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Life history of the bay anchovy, Anchoa mitchilli, in Chesapeake Bay

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Luo, Jiangang, Ph.D.

The College of William and Mary, 1991

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LIFE HISTORY OF THE BAY ANCHOVY, ANCHOA MITCHILLI, IN CHESAPEAKE BAY

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

By

Jiangang Luo

1991

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

Jiangang Luo

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Approved, December 1991

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ABSTRACT

Eggs from plankton samples in lower Chesapeake Bay indicated that the spawning season of the bay anchovy *Anchoa mitchilli* in 1988 was from early May to mid-September. Oocyte stages in adults were used to determine daily spawning time and frequency, as well as batch fecundity. Spawning was temporally synchronized and lasted for about 1.5 h each night. Spawning time became later each month (2000 h on 6 June to 2330 h on 31 August). Spawning frequency per individual was every 4 d in early June and 1.3-1.9 d in other months. Batch fecundity was a linear function of fork length and body weight; regression slopes on 6 July and 4 August were significantly higher than those on 6 June and 31 August. Estimated mean total spawnings per female in 1988 was 54. Total egg production for a fish of average size was 45,110, which is equivalent to 346% of body biomass energy. Age determination based on lagenar otoliths showed that some fish spawned when as young as 2.5-3 months.

Transport of the adult bay anchovy in darkness was studied in laboratory and field experiments. In a hydraulic flume, 99% of all fish were transported to the end of the flume in darkness at a current speed of 30 cm s^{-1}. In field experiments, fish marked with neutral red dye and released in a creek at flood tide were recaptured 5.1 km upstream 4 h after release at night, and were recaptured within 200 m of the release site 3 h after release in daylight. This nocturnal transport phenomenon may also exist in other marine and estuarine pelagic fishes, and may help in understanding behavior and distribution of pelagic estuarine fishes.

Historical trawl survey data indicate that bay anchovy is the most abundant species in lower Chesapeake Bay. The standardized CPUE data show long-term population fluctuations on the order of ten-fold. The bay anchovy population also has extensive seasonal variations which appeared attributable to winter migration or mortality, high spring and summer predation, and peak recruitment in fall. A Fourier analysis removed the seasonal (short-term) variation from the long-term data series. An autoregressive analysis of the residual series indicated that it contained a significant first-order autoregressive process component ($r^2 = 0.26$, $P \leq 0.0066$), which was interpreted as a spawner-recruit relationship. Cross-correlation analysis indicated that bay anchovy population abundance was positively correlated with winter water temperature ($r = 0.663$, $P \leq 0.0001$) and river flow ($r = 0.376$, $P \leq 0.027$), but negatively correlated with white perch abundance ($r = -0.437$, $P \leq 0.011$) and the squared function of residual wind speed ($r = -0.377$, $P \leq 0.026$). A multiple regression model indicated that temperature, white perch abundance and wind made significant contributions (accounting for 78% of the variation) to the model, with no significant contributions from other factors.

Life History of the Bay Anchovy, *Anchoa mitchilli* in Chesapeake Bay

GENERAL INTRODUCTION

The bay anchovy, *Anchoa mitchilli*, is one of the most abundant food resources of larger predatory species in Chesapeake Bay (Hildebrand and Schroeder 1928, Hildebrand 1963a, 1963b), and is very important to the energetic processes of the ecosystem. Therefore, understanding the life history of bay anchovy and its production is vital to the resource management of the ecosystem. It is surprising that only fragmentary information is available on the life history of this species, considering its abundance and its wide geographical range which extends from Cape Cod, Mass., U.S.A. to Yucatan Peninsula, Mexico (Bigelow and Schroeder 1953, Hoese and Moore 1977, Byrne 1982, Morton 1989).

Bay anchovy is a short-lived fish. Newberger (1989) found that few individuals ($\leq 0.1\%$) lived to age 3^+ years, and that the annual mortality rate was 89-95%. Adult bay anchovy attain a maximum size of 110 mm TL (Hildebrand 1963), and a mean fork length of age 1 fish is 55 mm fork length (FL) in mid-Chesapeake Bay (Newberger 1989).

Bay anchovy is a highly schooling, nektonic, and euryhaline species, and can be found in all types of habitats, from oligohaline estuarine water to coastal marine water, from open bays to muddy coves, from river channels to intertidal creeks, and from grassy areas to sandy beaches (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Kilby 1955, Reid 1955, Vouglitois *et al.* 1987).

Bay anchovy populations fluctuate widely from year to year. Although reliable estimates of population size are not available, preliminary analysis of trawl survey data from the Virginia Institute of Marine Science (VIMS) indicates 10-fold fluctuations in annual abundance of bay anchovy in lower Chesapeake Bay and its tributaries. Indices of bay anchovy abundance from summer beach seine surveys conducted by the Maryland Department of Natural Resource show variations more than 100-fold from 1958 to 1989 (Newberger 1989). Trawl survey data in mid-Chesapeake Bay indicate bay anchovy catch per unit of effort (CPUE) in 1986 was almost six times higher than that in 1987 (Newberger 1989).

Bay anchovy population fluctuations may have indirect effect on other commercially and recreationally important species because it is a key species in the Chesapeake Bay food web. Bay anchovy feeds mostly on zooplankton by selecting individual particles. Larvae prey mainly on copepod nauplii and rotifers. Juveniles feed on copepoda, crab zoea and other pelagic zooplankton. Adults are able to add mysids, ostracods, small fishes, small benthic mollusks, and crustaceans to their diets (Reid 1954, Darnell 1958, Sheridan 1978, Vazquez 1989, Johnson *et al.* 1990). Bay anchovy consumes 86, 90, 90, and 73% of total zooplankton consumed by all planktivorous fishes in summer, fall, winter, and spring, respectively, in mid-Chesapeake Bay (Baird and Ulanowicz 1989). Bay anchovy is an important food source for many larger species. Its predators include weakfish, striped bass, summer flounder, white perch, bluefish, and white catfish (Hollis 1952, Merriner 1975, Chao and Musick 1977, Homer and Boynton 1978, Safina and Burger 1989, Baird and

Ulanowicz 1989). Bay anchovy contributes 70, 90, and 60% to the diets of larger predatory fishes in summer , fall, and spring, respectively, in mid-Chesapeake Bay (Baird and Ulanowicz 1989). Therefore, to understand the dynamics of the ecosystem it is very important to understand the life history and the dynamics of bay anchovy.

A variety of natural factors are likely contributors to fluctuations in the population size of bay anchovy: (1) variability of spawning success of adult bay anchovy; (2) variability of egg and larval mortalities; (3) variability of predation pressure on juvenile and adult bay anchovy; and (4) variability of weather conditions causing changes in emigration and immigration patterns of bay anchovy in Chesapeake Bay, or extreme weather causing mortality.

Egg production is controlled primarily by the nutritional history of spawners, the availability of suitable spawning habitats, and the duration of the spawning season, and secondarily by abiotic and biotic environmental factors such as water temperature, salinity, dissolved oxygen, food abundance, and population density (Bagenal 1973, Dando 1984, Rothschild 1987, Jennings and Beverton 1991).

Recruitment variability due to changes in mortality rates of eggs and larvae is believed to be the cause of fluctuations in population size of many fish species (Cushing 1975, Steele *et al.* 1980, Houde 1987, 1989a, 1989b). Starvation, predation, and lethal environmental conditions are suggested major factors responsible for controlling the mortality rates of fish eggs and larvae. Starvation has long been considered an important factor in causing larval mortality (Hjort 1914) and may be a result of a temporal mismatch of seasonal plankton bloom with spawning (Cushing

1975) or the destruction of critical food patchiness (Lasker 1975, 1978). Houde (1978, 1987) suggested that a minimum food level of approximately 100 prey/l was required for larval growth and survival of bay anchovy based on laboratory experiments. But, in later *in situ* enclosure experiments in the Patuxent River, MD., Cowan and Houde (1990) obtained high growth rates and high survival rates at microzooplankton concentrations as low as 50 prey/l. More recently, some workers (Bailey and Houde 1989, Leak and Houde 1987, Houde 1987) have implicated predation as the major cause of early life mortality of fishes. Leak and Houde (1987) reported high egg mortality (85.6% / d) and high larval mortality (26 to 36% / d) of bay anchovy in Biscayne Bay, Florida. Govoni and Olney (1991) estimated maximum ctenophore (*Mnemiopsis leidyi*) predation on bay anchovy eggs ranging from 24.1 eggs/m^3/day to 753.8 eggs/m^3/day. Monteleone and Duguay (1988) also demonstrated in laboratory experiments that the ctenophore was an effective predator of bay anchovy eggs and larvae. Other potential predators are medusa *Chrysaora quinquecirrha*, adult bay anchovy, and other planktivorous fishes, such as Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic silverside (*Menidia menidia*).

Predation pressure on juvenile and adult bay anchovy by larger species can be changed significantly if the population size of predatory species changes. Bay anchovy contributes a major portion to the diets of larger predatory fishes (Baird and Ulanowicz 1989). Studies have shown large fluctuations in year classes of striped bass (Boreman and Austin 1985, Kline 1990, McGovern 1991) and weakfish

(Merriner 1973, McHugh 1980, Mercer 1983, Szedlmayer 1988), both are major bay anchovy predators.

In part of its range, bay anchovy migrates to deeper water in bays or the inner continental shelf in winter, and back to shallower water in spring (Vouglitois *et al. 1987*). The extent of migration is poorly known, but the process is probably controlled by water temperature. In colder winters it is probable that more bay anchovies migrate offshore than in warmer winters, and during extremely cold winters large numbers of bay anchovy can be killed by sudden drops of water temperature (Gunter and Hildebrand 1951, and personal observation).

In addition to seasonal migration, bay anchovy populations may exhibit short-term (tidal period) movements within the estuary. This is, because bay anchovy schools break up after dark, and fish swim in all directions at a greatly reduced speed (pers. obs.). This behavior makes bay anchovies susceptible to transport by tidal currents at night. Since the duration of flood and ebb tidal currents at night are usually asymmetrical (such as 6-h flooding and 2-h ebbing, depending on the time of the lunar period, season and latitude), bay anchovies are likely transported and segregated upstream during a period when flooding is dominant at night, and downstream during a period when ebbing is dominant at night. The resulting change in the spatio-temporal distribution may affect its food availability therefore growth rate and reproduction success, and may affect the predation pressure from larger predatory fishes.

The general goal of this study was to investigate aspects of bay anchovy life history that may be important to biological success in the highly variable estuarine environment. Wilbur *et al.* (1974) suggested that understanding a life history strategy would usually require knowledge of at least the following: (1) juvenile and adult mortality schedules; (2) age at first reproduction; (3) reproductive life-span; (4) fecundity; (5) fecundity-age regression; (6) degree of parental care; (7) amount of resources allocated to reproductive effort.

A life history is controlled by three basic biological processes: maintenance, growth, and reproduction (Gadgil and Bossert 1970). Since any organism has limited resources of time and energy at its disposal, the life history strategy of a species is to give an optimal allocation of resources among maintenance, growth and reproduction. But fitness is measured in terms of the contribution made to the gene pool of the next generation, and that is in terms of reproductive success (Mayr 1966). Since selection is in favor of reproductive success, the advantage of devoting resources to maintenance and growth occurs only so far as this enhances reproduction at further stages in the life history. Maintenance is essential to enable an organism to survive to reproductive age, and growth may enhance both survival and reproductive ability (Gadgil and Bossert 1970).

This dissertation consists of three chapters. The first chapter focuses on the characteristics of the reproductive biology of bay anchovy. This part of the study was designed to determine age and growth of larval and juvenile bay anchovy, age and size at sexual maturity, spawning time, spawning frequency, and batch fecundity.

The second chapter describes an important behavioral phenomenon: "tidal transport in darkness", which can be used to explain a variety of other behaviors of bay anchovy. The third chapter attempts to incorporate available life history information and available biological and physical data to determine possible factors causing fluctuations in population size.

CHAPTER 1

Reproductive Biology of the Bay Anchovy in Chesapeake Bay

INTRODUCTION

The bay anchovy, *Anchoa mitchilli*, exhibits a protracted spawning season (late April to late September) in Chesapeake Bay (Hildebrand and Schroeder 1928; Dovel 1971; Olney 1983; Dalton 1987). Rapid summer growth presumably allows it to spawn in late summer at an age of 3 months because individuals as small as 35-40 mm FL (fork length) can be mature (Hildebrand and Cable 1930; Fives *et al.* 1986). Alternatively, fish of this size may be as old as 10 months (Dovel 1971), but no daily age data are available for Chesapeake Bay. Stevenson (1958) believed that the bay anchovy spawned only once per year in Delaware Bay because he found a few fish with fully developed ovaries. Recent studies have shown that ovaries with hydrated oocytes are not rare in most engraulids, though they may seem rare because they are found only at particular times of year for a few hours each day (Hunter *et al.* 1985; Clarke 1987). The purpose of my study was to determine age and size at first sexual maturity, spawning frequency, and batch fecundity in bay anchovy from lower Chesapeake Bay.

MATERIALS AND METHODS

Age validation

I used laboratory-hatched fish and caged wild-caught fish to validate daily increments of lagenar otoliths. In the laboratory, bay anchovies were raised from eggs held at 25 ± 2 °C by methods similar to those of Houde (1978 and references therein). On 11 September, I immersed about 150 wild-caught bay anchovies in a 200-300 mg/L tetracycline bath for 24 h (Choate 1964; Weber and Ridgway 1967; Hettler 1984) after they had been acclimatized in a holding tank for a week. I then transferred the tetracycline-marked fish to a cage in the York River, a Virginia tributary of lower Chesapeake Bay. The cage was made of 6 mm nylon mesh and was 2 m in height and 1 m in diameter. No additional food was given to these fish. I assumed that natural planktonic prey organisms could pass easily through the mesh because most caged fish sampled had full stomachs.

Fish were removed periodically from laboratory (2-7 d) and cage (2-3 weeks) treatments, measured, and weighed. I removed otoliths (saccular and lagenar) from otic capsules and mounted them on glass slides with Flo-texx mounting medium. Otoliths were ground with 600 grit sandpaper and polished against a piece of microcloth containing 0.3 μm alumina oxide polishing compound. Polished otoliths were rinsed with water and etched with 5% EDTA (adjusted to pH 7.5 with KOH) for 30-60 s (Haake *et al.* 1982; Casselman 1983). I read prepared otoliths under a compound microscope.

Reproductive biology

To determine ovarian stage, spawning frequency, batch fecundity, and diel spawning time, I collected eggs and adult bay anchovies in lower Chesapeake Bay on 6 June, 6 July, 4 August, and 31 August 1988 over a 24-h period. I deployed a 5-m semiballoon otter trawl with a 3-mm mesh cod end liner and a 0.5-m diameter, 505-μm-mesh plankton net at 1-2 h intervals. An extra float was tied to the float line to keep the trawl off the bottom. The trawl was towed 5-10 min over bottom depths of 6-8 m. Adult bay anchovies were preserved in 10% formalin, and plankton samples were preserved in 50% isopropanol. In addition, adult bay anchovies were attracted with a light and collected with a 1-m diameter plankton net at a pier in the lower York River at night on 1, 2, 3, 8, 9, 10, 11, 12, and 14 July 1988. All these fish were examined for the presence of hydrated oocytes in fresh ovaries. During the nonspawning season (September-May), monthly samples were collected from a trawl survey.

Ovarian maturation.--I calculated the gonadosomatic index (GSI) as GSI = $100 \cdot$ GWT/BWT; GWT is gonad wet weight (mg) and BWT is gonad-free wet body weight (mg). Female bay anchovies from 6 July collections were classified as spawners if their ovaries contained oocytes greater than 0.34 mm in diameter; otherwise they were classified as nonspawners. To estimate the rates of oocyte development, ovaries of 10 spawners from each sample collected on 6 July (140 fish) were teased apart on a glass slide, and a few drops of glycerin were added to spread the oocytes. The major axis of 10 oocytes in the most advanced mode (represented by the darkest oocytes under transmitted light before hydration and by transparent oocytes after hydration) was measured to the nearest 0.01 mm with an ocular micrometer. To determine the oocyte size frequency distribution, I selected a fish with a mean oocyte size close to the grand mean of all fish in the sample, and we measured all oocytes larger than 0.30 mm in a 20-30 mg subsample (about 200 oocytes). Several ovaries of different developmental stages were examined histologically as described by Hunter and Macewicz (1985).

Spawning season and time.--From May to September 1988, I obtained plankton samples periodically (3-6 d) at a pier in the lower York River to determine the beginning and end of the spawning season. I used the presence of bay anchovy eggs in plankton samples as an indication of spawning activity because bay anchovy eggs hatch in about 24 h.

Eggs from plankton samples collected on 6 June, 6 July, and 31 August were classified in two categories; recently-spawned (stage I and II in Moser and Ahlstrom 1985), and well-developed (stage IX-XI) to determine the diel periodicity of spawning during the 1988 spawning season. I identified the start of spawning time by the first appearance of recently-spawned eggs (which were usually much less than 1% of total eggs), and the end of spawning time by the disappearance of ovaries with hydrated oocytes. No cruise was made in May to estimate spawning time, and on 4 August the cruise was not completed because of bad weather.

Spawning frequency and batch fecundity.--Because the hydrated oocyte stage lasted less than 4 h, spawning frequency (fraction of mature females spawning per day) was estimated as the percentage of females with hydrated oocytes (DeMartini and Fountain 1981; Hunter and Macewicz 1985; Hunter *et al.* 1985). Only samples collected 0.5

to 2 h before spawning time were used in estimating the spawning frequency and batch fecundity (number of eggs per spawn). I used a 10-20 mg subsample of the ovaries to estimate batch fecundities. The step-by-step procedure (hydrated oocyte method) is outlined in Hunter *et al.* (1985). I estimated the total number of batches spawned per female by integrating the area under the spawning frequency curve according to the method of Hunter and Leong (1981). Relative batch fecundity was defined as the number of eggs per spawn per gram body weight. Relative daily fecundity was defined as the number of eggs spawned per day per gram body weight.

I estimated energy output of spawning per day (E_p) as $E_p = F \cdot EWT \cdot Q_e/d$, where F is batch fecundity, EWT is dry egg weight (g), Q_e is egg energy value (J/g dry eggs), and *d* is spawning interval (d/batch). I estimated percentage of body energy spawned per day by dividing E_p by the body energy of bay anchovy. Dry egg weight data and egg energy value (22,916 J/g) of bay anchovy were from Tucker (1983). I used the energy value of 17,276(±739 SD) (J/g dry weight) for northern anchovy, *Engraulis mordax*, (Hunter and Leong 1981) to estimate the body energy of bay anchovy. I define spawning peak as a period when the daily energy output of spawning is at least 90% of the highest value.

Age and size at maturity.--I aged 93 bay anchovies collected on 31 August and examined them for maturity stages. The logistic equation was fitted to the percentage of mature individuals in each size class and in each age class (Gunderson 1977; Ni and Sandeman 1984).

Statistical procedures

I used simple linear regression with a 99% confidence interval of mean predicted value to evaluate the relationship between number of otolith increments and age of laboratory-hatched bay anchovy. I used Student's *t*-test to compare mean number of increments deposited after tetracycline marking with the number of days after tetracycline treatment. I performed analysis of covariance on percent mature fish as a function of age and size. I also tested heterogeneity of slopes for regressions of batch fecundity on size (both length and weight) and month with analysis of covariance. The square root of the mean square error for the regression of batch fecundity on fork length and on weight was used to compare the fit of the relationship (Hunter *et al.* 1985). The acceptable level for all type I errors was set at $P = 0.05$.

RESULTS

Age validation

Laboratory experiments ended 47 d after hatching when the fish were 18.6 - 24.1 mm FL (mean 21.7 mm). The slope (0.98) of the regression of number of otolith increments on age of fish was not significantly different from 1.0 (*t*-test, P = 0.50, Figure 1.1). The intercept was -23.1 d and the 99% confidence interval of mean predicted values extended from -21 to -25 d. This indicated increments were formed daily in the lagenar otoliths after their formation at the age of 23 ± 2 d.

Most cage-cultured fish sampled 18, 32, and 53 d after tetracycline treatment had a clear tetracycline mark in the lagenar otoliths (Table 1.1). Mean increment

Figure 1.1 Linear regression line (solid line) and 99% confidence limits (dashed lines) of mean predicted values of lagenar otolith increments versus known ages based on data from laboratory-raised bay anchovies. Several points represent more than one value.

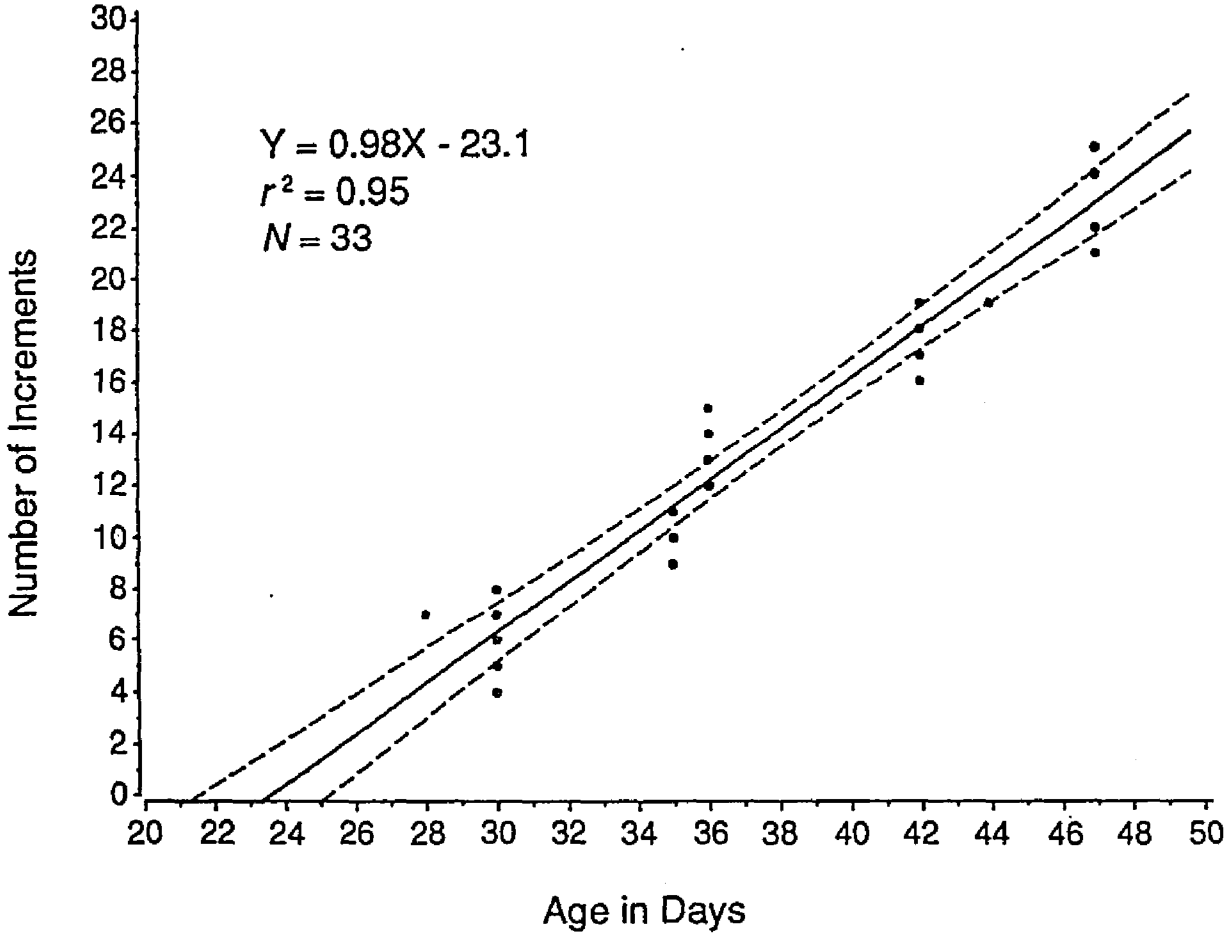

Y = 0.98X - 23.1
r² = 0.95
N = 33
Number of Increments
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
20
22
24
26
28
30
32
34
36
38
40
42
44
46
48
50
Age in Days

Table 1.1 Number of growth increments of lagenar otoliths after tetracycline treatment and growth rates of caged bay anchovies in Chesapeake Bay, 1988.

Date	Temperature (C)	*N*	Fork length (mm)		Days after treatment	Number of increments		Growth rate (mm/d)
			mean	SD		mean	SD	
12 Sep	23.3	14	39.7	4.8	0	0	0	
30 Sep	21.9	10	49.4	2.0	18	18.6	1.1	0.52
14 Oct	16.4	20	54.1	3.9	32	30.8	4.5	0.34
4 Nov	11.5	30	56.4	3.2	53	45.9	7.4	0.11

counts after the mark were 18.6, 30.8, and 45.9 respectively. Statistical analysis (*t*-test) indicated that the mean number of increments was not significantly different from the number of days after marking for the first two periods when water temperature exceeded 15°C (*P* = 0.1114 and 0.2694 respectively) and that it was significantly different for the third period when the temperature was below 12°C (*P* = 0.0001).

Reproductive biology

Ovarian maturation.--Oocytes smaller than 0.15 mm were found throughout the year, but those larger than 0.15 mm were found only during the spawning season (May to September). Histological sections revealed that these oocytes, in the primary growth stage (Wallace and Selman 1981), consisted of a scant basophilic cytoplasm and a disproportionately larger, centrally located nucleus containing either a single large basophilic nucleolus (oocytes smaller than 0.05 mm) or multiple perinuclear nucleoli (oocytes of 0.05-0.15 mm). The follicular epithelium was not well developed at this stage.

Ovaries in which the largest oocytes were 0.15-0.25 mm were found in maturing fish (maturing stage). These oocytes had a well-developed follicular epithelium and a dramatically increased basophilic cytoplasm in comparison with the primary growth stage. In the nucleus, basophilically stained nucleoli were seen at the perinuclear position. In the cytoplasm, neutrophilic spherical yolk vesicles appeared circumferentially at various depths. By the end of the maturing stage, yolk vesicles almost entirely filled the cytoplasm. These vesicles are the cortical alveoli precursors, and their contents cannot be termed yolk in the true sense (de Vlaming 1983).

True vitellogenesis became evident only in oocytes larger than 0.25 mm (mature stage). At this stage yolk proteins were deposited as acidophilically stained yolk granules, and the oocytes increased in size rapidly, growing from 0.25 to 0.35 mm over 24 h (6 July samples). As the accumulation of yolk continued, the germinal vesicle (nucleus) migrated toward the animal pole and the oocyte elongated. During the daily spawning peak, oocyte in the most advanced mode progressed very quickly toward maturation. The major axis increased from 0.35 to 0.60 mm and the gonadosomatic index increased from 3% to 8% in 20 h in spawners (Figure 1.2). The most advanced mode was completely separated from the next mode at 1700 hours when hydration was first observed (Figure 1.3).

Hydration started when the germinal vesicle arrived at the animal pole (1700 hours in 6 July samples, Figure 1.2). At the same time the dissolution of the germinal vesicle membrane occurred. During the 4-h process of hydration, oocytes rapidly absorbed fluids of lower specific gravity than seawater, and the yolk granules fused into yolk plates. The oocytes became progressively more transparent, and the major axis increased to 0.80-1.10 mm. The mean gonadosomatic index reached 20% at this stage.

Figure 1.2 Development of spawning bay anchovy ovaries over a day. Samples were collected from 1100 hours (Eastern Daylight Time) on 6 July to 0800 hours on 7 July 1988. Solid line connects means of oocyte length; dashed line connects means of gonadosomatic index; vertical lines = standard deviation.

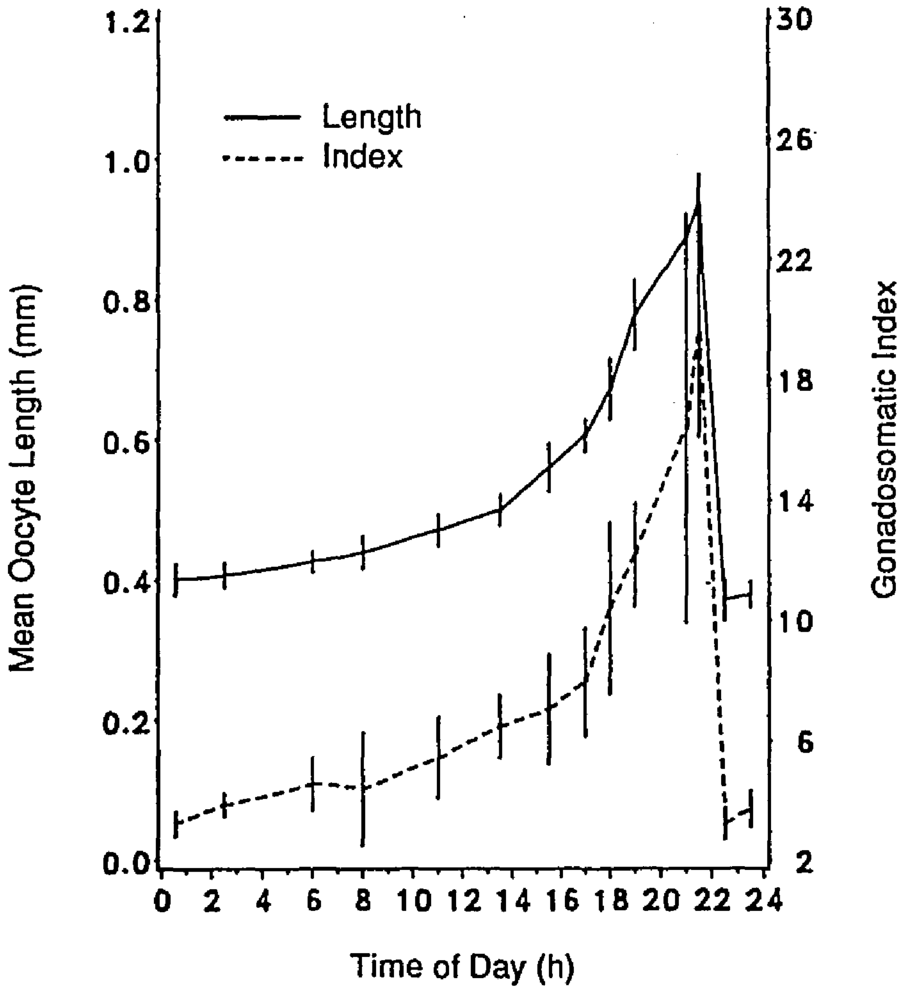
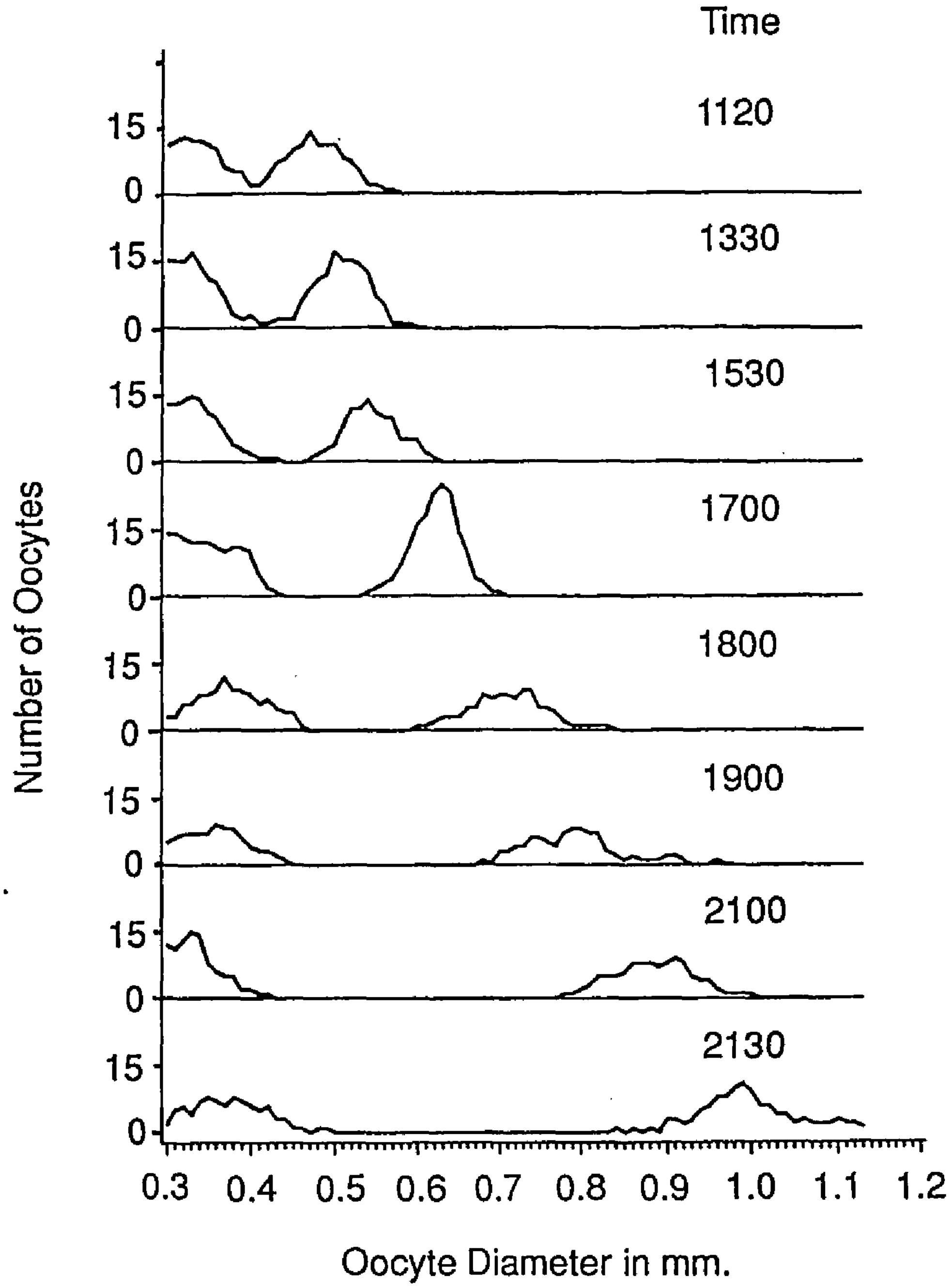

Length
Index
Mean Oocyte Length (mm)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Gonadosomatic Index
30
26
22
18
14
10
6
2
0 2 4 6 8 10 12 14 16 18 20 22 24
Time of Day (h)

Figure 1.3 Oocyte size frequencies of bay anchovy from 1120 hours to 2130 hours on 6 July 1988.


Time
1120
1330
1530
1700
1800
1900
2100
2130
15
0
Number of Oocytes
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
Oocyte Diameter in mm.

Spawning season and time.--Eggs collected from plankton samples in the York River indicated that the spawning season of the bay anchovy in 1988 was from early May to mid-September. Spawning occurred when the oocytes were fully hydrated, and it lasted about 1.5 h each night. Bay anchovy started to spawn by 2000 hours on 6 June, by 2100 hours on 6 July, and by 2300 hours on 1 August (Figure 1.4). One hour after spawning was first observed, the largest oocyte group in the ovaries had a mean of 0.35 mm and were at true vitellogenesis. At this time the postovulatory follicles were clearly distinguishable, but they were scarcely visible 16-21 h after spawning and none remained evident 21 h after spawning in July.

Spawning frequency and batch fecundity.--An analysis of data on ovaries with hydrated oocytes (Table 1.2) indicated that on average, bay anchovy spawned every 4 d in early June (based on 6 June samples); every 1.9 d in the beginning of July; and every 1.3-1.4 d (2-3 batches in 3-4 d) from 6 July to 31 August. Each mature female would spawn an average of 54 times between 6 June and 31 August 1988 based on the integration of the area under the frequency curve (Figure 1.5).

Batch fecundity varied from month to month with a mean of 429 eggs per batch on 6 June, 893 on 6 July, 1,186 on 4 August, and 562 on 31 August (Table 1.3). Batch fecundity was a linear function of fork length (Table 1.3) and of body weight (Figure 1.6). The square root of the mean square error showed no apparent differences between the relationship with fork length and with weight (142 versus 149

Figure 1.4 Spawning times (Eastern Daylight Time) of bay anchovy on three days in 1988. Circles represent percentage of spawning females; squares represent percentage of stage I and II eggs in plankton samples; start = start time of spawning; end = end time of spawning.

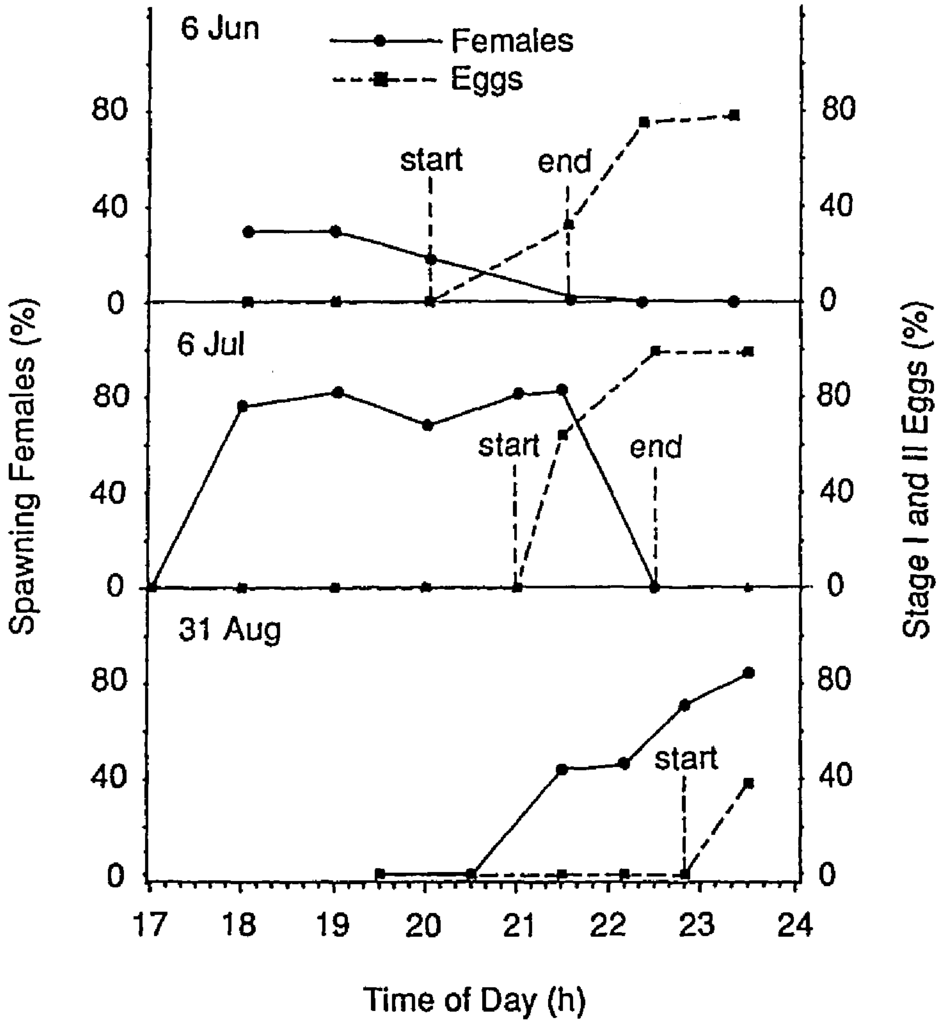

6 Jun
Females
Eggs
start
end
6 Jul
start
end
31 Aug
start
Spawning Females (%)
Stage I and II Eggs (%)
0
40
80
17
18
19
20
21
22
23
24
Time of Day (h)

Table 1.2 Sex ratio, percentage of females with hydrated oocytes (*N* = sample number used in estimating the mean), and spawning interval for bay anchovies in Chesapeake Bay, 1988. Spawning interval is the inverse of spawning frequency (*f*).

Date	t (°C)	Sex ratio (% female)	Number of fish	Percentage of females with hydrated oocytes mean (*f*)	range (*f*)	*N*	Spawning interval (*d*)
6 Jun	20.0	44	709	25	18-29	3	4.0
1-3 Jul	23.0	54	264	54	21-70	5	1.9
6 Jul	24.6	57	502	78	68-83	5	1.3
8-10 Jul	25.2	57	566	72	45-90	14	1.4
11-14 Jul	25.5	45	492	75	53-92	4	1.3
4 Aug	28.6	51	59	70	62-78	2	1.4
31 Aug	25.4	45	327	76	71-81	2	1.3

Figure 1.5 Fraction of mature bay anchovy females spawning per day (solid line) and percentage of body energy spawned per day for a fish of 55 mm fork length (dashed line) during the 1988 spawning season.

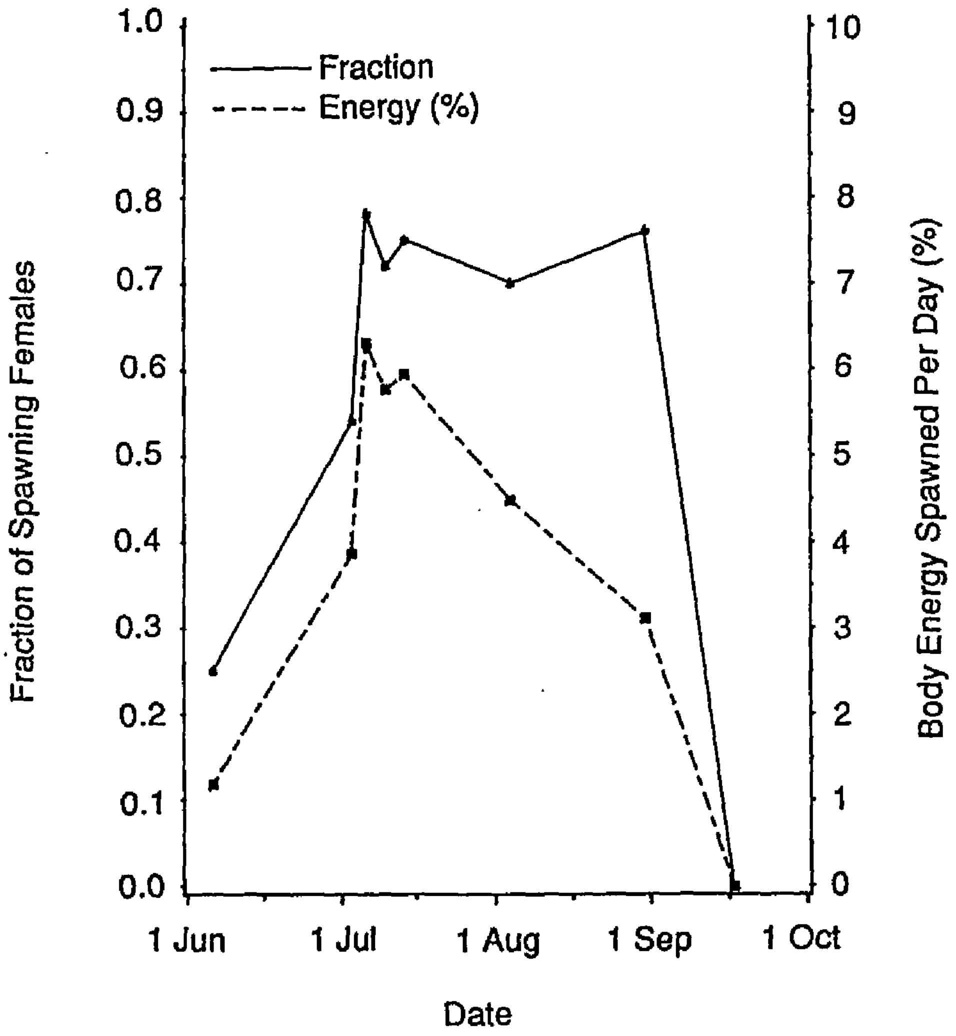
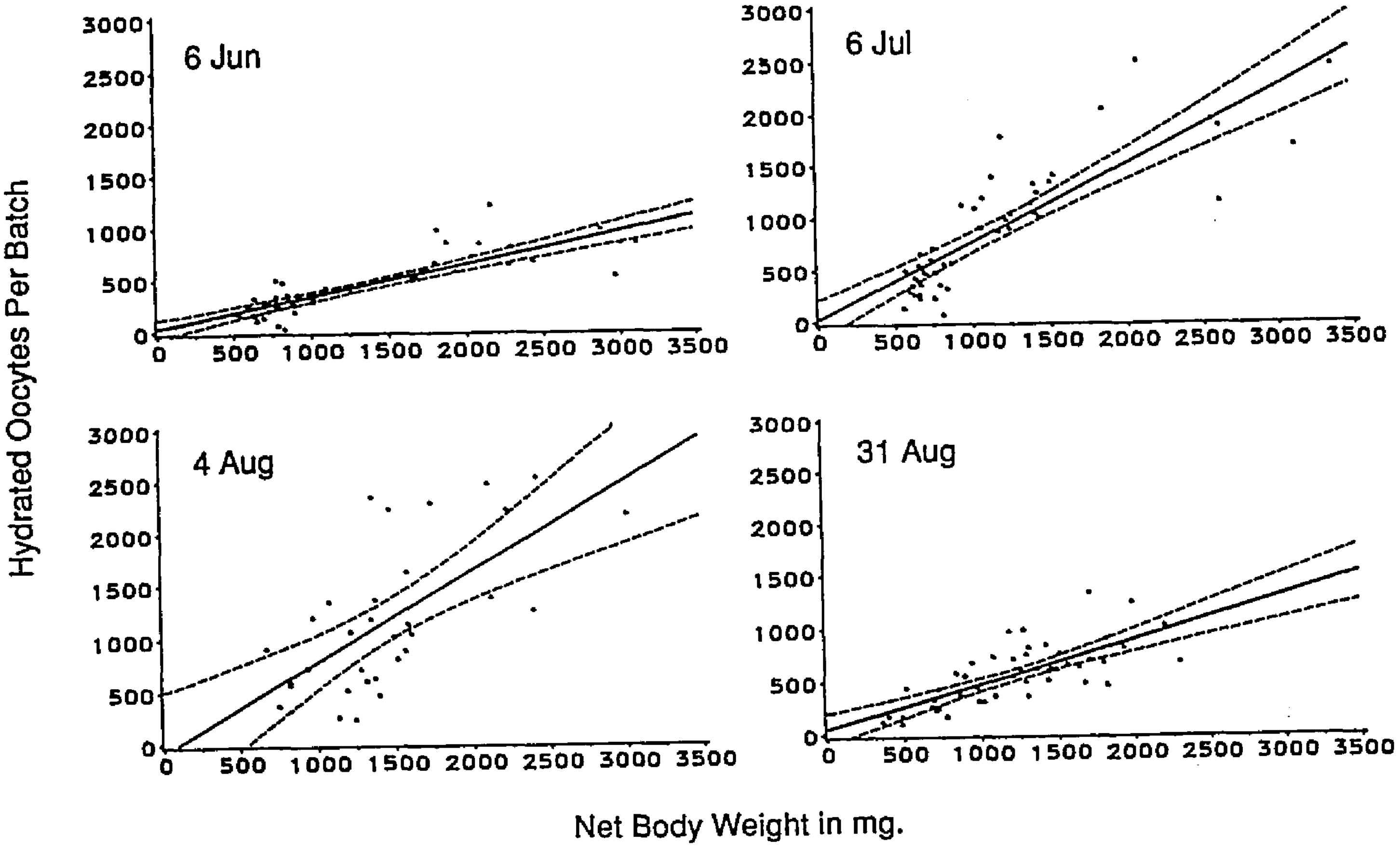

Fraction
Energy (%)
Fraction of Spawning Females
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Body Energy Spawned Per Day (%)
10
9
8
7
6
5
4
3
2
1
0
1 Jun
1 Jul
1 Aug
1 Sep
1 Oct
Date

Table 1.3 Statistics of least squares linear regressions of batch fecundity on fork length (FL, mm) and weight (mg) of bay anchovies, 1988. BF = batch fecundity (eggs); RBF = relative batch fecundity (eggs/g).

Statistics	6 June		6 July		4 August		31 August	
	FL	Weight	FL	Weight	FL	Weight	FL	Weight
N	50	50	48	48	32	32	50	50
Intercept	-1192	35	-2571	28	-2097	-74	-859	54
Coefficient	29.7	0.306	64.9	0.743	55.8	0.859	26.1	0.419
r^2	0.73	0.71	0.70	0.70	0.28	0.43	0.55	0.52
P value of rejecting b = 0	0.0001	0.0001	0.0001	0.0001	0.0016	0.0001	0.0001	0.0001
Mean ovary free weight	-	1291	-	1165	-	1468	-	1212
Mean FL	54.6	-	53.4	-	58.8	-	54.5	-
Mean BF	429		893		1186		562	
Mean RBF	334		740		803		464	
BF for a 55 mm fish	425		999		972		577	

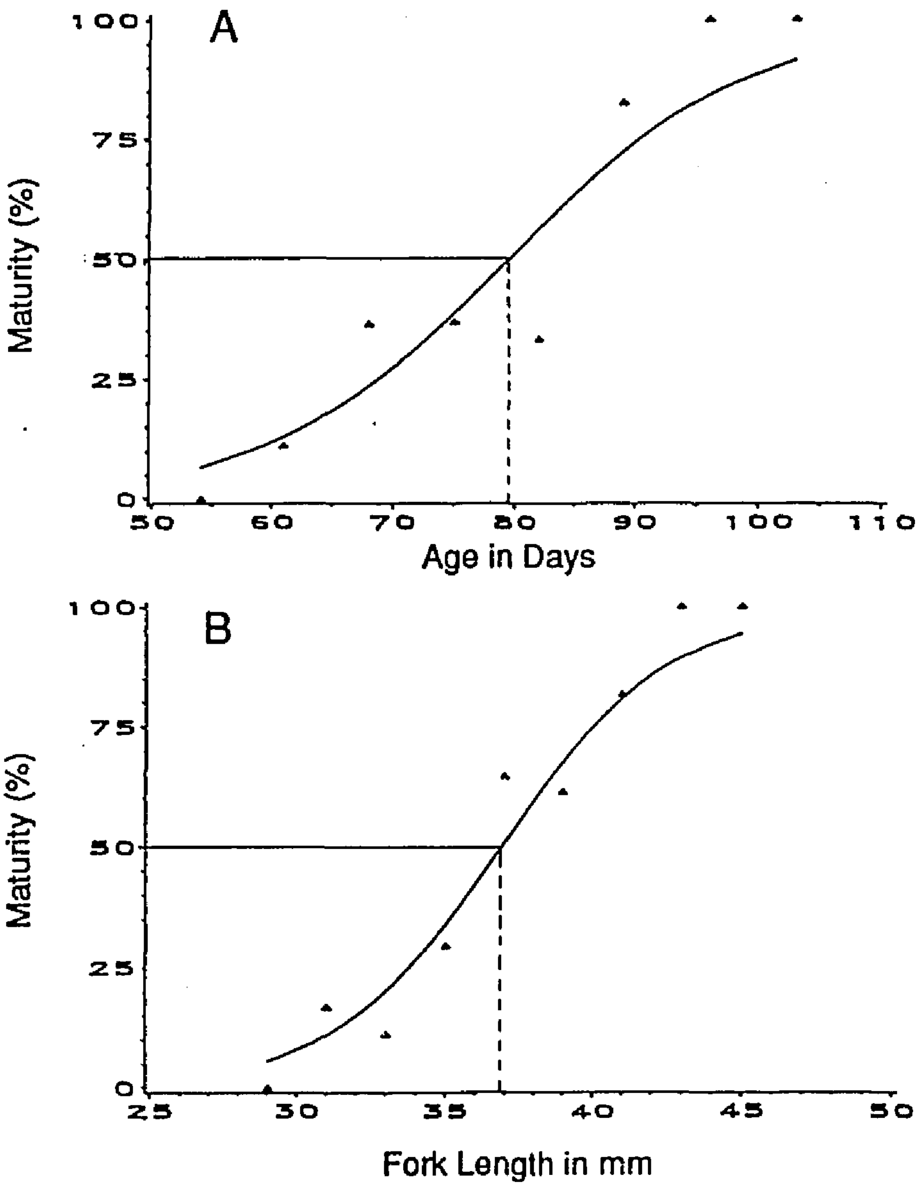
Figure 1.6 Linear regressions (solid lines) and 95% confidence limits (dashed lines) of mean predicted values of batch fecundity with ovary-free body weight (mg) of bay anchovy for four days in 1988.


6 Jun
6 Jul
4 Aug
31 Aug
Hydrated Oocytes Per Batch
Net Body Weight in mg.
0
500
1000
1500
2000
2500
3000
3500

on 6 June; 334 versus 334 on 6 July; 599 versus 537 on 4 Aug; 185 versus 192 on 31 August), probably because of the limited size range of spawning fish and the large variation in batch fecundity. Analysis of covariance indicated that regression slopes on 6 July and 4 August were significantly higher than those on 6 June and 31 August (6 June versus 6 July, $P = 0.0001$; 6 June versus 4 August, $P = 0.0153$; 6 June versus 31 August, $P = 0.6697$; 6 July versus 4 August, $P = 0.3983$; 6 July versus 31 August, $P = 0.0001$; 4 August versus 31 August, $P = 0.0060$). The overall egg production for the season was 45,110 eggs per female (55 mm FL fish), which was equivalent to 346% (area under the dashed line in Figure 1.5) of a females body energy. During peak spawning, daily spawning output was 6.3 ± 0.3% of body energy.

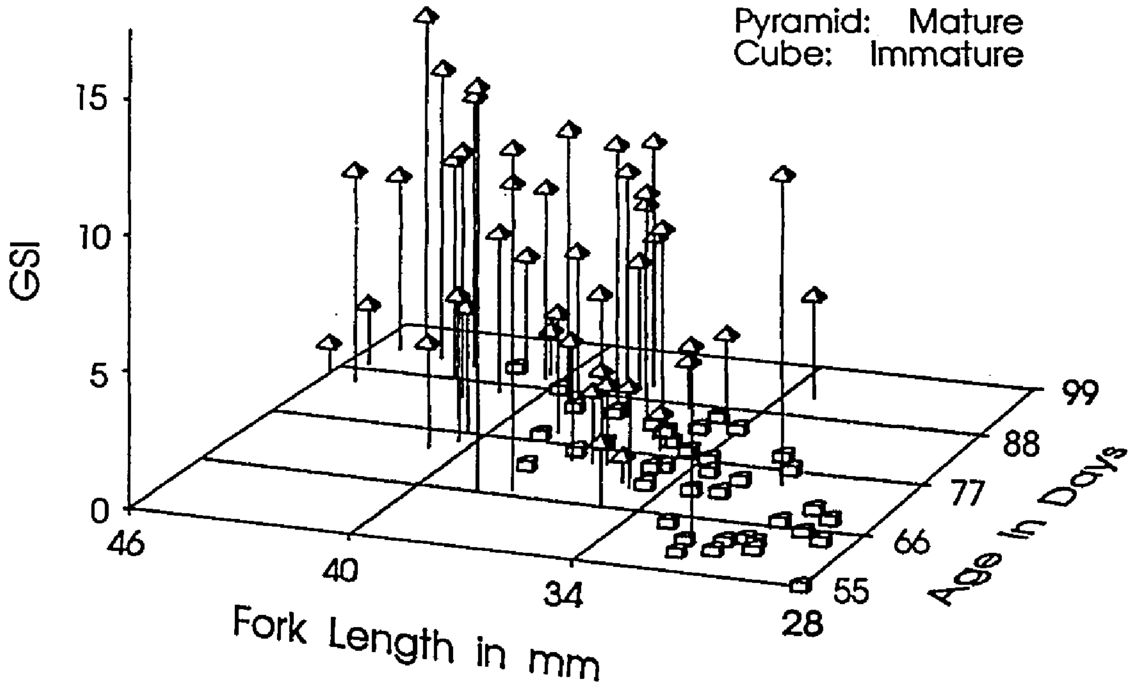
Age and size at maturity.--Maturity was determined by the presence of true vitellogenic oocytes. Histological examination showed that all oocytes larger than 0.25 mm were in the process of true vitellogenesis, and the gonadosomatic indices of these fish were larger than 2%. Therefore, this oocyte size and the index were used as criteria to determine the maturity of fish that were not examined histologically. Logistic curves fitted to the data of size, age and maturity indicated that the size at 50% maturity was 36.9 mm FL ($\% = 100/(1 + e^{(-0.35 \cdot FL + 13.02)})$, $r^2 = 0.88$) and the age at 50% maturity was 80 d ($\% = 100/(1 + e^{(-0.1022 \cdot Age + 8.11)})$, $r^2 = 0.75$, Figure 1.7). A plot of gonadosomatic index on fork length (FL in mm) and age (in days) showed that in each age group, the percent mature was higher in larger fish than in

Figure 1.7 (A) percentage of maturity versus age and (B) percentage of maturity versus fork length of bay anchovy. Curves are fitted logistic functions; dashed lines indicate age and size at 50% maturity.



A
Maturity (%)
100
75
50
25
0
50
60
70
80
90
100
110
Age in Days
B
Maturity (%)
100
75
50
25
0
25
30
35
40
45
50
Fork Length in mm

Figure 1.8 Age and size at sexual maturity of bay anchovy. GSI = gonadosomatic index; pyramid = mature fish (GSI > 2); cube = immature fish (GSI ≤ 2).


Pyramid: Mature
Cube: Immature
GSI
0
5
10
15
46
40
34
28
Fork Length in mm
55
66
77
88
99
Age in Days

smaller fish, and in each size group, percent maturity for older fish was higher than for younger fish (Figure 1.8). Analysis of covariance indicated that age had an effect on the maturity-size relationship ($P = 0.0019$, 0.0001, and 0.0311 for age, length, and length x age, respectively; for the model overall, $R^2 = 0.83$, $P = 0.0004$). The smallest fish with ovaries containing hydrated oocytes found in this study was 31 mm FL and 63 d old.

DISCUSSION

The lagenar otoliths (asterisci) in bay anchovy are useful for daily aging of juvenile and 3-4 month old adult fish. In most fishes, the lagenar otoliths are usually the smallest of the three pairs, but in clupeids, the lapilli are the smallest (Brothers 1983). My study shows that the asterisci in bay anchovy are thin and well defined, and they are well suited for aging juvenile fish. However, they cannot be used to age larval fish because they do not appear until 23 ± 2 d after hatching.

Although increments of lagenar otoliths in bay anchovy were deposited during summer, they were not deposited daily during winter. Cessation of daily increment formation could be a result of cessation of fish growth at low temperatures (Taubert and Coble 1977; Campana and Neilson 1985), given that the stomachs of my fish were full or at least half full. My later cage-culturing experiment showed that from 21 November 1988 to 15 March 1989, when water temperature was between 5 and 12°C, not a single increment was deposited on otoliths of bay anchovies (the 12 fish out of 60 that survived this 86 d experiment showed no growth).

Bay anchovy in Chesapeake Bay mature at a younger age and smaller size than I had expected. I found that fish hatched early in the spawning season were mature and able to spawn during the latter part of the season. Fast growth (0.45 ± 0.05 mm/d) during summer (temperature range 20-28 °C) enabled them to reach spawning size (36.9 mm; size at 50% maturity) in about 80 d (age at 50% maturity), and back-calculated birth dates indicated that these fish were hatched in May and June. However, first sexual maturity depended both on age and size. My study indicated that larger fish matured at younger ages and older fish matured at smaller sizes.

The spawning season of bay anchovy in Chesapeake Bay varies from year to year; the earliest spawning season reported lasted from 22 April to 22 August 1963 (Dovel 1971) and the latest from 13 June to 26 October 1974 (Dalton 1987). The most common estimates are from May to September (Dovel 1971; Olney 1983; Dalton 1987). I found that the 1988 spawning season ranged from early May to mid September.

My estimate of the time of day at which bay anchovy spawn differs from other reports. Bay anchovy at Beaufort, North Carolina (Hildebrand and Cable 1930) and at Peconic Bays, New York (Ferraro 1980) spawned between 1800 and 2100 hours. Zastrow *et al.* (1991) reported that bay anchovy in mid-Chesapeake Bay spawned between 2100 and 2400 hours in 1986 and 1988. My data showed that spawning time varied from month to month; it was delayed as the season progressed (2000 hours on 6 June to 2330 hours on 31 August, Figure 4). If the day-to-day variation of spawning time within a month was small, there must have been some factor responsible for the delay. There are many explanations for diel spawning periodicity, including synchronized reproduction between sexes (Aschoff 1964; Marshall 1967), reproductive isolation (Marshall 1967), avoidance of high levels of solar radiation (Bell and Hoar 1950; Perlmutter 1961), and predation reduction (Nikolsky 1963). None of these, however, explains the delay in time of spawning I observed.

One of the major assumptions underlying the estimation of spawning frequency from the fraction of females with ovaries containing hydrated oocytes is that a representative sample of the population is obtained. Spawning frequency would be overestimated if there were segregation of spawners and nonspawners or if nonspawners were less susceptible than spawners to capture by the sampling gear. However, I found only a small variation in percentage of females with hydrated ovaries in samples collected on 6 July (Figure 1.4), which indicated the samples came from a well-mixed population.

During the spawning peak, oocytes of bay anchovy developed from 0.35 mm to 0.90 mm (spawning size) in 24 h. This is the fastest rate reported for engraulids. Oocytes develop from 0.46 mm to the size at which hydration begins in about 7 d in northern anchovy (Hunter and Goldberg 1980) and about 6 d in Peruvian anchoveta *E. ringens* (Alheit *et al.* 1984, Alheit 1989). In Hawaiian anchovy *Encrasicholina purpurea*, 2 d are required for oocytes of 0.52 mm to develop to spawning size (0.80-1.00 mm, Clarke 1987).

I saw postovulatory follicles only within 21 h after spawning occurred in July. They were clearly distinguishable up to the first 8 h after spawning. They were also found in ovaries within 3-7 h of spawning, thus providing direct evidence that some bay anchovies spawned every day during the spawning peak. The spawning frequency estimated from the postovulatory follicles is 75%, which is very close to the 78% estimated from the fractions of females with hydrated ovaries on 6 July. Zastrow *et al.* (1991) reported that bay anchovy in mid-Chesapeake Bay spawned every day in July 1987.

Most spawning energy in bay anchovy must have been derived from daily feeding, not from fat reserves. In northern anchovy, 60% of spawning energy was supplied by fat reserves over the spawning season (20% of body energy, Hunter and Leong 1981). At the spawning peak, the daily energy output in bay anchovy was about 6% of body energy (Figure 5). If bay anchovy use 20% of body energy from fat reserves for spawning over the spawning season, less than 0.2% of body energy would be used daily. Therefore, the rest of the energy required has to be from daily feeding. Vazquez (1989) reported that bay anchovy were able to consume as much as 28% of their own body weight each day with an assimilation efficiency of over 60%. Thus, the assimilated energy was about 18% of body energy, which would be sufficient to support observed spawning activity as well as body growth and maintenance. Therefore, I conclude that bay anchovy are capable of spawning every day during peak spawning if there is sufficient food. Conversely, any shortage of food will immediately affect spawning output.

Relative daily fecundity may be a better index than relative batch fecundity for comparing egg production of different species, because some fish spawn more frequently than others (Table 1.4). Compared with other anchovy species, the bay anchovy has much higher relative daily fecundity and greater reproductive potential. This is probably an adaptation to highly variable environmental conditions characteristic of Chesapeake Bay and other temperate estuaries.

Table 1.4 Relative batch fecundity (RBF, eggs/g), spawning intervals (SPI, d), and relative daily fecundity (RDF, eggs/g/d) of four anchovy species (Engraulidae).

Species and sampling time	N	RBF (A)	SPI (B)	RDF (A/B)	Reference and location
Anchoa mitchilli					This study (lower Chesapeake Bay, Virginia)
6 Jun 1988	50	306	4.0	77	
6 Jul 1988	48	743	1.3	572	
4 Aug 1988	32	859	1.4	614	
31 Aug 1988	50	419	1.3	322	
30 Jul 1986	10	643	1	642	Zastrow *et al.* (991) (mid-Chesapeake Bay)
30 Jun 1987	10	731	1	731	
Encrasicholina purpurea					Clarke 1987 (Kaneohe Bay, Hawaii)
Summer	128	566	2	283	
Winter	94	368	2	184	
Engraulis capensis					Armstrong *et al.*(1987) (South Africa)
Spawning peak		530	5	106	
Engraulis mordax					Hunter and Macewicz 1980 (North Pacific, off California)
Central population (Spawning peak, Feb - Mar)	67	421	7	60	
Engraulis ringens					Minano 1968 (South Pacific, off Peru)
(Spawning peak, Aug - Sep)	83	651	6	109	
Aug/Sep 1981	254	637	6	106	Alheit (1989) (Peru)
Aug/Sep 1985	58	568	6	95	

CHAPTER 2

Tidal Transport of the Bay Anchovy in Darkness

INTRODUCTION

The schooling behavior of estuarine fishes has rarely been investigated in the field because of difficulties caused by low visibility and strong tidal currents. Most studies of fish schooling have been conducted in the open ocean, over coral reefs and in freshwater lakes, at times when visibility was high and water currents were weak. Moreover, most of these studies (reviewed in Pitcher 1986) emphasize the mechanisms and advantages of maintaining schools. Although it is widely known that schooling behavior in most fishes is not prevalent at night (Parr 1927; Loukashkin & Grant 1959, 1965; Blaxter & Holliday 1963; Whitney 1969; Shaw 1970, 1978; Radakov 1973; Blaxter & Batty 1985; Helfman 1986; Batty *et al.* 1990), there is little information about the fate of fish when schooling ceases.

The bay anchovy, *Anchoa mitchilli* (Valenciennes), is the most abundant fish in Chesapeake Bay (Chittenden 1989). It is a pelagic, schooling, and euryhaline species, and occurs in freshwater through salinities as high as 45‰ (Robinette 1983). In holding tanks bay anchovy schools break up after dark, and fish swim in all directions at a greatly reduced speed (pers. obs.). Houde and Brandt (pers. communi.), using acoustic estimates and trawl catches, found throughout the year that during daylight bay anchovy are in tight schools near bottom, and that at night fish are scattered throughout the water column and form only loose or scattered schools. If this behavior is common, bay anchovies may be susceptible to transport by tidal currents at night. Since the duration of flood and ebb tidal currents at night are usually asymmetrical (such as 6-h flooding and 2-h ebbing), depending on the time of the lunar period, season and latitude, the transport distance and direction will vary. The resulting change in the spatio-temporal distribution may be important to the energetic processes in the ecosystem.

The purpose of this study, using laboratory flume experiments and a field mark-recapture study, was to determine whether bay anchovies are transported by currents when schooling ceases in darkness.

MATERIALS AND METHODS

Definition of schooling

Although there are many definitions of schooling (Shaw 1970; Partridge 1982; Pitcher 1983), it is important to use one that gives a clear concept about the social behavior of fish under investigation. In this study, I employ the term 'schooling' for a synchronized swimming behavior as fish adjust speed and direction to that of their neighbors, and the term 'shoaling' for a social gathering in which fish may be either polarized or nonpolarized (Pitcher 1983). By these definitions, all schools are shoals, but not all shoals are schools.

Collection of anchovies

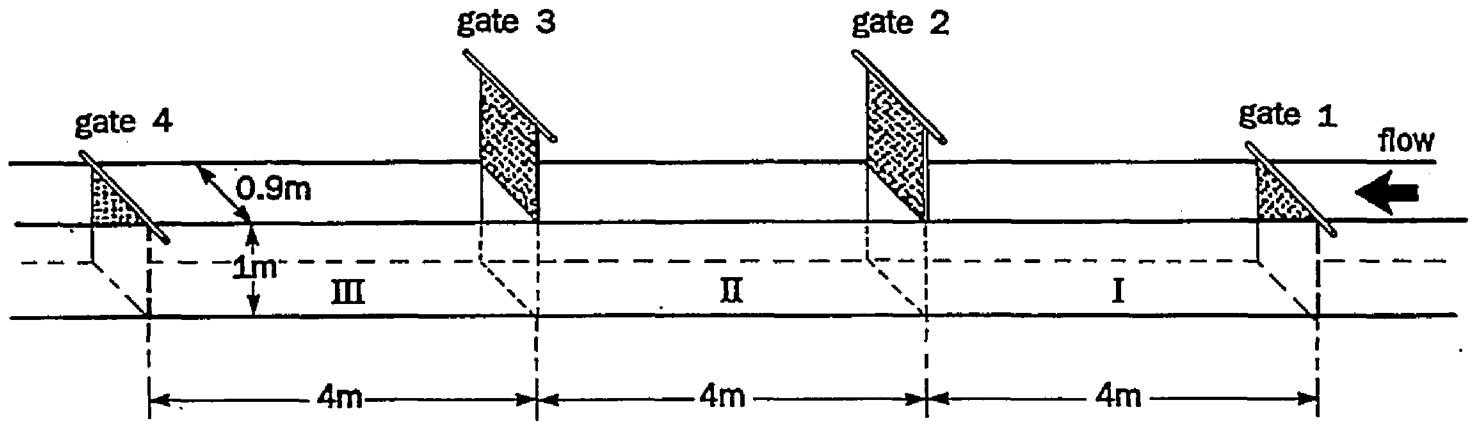
Bay anchovies were attracted with a light and collected by dip-netting at night with a 1-m, 505-um plankton net at a pier in the lower York River (Gloucester Point, Virginia, U.S.A.) from August to October 1989. The temperature was 25-28°C in August, 20-25°C in September and 16-20°C in October. Salinity was 19 ± 2°/$_{\infty}$ throughout the study. After collection, the fish (usually 50-300 individuals for each dipping, size range of 30-65 mm fork length) were transferred into an open-seawater holding tank with flow-through river water.

For the flume experiment, bay anchovies were acclimatized to freshwater by dilution in the holding tank for a period of one week. No fish died during the acclimatization period.

Laboratory experiment

An 18-m hydraulic flume filled with fresh water (22 ± 1°C) was used to test relative transport of bay anchovies in darkness. The test section of the flume was 12-m long, 0.9-m wide, and 1-m deep (water filled up to 0.9-m depth), and had a stainless steel bottom and glass side walls. Water speed in the test section could be adjusted from 2 to 75 cm s^{-1}, with essentially uniform speed within a cross section, except near the walls and bottom. Current speed was determined by measuring the transit time of a drogue between two laser beams 50 cm apart. The test section of the flume could be divided into three segments by inserting 2-mm mesh plastic screen gates (Figure 2.1). The flume room had no windows and was illuminated with 30 fluorescent lights (40 w each) on its ceiling. The light intensity measured on the surface of flume was about 400 lux. Darkness (<0.001 lux) was achieved by turning off all lights.

Figure 2.1 The test section of the hydraulic flume (the mechanical portion is not shown on the diagram).


gate 3
gate 2
gate 4
gate 1
flow
0.9m
1m
III
II
I
4m
4m
4m

After a preliminary trial on 10 August 1989 (Table 2.1), fish were tested at four current speeds (11, 16, 21, 30 cm s^{-1}) in trial 2 on 24 August 1989. First, all lights were turned on (about 400 lux) and the flume speed was adjusted to 5 cm s^{-1}. About 100 fish were released into Segment I of the flume. After 5 min acclimatization, gates 2 and 3 were removed, and speed was increased to the test value. At that time most fish were schooling; those not schooling were removed from the flume. When the school was positioned in the upstream portion of segment I, lights were turned down slowly. Darkness (< 0.001 lux) was maintained for the length of time necessary for the water to traverse the test section (i.e. 40 s for 30 cm s^{-1} speed). Gates 2 and 3 were lowered prior to turning on the lights. Numbers of fish in each segment were recorded, then gates 2 and 3 were removed and bay anchovies were allowed to resume schooling. Damaged fish were removed from the flume and the remaining school was then tested again at the same speed. After the second test, all fish were removed from the flume and the water flow restored to 5 cm s^{-1}. A different group of 100 fish was used at each speed.

Field experiment

Bay anchovies were marked with neutral red dye. The suitability of this vital stain depended on dye concentration, immersion time and salinity. From preliminary experiments, the best combination for the bay anchovy was 0.01 g l^{-1} for 1 h at 8-14 $^{\circ}/_{\circ\circ}$ salinity. After immersion the whole body of bay anchovy was bright pink, the survival rate was 100%, and the stain remained easily visible for at least 2 d. Studies using neutral red dye with other fishes have been successful and have reported insignificant behavioral effects (Cantrelle 1984; Pavlov & Gorin 1985).

Mark-recapture experiments were conducted in Queen Creek, a York River tributary about 10 km in length, 30-60 m in width and 2-3 m deep in the channel (Figure 2.2). A 5-m, 3-mm mesh otter trawl towed with the current from an 8-meter boat was used to recapture the fish. An extra float was tied to the head line to increase the vertical range of net, and each tow covered about a 100 m distance.

The first mark-recapture experiment was performed on a flooding tide during evening hours on 18 September 1989. About 2,500 bay anchovies, which had been kept in holding tanks for 3-4 d, were loaded to three 150-l tanks on the boat. Salinity in the tanks was adjusted to 14 ± 1‰ by adding fresh water. At the release site, creek water (13‰, 25°C) and neutral red dye (0.01 g l^{-1}) were added to the tanks. After 1 h immersion in the dye solution, all fish were transferred to a nylon screen cage (2-mm mesh, 1 m diameter and 1.5 m high) in the creek. At 2100 hours (about 30 min after the fish were caged) all fish were released by immersing the whole cage under water, turning it upside down and pulling it out of the water. At the same time, a lighted hydrographic near-surface drogue was released to monitor water movement. The drogue was designed to float 1 m below the surface. At 2200 hours the first otter trawl tow was made at the release site. Subsequently, 9 tows within 200 m of the drogue were made during the next 3 h, then 3 fixed stations were sampled after the drogue was picked up at the upper most station (Figure 2.2).

Similarly, a daytime experiment was conducted on 22 October 1989 in the same creek. Surface temperature was 16°C and salinity was 10 °/₀₀. Bay anchovies and the drogue were released at 1400 hours during flooding tide. Tows were made from 1500 to 1730 hours.

RESULTS

Laboratory experiment

In flume experiments, schools of bay anchovies were able to maintain position against a current (up to the maximum flume speed of 75 cm s^{-1}) during daylight conditions. All fish remained in Segment I during extended periods of light (400 lux). Schools broke up during nighttime conditions. In darkness, only 53% of fish were able to maintain position at a current speed of 5 cm s^{-1} (Table 2.1). As current speed was increased, most of the fish were flushed to the end of the flume and the percentage of fish in Segment I decreased. At 30 cm s^{-1}, no fish were found in Segment I and 99% of the fish were found in Segment III (Table 2.1).

The percentage of fish transported to the end of the flume increased exponentially as the speed increased (Figure 2.3). The following model was used to analyze the relationship:

$$Y=100\,(1-e^{-au^{b}})$$

Table 2.1 Distribution of bay anchovies in the flume at different velocities in darkness.

Measured velocity cm s^{-1}	Segment I		Segment II		Segment III		Total
	count	(%)	count	(%)	count	(%)	count
Trial 1							
5	24	(53)	6	(13)	15	(34)	45
14	6	(14)	13	(31)	23	(55)	42
25	1	(4)	3	(12)	21	(84)	25
Trial 2							
11	18	(22)	16	(19)	49	(59)	83
11	7	(16)	9	(20)	28	(64)	44
16	1	(1)	14	(16)	75	(83)	90
16	2	(3)	19	(27)	49	(70)	70
21	0	(0)	6	(7)	85	(93)	91
21	0	(0)	5	(14)	31	(86)	36
30	0	(0)	1	(1)	78	(99)	79

Figure 2.2 Map of the study site; for the night experiment, A is the release site; 1, 2, ..10 are tow numbers and F (tow 11, 12 and 13) is the fixed station; for the day experiment, B is the release site and the cross-hatched area is where all marked fish were recaptured.

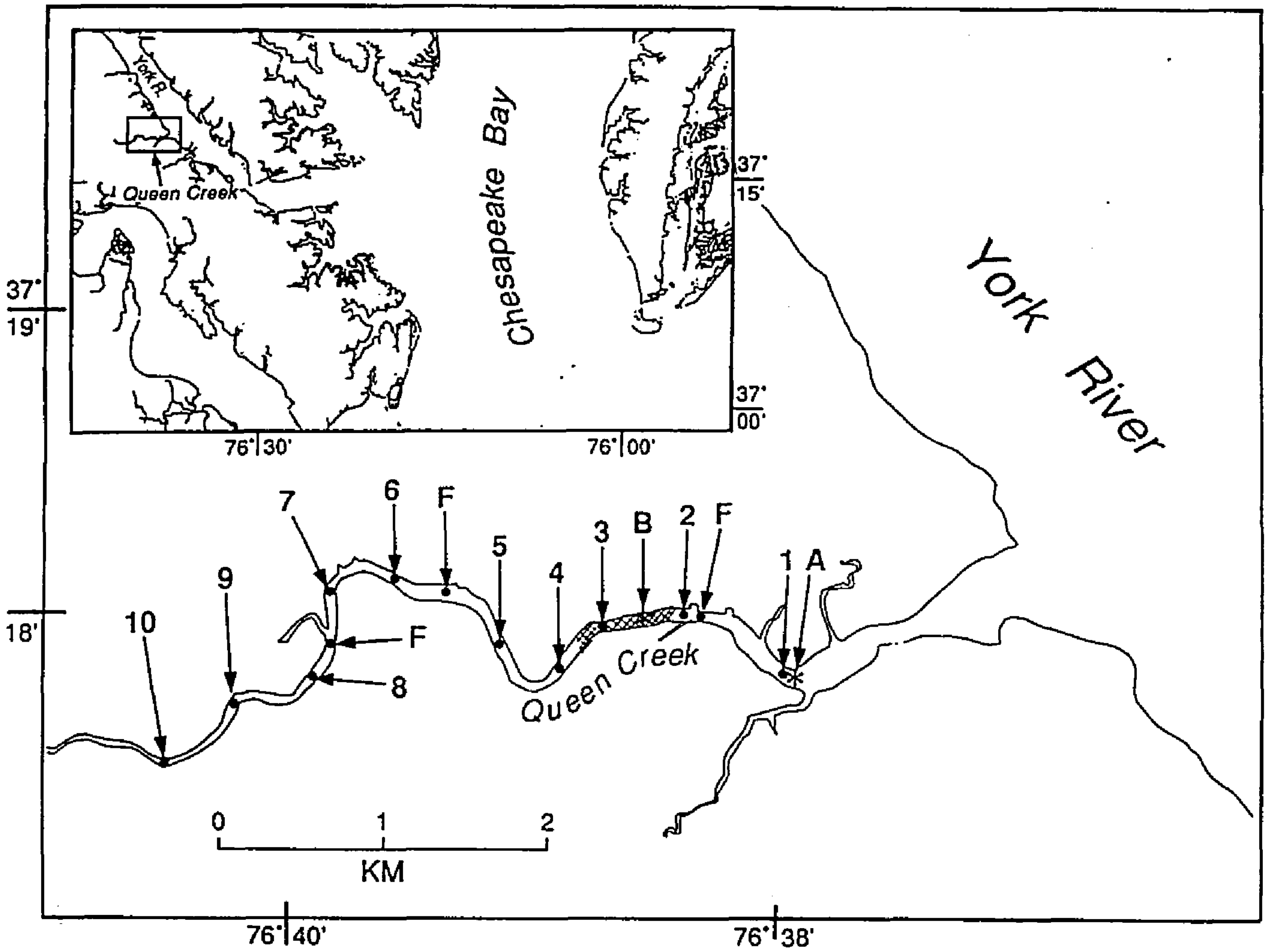
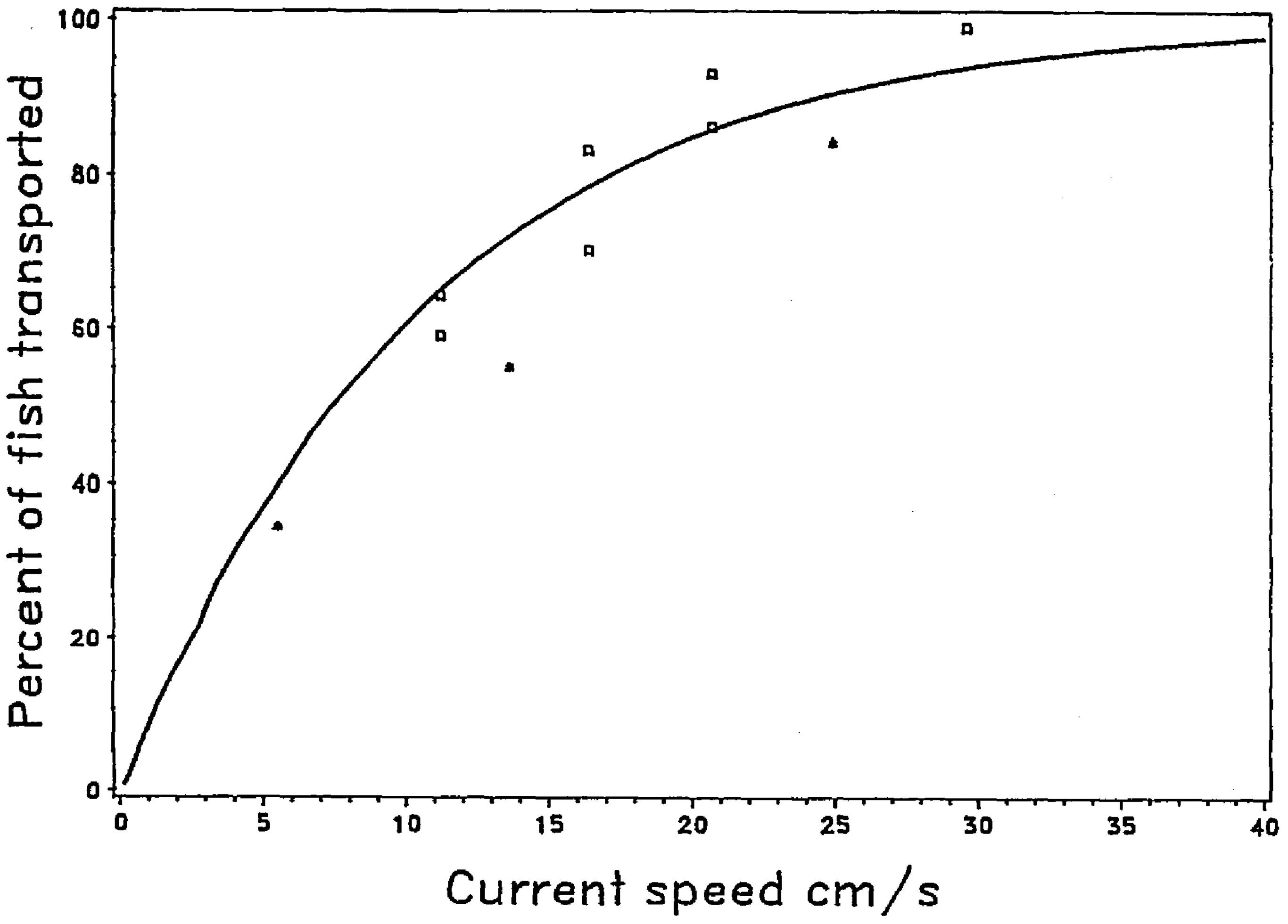

York R.
Queen Creek
Chesapeake Bay
37° 15'
37° 00'
76° 30'
76° 00'
37° 19'
18'
York River
Queen Creek
1
A
2
F
B
3
4
5
F
6
7
F
8
9
10
0
1
2
KM
76° 40'
76° 38'

Figure 2.3 Exponential relation between percent of transport and current speed; the vertical axis is the percent of fish in segment III; horizontal axis is the current speed; stars are data points from trial 1; squares are data points from trial 2.


Percent of fish transported
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
Current speed cm/s

where Y is the percent of fish in Segment III, u is the measured current speed (cm s^{-1}), a and b are parameters to be estimated, and 100% is the asymptote of the model. Analysis of covariance indicated no significant difference between the two trials ($P = 0.1037$) and data in Table 1 were pooled to estimate the parameters: a = 0.0889, b = 1.02 ($r^2 = 0.97$, p = 0.0001).

Field experiment

In the night experiment, marked bay anchovies were captured in the vicinity of the drogue in trawls as much as 5.1 km upstream from the release point for as long as 4 h after release. The drogue was picked up at this point because the boat could not go under a bridge across the creek (station 10 in Figure 2.2). The average current speed in the creek, estimated from the distance (5.1 km) and time interval (4 h), was 35 cm s^{-1}. Fifty-four marked fish all captured within 200 m of the drogue were collected in 9 tows (tow # 2-10 in Table 2.2). Marked fish comprised 0.7%-13.4% of the bay anchovies in each tow. No marked fish were captured at three fixed stations (tow 11-13 in Table 2.2) sampled after the drogue had passed. These stations were 1300, 3000 and 4500 m downstream from the bridge (tow locations are indicated in Figure 2.2).

In the day experiment, tows were made within 500 m downstream and 300 m upstream of the release site for 1-3 h after release (Table 2.3). Marked bay anchovies comprised 1.5-6.2% of those collected and were captured only within 200 m of the release site. The cross-hatched area in Figure 2.2 indicates the location where

Table 2.2 Distribution of recaptured bay anchovies in Queen Creek from night experiment; DFRS is the distance from the release site; DFHD is distance from the hydrographic drogue; slack before flood tide was at 2000 h.

Tow #	Time	DFRS (m)	DFHD (m)	Anchovies in catch	Marked anchovies	% of marked anchovies
Release	21:00	0	0			
1	22:00	0	1000	73	0	
2	22:05	900	100	67	9	13.4 %
3	22:20	1200	200	166	2	1.2 %
4	22:30	1500	100	166	17	10.2 %
5	22:50	2100	100	150	9	6.0 %
6	23:20	3000	100	33	3	9.1 %
7	23:40	3500	100	99	2	2.2 %
8	00:10	4000	100	137	1	0.7 %
9	00:30	4500	100	69	3	4.3 %
10	00:55	5100	100	78	8	10.3 %
11	01:15	4000	fixed	166	0	
12	01:35	2300	fixed	235	0	
13	02:00	1000	fixed	160	0	

Table 2.3 Distribution of recaptured bay anchovies in Queen Creek from day experiment; DFRS is distance from the release site, upstream positive, downstream negative; slack before flood tide was at 1300 h.

Tow #	Time	DFRS (m)	Anchovies in catch	Marked anchovies	% of marked anchovies
Release	14:00	0			
1	15:15	100	133	2	1.5 %
2	15:35	150	226	14	6.2 %
3	15:55	250	10	0	
4	16:15	-500	20	0	
5	16:30	-400	52	0	
6	16:45	0	34	0	
7	16:55	200	111	0	
8	17:10	0	205	4	2.0 %
9	17:30	0	125	6	4.8 %

marked fish were collected, but not all tows within the area captured marked fish. Current speed could not be determined because the drogue was stranded by gusty NW wind.

DISCUSSION

Results of the laboratory and field experiments in this study suggest that in darkness, bay anchovy schools break up and fish are transported by currents. The positive exponential relationship between percent of anchovies transported and current speed indicated that bay anchovies swam in darkness, but at slower speeds and in random directions. Blaxter & Batty (1985), using an infra-red television system, observed that herring schools broke up in darkness and individuals swam at greatly reduced speeds.

Parr (1927) and Shaw (1970) believed that schools broke up in darkness because vision was required for fish to school. Although some laboratory studies have shown that temporarily blindfolded fish were able to school if their posterior lateral lines were not cut (Partridge & Pitcher 1980), it is unknown whether this behavioral pattern applies to fish in the natural environment because fish in confinement have a much greater chance of encounter than fish in the natural environment. Partridge & Pitcher (1980) concluded from their study that vision is important for maintaining position and the lateral line system is important for monitoring speed and direction of other fish in the school. In addition, anchovies (and other clupeoids) have no posterior lateral lines; thus, vision probably plays a central role in anchovy schooling.

Mark-recapture experiments supported the results of the laboratory experiments. Daylight observations revealed that bay anchovies maintained a relatively fixed location. The night experiment showed bay anchovies were transported by tidal currents. From flume experiments and the estimated average current speed (35 cm s^{-1}) in the creek during the night experiment, it could be predicted that at least 95% of fish would be transported. The prediction is supported in that all marked fish were caught within 200 m of the drogue in the night experiment. In the York River, the average current speed is about 20 cm s^{-1} at neap tide and about 52 cm s^{-1} at spring tide (U. S. Department of Commerce, NOAA/NOS 1988).

Lyon (1904, 1909), Hoar (1953), Harden Jones (1968), and Smith (1985) suggested that fish which are both out of sight and touch of the bottom drift with the current. Pavlov *et al.* (1977) concluded from a study of juvenile fish migration that passive transport was associated with the loss of visual orientation by fishes and was observed only during nighttime. Arnold (1981) stated that loss of visual reference points at night may account for the downstream displacement of salmonid fry.

The threshold of light intensity for schooling was not investigated in this study. The lowest light intensity where feeding and schooling can be performed by clupeoids is 0.2-0.001 lux (Blaxter and Hunter 1982; Batty *et al.* 1990). It is expected that in a turbulent estuarine environment, the light intensity at night is well below 0.001 lux most of the time (Whitney 1969).

Transport of bay anchovies by currents at night may play an important ecological role in estuarine environments. In addition to seasonal migration, bay anchovies are likely transported and segregated upstream during a period when flooding is dominant at night, and downstream during a period when ebbing is dominant at night. This may affect food availability, growth rate and reproduction. This pattern of spatio-temporal distribution is also important to studies on fish community structure in estuaries. There have been some suggestions that microgeographic subpopulations of bay anchovy may exist in Chesapeake Bay and its tributaries. Conversely, the passive nocturnal transport noted in the present study would more likely lead to a panmictic population structure within the ecosystem although further studies are necessary.

This behavior may also exist in other marine and estuarine pelagic species. Preliminary tests with the Atlantic silverside (*Menidia menidia* L.) in a flume showed that its schools also broke up in darkness and fish were transported by currents (Unpubl. data).

CHAPTER 3

Population Variability of the Bay Anchovy,

in Chesapeake Bay

INTRODUCTION

The bay anchovy, *Anchoa mitchilli,* like most other anchovies, is a small species with rapid growth and early maturity; an 'r' selected species. Such species may exhibit large population fluctuations but little information is available about the population dynamics and factors affecting the population size of bay anchovy. Overfishing, often associated with fluctuation of fish populations, is not applicable to bay anchovy because there is no commercial fishing or bycatch of this species.

The purpose of this study is to examine a data set derived from a long-term trawl survey in order to define temporal patterns in population size of bay anchovy in Lower Chesapeake Bay, and to identify the possible factors which cause population fluctuations.

MATERIALS AND METHODS

Catch data were obtained from a long-term trawl survey program of the Virginia Institute of Marine Science (VIMS). A total of 15,438 tows was made from 1955-1990 covering the area from the mouth of Chesapeake Bay to the freshwater interface of the James, York, and Rappahannock Rivers. From 1955 to 1987 monthly samples were collected mainly in rivers, whereas from 1988 to 1990 both the bay and rivers were sampled extensively. Because trawls of different sizes have been used during the years, all catch and effort data were standardized to a unit effort: 5 min bottom time of a 30 foot semi-balloon otter trawl with 1.5" stretch mesh body, and a 1/4" stretch mesh cod end liner (Table 3.1). I standardized the sampling efforts of different gears by computing the ratio of the average catch of selected fish species in each gear relative to the average catch of the standard gear fished during the same time period.

To analyze the spatial distribution of bay anchovy, data from 1987 to 1989 were pooled within four seasonal periods: spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb). In each season, samples were split into four horizontal (lower bay, lower rivers, middle rivers, and upper rivers), and four bottom depth (<7 m, 7-9 m, 9-13 m, and >13 m) strata. I chose horizontal and depth strata arbitrarily to give similar numbers of samples in each section. Analysis of variance was used to determine whether there were significant differences in horizontal and depth distributions of bay anchovy from season to season, and the significance level was set at $\alpha = 0.05$ throughout this study.

From 1955-1985, usually only the fork lengths of 25 individuals were recorded from each sample. From 1986-1990, all individual lengths were measured or a subsample of 100-1000 individuals were measured if the total sample was too large to be practically measured. In this study, I selected the 1988 and 1989 length data for analysis of seasonal length-frequency distributions.

A multiple linear regression model was used to determine which factors could have caused bay anchovy population variation. Six types of data were used: bay anchovy CPUE, water temperature, wind speed, river flow, weakfish CPUE, and

Table 3.1 Major sampling gears used in VIMS trawl survey. Standardization was made by comparing the catches of different gears in the same year period. Q is the ratio of catch of any type of gear to the catch of the 30' lined semi-balloon trawl. A catch in each of the gears is multiplied by Q to obtain the CPUE.

Gear code	Gear description (Years used)	Q Bay anchovy	Weakfish	White perch
10	30' semi-balloon trawl, unlined. (1955-72)	7	1.3	1.2
33	30' semi-balloon trawl, lined. (1973-80)	1	1	1
35	16' semi-balloon trawl, lined. (1970-79)	2.2	3.8	4.3
70	30' semi-balloon trawl, lined, chain, bridle. (1980-90)	1	1	1

white perch CPUE. First, all data sets were transformed into compatible forms by a Fourier analysis. The purpose of Fourier analysis was to remove the seasonal variation from a data set, and to leave long-term variations for modelling. Then, cross-correlation analyses were performed on all the variable pairs after each series was filtered with an autoregressive process if it showed any significant autocorrelation. This is because "the interpretation of the sample cross-correlation function can be fraught with danger unless one uses the prefiltering procedure..." (Chatfield 1989, p. 139).

Fourier analysis was based on the following equation:

$$Y_t = a_o + \sum_{p=1}^{(N/2)-1} [a_p \cos(2\pi p t) + b_p \sin(2\pi p t)] + a_{N/2} \cos(\pi N t) + \xi_t$$

where t = year - 64 + (month-1)/12 for monthly index and t = year-64 + (season - 1)/4 for seasonal index, Y_t is the observation (ln[CPUE], log[FLOW], Wind speed and Temperature) at time t, N is the number of observations in a year, ξ_t is an error term, a_o, a_p, b_p, $a_{N/2}$ are parameters to be estimated from data, and p is a integer from 1 to (N/2 - 1). Only harmonics with significant contributions ($P \leq 0.05$) were used to predict the seasonal variation:

$$\hat{Y}_t = a_o + \sum_{p=1}^{K} [a_p \cos(2\pi p t) + b_p \sin(2\pi p t)]$$

where K equals the number of significant harmonics. Residuals (R_t) were obtained from the difference of the observed Y_t and the predicted $\hat{Y}_t$: $R_t = Y_t - \hat{Y}_t$.

Monthly bay anchovy CPUE was calculated for years when the sample size was larger than 100 collections (1964-1990). The Fourier analysis was performed on the natural logarithms of the monthly CPUE to remove seasonal variations. The residuals of the Fourier analysis were averaged by year to produce a yearly bay anchovy abundance index (BAAI, Table 3.2). Spawner index (SPAWNERI) was the first lag of BAAI because the prior year's fish are the parents of the subsequent year-class.

The yearly abundance index of weakfish (WFISHI), *Cynoscion regalis*, and white perch (WPERCHI), *Morone americana,* were calculated similarly to the bay anchovy from VIMS trawl survey data, and were used as predator indices because they were the most abundant known bay anchovy predators in the trawl catches. The predator indices were calculated with seasonal CPUE rather than monthly CPUE because of frequent missing values.

Average monthly river flow data were from the CBP Computer Center, EPA Chesapeake Bay Program, Annapolis, Maryland. The river flow index (FLOWI) was calculated from the sum of the river flow of James, York, and Rappahannock rivers in the same way as the bay anchovy index except that base ten logarithms were used instead of natural logarithms.

Water temperature and wind also were selected as abiotic factors. Temperature data were obtained from VIMS pier ambient monitoring program, recorded at Ferry pier. Wind speed data were obtained from National Weather Service, recorded at Norfolk International Airport. The Fourier analysis was

Table 3.2 Indices calculated from the residuals of the variables in Fourier analysis. BAAI is bay anchovy abundance index; FLOWI is the sum river flow index of James, York, and Rappahannock river; WFISHI is weakfish abundance index; WPERCHI is white perch abundance index; WINDI is summer wind speed index; and TEMPI is winter temperature index.

Year	BAAI	FLOWI	WFISHI	WPERCHI	WINDI	TEMPI
64	-1.073	-0.148	0.946	0.905	-0.084	-0.943
65	-1.047	-0.227	0.661	0.884	3.520	0.447
66	-0.957	-0.130	-0.366	0.701	1.370	-0.193
67	0.340	-0.385	0.777	1.365	-0.472	0.094
68	-0.474	0.009	0.272	0.983	-1.530	-0.910
69	-0.304	-0.076	-0.220	0.749	-1.030	-1.296
70	-1.112	-0.076	1.083	0.190	-2.239	-1.663
71	-0.037	-0.079	-0.001	0.713	-0.436	0.500
72	0.062	0.022	-0.589	-0.155	1.480	1.167
73	0.550	0.293	-1.004	-0.293	0.738	1.054
74	1.667	0.306	-2.020	0.278	0.137	2.777
75	1.648	0.079	-1.501	-2.223	0.178	2.770
76	0.893	0.168	-0.620	-1.637	0.072	0.554
77	-0.142	0.109	-0.920	0.346	-0.790	-2.826
78	-1.723	-0.117	-0.195	0.744	-2.260	-1.160
79	-0.749	0.153	-0.481	-0.882	-1.074	0.160
80	0.766	0.097	-0.060	-0.158	-0.853	-0.651
81	-0.051	0.236	-0.594	0.047	-2.066	0.251
82	-0.868	-0.316	0.492	0.398	0.755	-1.290
83	0.467	-0.011	0.358	-0.186	-2.249	1.670
84	0.352	-0.006	-0.518	-0.122	1.999	-0.050
85	0.590	0.200	0.377	-0.180	1.870	0.924
86	0.823	-0.047	0.526	-0.646	1.295	0.620
87	0.717	-0.049	0.439	-0.755	1.093	0.764
88	0.597	-0.047	1.271	-1.900	1.005	-0.230
89	1.153	-0.043	0.191	0.029	-0.083	0.974
90	-0.383	-0.301	0.618	-0.275	0.815	0.217

performed on monthly average temperature (°C) and monthly average wind speed (km/h). The temperature index (TEMPI) was the mean residual temperature of winter months (Dec, Jan, and Feb). The wind index (WINDI) was initially calculated by averaging the residual wind speed of summer months (June, July, and August), because wind conditions are presumed to have effects on the survival of eggs and larvae of bay anchovy during these months. However, after preliminary analysis indicated that August wind did not give a significant contribution, only the residuals of June and July were used.

The data set of this study was combined from historic data sets of a variety of projects with different objectives. Most data of this type lack consistency in sampling space, sampling method, and sampling time interval. This type of data is not ideal, but often it is the only data available to them. Although I have made my best effort to reduce the effects of inconsistencies in sampling, I could not rule out the probability that some aspects of the results were artifacts of the data.

RESULTS

Spatial distribution of bay anchovy:

Horizontal.--The bay anchovy was the most abundant species in the trawl survey catches and was found throughout the entire sampling area. In the 1987-1989 analysis, bay anchovies generally were more concentrated in the lower part of the rivers and in the Bay, but the spatial distribution showed some degree of seasonal variation (Figure 3.1). In fall, bay anchovies were relatively evenly distributed over the whole area when young-of-the-year recruited to the sampled population. Analysis of variance (ANOVA) indicated that fall CPUEs were not significantly different ($P \leq 0.073$) among areas. In winter, some bay anchovies migrated downriver and concentrated in the lower part of the rivers and in the Bay. The ANOVA indicated that winter CPUEs were significantly different ($P \leq 0.0046$) among areas. In spring, some bay anchovy migrated upstream. Although the spring CPUE was higher in the Bay and lower and middle parts of the rivers, there were no significant differences ($P \leq 0.068$) among areas. In summer, the CPUE was significantly lower ($P \leq 0.035$) upstream.

Depth.--Although trawl collections were made at bottom depths ranging from 3 to 30 m, most of the samples (94%) were collected in depths ranging from 5 to 20 m. Only 4% of the samples were collected in depths less than 5 m, and 2% in depths greater than 20 m. The pattern of depth distribution was related to horizontal distribution because the deeper waters are mostly in the Bay and mouths of the rivers. In general, the CPUE was higher at deeper water stations, but depth distribution also varied in some degree from season to season (Figure 3.2). Bay anchovies were nearly uniformly distributed over the depth range in fall when the young-of-the-year recruited to the population. Analysis of variance indicated no significant differences in fall ($P \leq 0.164$) over the depth range. In winter, many fish withdrew from shallow water to deeper water, and the ANOVA indicated that the CPUEs were significantly higher ($P \leq 0.0005$) at the deeper water stations. In spring, although some fish moved back to the shallow water, the CPUEs were still significantly higher ($P \leq 0.0035$) in deeper water. In summer, the CPUEs were not significantly different ($p = 0.2301$) over the entire depth range.

Variation in seasonal abundance of bay anchovy:

Bay anchovy populations showed great seasonal fluctuations. The seasonal variation is composed of a basic one year sinusoidal curve and its second and third harmonics (Table 3.3, Figure 3.3). Seasonal variation was the average over the 27 year period and contributed 17% of total variation. On the average, the highest CPUE was in November when young-of-the-year bay anchovy fully recruited to the population. In December and January, when water temperature dropped to its lowest value, CPUE dropped sharply due to probable offshore migration and migration to the deeper parts of the Bay where sampling was not conducted. CPUE reached its lowest values in January and February. In March, CPUE increased quickly as temperature rose and fish migrated back into the bay and its tributaries. By April, CPUE reached a secondary peak. After April the CPUE decreased sharply, presumably due to predation and migration of fish to other Bay areas. By June, CPUE reached a secondary low value, at the time when most fish were one year old, and were mature. Although fish started to spawn in May, young-of-the-year had not recruited yet to the sampling gear. In July-September, CPUE increased gradually as the young-of-the-year recruited to the population (Figure 3.4a, b).

Figure 3.1 Horizontal distribution of bay anchovy (average from 1987-1989). The height of block is the ratio of each stratum CPUE within a season to the sum CPUE of the same season. Horizontal strata were chosen arbitrarily to give similar numbers of samples in each stratum.

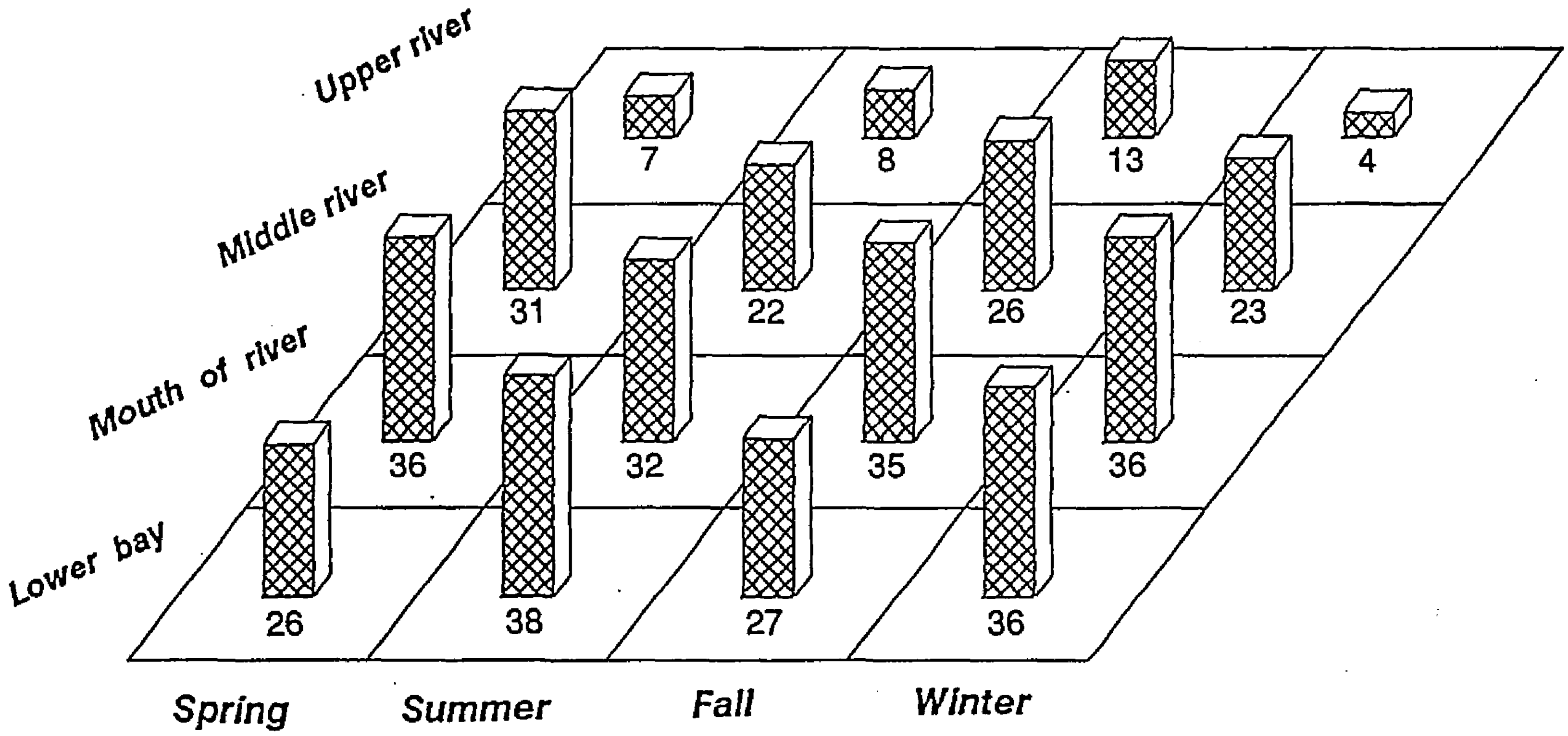

Upper river
Middle river
Mouth of river
Lower bay
7
8
13
4
31
22
26
23
36
32
35
36
26
38
27
36
Spring
Summer
Fall
Winter

Figure 3.2 Depth zone distribution of bay anchovy (average from 1987-1989). The height of block is the ratio of each stratum CPUE within a season to the sum CPUE of the same season. Depth strata were chosen arbitrarily to give similar numbers of samples in each stratum.

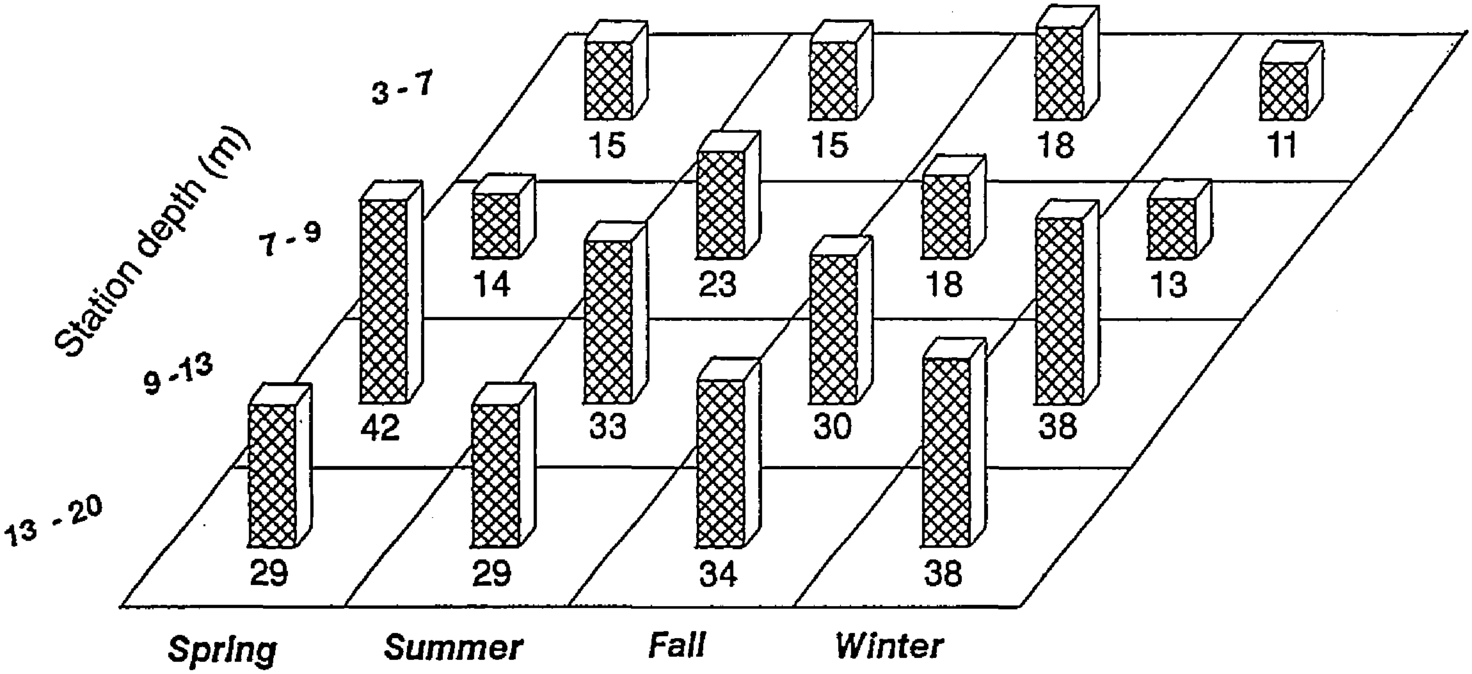

Station depth (m)
3 - 7
7 - 9
9 -13
13 - 20
15
15
18
11
14
23
18
13
42
33
30
38
29
29
34
38
Spring
Summer
Fall
Winter

Figure 3.3 Seasonal bay anchovy abundance derived from a Fourier analysis of 27-years of monthly CPUE data. It consisted of a basic one-year period sinusoidal curve and its second and third harmonics.

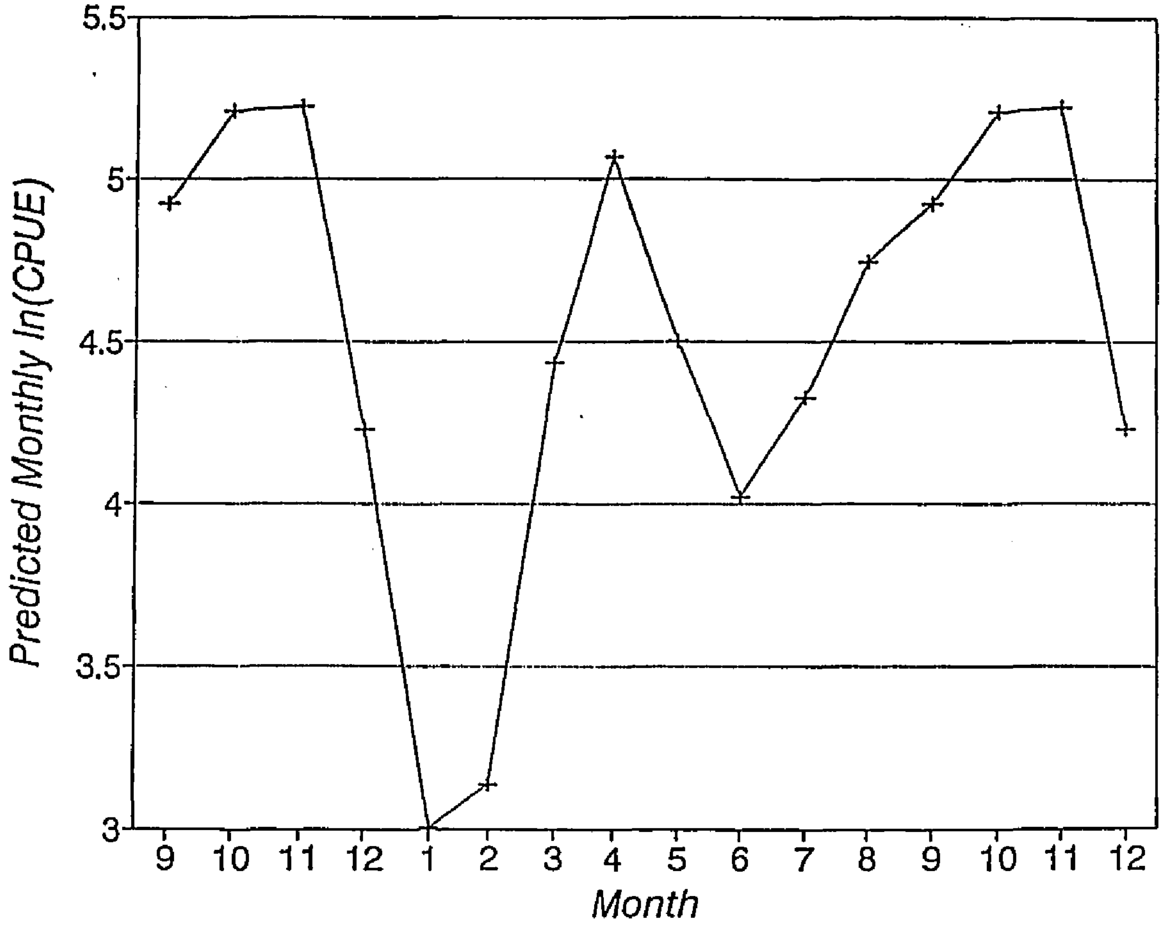

5.5
5
4.5
4
3.5
3
Predicted Monthly ln(CPUE)
9
10
11
12
1
2
3
4
5
6
7
8
9
10
11
12
Month

Table 3.3 Parameters of Fourier analysis. Estimated from multiple regression model. The period of the basic sinusoidal curve is one year.

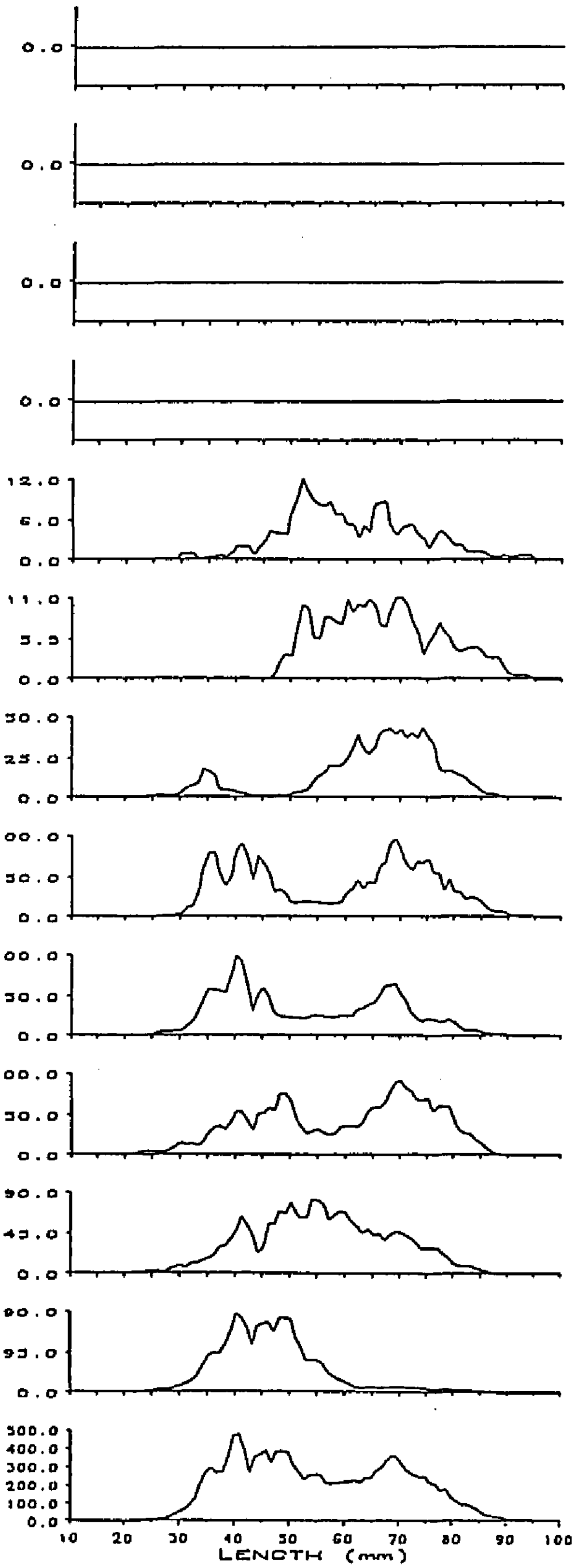
Series	Parameters of significant harmonics							R^2
	a_0	(a_1	b_1)	(a_2	b_2)	(a_3	b_3)	
CPUE	4.402	(-0.403,	-0.350)	(-0.737,	-0.106)	(0.257,	-0.281)	.17
WFISH	1.417	(-1.399,	-1.531)	(-0.371,	*)			.69
WPERCH	3.143	(1.192,	0.057)	(-0.262,	*)			.42
FLOW	4.045	(0.229,	0.262)					.42
WIND	13.454	(1.884,	0.627)	(-0.380,	0.051)	(0.006,	0.329)	.41
TEMP	15.660	(-11.097,	-3.052)	(-0.420,	-0.014)			.97

* Seasonal observations and its nyquist frequency is 2; b_2 is not present in the equation.

Figure 3.4 Monthly length frequency distribution of bay anchovy in 1988 (a) and in 1989 (b). Length is fork length in mm; vertical axis is a 3 point moving average of number of fish in each length unit (mm).

(a)

BAY ANCHOVY
1988 ALL RIVERS STATION



JANUARY 000000 — 000000

NO. CCHT. —	0	MEAN SIZE —	.
NO. MEAS. —	0	S.E. SIZE —	.
NO. HAULS —	0	MIN. SIZE —	.
CAT./HAUL —	.	MAX. SIZE —	.

FEBRUARY 000000 — 000000

NO. CCHT. —	0	MEAN SIZE —	.
NO. MEAS. —	0	S.E. SIZE —	.
NO. HAULS —	0	MIN. SIZE —	.
CAT./HAUL —	.	MAX. SIZE —	.

MARCH 000000 — 000000

NO. CCHT. —	0	MEAN SIZE —	.
NO. MEAS. —	0	S.E. SIZE —	.
NO. HAULS —	0	MIN. SIZE —	.
CAT./HAUL —	.	MAX. SIZE —	.

APRIL 000000 — 000000

NO. CCHT. —	0	MEAN SIZE —	.
NO. MEAS. —	0	S.E. SIZE —	.
NO. HAULS —	0	MIN. SIZE —	.
CAT./HAUL —	.	MAX. SIZE —	.

MAY 880523 — 880526

NO. CCHT. —	1149	MEAN SIZE —	58.5
NO. MEAS. —	228	S.E. SIZE —	0.8
NO. HAULS —	34	MIN. SIZE —	29
CAT./HAUL —	33.8	MAX. SIZE —	91

JUNE 880621 — 880624

NO. CCHT. —	1147	MEAN SIZE —	64.0
NO. MEAS. —	280	S.E. SIZE —	0.6
NO. HAULS —	34	MIN. SIZE —	40
CAT./HAUL —	33.7	MAX. SIZE —	91

JULY 880711 — 880714

NO. CCHT. —	952	MEAN SIZE —	63
NO. MEAS. —	952	S.E. SIZE —	0.4
NO. HAULS —	34	MIN. SIZE —	23
CAT./HAUL —	28	MAX. SIZE —	94

AUGUST 880808 — 880813

NO. CCHT. —	12555	MEAN SIZE —	56.3
NO. MEAS. —	2324	S.E. SIZE —	0.3
NO. HAULS —	34	MIN. SIZE —	26
CAT./HAUL —	369.3	MAX. SIZE —	103

SEPTEMBER 880914 — 880921

NO. CCHT. —	5569	MEAN SIZE —	51.6
NO. MEAS. —	1941	S.E. SIZE —	0.3
NO. HAULS —	34	MIN. SIZE —	22
CAT./HAUL —	163.8	MAX. SIZE —	91

OCTOBER 881002 — 881024

NO. CCHT. —	31654	MEAN SIZE —	57.7
NO. MEAS. —	2582	S.E. SIZE —	0.3
NO. HAULS —	34	MIN. SIZE —	11
CAT./HAUL —	931	MAX. SIZE —	89

NOVEMBER 881104 — 881117

NO. CCHT. —	5714	MEAN SIZE —	54
NO. MEAS. —	2281	S.E. SIZE —	0.3
NO. HAULS —	32	MIN. SIZE —	18
CAT./HAUL —	178.6	MAX. SIZE —	107

DECEMBER 881212 — 881215

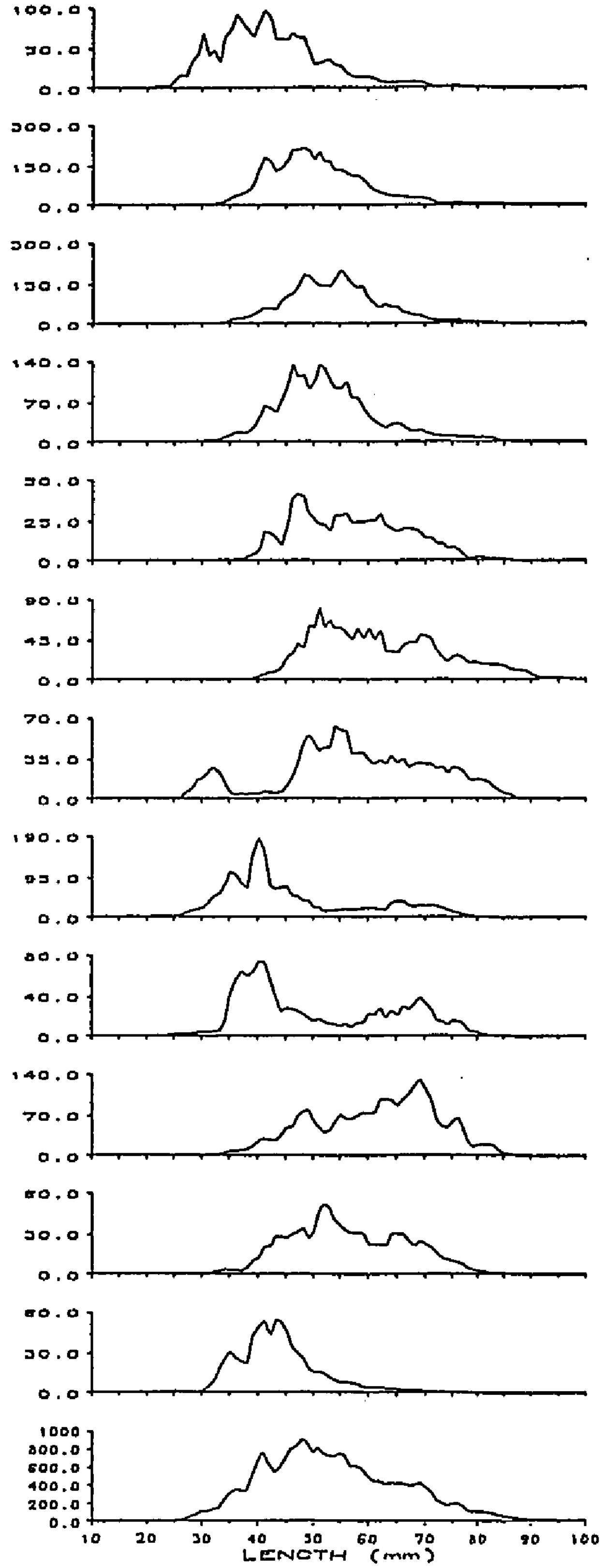
NO. CCHT. —	8366	MEAN SIZE —	44.3
NO. MEAS. —	3366	S.E. SIZE —	0.2
NO. HAULS —	21	MIN. SIZE —	15
CAT./HAUL —	398.4	MAX. SIZE —	88

JAN — DEC 880120 — 881215

NO. CCHT. —	67106	MEAN SIZE —	55.4
NO. MEAS. —	14158	S.E. SIZE —	0.1
NO. HAULS —	257	MIN. SIZE —	11
CAT./HAUL —	261.1	MAX. SIZE —	107

BAY ANCHOVY
1989 ALL RIVERS STATION

(b)



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JANUARY        890111    -    890117
NO. CCHT.  -  8765        MEAN SIZE -   40.3
NO. MEAS.  -  1831        S.E. SIZE -    0.2
NO. HAULS  -    25        MIN. SIZE -     18
CAT./HAUL  - 350.6        MAX. SIZE -     91

FEBRUARY       890208    -    890216
NO. CCHT.  - 33870        MEAN SIZE -     49
NO. MEAS.  -  4032        S.E. SIZE -    0.1
NO. HAULS  -    25        MIN. SIZE -     24
CAT./HAUL  -1354.8        MAX. SIZE -     90

MARCH          890314    -    890321
NO. CCHT.  - 12818        MEAN SIZE -   52.3
NO. MEAS.  -  3444        S.E. SIZE -    0.2
NO. HAULS  -    25        MIN. SIZE -     25
CAT./HAUL  - 512.7        MAX. SIZE -     91

APRIL          890411    -    890418
NO. CCHT.  -  4139        MEAN SIZE -     51
NO. MEAS.  -  2389        S.E. SIZE -    0.2
NO. HAULS  -    25        MIN. SIZE -     23
CAT./HAUL  - 165.6        MAX. SIZE -     87

MAY            890509    -    890516
NO. CCHT.  -  1212        MEAN SIZE -   54.7
NO. MEAS.  -   804        S.E. SIZE -    0.4
NO. HAULS  -    34        MIN. SIZE -     31
CAT./HAUL  -  35.6        MAX. SIZE -     88

JUNE           890613    -    890620
NO. CCHT.  -  2010        MEAN SIZE -   60.3
NO. MEAS.  -  1697        S.E. SIZE -    0.3
NO. HAULS  -    34        MIN. SIZE -     36
CAT./HAUL  -  59.1        MAX. SIZE -     98

JULY           890710    -    890717
NO. CCHT.  -  3234        MEAN SIZE -   56.2
NO. MEAS.  -  1473        S.E. SIZE -    0.4
NO. HAULS  -    34        MIN. SIZE -     26
CAT./HAUL  -  95.1        MAX. SIZE -     91

AUGUST         890805    -    890822
NO. CCHT.  - 12747        MEAN SIZE -   44.7
NO. MEAS.  -  2286        S.E. SIZE -    0.3
NO. HAULS  -    34        MIN. SIZE -     21
CAT./HAUL  - 374.9        MAX. SIZE -     87

SEPTEMBER      890911    -    890920
NO. CCHT.  - 10034        MEAN SIZE -   49.2
NO. MEAS.  -  1300        S.E. SIZE -    0.4
NO. HAULS  -    34        MIN. SIZE -     21
CAT./HAUL  - 295.1        MAX. SIZE -     84

OCTOBER        891009    -    891017
NO. CCHT.  - 13002        MEAN SIZE -   59.5
NO. MEAS.  -  2761        S.E. SIZE -    0.2
NO. HAULS  -    34        MIN. SIZE -     25
CAT./HAUL  - 382.4        MAX. SIZE -     88

NOVEMBER       891113    -    891120
NO. CCHT.  -  7943        MEAN SIZE -   54.6
NO. MEAS.  -  1053        S.E. SIZE -    0.3
NO. HAULS  -    34        MIN. SIZE -     31
CAT./HAUL  - 233.6        MAX. SIZE -     87

DECEMBER       891207    -    891213
NO. CCHT.  -  1675        MEAN SIZE -   42.2
NO. MEAS.  -   736        S.E. SIZE -    0.3
NO. HAULS  -    23        MIN. SIZE -     22
CAT./HAUL  -  72.8        MAX. SIZE -     79

JAN - DEC      860120    -    861218
NO. CCHT.  -111449        MEAN SIZE -   51.3
NO. MEAS.  - 23826        S.E. SIZE -    0.1
NO. HAULS  -   361        MIN. SIZE -     18
CAT./HAUL  - 308.7        MAX. SIZE -     98
```

Variation in long-term abundance of bay anchovy:

Trawl survey catch rates showed that bay anchovy population size has varied as much as 10-fold from year to year (Figure 3.5).

Autocorrelation analysis (Figure 3.6A) suggests that the bay anchovy abundance index time series contained a first-order autoregressive process: $x_t = \alpha_1 \cdot x_{t-1} + Z_t$, ($r^2 = 0.26$, $\alpha_1 = 0.497$, $P \leq 0.0066$), where x_t is the index at year t; x_{t-1} is the index of the previous year; and Z_t is an error process which may be controlled by other factors. Autocorrelation also showed that WFISHI and WPERCHI series contained significant first-order autoregressive processes ($r^2 = 0.29$, $\alpha_1 = 0.528$, $P \leq 0.0039$; $r^2 = 0.20$, $\alpha_1 = 0.434$, $P \leq 0.0210$, respectively).

To identify other factors, I performed cross-correlation analysis on all variable pairs. Results indicated that Z_t was significantly correlated with lag(0) TEMPI ($r_o = 0.662$, $P \leq 0.0001$), lag(1) FLOWI ($r_1 = 0.376$, $P \leq 0.027$), lag(1) F-WPERCHI (the prefix F indicating a filtered series, $r_1 = -0.437$, $P \leq 0.011$), and lag(0) of the square function of WINDI (SQWINDI, $r_o = -0.377$, $P \leq 0.026$), but was not significantly correlated with F-WFISHI in any lag (Table 3.4). There also were significant correlations between TEMPI and FLOWI1, and between TEMPI and F-WFISHI, which made it difficult to identify the true correlations between any pair of variables (i,e. they were not independent). Partial correlation using TEMPI as a controlling variable (remove the effect of TEMPI) resulted in a better correlation between Z_t and F-WPERCHI1, and between Z_t and SQWINDI, but reduced the correlation between Z_t and FLOWI1, and between Z_t and F-WFISHI.

Figure 3.5 Annual average bay anchovy catch per unit effort (CPUE) from 1964 to 1990. A unit effort is a 5 min bottom time of a 30-foot semi-balloon otter trawl with 1.5 inch stretch mesh body, and a 0.25 inch stretch mesh cod end liner; catch is number of fish.

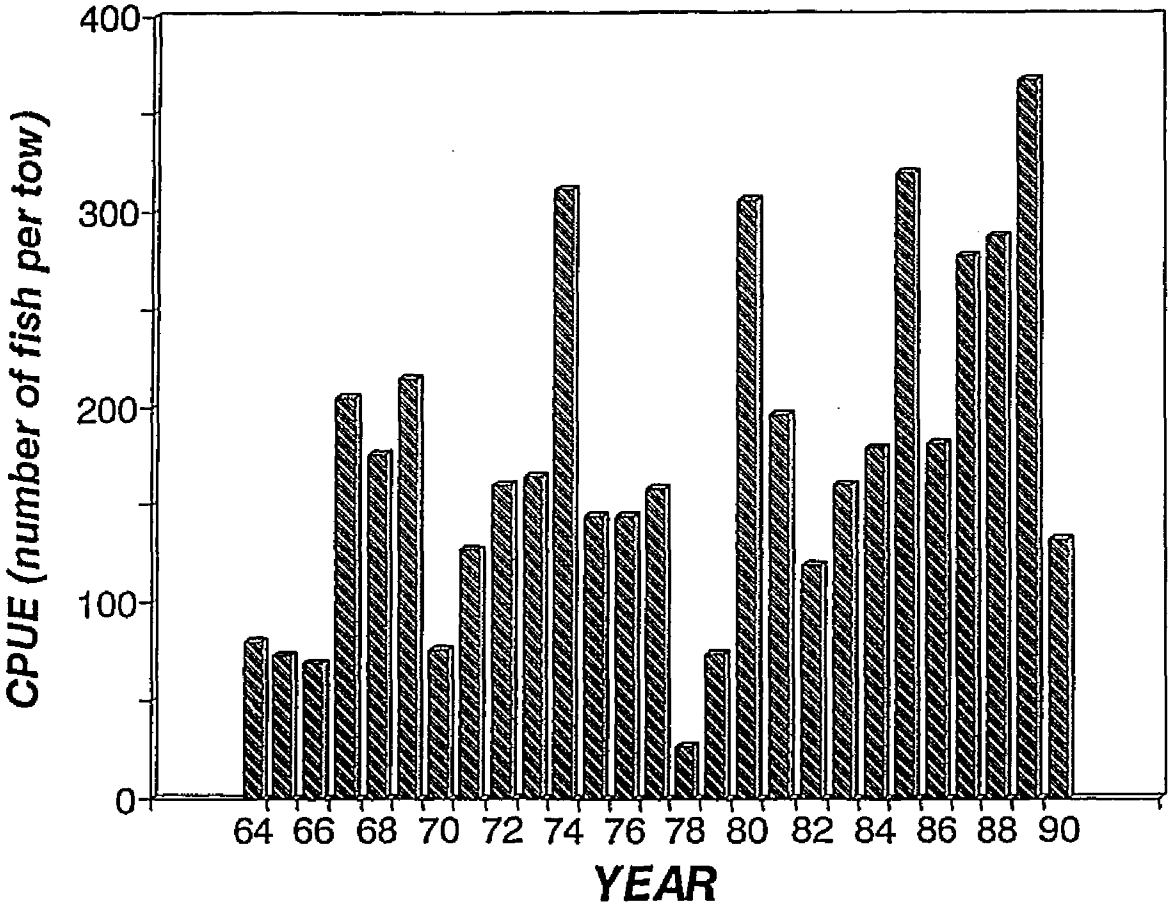
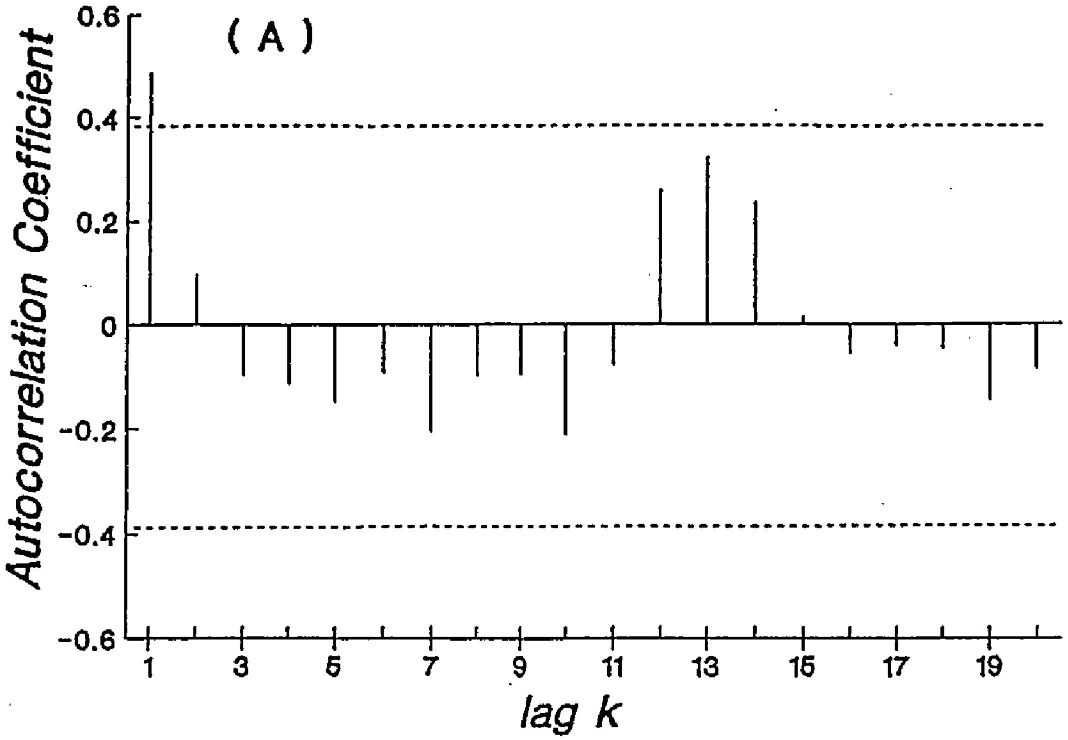

400
300
200
100
0
CPUE (number of fish per tow)
64
66
68
70
72
74
76
78
80
82
84
86
88
90
YEAR

Figure 3.6 Autocorrelation of bay anchovy abundance index (BAAI). A) before modelling; B) after modelling. Dashed lines are 95% confidence limits.


(A)
Autocorrelation Coefficient
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
1
3
5
7
9
11
13
15
17
19
lag k

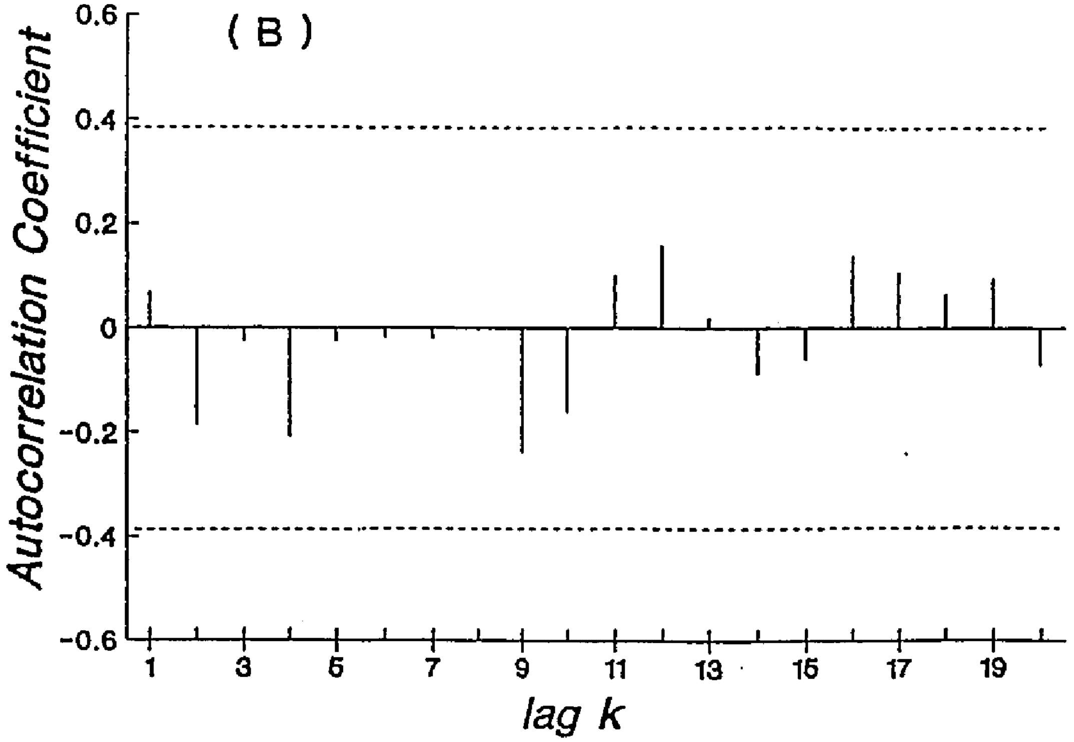

(B)
Autocorrelation Coefficient
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
1
3
5
7
9
11
13
15
17
19
lag k

Table 3.4 Pearson correlation between Z_t, FLOWI1, F-WFISHI, F-WPERCHI1, SQWINDI, and TEMPI. Values above the leading diagonal are simple correlations and those below are first-order partial correlations with the effect of temperature removed. The values in parentheses are the P-values that the correlation is significantly different from 0

	Z_t	FLOWI1	F-WFISHI	F-WPERCHI1	SQWINDI	TEMPI
Z_t	1	.3759	-.2950	-.4366	-.3774	.6625
		(.027)*	(.068)	(.011)*	(.026)*	(.000)*
FLOWI1	.2091	1	-.5467	-.3210	-.1465	.3455
	(.153)		(.002)*	(.051)	(.233)	(.039)*
F-WFISHI	-.0915	-.4846	1	.0642	-.1697	-.3484
	(.328)	(.006)*		(.375)	(.199)	(.037)*
F-WPERCHI1	-.5083	-.3114	-.0365	1	-.2737	-.0864
	(.004)*	(.061)	(.430)		(.084)	(.334)
SQWINDI	-.4521	-.1345	.1592	.2700	1	-.0595
	(.010)*	(.256)	(.219)	(.091)		(.384)

* Significant at 0.05 level.

A step-wise multiple regression model was constructed from information in the cross-correlation analysis. The dependent variable was the BAAI, and the independent variables were SPAWNERI, WFISHI, WPERCHI1, FLOWI1, SQWINDI, and TEMPI. In the first step, the BAAI was regressed on each variable independently, and five out of six variables were significant (Table 3.5). The TEMPI-model was the best one-variable model, and accountable for 46% of the total variance. In the second step, other variables were added into the TEMPI-model, and three of them gave additional significant contributions to the model. The TEMPI-SPAWNERI-model and the TEMPI-SQWINDI-model accounted for 61% and 64% of total variances, respectively, and the TEMPI-WPERCHI1-model was the best two-variable model, accounting for 71% of the total variance. In the third step, variables were added into the TEMPI-WPERCHI1-model, only SQWINDI gave an additional significant contribution to the model. The TEMPI-WPERCHI1-SQWINDI-model explained 78% of the total variance and was selected as a final predictive model because in the fourth to sixth steps none of the remaining variables gave additional significant contributions. The model is shown as below:

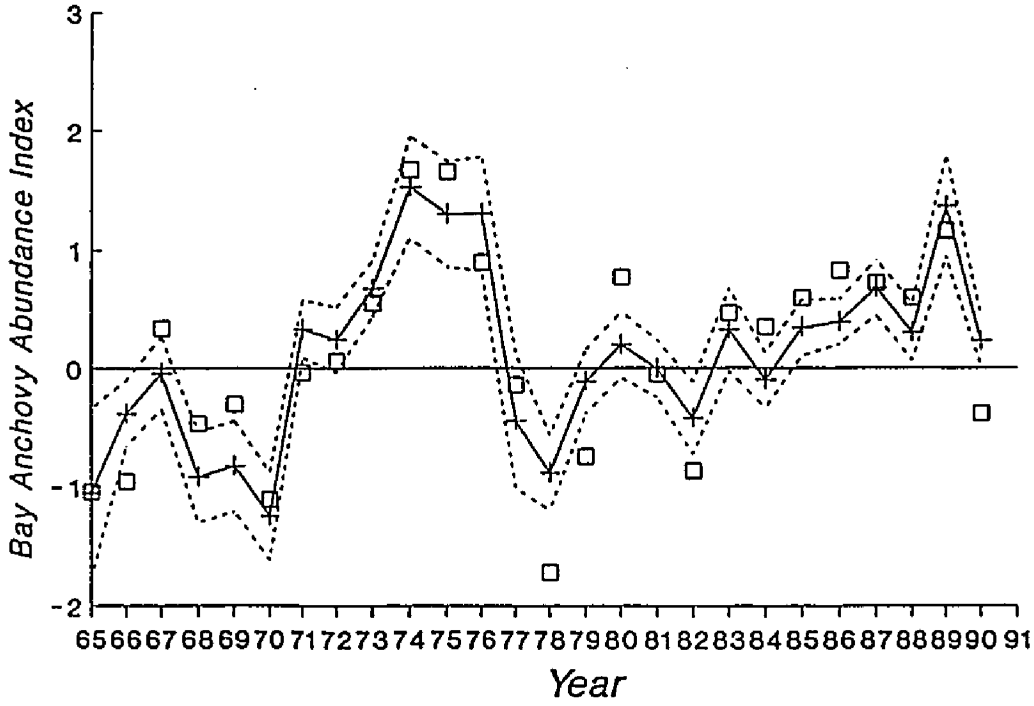
$$X_{o,t}=0.207+0.433T_t-0.384WP_{t-1}-0.0893W_t^2+\epsilon_t$$

where $X_{o,t}$ is the observed bay anchovy abundance index (BAAI) in year t; T_t is the temperature index (TEMPI) in year t; WP_{t-1} is the white perch abundance index of the previous year (WPERCHI1); W_t is the wind index (WINDI) in year t, and ϵ_t is the

Table 3.5 The improvement in R^2 in a step-wise multiple regression model. The dependent variable was the bay anchovy abundance index (BAAI) and the independent variables were added to the model such as to maximize the increase in R^2

Step	Variables included	R^2	*P* value of last var
1	FLOWI	0.21	0.0170
	SQWINDI	0.24	0.0108
	SPAWNERI	0.26	0.0066
	WPERCHI1	0.28	0.0049
	TEMPI	0.46	0.0001
2	TEMPI, SPAWNERI	0.61	0.0060
	TEMPI, SQWINDI	0.67	0.0021
	TEMPI, WPERCHI1	0.71	0.0001
3	TEMPI, WPERCHI1, SQWINDI	0.78	0.0185
4	TEMPI, WPERCHI1, SQWINDI, FLOWI1	0.78	0.3852
5	TEMPI, WPERCHI1, SQWINDI, FLOWI1, WFISHI	0.79	0.3274
6	TEMPI, WPERCHI1, SQWINDI, FLOWI1, WFISHI, SPAWNERI	0.80	0.3593

Figure 3.7 Observed (square) and predicted (plus and solid line) bay anchovy abundance index, and two standard errors (dashed lines).


3
2
1
0
-1
-2
Bay Anchovy Abundance Index
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
Year

residual error term of the model. The standard error (s_b) of each estimate of regression coefficient (b) is 0.0688, 0.105, and 0.0351 for T_t, WP_{t-1}, W_t^2, respectively. The standardized partial regression coefficient (b'), which indicates the relative contribution of each independent variable to the dependent variable (Zar 1972), is 0.637, -0.400, and -0.279, respectively. Autocorrelation analysis indicated that ϵ_t is not significantly different from a random process (Figure 3.6b), which supported the choice of the model.

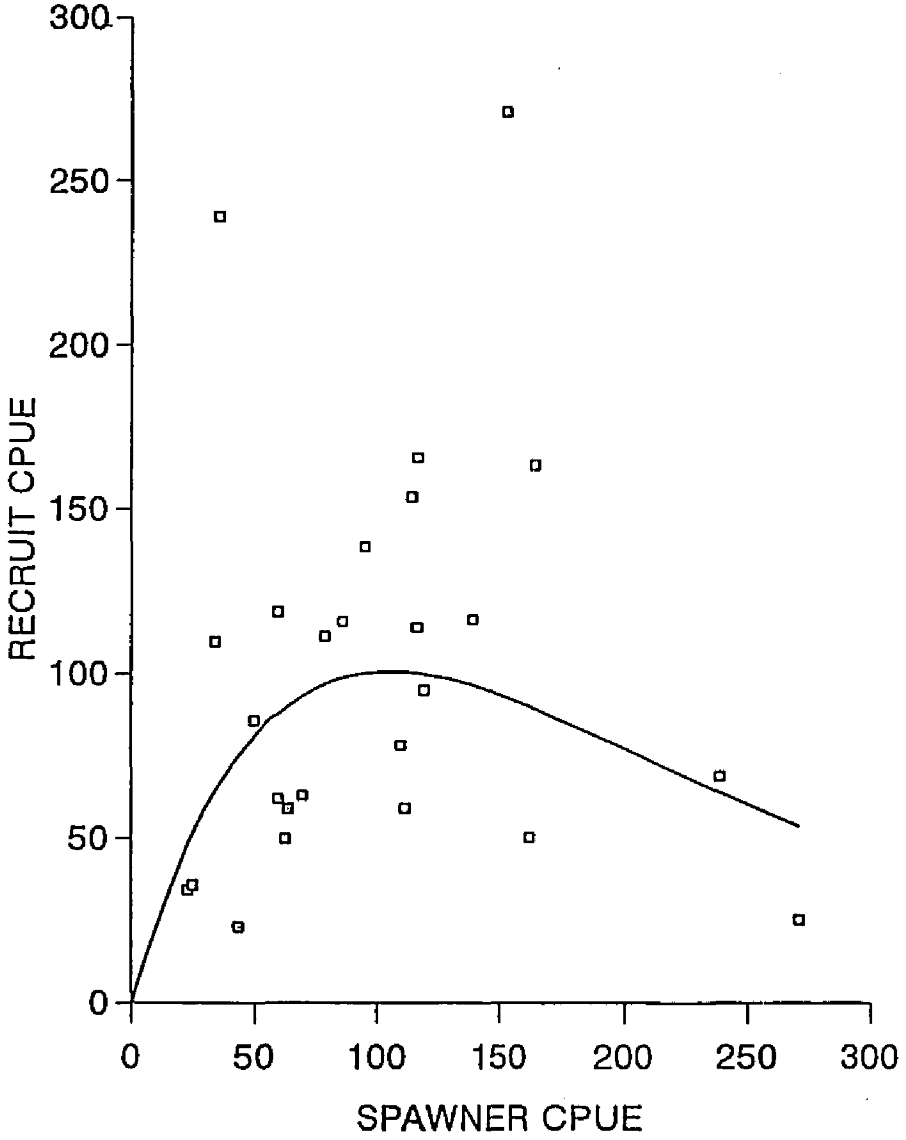
The observed and predicted bay anchovy abundance indices are shown in Figure 3.7. The bay anchovy population was below average level during the late 60's and late 70's, mostly due to low winter temperatures during those time periods. The population was much above its average level during the middle 70's, when there were extremely warm winters. From the beginning of the 80's to present, the bay anchovy population has been slightly above the average level.

DISCUSSION

Six independent variables (spawner, temperature, white perch, weakfish, river flow, and wind speed) selected for modelling in this study all had some physical or biological significance. But only three (temperature, white perch abundance, and wind speed) gave significant contributions to the multiple regression model (78%), and reduced the model residual to a white noise series. Other potentially important variables, such as the abundance of copepods known as major food of bay anchovy (Reid 1954, Darnell 1958, Sheridan 1978, Vazquez 1989) and the abundances of gelatinous zooplankton known as the major predators on eggs and larvae of bay anchovy (Monteleone and Duguay 1988, Govoni and Olney 1991), were not included in the analysis because I was not able to obtain a long-series of data of these variables. By omitting these factors, it is assumed that these variables were constant over the years. Salinity was also not included in the analysis because bay anchovy is a euryhaline species and the variation in salinity among years was very small compared with bay anchovy's wide salinity range (Massmann 1954, Simmons 1957, Dovel 1971). On the other hand, the fluctuation in salinity should have been reflected very well by the river flow index.

The bay anchovy abundance index was significantly correlated with the previous year's index ($r^2 = 0.27$, $P \leq 0.005$, $b = 0.3824 \pm 0.2436$). This relationship can be interpreted as a spawner-recruit relationship, because the bay anchovy is a short-lived fish and all individuals are mature at less than one year of age (Chapter 1). Thus, the prior year's recruits are the parents of the subsequent year-class. It is difficult to interpret the exact nature of the spawner-recruit relationship because of the transformed data. For a better interpretation, the bay anchovy abundance index was converted back to the same units as the CPUE after the effects of temperature were removed. Among three models (linear, Ricker, and Beverton-Holt model), the Ricker model was the only significant model ($Yr = 2.603 \cdot X \cdot e^{-0.00915 \cdot X}$, $r^2 = 0.52$, $P = 0.0001$, Figure 3.8), which suggests that bay anchovy population recruitment dynamics was density-dependent in Chesapeake Bay.

Figure 3.8 Ricker spawner-recruit model: $Yr = 2.603 \cdot X \cdot e^{-0.00915 \cdot X}$, $r^2 = 0.52$, $P = 0.0001$; where Yr and X are the recruit and spawner CPUEs with the effect of temperature removed.


RECRUIT CPUE
300
250
200
150
100
50
0
0
50
100
150
200
250
300
SPAWNER CPUE

The lower left-hand corner of the spawner-recruit curve shows that recruitment is nearly proportional to spawner stock. As the spawner stock increases, the rate of recruit begin t decline. This decline in recruitment is believed to reflect the operation of density-dependent factors in the relation of spawner stock to recruitment. Ricker (1954) suggested that cannibalism is the most natural candidate for density-dependent early mortality of eggs and larvae.

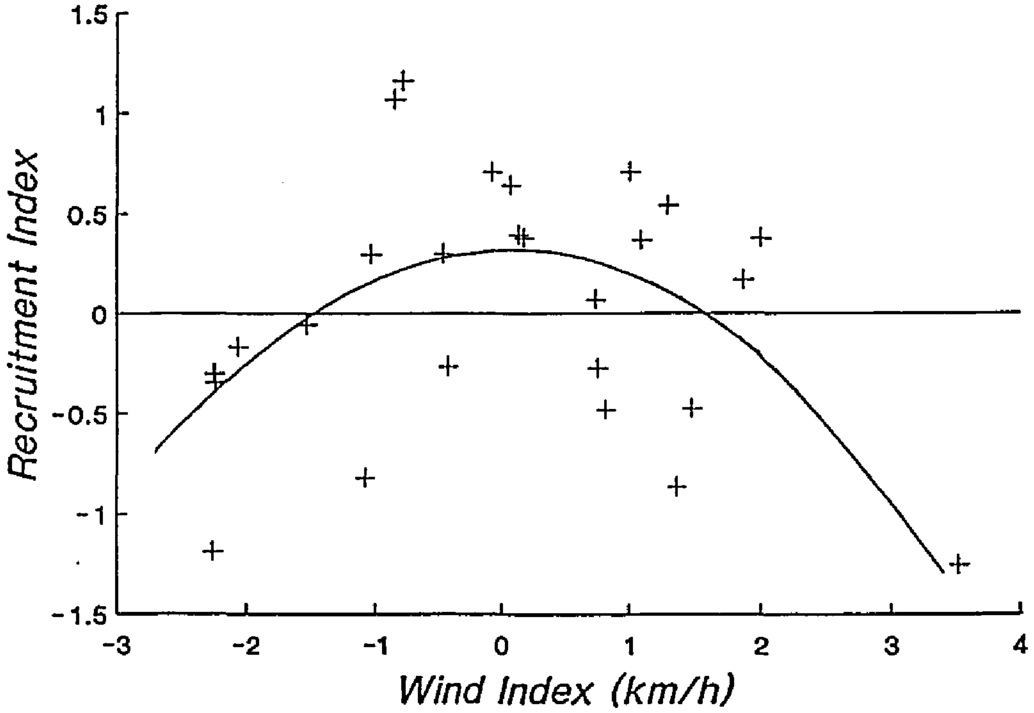
Winter water temperature made the most significant contribution to the model. The temperature effect can be explained in two ways. During colder winters, more fish migrated into deeper parts of the bay where sampling was not conducted (Markle 1976) or to offshore deeper waters (Vouglitois *et al.* 1987) where mortality might be higher (because most predators are in offshore deeper water in winter, i.e. striped bass, weakfish) and some fish may not return the following spring. During extremely cold winters (surface water temperature below 1°C), bay anchovies probably were killed by the low temperature in the bay and rivers (Gunter and Hildebrand 1951; personal observation).

Weakfish and white perch are major predators of the bay anchovy in the Chesapeake Bay (Baird and Ulanowicz 1989), therefore they were expected to have a negative effect on the bay anchovy abundance. This study showed that both were negatively correlated with bay anchovy abundance but only the white perch had a significant effect in the model. This can be explained partially by the natural distribution difference of the two species. The white perch is a resident species in the rivers and upper Bay. Weakfish is a seasonal visitor to the Bay system and is more abundant in the Bay than in the rivers. Since the data were primarily collected in rivers before 1988, it was more likely that the abundance index for white perch was better than that for weakfish. The result would be the opposite if the data were collected mainly in the Bay.

River flow was significantly positively correlated with bay anchovy abundance although it did not significantly contribute to the multiple regression model. This may be because river flow is positively correlated with water temperature. That is, the effects of river flow can be explained to some extent by the effects of temperature. Normally, increases in river flow would increase the primary production (Malone *et al.* 1988), thus increasing the secondary production and increasing the food of bay anchovy (Vazquez 1989).

This study found that bay anchovy abundance was not significantly correlated with the linear function of the wind index, but the squared function of the wind index ($BAAI = 0.318 - 0.138 \cdot W_t^2$, $r^2 = 0.34$, $P = \leq 0.002$; Figure 3.9), which also made a significant contribution to the multiple regression model. In this study, only the June-July wind index gave a significant contribution to the model. This is because the spawning peak of bay anchovy is usually in July and about 75% of total annual eggs are produced in June and July (Zastrow *et al.* 1991, Luo and Musick 1991). The highest wind index in this study is 3.52 km/h (Figure 3.9) which is a result of a storm occurred during 14-17 June 1965. It is seemly that this extreme point drives the relationship, but by excluding this point in the analysis it still results a significant quadratic function ($BAAI = 0.378 - 0.158 \cdot W_t^2$, $r^2 = 0.21$, $P \leq 0.020$).

Figure 3.9 Wind-recruit relationship (r^2 = 0.34, $P \leq 0.002$) of bay anchovy. The vertical axis is the bay anchovy abundance index with the effect of temperature removed, the horizontal axis is wind index.


Recruitment Index
1.5
1
0.5
0
-0.5
-1
-1.5
-3
-2
-1
0
1
2
3
4
Wind Index (km/h)

The effect of wind on the bay anchovy population is not a simple case. The ideal condition is moderate winds. Moderate winds increase the contact rates between larvae and their prey without reducing their feeding success (Mackenzie and Leggett 1991). High winds could generate an extremely turbulent environment which would allow prey to pass through the larva's visual field without being successfully captured because larva reaction times may be too slow to respond to fast-moving prey (Checkley 1982, Govoni *et al.* 1986), or because the reduced visibility of the water column reduces the ability of larvae to see their prey (Mackenzie and Leggett 1991). High winds would also destroy the patchiness of food that is essential during the early larval stage of fish (Lasker 1978). On the other hand, extended calm periods would reduce turbulence which otherwise increases contact rates, and could result in vertical stability of the water column leading to hypoxia in the lower water column (Goodrich *et al.* 1987) and a reduction in secondary production and the available space for adult fish.

Some of the unexplained variance in the model could have been caused from the errors in estimating the CPUE. That is, the CPUE might not indicate the true bay anchovy abundance in the Chesapeake Bay due to the following possible factors: (1) inconsistency in sampling locations, such as in some years more samples were collected in the rivers and in other years more in the Bay; (2) variability in catchability coefficient (q) of the same gear at different depths, i.e. in deeper water the otter trawl did not sample the overlying water column as effectively as in shallower water therefore under-estimating the abundance relative to shallower water;

(3) changes in gear from year to year (although some standardization has been applied, gear variation still is a major source of error in estimating the CPUE because of a lack of well-designed experiments).

The fluctuation in abundance of bay anchovy may have potential effects on the Bay ecosystem because it is a key species in the Chesapeake Bay food web. Bay anchovy links the zooplankton production to the biomass of larger predatory fishes. Therefore, the lower the abundance of bay anchovy the less zooplankton production will be converted into food for larger predatory fishes and the lower the fisheries output in the subsequent year or years. But many more studies are needed to quantitatively understand the importance of bay anchovy in the Chesapeake Bay food web.

In summary, this study indicated that the bay anchovy population size in lower Chesapeake Bay was mainly controlled by winter water temperature and the previous year's white perch abundances. When the environmental conditions were unfavorable (extreme low temperature in winter, strong or little wind in summer), the bay anchovy populations could drop five-fold from its average level in one year. On the other hand, during a favorable period (warm winter and moderate wind in summer), the bay anchovy population could recover quickly to its average level or above. An earlier study (chapter 1) indicated that bay anchovy has the reproductive potential (reproductive output is about 350% of body energy per year) to produce an almost explosive increase in population size.

GENERAL DISCUSSION

The present study examines certain important aspects of the life history of the bay anchovy. The life history of organisms represents a series of selective compromises to a suite of environmental variables. Components, such as age and size at maturity, fecundity, spawning frequency, body size, and longevity, constitute a life history "strategy", which implies a suite of adaptive responses accumulated over evolutionary time (Wilbur *et al.* 1974). Age and size at maturity are the life-history parameters most sensitive to environmental stress. An organism that encounters an unavoidable stress that results in slower growth its age at maturity could be changed to keep fitness as high as possible despite slower growth (Stearns and Grandall 1984). According to Giesel (1976), life histories that should be selected for are those in which the age-specific reproductive effort schedule is such that the overall fitness of the life history is maximized. He also noted that early reproduction, all else being equal, increases fitness over late reproduction.

The present study has shown that bay anchovies hatched in May and June could mature at a size of 36.9 mm FL in about 80 days. Fish which hatched early had high growth rates in summer and spawned before temperature and other environmental factors fell below optimal spawning conditions in late September. Fish hatched in July and August experienced different environmental conditions and nutrient levels from fish hatched earlier, and although they also were able to reach 35-40 mm by late September and October, the water temperature was usually too low for spawning. These fish delayed maturity until the next spawning season (May to September of next year) at an age of about 10 months and size of 45-55 mm. These results support Giesel's (1976) contention that reproductive effort and allocation of available energy may be regulated in response to variations in nutrient level and other environmental conditions, and that such phenotypic plasticity within reproductive patterns sometimes constitutes the major part of a reproductive strategy.

This study revealed that an individual bay anchovy spawns repeatedly in a spawning season. The spawning frequency was 0.25 batches per day (1 spawning every 4 days) at the beginning of the season (May to June) and increased to about 0.75 batches per day (3 spawnings every 4 days) in July and August. The estimated total number of batches in the 1988 spawning season was about 54. Calow (1979) suggested that life-span expressed in terms of the number of breeding seasons between birth and death is likely to be a more important criterion of life-history strategy than is longevity. Although multiple spawning in a season and iteroparity (repeated breeding at different ages, Cole 1954) are different by definition, their contributions to populations are the same: spreading of reproduction over a long time period to overcome the reproductive uncertainty resulting from variable biotic and abiotic environments. Moreover, multiple spawning in a season has some advantages over iteroparity: (1) multiple spawning increases the annual egg production; (2) high adult mortality has more of an effect on populations with iteroparity than on populations with multiple spawning.

Bay anchovy in Chesapeake Bay has high relative fecundity. The annual relative fecundity of 1-yr-old bay anchovy is about 450 times that of 4-yr-old striped bass and 8 times that of 12-yr-old striped bass (Westin and Rogers 1978). Among all anchovy species investigated (Table 3.4), the bay anchovy has highest relative daily fecundity. Calow (1979) suggested that the most satisfactory measure of the cost of reproduction is energy invested in reproduction as a proportion of energy taken in since it expresses reproductive output in terms of nutrient input. This study estimates that bay anchovy invests about 20% of calories consumed daily into daily reproductive output at spawning peak (Chapter 1). Hunter and Goldberg (1980) reported that for 1-yr-old female northern anchovy, 8% of consumed calories were used for reproduction.

The passive tidal transport of adult bay anchovy in darkness described in chapter 2 is an important ecological phenomenon. This transport pattern is important to studies on fish community structure in the estuaries because it is likely to result in unique spatio-temporal distribution of pelagic fishes. Disassociation of schools and drift may explain why most pelagic schooling fishes spawn in the evening or at night (Ferraro 1980), because the sterotypic polarized schooling behavior in daylight may preclude the complex behavioral interrelations that are required between mates for successful spawning. In terms of population genetics, tidal transport in darkness could result in a panmictic population structure within Chesapeake Bay.

The multiple linear model analysis (Chapter 3) suggested that the bay anchovy population in Chesapeake bay is primarily regulated by winter water temperature, predator abundance, and summer wind speed. Other studies (Lasker 1975, 1978, Hayman and Tyler 1980, Henderson and Holmes 1990) have shown that water temperature and wind conditions are two important density-independent factors that cause fluctuations in fish populations. Predation has been known as a major factor for regulating population sizes of small forage species (Wilbur *et al.* 1974), but quantitative studies of prey-predator relationships are rare. Other potentially important variables, such as the abundance of copepods known as the major food of bay anchovy (Reid 1954, Darnell 1958, Sheridan 1978, Vazquez 1989), and the abundance of gelatinous zooplankton known as the major predators on eggs and larvae of bay anchovy (Monteleone and Duguay 1988, Govoni and Olney 1991), were not included in the analysis because I was not able to obtain long-series data of these variables. The analysis also showed that bay anchovy abundance of a current year is significantly correlated with that of the previous year. The Ricker spawner-recruit model suggests that there may be a density-dependent mechanism in the bay anchovy population recruitment in Chesapeake Bay. The large variation of the observed values about the model indicated that the bay anchovy is a typical 'r' selected species.

Life history patterns have evolved along two major lines (Williams 1966, Murphy 1968, Schaffer 1974a, 1974b, Giesel 1976): (1) species that face high pre-reproductive mortality or low probability of reproductive success per reproductive effort should have long life, late maturity, and repeated reproduction (iteroparity); (2)

species that characteristically suffer high adult mortality should maximize early reproduction and have short life. Murphy (1967, 1968) suggested that fishes that face both high variable pre-reproductive mortality and high variable adult mortality would be unobservable because of extinction. Studies have shown that the bay anchovy suffers high adult mortality from larger carnivores and has a short life span (Hildebrand and Schroeder 1928, Stevenson 1958, Newberger 1989, Baird and Ulanowicz 1989). Other studies also have shown that bay anchovy suffers high egg and larval mortalities (Leak and Houde 1987). According to Murphy's theory, the bay anchovy should have become extinct: instead it is one of the most abundant fish species in Chesapeake Bay. Murphy did not consider the possibility of multiple-spawning of individual fish in a spawning season because batch spawning was poorly known until the 1980's (Hunter and Goldberg 1980, Hunter *et al.* 1985, Clarke 1987). It is probably this type of spawning tactic that overcomes the high egg and larval mortality, and ensures the reproductive success of the bay anchovy in Chesapeake Bay.

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VITA

ANN E. <u>ANCHOA MITCHILLI</u>

Born in the long, hot summer,
In the mouth of the York River.
Thrown out from the nursery one day after,
With thousands of brothers and sisters.

Most brothers and sisters died
Before reaching day nine.
Hard work traded for fast growth,
Harsh life matured them early.

Sexually active as teenagers,
With hundreds of unknown lovers.
Had many thousands of sons and daughters,
But only a few were survivors.

Called useless by politicians,
But deserves the highest recognition,
For being the important link in the chain,
That serves Chesapeake Bay.

VITA

Jiangang Luo

Born in Wenchow, China, 30 September 1958. Graduated from Luo-Fu High School, Yongjia County, Zhejinag Provence, China in 1975. After three years as a mechanics in a factory, entered Shanghai Fisheries College, Shanghai, China in 1978. Earned B. S. in Marine Fisheries Resource Management in 1982, and was an assistant teacher in Shanghai Fisheries College from 1982 to 1985. Came to U. S. A. and entered masters program in College of William and Mary, School of Marine Science, Virginia Institute of Marine Science in August 1985. Bypassed master and entered doctoral program in 1987, and defensed his dissertation on 22 November 1991.