations was 98.8 anchovies per tow. The 1986 and 1987 mean CPUE, based on all tows and all stations during the two-year study, were 307 and 34 anchovies per tow, respectively, based on 75 tows in 1986 and 242 tows in 1987. At the standard station (Station 7, Table 3), 63 tows were made from July to November 1986 and 75 tows were made between February and December 1987. The mean July-November CPUE at the standard station in 1986 and 1987 were 354 and 54 anchovies per trawl tow, respectively.

Although surface feeding schools of bay anchovy were regularly observed associated with the surface slick of a tidal front in the Patuxent River mouth, no significant CPUE differences (ANOVA $P>0.80$) were detected among the grid of stations (Table 4; Figure 8) sampled during the frontal zone study of 24-28 August 1987. Of 61 standardized trawl tows made during the five days of sampling, 46 tows yielded no anchovies and 56 tows yielded five or fewer. The mean CPUE varied more than ten-fold among the stations, but the largest mean CPUE, 30.9 (Table 4, Station F), resulted from a single large catch (309 anchovies) at that station. The correlation between mean CPUE and standard deviations (Kendall's coefficient of rank correlation, $P<.01$) indicated that the higher mean CPUE resulted from high catches occurring in only a few of the trawl tows at a station, which implies a patchy distribution of anchovy in the sampling area.

Interannual Analysis of Catches

Catch-per-unit-effort was higher in 1986 than in 1987 (Table 3, Figure 10). Because the trawling program differed during the two years, valid interannual comparisons of CPUE could only be made at the standard station (Station 7) during July through November when there was similar effort in both years of the study (Table 3). In that period the mean CPUE at the standard station was 354 in 1986 but only 54 in 1987. The nearly six-fold higher mean CPUE in 1986 was significantly higher than that in 1987 (ANOVA, $P<.001$).

Table 3. Summary of bay anchovy catch data for 1986 and 1987, indicating the mean catch-per-unit-effort (CPUE), number of trawl collections, and standard deviation of CPUE by month and station. Each standard collection was a 10-min tow of a 4.9 m semi-balloon trawl.

	1			2			3			5			7		
Month	n	CPUE	S	n	CPUE	S	n	CPUE	S	n	CPUE	S	n	CPUE	S
7/86	0			0			0			0			32	159.8	196
8/86	0			0			0			0			14	328.8	503
9/86	4	954.3	1131	4	28.0	41	4	11.0	13	0			8	1024.5	1001
10/86	0			0			0			0			4	146.5	121
11/86	0			0			0			0			5	110.6	204
TOTAL, MEAN	4	954.3		4	28.0		4	11.0		0			63	354.0	
2/87	0			0			0			0			2	4.0	4
3/87	0			0			0			0			2	26.0	20
4/87	2	156.0	156	2	0.0		2	1.5	2	2	1.0	1	5	19.2	27
5/87	2	84.0	80	2	8.0	4	2	14.0	14	2	47.0	43	4	31.5	52
6/87	8	27.1	52	4	0.8	1	5	18.8	28	4	40.0	61	17	19.6	25
7/87	4	21.0	36	4	0.0	--	4	124.0	140	4	0.8	1	14	95.8	252
8/87	3	0.0	--	3	0.0	--	3	128.3	181	3	3.0	4	13	13.8	32
9/87	5	8.2	15	5	1.6	3	5	150.2	295	3	54.7	46	10	129.4	159
10/87	2	0.0	--	2	0.5	0.5	2	77.5	78	1	0.0	--	4	28.0	30
11/87	1	0.0	--	1	15.0	--	1	0.0	--	1	119.0	--	2	3.0	3
12/87	1	0.0	--	1	0.0	--	1	0.0	--	1	0.0	--	2	0.0	0
TOTAL, MEAN	28	32.9		24	2.9		25	57.1		21	29.5		75	41.1	

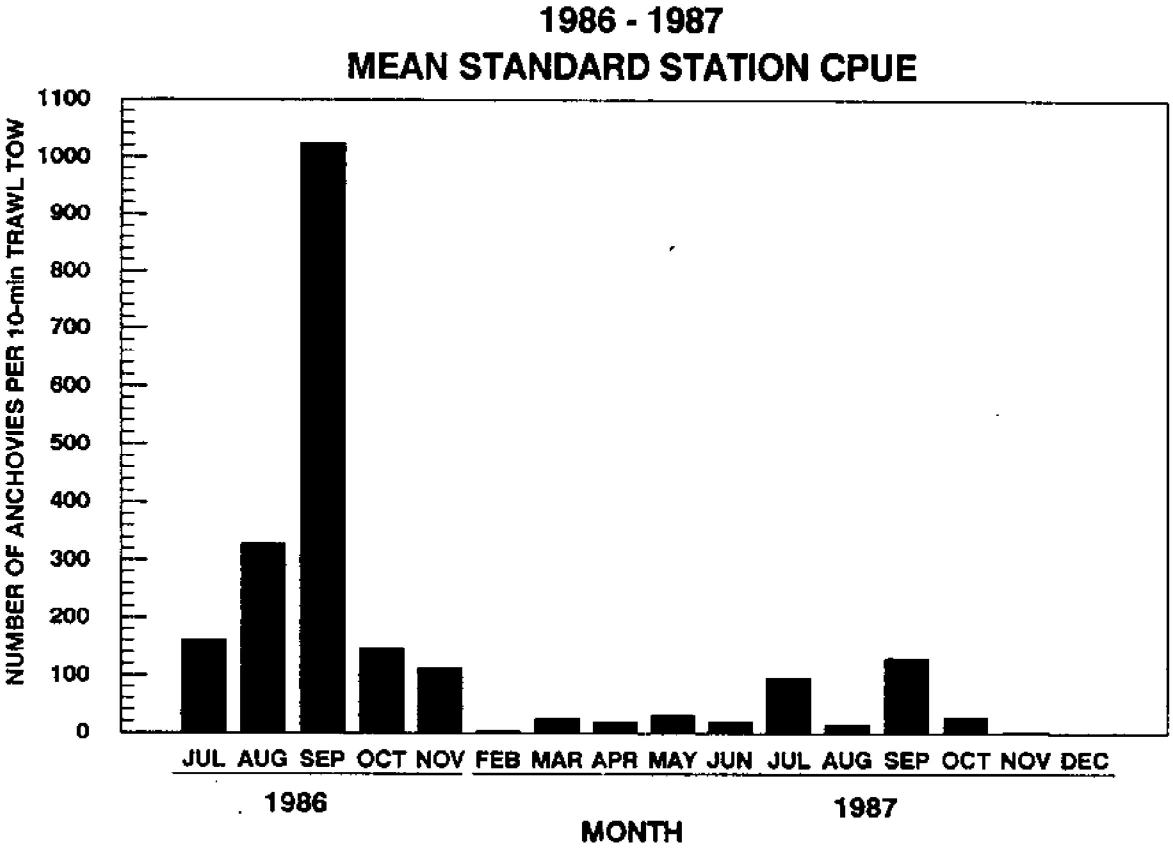

Figure 10. Bay anchovy monthly standard station (Station 7) catch-per-unit-effort.

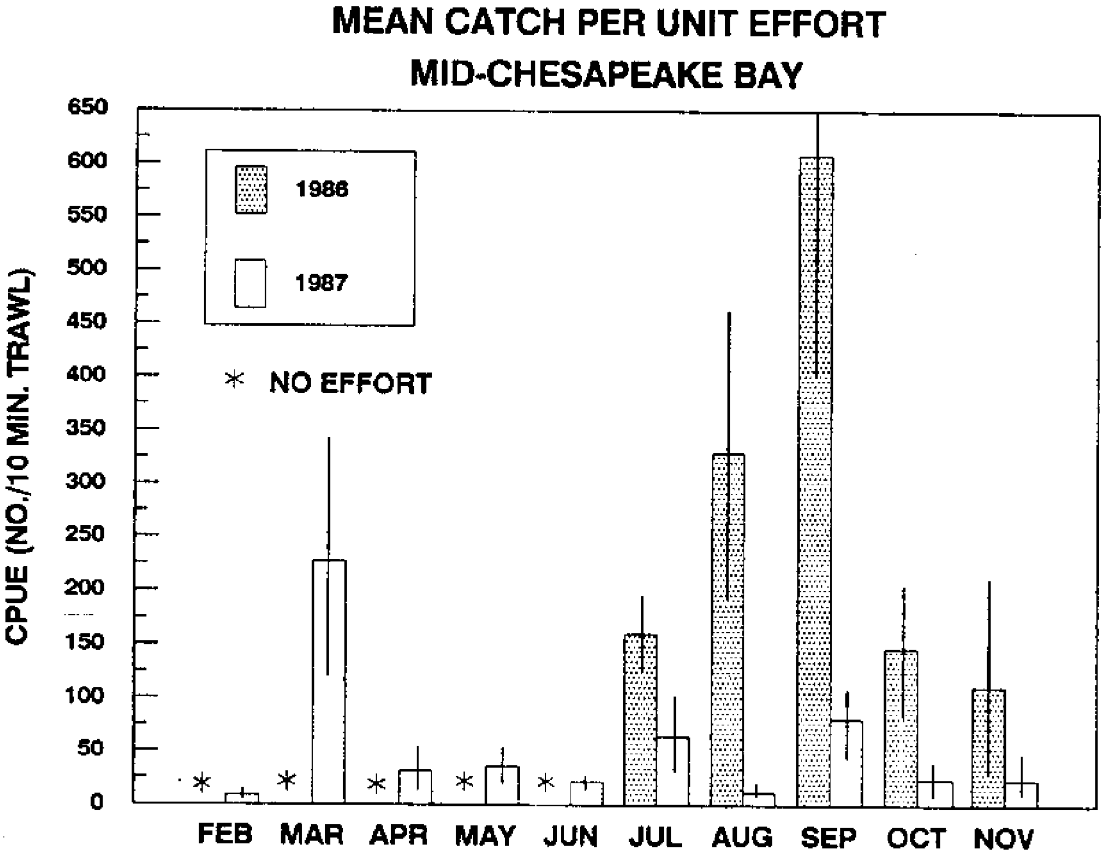

Figure 11. Bay anchovy mean catch-per-unit-effort, all trawl stations combined.

Table 4. Bay anchovy trawl catch statistics during the frontal zone study of 24-28 August 1987.

FRONTAL ZONE STUDY CATCH STATISTICS
24-28 August 1987

Station	Catch (Total)	Effort (# Tows)	CPUE (#/Tow)	S
A	35	6	5.8	13.8
B	11	6	1.8	2.5
C	0	4	0	0
D	36	10	3.6	6.5
E	25	6	4.2	10.2
F	309	10	30.9	97.7
G	5	6	0.8	2.0
H	3	6	0.5	0.8
I	0	7	0	0
TOTAL	424	61	$\bar{X} = 5.29$	

Intraannual Analysis of CPUE

Standard station CPUE among months varied approximately ten-fold in 1986 and nearly 50-fold in 1987 (Table 3, Station 7). In the July to November 1986 period mean CPUE ranged from 110.6 anchovies per tow in November to 1024.5 in September. During the same period in 1987, mean CPUE ranged from 3.0 anchovies per tow in November to 129.4 in September. There were no significant differences among mean monthly CPUE at the standard station in 1986 (ANOVA, $P>.30$). In 1987 significant differences were detected among the mean monthly CPUE at the standard station (ANOVA, $P<.05$). However, the specific monthly means that differed significantly in 1987 could not be unambiguously separated with an *a posteriori* multiple range test (Duncan's Test, $P>.05$).

Analysis of the pooled 1986-1987 July to November CPUE indicated seasonal CPUE variability in which the highest monthly CPUE occurred in September and October. The pooled monthly CPUE differences were significant (ANOVA, $P<.05$). The multiple range test indicated that overlap in mean CPUE occurred for all months except September and November (Duncan, $P<.05$), which had the highest and lowest mean CPUE, respectively.

Spatial Analysis of Catch Data

Mean CPUE among the transect stations (Figure 8, numbered stations) varied nearly 20-fold from 2.9 anchovies per tow at Station 2 to 57.1 at Station 3 (Table 3). Because there was little trawling effort at stations other than the standard station in 1986, spatial analysis was restricted to the 1987 catch data. There were significant differences in mean CPUE among the five stations (ANOVA, $P<.05$) but the multiple range test (Duncan, $P>.05$) was unable to clearly distinguish which stations had significantly different mean CPUE.

Diel Catch Data

Catches of bay anchovy generally were lower at night although relatively few tows were made on a diel basis (Table 5). The differences between day and night CPUE were not significant (Mann-Whitney Test, $P>.50$). Acoustic echo traces generally indicated that anchovy were more dispersed at night, while during the day large schools of anchovy often were observed.

Recruits

Age 0+ bay anchovy first became vulnerable to the trawling gear in late July in 1986 and mid-July in 1987. The smallest anchovies that were collected were 15 mm FL. Fish less than 25-30 mm were not fully vulnerable to the trawl, but their occurrence in catches indicated that recruitment began earlier in 1987 than in 1986. New recruits dominated the catches in both years from August to October (Figure 12). The level of recruitment appeared to be higher in 1986 than in 1987. During these months young-of-the-year anchovy represented nearly 85% of the total catch. Mean peak abundance of new recruits occurred in September of both years, representing 928 recruits per tow in 1986 and 109 recruits per tow in 1987. CPUE of recruits was more than eight times higher in 1986 than in 1987.

Table 5. Bay anchovy catch statistics for two-24 h trawl series. CPUE is number of anchovies per 10 min trawl tow.

Time	Mean CPUE	# Tows	S
	29 - 30 July 1986		
1000 - 1100	662	2	193.0
1700 - 1800	128	3	79.5
0001 - 0100	93	3	41.9
0700 - 1000	50	5	60.9
1400 - 1500	140	2	82.5
	30 June - 1 July 1987		
1200 - 1500	20	4	23.4
2100 - 2200	44	3	39.0
0300 - 0400	5	3	3.3
0900 - 1000	28	2	4.0

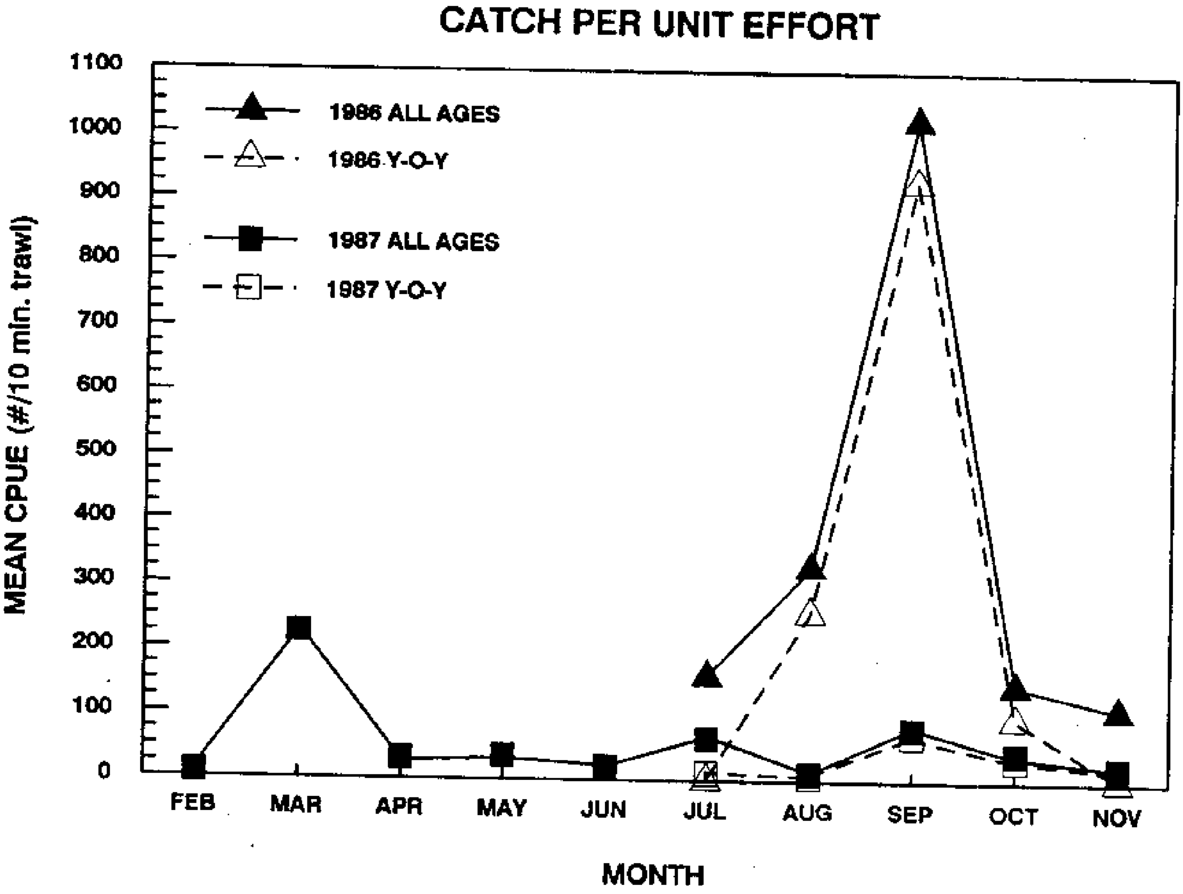

Figure 12. Bay anchovy age 0+ and total catch-per-unit-effort, all trawl stations included.

Other Abundance Indices

More than ten-fold annual variation in abundance of bay anchovy occurred in an index derived from beach seine samples (Figure 13a) collected by the Maryland Department of Natural Resources. The seine samples were collected from July to September of each year in relatively low salinity regions of Chesapeake Bay tributaries. The 30-year mean abundance index was 26.7 bay anchovies per seine haul (Figure 13a). The highest index value was 105.8 in 1967 and the lowest was 0.75 in 1958. The 1986 abundance index (44.3) was approximately four times higher than that of 1987 (12.1).

Interannual variability in abundance of bay anchovy in the Chesapeake Bay also was observed in bottom trawl data collected near Calvert Cliffs. Part of the preoperational ecological studies for the Calvert Cliffs nuclear power plant included year-round trawling between 1969 and 1981 (Horwitz 1987). The relative annual abundances (catch/30 min tow of a 7.6 m semi-balloon otter trawl) of bay anchovy ranged from 58 in 1976 to 974 in 1980 (Figure 13b). The 13-year mean was 708 anchovies per trawl tow. The extremely low abundance in 1976 was not observed in other years. Among the remaining years, less than three-fold variability of anchovy abundance occurred. The abundances in this series, from the Bay proper, did not correlate with the Maryland DNR abundance indices from the tributaries for corresponding years (Figure 13) (Kendall's tau, $P > .99$).

Sex Ratio

Females generally were more abundant in the collections (Table 6). The mean sex ratio for the 4,048 anchovies that were examined during the two-year study was 1.16 females per male (53.7% females). Monthly sex ratios significantly greater than 1.0 (Chi-square, $P < .05$) occurred in April, June, August and October 1987. The mean sex ratios for 1986 (1.13 females per male (53% female)), 1987 (1.17 females per male (54% female)) and the two years combined (1.16 females per male) all differed significantly from 1.0 (Chi-square, $P < .05$).

Length-Frequency Distributions

The length-frequency distributions of bay anchovy were multimodal from 1986 and 1987 trawl catches (Figure 14a-d). From late July through November the modes delineate age-groups, distinguishing age 0+ recruits from age 1+ and older anchovies. Modes representing young-of-the-year and age 1+ fish are most prominent. The first recruits (< 40 mm FL) were observed in the 15-31 July catches each year. Significant recruitment occurred earlier in 1987 than in 1986 and recruits dominated the catches by late August in each year. Modes that represent recruits and older anchovies were easiest to distinguish in 1986.

In both years, but especially in 1986, the length frequencies of new recruits apparently were bimodal during some months. Normal probability plots of anchovy lengths during these months (Figure 15) exhibited inflections within the range of lengths of young-of-the-year anchovies, suggesting the presence of more than one mode within the age 0+ class. The length frequencies of new recruits during these months (July - October 1986, July and

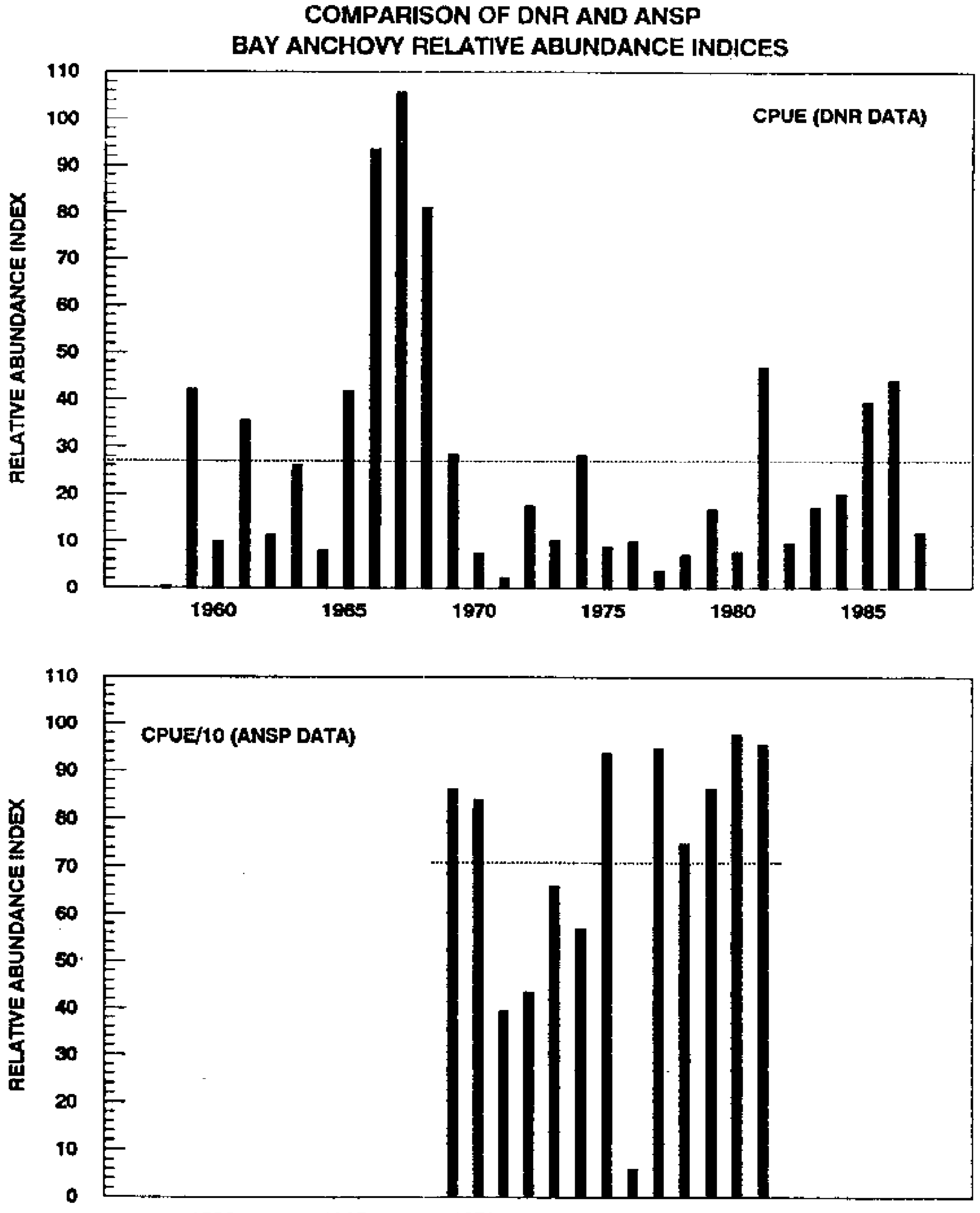

Figure 13a - b. Bay anchovy abundance indices from the Chesapeake Bay region. a) 30-year bay anchovy relative abundance index from Maryland Department of Natural Resources Chesapeake tributaries juvenile index seining survey. Horizontal line is the mean index value of 26.7. b) Academy of Natural Science of Philadelphia (ANSP) relative abundance index for bay anchovy from the Calvert Cliffs region (Horwitz 1987). Catch-per-unit-effort is the number of anchovies caught per 30 min. trawl tow of a 7.6 m semi-balloon trawl. Relative abundances were divided by 10 for scaling. Horizontal line is the 13 yr mean index of 708.

Table 6. Monthly sex ratios of bay anchovy collected during 1986-1987.

SEX RATIO SUMMARY

	1986		1987	
MONTH	F:M	n	F:M	n
March			1.03	325
April			1.35*	197
May			0.89	138
June			1.28*	565
July	1.12	914	1.02	448
August	1.14	90	1.43*	372
September	1.15	198	1.10	481
October			1.29*	305
November			0.66	15

Overall Mean Ratio = 1.16*

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* = ratio significantly different from 1:1
n = number of observations
F = Female
M = Male

Fig. 14(a)

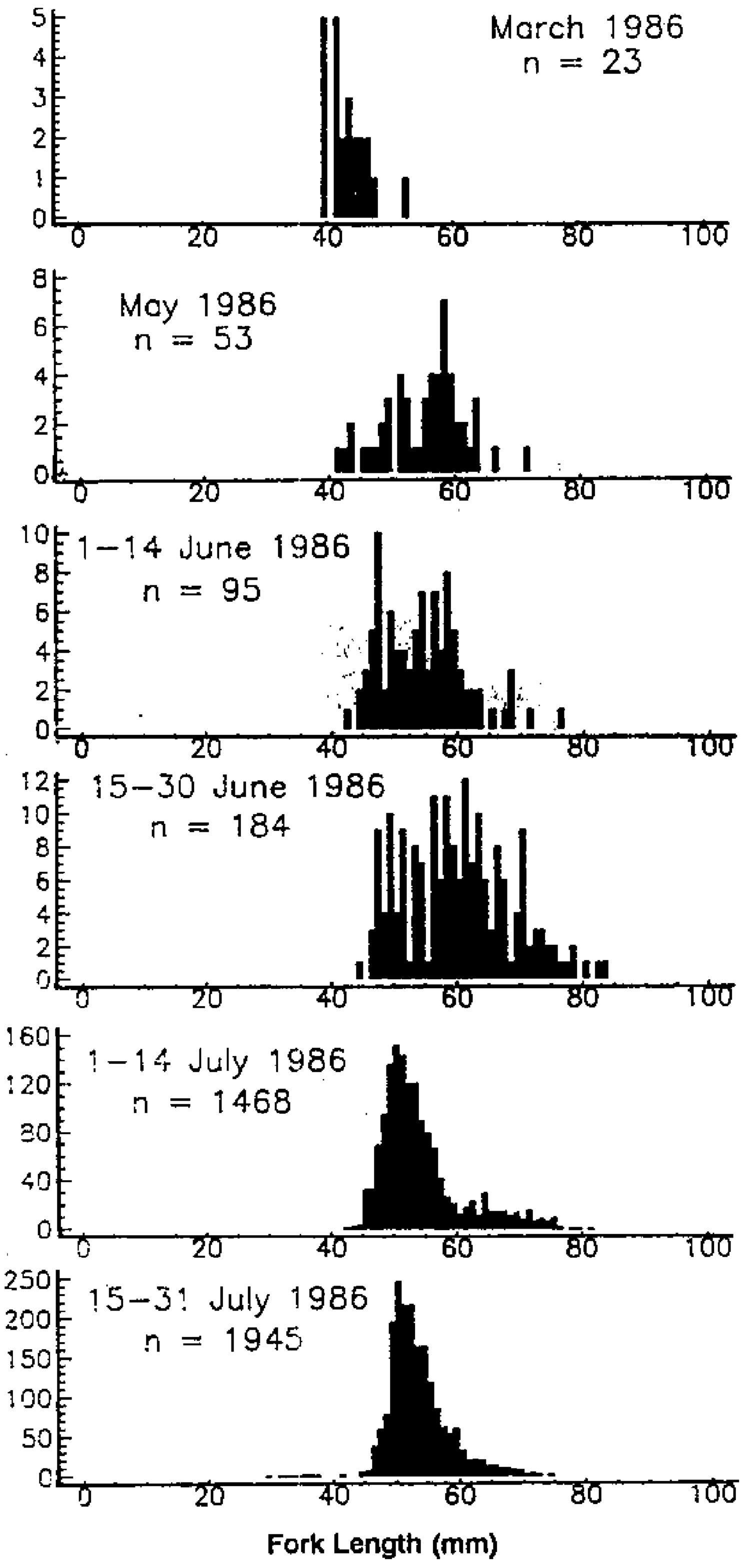
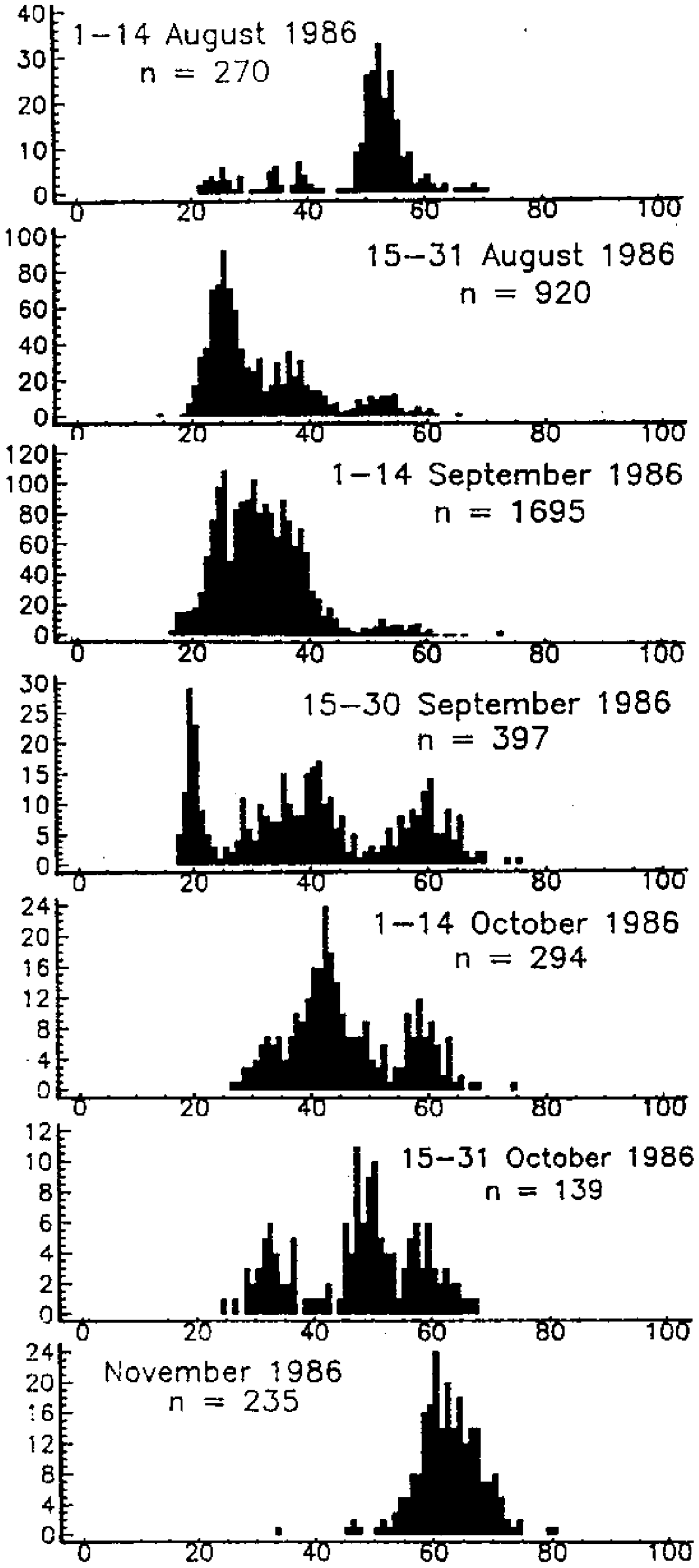


Figure 14a - d. Bay anchovy length frequency distributions in 1986-1987. The distributions are pooled from trawl catches by two-week intervals. The trawl had a 3 mm stretch-mesh cod-end liner. The y-axis scale varies among the two-week panels.

Fig. 14(b)



Fork Length (mm)

Fig. 14(c)

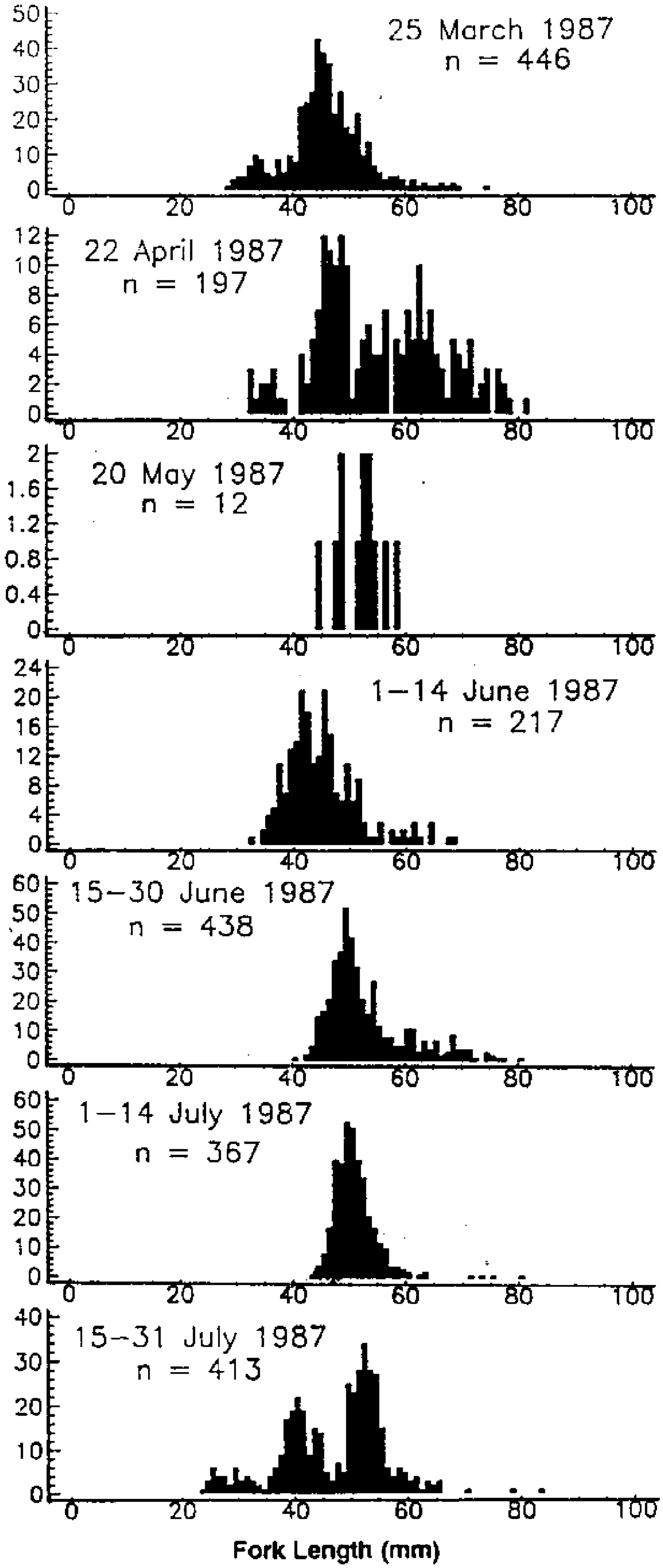
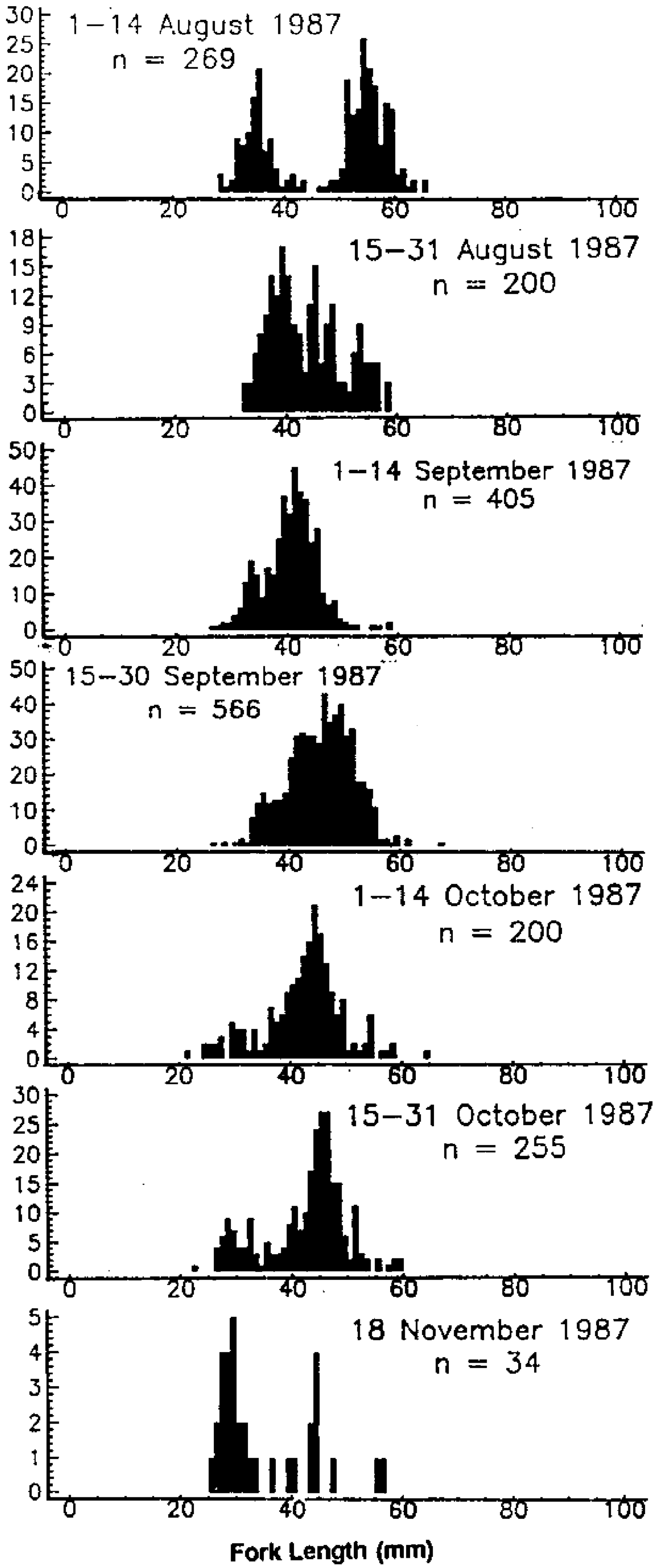

25 March 1987
n = 446
22 April 1987
n = 197
20 May 1987
n = 12
1–14 June 1987
n = 217
15–30 June 1987
n = 438
1–14 July 1987
n = 367
15–31 July 1987
n = 413
0
20
40
60
80
100
Fork Length (mm)

Fig. 14(d)


1-14 August 1987
n = 269
0
5
10
15
20
25
30
15-31 August 1987
n = 200
0
3
6
9
12
15
18
1-14 September 1987
n = 405
0
10
20
30
40
50
15-30 September 1987
n = 566
0
10
20
30
40
50
1-14 October 1987
n = 200
0
4
8
12
16
20
24
15-31 October 1987
n = 255
0
5
10
15
20
25
30
18 November 1987
n = 34
0
1
2
3
4
5
0
20
40
60
80
100
Fork Length (mm)

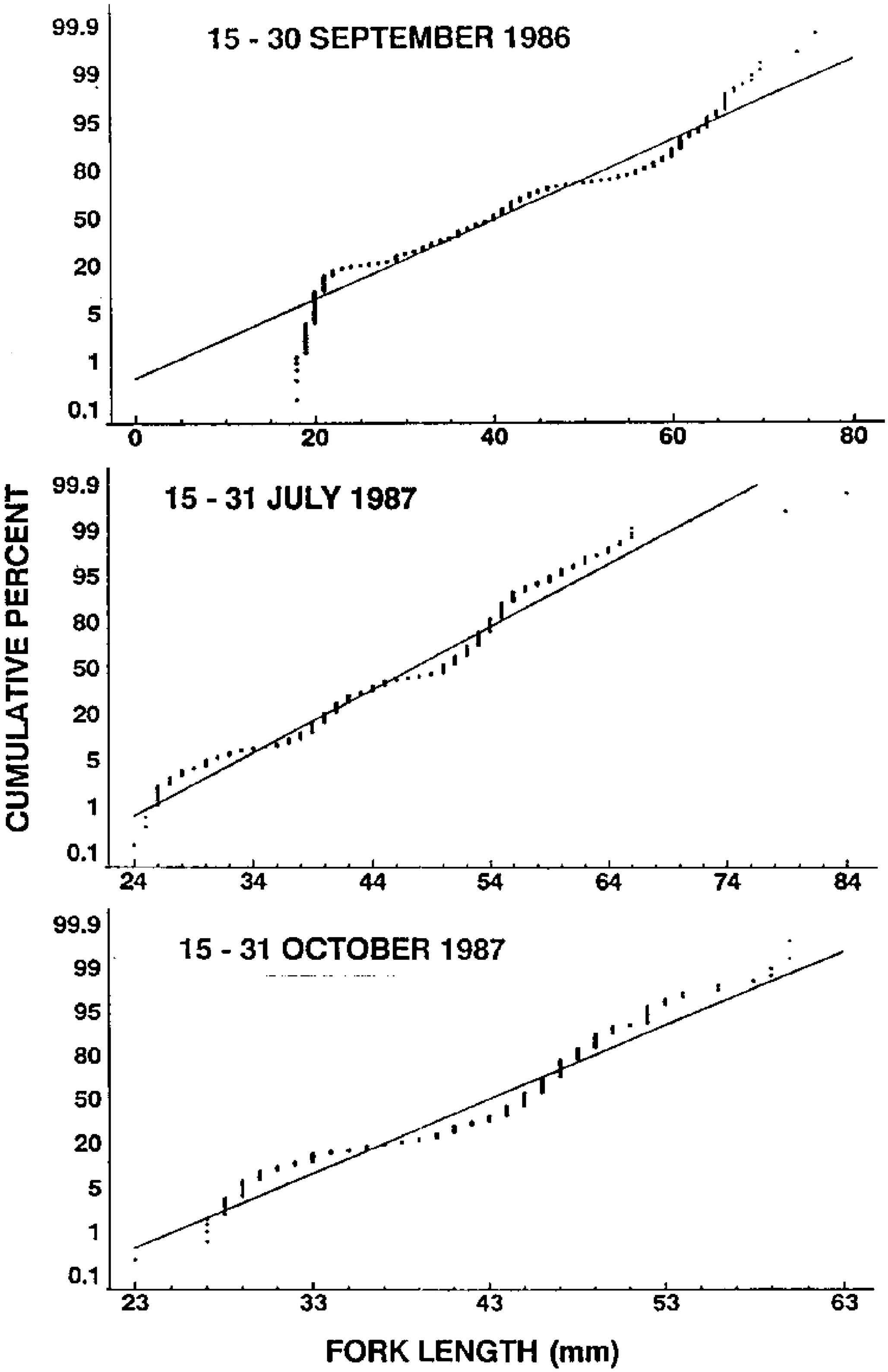


Figure 15. Normal probability plots of bay anchovy length-frequency data. The x-axis range varies among the panels.

October 1987) were both skewed and platykurtotic (T-test, g_1, g_2, $P<.05$). Skewed length frequencies of new recruits may indicate hatch-date-dependant differential mortality of egg and larval stages, or non-uniform spawning. The T-test that indicated significant platykurtosis in the length-frequency distributions also may indicate differential mortality or non-uniform spawning, but multimodal distributions also would be judged platykurtotic with this test.

Length-Weight Relationship

The length-weight relationship of bay anchovy, as indicated by the coefficient (b) of the power model (Table 7) varied seasonally. Because only two seasons, summer and fall, were represented in 1986 collections, interannual comparisons were restricted to July through November data. Seasonal comparisons were restricted to 1987 data. There were no significant differences in the coefficient (b) of the length-weight relationship between years (ANCOVA, $P>.60$) or between sexes (ANCOVA, $P>.50$). For the pooled sexes data, differences in the b coefficient among seasons were significant (ANCOVA $P<.001$). Each coefficient differed significantly from all others (Q-test, $P<.05$, Zar (1974)). For the two sexes combined, the seasonal coefficients in 1987 varied from 3.18 during summer to 3.49 in the spring.

Condition of bay anchovy, as indicated by the Fulton condition factors, varied seasonally (ANOVA $P<.001$). The seasonal condition changes may reflect annual reproductive, growth and recruitment cycles. Mean seasonal condition in 1987 was highest during Summer and lowest during Winter (Figure 16). All but two (Fall 1986 and Fall 1987) of the six mean seasonal condition factors that were compared were significantly different from each other (SNK test, $P<.05$). Significant differences in mean condition between sexes were not detected (ANOVA, $P>.50$)

Age and Growth

Based on presence of otolith annuli, anchovy of age 0+, 1+, 2+, and 3+ were represented in collections. The age composition of 863 otolith-aged anchovies (not a random population sample) was: 528 age 0, 287 age 1, 44 age 2, and 4 age 3. In addition, there were 162 (16%) non-readable otolith pairs that were rejected from the age analysis.

The rostral radius of the saggita was selected for measurements from which back-calculated lengths-at-age and growth models were calculated. Linear regression of anchovy fork-length on measurements from three otolith radii of the sagittae (rostral, posterior and antirostral; Figure 9) indicated that the rostral radius and the posterior radius predicted fork length best ($R^2 = 0.9616$ and 0.9611, respectively). The antirostral radius also was a excellent predictor of fork length ($R^2 = 0.9606$). Better measurement accuracy could be obtained along the rostral radius because annuli were more distinct along it. Based on the regression results and otolith observations, all otolith measurements for the age and growth analysis were made along the rostral radius.

Otolith marginal increments were minimal from mid May to early June (Figure 17). Because the mean minimal marginal increments occurred only once

Table 7. Coefficients of the length-weight relationship of bay anchovy by sex, season and year.

LENGTH-WEIGHT RELATIONSHIP																
YEAR	1986								1987							
SEX	MALE				FEMALE				MALE				FEMALE			
Season	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
$a(x10^6)$			2.045	3.727			1.851	3.051	1.122	1.210	3.727	1.851	1.674	0.919	4.552	1.515
b			3.37	3.20			3.40	3.25	3.49	3.44	3.22	3.37	3.37	3.53	3.16	3.42
n			473	46			531	53	18	264	551	371	15	296	639	430
r^2			.97	.99			.97	.99	.97	.95	.98	.95	.96	.97	.98	.97

Season 1 = December, January, February
Season 2 = March, April, May
Season 3 = June, July, August
Season 4 = September, October, November
a,b = coefficients of length-weight relationship
where: $\log_e(\text{weight}) = \log_e(a) + b * \log_e(\text{fork length})$
blank cells = no data
ANCOVA: b significantly different among seasons in 1987
$P < .0001$

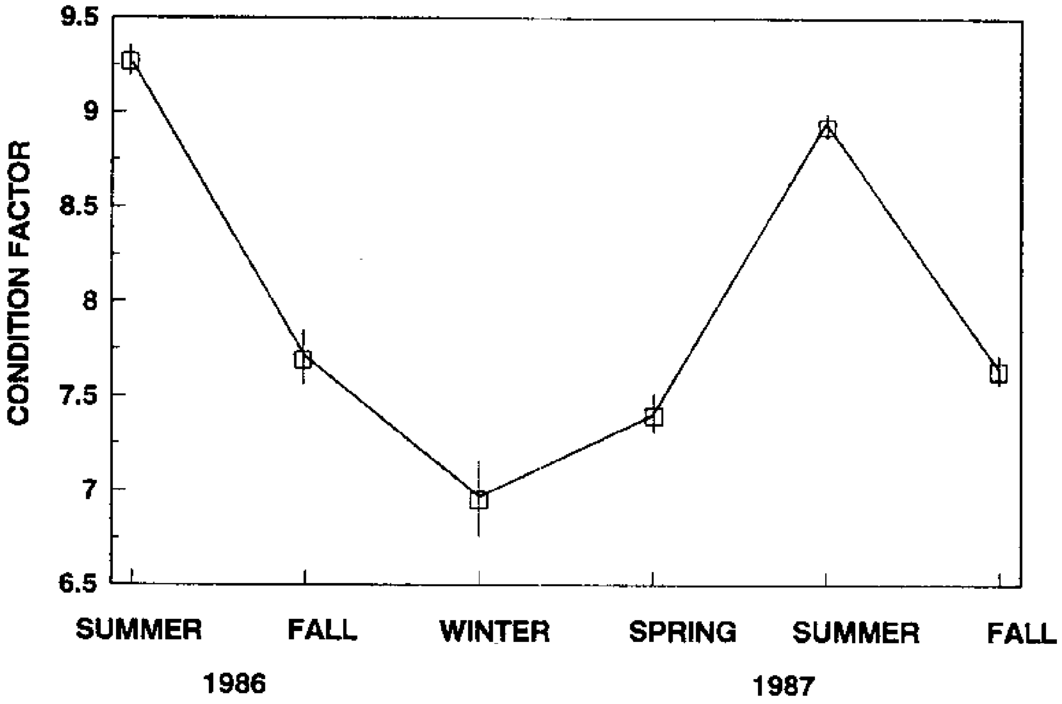


Figure 16. Seasonal Condition of bay anchovy, as indicated by Fulton condition factors. Vertical bars indicate ± two standard errors.

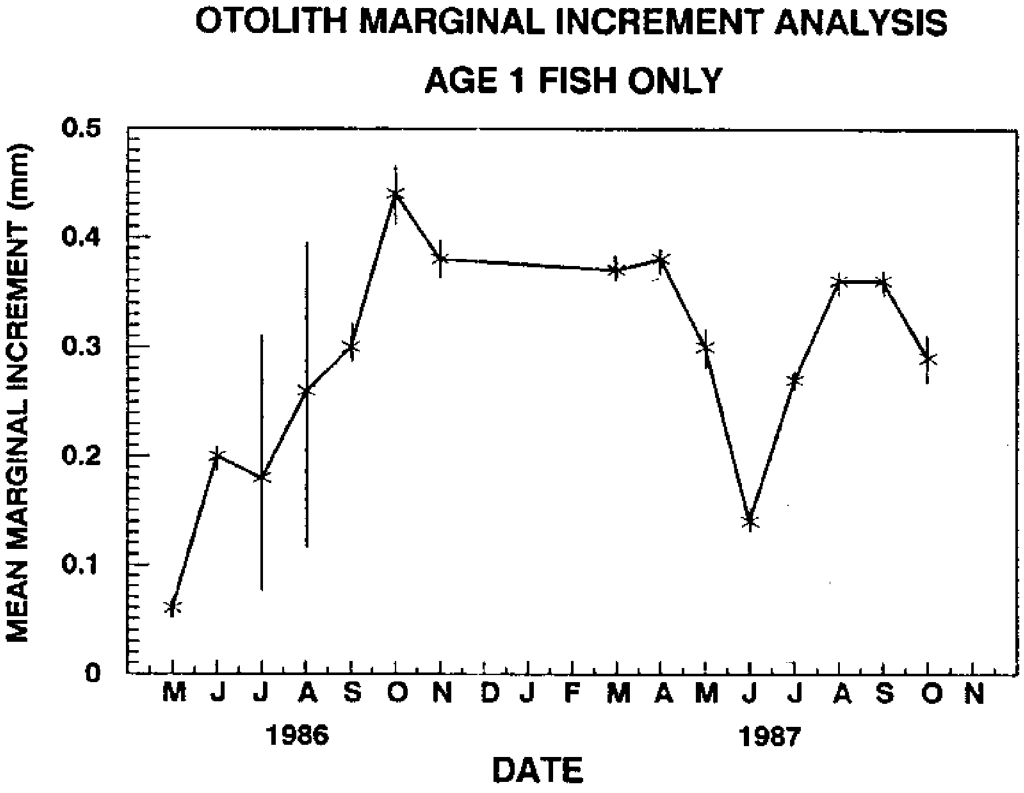


Figure 17. Mean monthly marginal increments on otoliths of age 1+ bay anchovy. Vertical bars indicate ± 1 standard error.

per year, mid May was judged to be the time of annulus formation and the annuli were judged to be valid indicators of bay anchovy age. The high standard errors associated with the July and August 1986 data (Figure 17) may have resulted from small sample sizes in these months.

The model that best described the otolith size - anchovy length relationship was a 3rd order polynomial (Figure 18). The linear regression of fork length on otolith radius had a similar coefficient of determination but it was a poor predictor of anchovy fork lengths for large otoliths. Therefore, the polynomial relationship that was accepted is:

$$\begin{aligned}\text{Fork length} = 15.64 &+ 32.03(\text{otolith radius}) \\ &+ 18.60(\text{otolith radius})^2 \\ &- 4.92(\text{otolith radius})^3,\end{aligned}$$

$R^2 = 0.94$. Because there was no significant difference between sexes in the relationship (ANCOVA, $P > .70$), the model given above, with data pooled for both sexes, was used in all subsequent calculations.

Based on the aging analysis, bay anchovy in mid-Chesapeake Bay apparently did not exceed age 3+ and individuals that attained this maximum age were rare. The largest bay anchovy collected during this study was 86 mm fork-length (equals 95 mm total length) and weighed 6.03 g wet-weight. Its age could not be confirmed as age 3+. A 95 mm fork-length (equals 105 mm total length) bay anchovy weighing 8.65 g wet-weight was collected on the eastern side of the mid-Chesapeake Bay in October 1988. Its age also could not be confirmed from otolith examination. Age 2+ bay anchovy were more common than age 3+ anchovy but still much less abundant than younger age-classes. Age 0+ bay anchovy were most abundant from late summer until the following spring when they became age 1. The age 1+ anchovy remained the most abundant age class until recruitment of young-of-the-year anchovy in late summer and fall.

Mean back-calculated lengths-at-annuli ranged from 42.9 mm at annulus 1 to 78.3 mm at annulus 3 (Table 8). Actual anchovy ages at annuli are not equal to the annulus "age" in years. Estimates of actual age-in-years were made by adjusting the otolith annulus age of an individual by its estimated hatch date and date of capture. Back-calculated lengths were variable among individuals. The protracted spawning season was a major source of variability. At the end of the first summer's growth (fall mark 1), back-calculated lengths ranged from 24 to 56 mm fork length. These differences are even more pronounced when considering individual weights, which varied from 0.1-1.5 g. The ranges of back-calculated lengths-at-age decreased with age. Part of this decrease may be attributable to much smaller sample sizes at older ages.

Means and ranges of back-calculated lengths-at-annuli were similar between years. Significant annual differences between mean back-calculated lengths-at-annuli were observed only for annulus 2 (T-test, $P < .05$). Because older anchovies were rare in the collections and the means and variances of the back-calculated lengths-at-annuli were similar between years, a single growth model was fit to the combined-years data, rather than fitting a separate model for each year.

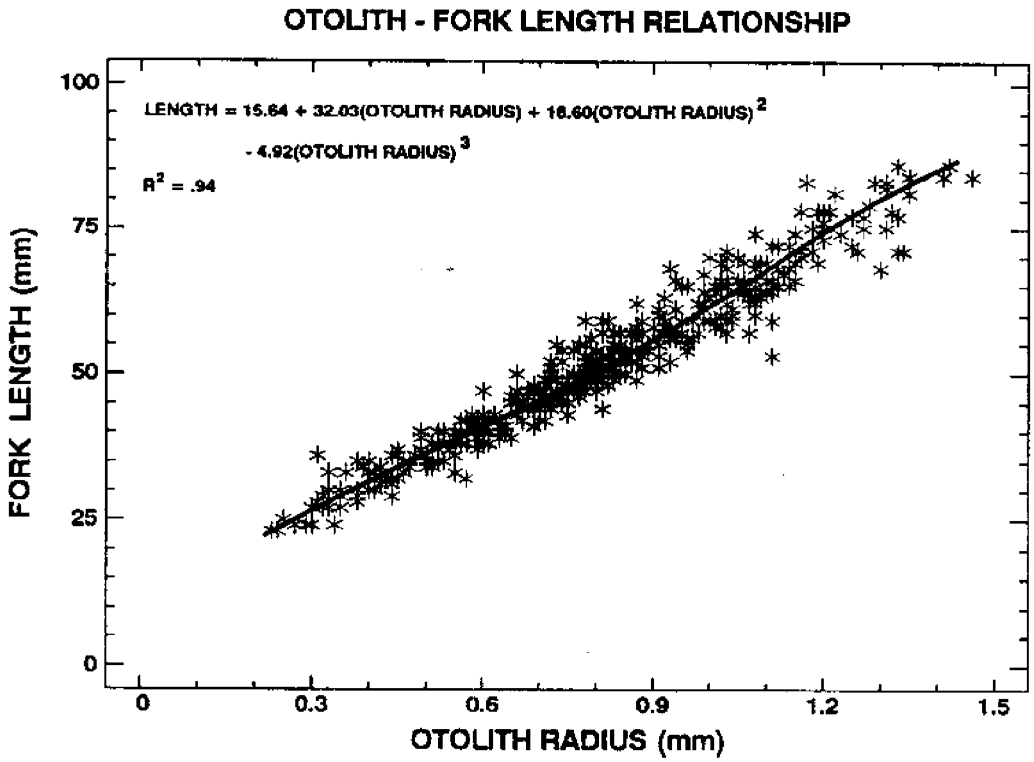


Figure 18. Third-degree polynomial relationship between otolith radius and fork length of bay anchovy.

Table 8. Summary of the back-calculated fork lengths at annuli and fall marks indicating the mean back-calculated lengths, the otolith annuli, the otolith fall marks, the standard deviation of the mean and the range of back-calculted lengths.

SUMMARY STATISTICS
OF BACK-CALCULATED LENGTHS

OTOLITH INCREMENT	RADIUS	N	MEAN LENGTH	S	RANGE
Fall Mark 1	R1	442	37.6	6.2	24-56
Annulus 1	R2	322	42.9	6.3	26-61
Fall Mark 2	R3	96	57.0	5.3	46-71
Annulus 2	R4	42	63.6	5.6	54-74
Fall Mark 3	R5	2	74.5	1.5	73-76
Annulus 3	R6	4	78.3	1.8	76-81
Fall Mark 4	R7	4	81.5	3.4	78-87

Growth in Length

Predicted fork lengths-at-age, calculated from the von Bertalanffy model, are: Age 1 - 50.9 mm, Age 2 - 67.7 mm, and Age 3 - 81.4 mm. The parameters of the model, fit to the combined years' mean back-calculated lengths-at-annuli (Table 8, Figure 19) are: L_∞ = 139.65 mm, k = 0.21, and t_0 = -1.16 yrs. Back-calculated lengths at annuli 1, 2, and 3 (Table 8) differ from the predicted lengths at ages 1, 2, and 3 because annulus formation occurs approximately two months earlier than the mean hatch date. Consequently, estimated ages at the time of otolith annulus formation are approximately two months less than the age in years indicated by the number of otolith annuli.

The von Bertalanffy parameters estimated from the model fit to measured (not back-calculated) fork lengths at adjusted age are: L_∞ = 131.0 mm, k = 0.23, and t_0 = -1.37 yrs (Figure 20). The age adjustments were made by adding or subtracting fractions of years to the otolith age based upon known capture dates, mean hatch date (July 15, Dalton 1987) and date of annulus formation. Predicted lengths-at-age calculated from the adjusted-age model are: Age 1 - 55.0 mm, Age 2 - 70.7 mm, and Age 3 - 83.1 mm.

In the fitted models (Figures 19 and 20) the data show a sinusoidal pattern about the fitted lines, indicating a seasonal pattern in growth. This pattern causes a significant overestimate by the model of length at annulus 1 (Figure 19) but only small errors at older ages.

Mean growth in length of young-of-the-year anchovy calculated from the mean back-calculated length at fall mark 1 and an estimated time between mean hatch date (Dalton 1987) and fall mark formation (present study) was 0.46 mm d^{-1}. Young-of-the-year growth rates estimated from modal length progression (1986, 0.33 mm d^{-1}; 1987, 0.20 mm d^{-1}) were less than the estimate from back-calculated length at fall mark 1. Growth rates derived from modal length progression did not include the larval and early juvenile growth periods that had occurred before anchovy became susceptible to the trawl. Thus, growth rates estimated from modal progression are expected to be lower than growth rate estimates that included larval growth.

Growth in Weight

The parameters of the von Bertalanffy model derived from the mean back-calculated weights-at-annuli and fall marks (Figure 21) are W_∞= 31.74 g, k = 0.21, and t_0 = -1.16 yrs. Predicted weights-at-age calculated from this model are: Age 1 - 1.05 g, Age 2 - 2.76 g, Age 3 - 5.12 g. The model parameters, derived from the weight-at-adjusted-age data (Figure 22), are W_∞= 25.57 g, k = .23, and t_0 = -1.37 yrs.

A Gompertz growth model fit to the mean back-calculated weight-at-annuli data (Figure 23) resulted in nearly identical predictions of weight-at-age. The parameter estimates of the model fit to the mean back-calculated weights-at-annuli and fall marks are: W_0 = 0.088, G = 4.44 and g = 0.81.

Mortality

Annual instantaneous mortality rates based on catch curves and assuming

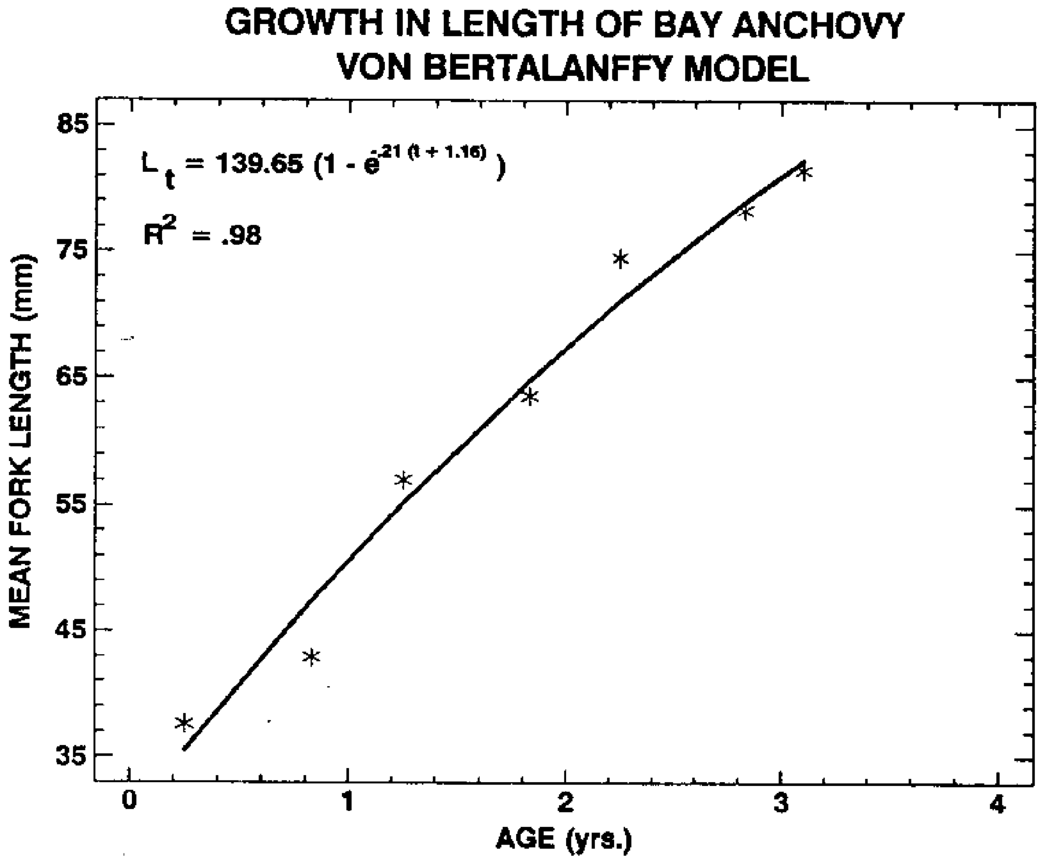


Figure 19. Von Bertalanffy growth model fit to the means of the 1986 and 1987 back-calculated fork lengths at annuli and fall marks for bay anchovy.

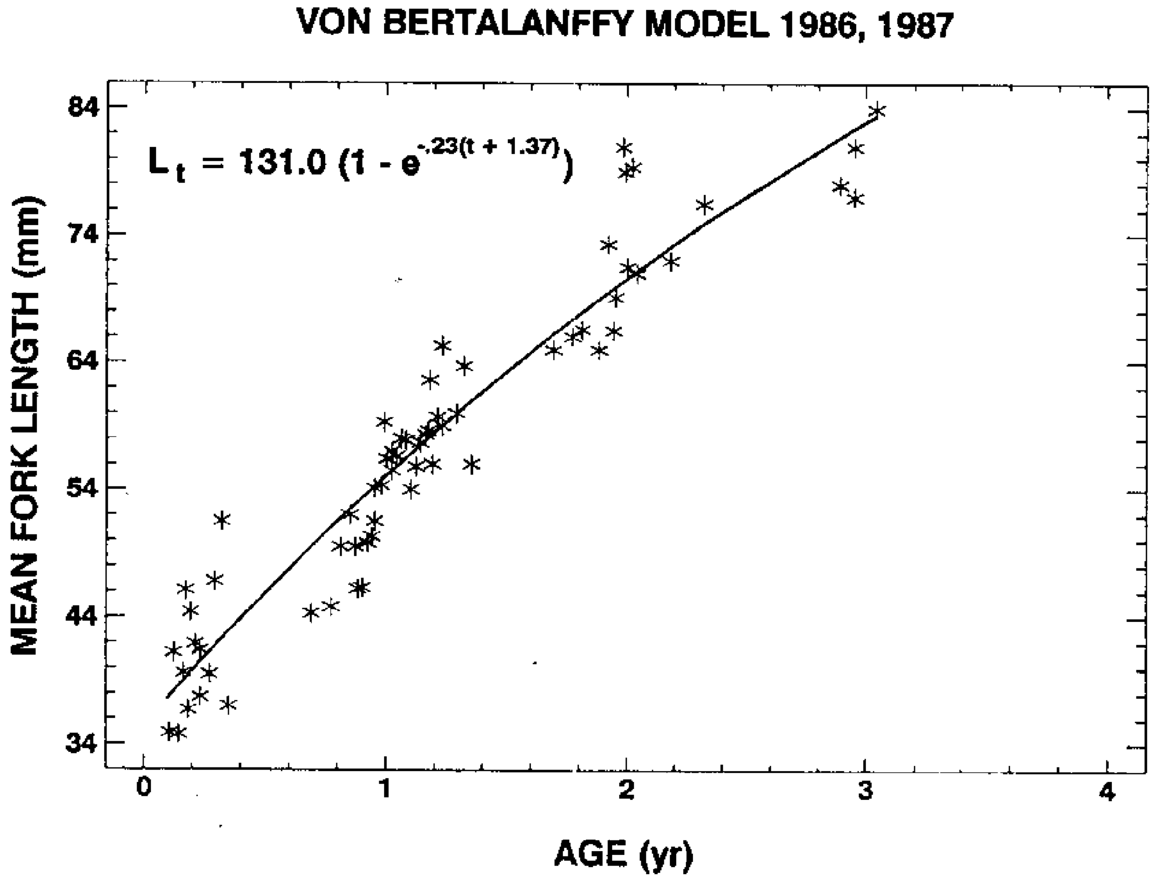


Figure 20. Growth in length form of the von Bertalanffy growth model fit to the means of the 1986 and 1987 lengths-at-adjusted-age data for bay anchovy.

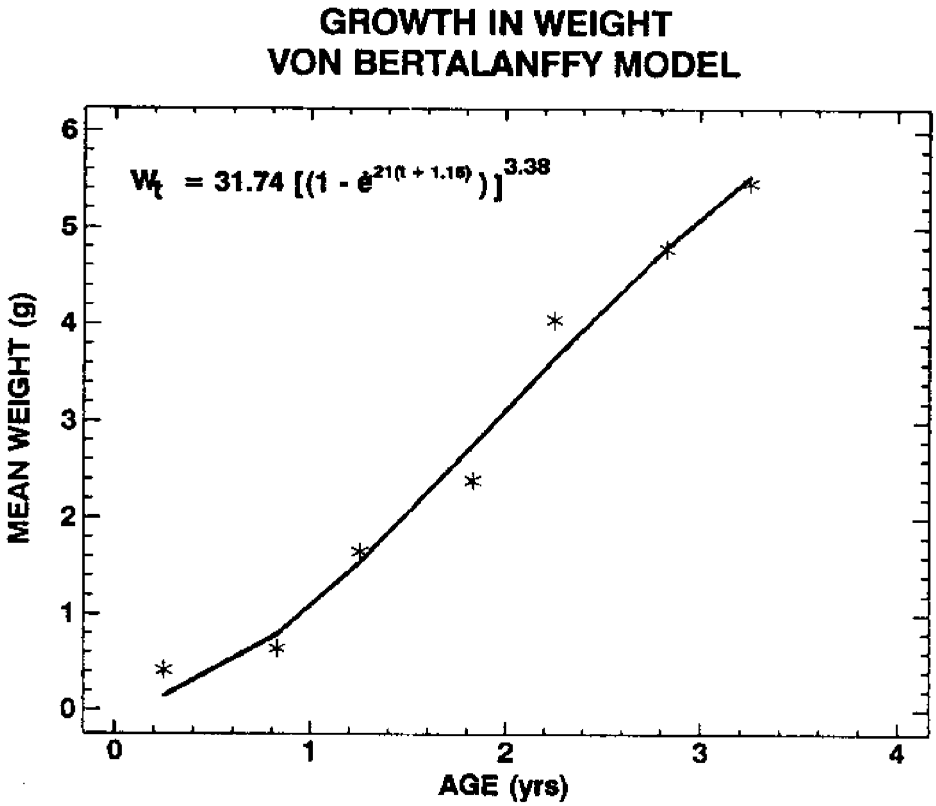


Figure 21. Growth in weight form of the Von Bertalanffy growth model fit to the means of the 1986 and 1987 back-calculated weights-at-annuli and fall marks for bay anchovy.

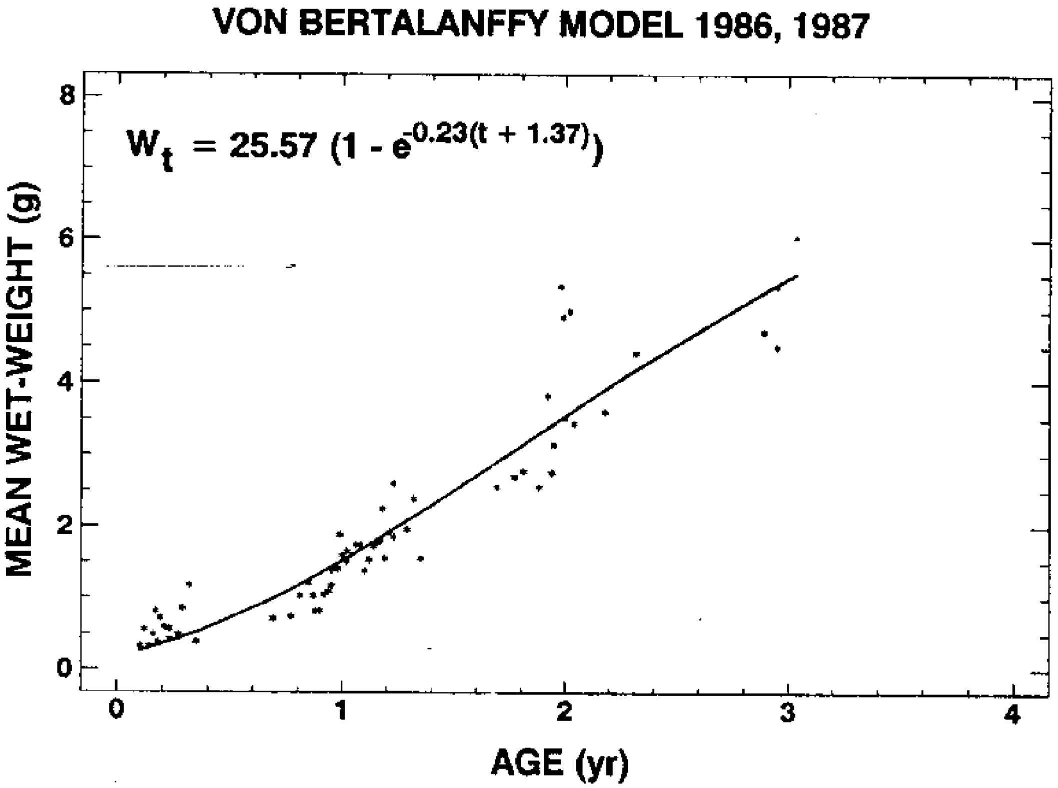


Figure 22. Growth in weight form of the von Bertalanffy growth model fit to the estimated mean weights of 1986 and 1987 adjusted otolith-aged data for bay anchovy.

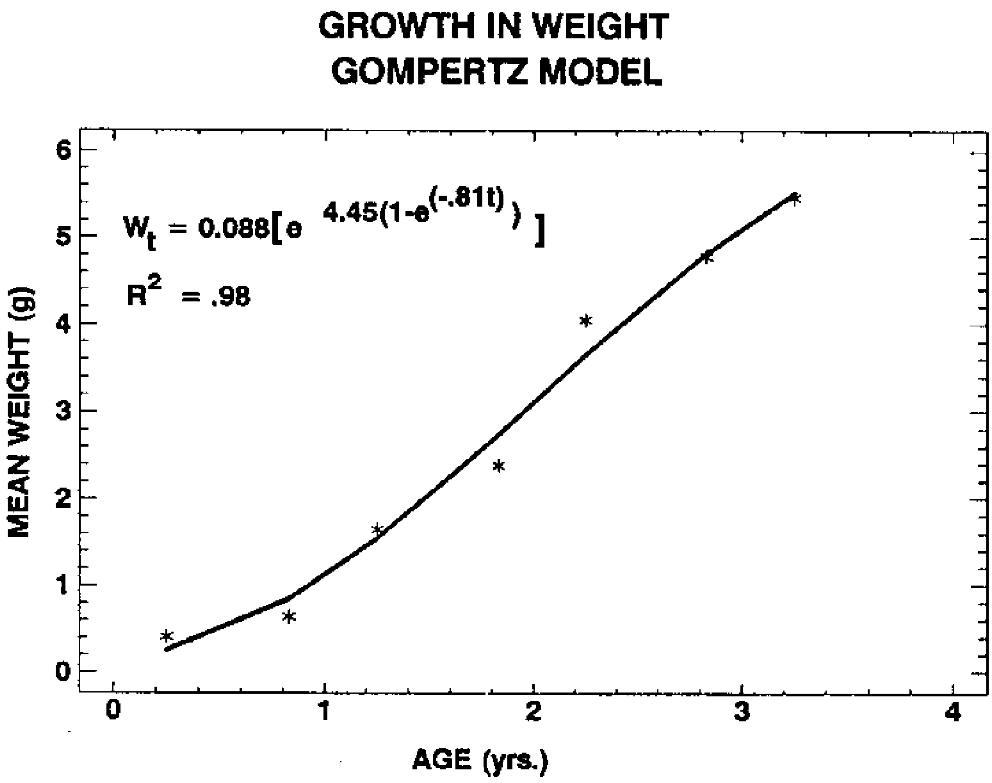


Figure 23. Growth in weight described by the Gompertz model fit to the means of the 1986 and 1987 back-calculated weights-at-annuli and fall marks data for bay anchovy.

different ages of full vulnerability to the trawl, ranged from Z = 2.19 to Z = 2.95, which is equivalent to 89 to 95% per year mortality (Table 9; Figures 24-26). The different assumptions regarding age at which anchovies became fully vulnerable to the trawl resulted in only small differences in estimates of mortality. The estimated instantaneous mortality rate of anchovy >0.5 yr. was 2.53 (S_Z = 0.58), equivalent to 92% annual mortality (Figure 24). If it is assumed that full vulnerability did not occur until age 1 the estimated instantaneous and percent annual mortality rates were 2.19 (S_Z = 0.77) and 89%, respectively (Figure 25). In an effort to reduce the variability, a third catch curve (Figure 26) was fit to abundance-at-age estimates averaged by three-month age intervals, with the assumption that bay anchovy was fully vulnerable to the trawl at age six months. Under that assumption, instantaneous and annual percentage mortalities of 2.95 (S_Z = 0.95) and 95%, respectively, were estimated.

The empirical methods all gave lower mortality rates than did the catch curve analyses (Table 9). Substituting L_∞ = 139.6 mm, mean environmental temperature = 15°C and k = 0.21 into Pauly's (1980) empirical relationship, the estimated instantaneous mortality rate was only Z = 0.31, (27% per year). Using parameters of the adjusted-age VBGF (L_∞ = 131 mm, k = 0.23) gave a similar mortality rate of Z = 0.34 (29% per year). These rates were the lowest of the six estimates that were made. Hoenig's (1983) longevity-based relationship gave an instantaneous rate of Z = 1.42, 76% per year, when age three years was assumed to be maximum age. If bay anchovy were assumed to live to a maximum of 3.5 years, then Hoenig's relationship predicted an instantaneous mortality of Z = 1.21, 70% per year. Substitution of 0.72 years for mean age and 0.14 years for age at first capture in Ssentongo and Larkin's (1973) empirical relationship gave an instantaneous mortality rate of Z = 1.0, 63% per year.

DISCUSSION

Interannual Abundances

Catch and effort data from the Maryland Department of Natural Resources (DNR) 30-year seining survey suggested that there was at least ten-fold interannual variability in bay anchovy abundance in tributaries of the Chesapeake Bay. The long time series and large spatial coverage of this sampling program provided an abundance index that may closely approximate actual abundance trends in low salinity tributaries of Chesapeake Bay. However, limitations of beach seine sampling to shallow littoral areas may bias such abundance estimates. Although bay anchovies generally are abundant along the shores during summer (Hildebrand and Schroeder 1928), smaller individuals may be relatively more abundant there (Stevenson 1958). The DNR index also is based on sampling where salinity usually is low, which may be an additional factor influencing availability of bay anchovy from year to year despite the wide temperature and salinity tolerance of the species (Hildebrand and Schroeder 1928; Morton 1989).

Ambient water column conditions, especially temperature and dissolved oxygen, may influence fish distributions differentially among years (Coutant 1987). Dissolved oxygen in the mainstem of the Chesapeake Bay varies annually and seasonally (Taft _et al_. 1980, Officer _et al_. 1984). Low dissolved oxygen conditions might have restricted bay anchovy to shallower water during anoxic

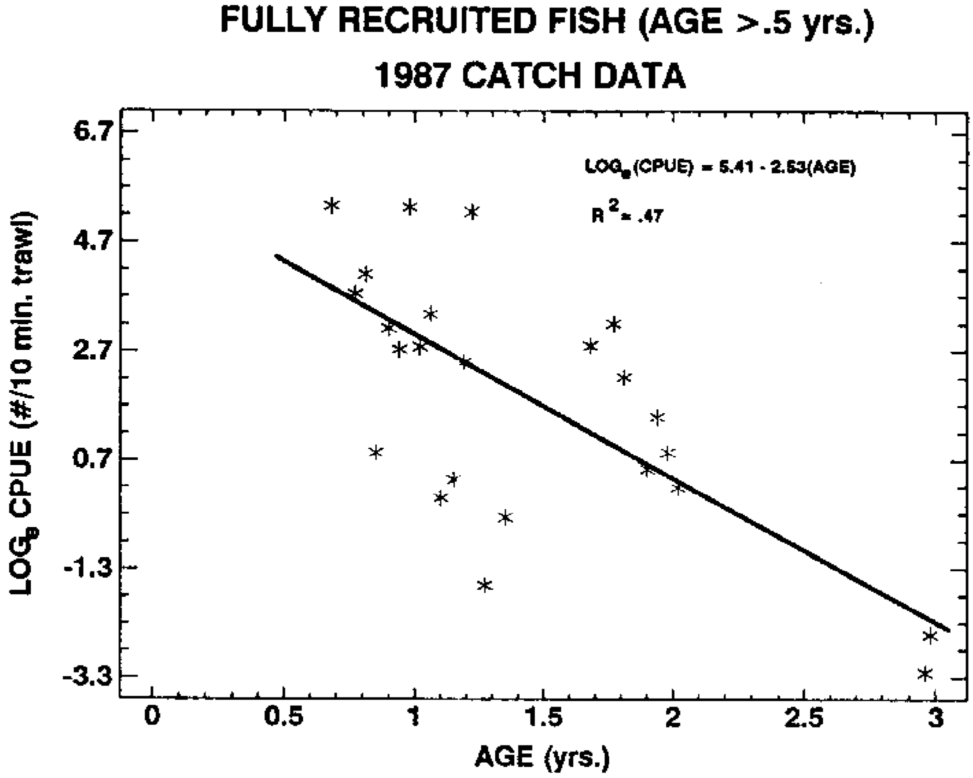


Figure 24. Catch curve for bay anchovy, assuming full vulnerability to the trawl at age 0.5 years.

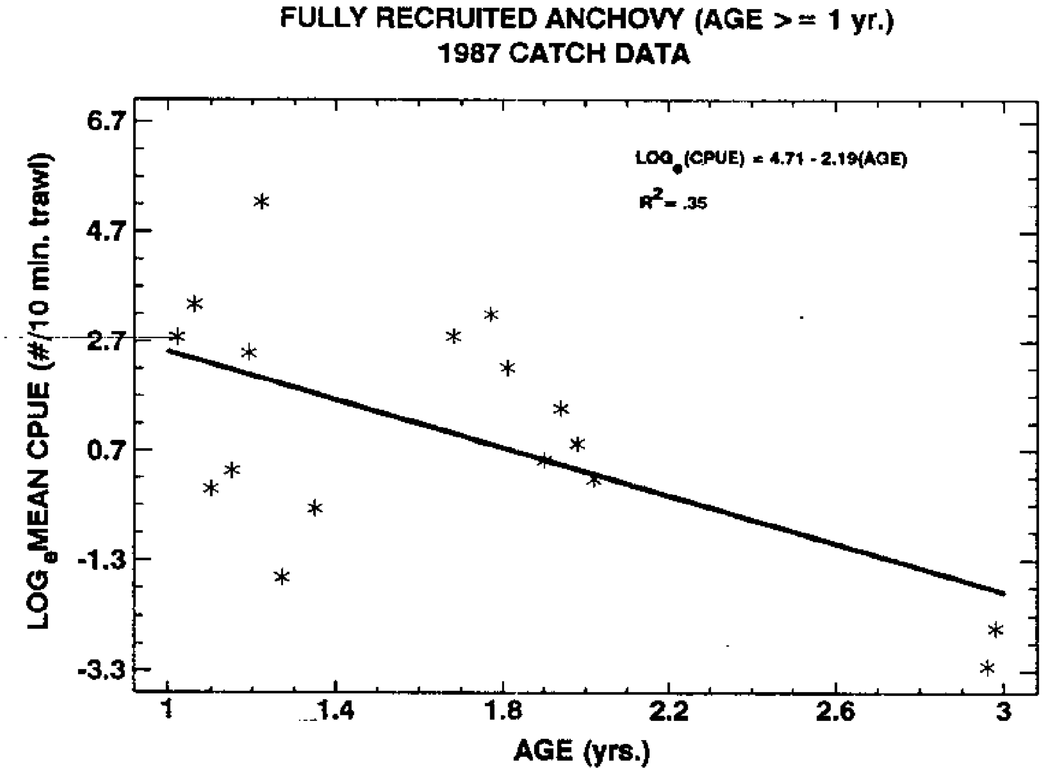


Figure 25. Catch curve for bay anchovy, assuming full vulnerability to the trawl at age 1.0 years.

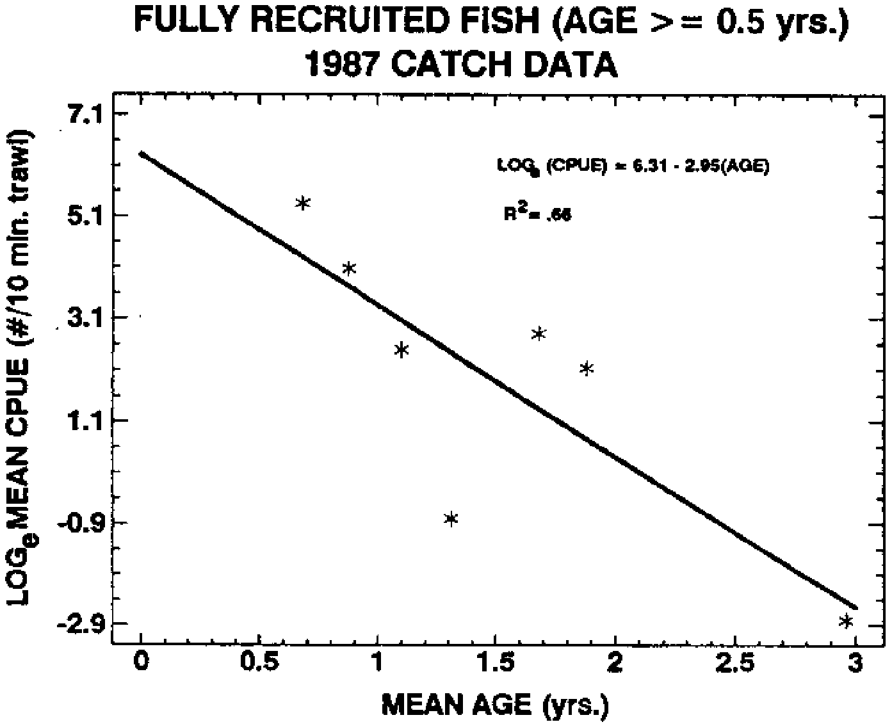


Figure 26. Catch curve for bay anchovy, fit to catch at age averaged over 3-month intervals. Full vulnerability was assumed at age 0.5 years.

Table 9. Bay anchovy mortality estimates summary. Catch curves and empirical estimates.

	BAY ANCHOVY MORTALITY		
METHOD	INSTANTANEOUS	STANDARD ERROR	ANNUAL (%)
Catch Curve 1[1]	2.53	0.58	92
Catch Curve 2[2]	2.19	0.77	89
Catch Curve 3[3]	2.95	0.95	95
Hoenig (1983)[4]	1.42		76
SSentogno and Larkin (1973)[5]	1.00		63
Pauly (1980)[6]	0.31		27

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[1] based on fully recruited fish (age >0.5 yrs)
[2] based on fish ≥1.0 yrs.
[3] fish grouped by 3-month age intervals
[4] empirical relationship based on longevity data
[5] empirical relationship based on age structure
[6] empirical relationship based on growth and temperature parameters

or hypoxic periods, or at least affected their vertical distribution, a factor that could have influenced trawl catch-per-unit-effort (CPUE) estimates of relative abundance in this study.

The trawling data indicated nearly 10-fold variation in anchovy abundance off the mouth of the Patuxent River between 1986 and 1987. The higher anchovy abundance estimate in 1986 compared to 1987 was similar to the result of the DNR seining index. However, the trawl study was restricted to a much smaller area than was the DNR seining survey, making direct comparisons tenuous at best.

Anchovy abundance estimates from 1969 to 1981 derived from research trawling near Calvert Cliffs on the Chesapeake Bay (Horwitz 1987) were not correlated with the DNR anchovy abundance indices for the same years. The Calvert Cliffs data were comparatively less variable among years except for one very low abundance estimate in 1976. Without the 1976 estimate, mean annual CPUE varied less than three-fold among years. The lack of correlation between the Calvert Cliffs and DNR anchovy abundance estimates suggests that one or both of the estimation procedures is biased. Because the DNR seining index was limited to the littoral zone of tributaries, it is possible that its large interannual variability resulted from local variation in salinity combined with baywide patterns of dissolved oxygen fluctuations that affect availability of bay anchovy to the collecting gear.

The trawling results in this study demonstrated that bay anchovy relative abundance varied significantly on annual temporal scales. It was not possible to conclusively attribute this variation to population abundance fluctuations, or to recruitment variability, although recruitment apparently was higher in 1986. Peak relative abundance of young-of-the-year anchovies occurred in September of both years but mean CPUE of young-of-the-year anchovies was more than 20 times higher in September 1986. Baywide recruitment might have been higher in 1986 but because the trawl study lasted only two years and was restricted to a small sampling area it was not possible to conclude that the estimated abundance variability was real or whether there were spatial distribution differences between years. Unbiased sampling over larger spatial and temporal scales is needed to determine how variable bay anchovy abundance is between years.

Seasonal Abundance

Considering the variable nature of trawl data, nonsignificant differences in bay anchovy abundances among months could result from too few samples. The CPUE data indicated that anchovy abundance generally was lowest in the winter months and highest in the late summer to early fall. Catches from both years, when combined into monthly CPUE estimates, indicated significantly higher CPUE in September than in other months. The large increase in CPUE in the late summer resulted from increased catches of young-of-the-year anchovy in which new recruits comprised approximately 80 percent of the total catch in each year. The decline in CPUE from late fall to winter possibly reflected high mortality and emigration either downbay or offshore from our trawling stations.

The summarized Calvert Cliffs trawl data (Horwitz 1987) indicated two annual anchovy abundance maxima (Figure 27): one in the spring (May) and one in the fall (September-November). The fall maximum was more than two times larger than the spring maximum. The three-month duration of the high fall abundance might have been an artifact from averaging 13 years of data which, if examined on a yearly basis might show temporal recruitment variation or temporal emigration differences among years. The fall maximum relative abundance off the Patuxent River mouth occurred during September in 1986 and 1987 and its duration was approximately one month in each year. Given many years of abundance data, the maximum fall abundance might occur in different months from year to year, possibly in response to temperature differences among years or other factors that might affect the temporal pattern of recruitment and emigration.

Vouglitois et al. (1987) reported that bay anchovy in Barnegat Bay, New Jersey, migrated in response to seasonal temperature changes. Anchovy moved offshore to the inner continental shelf in the fall as Barnegat Bay cooled rapidly, and returned to the Bay in the spring as the shallow waters warmed. In the Chesapeake Bay emigration of bay anchovy to the continental shelf has not been documented, and wintering anchovies are thought to remain primarily in the deeper regions of the estuary (Hildebrand and Schroeder 1928). Horwitz (1987) suggested that the relatively low CPUE of bay anchovy during the winter at the Calvert Cliffs sites resulted from offshore migration to the deeper regions of the Bay. Trawl data from the present study also indicated lower anchovy abundance during winter off the mouth of the Patuxent River. Catches were greater in deep water (30 m) in the main stem of the Bay during winter than at the standard trawling station (9 m) off the mouth of the Patuxent River. Two 10-min trawl tows at 30 m depth in March 1987 yielded 855 anchovies whereas two tows at the standard station (9 m) yielded only 52 anchovies. The differences were less pronounced in February 1987 when 26 and 8 anchovies were captured at 30 and 9 m, respectively, from two trawl tows at each depth.

The length frequencies of new recruits during some months (Figures 14 and 15, August - October 1986, July and October 1987) appeared to be bimodal, suggesting that there may have been two major periods of spawning and/or higher survival. Vouglitois et al. (1987) reported similar length-frequency distributions of newly-recruited bay anchovy in Barnegat Bay. They suggested that two major periods of spawning produced the bimodal frequency distributions - one offshore on the continental shelf and the other within the estuary. Based on egg abundance data PSEG (1984) also reported two peak spawning periods of bay anchovy, but both peaks were reported to occur within the Delaware Bay. Two peak spawning periods also could explain the bimodal length-frequency distribution observed in the Chesapeake Bay. In a large estuary like the Chesapeake Bay two peak spawning periods could occur entirely within the estuary if adults migrated into the Bay in the spring and then further up the Bay later in the season. Bay anchovy young-of-the-year hatched down-bay might then migrate or be transported up-bay. This component of the young-of-the-year population would be older than subsequent recruits hatched from later spawning farther up the Bay. This hypothesis is analagous to Dovel's (1971) conceptual model of upstream transport of anchovy larvae in the Chesapeake Bay. The young of many species including menhaden (Brevoortia tyrannus), spot (Leiostomus xanthurus), and croaker (Micropogonias undulatus) are transported or migrate into estuaries (Arenholz et al. 1987, Haedrich 1983, Norcross and Shaw 1984) and bay anchovy may behave similarly. However,

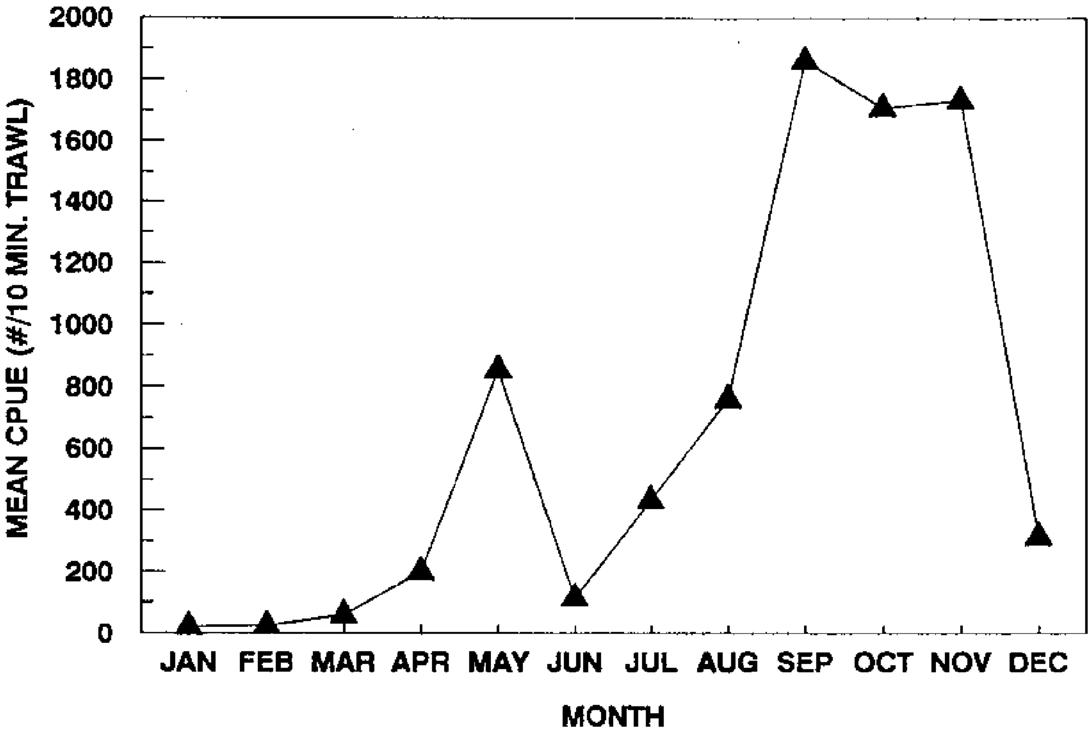


Figure 27. Mean catch-per-unit-effort by month for 13 years of trawling in the vicinity of Calvert Cliffs region of Chesapeake Bay (Figure derived from ANSP bottom trawl data, Horwitz 1987).

anchovy spawning apparently does not begin earlier in the lower Bay compared to the mid-Chesapeake Bay as indicated by monthly egg abundance data (Olney 1983; Dalton 1987) although high spawning activity may be sustained over a longer period in the lower Bay.

Differential egg and larval mortality within a spawning season also could result in bimodal or multimodal length frequencies of new recruits. One cause of high and variable mortality may result from predation, for example by gelatinous zooplankton such as the ctenophore *Mnemiopsis leidyi* (Monteleone and Duguay 1988), which co-occurs with spawning bay anchovy in the Chesapeake Bay (Johnson *et al*. 1986). If peak spawning occurs only once each year in the Chesapeake Bay and mortality of eggs and larvae were relatively constant, the expected length-frequency distribution of new recruits should be unimodal with the most abundant length class representing individuals hatched during peak egg densities. But, if all newly recruited bay anchovy originated from a peak period of spawning, then bimodal or multimodal length frequencies of recruits may reflect the effects of differential mortality rates within a spawning season. Peak egg densities usually occurred only once per year (approximately mid-July) in the Calvert Cliffs region of the Chesapeake Bay from 1971 - 1978 (Dalton 1987). Dovel (1971) found anchovy egg abundance to be associated with the seasonal peak in water temperature and day length in the upper Chesapeake Bay and Olney (1983) reported that peak spawning of bay anchovy in the lower Chesapeake Bay occurred from July to August, although relatively high egg densities occurred throughout the spawning season from May to August.

Sex Ratio

Female bay anchovy were more abundant than males and comprised 54% of the 4,048 anchovies examined during the two years of this study. Several studies have reported female:male (F:M) sex ratios of bay anchovy greater than 1.0 (Stevenson 1958; Kurtz 1977 and 1978; PSEG 1984; Vouglitois *et al*. 1987). Stevenson (1958) observed bay anchovy sex ratios favoring females in all but one collection from the Delaware Bay. The single collection that had a F:M sex ratio less than 1.0 included females in spawning condition. Stevenson (1958) suggested that females about to spawn attracted males in higher proportion than non-spawning females. PSEG (1984) observed F:M ratios significantly greater than 1.0 in all seasons except summer, also in Delaware Bay. Both Stevenson (1958) and PSEG (1984) suggested that as the spawning season neared the sex ratio apparently became approximately 1.0, which implies unequal vulnerability to capture by some gears during most of the year. My data indicated F:M ratio >1.0 (Table 6) during the spawning season and throughout the year. F:M ratios were significantly >1.0 in April, June, August and October 1987, but the tendency toward a sex ratio favoring females was present in all seasons in both years. Only two months' collections, May and November 1987, had F:M ratios <1.0 (not significantly less).

Because the length-weight relationships and growth rates of bay anchovy did not differ significantly between sexes, male and female anchovy presumably should be equally vulnerable to capture unless distribution of the sexes differs on spatial scales larger than those being sampled or behavior of males and females differs significantly. Parrish *et al*. (1986) reported that fishery-dependent data on northern anchovy *Engraulis mordax* gave a F:M ratio of 1.48. However, the ratio derived from fishery-independent trawl surveys, which covered much more area, was 1.02. The differences occurred because the sex ratio of northern anchovy is both size and age-dependent, with females more abundant in the older age classes. The directed effort of the fishery for larger northern anchovy biases sex ratios estimated from such collections (Klingbeil 1978). Hunter and Macewicz (1980) suggested that during the time of peak spawning activity (2200-2359) of the northern anchovy, higher abundance of males in the schools caused sex ratio biases in trawl catches. Picquelle and Stauffer (1985) have shown that during spawning by the northern anchovy, actively spawning females are more susceptible to capture than are non-spawning females. It is unlikely that spawning behavior influenced the observed bay anchovy sex ratios in this study because bay anchovy also spawn at night but almost all sampling was conducted during the day.

Length-Weight and Maturity

The length-weight relationship of bay anchovy from the Chesapeake Bay was similar to that of bay anchovy from other regions along the Atlantic coast. The weight of a 50 mm FL bay anchovy calculated from the mean 1987 length-weight parameters averaged across seasons was 0.98 g. Weights of 50 mm FL bay anchovy, derived from reported length-weight relationships that were summarized by PSEG (1980), are: 1.08 g (Wilk *et al*. 1978, New York Bight); 1.06 g (PSEG 1980, Delaware Bay); 0.99 g (Kurtz 1978, Barnegat Bay); and 0.99 g (Anderson *et al*. 1977, Folly Beach, S. Carolina). The estimate derived from PSEG (1980) was calculated from the parameter means of eight reported length-weight relationships.

Seasonal condition changes in bay anchovy were indicated by the length-weight relationships. For example, using the 1987 seasonal length-weight relationships, calculated weights by season of a 50 mm fork length anchovy were: Winter, 0.94 g; Spring, 0.91 g; Summer, 1.12 g; and Fall, 1.01 g. A 50 mm anchovy in spawning condition (during summer) was on average 23 percent heavier than an anchovy of the same length in the spring. The ratios of summer weights to spring weights, calculated from the length-weight relationships, indicated that the seasonal differences in weight decreased as anchovy length increased. Summer and fall weights always were heavier than winter and spring weights, but the differences among seasons became less pronounced for anchovy in larger size-classes. The calculated Fulton condition factors indicated a similar trend. However, the highest condition factor was calculated for bay anchovy collected during the summer and lowest condition factor was calculated for anchovy collected during the winter (Figure 16).

Seasonal condition changes paralleled gonad development as indicated by the Fulton condition factors and the gonosomatic index (the ratio of gonad weight to gonad-free somatic weight). In the mid-Chesapeake Bay, high gonosomatic indices from mid-May to early August delineate the spawning season (Zastrow and Houde, Chapter 4). The male GSI is higher than that for females. Bay anchovy testes during the spawning season weigh 10-12% of the somatic weight, whereas ovaries weigh from 5-7% of the somatic weight. Although differences in the gonosomatic index were found between sexes, condition differences between sexes (as indicated by Fulton condition factors) were not observed. Gonad weights of winter-collected anchovies of both sexes were less than 1.0% of somatic weight. The relationship between gonosomatic index and fork length during the spawning season indicated the length at maturity

(Zastrow and Houde, Chapter 4). Minimal length at maturity for both sexes is 40-45 mm fork length. Although young-of-the-year anchovy as large as 50 mm fork length were collected in September 1986 and 1987, none that were examined were mature or reproductively active (Zastrow and Houde, Chapter 4).

Age and Growth, Validation

Increment validation and age estimation using otoliths have been successful for many Clupeiform species including the northern anchovy *Engraulis mordax* (Collins and Spratt 1969), the European anchovy *Engraulis encrasicolus* (Erkoyuncu and Ozdamar 1989), and the southwest African anchovy *Engraulis capensis* (Melo 1984). Although daily increment formation in otoliths of bay anchovy larvae has been validated (Leak and Houde 1987, Fives *et al.* 1986) validation of annual increment formation by marginal increment analysis or other techniques (Bagenal and Tesch 1978) had not been reported for adult bay anchovy. Stevenson (1958) was not successful in aging bay anchovy using either scales or otoliths. His method of mounting otoliths in Balsam and observing a projected image may have decreased resolution and precluded recognition of annuli. Annual increments usually were easily recognized using a stereomicroscope at 25-50X in otoliths examined during this study. PSEG (1984) reported age and growth data based on presumed annual marks on otoliths for bay anchovy from Delaware Bay but validation of annulus formation by marginal incrent analysis was not reported.

A third order polynomial described the otolith size - fork length relationship best for 25-85 mm bay anchovy. Otolith size was a precise predictor of fork length. For example, for an otolith radius of 0.50 mm the predicted fork length is 35.7 mm with a 0.95 C.I. of 35.4-36.0 mm and for a 1.30 mm radius the model predicted mean fork length of 77.9 mm and a 0.95 C.I. of 77.1-78.7 mm.

The wide range of back-calculated lengths at annuli and fall marks in younger anchovy, which is believed to be real, almost certainly (Table 6) resulted from the protracted spawning season and the greater potential for fast growth in young anchovy compared to older individuals. Growth compensation later in life might have caused the range of lengths-at-age to narrow in older anchovy (Ricker 1975).

The two years of back-calculated length-at-age data were pooled and described by single growth models. Similarity of the means and variances of the back-calculated lengths-at-age between years indicated that a combined-years model was justified. The decision to fit only one model was dictated in part by the otolith degradation in the 1986 anchovy collections, which greatly reduced the number of readable otoliths for that year. In addition to the otolith sample size differences between years, very few older (age 3+) anchovies were caught in either year of the study. By combining the two years of data it was presumed that better estimates of back-calculated sizes at the oldest ages would result.

The von Bertalanffy model fit to the means of the back-calculated sizes at age provided the best estimate of adult bay anchovy growth. The length-based von Bertalanffy growth model derived here differs substantially from that reported for Delaware Bay anchovy (PSEG 1984) which includes a comparatively low L_∞ (68.435 mm), and a very high k (2.632) and t_0 (-0.012). The PSEG (1984) model does not appear to describe the observed lengths-at-age of bay anchovy found in either the mid-Chesapeake Bay or the Delaware Bay. The PSEG (1984) model overestimates younger anchovy lengths-at-age from the Chesapeake Bay whereas lengths-at-age of older anchovy from both the Chesapeake and Delaware bays are underestimated. The PSEG (1984) model was fit to lengths at observed ages (not to mean back-calculated lengths-at-age) and was forced to fit a length at time of hatch of 2 mm which was defined as t_0. This constraint contributed greatly to the high k (which describes the rate at which the asymptotic size is approached) in the PSEG model. As a result, PSEG reported the mean length of Delaware Bay bay anchovy at age 1 to be 10 mm longer than that determined for mid-Chesapeake Bay bay anchovy in this study. The low L_∞ reported by PSEG (1984) resulted mostly from the small estimated mean lengths at age 3 in their model. The smallest age 3+ anchovy found during our Chesapeake Bay aging analysis was 77 mm and the remaining age 3+ anchovy were all longer than 80 mm.

Back-calculation of anchovy lengths at time of otolith annulus and fall mark depostion increased the resolution of my model because two relatively accurate lengths-at-age were calculated per year of fish growth. Using this approach, back-calculation incorporates more information on the growth history of individuals, beyond what can be obtained from single point estimates of age. Nevertheless, sampling biases such as gear selectivity or size-dependent spatial and temporal distribution of anchovy may bias mean size-at-age estimates. By incorporating the fall marks into the back-calculated growth histories of individuals, the growth model derived here minimizes the potential for such bias.

Observed ages in the PSEG (1984) model were adjusted using an estimated median hatch date of 11 June but they were not adjusted based on a knowledge of time of annulus deposition. As a result, reported mean lengths after the first growing season were estimated from age 0+ anchovy captured in April to May under the assumption that no growth had occurred during the winter or during early spring. My data indicate that significant growth, especially among smaller age 0+ anchovy, occurred during early spring, before annulus deposition.

Stevenson (1958) estimated growth from modal length progression in Delaware Bay bay anchovy. His reported mean lengths of young-of-the-year bay anchovy were: July - 15 mm, August - 25 mm and October - 39 mm. Growth rates computed from those mean lengths (July-August, 0.33 mm d^{-1}; August-October, 0.23 mm d^{-1}) are at the low end of other reported larval and early juvenile bay anchovy growth rates, which ranged from 0.43 to 0.56 mm d^{-1} and 0.24 to 1.11 mm d^{-1} (Leak and Houde 1987, Fives _et_ _al_. 1986, respectively). Stevenson's (1958) bay anchovy length frequencies included larval fishes (standard lengths as small as 6 mm). His growth estimates should therefore be similar to larval growth estimates of Leak and Houde (1987) and Fives _et_ _al_. (1986). Estimated mean growth rate of young-of-the-year mid-Chesapeake Bay anchovy based upon the mean back-calculated length at fall mark 1 and a mean hatch date of 15 July (Dalton 1987) was 0.46 mm d^{-1} (this study) while growth rates estimated from modal progression were much lower, averaging only 0.33 and 0.20 mm d^{-1} in 1986 and 1987, respectively. The back-calculation based estimate compares favorably to young-of-the-year growth rate estimates based upon daily otolith increments of mid-Chesapeake Bay anchovy in 1986 and 1987 which was 0.47 mm d^{-1} (Morin and Houde, Chapter 5). Stevenson's (1958) reported monthly mean lengths may have been underestimated because continuous recruitment of small individuals probably occurred throughout much of the period in which he collected young-of-the-year anchovy. Consequently, mean length-at-age might have been underestimated.

Interpreting length-frequency distributions, Stevenson (1958) suggested that the earliest-spawned individuals attained a mean length of 60 mm at about age 1. It was unclear how he distinguished earlier-spawned anchovy from later-spawned individuals or from smaller age 2+ individuals. My data indicate that few age 1+ anchovy in Chesapeake Bay attained 60 mm fork length by 1 July. Furthermore, if these fish had been spawned early (May) then their estimated age would be 14 months, not one year.

The estimated parameter k in the VBGF is relatively low for bay anchovy compared to other species of anchovy. Table 10 lists for seven engraulid species the VBGF parameters and authors, and estimated natural mortality rates (Pauly 1979) compared to those for bay anchovy (this study). Only one of the species, the Argentine anchovy, Engraulis anchoita, had an estimate of k similar to that of bay anchovy (Bayliff 1967), although other authors (Brandhorst et al. 1974) reported a k value for the same species much higher than that of bay anchovy. The remaining k coefficients, except for Engraulis mordax and E. encrasicolus, were very much higher than that of bay anchovy, suggesting that in many engraulid species most growth occurs early in life with a subsequent sharp decline in somatic growth rate as asymptotic sizes are approached. In contrast, bay anchovy grows relatively fast throughout its short lifespan and thus approaches its asymtotic size at a relatively slower rate. The largest bay anchovy collected in this study was 86 mm fork length and one measuring 95 mm was observed subsequently. It seems improbable that bay anchovy ever survives long enough to grow to its L_∞ as estimated in the VBGF (139.6 mm). Although bay anchovy continued to grow quite fast in the last year of life (age 3+), no older survivors were observed.

Variability in bay anchovy back-calculated lengths-at-age declined as age increased, suggesting that growth compensation or size-selective mortality occurred during the first two years of life. Possible growth compensation of age 0+ anchovy also was indicated by the length-frequency distributions, in which the bimodal length-frequency distribution of 1986 young-of-the-year anchovy was no longer apparent at age 1+ in 1987. If earlier maturation of the oldest individuals in a newly recruited anchovy year class occurs, somatic growth rates in these reproductively active fish might decrease relative to the somatic growth rates of immature, later-spawned anchovy of the same year-class, effectively enhancing compensatory growth. Also, the general decline of somatic growth with age may indicate that at the onset of maturity, gonad development takes priority over somatic growth in bay anchovy.

Many studies suggest that allocation of energy to reproductive effort, versus somatic growth and maintenance, regulates timing of spawning, size and age at maturity, adult longevity and maximum size attained (Calow 1985). For example, gonad maturation markedly affects the somatic growth of plaice, Pleuronectes platessa (Dawson and Grimm 1980). At the time of gonad maturation (a period of no feeding), a major translocation of protein from somatic

Table 10. Von Bertalanffy growth parameters and natural mortality estimates for eight Engraulid species, including bay anchovy.

SPECIES	L_∞ (mm)	K	M	REFERENCE
Stolothrissa tanganicae	89	2.66	5.2	Coulter 1977
Cetengraulis mysticetus	180	1.99	2.4	Bayliff 1967
Engraulis anchoita	232	0.27	1.42	Bayliff 1967
Engraulis anchoita	173	0.71	0.90	Brandhorst *et al*. 1974
Engraulis encrasicolus	149	1.13	1.80	Bayliff 1967
Engraulis encrasicolus	168	0.32	--	Erkoyuncu and Ozdamar 1989
Engraulis japonicus	177	1.80	1.63	Bayliff 1967
Engraulis mordax	164	0.45	1.70	Bayliff 1967
Engraulis ringens	170	1.40	1.00	Bayliff 1967
Engraulis ringens	150	1.70	1.52	Boerema *et al*. 1965
Anchoa mitchilli	139	0.21	2.19-2.95	Present Study

tissue to ovary occurred. In a comparison of two distinct populations of the river sculpin, Cottus hangiongensis, Goto (1989) observed marked growth decreases after the first sexual maturity was attained. In yellow perch, Perca flavescens, Tanasichuk and Mackay (1989) reported differences in both timing and extent of somatic growth among age-sex groups. Craig et al. (1989) reported that differences in somatic growth between male and female goldeye, Hiodon alosoides, may result from the differences in gonad growth between the sexes, implying a competitive interaction between somatic and gonad growth. A competitive interaction between somatic and gonadal growth also was indicated by the onset of maturity in the catfish, Silurus glanis, which occurred simultaneously with decreased annual somatic growth (Orlova 1988). Although bay anchovy growth rate continued to be significant throughout life, it never approached the high rates observed during the first growing season in subsequent growing seasons. Bay anchovy become reproductively mature early in their second growing season and allocation of resources to reproductive effort is one cause of lower somatic growth rates. Clarke (1987) suggested that prevailing mortality rates of adult and early life history stages of fish might be the selection pressure that dictates resource allocation to somatic or gonad growth.

Seasonal growth rate differences in bay anchovy seem probable based upon the observed sinusoidal pattern of mean back-calculated lengths-at-age (Figure 19). Most growth occurred during the period between annulus deposition (May) and fall mark deposition (approximately October). Consequently, predicted lengths-at-age from the model may be overestimated or underestimated, to some extent, depending upon the season in which the estimate was made. Predicted lengths at fall marks tend to be underestimated whereas predicted lengths at annuli are overestimated by the model. The difference between predicted and mean back-calculated lengths at annuli and fall marks are: fall mark 1 (-2.7 mm), annulus 1 (+4.8 mm), fall mark 2 (-2.2 mm), annulus 2 (+1.5 mm), fall mark 3 (-3.7 mm), annulus 3 (+0.9 mm).

Seasonal growth rate differences in fish are common in temperate environments (Iles 1974, Flath and Diana 1985). Modifications of the von Bertalanffy growth function have been proposed to describe seasonal growth variation in temperate fish species (Pitcher and Macdonald 1973; Lockwood 1974; Pauly and Gaschutz 1979). Although temperature is an important factor alone that influences growth in fish, interactions between temperature and other seasonally varying abiotic or biotic processes such as day-length, oxygen, food availabilty, and competition also can significantly affect growth (Brett 1979). Vazquez and Houde (Chapter 6) documented the effects of temperature and ration level on growth of bay anchovy in the laboratory. Feeding experiments at three diet levels (10%, 20%, and 40% of anchovy wet-weight per day) and three temperatures (19, 23, and 27°C) demonstrated that both factors significantly influenced bay anchovy growth. Generally, higher weight-specific growth rates were attained at higher temperatures and ration levels. These and other factors vary with season in the Chesapeake Bay. It is certain that overwintering bay anchovy are subject to low temperatures and shorter day-lengths, and feeding rates will be low under winter conditions.

Because two points of reference per year were visible on bay anchovy otoliths (the annulus and the fall mark) summer growth increments on otoliths were distinguishable from winter growth increments. Young-of-the-year bay anchovy exhibited the most extreme seasonal growth rate differences. Mean seasonal instantaneous growth rates derived from the mean back-calculated lengths at fall marks and annuli for young-of-the-year anchovy declined from 1.13 mo^{-1} (13.8 mm mo^{-1}) during summer to 0.018 mo^{-1} (0.70 mm mo^{-1}) during winter. Back-calculated seasonal growth rate differences declined as age increased. Mean seasonal instantaneous growth-in-length of age 1+ anchovy varied four-fold from 0.061 mo^{-1} in summer to 0.015 mo^{-1} in winter. Mean seasonal instantaneous growth rates of age 2+ anchovy varied nearly five-fold from 0.034 mo^{-1} during summer to 0.007 mo^{-1} during winter.

Mortality

No bay anchovy older than age 3+ were observed, indicating a short life-span and corresponding high mortality rates. Results of the catch curve analysis indicated that mortality rates ranged from 89 95% per year for fully recruited juveniles and adults. Such high mortality rates are common among engraulid species (Beverton 1963). Pauly (1979) compiled growth and mortality parameters for many species of fish and reported instantaneous mortality rates for engraulids (Table 10) ranging from 0.90 to 5.20 (59 to >99% yr^{-1}). Bay anchovy rates from catch curve analysis fall in the upper part of that range.

The assumptions of catch curve analysis include equal recruitment among years and equal vulnerability to the sampling gear of individuals larger than some minimum size (Chapman and Robson 1960). If the variable relative abundance estimates in 1986 and 1987 are indicative of recruitment differences between years, or if larger anchovy avoided the trawl, then the catch curve estimates may be biased. The survivors of relatively high recruitments in older age-classes would cause mortality to be underestimated whereas large recruitments of younger age-classes would lead to overestimates of mortality. Underestimation of older age-class abundances through gear avoidance by larger individuals also would cause overestimates of mortality.

Application of Pauly's (1979) temperature and growth-parameter procedure gave a very low mortality rate (Table 9). The estimated mortality generated from Pauly's (1979) method was not believed to be accurate because the growth parameters of most fishes used to develop his model differ substantially from those of bay anchovy. Bay anchovy have a relatively low k and high L_∞ for the age structure of the population observed in the Chesapeake Bay.

Another possible source of error in Pauly's (1979) method could result from applying an incorrect mean environmental temperature (15°C) for bay anchovy. Although bay anchovy are found in the Chesapeake Bay year round, it is possible that some anchovy may emigrate to warmer continental shelf water in winter as they do in Barnegat Bay (Vouglitois _et_ _al_. 1987). If such an emigration occurs in the Chesapeake Bay, the mean environmental temperature experienced by bay anchovy would be higher than that estimated for the mid-Chesapeake Bay. The sensitivity of Pauly's (1979) model to temperature was tested by arbitrarily substituting a five degree higher environmental temperature into his model. Under that condition an instantaneous mortality rate of 1.04 (64% yr^{-1}) was predicted for bay anchovy, which is approximately 2.5 times higher than that (27% yr^{-1}) using the mid-Chesapeake Bay mean water temperature, but it is still low compared to the catch curve estimates.

Based upon mean age of collected bay anchovy and age at first capture, Ssentongo and Larkins's (1973) model provided an instantaneous mortality rate estimate of 1.00 (Table 9), a low result compared to the catch curve estimates. A potential error associated with this method lies in inaccurate estimation of age at first capture, which assumes that older fish are fully vulnerable to the trawl. It was difficult to estimate age at full vulnerability for bay anchovy. The age selected (0.14 yr) for the Ssentongo and Larkin (1973) analysis probably was underestimated because anchovy of this age were only beginning to recruit to the gear. Perhaps a better way to estimate the age of full vulnerability is to examine dates of maximum CPUE of young-of-the-year anchovy relative to peak spawning date. Peak spawning of bay anchovy occurs in mid-July (Dalton 1987) in the mid-Chesapeake Bay and maximum CPUE of age 0+ anchovy occurred in mid to late September. Assuming that bay anchovy is fully vulnerable at the time of maximum CPUE for age 0+ fish, the age at full vulnerability is between 60 and 75 days (0.16-0.20 yr) posthatch. Substitution of these ages into Ssentongo and Larkin's (1973) equation caused only small changes in instantaneous mortality rates ($Z = 1.02$ and 1.09, equal to 64-66% annual mortality).

The second parameter of concern in Ssentongo and Larkin's (1973) method is the estimated mean age of captured bay anchovy. Age 0.72 years was derived from the relative abundance-at-age that was generated for the catch curve analysis. Gear avoidance by larger anchovies could have biased this estimate, causing an underestimate of mean age, which in turn would cause an overestimation of mortality. Because the largest bay anchovy adults were <90 mm FL the assumption of equal vulnerability may hold, although avoidance of the 4.9 m trawl by anchovy was not evaluated. Furthermore, because the estimated mortality rate derived from Ssentongo and Larkin's (1973) method was relatively low, the assumption of equal vulnerabilty was supported. Had gear avoidance by the oldest anchovy been serious, mean age of anchovy would have been underestimated, leading to a high mortality rate estimate.

The third empirical method (Hoenig 1983) regressed mortality rate on longevity, based on literature-derived estimates of natural mortality rate and maximum observed age for several groups of organisms including fish, molluscs and cetaceans. The age of the four oldest bay anchovies collected during this study ranged from 2.9-3.1 years although it is conceivable that some bay anchovy might live longer. Substitution of age 3.0 into Hoenig's (1983) regression model provided an instantaneous mortality rate of 1.42 (Table 9) a 76% yr^{-1} annual mortality. If bay anchovy attain age 3.5 yr., then Hoenig's equation predicts an instantaneous mortality rate of 1.21, a 70% annual mortality.

Compared to catch curve estimates of bay anchovy mortality, all of the empirical estimates are low, although the estimate obtained from Hoenig's (1983) equation compared more favorably to the catch curve estimates. Because the empirical procedures gave such variable results and because clupeiform species have been demonstrated to be prone to error in empirical mortality estimation procedures (Beverton 1963; Pauly 1979) the catch curve methods probably produced the best estimates of bay anchovy mortality. Annual mortality of 89-95% probably applies to the recruited population of bay anchovy in Chesapeake Bay. Given annual mortality in the 89-95% range, the population of bay anchovy in late summer will be dominated by young individuals. If $Z = 2.2$

(i.e. 89% per year), then the age structure of the recruited population (>30 d posthatch) will include 85.10% age 0+, 13.27% age 1+, 1.47% age 2+ and 0.16% age 3+ anchovies.

Bay anchovy must balance high mortality rates with high reproductive capacity. Zastrow and Houde (Chapter 4) found that virtually all adult females spawned >400 eggs g^{-1} body weight each night during an approximate 45-day peak period of the 1986-1987 spawning season in the mid-Chesapeake Bay. High reproductive effort also is evident from the dominance of bay anchovy eggs and larvae in ichthyoplankton from the Chesapeake Bay and many other estuaries along the east coast of the United State (Olney 1983, Dovel 1971 and 1981, Houde and Lovdal 1984).

Another indicator of high reproductive effort and high mortality rates is the young age of estimated maximum biomass. By modeling the decline in numbers and growth in weight of a hypothetical cohort of bay anchovy, the age at which biomass was maximum was estimated. Because growth and mortality rates differ substantially between larval and adult stages, the growth and mortality parameters derived here for adult bay anchovy were applied to a hypothetical cohort after the approximate age of metamorphosis (30 d). The estimated age of maximum biomass ranged from <0.1 to 0.8 years (Table 11), depending on the mortality rate used in the model. The oldest age of maximum biomass (0.8 yrs.) was estimated by applying an instantaneous mortality rate of 1.4 (derived from Hoenig's (1983) method) and probably is an overestimate. Applying the estimated mortality rates from catch curve analysis indicated much younger ages at maximum biomass (<0.1 to 0.17 yrs.), at lengths from 18 to 36 mm, respectively. These results suggest that age of maximum biomass occurred in late summer near the time of metamorphosis or shortly thereafter. Even if the lower mortality rates apply, bay anchovy maximum biomass in the Chesapeake Bay is expected to be achieved well before individuals are one year of age.

Table 11. Biomass model of a hypothetical cohort of bay anchovy with an initial abundance of 10^6, subjected to three different instantaneous mortality rates. Weight-at-age was estimated from the weight form of the von Bertalanffy model. Mortality rates were applied to ages older than age-at-metamorphosis (T_o = 30 d (0.082 yr)).

BIOMASS MODEL

		Z = 1.4		Z = 2.2		Z = 2.5	
AGE(yr)	Individual Weight	Cohort Abundance	Cohort Biomass (kg)	Cohort Abundance	Cohort Biomass (kg)	Cohort Abundance	Cohort Biomass (kg)
0.10	0.229	975115	223.40	961174	220.21	955997	219.02*
0.11	0.235	961558	225.50	940259	220.50	932394	218.66
0.12	0.240	948190	227.56	919799	220.75	909373	218.25
0.13	0.246	935008	229.60	899784	220.95	866920	217.79
0.14	0.251	922009	231.61	880205	221.11	865022	217.29
0.15	0.257	909191	233.59	861052	221.22	843665	216.76
0.16	0.263	896551	235.54	842316	221.29	822835	216.17
0.17	0.269	884087	237.46	823987	221.32*	802519	215.55
0.18	0.275	871796	239.35	806058	221.31	782705	214.89
0.19	0.281	859676	241.22	788518	221.25	763379	214.20
0.20	0.287	847724	243.05	771360	221.15	744532	213.46
0.30	0.352	736976	259.65	619030	218.10	579842	204.29
0.40	0.426	640696	273.05	496784	211.71	451582	192.45
0.50	0.508	556994	283.20	398678	202.70	351692	178.81
0.60	0.599	484227	290.18	319947	191.73	273898	164.14
0.70	0.699	420967	294.13	256763	179.40	213312	149.04
0.80	0.807	365971	295.28*	206057	166.25	166127	134.04
0.90	0.924	318160	293.86	165365	152.74	129380	119.50
1.00	1.049	276595	290.17	132708	139.22	100761	105.71
2.00	2.751	68207	187.61	14704	40.45	8271	22.75
3.00	5.110	16819	85.95	1629	8.33	679	3.47

* Indicates maximum biomass

CHAPTER 4. MATURITY, SPAWNING AND FECUNDITY OF BAY ANCHOVY (*ANCHOA MITCHILLI*) IN MID-CHESAPEAKE BAY

C.E. Zastrow and E.D. Houde

INTRODUCTION

The bay anchovy spawns over a protracted reproductive season that may extend throughout the year in southern parts of its range (Houde and Lovdal, 1984) but is shorter at higher latitudes. The spawning season near Beaufort, North Carolina extends from late April to early September, with peak spawning in July (Kuntz, 1914). In Barnegat Bay, New Jersey, the spawning season may begin as early as April, peaks in June and July and is completed in August, although anchovy eggs have been encountered as late as November (Vouglitois *et al*., 1987).

It has been suggested that Chesapeake Bay is the center of major spawning activity for bay anchovy (Dovel, 1971; Olney, 1983). In the lower Chesapeake Bay, bay anchovy eggs and larvae dominate the ichthyoplankton from May until September (Olney, 1983). Dalton (1987) reported that bay anchovy eggs comprised 99% of all fish eggs and 67% of all fish larvae collected in a seven-year study in mid-Chesapeake Bay, and that spawning occurred from May-September. There is no published information on fecundity, size at maturation or spawning frequency in mid-Chesapeake Bay, although Luo and Musick (submitted) have reported on reproductive characteristics of bay anchovy collected near the York River at the mouth of the Chesapeake Bay.

The reproductive ecology of bay anchovy in mid-Chesapeake Bay was examined based on 1986 and 1987 trawl collections of adults. Objectives were to determine:

1) Size and age at first maturity
2) Seasonal maturation cycle
3) Time and frequency of spawning
4) Fecundity of bay anchovy

METHODS

In 1986, bay anchovy were collected in a 4.9 m width otter trawl with 3 mm mesh codend. Collections were made at stations described by Newberger *et al*. (Chapter 3) in March, and in each month from May through November. In 1987, fish were trawled in February, and in each month from April through November. Gonads were removed from a random sample of up to 20 males and 20 females ≥40 mm fork length on a monthly basis and more frequently when samples were available. Each anchovy had been measured to the nearest 1.0 mm fork length and weighed to the nearest 1.0 mg. Gonads were preserved in 70% ethanol.

Gonosomatic indices (GSI) were calculated for fish ≥40 mm fork length to discern the spawning season. GSI was determined by weighing the gonad and each anchovy minus its gonad. Gonads and fish were blotted on paper towels and then weighed to the nearest 0.1 mg and 1.0 mg, respectively. GSI, expressed as a percent, was calculated as:

$$GSI=100\,[\text{gonad weight}/(\text{anchovy weight}-\text{gonad weight})]$$

GSI also was estimated for anchovies from additional separate samples of anchovies in the 35-42 mm fork-length range from June through September to ascertain the length at first maturity to determine if the smallest one-year-olds (collected in June) were mature, and to determine if the largest age 0+ anchovy might spawn during August and September.

Measurements on ova from preserved ovaries from 18 females were made on samples collected in July, August and November 1986 and in April 1987. The ovaries of four females from each sample date were selected and diameters of 100 ova from a randomly selected portion of the ovary were measured under a dissecting microscope with ocular micrometer. The near-spherical ova were measured along whichever axis fell along the micrometer scale. For two females collected on July 16, 1986, 100 ova were measured from each of four sections in the ovary: anterior left, posterior left, anterior right and posterior right to determine if ova sizes differed among locations in the ovary.

To examine daily spawning periodicity and batch fecundities of females, trawl collections were made repeatedly over a 29-hr period on 29-30 July, 1986 and over a 24-hr period on 30 June-1 July, 1987. The twelve samples of anchovies in 1986 provided 397 ovaries and the eleven samples of anchovies in 1987 provided 173 ovaries. These ovaries were examined for ova in hydrated condition. An additional 88 ovary samples from other collection dates in late afternoon or early evening during the spawning season were examined. Batch fecundity, defined as the number of ova released per spawn, was determined by counting hydrated ova, which are in the final stage of maturation, having rapidly accumulated ovarian fluid just prior to being spawned (Hunter et al., 1985). In 1986, ovaries from up to 50 females were randomly selected and examined for each sample time in the 29-hr series. In the 1987 24-hr series, which had smaller sample sizes, all females were examined except for one large sample in which 63 females were examined. Females were measured, weighed and their excised ovaries preserved in 10% formalin. Ovaries were examined under a dissecting microscope for evidence of hydrated condition. The percentage of females in a sample that were about to spawn on that day was determined from the ratio of females with hydrated ova to the total number of females in the sample (Hunter and Macewicz, 1985).

Ovaries from up to 10 females in hydrated condition at each sampling time were randomly selected and hydrated ova counted to determine batch fecundity. Ovaries were placed in Gilson's solution at least 24 hr prior to examination to break apart ovarian connective tissue and thus facilitate counting under a dissecting microscope. All hydrated ova in the left and right ovaries were counted to obtain the batch fecundity. Relative batch fecundity was calculated as the number of ova per g of ovary-free female weight. Regression relationships between batch fecundity and female weight, ovary-free female weight, fork-length and ovary weight were determined.

Relative egg production by individual size-classes of female bay anchovy during the peak spawning season was estimated. Length-frequency distributions of adult-size bay anchovy from July collections in 1986 and 1987 (Newberger et al., Chapter 3) were used to estimate the percent egg production by length classes and age groups in each year.

RESULTS

Gonosomatic Index (GSI)

The GSI for 416 male bay anchovy ≥35 mm ranged from 0.04% to 12.25%. The GSI for 417 female bay anchovy ≥35 mm ranged from 0.15 to 7.53% (Table 12). Based on GSI, neither male nor female bay anchovy were sexually mature until 40-45 mm fork length (Figure 28). A linear regression of GSI on fork length for female bay anchovy ≥43 mm fork length collected from June through August indicated that there was a significant decline in GSI as length increased ($P=0.015$). However, the coefficient of determination was very low ($r^2=0.0592$). There was no significant regression of GSI on fork-length for male bay anchovy ≥43 mm. The mean GSI for ≥43 mm male and female bay anchovy during the spawning season was 7.15% and 4.36%, respectively. ANOVA indicated that for both male and female anchovy ≥43 mm from May - August mean GSI did not differ significantly between years ($P>.90$). However, the GSI was significantly higher for mature male anchovy than for mature female anchovy ($P<0.0001$).

GSI for both males and females ≥40 mm was low in March, increased in April and May, and peaked in July, before decreasing in August to a low level in fall and winter (Figure 29). Based on GSI, the 1986 and 1987 spawning seasons in mid-Chesapeake Bay extended from mid-May to mid-August.

The mean GSI values for <43 mm FL male and female bay anchovy indicated that they were not mature (Table 12). Fish collected in June and July of 1987 were small age 1 individuals. Fish <43 mm collected in August and September of 1986 and 1987 were fast-growing age 0+ individuals. The low GSI values for the age 0+ anchovy (<1.0) indicated that these fish probably had not spawned (Table 12) and would not mature until the following year. The GSI values for the <43 mm, age 1 anchovy were slightly higher than those of the age 0+ anchovy but still much lower than the GSI of mature individuals. It is possible that the smallest age 1 anchovy also may not have spawned until the following year.

Ova Sizes

There was no significant difference in mean ovum diameters among four sections in the ovary (ANOVA; $P>.35$ and $P>.75$) for the two females that were analyzed (Table 13). Therefore, the section of an ovary from which mean ovum diameters were obtained for the remaining 16 females (Table 13) was selected at random.

Mean ovum diameters did not differ significantly among females collected on the same date except on 14 August 1986, when the mean for the 51 mm female was significantly smaller than that for the three larger females (ANOVA; $P<0.0001$) (Table 13). Mean ovum diameters were smallest in November (0.114-.118 mm), increased slightly in April (.129-.145 mm), reached a maximum in July (.211-.360 mm), and decreased in August (.115-.233 mm). Yolked

Table 12. Mean monthly gonosomatic indices of female bay anchovy in 1986 and 1987. Anchovies are ≥40 mm fork length.

DATE	N	$\bar{x}$ SL	2 S.E.	GSI	2 S.E.
4 MAR 86	10	44.92	1.92	0.86	0.10
29 MAY 86	20	57.95	2.42	3.95	0.50
3 JUL 86	20	55.35	3.18	5.20	0.58
16 JUL 86	20	57.95	2.72	5.71	0.54
14 AUG 86	20	49.60	2.38	1.39	0.62
29 AUG 86	20	55.81	2.86	0.81	0.16
24 SEP 86	20	60.85	1.86	0.83	0.08
8 OCT 86	20	59.75	1.86	0.83	0.08
24 OCT 86	20	55.75	2.98	0.69	0.06
10 NOV 86	20	67.40	3.30	0.89	0.10
26 FEB 87	14	43.46	1.84	1.01	0.14
22 APR 87	20	67.10	2.90	1.85	0.20
5 MAY 87	20	56.80	3.84	1.79	0.22
24 JUN 87	20	55.95	3.66	7.40	0.58
7 JUL 87	20	53.45	3.70	6.29	1.08
22 JUL 87	20	54.80	2.32	7.53	0.88
12 AUG 87	20	59.45	1.12	1.06	0.26
15 SEP 87	16	57.13	1.18	0.47	0.05

Mean gonosomatic indices of female anchovy 35-42 mm FL from June-September in 1986 and 1987.

DATE	N	$\bar{x}$ SL	2 S.E.	GSI	2 S.E.
21 AUG 86	9	40.67	1.52	0.15	0.03
10 SEP 86	10	41.20	1.84	0.21	0.08
3 JUN 87*	11	39.31	1.18	1.13	0.28
JUL 87*	26	38.64	1.20	0.37	0.12
12 AUG 87	10	39.20	1.66	0.16	0.08
11 SEP 87	10	39.70	1.88	0.19	0.06

---

* One-year-old bay anchovy hatched late in the 1986 season.

Table 12. continued

Mean monthly gonosomatic indices of male bay anchovy in 1986 and 1987. Anchovies are ≥40 mm fork length.

DATE	N	$\bar{x}$ SL	2 S.E.	GSI	2 S.E.
4 MAR 86	12	43.80	1.90	0.24	0.06
29 MAY 86	20	58.35	2.10	8.28	1.44
3 JUL 86	20	55.05	1.82	9.82	0.72
16 JUL 86	20	57.45	2.26	10.17	1.26
14 AUG 86	20	52.95	2.08	1.33	0.66
29 AUG 86	16	55.20	2.08	0.39	0.18
24 SEP 86	20	59.00	3.06	0.28	0.06
8 OCT 86	20	60.25	2.90	0.21	0.04
24 OCT 86	20	58.00	2.06	0.19	0.04
10 NOV 86	20	65.25	3.12	0.25	0.02
26 FEB 87	13	42.93	1.40	0.19	0.04
22 APR 87	20	67.20	3.94	0.95	0.18
5 MAY 87	20	58.60	3.84	2.07	0.54
24 JUN 87	20	54.10	3.04	10.74	0.78
7 JUL 87	20	50.00	1.28	9.65	1.08
22 JUL 87	20	54.25	1.68	12.25	1.72
12 AUG 87	20	58.80	1.20	0.93	0.26
15 SEP 87	16	54.44	1.22	0.13	0.03

Mean gonosomatic indices of male anchovy 35-42 mm FL from June-September 1986 and 1987.

DATE	N	$\bar{x}$ SL	2 S.E.	GSI	2 S.E.
21 AUG 86	9	40.11	1.78	0.04	0.01
10 SEP 86	10	41.10	1.82	0.04	0.02
3 JUN 87*	13	39.09	1.24	1.04	0.74
JUL 87*	28	38.92	1.14	0.51	0.30
12 AUG 87	10	38.30	1.80	0.04	0.01
11 SEP 87	10	40.10	1.20	0.04	0.02

* One-year-old bay anchovy hatched in the 1986 season.

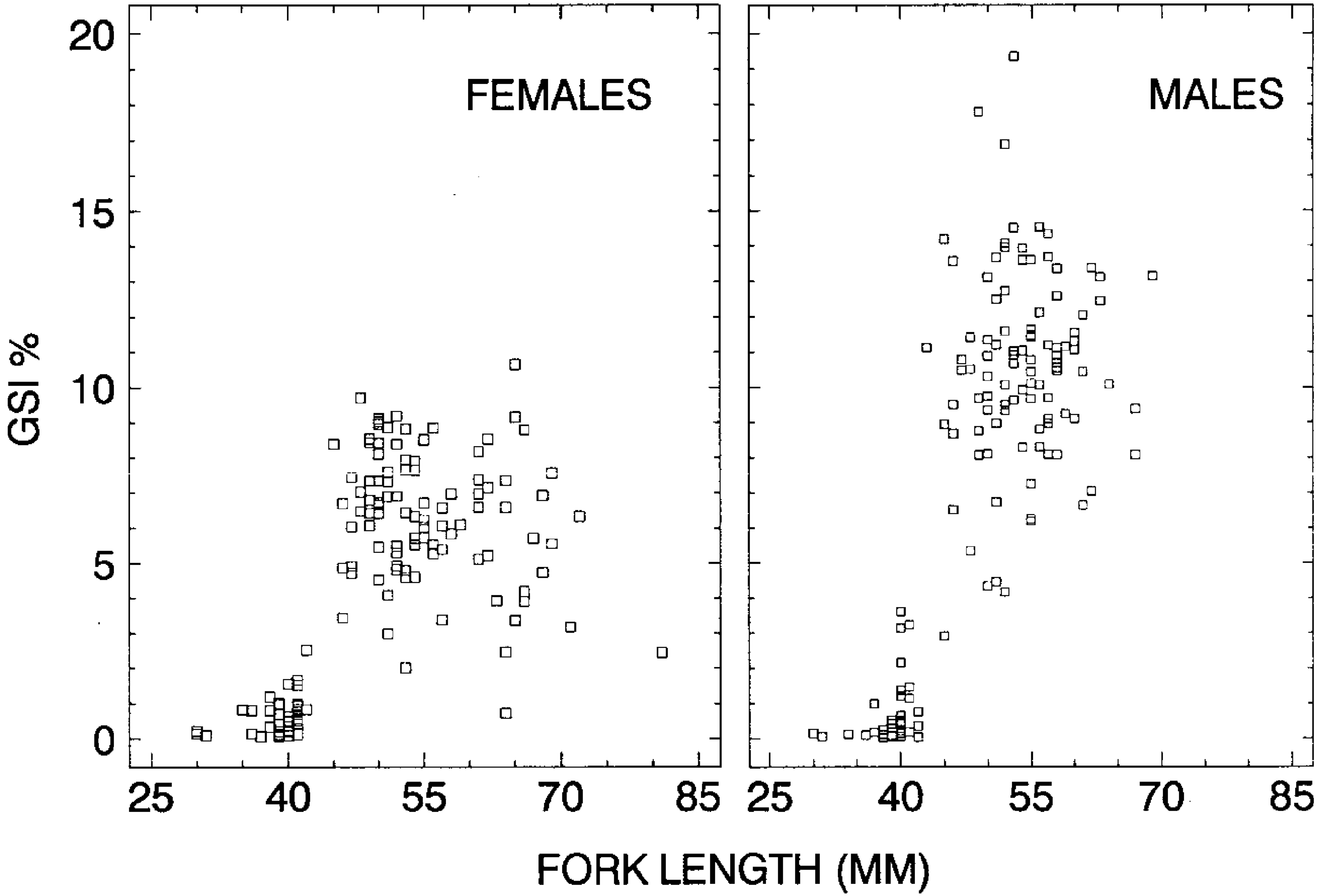


Figure 28. Gonosomatic index in relation to fork length for female and male bay anchovy from mid-Chesapeake Bay June through July, 1986 and 1987.

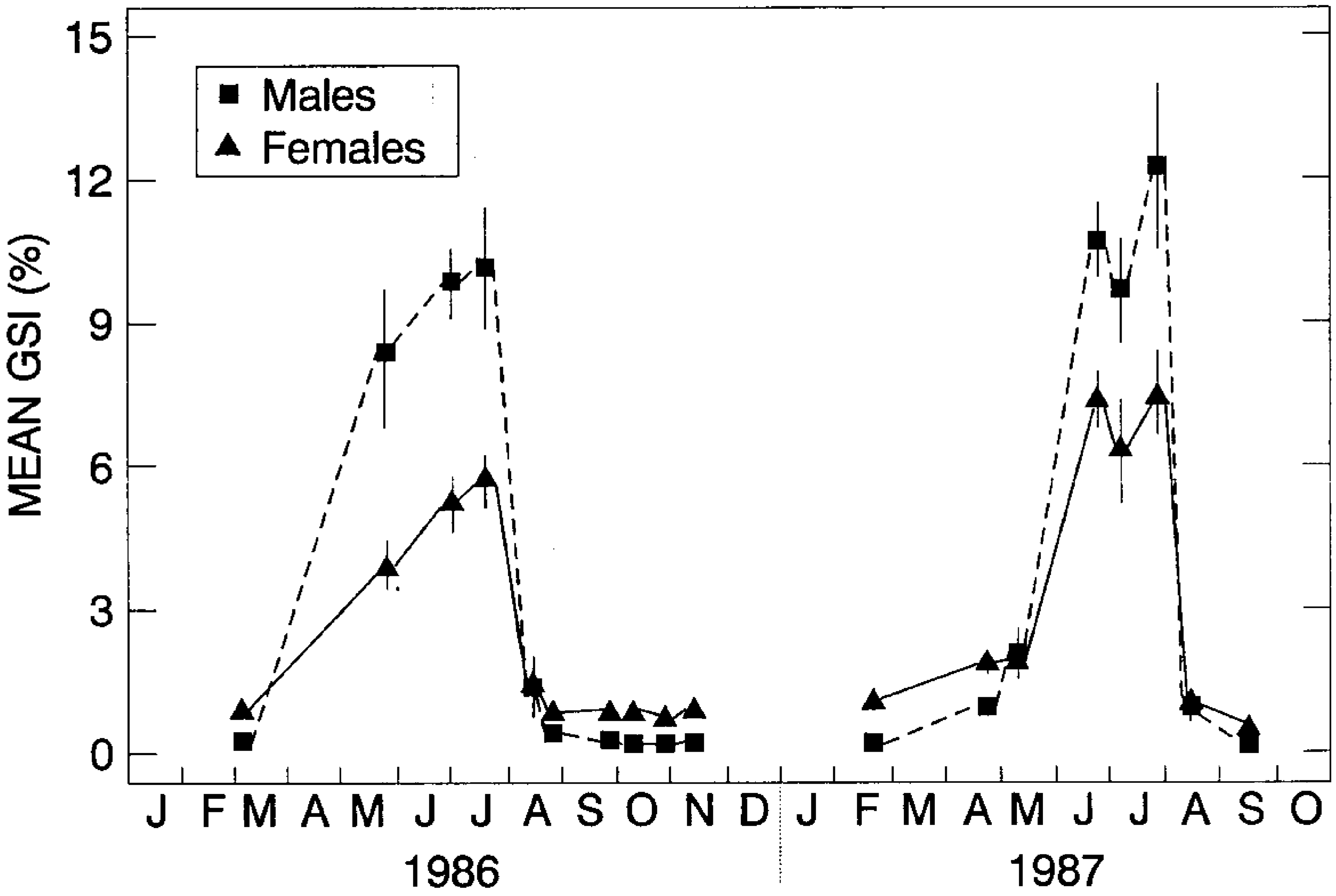


Figure 29. Mean gonosomatic index in relation to month of collection for male and female bay anchovy ≥40 mm FL from mid-Chesapeake Bay for 1986 and 1987.

Table 13. Mean ovum diameters of bay anchovy in mid-Chesapeake Bay. Data from females collected in four sample months are presented as are means of yolked ova >0.2 mm and means of all ova from four different sections within the ovaries.

Date	Female Fork Length	Number Of Ova	$\bar{x}$	Standard Deviation	Min.	Max.
11/10/86	51	100	0.114	0.020	0.054	0.153
11/10/86	53	100	0.116	0.024	0.053	0.163
11/10/86	72	100	0.113	0.027	0.057	0.173
11/10/86	74	100	0.118	0.027	0.058	0.182
11/10/86	Yolked ova >0.2mm	0	-	-	-	-
04/22/87	61	100	0.138	0.041	0.048	0.250
04/22/87	63	100	0.129	0.039	0.056	0.242
04/22/87	65	100	0.145	0.053	0.069	0.306
04/22/87	79	100	0.134	0.034	0.050	0.220
04/22/87	Yolked ova >0.2mm	31	0.232	0.026	0.201	0.306
07/03/86	53	100	0.256	0.207	0.079	1.333
07/03/86	61	100	0.280	0.244	0.071	0.874
07/03/86	63	100	0.240	0.183	0.069	0.898
07/03/86	71	100	0.211	0.153	0.075	0.781
07/03/86	Yolked ova >0.2mm	147	0.443	0.216	0.202	1.333
08/14/86	51	100	0.186*	0.158	0.054	0.697
08/14/86	53	100	0.230	0.214	0.049	1.030
08/14/86	55	100	0.233	0.173	0.055	0.773
08/14/86	56	100	0.115	0.033	0.063	0.218
08/14/86	Yolked ova >0.2mm	89	0.450	0.185	0.200	1.030
07/16/86	54 Left Ant.	100	0.314	0.241	0.062	0.842
07/16/86	54 Left Post.	100	0.360	0.253	0.075	0.977
07/16/86	54 Right Ant.	100	0.310	0.241	0.058	0.876
07/16/86	54 Right Post.	100	0.311	0.242	0.062	0.858
07/16/86	Yolked ova >0.2mm	206	0.518	0.192	0.202	0.977
07/16/86	65 Left Ant.	100	0.235	0.188	0.083	0.774
07/16/86	65 Left Post.	100	0.211	0.186	0.057	0.803
07/16/86	65 Right Ant.	100	0.225	0.161	0.054	0.792
07/16/86	65 Right Post.	100	0.232	0.184	0.069	0.927
07/16/86	Yolked ova >0.2mm	138	0.417	0.189	0.201	0.927

* Differs significantly from means of other females on this date.

oocytes, which were >0.20 mm, were not present in November, appeared in April and had increased in size by July and August (.417 to .518 mm) (Table 13). Ova size-frequency distributions for four sampling dates, based on pooled measurements of ova from all females examined on that date, shows a progression from the single mode of small (<0.20 mm) primary oocytes in November to the addition of larger yolked oocytes in July and August (Figure 30). Two modes of yolked oocytes, at approximately 0.4 and 0.7 mm, may be present in the July and August samples. Two ova >1.0 mm were observed, one in July and one in August (Figure 30). Those ova probably had ripened but were not spawned and were undergoing atresia.

Spawning Frequency

Hydration of ova occurs in the evening beginning about 1800 hr. No hydrated ova were observed after 00:33 hr, when presumably anchovy have completed spawning (Table 14; Figure 31). From 67 to 100% of the females that were collected between 17:57 and 23:00 hr had hydrated ova in June and July 1987. On 10 June 1987, the weighted mean percentage of 11 females with hydrated ova was 81.9%. On the remaining June and July 1987 dates, all females had hydrated ova indicating that virtually all mature bay anchovy females spawned each night during the peak of the 1987 spawning season in mid-Chesapeake Bay.

Fecundity

Hydrated ova numbers, which correspond to daily batch fecundities, ranged from 618 to 1478 in 1986, and from 514 to 2026 in 1987. Mean relative fecundity was 642.9 ova/g in 1986 and 730.2 ova/g in 1987 (Table 15). The mean relative fecundities did not differ significantly between 1986 and 1987 (t-test P >0.25).

There were significant regression relationships of batch fecundity on female fork length (mm), female weight (g), ovary-free female weight (g) and ovary weight (g) (P=0.0001-0.0002). These relationships did not differ between the two years (ANCOVA P=.166-.840). For the pooled data from both years the regressions are:

hydrated eggs = -1038.11 + 38.319 (fl)- r^2 =0.592
hydrated eggs = 304.79 + 404.64 (female wt) r^2 = 0.710
hydrated eggs = 393.67 + 421.84 (ovary-free wt) r^2 =0.629
hydrated eggs = 244.16 + 3011.94 (ovary wt) r^2 =0.759

The relationship between batch fecundity (i.e. hydrated ova) and female ovary-free weight (Figure 32) indicates that batch fecundity increased by 421.8 eggs for each 1.0 g increase in female ovary-free weight. A one-year-old female of mean weight 1.47 g would spawn 899 eggs per evening during the peak spawning season.

In July of 1986 and 1987, female anchovy in the 50-55 mm length range contributed most to the total egg production in mid-Chesapeake Bay. Anchovy of these lengths are one year of age. Age 1 fish ranged from 45-74 mm FL and Age 2+ individuals ranged from 71-87 mm FL in July of 1986. In July of 1987, Age 1 fish ranged from 38-68 mm; Age 2+ fish were 68-84 mm FL (Newberger

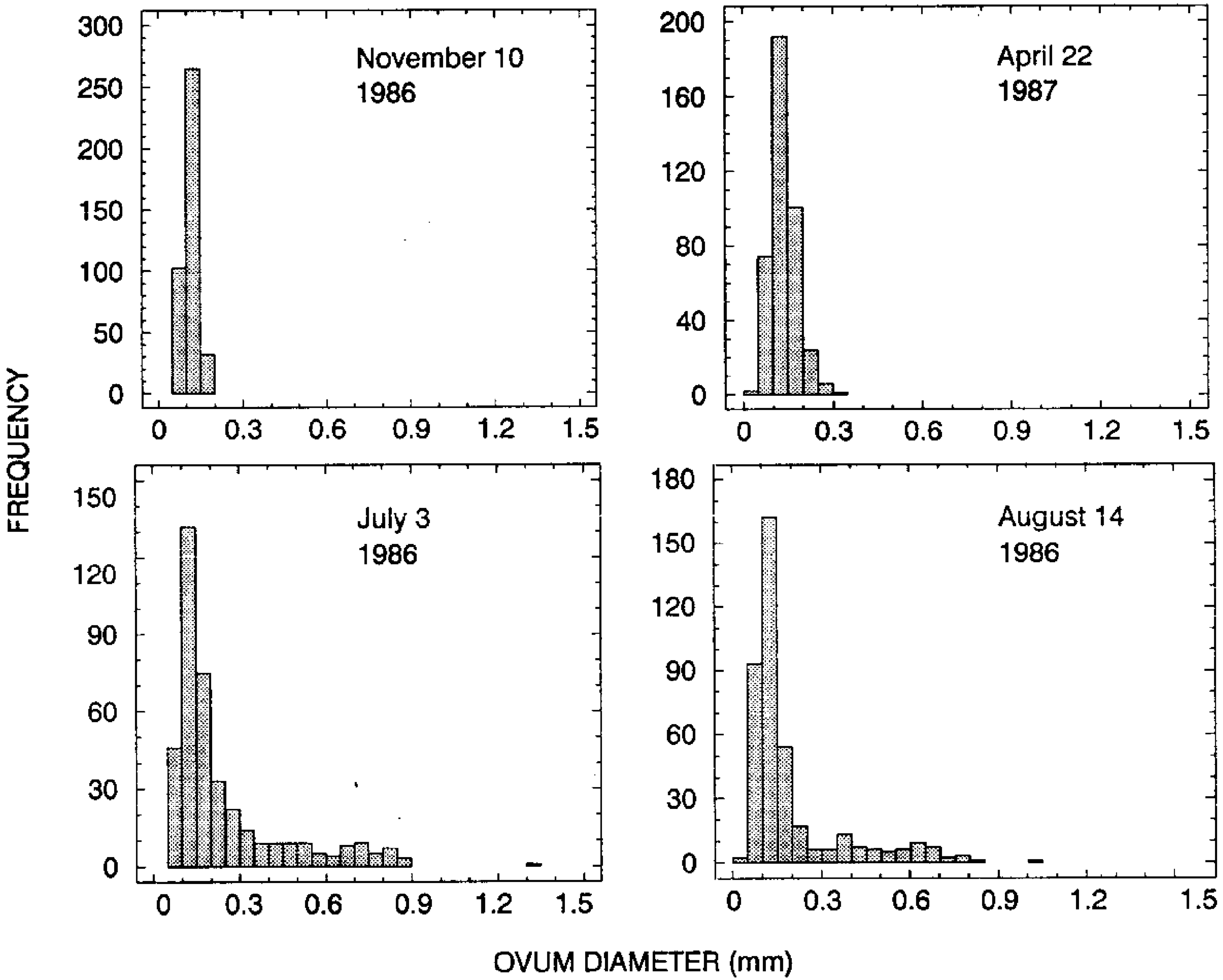


Figure 30. Size-frequency distributions of 100 ova from four female bay anchovy on four collection dates (N = 4 females and N = 400 ova for each distribution).

Table 14. Estimated spawning frequency (i.e. percent hydrated) of female bay anchovy in mid-Chesapeake Bay during 1986 and 1987. Data for a 24- and 29-hr time series along with additional late afternoon/early evening samples are presented.

Date	Time	Female Fork Length	Number of Females Examined	Number of Females with Hydrated Eggs	% Females in in Hydrated Condition
		Range			
7/29/86	1035	48-63	50	0	0
7/29/86	1105	51-68	44	0	0
7/29/86	1652	47-75	43	0	0
7/29/86	1721	36-70	9	0	0
7/29/86	1750	47-70	43	0	0
7/30/86	0001	45-69	50	47	94.0
7/30/86	0033	35-63	16	2	12.5
7/30/86	0100	33-57	14	0	0
7/30/86	0705	50-57	4	0	0
7/30/86	0804	47-64	49	0	0
7/30/86	1427	46-72	27	0	0
7/30/86	1451	-	48	0	0
*6/10/87	1807	50-53	5	4	80.0
*6/10/87	1824	51-70	3	2	67.0
*6/10/87	1842	46-52	3	3	100.0
*6/16/87	1734	50-65	9	0	0
*6/16/87	1757	45-54	7	7	100.0
*6/16/87	1815	44-62	10	10	100.0
*6/24/87	1803	48-69	4	4	100.0
*6/24/87	1821	62	1	1	100.0
6/30/87	1005	49-56	2	0	0
6/30/87	1158	49-54	6	0	0
6/30/87	1404	47-79	39	0	0
6/30/87	1426	49-71	3	0	0
6/30/87	1445	66-68	2	0	0
6/30/87	2052	44-69	14	14	100.0
6/30/87	2103	45-69	63	63	100.0
7/01/87	0323	50-72	3	0	0
7/01/87	0348	46-50	3	0	0
7/01/87	0855	48-74	18	0	0
7/01/87	0920	48-59	20	0	0
*7/22/87	1717	48-60	13	0	0
*7/22/87	1735	49-58	9	0	0
*7/28/87	1611	63-67	2	0	0
*7/28/87	2300	83	1	1	100.0
*8/21/87	1830	39-56	20	0	0

* Additional samples not part of 24 and 29-h series.

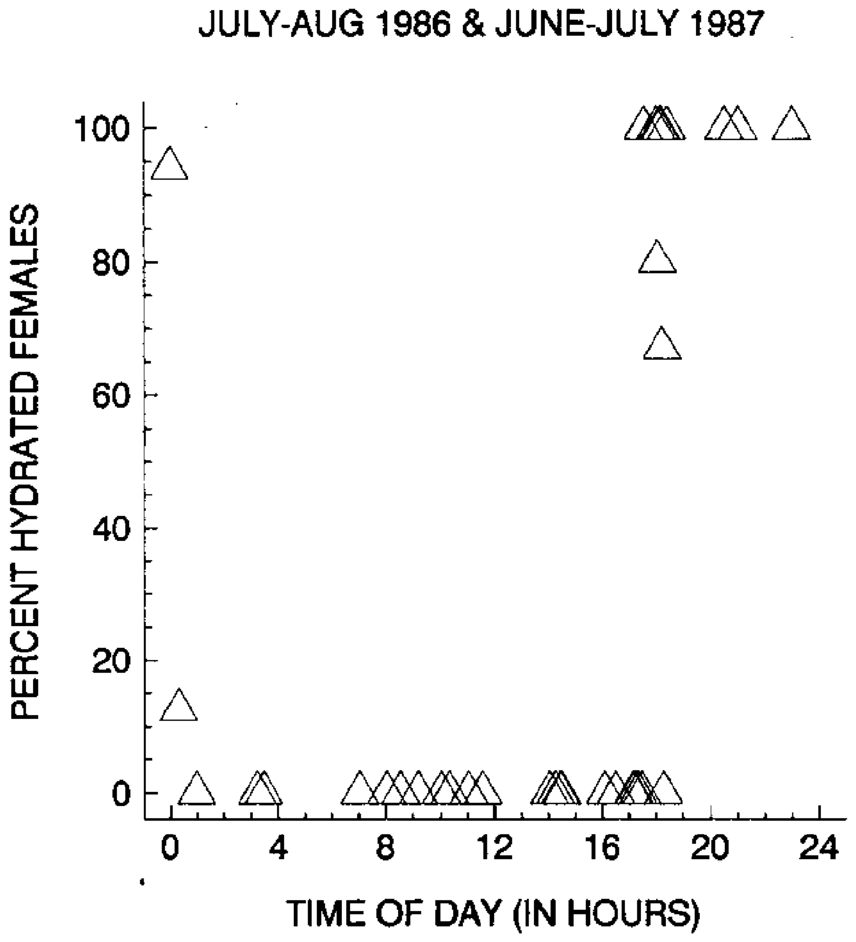


Figure 31. Percent of female bay anchovy in hydrated condition in relation to time of day, July-August 1986 and June-July 1987.

Table 15. Hydrated ova counts (batch fecundity) and relative fecundity (number of hydrated ova/ovary-free female weight) for 20 female bay anchovy in mid-Chesapeake Bay in 1986 and 1987.

Date	Female Fork Length (mm)	Female Weight (g)	Wet Weight of Ovary (g)	Number of Hydrated Ova	Relative Fecundity (ova/g)
7/30/86	69	2.97	0.247	1203	441.79
7/30/86	68	3.30	0.364	1478	503.41
7/30/86	63	2.65	0.357	1340	584.39
7/30/86	58	2.30	0.283	1127	558.75
7/30/86	55	1.99	0.366	1332	820.20
7/30/86	55	1.85	0.242	1109	689.68
7/30/86	53	1.59	0.167	819	569.22
7/30/86	50	1.45	0.194	797	634.55
7/30/86	47	1.12	0.247	802	918.67
7/30/86	45	1.09	0.218	618	708.72
					X = 642.94
					SD = 145.26
6/30/87	69	3.67	0.624	2026	665.13
6/30/87	69	3.41	0.446	1767	596.15
6/30/87	60	2.41	0.228	1020	467.46
6/30/87	58	2.00	0.316	1369	812.95
6/30/87	55	1.89	0.299	1526	959.15
6/30/87	55	1.47	0.169	524	395.08
6/30/87	55	1.75	0.282	977	665.53
6/30/87	53	1.52	0.409	1053	947.79
6/30/87	48	1.30	0.250	1001	953.33
6/30/89	46	1.01	0.168	707	839.67
					X = 730.22
					SD = 204.42

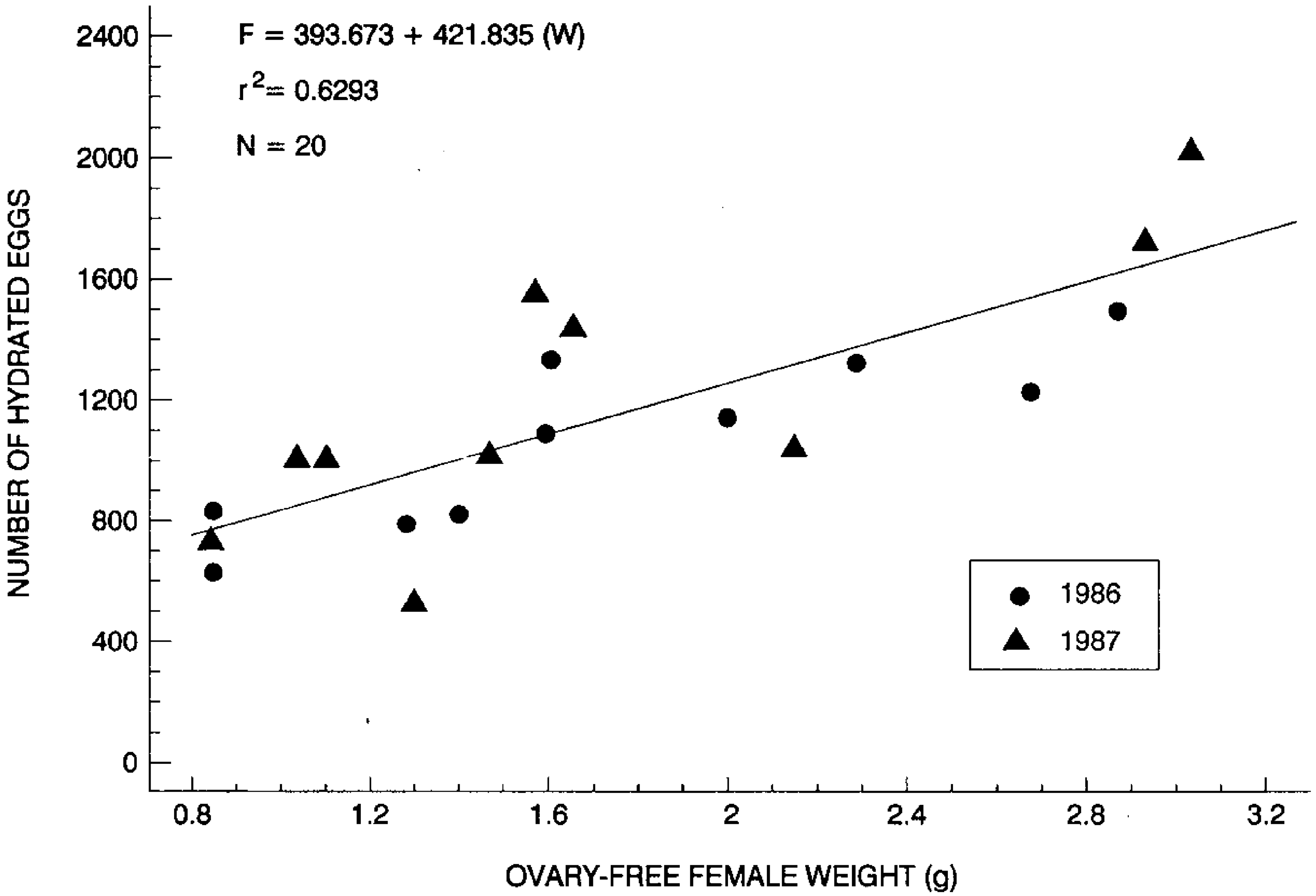


Figure 32. Relationship between batch fecundity (number of hydrated ova) and ovary-free female weight for 20 female bay anchovy; data from 1986 and 1987.

et al., Chapter 3). Anchovy in the 50-55 mm length classes contributed 58.7 and 52.5% to egg production in 1986 and 1987, respectively (Figures 33a and 33b). Age 1 females produced 99.2 and 92.8% of the eggs in July 1986 and July 1987, respectively. Age 2+ females produced only 0.8 and 7.2% in July of those years.

DISCUSSION

Most male and female bay anchovy in mid-Chesapeake Bay matured at approximately 40-45 mm FL in 1986 and 1987. Based on Newberger et al. (Chapter 3), age of first maturity was approximately 10 months posthatch, assuming median hatch date of 15 July (Dalton 1987) and maturation on 15 May of the following year. We had hypothesized that some bay anchovy might mature and spawn at age 0+ when only 3 months posthatch, but we observed no mature age 0+ individuals in late summer of 1986 and 1987 based upon gonosomatic index values and examination of ovaries for hydrated ova. It is possible that a few anchovy may mature during their first summer in mid-Chesapeake Bay as Hildebrand and Schroeder (1928) had suggested. Luo and Musick (submitted) did observe some female bay anchovy from the lower Chesapeake Bay that had matured at age 0+ and <40 mm FL in late summer 1988. Stevenson (1958) found some bay anchovy 35-40 mm FL that were mature in the Delaware Bay and suggested that they were young-of-the-year although he did not age the fish. Size and age at maturity may vary among engraulid species. For example, northern anchovy Engraulis mordax mature at 104-197 mm standard length and age 2 (LaRoche and Richardson 1980), while the small, tropical nehu Encrasicholina purpurea may mature at only 40 mm standard length and less than one year of age (Clarke 1987).

In both 1986 and 1987, most spawning in mid-Chesapeake Bay was by age 1 bay anchovy. More than 50% of the total egg production in each year was by anchovy in the 50-55 mm length-class. Most of these anchovy were 10-15 months of age (Newberger et al., Chapter 3) during the approximate three-month spawning season. Egg production during the peak spawning month of July was most dependent on spawning by age 1 females in each year. Spawning by older age-classes accounted for only 0.8 and 7.2% of egg production in 1986 and 1987, respectively. Because anchovy mortality is high, mature anchovy are uncommon at ages 2 and 3. Thus, a recruitment failure that greatly reduced numbers at age 1 would have a major impact on egg production in this species.

The typical spawning season reported in Chesapeake Bay is from May to September (Dovel 1971; Olney 1983; Dalton 1987; Luo and Musick, submitted). Clupeiform fishes typically have protracted spawning seasons (Alheit, 1988). This is true of the bay anchovy in mid-Chesapeake Bay. We found that the spawning season for bay anchovy in mid-Chesapeake Bay in 1986 and 1987 extended from mid-May through mid-August. Gonosomatic indices and incidence of hydrated ova indicated that the major spawning activity was in July. Dalton (1987) found that bay anchovy egg abundances in mid-Chesapeake Bay peaked in mid-July during a six-year ichthyoplankton study in the 1970s. The spawning season for bay anchovy in Delaware Bay and Barnegat Bay, New Jersey also occurs primarily from May to August with peak spawning in July (PSEG 1984; Vouglitois et al. 1987). In the southern part of its range, bay anchovy may spawn throughout the year (Houde and Lovdal 1984).

Figure 33a

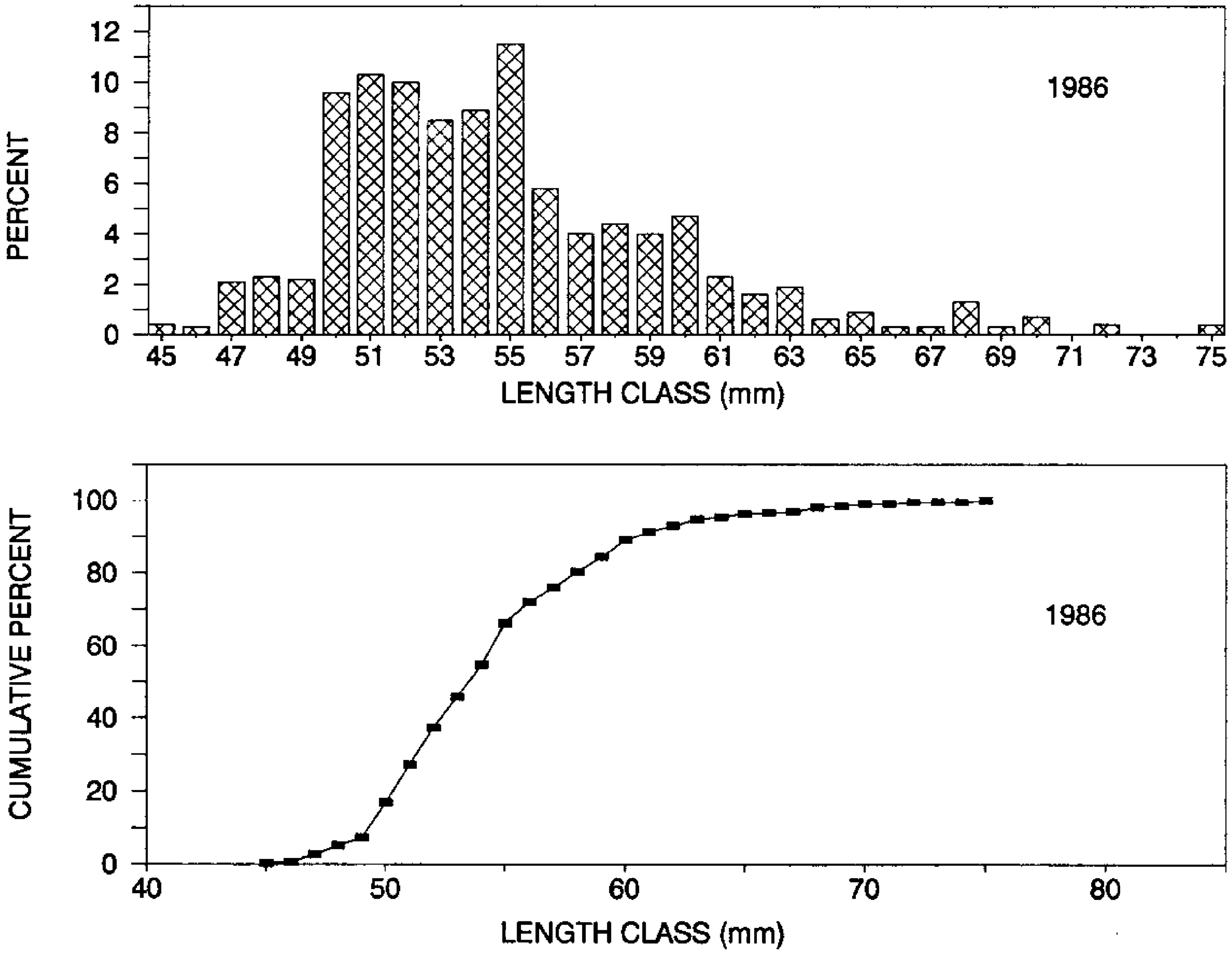
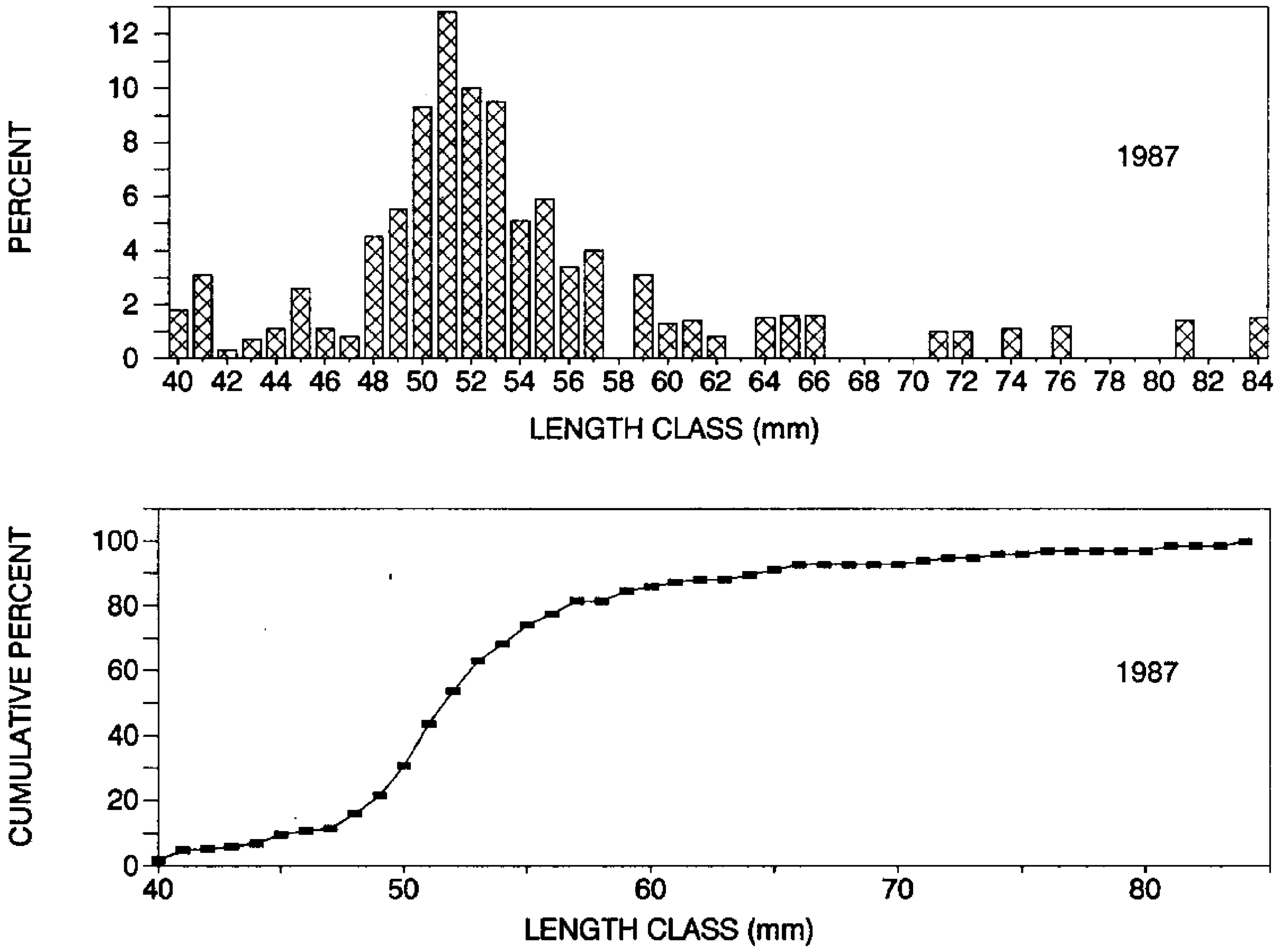


Figure 33a and b. Relative contribution to total egg production by female bay anchovy in 1 mm length-classes July 1986 (a) and July 1987 (b).

Figure 33b


PERCENT
12
10
8
6
4
2
0
40 42 44 46 48 50 52 54 56 58 60 62 64 66 68 70 72 74 76 78 80 82 84
LENGTH CLASS (mm)
1987
CUMULATIVE PERCENT
100
80
60
40
20
0
40 50 60 70 80
LENGTH CLASS (mm)
1987

Bay anchovy, like many pelagic species, spawn in the evening. Spawning by bay anchovy near Beaufort, N.C. and in Peconic Bay, New York occurred between 1800 and 2100 hr (Hildebrand and Cable 1930; Ferraro 1980). Spawning was contained within a 1.5-hr time period in the York River which occurred later in the evening as the spawning season progressed. Spawning began at 2000 hr in June and 2330 hr in September (Luo and Musick,submitted). We found females with hydrated ova from 1757 to 0033 hr. The majority of spawning probably occurred between 2100 and 2400. Sixty-six females examined between 2400 and 0001 during the peak spawning season included fish with partially and fully spent ovaries.

Other anchovy species also have diel spawning periodicity. The northern anchovy spawns only at night between 2000 and 0400 (Smith 1978). The Hawaiian anchovy (nehu) also spawns in the evening for a short 1-2 h period after sunset (Clarke 1987). Advantages of diel spawning periodicity include predator avoidance by the adults (Nikolsky, 1963) and protection from predators of eggs that otherwise might be vulnerable to visual predators immediately after being spawned and before they have had opportunity to disperse (Johannes 1978; Bailey and Houde 1989).

Clupeiform fishes such as anchovies, sardines and sprats are serial (batch) spawners (Alheit 1988). We found that 67-100% of the female bay anchovy collected in June and July 1987 were about to spawn (i.e. had hydrated ova). After 10 June 1987 and throughout July, 100% of the 100 females examined during the evening (Table 14) were in spawning condition, indicating that virtually all mature female bay anchovy spawned nightly in mid-Chesapeake Bay in July 1987. A possible source of error in the hydrated ovary method for determining spawning frequency is that females in hydrated condition may be more vulnerable to trawls, as was observed for northern anchovy (Hunter and Macewicz 1985). Females that were not hydrated were vulnerable to daytime trawling and to trawling after 0100 h. But, in July 1987, 100% of females collected from 1757-2300 were hydrated. The evidence seems quite strong that nearly 100% of female bay anchovy during the peak spawning season (mid-June through July) spawned daily.

Bay anchovy females in the James River during 1988 had spawning frequencies ranging from 25% in early June to 81% in mid-July (Luo and Musick, submitted). Thus, spawning interval was every four days in June and 1.3 days, on average, during other months of the spawning season. Luo and Musick (submitted) calculated the average annual spawnings per female per year to be 55. Although we had insufficient data to calculate the average number of spawnings per female, it is clear that each female must have spawned a minimum of 50 times in the 1 June to 15 August period based on the hydrated condition data in Table 14. Our results and those of Luo and Musick (submitted) contradict those of Richardson (1958) who believed that bay anchovy in Delaware Bay spawned only once in each spawning season. Richardson (1958) based his findings on ova-size distributions from a few ovary samples.

The percentage of females that spawn each day for other engraulids is generally lower and more variable than for bay anchovy. At peak spawning, the spawning frequency for northern anchovy females varied from 9.4-16.0% in 1980-1985 (Bindman 1986) and was 12-16% in March 1977 and February 1978 (Hunter and Goldberg 1980). The spawning frequency for Peruvian anchoveta Engraulis ringens was 16% in 1981 (Alheit et al. 1984). European anchovy, Engraulis encrasicholus in the Bay of Biscayne spawned at 3-day intervals in 1987 and 1988 (Sanz et al. 1989; Santiago and Sanz 1989). The spawning frequency of the nehu was 50%, indicating that females spawned every other day (Clarke 1987).

Relative fecundity of Clupeiform fishes may vary annually and intraseasonally (Alheit 1988). In bay anchovy, relative batch fecundity did not differ significantly between 1986 and 1987, although the estimated mean relative fecundity was 87 ova/g higher in 1987. The variability in relative fecundity may have been higher (Table 4) in 1987. Our estimates of relative fecundity in July (642 in 1986 and 730 in 1987) are similar or somewhat lower than the July 1988 values reported in the York River (743) (Luo and Musick, submitted). We found significant regression relationships between batch fecundity and female length or weight, ovary-free weight and ovary weight. There were no significant differences in any of the regression relationships of batch fecundity between July 1986 and July 1987. These relationships proved useful to predict batch fecundities and relative contributions by size-classes to population egg production in mid-Chesapeake Bay. Luo and Musick (submitted) also found significant relationships between batch fecundity and female length and weight. They found that the relationships between batch fecundity and female fork-length or female weight differed among months in the June to September period and they developed separate equations for each month. A 55 mm FL anchovy would produce between 442 (June) and 999 (July) hydrated ova using Luo and Musick's (submitted) equations, whereas a 55 mm fish would produce 1,069 hydrated ova using our equation (for July 1986 and 1987 data). Similarly, a 1.5 g anchovy would produce 355 (June) and 1,215 (August) ova, based upon Luo and Musick's (submitted) equations and 912 ova based upon our equation. If we had sampled hydrated ovaries in months other than July, differences in batch fecundity among months might have been observed in mid-Chesapeake Bay anchovy.

The relative fecundity of Anchoa naso in Ecuador was 885 (Joseph 1963). This species of Anchoa has higher relative fecundity than that of bay anchovy. Relative fecundity of the northern anchovy ranged from 421 ova/g for a central subpopulation off California (Hunter and Macewicz 1985) to 826 ova/g for a northern subpopulation off Oregon and Washington (LaRoche and Richardson 1980). This two-fold difference in batch fecundity was attributed to latitudinal and racial differences (Alheit 1988, LaRoche and Richardson 1980). Relative batch fecundity for Peruvian anchoveta ranged from 466 in 1985 for a northern population to 637 for a central population in 1981 (Alheit and Alegre 1986) while that for Hawaiian anchovy ranged from 368 in winter to 566 in summer (Clarke 1987).

Compared to most engraulids, bay anchovy has higher fecundity and, because it spawns more frequently, has a higher spawning potential. The bay anchovy spawning strategy, which entails batch spawning over a protracted season is risk-minimizing. Houde (1978) categorized bay anchovy larvae as "prey-sensitive", indicating that they were more susceptible to starvation mortality than many species. Leak and Houde (1987) demonstrated that daily mortality rates of bay anchovy larval cohorts in Biscayne Bay were very high, averaging 31%, but varying from 26 to 36% per day. By broadcasting its eggs repetitively during a long spawning season, bay anchovy improves the probability that some eggs and larvae will encounter the favorable environmental conditions that are necessary for survival and eventual recruitment to the adult population.

CHAPTER 5. YOUNG-OF-THE-YEAR GROWTH RATES AND HATCH-DATES OF BAY ANCHOVY (*ANCHOA MITCHILLI*) IN MID-CHESAPEAKE BAY

L.G. Morin and E.D. Houde

INTRODUCTION

Abundance of bay anchovy in the Chesapeake Bay varies significantly from year-to-year (Horwitz 1987; Newberger *et al*., Chapter 3). Patterns and levels of recruitment probably cause the large annual fluctuations in abundance of this short-lived species.

Pannella (1971) first demonstrated daily growth increments in the otoliths of temperate fishes. Since then, otoliths have become an important tool for accurately aging larval and juvenile fishes. Two of the earliest applications of the technique were on anchovy species. Daily increments were observed in the otoliths of northern anchovy (Brothers *et al*. 1976) and also in otoliths of Hawaiian anchovy *Stolephorus purpureus* (Struhsaker and Uchiyama 1976). Growth rates of northern anchovy larvae were estimated from otolith ages (Methot and Kramer 1979). Methot (1983) examined recruitment patterns and correlated seasonal patterns of larval survival of northern anchovy *Engraulis mordax* with environmental conditions after estimating hatch dates by otolith-aging. Leak and Houde (1987) used otolith-aging to estimate growth and survival rates of bay anchovy larvae in Biscayne Bay, Florida and Fives *et al*. (1986) estimated growth rates in a North Carolina population.

Otoliths have been demonstrated to be excellent integrators of environmental conditions and to permanently record important life history events (Radtke 1984). Attributes of the daily increment method have been reviewed, methods developed, and assumptions discussed in several recent papers (Campana and Neilson 1985; Jones 1986; Brothers 1987).

The objective of the present study was to document the annual hatching-date patterns and growth rates of young-of-the-year bay anchovy during 1986 and 1987 in the mid-Chesapeake Bay. Newberger *et al*. (Chapter 3) had observed an earlier recruitment in 1987 than in 1986. The growth rates and hatch dates of the 1986 and 1987 age 0+ recruits are estimated here by applying otolith-aging techniques to a subsample of the bay anchovy collections.

METHODS

Sagittal otoliths were removed from 227 young-of-the-year bay anchovy. Prior to otolith removal, all anchovy were measured to the nearest 0.5 mm standard length. The composition of this sample is summarized in Table 16.

Otoliths were embedded onto microscope slides, lateral surface up, with several drops of Polybed 812 epoxy resin. The resin was polymerized by placing the slides on a slide warmer set to 60^{o}C for 24-hr. Otoliths were ground sagitally with 400 and 600 grit wet/dry silicon carbide paper which was fastened to a rigid plastic block. These preparations subsequently were polished with 0.3-µm alumina paste.

Table 16. Young-of-the-year bay anchovy from mid-Chesapeake Bay that were examined to estimate growth rates and hatch dates, 1986 and 1987.

	STANDARD LENGTH (mm)			
YEAR	$\bar{X}$	S	RANGE	N
1986	31.7	7.44	17.5 - 48.0	124
August	25.3	6.24	17.5 - 42.0	17
September	29.0	6.05	20.0 - 47.0	64
October	38.2	4.54	29.5 - 48.0	43
1987	38.8	4.53	28.0 - 49.5	103
September	37.3	3.97	28.0 - 47.5	62
October	41.0	4.38	30.0 - 49.5	41

Otolith growth increments (a light incremental zone followed by a dark discontinuous zone) were counted directly from a 1000x image on a monitor interfaced to a light microscope via a video camera. Polarizing filters were used to enhance contrast. A subsample of 30 randomly-selected otoliths was read by a second person and then read again by the first reader to check the accuracy and precision of increment counts (i.e. aging).

Recent experiments with laboratory-reared bay anchovy larvae from eggs of Chesapeake Bay stock origin (unpublished data) demonstrated that increments were deposited daily, beginning on the third day posthatch at 23-26°C. This observation agrees with that of Leak and Houde (1987). Fives et al. (1986) did not observe increment deposition in bay anchovy otoliths until 5 days posthatch. The ambient temperatures of their laboratory experiments were as much as 5°C cooler than those used by us and by Leak and Houde (1987). Appearance of the first increment may be temperature-dependent. Young-of-the-year bay anchovy from the 1986 and 1987 collections had experienced temperatures in the 26-29°C range during their larval life (Houde et al., Chapter 2). We have assumed that the first otolith increment in bay anchovy was deposited on the third day posthatch. Therefore, age at capture was estimated as number of increments plus 2.

Age data and standard length measurements were fit to simple linear regressions to estimate growth rates of young-of-the-year anchovy in each year-class. Growth rates of individual anchovy also were calculated from:

$$G = \Delta SL \div (\text{otolith increments} + 2)$$

where G = growth rate (mm d^{-1}), ΔSL = observed length at capture minus 2.0 mm - the length at hatch, and otolith increments + 2 - the age of the individual.

Hatch dates were estimated from the daily increment counts on individual otoliths from young-of-the-year bay anchovy collected during late August to October. Hatch-date frequency distributions were generated for the 1986 and 1987 year-classes. Hatch-date frequencies were aggregated into weekly or biweekly groups to determine the modal hatch dates and distribution of hatches of anchovy that had survived to the juvenile stage.

RESULTS

Growth of 1986 and 1987 young-of-the-year bay anchovy, based on the regression estimates of standard length on age (Figure 34) indicated that growth rate of anchovy in 1986 was significantly faster than in 1987 (0.46 mm d^{-1} and 0.32 mm d^{-1}, respectively). But, mean individual growth rates, calculated from the ΔSL and increment-defined ages were nearly identical (Table 17) at 0.474 and 0.468 mm d^{-1} in 1986 and 1987, respectively. The growth-rate frequency distributions of individuals in 1986 and 1987 (Figure 35) were similar. Most growth rates in each year were in the range 0.44-0.50 mm d^{-1}. The range of estimated growth rates was broader in 1986 (Figure 35).

Hatch-date frequencies, based on estimated age-at-capture, were generated for each year class and grouped into weekly (Figure 36) and biweekly (Figure 37) sets. A Wilcoxon's paired sample test on a randomly-selected subset of 30 of the 227 otoliths that were analyzed indicated that two

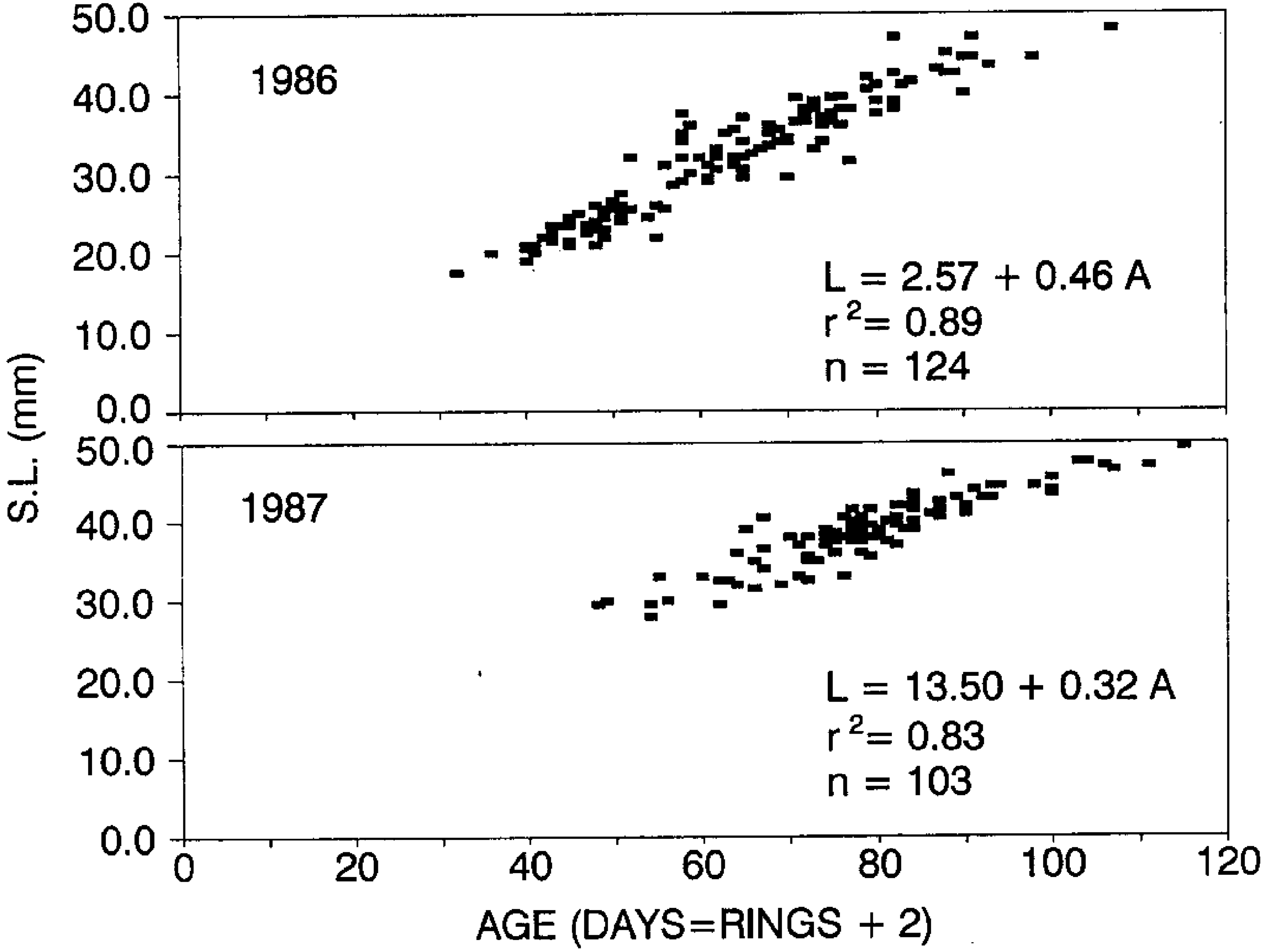


Figure 34. Linear regressions of standard lengths on estimated age (otolith increments +2) for young-of-the-year bay anchovy collected in mid-Chesapeake Bay, 1986 and 1987. Slopes of the regressions are estimated daily growth rates (mm d^{-1}).

Table 17. Bay anchovy growth rates in 1986 and 1987, based on standard lengths and estimated ages (i.e. G = ΔSL ÷ age. See text).

GROWTH RATE (mmd-1)

Sample	$\bar{X}$	S	Range	N
1986 (combined)	0.47	0.04	0.36 - 0.61	124
August	0.45	0.04	0.36 - 0.51	17
September	0.48	0.04	0.38 - 0.61	64
October	0.47	0.03	0.42 - 0.54	43
1987 (combined)	0.47	0.04	0.41 - 0.58	103
September	0.48	0.03	0.41 - 0.58	62
October	0.45	0.03	0.41 - 0.57	41

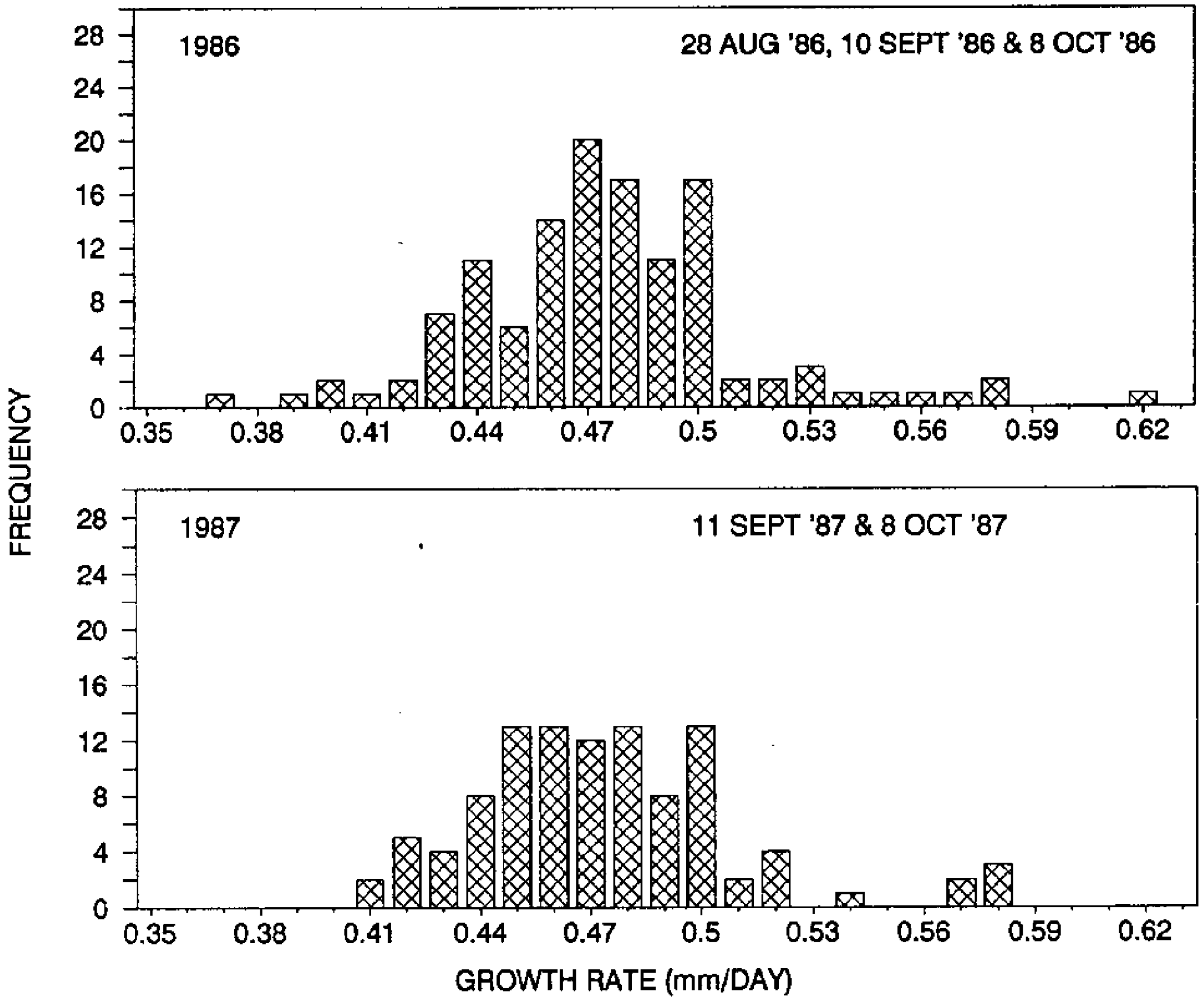


Figure 35. Growth-rate frequencies of young-of-the-year bay anchovy derived from otolith increment age estimates in 1986 and 1987.

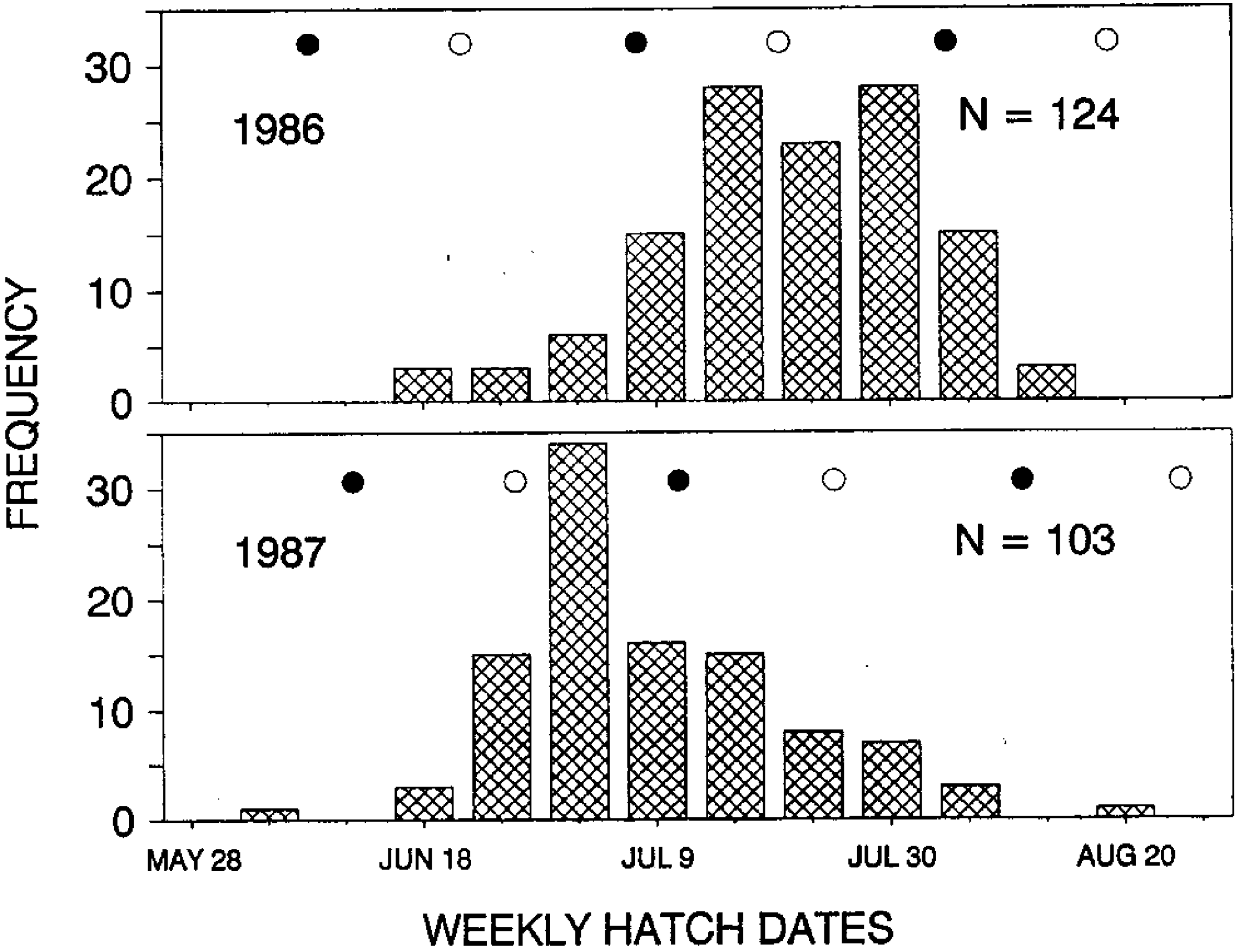


Figure 36. Hatch-date frequency distributions of bay anchovy in 1986 and 1987. Data are aggregated into weekly hatch-date groups. Moon phases are indicated: ● new moon; ○ full moon.

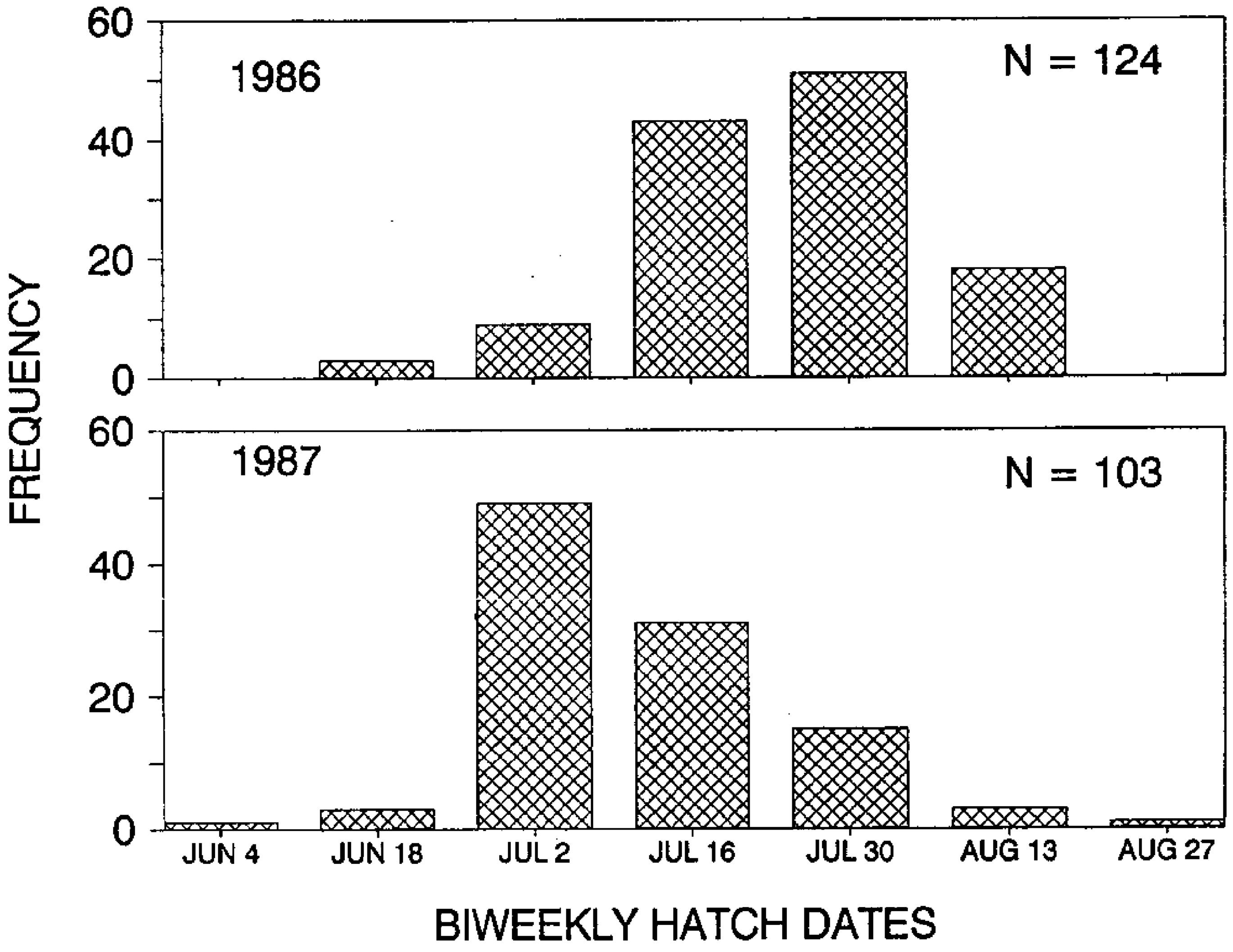


Figure 37. Hatch-date frequency distributions of bay anchovy in 1986 and 1987. Data are aggregated into biweekly hatch-date groups.

different otolith readers had assigned different ages and consequently, different otolith-aged anchovy were aggregated into either weekly or biweekly cohorts, no differences in hatch-date frequencies between readers were detected.

The weekly and biweekly hatch-date frequency distributions indicated that hatching occurred and peaked earlier in 1987 than in 1986 (Figures 36 and 37). In 1987, hatching was first estimated to occur in early June and continued through late August, with peak hatching from 19 June-2 July. In 1986, hatching was not evident until the second week in June and was not observed after the second week in August. Peak hatching in 1986 was observed from 9-30 July. Cumulative estimates indicated that >80% of the observed recruits had hatched by 30 July and 15 July in 1986 and 1987, respectively. More than 95% of the recruits had hatched by 6 August and 30 July in 1986 and 1987.

DISCUSSION

Mean growth rates of young-of-the-year bay anchovy, based on the $\Delta SL \div$ age method, were similar in 1986 and 1987. They also were similar to the larval growth rates reported by Cowan and Houde (1989) in mesocosm experiments in the Chesapeake Bay, and by Leak and Houde (1987) in Biscayne Bay, Florida. In addition, the five mean growth rates derived from anchovy collections in individual months and estimated by this method (Table 17) all were similar, indicating that the method gave consistent results. The regression analysis estimate in 1987 produced a significantly lower growth rate (Figure 34). This result may have been obtained because relatively older age classes of anchovy were included in the 1987 analysis, a consequence of the earlier recruitment in that year (Table 16). Individuals still in the larval stage (<25 mm SL), and which had relatively fast growth rates, were not represented in the 1987 regression analysis.

Newberger _et al_. (Chapter 3) estimated the mean young-of-the-year growth rate of bay anchovy from pooled 1986-87 data and a von Bertalanffy growth model. Their estimate of 0.46 mm d^{-1} is nearly identical to the 0.47 mm d^{-1} estimated here by the $\Delta SL \div$ age method. An attempt by Newberger _et al_. (Chapter 3) to estimate young-of-the-year growth rates by length-mode progressions during the sampling season gave rates of only 0.33 and 0.20 mm d^{-1} in 1986 and 1987, respectively. They argued that this method did not include growth during the larval period, leading to an underestimate of the actual mean growth rate during the first three months of life, an argument like that which we have proposed to explain our 1987 regression analysis result. The rates based on length-mode progression (Newberger _et al_., Chapter 3) and the 1987 regression of standard lengths on age do indicate that juvenile growth-in-length, while still rapid, is only approximately one-half that during the pre-metamorphosis stage in the Chesapeake Bay.

The average age of 1986 and 1987 anchovy in the present study, as determined by otolith aging, was 63.2 days (s=15.3, n=124) and 79.1 days (s=12.9, n=103), respectively. After 30-40 days posthatch, the sagittal otoliths of bay anchovy change shape with the development of the rostrum and antirostrum. This results in a lack of continuous counting paths in otoliths of anchovy older than 60 days. Therefore, anchovy more than 60 days of age became increasingly difficult to age accurately. Jones and Brothers (1987) made the same observation on otoliths of laboratory-reared striped bass. In their study, ages of fish older than two months tended to be underestimated. Despite the difficulty in aging the oldest anchovy, we did not discard such otoliths because of the probable bias in hatch-date estimation that might occur if older anchovy were selectively removed from the sample.

Growth increment counts by two different otolith readers on a subset of the otoliths used in this study resulted in assignment of different hatch dates to the same anchovies. Because we could not determine if increment counts were low, high or correct, otolith-aged anchovy were aggregated into weekly or biweekly hatch-date intervals, effectively removing the differences in counts assigned by the two readers. This decision eliminated the possibility of assigning each larva to an individual hatching date, but assured that weekly or biweekly cohorts were accurately assigned. The earlier hatch dates observed in 1987 probably were attributable to environmental factors in the Chesapeake Bay. Water temperatures during the 1986 and 1987 spawning seasons were higher in 1987 than in 1986 and mean August surface temperatures were 2.7°C higher in 1987 (Houde et al., Chapter 2, Table 1). The peak period of bay anchovy hatching in mid-Chesapeake Bay occurs in July (Dalton 1987). The long-term mean surface temperature in July is 26.7°C (Kelly 1988), lower than the temperatures observed in either 1986 and 1987. Salinities during July were higher in 1986 and 1987 (Houde et al., Chapter 2, Table 1) than the long-term mean (Kelly 1988).

Moon phase might have influenced spawning behavior of bay anchovy and resulting hatch-date frequency distributions. In French grunt Haemulon flavolineatum (McFarland et al. 1985), settlement onto reefs was demonstrated to be keyed to biweekly moon-phase events associated with spawning peaks. There did not appear to be a relationship between new or full-moon phases and bay anchovy hatch-date frequencies in mid-Chesapeake Bay (Figure 36). It seems more likely that anchovy spawning and hatch-date frequencies were keyed to temperature and light cycles. It is possible that the observed hatch-date frequencies are different from the actual egg-production frequencies if survival of cohorts is variable during the reproductive season. Unfortunately, we have no data to test that possibility at this time.

CHAPTER 6. ENERGETICS OF BAY ANCHOVY, *Anchoa mitchilli*: RATION LEVELS AND TEMPERATURE EFFECTS

A.V. Vazquez and E.D. Houde

INTRODUCTION

Fish energetics studies provide insight into interactions of biotic and abiotic factors that control food intake and growth in fishes (Durbin and Durbin 1983). The first fish energetics studies of note were conducted by Ivlev (1939; 1945), who developed energy budgets for individuals by quantifying the feeding and growth relationships. Ivlev's pioneering ideas were followed by Winberg's (1956) contributions. Continued research led to the formulation of energy budgets for individual animals (Warren and Davis 1967). For example, Pandian (1967) studied the intake, digestion, absortion and conversion of food in the fishes, *Megalops cyprinoides* and *Ophicephalus striatus*. Energetics studies to date have been carried out on many species, including perch, (*Perca fluviatilis*) (Solomon and Brafield 1972), largemouth bass, (*Micropterus salmoides*) (Niimi and Beamish 1974), tilapia (*Sarotherodon mossambicus*) (Minorova 1974), rainbow trout, (*Salmo gairdneri*) (Staples and Nomura 1976), brown trout, (*Salmo trutta*) (Elliott 1976), yellow perch, (*Perca flavescens*) (Mills and Forney 1981), Peruvian anchoveta, *Engraulis ringens* (Villavicencio *et al*. 1981), sockeye salmon, (*Oncorhynchus nerka*) (Brett 1983), menhaden, (*Brevoortia tyrannus*) (Durbin and Durbin 1983), cod, (*Gadus morhua*)(Jobling 1988), walleye pollock, (*Theragra chalcogramma*) (Smith *et al*. 1988), and some cyprinids (Cui and Wootton 1988a; 1988b; 1989). In addition, bioenergetics models recently have been developed for several species (Kitchell *et al*. 1977; Stewart and Binkowski 1986; Cui and Wootton 1989).

An energy budget is a balance of energy income against energy expenditure (Brafield 1985). Energy budgets were developed from the relationship:

$$I = G + M + F + U$$

where I = energy value of the food consumed; i.e. ingestion

G = energy to growth
M = energy to metabolism
F = energy value of feces
U = energy value of materials excreted in the urine or through the gills or skin.

This budget is a generalization (Brett and Groves 1979) but it can serve to quantify energetics relationships that may vary as food quantity, food quality or environmental conditions change.

If fecal energy (F) is subtracted from the ingested energy (I), the energy absorbed and assimilated by the fish (G + M + U) is obtained (Brafield 1985); the nitrogenous waste (U) is excreted and the remainders (G + M) are the metabolizable energy. Because the estimation of ingestion lost in feces and excretory products is experimentally difficult and time consuming

(Braatten 1979), urine often is assumed to be 7% of ingestion, a mean value for carnivorous fishes (Brett and Groves 1979), and feces is the remainder of the ingested ration after the physiologically useful energy available for growth and metabolism has been determined.

The energetics study conducted here was designed to determine bay anchovy growth and metabolism. Through the development of energy budgets, the growth and assimilation efficiencies at different diet levels and temperatures were compared. The study is a first step toward eventually estimating population-level consumption by bay anchovy in the Chesapeake Bay.

Extensive research has been conducted on fish growth. However, little was known about the growth of bay anchovy in the Chesapeake Bay. Growth and aging data are available for larval bay anchovy (Houde 1978; Houde and Schekter 1981; Fives et al. 1986; Leak 1986). Stevenson (1958) and PSEG (1984) reported growth rates of juvenile and adult bay anchovy from Delaware Bay. Recently, growth of the juvenile and adult bay anchovy population in the Chesapeake Bay was described and a von Bertalanffy growth model was fit to size-at-age data (Newberger et al. Chapter 3; Newberger 1989). Although the von Bertalanffy model is useful to fit growth data for studies based on changes of weight or length over time, it gives little insight into the factors influencing metabolism and growth (Ricker 1979). Energy budgets are required to better understand the physiological aspects of growth. The energetics approach may be viewed as the elaboration of the growth process, including negative growth, as measured by changes in biomass, proximate body composition and energy content (Beamish et al. 1975).

Estimates of gross growth efficiency, K_1=G/I, are an important derivation of growth studies; K_1 reflects the fraction of ration that is retained as body substance (Braaten 1979). Estimates of assimilation (G+M+U)/I and of net growth efficiency, K_2=G/(I-F), the proportion of the assimilated ration that is retained as body substance, also are important products derived from energy budgets.

METHODS

Obtaining, Acclimating and Rearing Bay Anchovy

Juvenile bay anchovies for experiments were collected in late summer and fall 1988 near the Patuxent River mouth using a 4.9 m semi-balloon otter trawl with 3 mm mesh cod-end liner. The trawl was towed from an outboard-powered vessel, generally in midwater at 4-7 m depth. Immediately after trawling, the fish were carefully transported in styrofoam coolers to the laboratory.

Approximately 350 juvenile anchovies were acclimated for 21 days in an 800-liter, flow-through cylindrical tank supplied with 5-um filtered Patuxent River water. Airstones provided oxygen in the tank, and the light-dark cycle was set at 12-12 hr.

An acclimation period of 2 weeks is often recommended for energetics studies (Niimi and Beamish 1974; Brett and Shelbourn 1975). During the first week of the bay anchovy acclimation period, temperature was slowly increased by 1°C/day until the experimental temperature (27°C) was reached. Anchovies were held at the desired temperature for 2 weeks before beginning the experiment. During the acclimation period, fish were fed daily with newly hatched *Artemia* nauplii.

Feeding Experiments

Feeding experiments at three ration levels were conducted at three temperatures in 800-liter, cylindrical tanks, each holding 50 anchovies. Each experimental tank had the same dissolved oxygen ($\bar{X}$ = 6.6 mg/l), light (12/12 hr light-dark cycle), and salinity (15.5-18.0 ‰).

Flow rates were maintained at 2 l/min to replace water in each tank at least four times a day. On occasion flow rates were reduced to help maintain experimental temperatures. Salinity ranged from 15.5 to 18.5‰.

All experiments were not conducted simultaneously because of (1) lack of tanks and space in the laboratory and (2) availability of anchovies. Anchovies collected on 8 September 1988 were used in the first feeding experiment (27°C). Anchovies used in the 23°C experiment were mostly from a 26 October collection. Some fish that had been acclimated from the 8 September collection were also used in this experiment. In the 19°C experiment, a mix of anchovies that were held in the laboratory from the previous collections and fish collected on 4 November was used.

Experiment duration varied. The duration was 21 days at 27°C, 28 days at 23°C and 35 days at 19°C (Table 18). The longer durations at lower temperatures assured measurable growth responses.

Ingestion Estimates

The diet levels that were offered, on a wet to wet weight basis, were 10, 20 and 40% of the fish body weight. Anchovies were fed newly-hatched *Artemia* nauplii at a concentration sufficient to provide the desired nominal ration level. The amounts of *Artemia* to be fed were calculated based on the estimated wet weight of an individual Colombian strain *Artemia* nauplius, which was 6.12×10^{-6}g. Food was dispensed by automatic feeders that released small quantities of the *Artemia* for approximately 8-hr each day. The amount of *Artemia* offered but not consumed was estimated on each day by counting *Artemia* nauplii in 3 ml aliquots of those that had been flushed onto 100-um mesh collectors below the outflow standpipes.

Weight-specific ingestion rates ($g.g^{-1}.d^{-1}$) were estimated on a dry weight basis and exponential models of ingestion in relation to diet level were fit to the data at each temperature.

Growth Experiments

Growth was measured weekly by randomly netting 10 anchovies from each experimental tank. Each fish was weighed to the nearest 0.01g in a beaker with water.

Growth was expressed as daily weight-specific growth rate using the

Table 18. Experimental design. Rations were newly-hatched *Artemia* nauplii. Diet levels (% of body weight per day) were calculated on a wet weight to wet weight basis. Fifty anchovies were tested in each treatment combination.

TEMPERATURE (°C)	DIET LEVEL (% of b. wt. offered)			EXPERIMENT DURATION (days)
19	10	20	40	35
23	10	20	40	28
27	10	20	40	21

exponential model recommended by Ricker (1979):

$$G = (\ln W_t - \ln W_0)/t$$

where, G is the specific growth rate in g/g/d.

W_t and W_0 are the wet weights of the anchovies (in g) at the end and at the beginning of a growth period of t days.

To express weight-specific growth in percent per day, the following formula was used:

$$\% \, d^{-1} = 100(e^G - 1)$$

Exponential growth models were fit to the data for individual anchovy weights on time, from which the equation $W_t = W_0 e^{Gt}$ was obtained. The weight-specific growth coefficient (G) was then estimated for each treatment. The growth coefficients in these models were used to describe the daily increase in weight during each experiment and to estimate the growth component in energy budgets. The growth rates of anchovy tested at different temperatures and diet levels were compared.

Oxygen Consumption Experiments

System Description. The oxygen uptake experiments were conducted in a recirculating respirometry system (Figure 38). Water in a 270-l reservoir was pumped up to a 113-l head-box holding filtered, aerated sea water. The desired temperature (19, 23 or 27°C) in the head-box was maintained with a circulating heater and thermostats. The box was plumbed to allow water to flow by gravity through a manifold with three valves, two serving the respirometers (carboys of 20-l capacity) and one for measurements of oxygen concentration at the inflow to each carboy.

Experimental Procedure. On the day before an experiment, two carboys were washed, acid rinsed and autoclaved along with required tygon and glass tubing. In the morning of an experiment the head-box and reservoir were filled with filtered-ambient sea water. The pump was set to circulate the water through the system and the heater/circulator, thermostats and aerators were activated. The respirometers were placed inside the reservoir and filled. Tygon tubing was attached to the valves and repirometer glass tubing. The valves were adjusted to prevent reservoir overflow but to allow sufficient water to pass through the pump and respirometers.

From 10-14 anchovies per respirometer were transferred from the 800-l holding tank and/or experimental tanks. The anchovies had not been fed for 12-15 hr prior to an oxygen uptake experiment. The anchovies were carefully placed in each carboy and acclimated for at least one hr before the first oxygen reading. Sometimes it was necessary to wait 3-4 hr for the fish to appear calm before beginning an experiment. Control oxygen uptake experiments, without anchovies in the respirometers, were conducted at the three experimental temperatures to measure any significant uptake by microorganisms in the system.

Oxygen Readings and Calculations. A YSI model 58 dissolved oxygen meter with

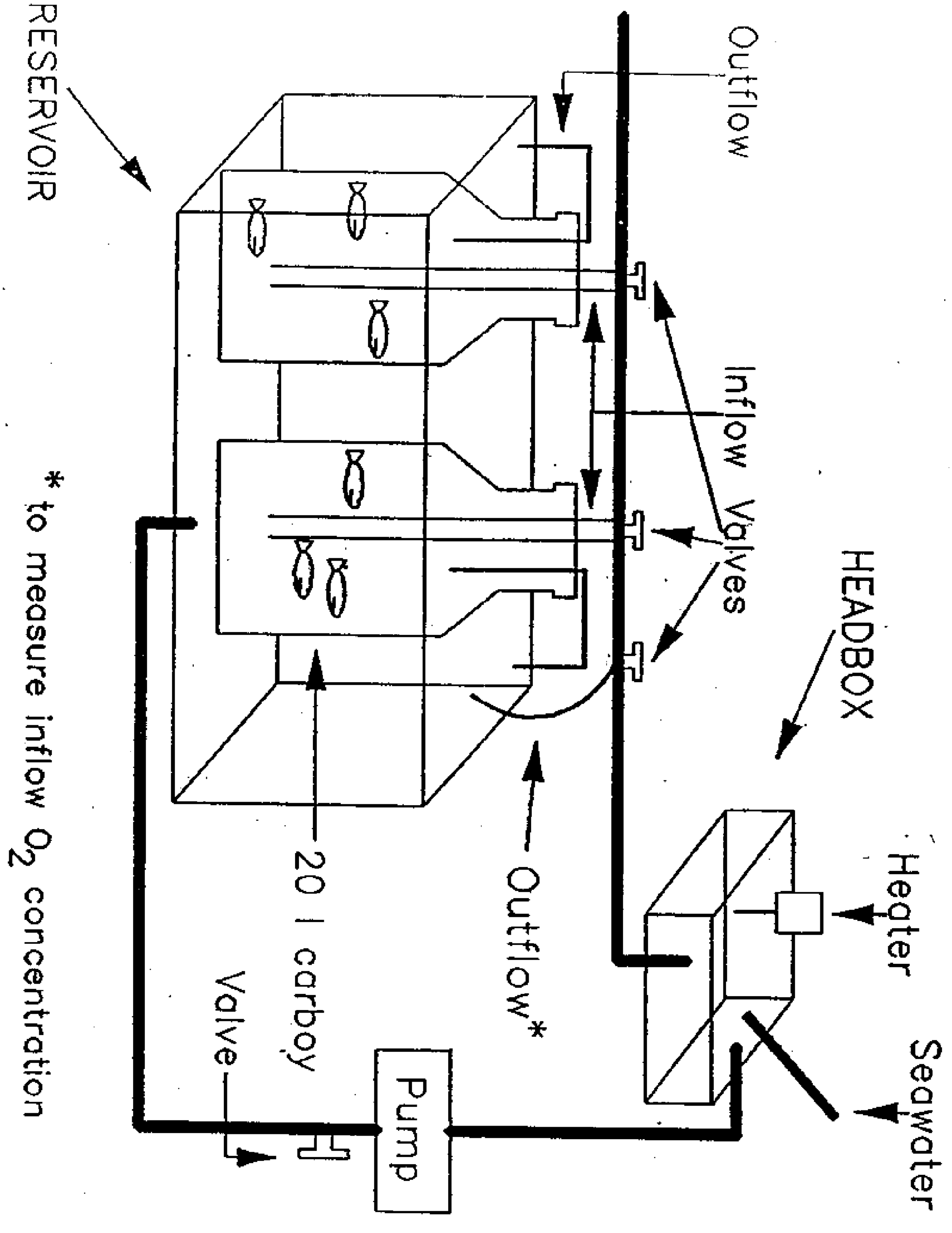


Figure 38. Design of respirometry apparatus.

a YSI 5739 probe was used to determine oxygen concentration in the inflow and outflow waters of the respirometers. After calibration of the apparatus, readings were recorded every hour for 6-14 hr. Some of the oxygen uptake experiments were extended to 12-14 hr to obtain more stable oxygen uptake values when the anchovies appeared to be very excited.

At the end of an oxygen uptake experiment the anchovies were removed from the carboys. Each fish was weighed to the nearest 0.01g in a beaker with water if it was to be returned to the holding tank, or to the nearest 0.001g and frozen for proximate analysis if it was from an experimental tank at the end of a feeding experiment.

To calculate weight-specific oxygen uptakes (mg O_2/g/h=Q_{O2}) for the anchovies in each respirometer the equation:

$$Q_{O2} = (O_2 \text{ inflow} - O_2 \text{ outflow}) / [(\text{Biomass})(\text{flow rate})]$$

was used to estimate weight-specific oxygen uptake. The mean value of the last two Q_{O2} measurements was used as the oxygen uptake estimate at each tested temperature. Weight-specific oxygen uptakes were converted to respiration rates by multiplying Q_{O2} by mean weight of the anchovies in an experiment.

The relationship between oxygen uptake and anchovy weight was described by the power model:

$$R = aW^b$$

where R = rate of oxygen consumption (mg O_2/h)
W = fish body weight (g)

a and b are coefficients characteristic of a given species (Brett and Groves 1979). The exponent (b) and intercept (a) were estimated for bay anchovy at each temperature.

The expected change in O_2 uptake over a 10°C interval, defined as the temperature coefficient (Q_{10}) was estimated from the equation:

$$Q_{10} = \left[\frac{QO_2\ (1)}{QO_2\ (2)}\right]^{\frac{10}{T1 - T2}}$$

where $Q_{O2(1)}$ and $Q_{O2(2)}$ are the oxygen uptake rates at temperatures T_2 and T_1, respectively (Bayne and Newell 1983).

Energy Budgets. Daily energy budgets, expressed in calories, were developed for the three experimental temperatures and ration levels using the relationship:

$$I = G + M + U + F$$

where I=ingestion, G=growth, M=metabolism, U= urine, and F=feces (Brett and Groves 1979).

Ingestion. The amount of *Artemia* consumed daily was estimated by difference based on the number of *Artemia* dispensed into the holding tank minus the number recovered in the outflow. The dry weight of *Artemia* consumed was obtained by multiplying the number of nauplii consumed by the dry weight conversion for *Artemia* nauplii ($1.74\text{x}10^{-6}$g) (Vanhaecke and Sorgeloos 1983). The dry weight of ingested *Artemia* was converted to a caloric equivalent using the ash-free dry mass value of 5780 cal/g (Emmerson 1984), which assumes an average of 10% ash content in dry mass of *Artemia* (Watanabe *et al*. 1983).

Growth. Wet weight growth rates were converted to dry weight rates using wet to dry conversion factors obtained for each treatment. The conversions were obtained by weighing samples of anchovies both wet and dry at the beginning and end of each feeding experiment. Dry weights were converted to ash-free dry weights by multiplying each dry weight by the percentage of protein and lipid in anchovies from each treatment group, based on data from proximate composition analysis (see Vazquez *et al*. Chapter 8).

Ash-free dry weights of anchovies were multiplied by the protein and lipid percentages to determine the proportions of weight gained as protein and lipids. Subsequently, the weights gained as protein and lipids were converted to calories based on their caloric equivalents (5650 and 8500 cal/g, respectively) (Jobling 1983; Henken *et al*. 1986).

Metabolism. Oxygen uptakes, based on the power function $R=aW^b$ were multiplied by 24-hr to obtain the daily metabolic rates of anchovy of mean weight in each experiment. The daily metabolic rate was converted to calories using an oxycalorific equivalent of 3.258 cal/mg O_2 (Brett and Groves 1979).

Excretion. The two major components of excretion are feces and urine (F+U). Urine was assumed to be 7% of the ingested calories, the mean value for young, carnivorous fish (Brett and Groves 1979). Feces then was estimated by difference, after determining other components of the budget.

Growth and Assimilation Efficiencies. Gross growth efficiency (K_1=G/I), net growth efficiency [K_2=G/(I-F)], assimilation (A=I-F), and assimilation efficiency (A/I) were estimated. Assimilation was calculated as the total metabolizable energy or (G+M+U). To estimate the proportion of the physiologically useful energy that goes into growth or metabolism, the expressions G/(G+M) and M/(G+M) were used, respectively.

Energy budgets were standardized and are presented as cal/g/day. To obtain budgets as Joules/g/day, budget components must be multiplied by 4.2 J/cal (Calow 1985).

Maintenance Ration Determinations. Maintenance rations were estimated from the weight-specific oxygen uptake (Q_{O2}) estimates, by calculating the energy (cal/g/d) required in routine respiration for anchovies in each treatment. The cal/g/d required to fulfill this metabolic demand were converted into g of *Artemia* and then into numbers of *Artemia* from the dry weight-calorie conversion for *Artemia*. Finally, the percentage of an anchovy's body weight, as *Artemia*, that would have to be consumed daily to meet routine respiratory needs was calculated. The estimated mean maintenance rations were calculated for each diet level and temperature.

RESULTS

Ingestion

Weight-specific ingestions were less than the diet levels that were offered (Table 19). Mean consumption rates ranged from 6.8-28.0% of body weight. Relative percent of the diets offered that were consumed ranged from 66-78%. The actual consumption, relative to nominal levels, was lowest at 19°C and highest at 27°C (Table 19). The Analysis of Variance (ANOVA) that was conducted resulted in no significant differences among temperatures ($P>0.05$). Despite the lack of significance, Table 19 values indicate small decreases in the weight-specific ingestion rates as diet level increased at a specific temperature, suggesting that the highest relative percent consumed was at 10% and the lowest at 40%.

The exponential regressions of weight-specific ingestion rates in relation to diet level for the 19, 23 and 27°C experiments indicated that ingestion increased by >4% for each one percent increase in diet level at each of the temperatures (Figure 39). The ANOVA was highly significant among diet levels ($P<0.01$).

The weight-specific ingestion equations are:

19°C experiment	$I=0.0463e^{0.0408d}$
n=15	$r^2=94.97\%$
	$(S_b = 0.0026)$
23°C experiment	$I=0.0504e^{0.0415d}$
n=12	$r^2=92.18\%$
	$(S_b = 0.0038)$
27°C experiment	$I=0.0527e^{0.0424t}$
n=9	$r^2=90.12\%$
	$(S_b = 0.0053)$

The exponents of the weight-specific ingestion regressions did not differ (analysis of covariance; $P>0.30$) indicating that the rate of increasing consumption relative to diet level did not differ among the three temperatures.

Growth Experiments

Mean growth at 19°C was 0.347 g at the 10% diet level, 0.717 g at the 20% diet level and 0.853 g at the 40% diet level. The anchovies more than doubled their weight at the 20% and 40% diets in the 35-day period, and had a 57% weight gain at the 10% diet level (Table 20). The growth coefficient (G) was significantly lower at the 10% diet level than at the 20% and 40% levels (ANCOVA; $P<0.0001$). The growth coefficient at the 20% and 40% diet levels did not differ (ANCOVA; $P>0.20$) at 19°C. Daily percentage weight gains at 19°C ranged from 1.50 to 2.32% (Table 21).

Mean growth at 23°C was 0.085 g at the 10% diet level, 0.235 g at the 20%

Table 19. Mean weight-specific wet weight ingestion rates (g/g/day)(±SE) and the relative percentage of the diet offered that was actually consumed by the bay anchovies.

TEMPERATURE	DIET LEVEL OFFERED (%)					
(°C)	10%		20%		40%	
	(g/g/d)	Relative %	(g/g/d)	Relative %	(g/g/d)	Relative %
19	0.0683 (0.0067)	71.9	0.124 (0.0197)	65.5	0.250 (0.0353)	65.8
23	0.0695 (0.0060)	73.2	0.136 (0.0184)	71.8	0.259 (0.0526)	68.1
27	0.0740 (0.0069)	77.9	0.142 (0.0261)	74.8	0.280 (0.0638)	73.6

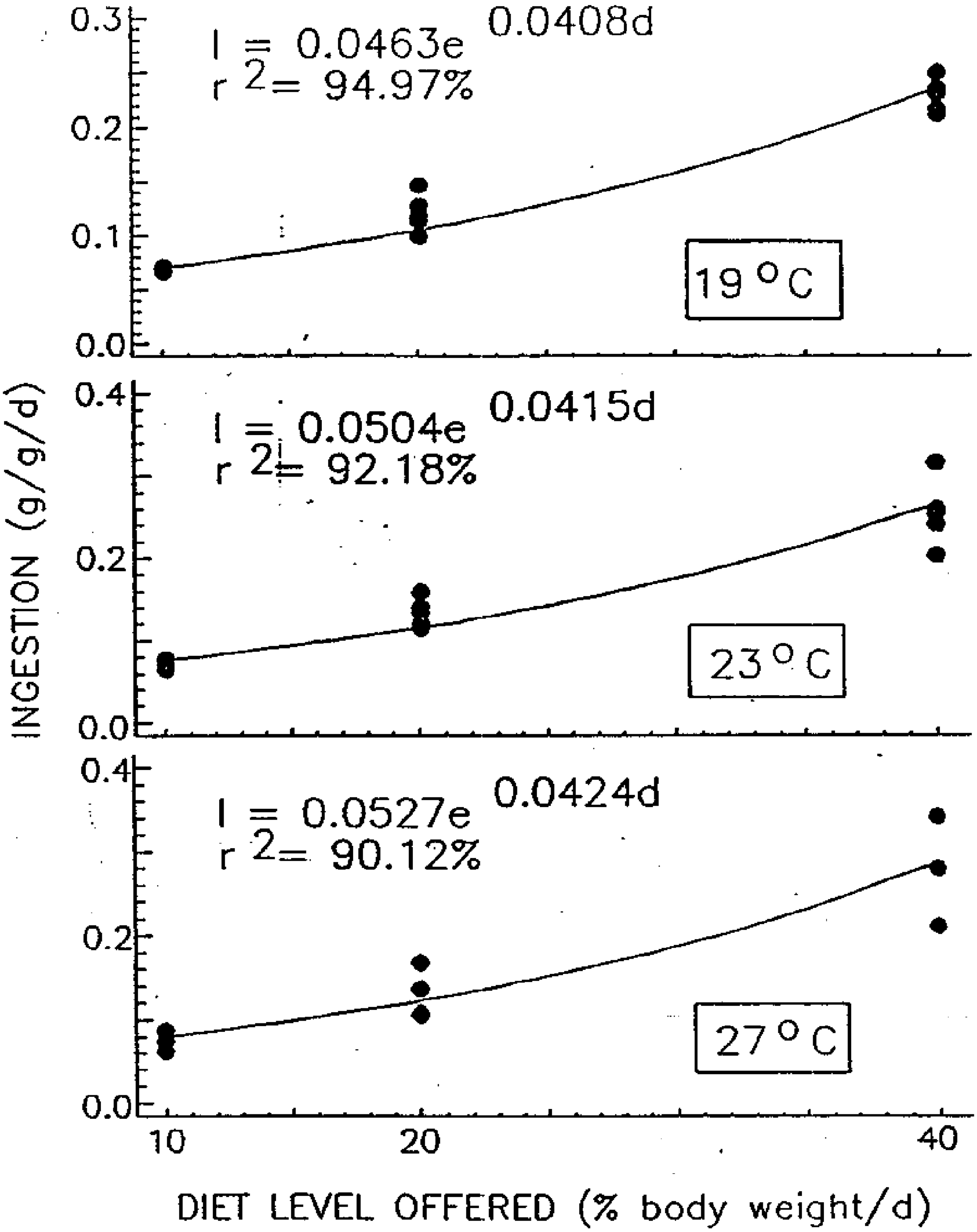


Figure 39. Exponential regressions of weight-specific ingestion rates in relation to offered diet levels at 19, 23 and 27°C.

Table 20. Bay anchovy initial and final wet weights (g), mean daily growth increments and mean weight-specific growth rates (G) for the 19°C experiment (duration of the experiment 35 days). The G estimates are from exponential growth models fit to weekly weight data (±SE).

DIET LEVEL (% body weight)	INITIAL WEIGHT (g)	FINAL WEIGHT (g)	MEAN GROWTH INCREMENTS (g/d)	MEAN WEIGHT-SPECIFIC GROWTH RATE (G)
10	0.606	0.953	0.0099	0.0149±0.0020
20	0.606	1.323	0.0205	0.0214±0.0029
40	0.606	1.459	0.0244	0.0229±0.0026

Table 21. Mean daily percentage growth of Bay Anchovy at three temperatures and diet levels. Diet offered in % of body weight per day.

TEMPERATURE	DIET LEVEL OFFERED (%)		
(°C)	10%	20%	40%
19	1.50	2.16	2.32
23	0.75	1.15	2.50
27	1.17	1.79	4.49

diet level and 0.806 g at the 40% diet level. Anchovies more than doubled their weight at the 40% diet in 28 days and had weight gains of 11.6 and 32.0% at 10 and 20% diets, respectively (Table 22). Growth coefficients (G) increased significantly with each increase in diet level at 23°C (ANCOVA; $P<0.0001$). Daily percentage weight gains at 23°C ranged from 0.75 to 2.50% (Table 21).

Mean growth at 27°C was 0.051 g at the 10% diet level, 0.228 g at the 20% diet level and 0.832 g at the 40% diet level. Anchovies more than doubled their weight at the 40% diet in 21 days and had 9.4 and 42.1% weight gains at the 10 and 20% diets, respectively (Table 23). Growth coefficients (G) increased significantly at each diet level at 27°C (ANCOVA; $P<0.0001$). Daily percentage weight gains ranged from 1.17 to 4.49% (Table 21).

Comparisons of the weight-specific growth rates among temperatures at each diet level indicated that at both 10% and 20% diet levels the lowest weight-specific growth rates were obtained at 23°C and the highest at 19°C (ANCOVA; $P>0.0001$). At the 40% diet level the lowest weight-specific growth rate was obtained at 19°C and the highest at 27°C (ANCOVA; $P>0.0001$). There was no significant difference between G at 19° and 23°C for the 40% diet (ANCOVA; $P>0.10$) or between G at 19° and 27°C for the 10 and 20% diet levels (ANCOVA; $P>0.09$).

The exponential growth models fitted to the data on anchovy weight in grams regressed on time in days are provided for each temperature (Figures 40, 41 and 42). All of the regressions are significant ($P<0.05$). At each temperature the growth coefficient (exponent in the models) increased with diet level. The variability in weight among the 10 fish weighed weekly decreased as ration increased at each temperature. The low r^2 values in the regression models (Figures 40, 41 and 42) reflect the relatively large variances, although the predictive regression lines appear to reasonably represent the average growth in each experiment.

The exponential growth models at 19°C (Figure 40) are:

10% Diet level offered n=60	$W=0.5972e^{0.0149t}$ $r^2=49.08\%$ $(S_b = 0.0020)$
20% Diet level offered n=60	$W=0.6674e^{0.0214t}$ $r^2=48.08\%$ $(S_b = 0.0029)$
40% Diet level offered n=60	$W=0.6626e^{0.0229t}$ $r^2=58.29\%$ $(S_b = 0.0026)$

The exponential growth models at 23°C (Figure 41) are:

10% Diet level offered n=75	$W=0.6874e^{0.0075t}$ $r^2=16.01\%$ $(S_b = 0.0023)$

20% Diet level offered $W=0.6992e^{0.0114t}$
n=75 $r^2=23.78\%$
$(S_b = 0.0027)$

40% Diet level offered $W=0.7733e^{0.0247t}$
n=50 $r^2=54.45$
$(S_b = 0.0033)$

The exponential growth models at 27°C (Figure 42) are:

10% Diet level offered $W=0.5288e^{0.0116t}$
n=75 $r^2=22.14\%$
$(S_b = 0.0025)$

20% Diet level offered $W=0.5426e^{0.0177t}$
n=40 $r^2=44.96\%$
$(S_b = 0.0032)$

40% Diet level offered $W=0.5731e^{0.0439t}$
n=40 $r^2=62.41\%$
$(S_b = 0.0055)$

Power function models described the increase in the daily weight-specific growth rates in relation to diet (Figure 43).

The power functions for each temperature are:

19°C experiment $G = 0.0084C^{0.3274}$
n=180 $r^2=83.77\%$
$(S_b = 0.144)$

23°C experiment $G = 0.0012C^{0.9037}$
n=150 $r^2=96.52\%$
$(S_b = 0.172)$

27°C experiment $G = 0.0014C^{1.0032}$
n=120 $r^2=96.27\%$
$(S_b = 0.197)$

The exponential coefficients were significantly different at each of the temperatures (ANCOVA; $P<0.0001$). The coefficients increased in relation to temperature, indicating that growth rate increased faster as ration increased at higher temperature than at lower temperature.

Oxygen Consumption

Oxygen uptake rates (R), in mg O_2/fish/hr, increased as anchovy weight increased at each temperature (Figure 44, Table 24). Weight-specific oxygen uptake (QO_2), in mg O_2/g fish/hr, decreased as mean weight of anchovies increased (Figure 45, Table 24).

Oxygen uptake rates at 19°C ranged from 0.188 to 0.331 mg hr^{-1} for anchovies weighing 0.69 to 1.39g. At 23°C the rates ranged from 0.283-0.558 mg/hr

Table 22. Bay anchovy initial and final wet weights (g), mean daily growth increments and mean weight-specific growth rates (G) for the 23°C experiment (duration of the experiment 28 days). The G estimates are from exponential growth models fit to weekly weight data (±SE).

DIET LEVEL (% body weight)	INITIAL WEIGHT (g)	FINAL WEIGHT (g)	MEAN GROWTH INCREMENTS (g/d)	MEAN WEIGHT-SPECIFIC GROWTH RATE (G)
10	0.734	0.819	0.0030	0.0075±0.0023
20	0.734	0.969	0.0084	0.0114±0.0027
40	0.734	1.54	0.0288	0.0247±0.0033

Table 23. Bay anchovy initial and final wet weights (g), mean daily growth increments and mean weight-specific growth rates (G) for the 27°C experiment (duration of the experiment 21 days). The G estimates are from exponential growth models fit to weekly weight data (±SE).

DIET LEVEL (% body weight)	INITIAL WEIGHT (g)	FINAL WEIGHT (g)	MEAN GROWTH INCREMENTS (g/d)	MEAN WEIGHT-SPECIFIC GROWTH RATE (G)
10	0.542	0.593	0.0024	0.0116±0.0025
20	0.542	0.770	0.0109	0.0177±0.0032
40	0.542	1.374	0.0396	0.0439±0.0055

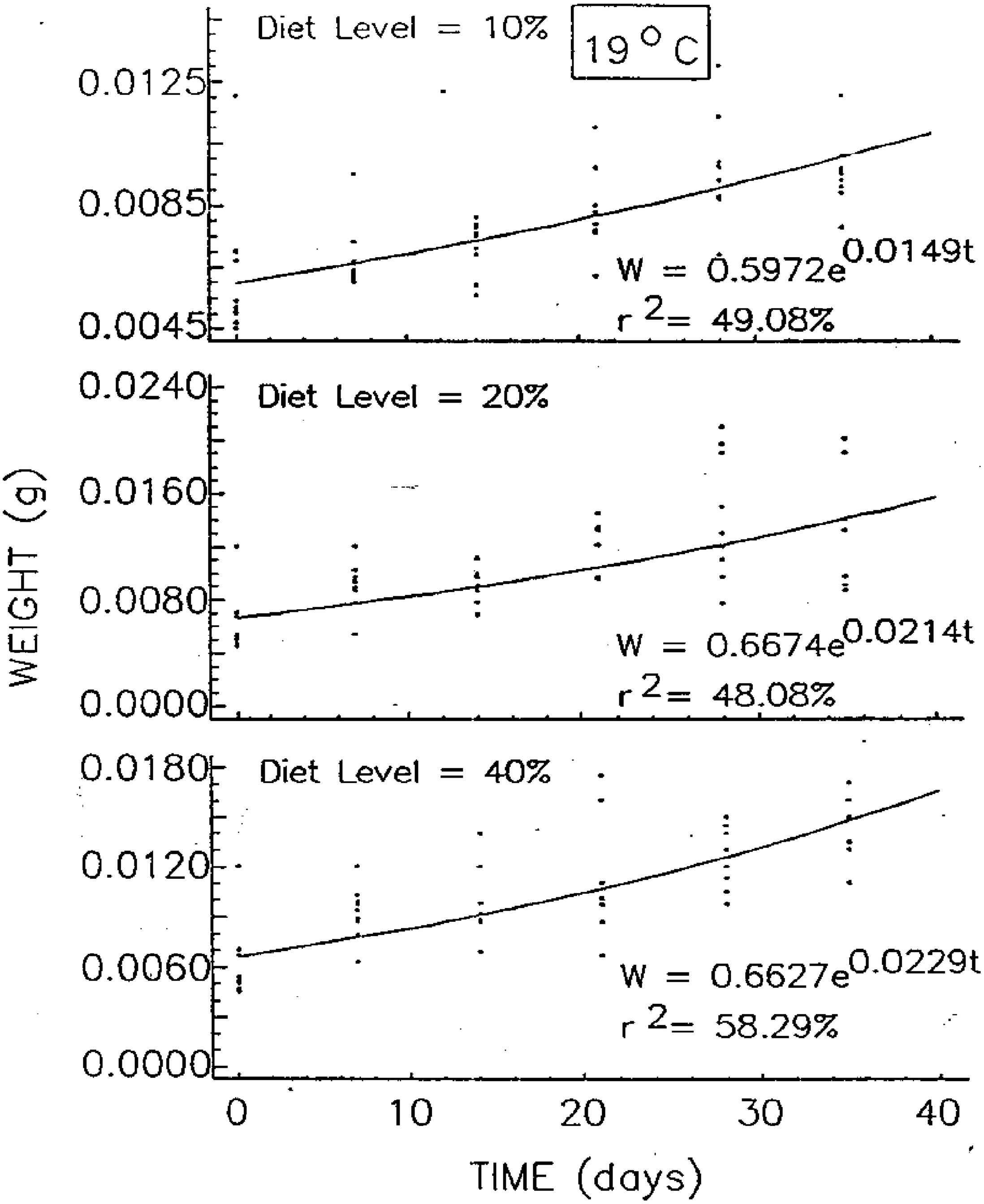


Figure 40. Exponential growth models of anchovy wet weights regressed on time for the three diet levels at 19°C.

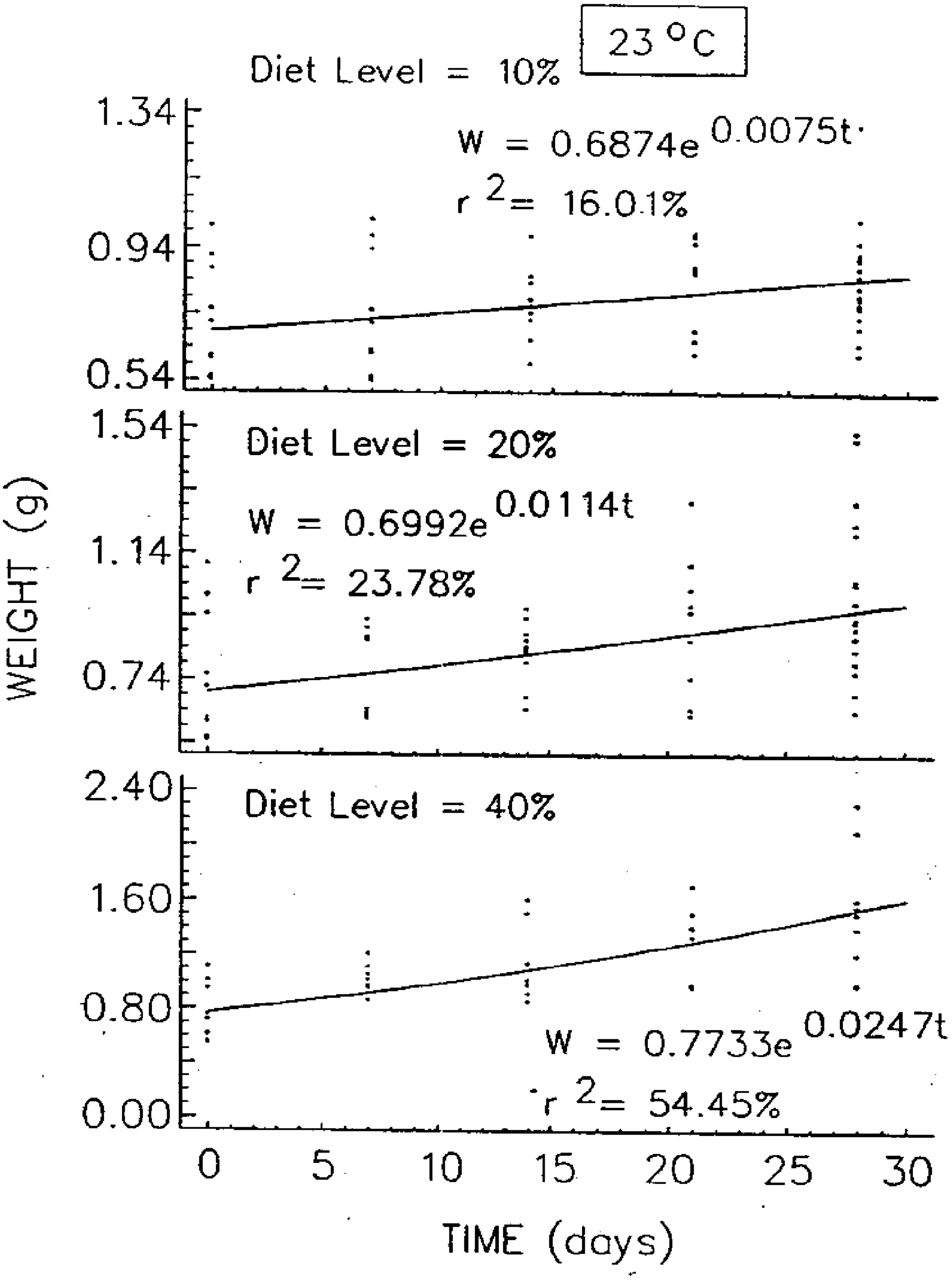


Figure 41. Exponential growth models of anchovy wet weights regressed on time for the three diet levels at 23°C.

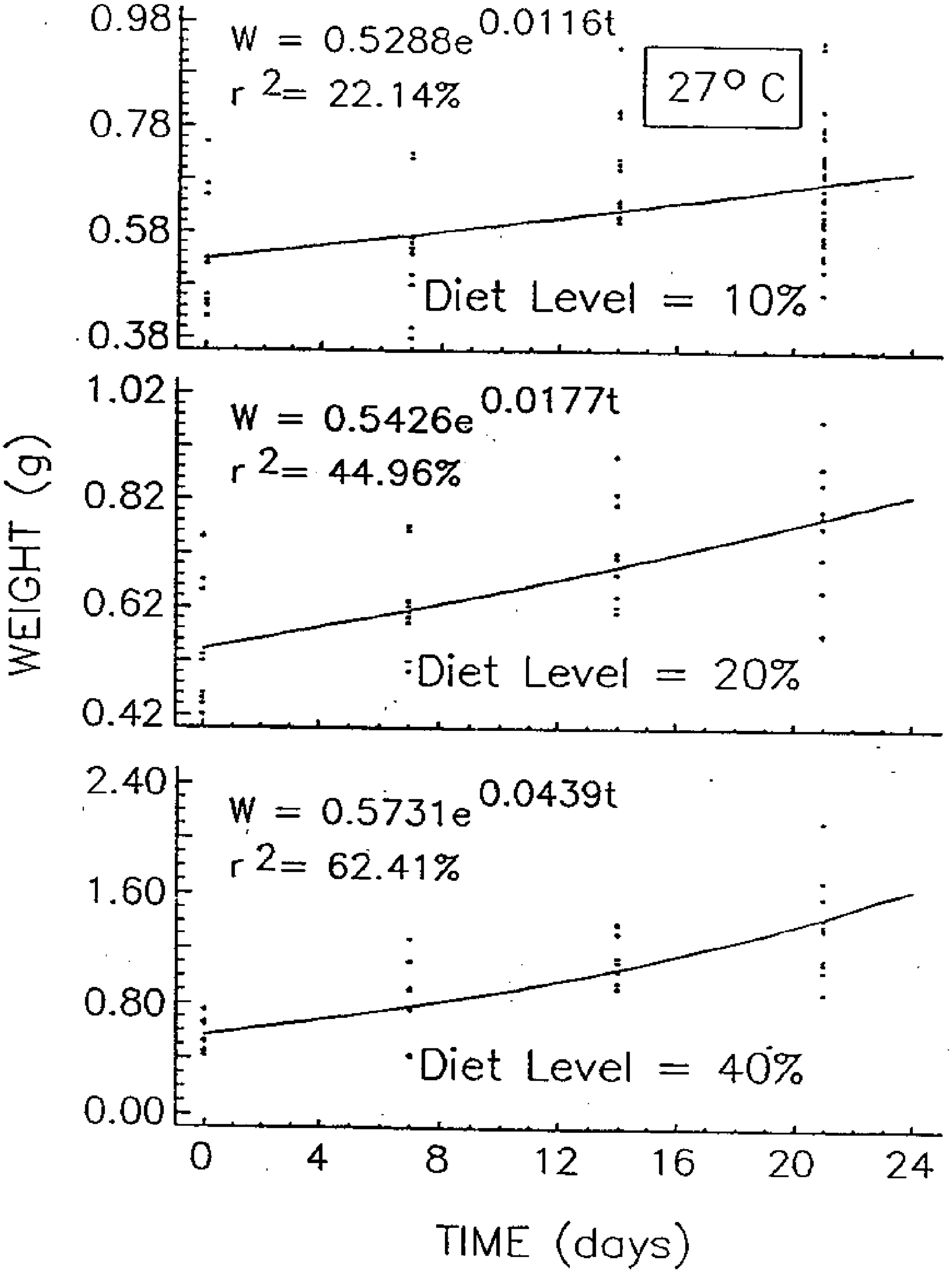


Figure 42. Exponential growth models of anchovy wet weights regressed on time for the three diet levels at 27°C.

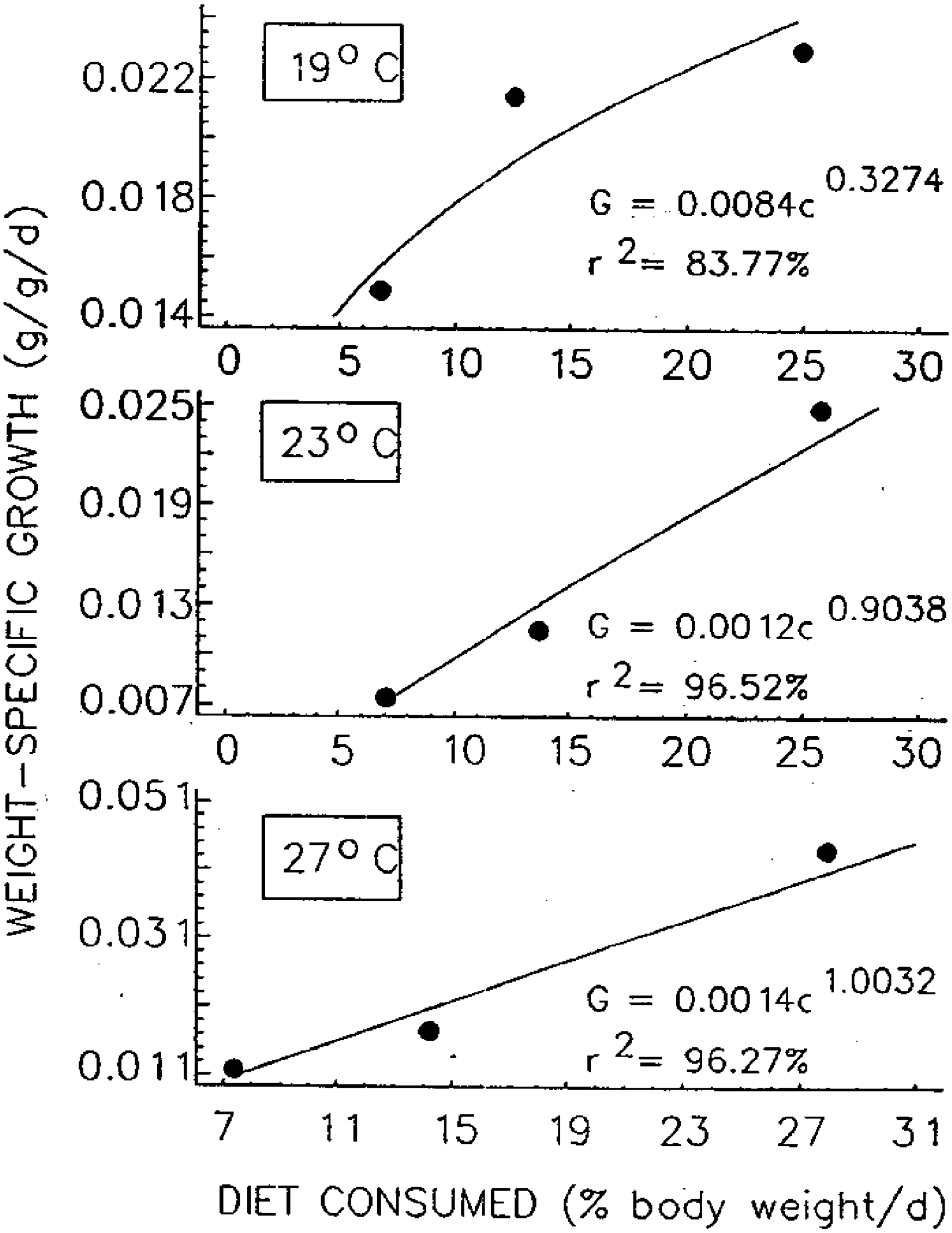


Figure 43. Power functions of bay anchovy daily weight-specific growth rates in relation to diet level for the three experimental temperatures.

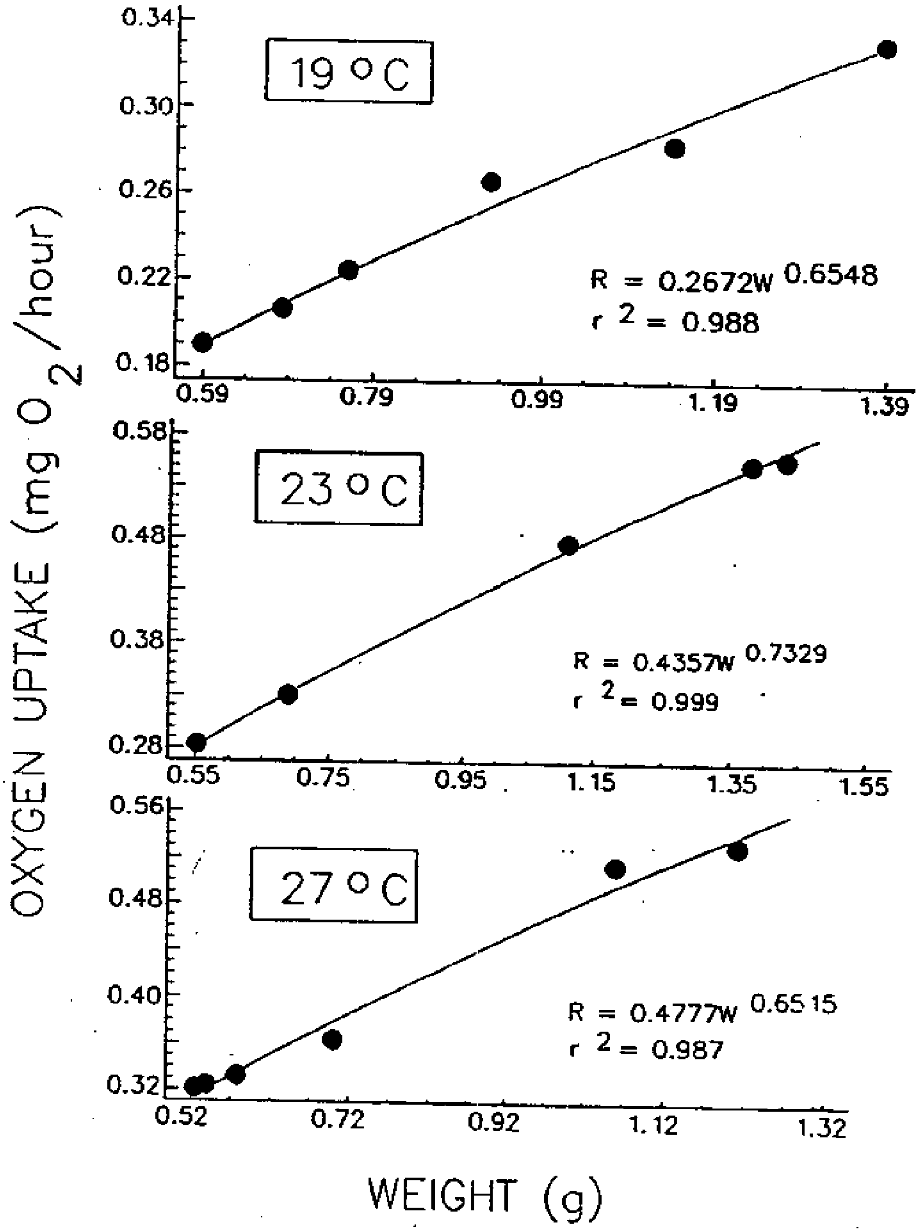


Figure 44. Power functions of oxygen uptake related to the weight of bay anchovy at the three experimental temperatures.

Table 24. Mean oxygen uptakes by bay anchovy. N = 12 to 14 anchovies in each experiment.

TEMPERATURE (°C)	MEAN WEIGHT (g)	QO_2 ($mgO_2/g/h$)	R (mgO_2/h)
19	1.39	0.238	0.331
	1.14	0.249	0.284
	0.93	0.286	0.266
	0.76	0.295	0.223
	0.69	0.301	0.188
23	1.43	0.390	0.558
	1.38	0.403	0.556
	1.11	0.429	0.476
	0.70	0.478	0.333
	0.69	0.479	0.332
	0.55	0.511	0.283
27	1.21	0.439	0.531
	1.06	0.486	0.515
	0.70	0.521	0.365
	0.58	0.572	0.332
	0.54	0.598	0.322
	0.53	0.608	0.320

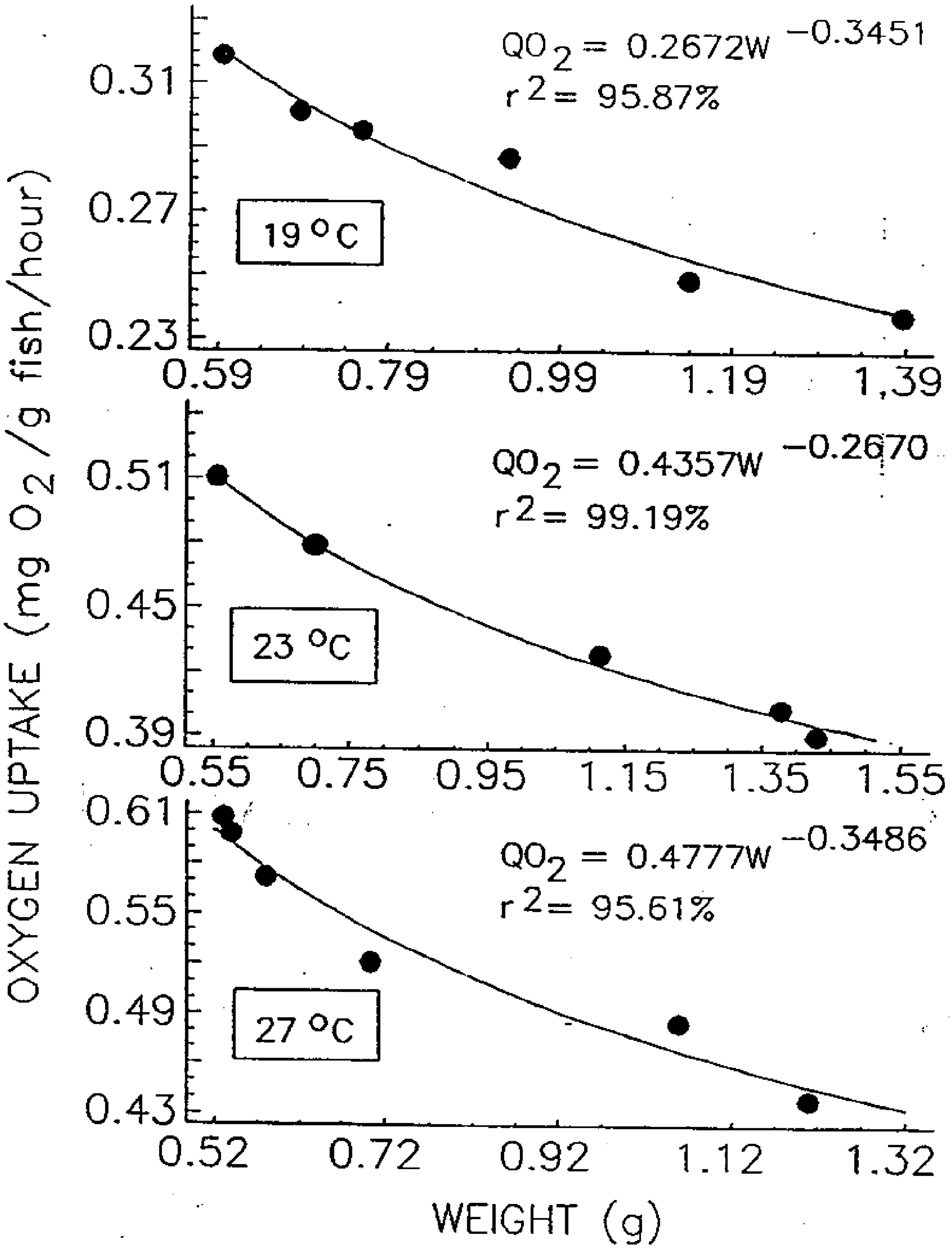


Figure 45. Power functions of weight-specific oxygen uptake related to the weight of bay anchovy at the three experimental temperatures.

for anchovies weighing 0.55 to 1.43 g and, at 27°C the rates ranged from 0.320-0.531 mg hr^{-1} for anchovies weighing 0.53-1.21 g (Table 24, Figure 44).

Weight-specific oxygen uptake at 19°C ranged from 0.238 to 0.301 for anchovies of 1.39 to 0.69 g. At 23°C QO_2 ranged from 0.390 to 0.511 for fish of 1.43 to 0.55 g. At 27°C QO_2 ranged from 0.439 to 0.608 for anchovies of 1.21 to 0.53 g (Table 24, Figure 45).

Power functions relating oxygen uptake (R) to weight of anchovy (W) (Figure 44) are:

19°C experiment	$R=0.2672W^{0.6548}$
n=12	$r^2=98.82\%$
(S_a = 0.0116)	(S_b = 0.0358)
23°C experiment	$R=0.4357W^{0.7329}$
n=12	$r^2=99.89\%$
(S_a = 0.0046)	(S_b = 0.0121)
27°C experiment	$R=0.4777W^{0.6515}$
n=12	$r^2=98.70\%$
(S_a = 0.0171)	(S_b = 0.0374)

The regression equations were highly significant ($P<0.0001$). The weight exponents of the regressions ranged from 0.6548 at 19° to 0.7329 at 23°C. The exponents did not differ significantly among temperatures (ANCOVA; $P>0.20$), indicating that the increasing rates of oxygen uptake were similar at each temperature. The intercepts were significantly different among experiments ($P<0.0001$), indicating that the mean level of oxygen uptake was strongly affected by temperature.

The regressions relating weight-specific oxygen uptake, Q_{O2} to weight of anchovy are:

19°C experiment	$QO_2=0.2672W^{-0.3450}$
n=12	$r^2=95.87\%$
(S_a = 0.0116)	(S_b = 0.0358)
23°C experiment	$QO_2=0.4357W^{-0.2670}$
n=12	$r^2=99.19\%$
(S_a = 0.0046)	(S_b = 0.0121)
27°C experiment	$QO_2=0.4777W^{-0.3486}$
n=12	$r^2=95.61\%$
(S_a = 0.0171)	(S_b = 0.0373)

The exponents of the Q_{O2} regressions also were not significantly different (ANCOVA, $P>0.20$) but the intercepts were different (ANCOVA; $P<0.0001$).

The calculated Q_{10} for weight-specific oxygen uptake was 2.247, indicating a more than twofold expected increase in Q_{O2} for a 10°C increase in temperature.

Energy Budgets

The calories allocated to growth and metabolism increased at each ration level for all temperatures (Tables 25-27). The relative amount of calories ingested which were allocated to metabolism decreased with ration level while the relative allocation to growth was variable (Table 28). The relative allocation of calories to growth decreased as diet level increased at 19°, showed no trend at 23° and increased at 27°C (Table 28). At the 20% and 40% rations, 50% or more of the ingested calories were in feces and urine at 19° and 23°C, although smaller allocations to (F+U) occurred at 27°C. Ingestions at each diet level were similar among temperatures, indicating that temperature within the test range had relatively small effects on food intake (Tables 25-27).

Overall assimilation efficiencies ranged from 34 to 88%. They generally were lowest at the highest diet level (Table 29). The highest assimilation efficiencies (>82%) occurred at each temperature for the 10% offered diet level. Assimilation efficiencies at 27°C were higher for the 20 and 40% offered diet levels than at 19 or 23 °C (Table 29; Figure 46).

Energy into growth and Growth Efficiencies

Gross growth efficiencies ranged from 14.4 to 38.3% (Table 30). The highest gross growth efficiencies (K_1) were estimated at 19°C, 10% diet level, and at 27°C, 40% diet level. The lowest K_1 were estimated at 23°C, for the 20% and 10% diet levels. Gross growth efficiency tended to decrease as diet level increased at 19°C, was nearly constant across diet levels at 23°C, and increased as diet level increased at 27°C.

Net growth efficiencies (K_2) ranged from 18.5 to 59.0% (Table 31). Net growth efficiencies generally increased as diet level increased at each of the temperatures, and increased most at 27°C. The highest K_2 were estimated at the 40% diet level, ranging from 47 to 59%. The two lowest K_2 were estimated for the 10% diet level at 23° and 27°C. The results (Table 31) indicated that a high net growth efficiency is achieved by bay anchovy at all diet levels when temperature is low but that high K_2 can be achieved at high diet levels only if the temperature is high.

It appears that the "physiologically useful" energy was highest at low diet levels and decreased as ration increased at each temperature (Table 32). The proportion of the physiologically useful energy that went to growth had its highest values at 19°C for all diet levels (Table 33). More than 55% of the physiologically useful energy was allocated to growth at each temperature for the 40% diet level.

Energy into Metabolism

The amount of energy that was allocated to metabolism declined consistently as ration level increased (Table 34). The energy of metabolism from the physiologically useful energy was highest at 23°C (43.5-79.9%) and lowest at 19°C (33.3-49.4%).

Comparing the three experiments at any of the diet levels, the lowest

Table 25. Standarized energy budgets (cal/g/d) and efficiencies for bay anchovy reared at 19°C, and fed at 10, 20 and 40% of the fish body weight with newly hatched *Artemia* nauplii. Mean weights of anchovies were 0.775, 0.970, and 0.990 g for the 10, 20 and 40% diet levels.

BUDGET COMPONENT	DIET LEVEL OFFERED		
	10%	20%	40%
I	61.07	117.29	230.95
G	23.39	37.74	41.94
M	22.81	21.11	20.96
F	10.59	50.22	151.88
U	4.27	8.21	16.16
A=I-F	50.48	67.07	79.07
EFFICIENCIES			
K_1=G/I	0.38	0.32	0.18
K_2=G/I-F	0.46	0.56	0.53
A/I	0.83	0.51	0.34
M/A	0.45	0.31	0.27
(G+M)/I	0.76	0.50	0.27
G/(G+M)	0.51	0.64	0.67
M/(G+M)	0.49	0.36	0.33

Table 26. Standarized energy budgets (cal/g/d) and efficiencies for bay anchovy reared at 23°C, and fed at 10, 20 and 40% of the fish body weight with newly hatched *Artemia* nauplii. Mean weights of anchovies were 0.763, 0.820 and 1.09 g for the 10, 20 and 40% diet levels.

BUDGET COMPONENT	DIET LEVEL OFFERED		
	10%	20%	40%
I	57.42	112.61	214.02
G	9.20	16.24	43.33
M	36.63	35.91	33.34
F	7.56	52.57	122.37
U	4.02	7.88	14.98
A=I-F	49.86	60.04	91.65
EFFICIENCIES			
K_1=G/I	0.16	0.14	0.20
K_2=G/I-F	0.18	0.27	0.47
A/I	0.88	0.53	0.43
M/A	0.73	0.60	0.36
(G+M)/I	0.80	0.46	0.36
G/(G+M)	0.20	0.31	0.57
M/(G+M)	0.80	0.69	0.43

Table 27. Standarized energy budgets (cal/g/d) and efficiencies for bay anchovy reared at 27^{o}C, and fed at 10, 20 and 40% of the fish body weight with newly hatched *Artemia* nauplii. Mean weights of anchovies were 0.600, 0.654 and 0.909 g for the 10, 20 and 40% diet levels.

BUDGET COMPONENT	DIET LEVEL OFFERED		
	10%	20%	40%
I	73.28	102.71	206.45
G	14.30	25.02	76.38
M	44.72	43.30	38.60
F	9.13	27.20	77.00
U	5.13	7.19	14.46
A=I-F	64.15	75.50	129.44
EFFICIENCIES			
K_1=G/I	0.20	0.24	0.37
K_2=G/I-F	0.22	0.33	0.59
A/I	0.88	0.74	0.63
M/A	0.70	0.57	0.30
(G+M)/I	0.81	0.67	0.56
G/(G+M)	0.24	0.37	0.66
M/(G+M)	0.76	0.63	0.34

Table 28. Relative energy budgets for bay anchovy fed at 3 different diet levels at 19°, 23° and 27°C.

TEMPERATURE (°C)	DIET LEVEL (%)	G	M	F	[F+U]
19	10	0.3830	0.3735	0.1735	0.2435
	20	0.3218	0.1800	0.4281	0.4981
	40	0.1816	0.0908	0.6576	0.7276
23	10	0.1602	0.6381	0.1317	0.2017
	20	0.1443	0.3189	0.4668	0.5368
	40	0.2025	0.1558	0.5718	0.6418
27	10	0.1952	0.6103	0.1245	0.1945
	20	0.2435	0.4215	0.2649	0.3349
	40	0.3700	0.1870	0.3730	0.4430

Table 29. Assimilation efficiencies of bay anchovy.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	20%	40%
19	0.8265	0.5719	0.3424
23	0.8778	0.5332	0.4282
27	0.8755	0.7351	0.6270

Table 30. Bay anchovy percent gross growth efficiencies (K_1=G/I) for the three temperatures and three diet levels.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	20%	40%
19	38.3	32.2	18.2
23	16.0	14.4	20.3
27	19.5	24.4	37.0

Table 31. Bay anchovy percent net growth efficiencies (K_2=G/A) for the three temperatures and three diet levels.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	20%	40%
19	46.3	56.3	53.0
23	18.5	27.1	47.3
27	22.3	33.1	59.0

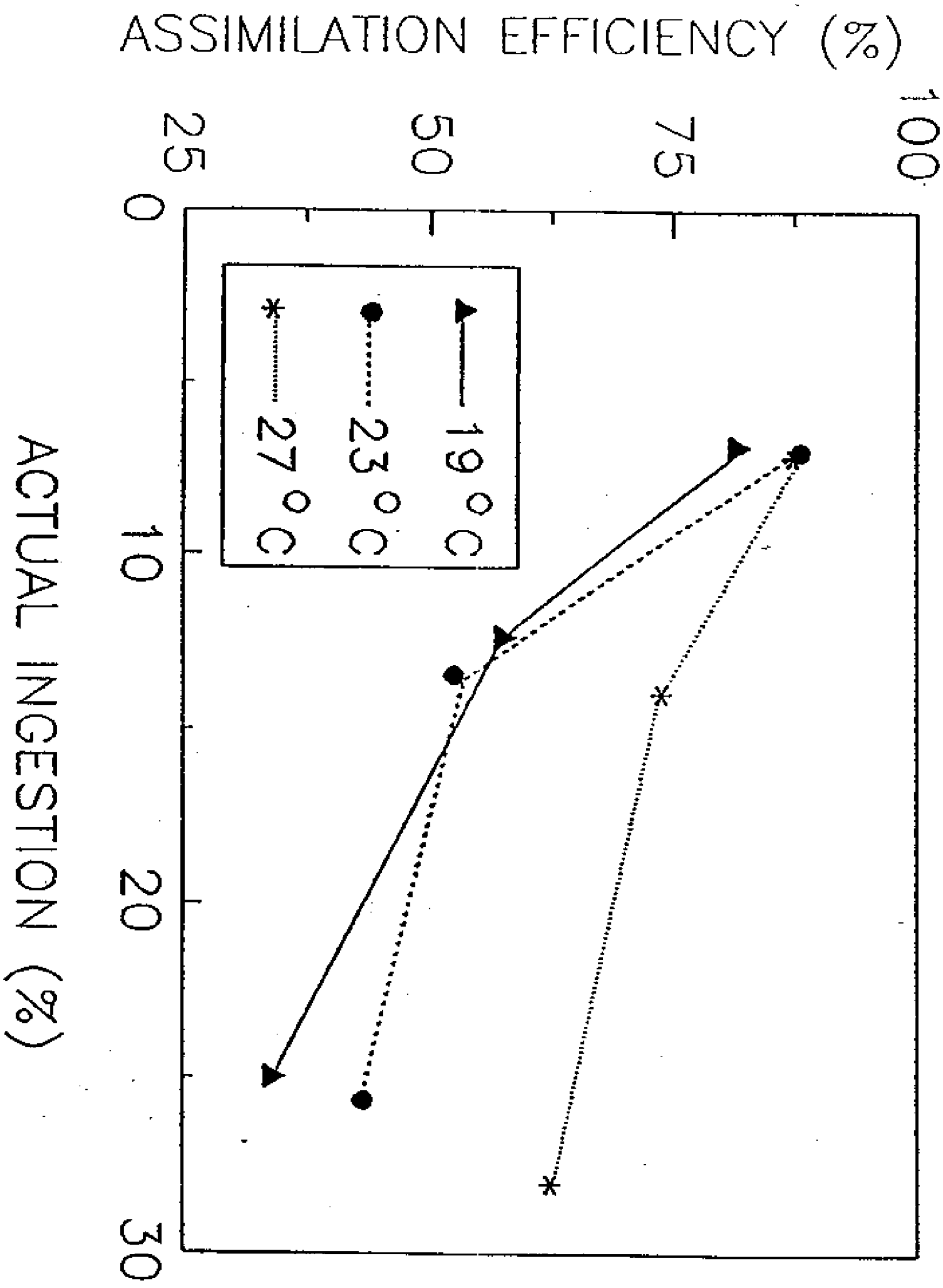


Figure 46. Assimilation efficiency (%) related to the ration (percentage of wet body weight) actually consumed by bay anchovy at the three experimental temperatures.

Table 32. "Physiologically useful ration" for bay anchovy. Relative amount of energy (%) allocated to growth and metabolism (G+M)/I.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	 20%	 40%
19	75.7	50.2	27.2
23	79.8	46.3	35.8
27	80.6	66.5	55.7

Table 33. Proportion of physiologically useful rations (G+M) allocated to growth (i.e. G/(G+M)) for bay anchovy.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	 20%	 40%
19	50.6	64.1	66.7
23	20.1	31.2	56.5
27	24.2	36.6	66.4

Table 34. Proportion of the physiologically useful ration (G+M) allocated to metabolism (i.e. M/(G+M)) for bay anchovy.

TEMPERATURE (^{o}C)	DIET LEVEL OFFERED 10%	 20%	 40%
19	49.4	35.9	33.3
23	79.9	68.9	43.5
27	75.8	63.4	33.6

relative amounts of energy allocated to metabolism (M/I) were estimated at 19°C (Table 28), ranging from 9.1 to 37.4% as diet level decreased. The highest M/I percentages were estimated at 27°C (Table 28) for the 10 and 20% diet levels (61.0 and 42.2% respectively), and at 23°C, 10% diet level (63.8%) (Table 28). In each experiment the relative amount of energy allocated to metabolism decreased as diet level increased.

Energy into Excretion

The relative amount of energy that was excreted (F+U)/I ranged from 19.5 to 72.8% (Table 35). At each temperature the relative amount of energy that was excreted increased as diet level increased. The actual calories excreted (Tables 25-27) were highest at 19°C for all diet levels, except for the 23°C, 20% diet level. The lowest excretion rates, both relative and actual, were found at 27°C at each diet level.

Maintenance Rations

The calculated maintenance rations from the routine metabolic rates (Table 24) for the three experimental temperatures were 19°C, 2.62% (SE = 1.27); 23°C, 4.92% (SE = 1.97) and 27°C, 7.31% (SE = 2.74). The estimated maintenance ration increased by a factor of 2.79 from 19°C to 27°C. The estimated ration at 27°C, 10% diet level (7.4%) was close to the estimated maintenance ration (7.31%) derived from the Q_{02} relationship. Because the variance in the estimated maintenance ration at 27°C is high, it is possible that the maintenance ration at 27°C actually was considerably lower than 7.31%.

DISCUSSION

Food Consumption by the Bay Anchovy

Appetites of fish increase with increasing temperature, reach a peak and then decline as temperature continues to increase above optimal (Jobling 1988). Therefore, temperature may have an important effect on the rate of food intake in fishes (Pandian and Vivekanandan 1985). In the present study, although the actual ration and percent of the offered diet that was consumed by bay anchovy increased with temperature at each diet level (Table 19), the weight-specific ingestion rates did not differ significantly among temperatures at any of the diet levels. Apparently, temperature changes of 4-8°C had only a small effect on increasing the rate of food consumption by bay anchovy. The relative percentages of the offered diets that were consumed tended to decrease slightly as diet level increased, indicating that a higher percentage of the nominal *Artemia* diet level was consumed at the lowest diet level compared to the highest diet level.

Growth

Growth rates of bay anchovy increased as ration increased at each temperature. The only non-significant difference in growth rate was at 19°C for the 20% and 40% diet levels. The results also indicated that at lower temperatures the anchovies were less efficient in converting their ingested energy into growth as ration increased. In contrast, at higher temperatures,

Table 35. Percentage of the ingested energy for bay anchovy that was excreted, i.e. [F+U]/I.

TEMPERATURE (°C)	DIET LEVEL OFFERED 10%	20%	40%
19	24.4	49.8	72.8
23	20.2	53.7	64.2
27	19.5	33.5	44.3

both assimilation and growth efficiencies increased in response to increasing metabolic rates and, to a lesser extent, small increases in amounts ingested.

The relation between growth and ration level has been studied for several fishes. Durbin and Durbin (1983) obtained an almost linear relationship between growth and ration size of Atlantic menhaden at moderately high plankton densities; this relationship became asymptotic at lower plankton levels because of a decrease in the foraging speed; therefore, less of the ingested energy was used in metabolism and more energy is available for growth when swimming speed was slow. In contrast, Ivlev (1960) found that for particulate-feeding planktivore fishes growth increased asymptotically rather than linearly with increasing food concentration, because particulate planktivores feed in a series of discrete events; consequently, there is a maximum ingestion rate set by the time required to capture and handle each prey. Similar results were obtained for brown trout by Elliott (1979; 1982). Cui and Wootton (1988a) found for the minnow, Phoxinus phoxinus, that at high rations, further increases in ration resulted in little or no increase in growth rate. The ration above which there is no increase in growth rate is what Brett et al. (1969) defined as maximum ration for Oncorhynchus nerka, or what is termed by Elliott (1979) the ad libitum ration.

One explanation for the failure to detect an increase in growth rate in bay anchovy at 19°C, 40% diet level, compared to the growth at 20% diet level, is that the fish probably were near the maximum ration for that temperature-diet level combination. In contrast, at 23 and 27°C, growth did increase significantly at the 40% diet compared to the 20% offered diet, indicating that maximum ration increased as temperature increased.

The combined effect of temperature and ration on growth rate of bay anchovy is complex. At the two lowest rations (10% and 20% offered diet levels) the growth rate of anchovies was higher at the lowest temperature (19°C). However, at 40% diet level growth rate was highest at the highest temperature (27°C). Similar results were obtained by Allen and Wootton (1982) for growth rate of stickleback, Gasterosteus aculeatus, where growth rate increased with increasing temperature at high rations but decreased as temperature increased when low rations were fed. The same pattern was observed below the optimum temperature for growth in O. nerka (Brett et al. 1969) and in S. trutta (Elliott 1979, 1982). Furthermore, Cui and Wootton (1988a) found that for the minnow growth rate at low rations decreased as temperature increased.

The growth results obtained for bay anchovy suggest that 27°C was not an especially high temperature for bay anchovy because maximum growth and high growth efficiency were obtained at the highest ration at 27°C. Growth rate of fishes at maximum ration is usually highest at an intermediate temperature termed the optimum temperature for growth (Brett 1979; Elliott 1979, 1982). In general, the amount of food available for growth in fishes is maximized at an intermediate temperature, which is slightly below the temperature at which appetite is greatest (Jobling 1988). It is probable that 27°C is below the optimum temperature for bay anchovy. Therefore, the maximum ration, and its associated growth rate, would be expected at higher temperature.

The lowest growth rates were obtained at 23°C, 10% and 20% diet levels, although intermediate growth responses had been expected. A possible explanation of this result may be that the anchovies at the beginning of the 23°C experiment were bigger than at the beginning of the other experiments. They weighed 21% more, on average, than did anchovies at 19°, and 35% more than did anchovies at 27°C. Bigger fish have relatively less potential to grow than do small fish (Jobling 1988). Bigger fish must also allocate relatively more energy to metabolism than small fish. This may explain in part why anchovies at 23°C put more energy into metabolism than did anchovies at other temperature (Table 34).

The variability in weight among individuals tended to be higher at the low diet levels at each temperature (Figures 40, 41 and 42), suggesting that competition for food was higher at lower rations. The variability in weights of anchovies was highest at high temperatures and low rations, which would be expected if competition were important. At the highest ration bay anchovy tended to grow more homogeneously at each temperature suggesting that food was more available for each individual and that competition was reduced.

Oxygen Consumption

The mean oxygen uptake values increased as anchovy weight and temperature increased. This result was expected and is in agreement with many studies on fishes, among them studies on the clupeid fishes menhaden and gizzard shad (Hettler 1976; Durbin *et al*. 1981; Pierce *et al*. 1981; Durbin and Durbin 1983). The mean QO_2 obtained at each temperature in the present study were high (Table 24) compared to results for non-feeding 302g Atlantic menhaden at 20°C, (0.10 mg O_2/g/hr) (Durbin and Durbin 1983) and closer to the Q_{O2} obtained for feeding adult menhaden (0.48 mg O_2/g/hr) (Durbin *et al*. 1981). The Q_{O2} for bay anchovy was lower than the values obtained for gizzard shad (1.2-2.6 mg O_2/g/hr) which ranged in weight from 0.7-256.9 g in a temperature range of 9.1-24.5°C (Pierce *et al*. 1981).

The exponent in the oxygen consumption-body weight relationships ranged from 0.65 to 0.73 for the bay anchovy. These values are low compared to the mean of 0.86 ± 0.03 reported by Brett and Groves (1979). A broad range (0.59 to 1.28) was reported by Glass (1969). The exponent ranged from 0.7 to 0.9 for several species, including Pacific and Atlantic cod (*Gadus macrocephalus* and *G. morhua*, respectively) walleye pollock (*Theragra chalcogramma*) (Paul 1986; Paul *et al*. 1988). Relatively small values of the weight exponent for hourly (0.44) and daily rates (0.48) were observed for gizzard shad (Pierce *et al*. 1981) weighing 0.7 to 256.9 g in the temperature range 9.1 to 24.5°C. Healey (1972) and Hoss (1974) reported low weight exponents (0.43-0.83) for the sand goby, *Gobius minutus* and the pinfish, *Lagodon rhomboides* (0.62), respectively. In each of those species the values were stated to be estimates of routine metabolism of unfed fish. A wide range of weight exponents perhaps is expected when comparing fish of different sizes over a range of temperatures. For example, Brett (1979) found weight exponents ranging from 0.78 to 0.97 for sockeye salmon of different sizes and for temperatures varying from 5°-20°C. In the bay anchovy oxygen uptake experiments, a relatively small weight range was used although the temperature range over which tests were run was substantial.

Oxygen consumption rates were difficult to estimate accurately for bay anchovy because the fish often did not calm down during an experiment and did not swim normally (i.e. schooling) in the 20-liter respirometer. In most of the experiments one or two fish remained "excited", trying to escape at the mouth of the carboy through most of the test, which made O_2 uptake readings variable. For this reason oxygen uptakes were calculated based on the last two measurements of oxygen uptake during an 8 to 12-hr experiment, when the uptake rates usually became more stable.

The estimated Q_{10} for oxygen uptake by bay anchovy was 2.247, which is in the range (2-3) suggested by Saunders (1963) and Paul (1986). Values of Q_{10} usually approximate 2.0 for standard and active metabolism in juvenile and adult fish (Fry 1971). In contrast, Rombough (1988) found Q_{10} values of 3.0 for salmonid embryos and alevines and reported a range of 3.0 to 5.0 from results found by Gruber and Wieser (1983). Values of 2.48 to 3.2 has been reported for some cod and pollock species (Saunders 1963; Paul 1986). The bay anchovy Q_{10} value is somewhat lower than the Q_{10} of 2.6 estimated for Peruvian anchoveta (Villavicencio 1981).

Energy Budgets

Gross growth efficiencies (K_1) of bay anchovy varied with diet levels and temperatures. K_1 tended to decrease as ration increased at the lowest temperature (19°C); it remained nearly constant at the intermediate temperature (23°C) and increased as ration increased at the highest temperature (27°C). Consequently, the highest gross growth efficiencies were found at 19°C (10% diet level) and 27°C (40% diet level).

Despite decreasing assimilation efficiencies, the anchovies had better growth at higher temperature and ration levels. Fish fed at ration levels higher than the level of maximum growth efficiency tend to have decreases in assimilation efficiency, but growth rate may still increase (Paloheimo and Dickie 1966; Brett and Groves 1979). Wurtsbaugh and Davis (1977) found that gross growth efficiency of rainbow trout, *Salmo gairdneri*, increased from zero at a maintenance ration and was highest at intermediate consumption rates. The authors pointed out that in some cases the efficiency declined slightly at repletion feeding levels. Durbin and Durbin (1983) found that gross growth efficiency increased asymptotically as ration increased for the Atlantic menhaden at a single temperature, 20°C. According to Paloheimo and Dickie (1966) the logarithm of gross growth efficiency declines with increasing ration levels from a maximum at low feeding levels. However, Warren (1971) pointed out that the curve relating efficiencies to consumption must increase initially as ration increases and sometimes declines at high ration levels. When declines in gross growth efficiency occur at high ration levels, they can be attributed to increases in specific dynamic action, decreases in assimilation efficiency and/or to increases in fish activity (Wurtsbaugh and Davis 1977).

The bay anchovy results indicate that gross growth efficiency (K_1) is a complex function of ration and temperature. High efficiencies are obtained at low temperatures and low to medium rations but also at high temperatures when ration is high. The K_1 of anchovy for the nine treatments ranged from 14-38%, which is a wider range than that suggested by Brett and Groves (1979) for young carnivorous fishes (29±6%). The K_1 for the three diet levels at 23°C were relatively low (mean of 17%), but K_1 at 19° and 27°C were in the range suggested by Brett and Groves (1979) (mean of 30% and 27%, respectively). Net growth efficiencies (K_2) in the three experiments increased as ration level increased. This indicates that the efficiency of converting the assimilable part of the diet into growth increased as consumption increased at each temperature. The highest mean K_2 was observed at 19°C (mean = 52%). The lowest K_2 (mean = 31%) occurred at 23°C.

The metabolic component of the energy budget should be interpreted carefully. The energy allocated to metabolism was calculated from the respiration models obtained from the oxygen uptake experiments on non-feeding fish. It was assumed that these values represent routine metabolic rates (Brett and Groves 1979). The metabolic rate will increase in feeding fish if they become more active and require more energy for ingestion, digestion and absorption of food (Jobling 1981). The metabolic expenditures of the bay anchovy may be higher than those calculated in the budgets under usual conditions in the estuary. The routine metabolic rates that were estimated perhaps should be multiplied by a factor to convert them to active metabolic rates. However, if such an approach were followed, the fact that some anchovies remained "excited" during an oxygen uptake experiment also must be considered.

Energy allocated to metabolism was on average low for the 19°C experiment (21.5%) compared to the range indicated by Brett and Groves (1979) for carnivorous fish of 37% to 51%. However, the values obtained for the 23 and 27°C experiments (37 and 41%, respectively) were in that range.

The mean values of calories allocated to metabolism at different diet levels ranged from 21.6 to 42.2 cal/g/d (mean 32.8) for bay anchovy in the temperature range 19°-27°C. Similar results were obtained for the northern anchovy, <u>Engraulis mordax</u> (Lasker 1970) and the Peruvian achoveta, <u>Engraulis ringens</u> (Villavicencio 1981). The northern anchovy had a mean metabolic allocation of 20.8 cal/g/d for a range of temperature of 11°-20°C, and the Peruvian anchoveta had a range of 12.1 to 22.4 cal/g/d in a temperature range of 14°-20°C.

A linear regression model describing the relationship between metabolic rate increase and temperature for the three anchovy species is presented in Figure 47. Metabolic rate increases by 2.2 cal/g/d for each 1° rise in temperature according to the regression model. The relatively good fit suggests that this model could be used to predict routine metabolism of anchovies and that it may be useful in future energetics studies on other engraulid species.

The proportions of physiologically useful energy (G+M) that were allocated to metabolism ranged from 33.3 to 79.9%. M/(G+M) often were lower than the mean of 60% reported for young carnivorous fish (Brett and Groves 1979). But, the anchovy values at 10 and 20% diet levels at 23 and 27°C were higher than the mean value, emphasizing the importance of the combined effects of temperature and ration level.

Assimilation efficiencies of bay anchovy decreased as diet level increased at each temperature. Mean assimilation efficiencies were 85% at the 10% diet level, 61% at the 20% diet level, and 47% at the 40% diet level. These values, except for the 10% diet level, are lower than the 80-90%

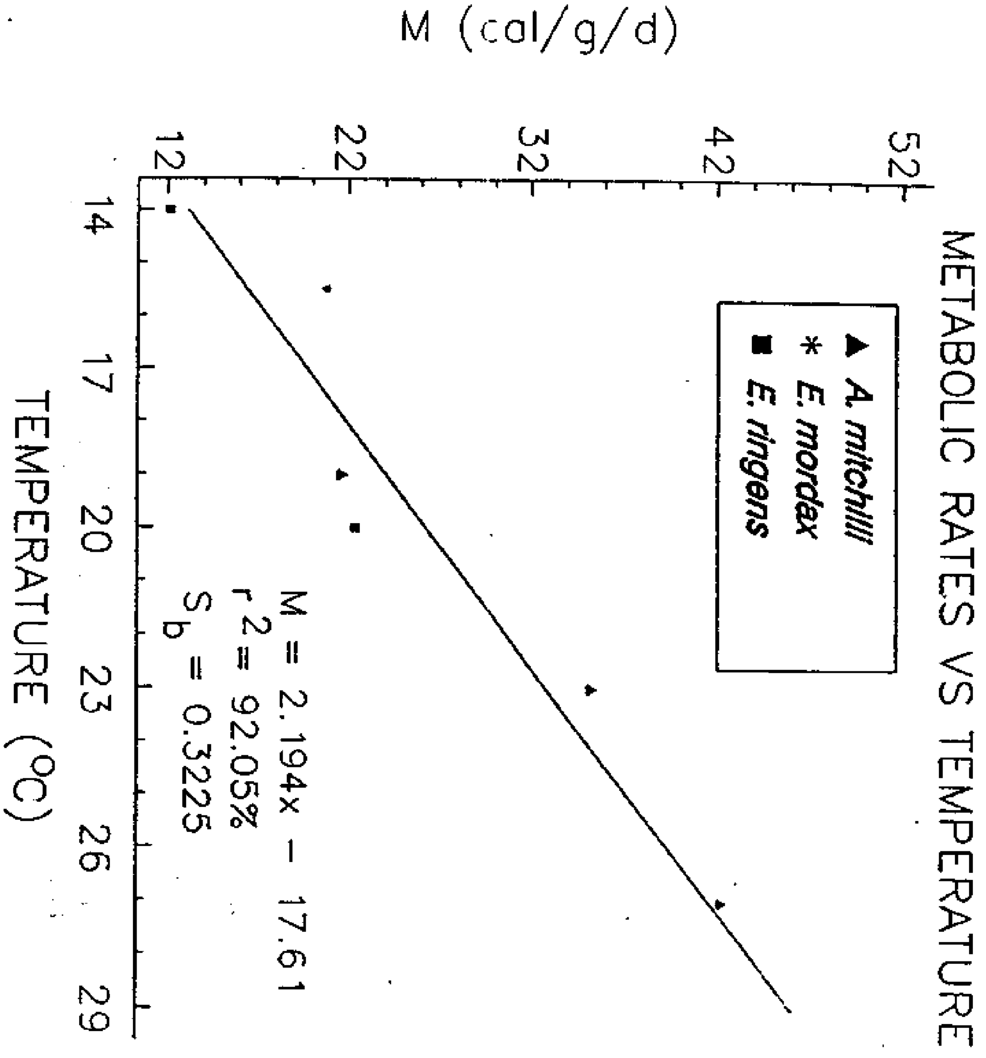


Figure 47. Comparison of metabolic rates in cal/g/d vs temperature for three anchovy species. Data for the northern anchovy are from Lasker (1970), data for the Peruvian anchoveta are from Villavicencio (1981) and data for the bay anchovy are from the present study.

reported by Brett and Groves (1979) for young carnivorous fish. The results are in contrast to findings obtained for Atlantic menhaden fed on phytoplankton; menhaden showed an increase in assimilation efficiency as ration increased, except at the highest ration where assimilation was reduced (Durbin et al. 1981). Menhaden had mean assimilation efficiencies of 89.5% for fish fed on phytoplankton and 87.7% for fish fed on zooplankton. These values are similar to the assimilation efficiencies of bay anchovy at the lowest rations (mean of 87.7%). Staples and Nomura (1976) found that assimilation efficiency was independent of ration size in rainbow trout, Salmo gairdneri. Durbin and Durbin (1983) assumed a constant assimilation efficiency for menhaden as ration increased, while other studies have reported decreases in assimilation efficiency as ration increased in brown trout, Salmo trutta and perch, Perca fluviatilis (Elliott 1976; Solomon and Brafield 1972).

Durbin and Durbin (1983) found that the major energy outputs by Atlantic menhaden were respiration and excretion. For bay anchovy at the lowest temperature (19°C) and higher diet levels (20 and 40%) the major outputs were to growth and excretion. At 23 and 27°C for the 40% diet level the major outputs were to growth and metabolism. Therefore, the relative allocations can shift as a function of variable temperature and diet levels.

The estimated (F+U)/I values for bay anchovy generally were much higher than the mean value of 27±3% given by Brett and Groves (1979) for young carnivorous fish, with the exception of the 10% diet level, where (F+U)/I was lower than the mean. A possible explanation is that 20-40% diet levels are not eaten commonly by most fish species, either in the wild or in culture, and experimental results on F+U may be unavailable at such high diet levels. The increase in F+U at high ration levels in bay anchovy was accompanied by a decline in assimilation efficiency (Table 31). Allocation to growth can still increase at high rations even when assimilation is low. Such results were reported by Houde and Schekter (1983) for bay anchovy larvae and by Borgmann and Ralph (1985) for white sucker (Catostomus commersoni) larvae and young common shiners (Notropis cornutus). In general, growth rate may continue to increase at high feeding levels but assimilation efficiency often decreases (Paloheimo and Dickie 1966; Brett and Groves 1979).

Maintenance Rations

The estimated maintenance ration of bay anchovy increased from 2.6% at 19°C to 7.3% at 27°C. Thus, the maintenance requirement increased by a factor of 2.8 for the 8°C temperature increase. This result is similar to that obtained for the Peruvian anchoveta, Engraulis ringens (Villavicencio and Muck 1985). In which the authors found that the metabolic expenditures increased by a factor of 3 between 17°C and 27°C. The estimated maintenance ration for the anchoveta was 2.3% at 15°C and that of the sardine, Sardinops sagax, 3.1% at 20°C (Tsukayama and Sanchez 1981; Villavicencio and Muck 1983).

Several studies on fishes have recorded increased maintenance ration as temperature increases (Brett et al. 1969; Elliott 1975). Wurtsbaugh and Davis (1977) found that with a temperature increase from 6.9 to 22.5°C, the maintenance ration of rainbow trout, S. gairdneri increased markedly from 2.2 to 7.5% of the body weight per day. The authors pointed out that the increase is expected because standard metabolism increases rapidly as temperature rises, which may also explains the result in bay anchovy.

The increased maintenance ration at high temperature probably caused the reduction in gross growth efficiency of bay anchovy at the two lowest diet levels. Wurtsbaugh and Davis (1977) found that K_1 of rainbow trout fed on small rations decreased as temperature increased, while the efficiency of trout fed near satiation was not affected by increasing temperature. Several studies on sockeye salmon, Oncorhynchus nerka (Brett et al. 1969) and largemouth bass, Micropterus salmoides (Lee 1969) reported that at high ration levels growth efficiency increased with temperature, a result similar to that observed for bay anchovy. In contrast, two studies gave opposite results: for largemouth bass, K_1 decreased as temperature increased over the range of tested ration levels (Niimi and Beamish 1974), and for brown trout (Elliott 1975) temperature increases usually resulted in decreased gross growth efficiencies at all ration levels.

The estimated maintenance ration, based upon the weight-specific oxygen uptake was 7.3% at 27°C. The estimated ration consumed at 10% diet level, 27°C was 7.4%; however, the anchovies grew, on average, 1.17% daily. It is possible that the maintenance ration at 27°C was overestimated because it was calculated as the mean for the three diet levels at each temperature, under the assumption that metabolic demands were constant with increasing diet level. This assumption may be erroneous (Jobling 1981).

Estimates of maintenance rations are useful to study fish production. For example, during the summer, when Chesapeake Bay temperatures are >27°C there will be an increase in metabolic demands of bay anchovy such that the density of zooplankton available as prey might not be sufficient to allow the maintenance ration to be exceeded and thus to allow growth. Under such conditions all assimilated energy would be allocated to active metabolism and the fish would be starving, resulting in a decline in production of bay anchovy. Wurtsbaugh and Davis (1977) observed for rainbow trout that if food was available, growth could be enhanced by increasing temperature. But, when food of wild trout was limited, as indicated from estimates of food consumption, then a substantial temperature increase resulted in decreased growth. Similarly, bay anchovy production would be expected to increase only if temperature increases were accompanied by concomitant increases in the production of.zooplankton or if zooplankton densities were always high enough to not be a factor limiting anchovy growth.

SUMMARY

The energetics study has provided insight into the complex process of bay anchovy growth and metabolism under different temperature and feeding conditions. Temperatures ranged from 19-27°C and diet levels offered ranged from 10-40% of bay anchovy body weight. The ration of Artemia consumed by bay anchovy increased as temperature increased although the percentage of the diet offered that was consumed tended to decrease as diet level increased. Bay anchovy consumed from 6.8-28.0% of their body weight per day and grew from 0.75-4.49% per day on a weight-specific basis. Growth rates were affected by both temperature and diet level. Mean daily growth rates at 10% and 20% diet levels were highest at the lowest temperature (19°C). At the 40% diet level, growth was highest at the highest temperature (27°C).

Mean oxygen uptakes increased significantly as anchovy weight and temperature increased. However, the weight exponents of the oxygen uptake regressions did not differ significantly among temperatures, indicating that the increasing rates of oxygen uptake as weight increased were similar at each temperature.

The maximum gross growth efficiency (K_1) of 37-38% was obtained at the two extreme treatments; K_1 was highest at the lowest diet level and temperature (10%, 19°C) and at the highest diet level and temperature (40%, 27°C). Increased temperatures resulted in increased metabolic demands of the anchovies, decreasing the potential energy available for growth, at low diet levels. The opposite result was obtained at the highest ration (40%) where anchovy growth became more efficient as temperature increased.

Assimilation efficiencies of bay anchovy decreased as diet level increased at each temperature. Assimilation efficiencies exceeded 80% at the 10% diet level but declined at 20% and 40% diet levels to values well below the 80-90% range indicated by Brett and Groves (1979) for young carnivorous fish. Although assimilation efficiency declined as diet level increased, the anchovies grew at all diet levels, because increased consumption and increased net growth efficiencies (K_2) were observed at the high diet levels. The lowest assimilation efficiency was estimated at 40% diet level and 19°C.

At the 20% and 40% diet levels,The excretion component of the budgets (F+U) was higher than the 27±3% given by Brett and Groves (1979) indicating that such high diet levels could not be efficiently utilized by bay anchovy. At 19 and 23°C, ≥50% of the ration at the 20 and 40% offered diet levels, were excreted as feces and urine.

Comparing energetics parameters for bay anchovy in laboratory feeding experiments with the estimated food consumption in the natural habitat (Vazquez and Houde, Chapter 7) is a potentially useful approach to understand the relationship between anchovy population growth and zooplankton availability. The effects of temperature and variable food availability could be used to examine seasonal production potential of bay anchovy. Additional field, laboratory and bioenergetics modeling studies are needed to extend results of this study to the bay anchovy population in Chesapeake Bay.

CHAPTER 7. FOOD HABITS AND DAILY RATION OF BAY ANCHOVY *Anchoa mitchilli* IN CHESAPEAKE BAY

A.V. Vazquez and E.D. Houde

INTRODUCTION

Food consumption and rations of bay anchovy (*Anchoa mitchilli*) had not been estimated previously, although its foods and feeding habits in many coastal bays have been described. (Hildebrand and Schroeder 1928; Darnell 1958; Odum and Heald 1972; Homer and Boynton 1978; Matlock and Garcia 1983; Din and Gunter 1986). Results of these studies emphasized the ecological importance of bay anchovy as a major plankton consumer. The seasonal frequencies of food items in stomachs during day or night at two stations in the Chesapeake Bay was described by Homer and Boynton (1978). Din and Gunter (1986) described the diel feeding pattern of bay anchovy from Biloxi Bay, Mississippi. Observations of diel feeding rhythm to determine diurnal variations in stomach contents and to estimate daily ration for bay anchovy in the Chesapeake Bay or elsewhere are not available.

We determined the diurnal variations of weight-specific stomach contents and estimated the daily ration of bay anchovy. A common way to determine the diel pattern of feeding in fish is to observe daily stomach content variability over a 24-hr period (Darnell and Meierotto 1962; Swenson and Smith 1973; Eggers 1977). The amount of food in the stomach varies as a function of the rates of food ingestion and gastric evacuation (Eggers 1977). Instantaneous gastric evacuation rates, estimated in the laboratory, can be applied to field data on stomach contents in the daily ration determination (Elliott and Persson 1978; Houde and Berkeley 1982; Jobling 1986; Persson 1986; Olson and Mullen 1986; Yang and Livingston 1988; Smith *et al*. 1989).

The estimated daily rations can provide information on potential production of bay anchovies in different seasons when zooplankton availability may vary and when results of laboratory energetics studies on bay anchovy (Vazquez and Houde, Chapter 6) can be applied to understand bay anchovy growth and metabolism. Based on energetics studies and a knowledge of feeding rhythm and estimated rations in the Bay, the impact of the bay anchovy on the zooplankton community could be estimated if anchovy biomass data were available. Production and potential energy transfer from the pelagic fish to higher trophic levels also could be assessed.

METHODS

Stomach Content Analysis

Stomach contents of 192 bay anchovies were analyzed from two 24-hr series of otter trawl collections on 29-30 July 1986 and 30 June-1 July 1987 (Table 36). Fish were collected at a single station near the mouth of the Patuxent River over a water depth of 9 meters. Salinity during the 1986 collections ranged from 16.8-17.8 $^{o}/oo$ and in 1987 ranged from 13.8-14.2$^{o}/oo$. Temperature varied from 27.3-28.8^{o}C during the 1986 collections and from 24.7-25.6^{o}C during 1987 collections.

Table 36. Dates and time of the day that bay anchovy were collected for stomach content analysis. Mean and range in length, and number of stomachs analyzed.

COLLECTION DATE	TIME OF DAY	MEAN AND RANGE OF LENGTH (mm)	NUMBER OF STOMACHS EXAMINED
7-29-86	10:35	58 46-70	24
	17:00	58 46-70	20
7-30-86	00:01	55 40-70	26
	08:04	55.5 46-65	19
	14:51	57.5 45-70	19
6-30-87	11:58	57.5 45-70	10
	14:04	60 45-75	34
	20:52	55 40-70	18
7-1-87	03:48	53 46-60	9
	09:20	53 46-60	13
TOTAL			192

Immediately upon collection anchovies were fixed in 10% buffered formalin and transferred later to 95% ethanol in the laboratory. Fish were weighed to the nearest 0.01g; fork lengths were recorded to the nearest 1.0 mm.

In the laboratory fish were dissected, their digestive tracts and gonads removed and preserved in 10% buffered formalin and later transferred to 95% ethanol. Preserved stomachs were opened, their food contents removed and identified to major taxonomic groups. A plankton guide (Smith 1977) was used to identify organisms in the stomachs. Stomach content analysis was conducted to obtain weight-specific stomach contents by time of the day to estimate daily rations. Quantitative analysis of individual food items was not performed; however, the food items found and their frequency of occurrence in the stomachs during day or night samples were recorded. Percent of empty stomachs during day or night for each 24-hr series was estimated.

The stomach contents were placed in a weighing pan. Dry weights of each stomach's contents were obtained by drying in an oven at 60°C for 36-hr (Elliott 1975). The weighing pan and stomach contents were cooled in a desiccator. Stomach contents were weighed to the nearest 0.001 mg on a microbalance. Wet weights of whole anchovies were converted to dry weights using a dry-to-wet-weight conversion estimated in the laboratory (Vazquez, Harvey and Gooch, Chapter 8).

The mean weight-specific stomach contents (g/g) were calculated as:

Mean dry wt of stomach content/mean dry wt of anchovy

Dry weights of anchovy were obtained from the total wet weight before dissection and converted to dry weight using the wet to dry weight conversion for wild bay anchovy (Vazquez, Harvey and Gooch, Chapter 8).

Stomach contents by length class were analyzed to establish if there was a relationship between stomach content weight and length of bay anchovy. Power models of the stomach content weight in relation to length of anchovy were fit to obtain the regressions:

$$S = aL^b$$

where S = stomach content weight (g) and L = fork length (mm)

Evacuation Rate and Digestion Time - Laboratory Experiments

Stomach evacuation experiments were conducted at 3 temperatures (19, 23 and 27°C) to determine time of digestion. After a fasting period of 24-hr, anchovies were placed in a 250-l tank and fed to satiation on *Artemia* nauplii. The tank was drained, refilled and the flow rate increased to exchange the water and remove any unconsumed *Artemia*. Periodically, three anchovies were sacrificed, beginning 30 minutes after feeding stopped and subsequently every hour, to determine the duration of stomach evacuation. Some anchovies were sacrificed as long as 12-14 hr after feeding to determine total digestive tract evacuation time. The sacrificed anchovies were frozen immediately for later stomach content weight determination.

The anchovies were thawed, wet-weighed to the nearest 0.1 mg on an electronic analytical balance and dissected. Food contents were removed separately from the stomach and the intestine, and dried at 60°C for 24-hr then placed in a desiccator and later weighed to the nearest 0.001 mg on a microanalytical balance. The stomach evacuation rate was estimated using Elliott's (1972) equation,

$$S_t = S_o e^{-rt}$$

where S_t = remaining weight-specific stomach contents (g/g), S_o is an estimate of initial weight-specific stomach contents (g/g), t is time since feeding stopped (hr) and r is the weight-specific stomach evacuation rate (h^{r-1}).

Exponential models of the relationship between weight-specific stomach contents and hours since feeding were fit to the data. Based on these models stomach evacuation rates and times to 95% digestion were estimated for 19, 23 and 27°C.

Daily Rations Under Natural Conditions Estimations

Daily rations were calculated by applying Elliott and Persson's (1978) model. This model assumes that the rate of gastric evacuation (r) is exponential and temperature-dependent, and that the fish did not feed at the same rate throughout the day. Therefore, the amount of food consumed in t hours is given by:

$$C_t = (S_t - S_o e^{-rt})(rt)/(1-e^{-rt})$$

where C_t is consumption of food by a fish over a time interval t, S_t is the mean weight of food present in the stomach at the end of the interval, S_o is the mean weight of food in the stomach at the beginning of the interval and r is the instantaneous evacuation rate.

The daily rations were estimated for 19, 23 and 27°C by using the respective evacuation rates (r) obtained from the laboratory experiments. Rations were estimated for each 6-hr period during the day using their respective mean weight-specific stomach contents $\bar{S}$. The equation of Elliott and Persson (1978) was used to estimate the daily ration:

$$R = \sum_{t=1}^{4} C_t$$

where R is daily ration and the C_t correspond to the amounts of food consumed during each time period.

RESULTS

Stomach Content Analysis

Forty-seven of the 192 stomachs analyzed were empty (24.5%). Empty stomachs occurred most often during the night. For the 24-hr series in 1986, only 15 of the 82 stomachs examined during the day were empty (18.3%) while at night 12 of the 26 anchovies had empty stomachs (46.2%). In the 1987 24-hr series, 9 of 57 day-collected anchovies (15.8%) and 11 of 27 night-collected anchovies (40.7%) had empty stomachs.

The mean weight-specific stomach content ($\bar{S}$) of bay anchovy for the two-24-hr series ranged from 0.21 to 3.54% of the fish body weight (Table 37). The mean weight-specific stomach contents for both years over a 24-hr period was 2.1%. For the day-time samples $\bar{S}$ ranged from 1.61% (at 17:00) to 3.54% (at 09:20). During the night $\bar{S}$ varied from 0.21% (at 03:48) to 1.42% (at 20:52). Variability in stomach content weights was much higher during the day than at night (Table 37).

Mean weight-specific stomach contents for the 1986 samples were 2.0% and 0.53% for the day and night samples, respectively. For the 1987 samples, $\bar{S}$ averaged 2.0% and 0.82% for the day and night samples, respectively.

Twelve groups of mostly planktonic organisms were eaten by bay anchovy (Table 38). The percent frequencies of occurrence of stomachs with food items was consistent between years (Table 38).

Copepods were the predominant food item found in the anchovies. Copepods were present in 92% of the stomachs analyzed (Table 38). Stomachs with no copepods were found mostly at night (00:01 and 03:48 samples). Copepods were present in all except one stomach analyzed during the day and they occurred in 67% of the stomachs examined at night.

The food items present in >75% of the stomachs of both series were copepods, tintinnids, detritus and diatoms. Tintinnids and diatoms were found in a higher proportion of stomachs collected during the day than at night. Diatoms, for example, were present in 93% of the daytime stomachs but only 37% of the nighttime samples.

Cladocerans, bivalves and ostracods were present in >30% but <60% of the stomachs analyzed for both years. Cladocerans and ostracods were found in both day and night samples in both years. Bivalves were found only in daytime samples. Polychaetes, which occurred in 15 to 23% of the total stomachs, were found only at night when they were present in 90% of the stomachs examined (Table 39). A single barnacle nauplius was found at 17:00, and another at midnight in 1986. One crab zoea was found at noon in 1987. The only amphipod was found at midnight in 1986 and the single mysid was present at 14:04 in 1987.

Parasites (trematodes) were found in 37 of the 192 stomachs (19.3%); 23 of these stomachs were from the 1986 collection. In those stomachs in which trematodes were found, they represented, together with copepods and tintinnids, the most abundant items. The weights of the trematodes were included with the weights of food in calculating weight-specific stomach contents. Thus, their presence led to a bias and overestimate of mean stomach contents.

Stomach Content Weight in Relation to Size of Fish

The power function models of stomach content weight in relation to length of bay anchovy indicated a strong positive correlation between the length of the fish and the amount of food in its stomach at each time of day (Figure 48).

Table 37. Mean weight-specific stomach content ($\bar{S}$) at each time of the day. Each mean value represents approximately 30 anchovies (five fish from each of 6 length-class subdivisions).

HOUR	MEAN WEIGHT-SPECIFIC STOMACH CONTENT	STANDARD ERROR	C.V.
00:01	0.0053	0.0008	15.4
03:48	0.0021	0.0005	24.8
08:04	0.0353	0.0144	54.1
09:20	0.0354	0.0092	40.2
10:35	0.0318	0.0161	62.9
11:58	0.0301	0.0101	59.8
14:04	0.0209	0.0081	43.1
14:51	0.0213	0.0095	46.9
17:00	0.0161	0.0050	37.5
20:52	0.0142	0.0050	35.2

Table 38. Frequency of occurrence (%) of stomachs with food items for bay anchovy in 1986 and 1987. $\bar{X}$ = the mean frequency of occurrence for both years. Empty stomachs were excluded.

FOOD ITEM	1986 (n=81)	1987 (n=64)	$\bar{X}$ (n=145)
COPEPODA	92.6	92.2	92.4
PROTOZOA (Tintinnids)	90.1	85.9	88.3
DIATOMS	85.2	76.6	81.4
DETRITUS	82.7	76.6	80.0
CLADOCERA	46.9	59.4	52.4
BIVALVIA (Clams)	35.8	34.4	35.2
OSTRACODA	43.2	42.2	42.6
POLYCHAETA	14.8	23.4	18.6
CIRRIPEDIA (nauplii)	2.47	0.00	1.38
BRACHYURA (zoeae)	0.00	1.56	1.38
AMPHIPODA	1.23	0.00	1.38
MYSIDACEA	0.00	1.56	1.38

Table 39. Frequency of occurrence (%) of stomachs with major food items of bay anchovy in day and night samples during 1986 and 1987, excluding empty stomachs. The frequencies are based on the total number of stomachs with food (n=145). $\bar{X}$ = 1986 and 1987 day or night samples combined.

	DAY			NIGHT		
FOOD ITEM	1986 (n=67)	1987 (n=48)	$\bar{X}$ (n=115)	1986 (n=14)	1987 (n=16)	$\bar{X}$ (n=30)
COPEPODA	98.5	100	99.1	64.3	68.8	66.7
PROTOZOA (Tintinnids)	91.0	87.5	89.6	85.7	81.2	83.3
DIATOMS	95.5	89.6	93.0	35.7	37.5	36.7
DETRITUS	82.1	79.2	80.9	85.7	68.8	76.7
CLADOCERA	46.3	62.5	53.0	50.0	50.0	50.0
OSTRACODA	41.8	43.8	42.6	50.0	37.5	43.3
BIVALVIA (Clams)	43.3	45.8	44.3	0.0	0.0	0.0
POLYCHAETA	0.0	0.0	0.0	85.7	93.8	90.0
CIRRIPEDIA (nauplii)	1.49	0.0	0.87	7.14	0.0	3.33
BRACHYURA (zoeae)	0.0	2.08	0.87	0.0	0.0	0.0
AMPHIPODA	0.0	0.0	0.0	7.14	0.0	3.33
MYSIDACEA	0.0	2.08	0.87	0.0	0.0	0.0

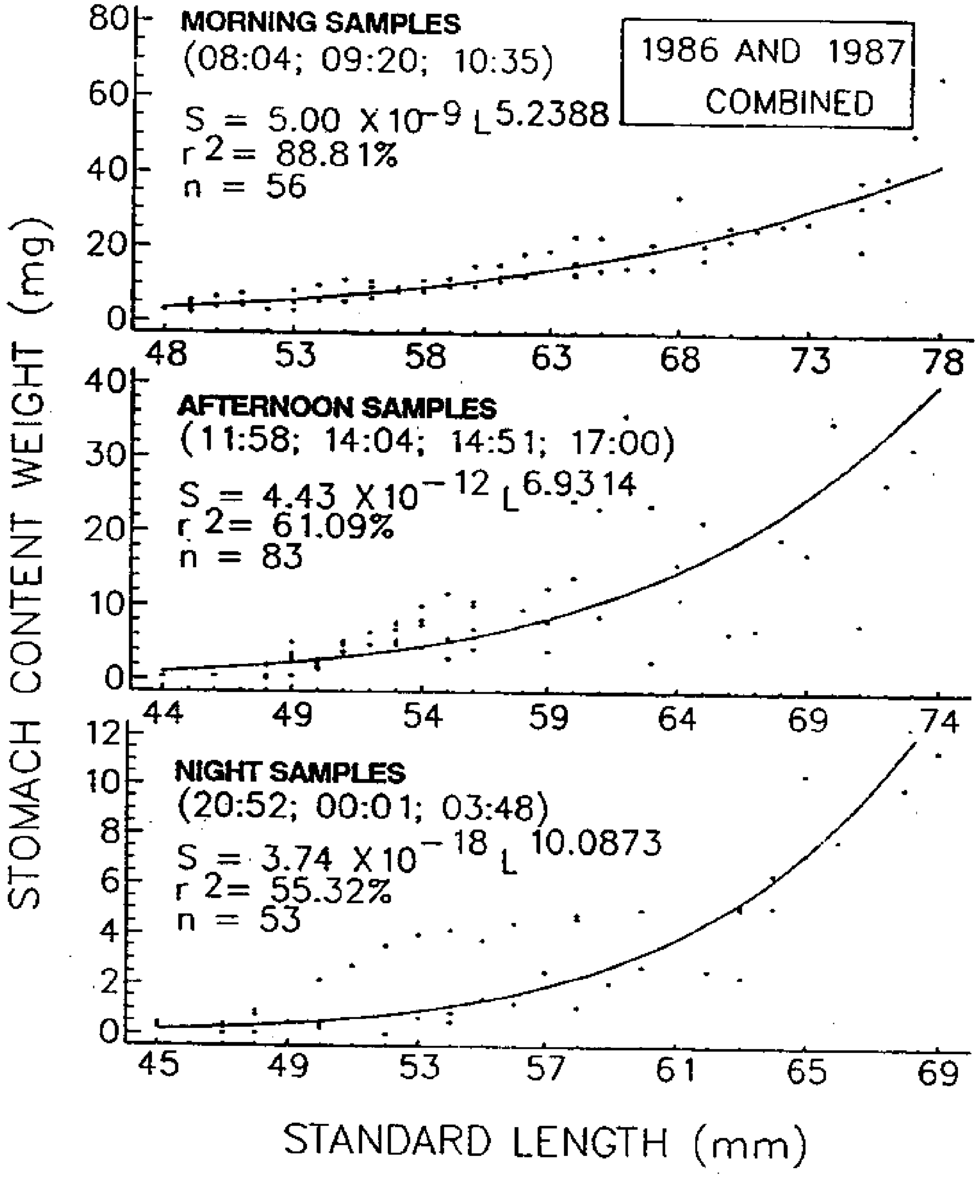


Figure 48. Power functions of weights of stomach content regressed on lengths of bay anchovy collected during a 24-h series on July 29-30 1986 and June 30-July 1 1987. Weights of stomach contents were grouped by morning, afternoon and night hours. Y-axis scale changes among the three panels.

The exponents were significantly different among the three regressions (ANCOVA; $P<0.0001$). Stomach contents of anchovy of each length were higher during morning and afternoon samples than at night. From these regressions S at each time of day for bay anchovy of 45-75 mm length could be predicted.

Feeding Rhythm

The feeding rhythm patterns, illustrated by weights of stomach contents, observed for the two 24-hr series in 1986 and 1987, indicated that in both years the major feeding activity occurred in early to mid-morning (Figure 49). Stomach content maxima were observed from 08:04 to 10:35. Minimum stomach contents in both years were observed from early evening until predawn hours. Because the amounts of weight-specific stomach contents and the feeding patterns were similar in both years, data were pooled to better illustrate the diurnal variations in the weight of the stomach contents (Table 37; Figure 50).

Stomach content weights were most variable when mean stomach content weights were highest (Table 37, Figures 49 and 50). Variability of stomach contents among individuals decreased considerably during the night samples, especially at 0001 and 0348. Analysis of variance indicated that the only statistically significant difference among daytime samples was between the 09:20 and the 17:00 sample ($P<0.05$). The weight-specific stomach contents at 00:01 and 03:48 were significantly lower than all other mean stomach content weights during the 24-hr period ($P<0.01$). In addition, the mean weight-specific stomach content at 20:52 was significantly different from those at 08:04, 09:20 and 11:58 but not from that of the highly variable 10:35 sample.

Evacuation Experiments

Digestion was approximately 95% completed in 2.26, 1.33 and 1.20 hr for the 19, 23 and 27°C experiments, respectively (Figure 51).

The exponential regressions of weight-specific stomach contents on time in hours are:

19°C experiment $S_t=0.0245e^{-1.3235t}$
n=30 $r^2=93.81\%$
(S_b = 0.0850)

23°C experiment $S_t=0.0534e^{-2.2605t}$
n=36 $r^2=90.05\%$
(S_b = 0.1878)

27°C experiment $S_t=0.0333e^{-2.5046t}$
n=36 $r^2=90.81\%$
(S_b = 0.2210)

The instantaneous evacuation rates (r) are the exponents in these regressions. The stomach evacuation rates differed significantly, increasing as temperature increased (ANCOVA; $P<0.0001$). The Y-axis intercepts at the three temperatures did not differ significantly (ANCOVA; $P>0.50$).

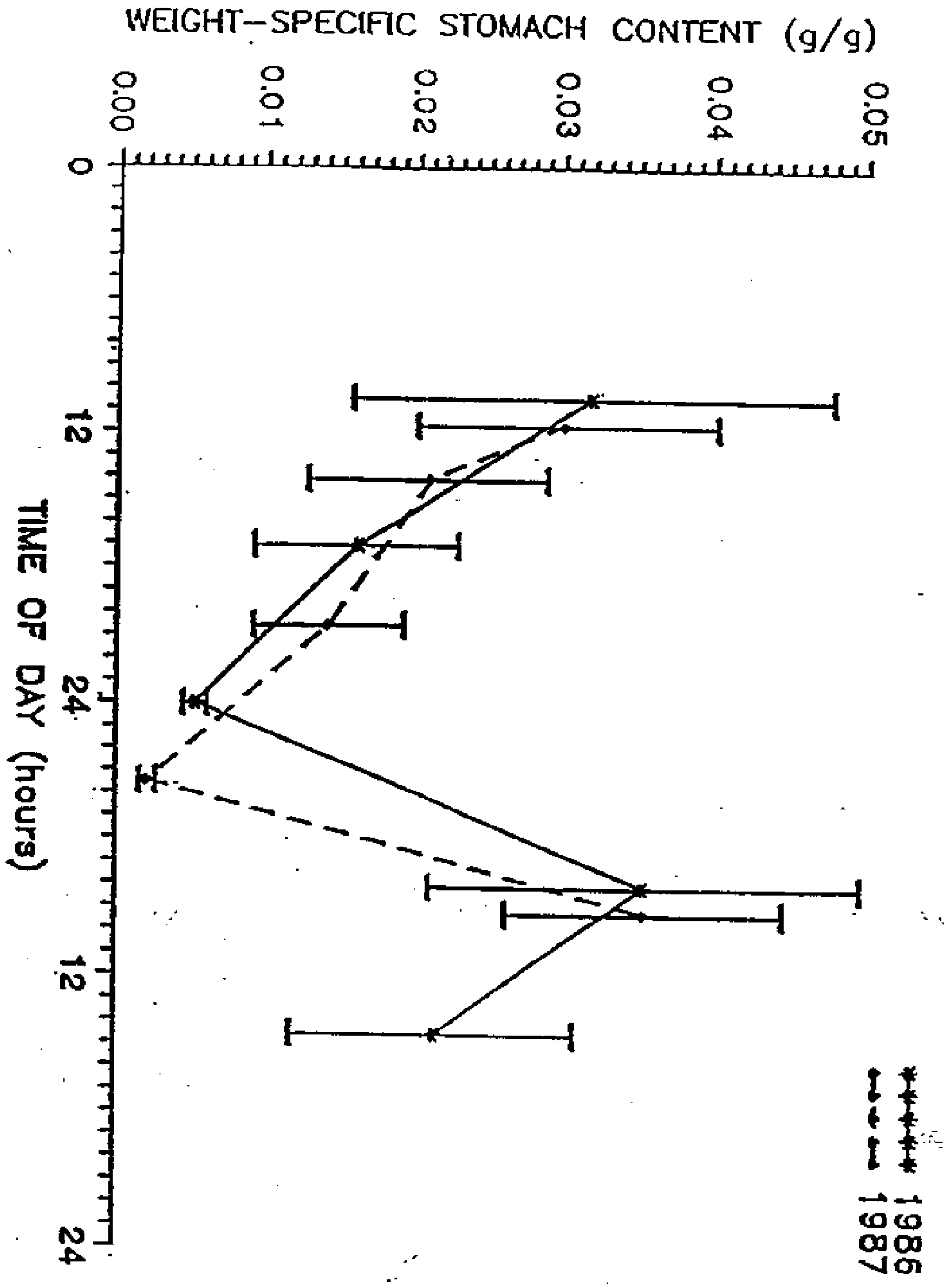


Figure 49. Feeding periodicity of bay anchovy. Diurnal variations in weight-specific stomach contents for a 24-h series in 1986 and 1987. (mean ± S.E.).

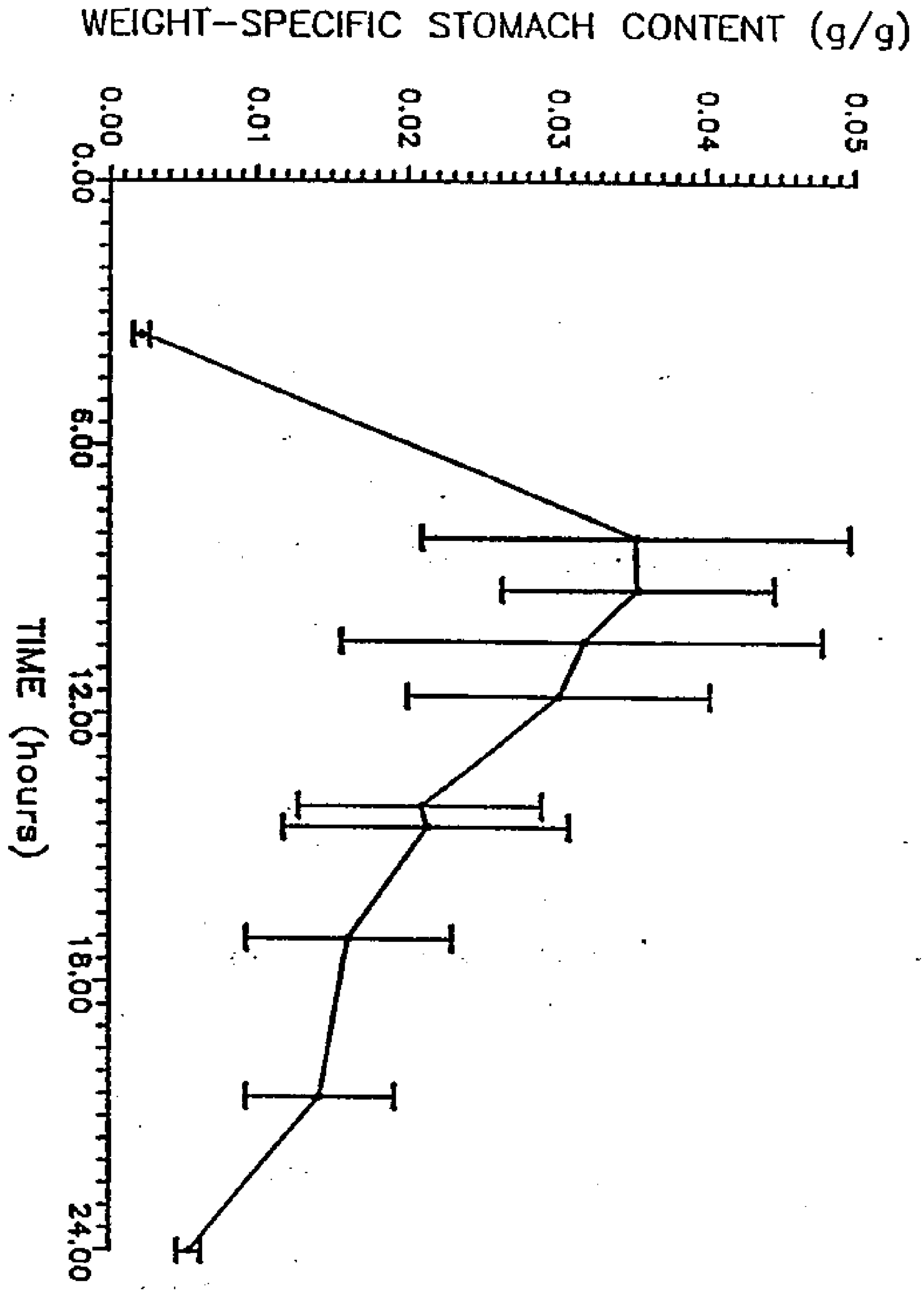


Figure 50. Feeding periodicity of bay anchovy. Diurnal variations in weight-specific stomach content from a 24-h series in 1986 and 1987.

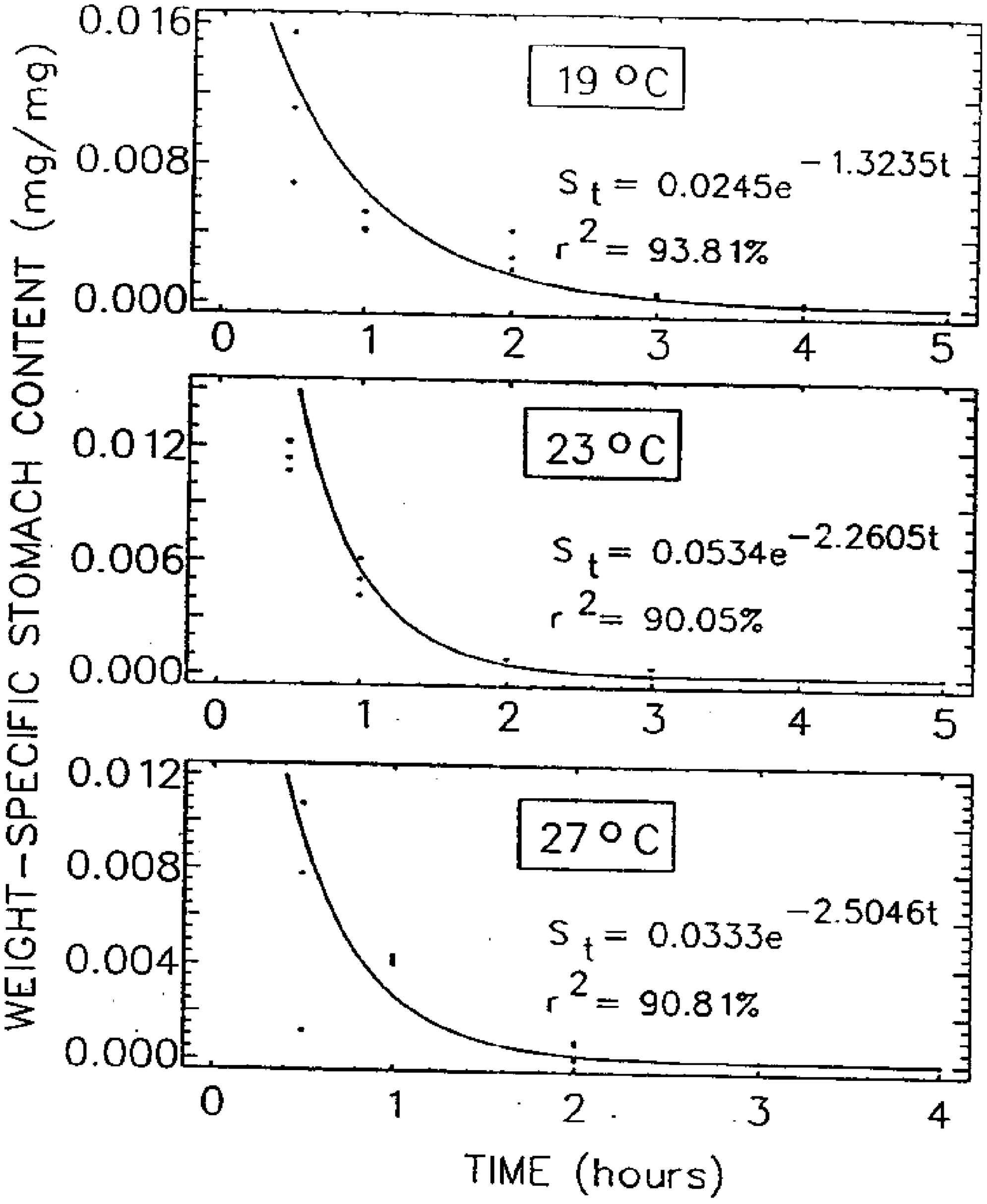


Figure 51. Relationships between weight-specific stomach contents and hours after bay anchovy were fed *Artemia* nauplii. Stomach evacuation rates and digestion time were estimated from these regressions.

Daily Rations

The estimated daily rations for bay anchovy of 40 to 76 mm FL were 9.0%, 13.1% and 16.2% of the fish body weight at 19°C, 23°C and 27°C, respectively. Daily consumption at 27°C was estimated to be 1.8 times more than that at 19°C (Table 40). Bay anchovy consumed 10-20% of their body weight daily under the feeding conditions observed in June-July 1986 and 1987.

DISCUSSION

Stomach Contents and Feeding Periodicity

Bay anchovy stomachs contained the most food between 0800 and 1030 with a peak around 0920 for both the 1986 and 1987 24-hr series. The major feeding activity must have occurred prior to the hours when maximum stomach content was observed. Peak feeding activity probably took place from 0600 to 0900, during the first hours of daylight. Another indication that considerable feeding took place before 0800-0900 was the observation of mostly digested matter around 1000 in the majority of stomachs examined. Most empty stomachs were found at night, when 43.4% contained no food. This result was similar to that of Homer and Boynton (1978) who found that 46.3% of night-collected bay anchovy from the Chesapeake Bay had empty stomachs.

The mean weight-specific stomach contents during the day was approximately three times higher than the mean during the night. Similar results were found for other species of anchovies (Darnell 1958; Laukashkin 1965) and sardines (Muzinic 1960). Because feeding occurs more during the day, it has been suggested that vision is involved. However, Homer and Boynton (1978) did report night feeding by bay anchovy in Chesapeake Bay and Din and Gunter (1986) found a minor peak of feeding activity by bay anchovy after midnight in Biloxi Bay. The weight of stomach contents during the night and the feeding periodicity pattern of bay anchovy indicated that relatively little feeding activity occurs at night. Nevertheless, some stomachs from night samples did contain undigested food items, good evidence that night feeding occurred. It may be that night feeding increases when skies are clear or when moonlight allows it. This hypothesis is supported by reports that anchovy vision is involved in locating food (Darnell 1958; Muzinic 1960). Future studies should consider the effects of lunar cycles and prevailing weather conditions on feeding behavior and, more importantly, the daily ration of bay anchovy.

Crustaceans, especially copepods, were the most abundant food items found in the stomachs of bay anchovy. Copepods have been reported previously as the most important food of bay anchovy in the Chesapeake Bay (Hildebrand and Schroeder 1928; Homer and Boynton 1978), in Delaware Bay (Stevenson 1958; PSEG 1984), in Louisiana, (Darnell 1958), in Florida, (Carr and Adams 1973) and in Biloxi Bay, Mississippi (Din and Gunter 1986). However, the abundance of copepods in stomachs was reduced when other food items such as tintinnids were present in high abundances. It was suggested by Din and Gunter (1986) that the rate of feeding on specific organisms may depend mainly on the density of that organism in the anchovy's environment.

No attempt was made to study the relationship of food item size to size of anchovy but it was observed that larger and more diverse food items were

Table 40. Mean weight-specific stomach contents ($\bar{S}$), estimated ration per time interval (C_t) and daily ration $\Sigma(C_t)$=R at 19, 23, and 27°C. Stomach contents and rations are expressed on a dry weight basis.

		WEIGHT-SPECIFIC STOMACH CONTENTS (g/g)		
TIME PERIOD	$\bar{S}$	C_t 19°C	C_t 23°C	C_t 27°C
00:00-06:00	0.0037	0.0051	0.0047	0.0027
06:00-12:00	0.0332	0.0481	0.0696	0.0830
12:00-18:00	0.0194	0.0233	0.0349	0.0455
18:00-24:00	0.0142	0.0139	0.0218	0.0313
ΣC_t =R		0.0902	0.1310	0.1625

found more frequently in bigger anchovies. Th . relationship has been well documented for bay anchovy (Hildebrand and Schroeder 1928; Stevenson 1958; Carr and Adams 1973; Homer and Boynton 1978) and for the northern anchovy (Leong and O'Connell 1965). For bay anchovy the authors pointed out that copepods and clam larvae (Carr and Adams 1973) were the major prey found in young anchovies (40-55 mm), and that there was a gradual change in diet with growth to include larger prey items (Stevenson 1958; Carr and Adams 1973). In addition, Homer and Boynton (1978) reported an increase in the polychaete Nereis in larger anchovies.

Bottom feeding, based on the presence in guts of benthic organisms, has been reported for bay anchovy (Homer and Boynton 1978; Din and Gunter 1986). The presence in stomachs of benthic or suprabenthic organisms such as polychaetes, amphipods and mysids in the present study support these findings, although all of these organisms could have been eaten while in the water column.

Sand and very small unidentified particles were classified as detritus. Most bay anchovy had detritus in their stomachs (Tables 38 and 39). Homer and Boynton (1978) reported a similar result. Detritus may be an important component in the diet of planktivorous fishes, including Atlantic menhaden, Brevoortia tyrannus, and gulf menhaden, Brevoortia patronus (Darnell 1958, 1964; Jeffries 1975; Peters and Schaaf 1981). In North Carolina estuaries, detritus constituted 70% of the diet of juvenile menhaden (Peters and Kjelson 1975). Detritus represented a potentially important energy source for the menhaden (Peters and Schaaf 1981), which also could be true for bay anchovy. The relatively high frequency of detritus of unknown nutritional quality, which was found in the stomachs of most bay anchovy, should be considered if laboratory energetics studies are used to predict energy budgets of bay anchovy under natural conditions. Although assimilation and growth efficiencies of organisms fed on detritus have been reported to be lower than for organisms fed on living foods, Raymont (1983) and Peters and Schaaf (1981) considered detritus to be a major potential food source in estuaries because of its abundance and apparent nutritional value.

The trematodes in stomachs were weighed as part of the stomach contents. These parasites did not represent food. Therefore, in the 37 stomachs (19.3%) that contained trematodes, the weight-specific stomach contents were overestimated which led to a subsequent error in calculation of daily ration. The errors are unevaluated and hard to avoid because it was difficult to extract trematodes without removing food items or digested matter. Nevertheless, better estimates of stomach contents and rations could be obtained if the weights and frequencies of trematodes were determined and substracted from total stomach contents. Because less than 20% of bay anchovy in this study had trematodes in the stomach, it is presumed that the stomach content and ration estimate errors are small and relatively unimportant.

Cannibalism is another feeding behavior that has been reported for bay anchovy (Hildebrand and Schroeder 1928; Stevenson 1958) although it was not observed in the present study. Din and Gunter (1986) found juvenile bay anchovies in the diet of adults, sometimes representing the most important food item by biomass. Based on their observations, they considered that cannibalistic feeding behavior is practiced when other food organisms are limited.

Cannibalism on eggs has been reported for the northern anchovy, Engraulis mordax (Hunter and Kimbell 1980), for the South African anchovy, Engraulis capensis (Valdes et al. 1987) and for the Peruvian anchoveta, Engraulis ringens (Alheit 1987). Cannibalism by late-stage larvae on eggs and newly-hatched larvae of the cape anchovy, Engraulis capensis was observed under laboratory conditions (Brownell 1985). Cannibalism by cape anchovy was reduced when copepods were added as alternative prey. Although not observed in the present study, cannibalism by bay anchovy probably occurs at times in the Chesapeake Bay and its importance should be evaluated.

Stomach Content Weight Related to Size of Anchovy

There is a clear relationship between weight of stomach contents and length of anchovy that varies by time of day (Figure 48). From the equations in Figure 48 the stomach contents expected to occur in anchovy of specified lengths and at specific times of the day can be estimated. For example, predicted stomach contents for 40, 50, 60 and 70 mm anchovy were calculated (Table 41). The predicted values give estimates of stomach content weights that are close to those that were observed. The predicted values could be used as estimates of mean stomach content weights and the method of Elliott and Persson (1978) applied to calculate daily ration for anchovy length-classes. If the length-frequency distributions and abundances of bay anchovy in Chesapeake Bay were known, consumption by the anchovy population could be estimated. The applicability of such a procedure would depend upon the assumptions that mean stomach contents did not differ significantly as a function of temperature or prey availability. There was no indication that the approximate 3°C difference in water temperature between the 1986 and 1987 series affected the mean stomach contents illustrated in Figure 48. Possible differences in plankton availability during the 1986 and 1987 24-hr series are not known but there were no obvious differences in observed stomach contents between the two years.

Daily Rations

The relationship between temperature and rate of stomach evacuation has been determined for many fish species (Elliott 1972; Durbin and Durbin 1983; Persson 1986; Olson and Mullen 1986; Jobling 1986 1987; Smith et al. 1989). As expected, gastric evacuation rates of bay anchovy increased significantly as temperature increased. Controversy exists regarding whether meal size has an effect on the gastric evacuation rate in fishes, but Elliott (1972) has shown that there was little or no effect on gastric evacuation rate as meal size increased in brown trout, Salmo trutta. In contrast, Flowerdew and Grove (1979) studied the effects of body weight and meal size on gastric evacuation rates in turbot, Scophthalmus maximus, and concluded that large fish emptied a meal of a given size from the stomach at a faster rate than did small fish, and that large meals were processed at a faster rate than small meals. Daan (1973) found that the ration (as percent body weight) decreased with increasing fish size for Atlantic cod, Gadus morhua, concluding that small cod generally consumed proportionately more food per unit of weight. In the present study, there was variability in remaining stomach contents among the three anchovies that were periodically sacrificed. In most cases the lowest amounts of food remaining were in the bigger anchovies, suggesting that stomach evacuation may have been faster in the bigger fish.

Table 41. Predicted dry weights (mg) of stomach contents of bay anchovy at four lengths at specific times of the day. Estimates are from the power function equations in Figure 48.

TIME	STANDARD LENGTH (mm)			
	40	50	60	70
08:00 10:30	1.23	3.98	10.34	23.18
12:00 17:00	0.56	2.65	9.36	27.26
20:52 04:00	0.054	0.51	3.23	15.32

Comparisons of daily rations under natural conditions and energetics parameters of bay anchovy in the laboratory have a potential application to understand relationships between anchovy growth and zooplankton abundance. Further analysis of bay anchovy consumption during different seasons, when changes in temperature and plankton biomass occur, will be useful to determine the annual consumption and potential production of bay anchovy in the Chesapeake Bay. It is possible to estimate the number of copepods consumed by an individual anchovy in one day based upon the daily ration estimates obtained in this study. For example, at 27°C the estimated ration of a 0.35 g dry weight anchovy (mean weight of anchovies examined) was 16.2% of its body weight per day (Table 40), a consumption of 0.057 g dry weight. A 0.35 g dry weight (=1.18 g wet weight) anchovy would consume approximately 6,450 copepods each of dry weight 8.8×10^{-6} g (mean dry wt of an Acartia sp. copepod, Raymont 1983) per day if copepods were the only diet item.

An estimate of the impact of bay anchovy on the zooplankton community can be made by examining the relative abundance of major food items and applying the energetics requirements of bay anchovy in the Chesapeake Bay. Variations in mean daily rations with season will depend upon the anchovy population size-structure, the temperature and perhaps zooplankton density. For example, Spanovskaya and Grygorash (1977) reported that young Perca fluviatilis consumed from 7-28% of their body weight per day. They attributed the differences in ration to variation in zooplankton abundance. Results of the bay anchovy study reported here indicated that large differences in estimated consumption may be attributable to temperature effects. Estimated ration of bay anchovy at 19°C was only 56% of that estimated at 27°C (Table 40).

Future studies on the consumption of food and production of bay anchovy in relation to fluctuating temperature and food availability should be considered. The laboratory (Vazquez and Houde, Chapter 6) and field approaches reported here have provided the foundation for future research on population-level energetics studies of bay anchovy in the Chesapeake Bay.

CHAPTER 8. CHEMICAL COMPOSITION OF BAY ANCHOVY (*Anchoa mitchilli*)

A.V. Vazquez, H.R. Harvey and J.W. Gooch

INTRODUCTION

The main constituents of fish body composition are water, protein, lipid and ash. Carbohydrates are present but occur in such small amounts that they are usually ignored in fish energetics studies (Cui and Wootton 1988b). In addition, fish utilize dietary carbohydrate poorly due to their low capacity to metabolize ingested carbohydrate (Brett and Groves 1979).

Some fish energetics studies assume that the relative energy content of the fish body is constant. However, laboratory studies conducted with channel catfish (*Ictalurus punctatus*), brown trout (*Salmo trutta*) and minnow (*Phoxinus phoxinus*) on the effect of ration and temperature on the body composition and energy content have demonstrated that both the proportion of the constituents and the energy content change with environmental conditions (Andrews and Stickney 1972; Elliott 1976; Cui and Wootton 1988b). When conducting fish energetics studies, it is important to determine how the proportion of each constituent of the fish body varies to estimate the amount of energy that may be available for growth under different feeding regimes and temperatures.

In this chapter the effects of offered diets (from 10% to 40% of the fish body weight) and temperature (19°-27°C) on the body composition and indices of condition of the bay anchovy are presented. Chemical composition and condition indices are used as indicators of the effect of environmental factors on fish nutritional status.

The second part of the chapter presents a detailed analysis of the fatty acid composition of the bay anchovy under various feeding and temperature conditions. Fatty acid composition frequently is used in fish nutrition studies as an indicator of the nutritional status (Watanabe 1982; Fraser and Sargent 1987; Fraser *et al*. 1988; Anderson and Arthington 1989). Fish require lipids as a source of both metabolic energy and to maintain the structure and integrity of cellular membranes (Cowey and Sargent 1979). The amount of fatty acids in fish oils varies widely with species, age, sex, and temperature and can be influenced greatly by diet (Lee and Sinnhuber 1972).

METHODS

Moisture and Ash Determination

Moisture and ash analyses were performed on 10 anchovies from each of nine feeding experiments (see Vazquez and Houde, Chapter 6). For each experiment five anchovies were frozen before and five after ending an experiment. Another 55 anchovies from field collections or from the holding tank also were analyzed.

For the moisture analysis, the frozen anchovies were thawed, and length and wet weight measurements (to the nearest 0.1 mg) taken. The fish then were dried in an oven at 60°C for 48-hr. Fish were removed from the oven, cooled in a desiccator, and dry weight measurements made. The moisture content was estimated by the difference of wet and dry weights. The percent moisture was calculated based upon the wet weight of the fish.

Following moisture analysis, the same anchovies were used for ash content determination. Each anchovy was placed in a dry, tared, porcelain crucible and combusted in a temperature-controlled muffle furnace (Thermolyne type 30400) at 550°C for 18-hr. After cooling, the crucibles were placed in a desiccator at room temperature and later weighed. Ash percent was calculated based upon dry weight of the fish.

Protein Determination

Two anchovies before and two after each feeding experiment were frozen and subsequently analyzed to determine the protein content. Frozen fish were thawed, weighed and dried at 60°C for 48-hr. Dry weight measurements were recorded after fish were cooled in a desiccator. Two dry anchovies from each treatment were finely ground with a mortar and pestle, dried again at 60°C overnight, and cooled in a desiccator. Duplicate samples for each treatment were weighed and carbon, nitrogen and hydrogen analysis performed using an elemental analyzer (Control Equipment model 240XA) with a high temperature combuster and a thermocouple.

To obtain protein percent, the Kjeldahl method was used; the percent nitrogen from the CHN analysis was multiplied by 6.25 (AOAC, 1975).

Fatty Acid Content and Composition Analysis

Three frozen anchovies from the beginning and three from the end of each feeding experiment were used for fatty acid analysis. Fish were weighed, cut in small pieces, and transferred into glass tubes with teflon caps.

For the extraction and methylation of fatty acids, the method described by Barnung and Grahl-Nielsen (1987) was applied. Fish were methanolyzed with 5 ml of 2N anhydrous methanolic HCl for a minimum of 15-hr at 100°C. After cooling, 1 ml of distilled water was added and the fatty acid methyl esters were extracted 5-7 times into hexane. The extracts were dried at 40°C by rotary evaporation. The residue was diluted in 8.85 ml of CH_2Cl_2 per gram of fish and one ml of each dilution was transferred into special gas chromatography glass ampoules and sealed. For larger anchovies, further dilutions (2X, 3X or 4X) were required.

Fatty acids were analyzed by capillary gas chromatography. The fatty acids were separated on a 25m x 0.3 mm DB-5 fused silica capillary column (J+W Scientific) with a stationary phase of 5% phenyl, 95% methyl silicone of 0.33 um thickness. The oven was programmed from 110°C to 280°C at a rate of 4°C/min. Flame ionization detector (FID) temperature was set at 325°C and injector at 250°C. H_2 was used as a carrier gas.

Peak integration and quantification was done using a dedicated data system (Waters-Maxima) with internal and external standards. Calculations of peak areas were based on injection of the 19:0 fatty acid methyl ester (FAME) as standard.

Structural identification of FAMES was performed on a HP 5985 GC-MS system using similar conditions as for GC with He as carrier gas. Electron impact mass spectra (70 eV, 0.5 scan/sec) were acquired and processed using an HP dedicated data system. Molecular identification of all components was made on the basis of co-injection with authentic standards and comparison with reference and/or literature spectra.

Total fatty acid content was calculated from the peak areas using the internal standard to determine the area in ng. The amount of total fatty acid then was estimated by multiplying the converted peak areas by the volumes in the previous dilutions. The mg of fatty acid per mg of anchovy were then determined.

The mean coefficient of condition (K) was calculated for the anchovies prior to and after a feeding experiment by the formula (Lagler 1956):

$$K = 10^5 W/L^3,$$

where, W = wet weight (g), and L = total length (mm).

The effects of temperature and ration level on the body composition of the anchovies were analyzed by a multifactor analysis of variance. ANOVAs were conducted for moisture, ash, and protein percentages. Total lipid content was estimated by difference. Arcsine transformations (Sokal and Rohlf 1987) of percentile data for the different fatty acid groups was performed. Multiple range tests by the Scheffe method (Lehmann 1986) were used to compare means.

RESULTS

Body Composition of Bay Anchovy

Overall ranges of body composition of wild and laboratory reared anchovies were: moisture, 70.0-77.4%; ash, 9.4-14.5%; protein, 56.1-75.3% and lipid, 11.2-33.7%. Mean values of moisture, ash, protein and lipid percentages at each diet level and temperature are listed in Table 42.

Effect of Temperature

The effect of temperature on the proximate composition of bay anchovy was variable for the different components. At the lowest temperature (19°C), the percentages of moisture and ash were lower at any of the diet levels than at 23 or 27°C ($P<0.05$) (Table 42 and Figure 52). No significant difference in percent ash or moisture was found between the 23 and the 27°C experiments ($P>0.05$). No significant difference in the percent of protein was detected among the three temperatures at any of the ration levels.

Multifactor analysis of variance of total fatty acid content indicated that temperature had no significant effect on the amount of total fatty acid ($P>0.05$) (Figure 53). However, analysis by diet level demonstrated that at the 10% diet level the lowest amount of fatty acid (corresponding to the low total amount of lipid in this sample) was found at the highest temperature

Table 42. Chemical composition of bay anchovy in relation to diet level offered (% body weight) and temperature. Each component is shown as percentage of dry weight (mean±S.D.)

TEMPERATURE (°C)	DIET LEVEL (% b.w)	MOISTURE (% d.w) n=60	ASH (% d.w) n=60	PROTEIN (% d.w) n=24	LIPID (Estimated)
19	Start	71.6±0.4b	14.3±0.2a	71.2	14.5
	10	72.1±1.7b	10.8±0.3b	68.4	20.7
	20	70.0±0.6c	9.7±0.2b	62.7	27.6
	40	70.2±0.5bc	9.4±0.2b	58.3	32.2
23	Start	73.4±0.8ab	13.5±0.1a	75.3	11.2
	10	77.4±0.4a	14.4±0.5a	66.6	19.0
	20	73.9±0.9ab	12.9±1.0a	68.1	19.0
	40	71.0±0.8b	10.2±0.4b	57.9	32.0
27	Start	75.1±0.6a	13.8±1.1a	72.2	14.0
	10	76.2±1.2a	14.5±0.9a	73.1	12.4
	20	74.1±0.9a	12.9±0.8a	66.7	20.4
	40	71.3±0.3b	10.3±0.4b	56.1	33.7

Letters after each value indicate results of Scheffe's test after multifactor analysis of variance. Means with same letter are not significantly different from each other at the P=0.05 level. Protein percentage represents the mean of two replicates.

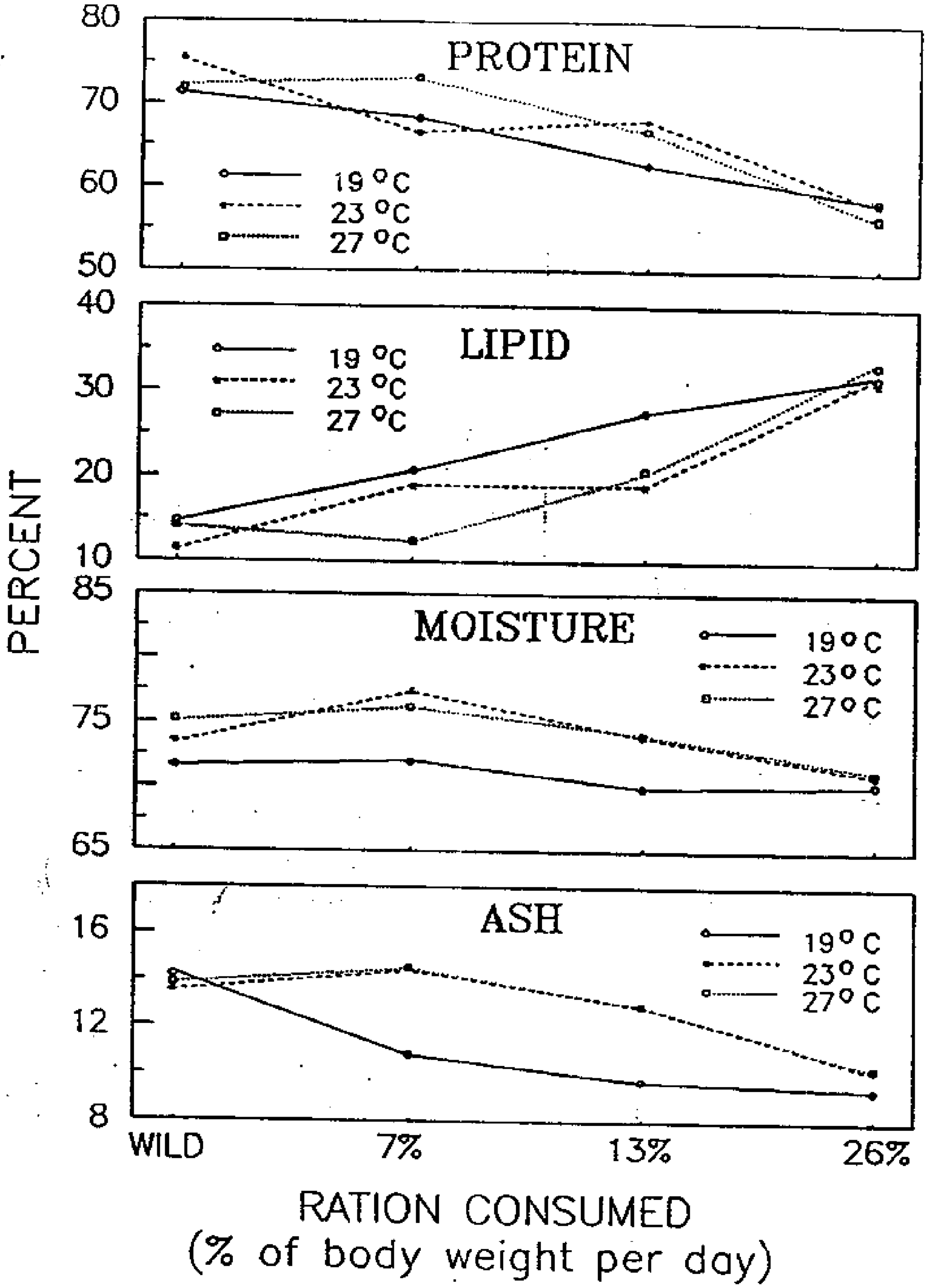


Figure 52. Percentage of protein, lipid, moisture and ash in <u>Anchoa mitchilli</u> with increasing ration level for the three temperatures tested.

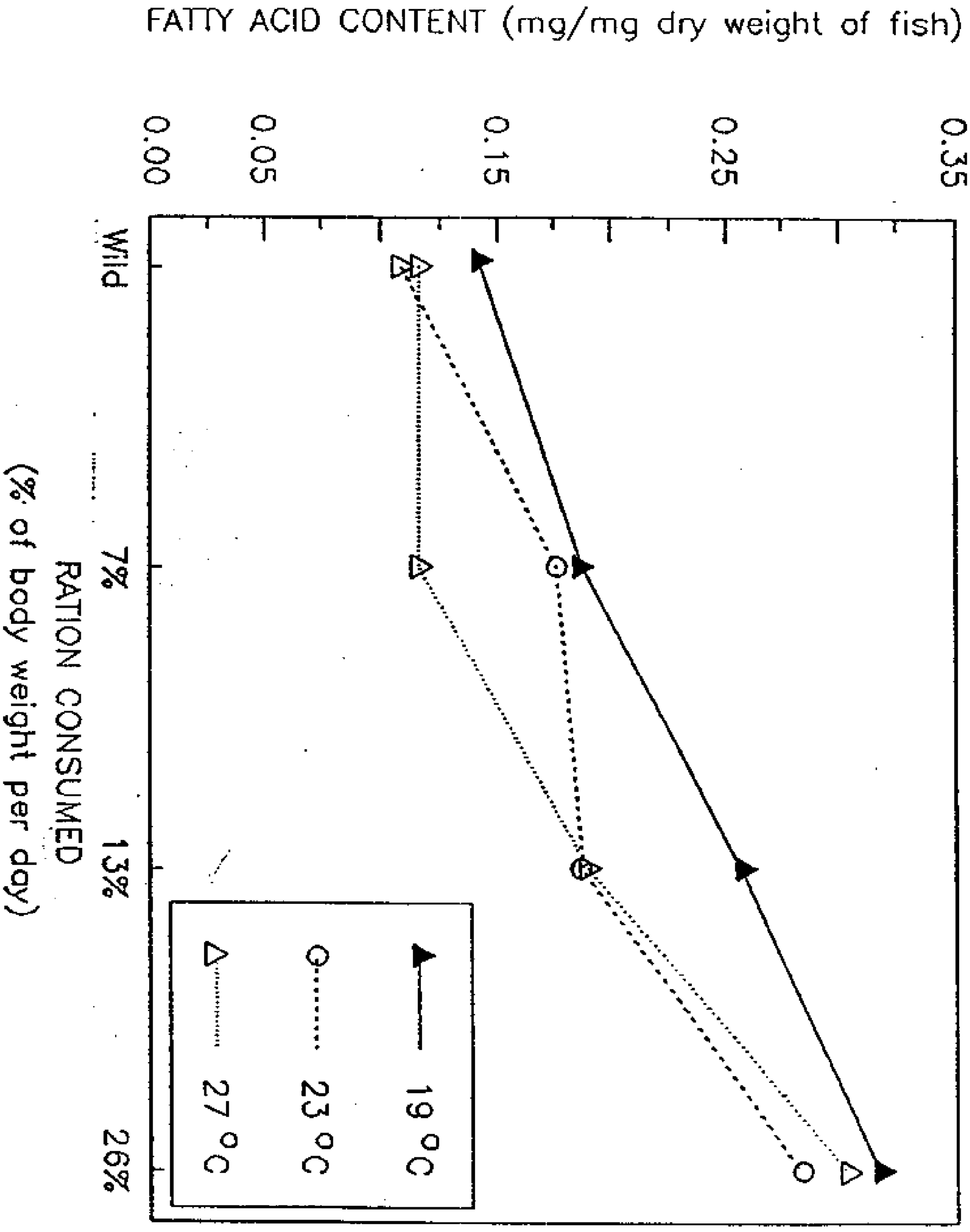


Figure 53. Total fatty acid content (mean ± S.D.) of bay anchovy fed *Artemia* at three experimental temperatures and ration levels.

(27°C) (Table 42). No significant difference in fatty acid content was found between the other two temperatures (19° and 23°C). At the 20% diet level, the highest amount of fatty acid was observed at the lowest temperature (19°C), while no significant difference in fatty acid amounts was detected between the two highest temperatures. No significant differences in fatty acid amounts were detected at any temperature at the 40% diet level.

The proportion of carbon to nitrogen, was not significantly different among temperatures, with two exceptions, one at the 10% diet level and 27°C where C/N ratio was lower than at 23° or 27°C, while 23° and 27°C did not differ significantly ($P>0.05$). The other exception was at the 20% diet level and 19°C where the C/N ratio was higher than at 23° or 27°C. No significant difference in C/N ratio was found for the 20% diet level between 23° and 27°C ($P>0.05$). Temperature did not have a significant effect on the condition indices (Table 43).

Effect of Ration

Ration had a significant effect on the percent of ash, moisture, protein and lipid contents (Table 42). The relationships between ration and protein, lipid, moisture and ash content for the three temperatures are illustrated in Figure 52. The general trend observed was a decrease of protein, moisture and ash content with increasing ration for any of the three temperatures tested. However, the percent of ash, moisture and protein were significantly lower than for any of the other rations or starting points only at the highest ration. In contrast, lipid content, condition index and the C/N ratio increased with increasing ration (Figures 52 and 54, Table 43). The indices of condition and the C/N ratio were significantly higher at the highest ration, with the exception of the 19°C experiment in which no statistically significant difference was found between the 20% and the 40% rations ($P>0.05$). No significant differences in lipid, C/N or condition index were found among the starting points (i.e. wild fish), the 10% diet level and the 20% diet level.

Fatty Acid Composition of the Bay Anchovy

Major differences were found in the fatty acid profiles of the anchovies frozen prior to starting the experiments (Table 44). The anchovies used for the first experiment (27°C) were acclimated the longest in the laboratory (three weeks; see methods in Vazquez and Houde, Chapter 6). The anchovies used for the 19°C and 23°C experiment were a mixture of wild fish (obtained prior to the beginning of the experiment) and fish held in the laboratory from 1-5 weeks. The fatty acid composition of the anchovies at the beginning of experiments at 19°C and 23°C were more similar to the fatty acid composition of wild anchovy than anchovy that had fed on *Artemia*. The fish held in the laboratory prior to the beginning of the 27°C experiment had a fatty acid profile that reflected three weeks of feeding on *Artemia*.

More specifically, the major differences found between the anchovies at the beginning of the 19°C and 23°C experiments compared with the anchovies at the beginning of the 27°C experiment were: (1) a relatively much higher quantity of the fatty acids 20:5 and 22:6 (average 10% and 20%, respectively) in anchovies at the beginning of the 19°C and 23°C experiments compared to

Table 43. Nitrogen and carbon percentages, C/N proportions and condition indices in relation to diet levels (% body weight) and temperature (mean±S.D.)

TEMPERATURE (°C)	DIET LEVEL (% b.w)	NITROGEN (%)	CARBON (%)	C/N	CONDITION INDEX
19	Start	11.4±0.2	46.1±0.8	4.1	0.49±0.08a
	10	10.9±0.2	50.1±0.2	4.6	0.57±0.03a
	20	10.0±0.3	52.7±0.1	5.2	0.59±0.03ab
	40	9.3±0.2	54.4±0.1	5.8	0.64±0.05b
23	Start	12.0±0.1	46.7±0.6	3.9	0.44±0.14a
	10	10.6±0.1	49.4±0.1	4.6	0.57±0.06a
	20	10.9±0.8	49.9±0.3	4.7	0.57±0.04a
	40	9.3±0.7	51.4±0.6	5.6	0.64±0.05b
27	Start	11.5±0.1	47.4±0.1	4.1	0.480.04a
	10	11.7±0.0	47.7±0.1	4.1	0.51±0.07a
	20	10.7±0.7	49.5±0.2	4.6	0.57±0.08a
	40	9.0±0.2	55.0±1.1	6.1	0.67±0.06b

Letters after each value indicate results of Sheffe's test after multifactor analysis of variance. Means with same letter are not significantly different from each other at the P=0.05 level.

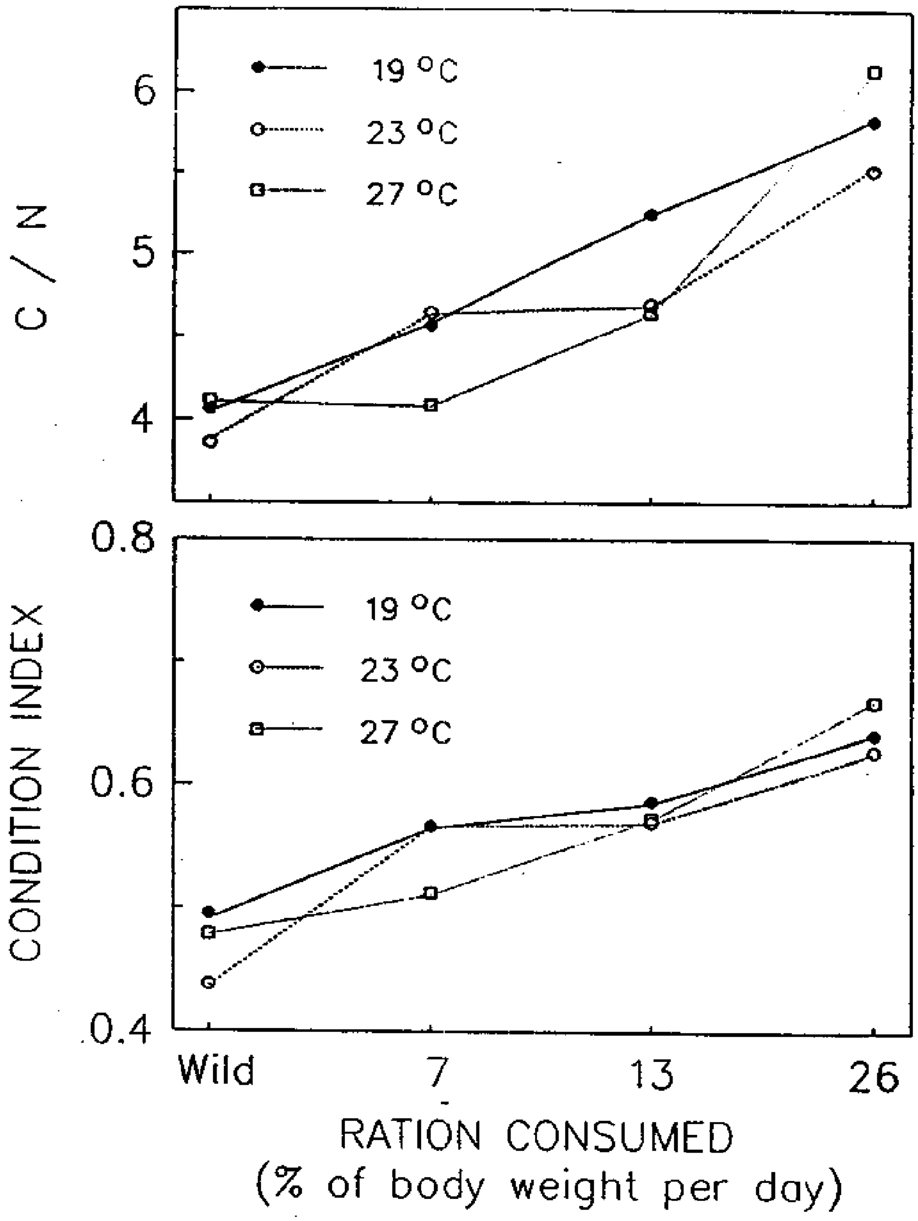


Figure 54. Carbon and nitrogen ratio and condition indices of *Anchoa mitchilli* with increasing ration level for the three experimental temperatures.

Table 44. Fatty acid composition of *Artemia* and bay anchovy at the beginning of the experiments (±SD).

FAME

SATURATED	START (19°C)	START (23°C)	START (27°C)	ARTEMIA
14:0	6.2 (1.3)	4.0 (1.4)	3.2 (1.2)	1.1
16:0	28.6 (1.7)	30.8 (4.0)	26.3 (3.6)	16.3
17:0	1.0 (2.3)	1.0 (0.2)	0.6 (0.8)	0.9
18:0	6.4 (0.5)	6.7 (0.5)	6.1 (0.6)	7.4
20:0	0.4 (0.5)	0.2 (0.3)	0.3 (0.5)	1.6
24:0	1.3 (1.2)	1.5 (1.4)	2.3 (2.5)	nd
TOTAL	43.9	44.2	38.8	27.3
MONOUNSAT				
16:1	6.4 (2.0)	5.7 (2.1)	5.5 (0.4)	3.7
$18{:}1^{\wedge 9}$	6.8 (1.4)	6.9 (0.2)	21.1 (9.0)	45.2
$18{:}1^{\wedge 11}$	5.1 (1.4)	3.8 (0.2)	8.4 (7.4)	12.3
20:1	nd	nd	0.7 (1.2)	nd
22:1	0.2 (0.2)	2.7 (2.3)	0.5 (0.6)	nd
TOTAL	18.5	19.1	36.2	61.2
POLYUNSAT				
16:2	nd	nd	nd	2.0
18:3	3.2 (1.0)	2.7 (0.9)	1.2 (0.2)	2.2
18:2	3.8 (0.4)	3.2 (0.6)	11.3 (2.5)	5.1
20:5	10.0 (1.0)	9.7 (0.7)	5.5 (2.8)	2.1
20:2	nd	nd	nd	0.2
22:6	21.3 (1.4)	20.6 (5.4)	6.6 (2.8)	nd
22:5	0.3 (1.4)	0.5 (0.4)	0.8 (0.9)	nd
TOTAL	38.6	36.7	25.4	11.5

nd-not detected

those at the beginning of the 27^{o}C experiment (5.5% and 6.6%, respectively), and (2) a higher proportion of $18{:}1^{\wedge 9}$ and 18:2 in the anchovy prior to the 27^{o}C experiment compared to anchovies used in the 19 and 23^{o}C experiments.

In the anchovies at the end of the experiments temperature did not have a significant effect on individual fatty acid composition or on the relative amount of saturated, monounsaturated or polyunsaturated classes within the anchovies. Therefore, results from the three temperatures tested were pooled by diet level (Table 45). Although there was no significant difference among ration levels for the saturated fatty acids (ANOVA, $P>0.05$), the percentage of monounsaturated fatty acids was significantly lower at the 10% ration than at the 20 and 40% rations. The percentage of polyunsaturated fatty acids was significantly lower at the 40% ration ($P<0.05$).

An increase in ration level generally elevated the amount of monounsaturated and depressed the amount of polyunsaturated fatty acids in bay anchovy, which tended to cause the fatty acid profile of the experimental anchovy to resemble that of Artemia. Oleic acid ($18{:}1^{\wedge 9}$) comprises almost half of the total fatty acids of Artemia. The percent of $18{:}1^{\wedge 9}$ increased proportionally with increasing ration level in the experimental fish. Linoleic acid (18:2) also increased in the experimental fish compared to their starting levels. However, this fatty acid is present in a relatively smaller amount in the Artemia compared to anchovy that have been fed on Artemia (Table 45).

DISCUSSION

Proximate Composition

The results obtained in the present study on bay anchovy are similar to those found for clupeid fishes by Strange and Pelton (1987) (Table 46). The percentage of moisture and protein obtained in the present study (70.0-77.4% and 56.1-75.3%, respectively) are similar to those for the three clupeid species that they studied (69.7-84.9% for moisture and 45.4-79.1 for protein). The percentage of ash in the present study (9.4-14.5%) is closest to that obtained for alewife (12.0-23.5%). Strange and Pelton (1987) found that total lipid ranged from 3.3 to 31.5% while for bay anchovy the values varied between 11.2 and 33.7%. It is possible that the lowest values obtained by Strange and Pelton (1987) were measured during the winter when feeding is diminished and lipid stores might be expected to fall. This would cause the mean values to be lower than those for the bay anchovy under continuous feeding conditions. Alternately, there may be real differences in lipid storage among species. It is also possible that seasonal and/or geographic variations, including changes in temperature and food availability and perhaps size of the fish have a bigger effect on the proximate composition than does interspecific variation. Implications of seasonal or age-specific changes in lipid content will be important to fully appreciate bay anchovy population biology and productivity.

Inconsistent results have been obtained for temperature effects on the proximate composition of fishes. The body composition of sockeye salmon, *Oncorhynchus nerka*, fed at different rations was constant at different temperatures (Brett *et al*. 1969). Niimi and Beamish (1974) found in *Micropterus salmoides* that lipid content was highest and water content lowest,

Table 45. Mean fatty acid composition of bay anchovy for different diet levels and for *Artemia*(±SD).

FAME	DIET LEVEL			
SATURATED	10%	20%	40%	ARTEMIA
14:0	2.9 (1.3)	1.9 (0.9)	1.7 (0.9)	1.1
16:0	21.2 (1.4)	21.4 (1.9)	24.0 (1.1)	16.3
17:0	0.4 (0.3)	0.1 (0.2)	0.1 (0.2)	0.9
18:0	4.6 (0.8)	4.6 (0.7)	4.0 (0.4)	7.4
20:0	0.2 (0.2)	nd	0.03 (0.1)	1.6
24:0	0.6 (0.7)	0.7 (0.7)	0.4 (0.6)	nd
TOTAL	29.9	28.7	30.2	27.3
MONOUNSAT				
16:1	5.5 (1.9)	4.1 (1.9)	5.1 (1.6)	3.7
$18:1^{\Delta 9}$	22.0 (2.4)	25.1 (2.2)	27.3 (2.1)	45.2
$18:1^{\Delta 11}$	8.5 (2.8)	10.9 (1.0)	10.3 (1.1)	12.3
22:1	1.9 (4.8)	1.5 (2.3)	0.5 (1.0)	nd
TOTAL	37.9	41.6	43.2	61.2
POLYUNSAT				
16:2	nd	nd	nd	2.0
18:3	2.3 (1.2)	2.5 (0.7)	2.9 (0.8)	2.2
18:2	19.8 (4.0)	23.0 (3.5)	20.4 (3.3)	5.1
20:5	3.8 (1.3)	2.6 (0.9)	2.5 (0.5)	2.1
20:2	nd	nd	nd	0.2
22:6	4.6 (2.7)	1.8 (1.7)	0.8 (1.0)	nd
22:5	0.2 (0.3)	nd	nd	nd
TOTAL	30.7	29.9	26.6	11.6

nd-not detected

Table 46. Proximate composition analysis of bay anchovy, *Anchoa mitchilli*, compared to three clupeid fishes (Gizzard shad, *Dorosoma cepedianum*; threadfin shad, *D. petenense*; alewife, *Alosa pseudoharengus*). Data on all species except bay anchovy were obtained from Strange and Pelton (1987).

SPECIES	% MOISTURE	% ASH	% PROTEIN	% LIPID
Gizzard shad	69.7-84.9	15.0-32.5	45.4-70.1	3.3-31.5
Threadfin shad	75.1-83.3	15.9-21.2	55.9-72.7	3.8-19.0
Alewife	71.6-84.0	12.0-23.5	52.7-79.1	5.8-20.8
Bay anchovy	70.0-77.4	9.4-14.5	56.1-75.3	11.2-33.7

at the lowest temperature while protein and ash content did not vary with temperature.

Differences in proximate composition of bay anchovy among the treatments did not appear to be a result of changes in temperature alone (Table 42). It appeared more likely that variations in body composition were the results of combined effects of temperature and diet level. The metabolic rate of fish determines the caloric requirement for energy and its availability for growth. If the food level is kept constant and metabolic requirements are lowered due to a decrease in temperature, fish will tend to accumulate lipids. Total fatty acid concentrations of bay anchovy fed at specific rations increased most at lower experimental temperatures, suggesting a decrease in metabolic demands.

Although storage lipids (i.e., triacylglycerols) were not measured directly, the fact that lipid content increased with ration level can be explained by the observed increase in fatty acid content because fatty acids represent more than 90% of total lipid. The increases were probably due to stored triacylglycerols (Brett and Groves 1979). Lipid accumulation in fishes is generally observed at higher food levels. In this regard bay anchovy results are similar to those obtained by Andrews and Stickney (1972) for channel catfish. In bay anchovy and in channel catfish the relative amounts of moisture and ash decreased proportionally in relationship to the increase in lipid content.

Condition indices are usually affected by temperature. Cui and Wootton (1988b), for example, found that the minnow (Phoxinus phoxinus) fed on restricted rations exhibited significant declines in condition indices as temperature increased. This suggests that increased metabolic demands at higher temperatures lower the condition of fish at a given ration. However, for bay anchovy temperature did not seem to have an effect on the condition indices. One possible explanation is that the range of temperature used in our experiments was not wide enough to show effects on the condition indices.

Ration level affected both the chemical composition and the condition indices of the anchovies. At the highest diet level (40%), the relative proportion of ash, moisture and protein decreased, almost certainly due to the increase in lipid content (reflected in the fatty acid analysis) noted previously. This result coincided with higher indices of condition and C/N ratios. Similar results were obtained by Cui and Wootton (1988b) for the minnow.

Protein and ash proportions obtained in this study differed from some other studies. In Onchorhynchus nerka, water content decreased while both lipid and protein content increased as ration increased at each temperature (Brett et al. 1969). In Micropterus salmoides, dry matter content and lipid content increased with ration while protein and ash content did not change (Niimi and Beamish 1974). In Salmo trutta, Elliott (1976) found that as ration increased moisture decreased, lipid and protein increased and ash remained relatively constant.

The C/N ratio has been used previously as an intraspecific index of the relative condition of similar size fish (Harris et al. 1986). With increasing ration, and consequently size as fish grow, the percentage of C, the C/N ratio and lipid content all increase while percentage protein decreases. Protein has a C/N value of approximately 3 (Harris et al. 1986). Consequently, increased amounts of lipids increase the C/N values. Although total lipid content was not directly measured in the present study, the results from the fatty acid content analysis and the C/N values from the carbon and nitrogen analysis indicated an increase in lipid relative to protein with increasing ration level. The C/N ratios increased by >40% at the highest diet levels compared to the ratios observed in wild bay anchovy at the start of experiments.

Fatty Acid Composition

The results obtained for the Colombian strain of Artemia used to feed the anchovies in the laboratory were most like the results obtained by Seidel et al. (1982) for Brazilian Artemia compared to other strains that they analyzed. The polyunsaturated fatty acids most common in zooplankton, including a variety of copepods, and phytoplankton, are 20:5 and 22:6 (Lee et al. 1971; Cowey and Sargent 1979; Muje et al. 1989). Planktivorous marine fish such as herring, capelin, menhaden and young salmon are rich in 20:5 and 22:6 fatty acids. In general, these are the major polyunsaturated fatty acids of marine and freshwater fish (Cowey and Sargent 1979).

As the anchovies were held in the laboratory and fed on Artemia, their fatty acid composition changed and began to reflect the fatty acid composition of Artemia. In particular, the main changes were an increase of the fatty acid 18:1$^{\wedge 9}$ and a decrease of the fatty acids 20:5 and 22:6. The most common fatty acid found in Artemia was 18:1$^{\wedge 9}$ while 20:5 was present only as a small proportion and 22:6 was not detected. At the start of the experiment the anchovies used for the 19° and 23°C treatments had fatty acid compositions characteristic of wild fish. The anchovies at the beginning of the 27°C experiment had a fatty acid composition which was more like that of experimental fish, and therefore Artemia, than that of wild fish. As noted previously this was most likely because the fish used in the 27°C experiment were held longer in the laboratory and were fed Artemia during acclimation. The high proportion of 20:5 and 22:6 in the fish at the beginning of the 19 and 23°C and low proportion of fatty acids common to Artemia suggest that these were wild fish that had been recently brought to the laboratory, and had not fed on Artemia long enough to show a change in their fatty acid composition. In addition, the saturated fatty acid 16:0, a prominent component of zooplankton and phytoplankton (Cowey and Sargent 1979), was also prominent in the wild anchovy. The 20:5 and 22:6 fatty acids both decreased with ration level as anchovy were fed on Artemia.

The increase of the fatty acid 18:1$^{\wedge 9}$ in the experimental anchovy as they were fed on Artemia reflects its presence as the most common fatty acid in Artemia. However, the fatty acid 18:2 also increased in fish fed Artemia despite the fact that it represented only 5.1% of the fatty acids of Artemia . This may be the result of some 18:1$^{\wedge 9}$ being transformed to 18:2 via the oleic-linoleic pathway (Cowey and Sargent 1979). The anchovy that were given diets deficient in polyunsaturated fatty acids may have elongated and further desaturated oleic acid 18:1$^{\wedge 9}$. Planktivorous marine fishes such as the Peruvian anchoveta, are also active in chain elongating and desaturating short chain dietary polyunsaturated fatty acids (Cowey and Sargent 1979). However, from the fatty acid composition observed for the bay anchovy in this study, it seems more likely that bay anchovy accumulated 18:2 rather than elongating it to the 20 and 22 carbon polyunsaturated fatty acids. Cowey and Sargent (1979) emphasized that marine carnivorous fish do not always convert 18:1, 18:2 or 18:3 to higher polyunsaturated fatty acids. Turbot, for example, fed on diets rich in these fatty acids did not show increased amounts of polyunsaturated fatty acids.

Fish nutrition studies recommend diets high in 18:2w6 and 18:3w3 for fast growth and efficient food conversion (Watanabe 1982). It is likely that 18:2w6 is an efficient storage form under feeding conditions which favor lipid deposition, the situation that apparently was observed in bay anchovy.

Laboratory studies on energetics and chemical composition of bay anchovy are essential to begin to understand the energetics and trophic dynamics of bay anchovy in the Chesapeake Bay. Proximate composition analysis on a seasonal basis can give insight into how the proportion of the different components change when temperature changes or when prey abundance changes. The continuation of ecological, physiological and chemical studies will be important to better understand bay anchovy production and also production at other trophic levels in Chesapeake Bay food webs.

CHAPTER 9. LABORATORY STUDIES ON THE EFFECT OF HYPOXIC WATERS ON THE SURVIVAL OF EGGS AND YOLK-SAC LARVAE OF THE BAY ANCHOVY, *ANCHOA MITCHILLI*

E. J.Chesney and E.D. Houde

INTRODUCTION

Fish population dynamics are strongly influenced by events that take place in the egg, larval or juvenile stages when they are most vulnerable to a variety of mortality agents. Prominent among these are the variability of food supply to first-feeding larvae and influences of predation on the highly vulnerable larval stages of fish. Fewer studies have looked at environmental stresses such as hypoxia or anoxia which might affect fish populations by influencing survival of fish larvae directly, or reducing survival indirectly by reducing growth, food supply or changing predator-prey interactions. Environmental stresses such as anoxia also have been hypothesized to influence fish recruitment indirectly through effects on adult condition, their prey distributions and reductions in adult habitat (Swanson and Sindermann 1979; Pavela *et al*. 1983; Leming and Stuntz 1984; Coutant 1985; Renaud 1986; Kramer 1987).

Environmentally stressed habitats are becoming increasingly more common, especially in nearshore and estuarine areas. Chesapeake Bay is experiencing an extensive and potentially worsening problem with anoxic and hypoxic waters (Officer *et al*. 1984; Magnien 1988). The problem is widespread, with other estuaries and coastal zones suffering similar problems. For example, Long Island Sound, Mobile Bay and the Louisiana inner continental shelf all suffer from an extensive seasonal period of low oxygen (Swanson and Sindermann 1979; Boesch 1983; Rabalais *et al*. 1985; Swanson and Parker 1988). These hypoxic (<2.0 mg/L) O_2 and anoxic (<0.1 mg/L) bottom waters can be extensive, sometimes covering areas of 8,000 Km^2 or more (Rabalais *et al*. 1985; Rabalais and Boesch 1987).

Hypoxic waters are probably most detrimental in enclosed areas such as estuaries and embayments, where the potential to limit habitat and migration, and to trap organisms as hypoxia develops, would be greatest. Demersal and benthic organisms, including fish, crabs, shrimp and benthic infauna are either displaced by the anoxia or, if unable to emigrate, are killed by it (Swanson and Sindermann 1979; Gaston 1985). Finfish can escape the direct effects of hypoxia and anoxia by vertically migrating or emigrating from the area, but they still must contend with the changes in their habitat that low oxygen waters cause (Pavela *et al*. 1983; Leming and Stuntz 1984; Renaud 1986; Kramer 1987).

Within Chesapeake Bay, the bay anchovy, *Anchoa mitchilli*, is an abundant fish likely to be impacted by anoxia. It spawns from May to September throughout the Bay with a peak of spawning in July (Olney 1983; Dalton 1987). We conducted laboratory experiments to determine the potential of hypoxia to cause mortality of the egg and yolk-sac stages of the bay anchovy.

METHODS

Laboratory experiments were conducted under controlled conditions to test the effects of reduced oxygen concentration on the hatchability and survival of bay anchovy, Anchoa mitchilli eggs and yolk-sac larvae. A population of approximately 100 bay anchovy adults was maintained and spawned in the laboratory by adjusting temperature and photoperiod to summer temperatures (27-28°C) and daylength (16L-8D). Once the adults were conditioned and began spawning, they spawned each evening after the dark cycle began (2100 hrs) at a rate of 50-500 eggs per day. The pelagic eggs were collected at the tank outlet in a collector. Eggs used in the experiments were always approximately 12-hr post-fertilization. Bay anchovy eggs hatch in approximately 20-22 hr at 26-27°C. All egg experiments were of 12-hr duration to allow sufficient time for eggs to hatch. For consistency, larval experiments also were of 12-hr duration. Bay anchovy larvae were hatched and held in aerated temperature-controlled (26°C) 2-L beakers of seawater and held overnight until they were used for experiments. All yolk-sac larvae tested were 12-14 hr post-hatch.

Each experiment consisted of placing either 30 eggs or 25 larvae in a 185 ml plexiglas chamber filled with partially deoxygenated seawater (15-18o/oo). A batch of seawater was partially deoxygenated by bubbling with nitrogen gas. The pH of this solution was checked to insure that pH was not significantly altered by nitrogen stripping of gases.

Eggs and larvae were sealed in the chambers, which were placed in a circulated temperature-controlled bath (26.5°C) and initial oxygen concentration measured in each chamber. The seawater in the chambers was gently circulated with a micro-magnetic stirbar. An experiment typically consisted of four chambers unless we lacked sufficient eggs or larvae to fill all four chambers on a given day. Oxygen partial pressures were monitored continuously in two chambers with a pair of Radiometer^{TM} acid-base analyzers fitted with dissolved oxygen modules. Temperature was monitored in a third chamber. At the end of each experiment oxygen levels were measured in all experimental chambers. Because of system respiration and the respiration of the eggs and larvae, the eggs and larvae were exposed to a gradual decrease of oxygen tension over the 12-hr experimental period. Mean delta O_2's for the egg experiments were $0.15+0.04$ mg L^{-1} hr-1 and $0.19+0.07$ mg L^{-1} hr-1 for the larval experiments. The results are considered relative to the final oxygen concentration reached during the experiments, rather than the means, to best represent the most severe conditions to which the eggs and larvae were exposed.

At the end of each experiment the contents of each chamber were poured into a culture dish and the eggs and larvae counted and examined under a dissecting microscope. Results of experiments on eggs were classified into four categories: unhatched-dead, unhatched-alive, hatched-dead or hatched-alive. In the larval experiments, larvae were classified as alive, alive but dying, or dead. Inactive larvae were judged to be alive if a heartbeat could be observed under the microscope. Unaccounted individual eggs or larvae were noted and subtracted from the starting number before calculating percentages in the various categories. If more than 20% of the eggs or larvae could not be accounted for in a given experiment, results from that chamber were not included.

The 50% lethal doses (LC_{50}) for the exposures were estimated by converting the percentage mortalities or survivorship to probits (Finney 1971), plotting the probits against log of oxygen concentration, and then fitting a linear regression to the relationship.

RESULTS

Hatchability of anchovy eggs declined abruptly below 2.5 mg O_2 L^{-1} (Figure 55a). Survival rates of larvae in these experiments that did hatch were similar to egg-stage rates (Figure 55b). Among the eggs that did not hatch a significant number were exposed to oxygen tensions in the 1-3 mg O_2 L^{-1} range and were unhatched but alive at the end of the 12-hr experiments (Figure 56b, 57a). The possibility that those eggs did not have time to hatch under the given conditions was tested by sorting the unhatched-alive eggs into fresh well-aerated seawater and re-examining them 12-hr later. These eggs remained unhatched, ruling out the possibility that hatching time was insufficient. The percentage of dead eggs increased below 3.0 mg O_2 L^{-1} and again below 1.5 mg O_2 L^{-1} (Figure 56a). Total survival in all categories appears to drop off abruptly below 1.5 mg O_2 L^{-1} (Figure 56b). Again, those individuals that were alive but unhatched contribute to the appearance of an abrupt decline in survival at 1.5 mg O_2 L^{-1}.

Bay anchovy larvae 12-24 hr posthatch apparently were more tolerant of exposure to low oxygen than the egg stage or the larvae hatched in the egg experiments. These larvae showed good survival above 2.0 mg O_2 L^{-1} and fair survival above 1.0 mg O_2 L^{-1} (Figure 58a). Exposures below 1.0-1.5 mg O_2 L^{-1} showed high percentages of dead or dying larvae (Figure 58b). Estimated LC_{50}'s for the exposure conditions were 2.8 mg O_2 L^{-1} for anchovy eggs and 1.6 mg L^{-1} for 12-24 hr old yolk-sac larvae (Figures 55a, 58b). The estimated LC_{50} for the larvae that hatched during the egg experiments was 2.4 mg O_2 L^{-1} (Figure 55a).

DISCUSSION

Numerous studies and literature reviews have addressed the effects of reduced oxygen levels on eggs and larvae of fishes (see Rombough 1988 for the latest review). Tolerance of individual species appears to be related to the habitat conditions normally encountered by each species, especially with regard to seasonal temperature ranges likely to be encountered. It is not surprising that anchovy eggs and yolk-sac larvae are moderately tolerant to low oxygen conditions compared to at least some species that have been tested. For example, DeSilva and Tytler (1973) reported 12-hr LC_{50}'s for yolk-sac larvae of <u>Clupea</u> <u>harengus</u> and <u>Pleuronectes</u> <u>platessa</u> of 2.8 and 3.9 mg O_2 L^{-1}. Bay anchovy larvae were less tolerant to low oxygen than the benthic, naked goby, <u>Gobiosoma</u> <u>bosci</u> larvae that had a 24-hr LC_{50} of 1.3 mg O_2 L^{-1} (Saksena and Joseph 1972), especially considering the much longer exposure time for the naked goby.

Hatchability of fish eggs is known to be influenced by the oxygen concentration to which the eggs are exposed during incubation (Rombough 1988). In previous studies, hyperoxic conditions prolonged or delayed hatching indefinitely, while hypoxic conditions generally caused premature hatching. These effects have been reported for stranded eggs of <u>Fundulus</u> <u>heteroclitus</u> (Taylor et al. 1977). This effect appears to convey a selective advantage to intertidal mummichog eggs, allowing them to develop and then hatch immediately upon exposure to water. For bay anchovy, we observed a significantly different pattern. First, bay anchovy eggs were clearly less tolerant to reduced dissolved oxygen than their yolk-sac larvae. Secondly, there was a marked increase in eggs that were unable to hatch but remained alive at low D.O. concentrations (1.5-3.0 mg O_2 L^{-1}).

Our results demonstrate that survival rates of bay anchovy eggs and larvae are likely to be affected when exposed to oxygen concentrations less than 3.0 mg L^{-1} and 2.5 mg L^{-1}, respectively. Although the potential for hypoxia to reduce survival rates of bay anchovy larvae within Chesapeake bay is certain, several key questions must be answered before a valid assessment of possible effects at the population level can be made.

First, more detailed information is needed on the vertical distribution of eggs and larvae and their dynamics within the water column. How does egg buoyancy change with temperature and salinity? How capable are larvae of avoiding hypoxic waters? Previous data have indicated that eggs and larvae of bay anchovy can be abundant in the lower half of the water column in Chesapeake bay (Dalton 1987) where water is potentially hypoxic. However, it is unclear whether the eggs that occurred in the lower half of the water column were alive, were dead as the result of mortality induced by hypoxia, or if they were dead eggs that had reduced buoyancy and had sunk into bottom waters. Second, an understanding of the physical processes, such as vertical mixing within the Bay, which are likely to play a role in exposing eggs and larvae to hypoxic and anoxic waters, is needed to interpret and predict the probability of eggs and larvae being mixed into or with hypoxic waters. Finally, results of these laboratory studies present a conservative estimate of the potential effects of hypoxic conditions on eggs and larvae of bay anchovy. More laboratory and in situ field studies are needed to assess the effects of length of exposure to lowered oxygen, size or stage-specific effects on older larvae and effects of the more complex water chemistry (i.e. hydrogen sulfide) that would be encountered by eggs of larvae in the Bay.

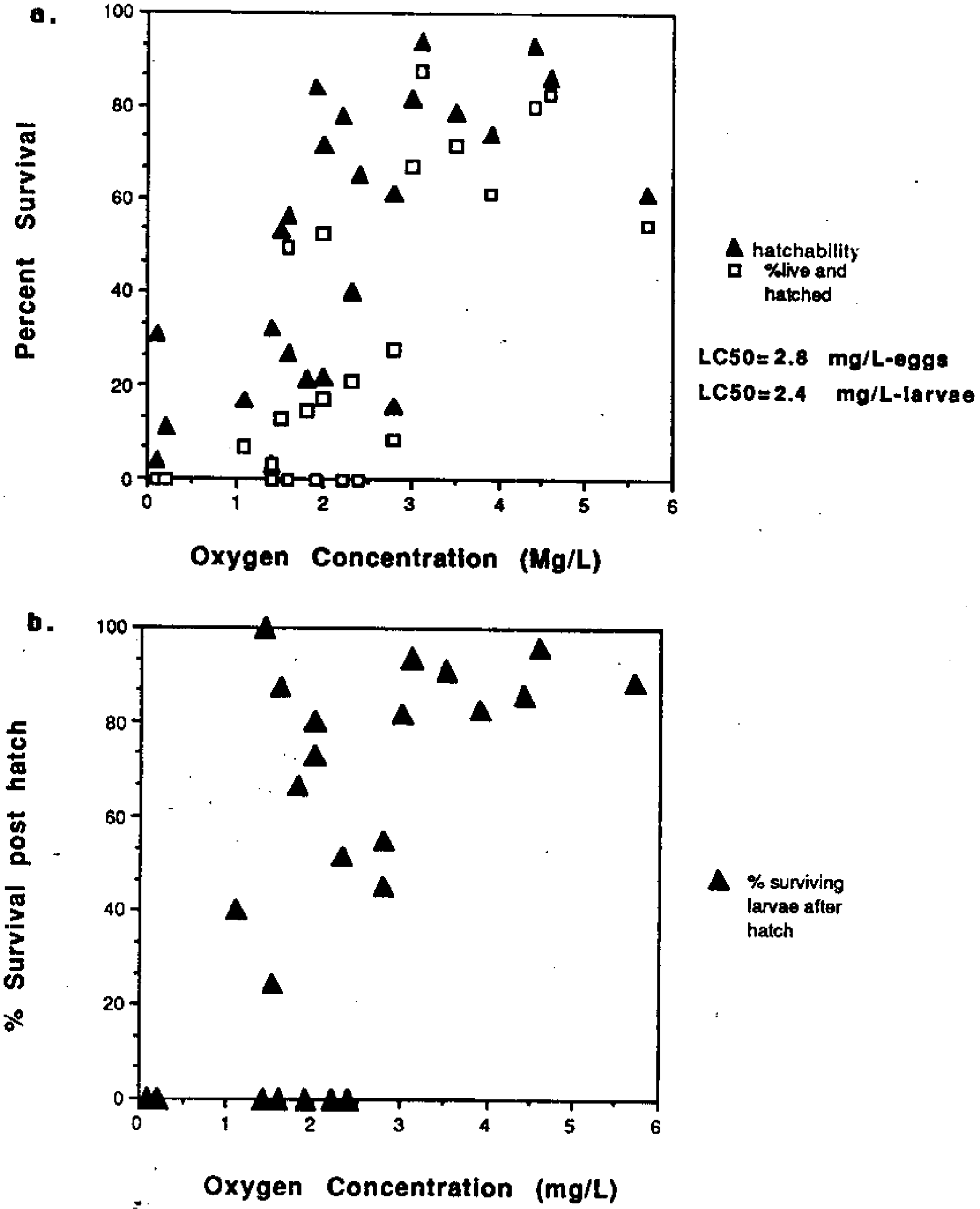


Figure 55. Percent hatchability (a) of anchovy eggs in relation to oxygen concentration and (b) survival of the hatched larvae.

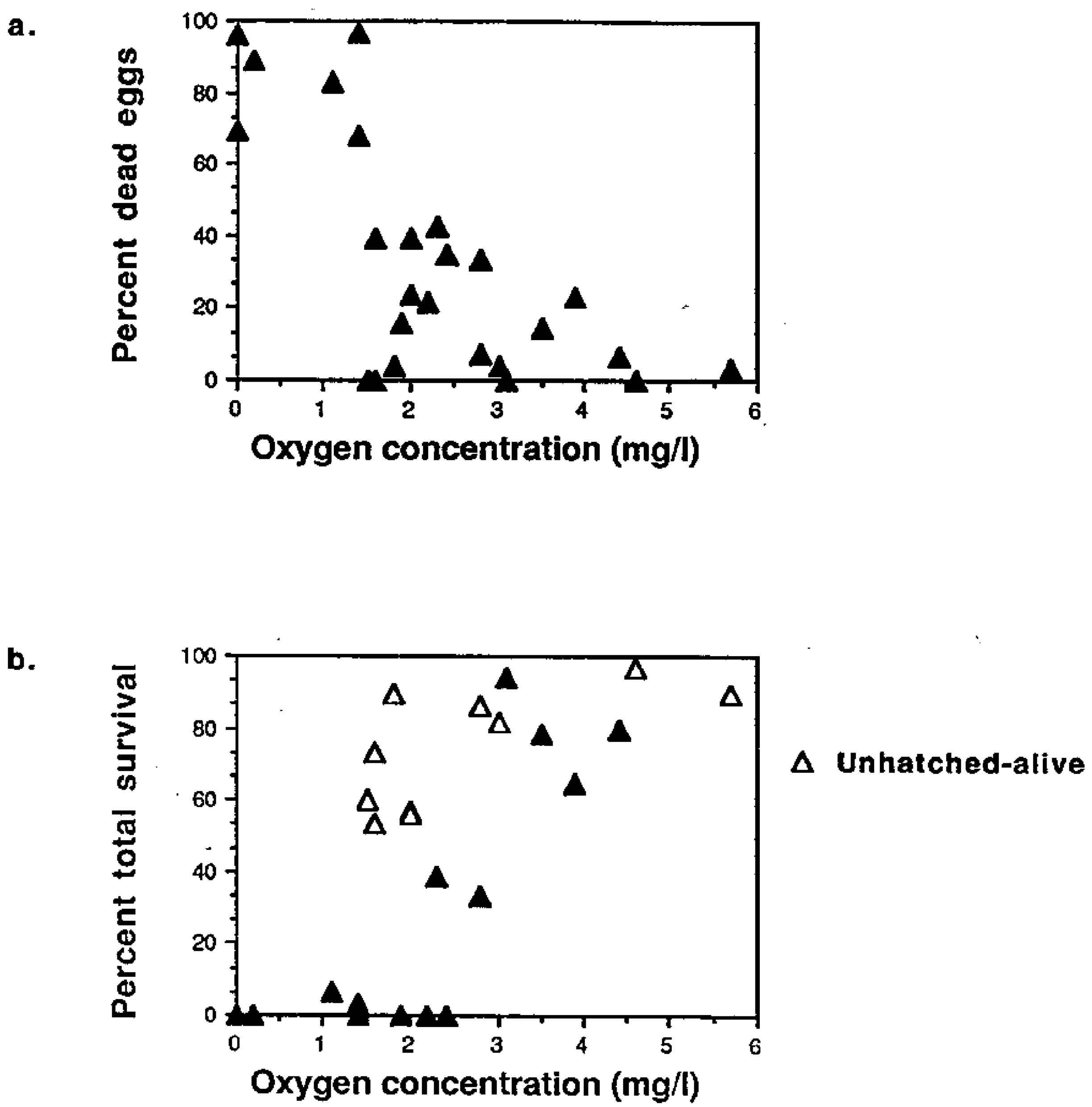
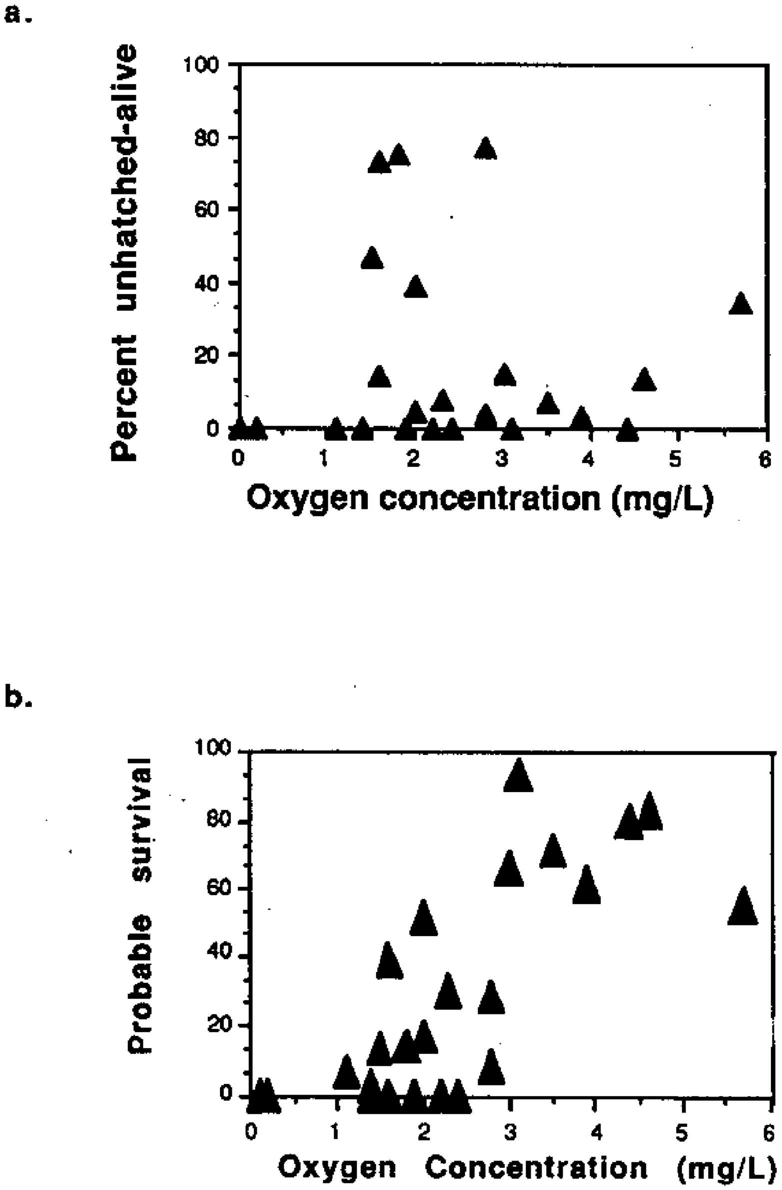


Figure 56. Percentage of dead bay anchovy eggs (a) and percent total survival (b) of hatched and unhatched eggs exposed to the various oxygen concentrations. Open triangles (b) represent experiments where 15% or more were unhatched and alive at the end of the experiment.



LC50=2.4 mg/L

Figure 57. Percent unhatched but alive bay anchovy eggs (a) and probable survival if live-unhatched never hatch (b) after exposure to the various oxygen concentrations.

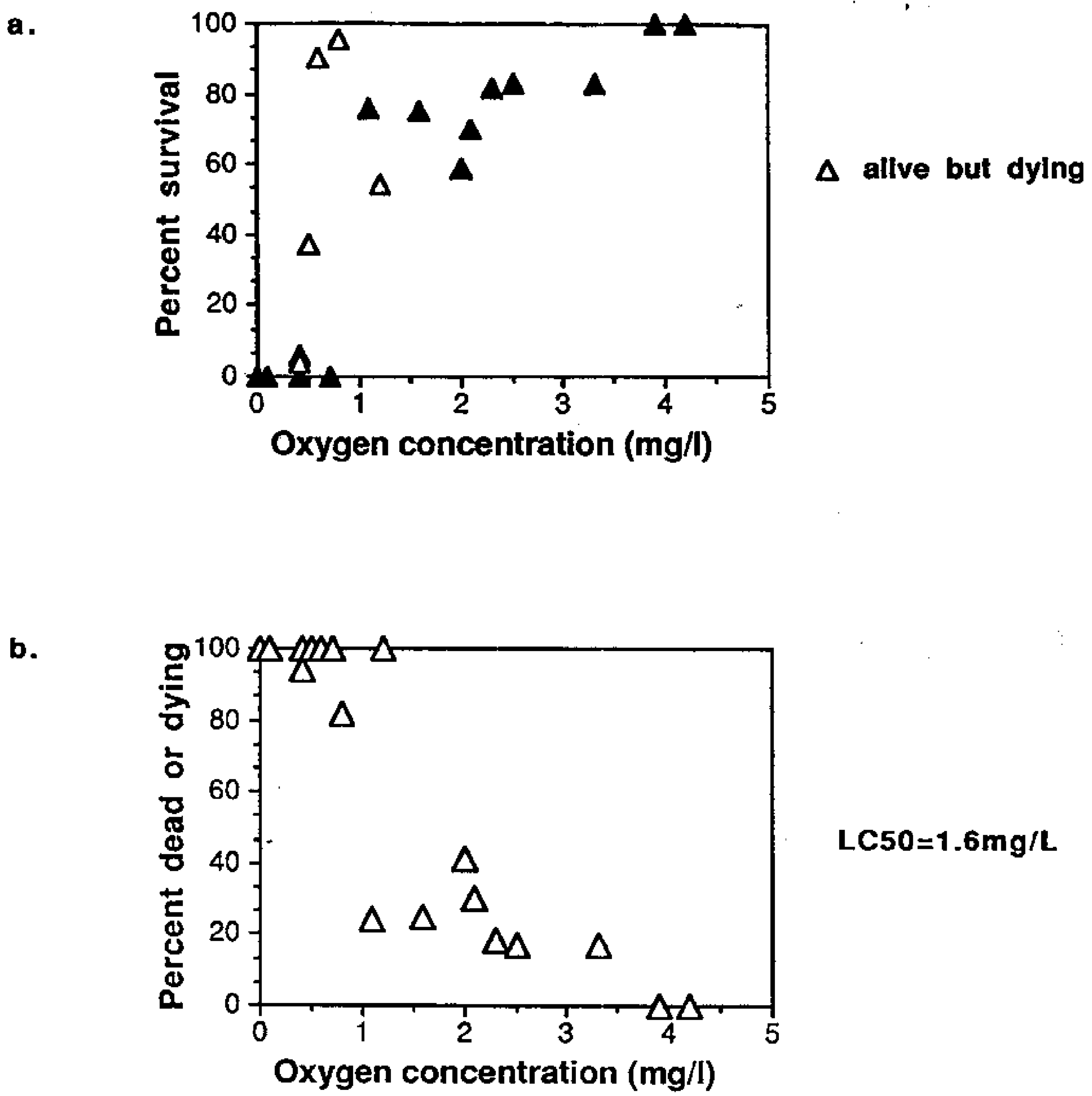


Figure 58. Percentage of surviving (a) and dead or dying (b) bay anchovy larvae at the various oxygen concentrations tested. Open triangles in the upper graph represent the experiments with a high percentage of dying larvae among the survivors.

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