

Bay anchovy *Anchoa mitchilli* in Narragansett Bay, Rhode Island. I. Population structure, growth and mortality

Amy E. Lapolla*

Box 200, University of Rhode Island, Graduate School of Oceanography, South Ferry Road, Narragansett, Rhode Island 02882, USA

ABSTRACT: Population structure, growth and mortality of *Anchoa mitchilli* were evaluated in Narragansett Bay (Rhode Island, USA), an estuary near the northern extent of this species' broad latitudinal range. The Narragansett Bay population was dominated by young fish (Age 1 and young-of-the-year, YOY); no fish were found to have survived a third winter. Growth rates were rapid, particularly during the first year of life, and annual mortality rates were estimated at >90%. A von Bertalanffy growth model fit to length-at-age data yielded parameters of asymptotic length $L_{\infty} = 89.97$, growth coefficient $K = 1.15$ and age at zero length $t_0 = -0.31$. Comparison of my results to those of an earlier study from Chesapeake Bay suggests that Narragansett Bay anchovies grow more rapidly during the first year of life, and subsequently attain a greater length-at-age, than their conspecifics at lower latitudes. Latitudinal differences are also indicated by comparison of the weight-length relationships and Fulton's condition factors of Narragansett Bay and Chesapeake Bay data. Narragansett Bay fish seem to be allocating energy preferentially to length versus weight compared to fish in Chesapeake Bay, which may be a reflection of this species' growth strategy at this latitude.

KEY WORDS: Bay anchovy · *Anchoa mitchilli* · Population biology · Narragansett Bay · Latitudinal differences

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INTRODUCTION

Ranging along the western North Atlantic from Maine to Florida and around the Gulf of Mexico to Yucatan, the bay anchovy *Anchoa mitchilli* is one of the most abundant fishes in the coastal western North Atlantic (Hildebrand 1943, 1963, Newberger & Houde 1995). Inshore abundance in coastal bays and estuaries generally peaks in the summer months and subsequently declines, with fall migrations offshore to deeper water (Hildebrand 1963). The bay anchovy is a small, short-lived engraulid, linking zooplankton production to piscivores, including striped bass *Morone saxatilis*, bluefish *Pomatomus saltatrix*, weakfish *Cynoscion re-*

galis, and fluke *Paralichthys dentatus* (Hildebrand 1963, Baird & Ulanowicz 1989). While not exploited commercially, recognition of the bay anchovy's trophic importance has precipitated a great deal of work in recent years to quantify many aspects of its biology, particularly in Chesapeake Bay (Luo & Musick 1991, Zastrow et al. 1991, Newberger & Houde 1995).

The bay anchovy may be the most abundant fish in Narragansett Bay (Fig. 1) during the summer months (Rhode Island Department of Environmental Management, Division of Fish and Wildlife [RIFW], Narragansett Bay, unpubl. data). Despite the potentially significant trophic role of *Anchoa mitchilli* in this estuarine system, only cursory information exists on its biology and ecology within Narragansett Bay. In addition, the location of this study site near the northern extent of the range of the bay anchovy would provide

*E-mail: amyla@gso.uri.edu and amylapolla@hotmail.com

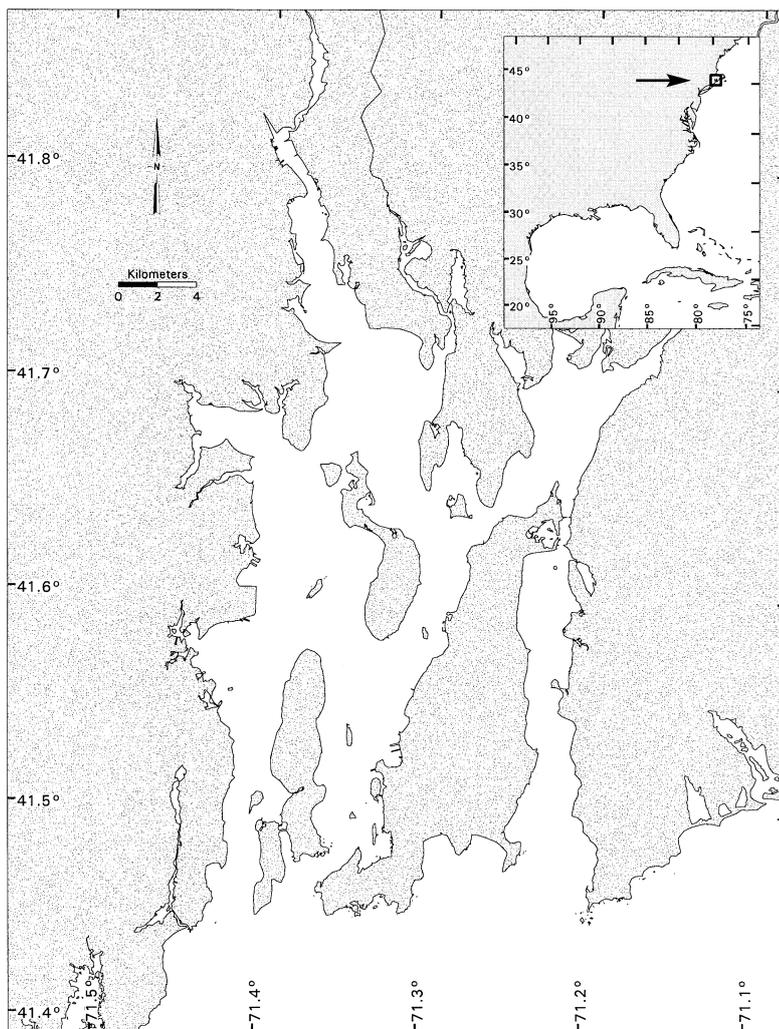


Fig. 1. Narragansett Bay, Rhode Island. Inset encompasses range of the bay anchovy *Anchoa mitchilli*, a coastal species

data suitable for investigating possible latitudinal differences in bay anchovy ecology when compared to published data collected at lower latitudes.

Environmental conditions that vary with latitude may be manifested in spatial phenotypic (and perhaps genotypic) variation of a species that has an extensive latitudinal range. It has been suggested that factors affecting bay anchovy recruitment (to a given bay or estuarine system) differ with latitude, in that overwintering losses to migration and overwintering mortality often increase with increasing latitude (Vouglitois et al. 1987). Conspecifics may also utilize different energy allocation and accumulation strategies at different latitudes in response to stresses associated with seasonality, as seen in another small coastal fish, *Menidia menidia* (Schultz & Conover 1997). In addition, there is mounting evidence for countergradient variation in growth rate in a number of fish species, such

that fishes at northern latitudes tend to grow faster in a given time period than more southerly conspecifics (Conover 1990, Conover & Present 1990, Conover et al. 1997).

The objectives of this study were: (1) to quantify aspects of the population dynamics of this species in Narragansett Bay, including age structure and size-at-age, sex ratio, and growth and mortality rates; and (2) to compare these results to published data from lower latitudes, particularly those of Newberger & Houde (1995).

METHODS

Field collections. *Anchoa mitchilli* were collected at monthly intervals from May through October 1997 at 13 stations within Narragansett Bay by the RIFW. Fish were collected by an otter trawl equipped with a 0.625 cm mesh cod-end towed for 20 min at approximately 4.6 km h⁻¹. Captured fish were counted, individual fork lengths were measured (to nearest cm), and total anchovy biomass (kg) was recorded. A random subsample of anchovies were chilled on ice, brought back to the laboratory, and preserved in 95% ethanol. Several additional samples (excluded from abundance calculations but used for all other analyses) were collected by the RIFW juvenile finfish survey with a 60 m beach seine (depth = 3 m; mesh size = 0.5 cm bag, 0.625 cm body), and by the University of Rhode Island Graduate School of Oceanography Narragansett Bay trawl survey with an otter trawl (tow duration = 30 min; tow speed = 4.6 km h⁻¹; cod-end mesh size = 5 cm). Some of these additional samples were frozen for up to 1 wk before being preserved in 95% ethanol.

Laboratory procedures. Within 2 wk of collection, the fork length (to nearest mm) and wet weight (to nearest 0.01 g) were measured for approximately 100 randomly selected adult anchovies from each station (or the total number of adult fish from stations where fewer than 100 fish were collected). Once young-of-the-year (YOY) were recruited to the trawl, the same measurements were taken from approximately 100 YOY individuals from each station (in addition to the 100 adults). Length and weight measurements were not adjusted for potential shrinkage due to death or

preservation. Each sample was divided into as many as 15 length classes of 5 mm increments (15–19 mm to 85–89 mm), and sagittal otoliths from up to 15 fish in each length class were removed. Sex was determined by visual gonad examination.

Otolith analysis. The radii, lengths and widths of all whole sagittal otoliths collected were measured using a stereomicroscope linked to an image-analysis system (Optimas: BioScan 1989). Five otoliths from each represented length class per sample were mounted in 'cubes' of epoxy and were affixed to a microscope slide with thermoplastic (Crystal-Bond). The otoliths were then cross-sectioned by grinding down from the rostral and anti-rostral surfaces with fine (220 to 600 grit) sandpaper and 30 μm lapping film (3M Imperial), and polished with 0.3 μm alpha alumina paste (Union Carbide Buehler micropolish). These cross-sections were examined under a stereomicroscope linked to the image-analysis system. The age of each fish was determined to the nearest year by counting annuli (Fig. 2) as described by Newberger & Houde (1995). Widths at the annuli (end of winter growth, seen as the edge of a dark zone) were measured to the nearest 0.01 mm. YOY were easily aged as such on the basis of their small size and sudden appearance in the trawls, starting in August. These age data were combined with the length data to form an age-length key for anchovies captured during 1997 in Narragansett Bay (Hilborn & Walters 1992).

Annuli were validated by marginal increment analysis. The otolith marginal increment (MI), a measure of fish growth from most recent annulus formation to capture, was defined as:

$$MI = OW_c - OW_{a(\text{last})}$$

where OW_c is the otolith width at capture and $OW_{a(\text{last})}$ is the otolith width at the outermost apparent annulus (Newberger & Houde 1995).

Morphometric analyses. The weight-length relationship of adults and YOY for each month was described by the equation $W = aL^b$, where W is wet weight (g) and L is fork length (mm). Fulton's condition factor (C) was calculated from the weight-length data according to the equation $C = W/L^3$ (Ricker 1975). Condition factors obtained for June, July, and August fish were pooled and compared to that calculated for the same period by Newberger & Houde (1995) with a Student's t -test assuming unequal variance (Sokal & Rohlf 1995).

Age and growth. Ages used in the following analyses were considered to be relative to catch date, with hatch date taken as July 15. The assumption has been made that small (1 to 3 mo) differences in actual age will not adversely affect conclusions drawn from the aged-based analyses used here.

The age distribution (relative abundance-at-age) for the Narragansett Bay anchovy population was estimated based on subsampled anchovies from the RIFW trawl survey. These fish were divided into 5 mm length-classes, and assigned an age-at-length with an age-length key developed from the otolith-analysis data.

Two forms of the von Bertalanffy growth model were fitted to length-at-age data determined by otolith analysis (observed data): (1) a traditional version (TVB: Ricker 1975), and (2) a seasonally oscillating version (SOVB: Hanumara & Hoenig 1987). These models are:

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

$$L_t = L(1 - e^{-K(t-t_0) + cK/2^1 \sin[2^1(t-t_0)]}) \quad (2)$$

where L_t is the estimated length at age, L_∞ is the mean asymptotic length, K is the growth coefficient, c represents the amplitude of the oscillations, t is age, t_0 is the hypothetical age at which a fish would have

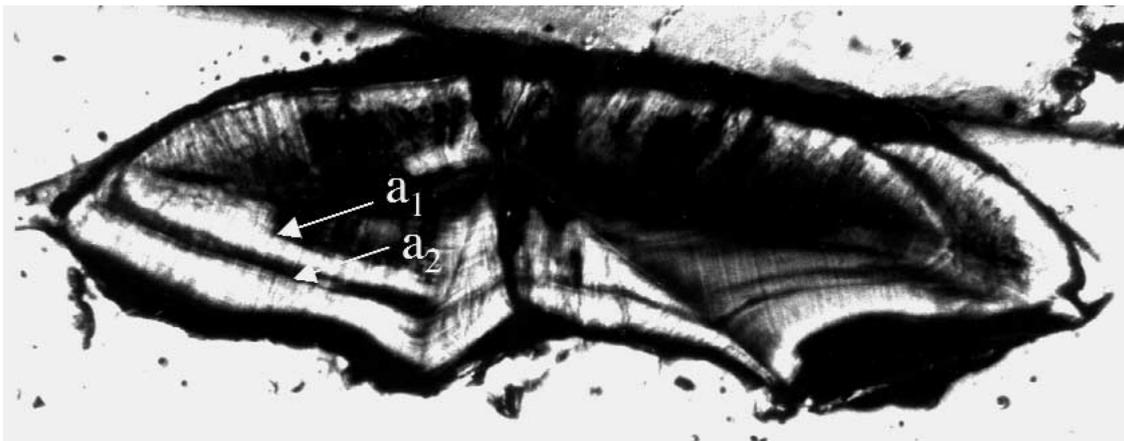


Fig. 2. *Anchoa mitchilli*. Cross-sectioned bay anchovy otolith. This fish had survived its second winter and entered Narragansett Bay for its second adult summer. Two annuli are visible (a_1 and a_2)

zero length had it always grown according to the equation, and t_s is the age at which oscillations begin. These models were fit by a non-linear least-squares procedure (Microsoft Excel Solver Tool). Growth rates (mm d^{-1}) were calculated from model estimates of lengths-at-age and from observed lengths-at-age.

Mortality. Mortality was estimated via abundance-at-age (catch-analysis) methods as well as life-history parameter methods. Three catch-analysis methods (Heincke 1913, Robson & Chapman 1961, Ricker 1975) used RIFW catch data partitioned by age with the age-length key developed in this study. Three life-history parameter methods (Alverson & Carney 1975, Pauly 1981, Hoenig 1983) used parameters (K, L_∞, t_0) from the TVB model. The TVB model 95% confidence interval values of K and L_∞ were used to calculate mortality confidence intervals for the life-history-based methods. Instantaneous mortalities were converted to annual mortalities based on the equation:

$$A = 1 - e^{-Z}$$

where A = annual mortality rate and Z = instantaneous mortality rate (Ricker 1975).

RESULTS

Sex ratio

The overall mean female to male sex ratio for 936 adult *Anchoa mitchilli* was 1.11:1 (Table 1). Females were more abundant in all months sampled, and comprised from 51% (August) to 71% (September) of the total sample. However, the overall mean sex ratio was not significantly different from 1:1 at the $\alpha = 0.05$ level ($\chi^2 = 2.46, df = 1, p > 0.1$).

Table 1. *Anchoa mitchilli*. Sex ratio by month, and overall sex ratio for bay anchovies in Narragansett Bay. Females outnumber males in each monthly sample. Note small sample size in September

Month	No. of females	No. of males	Ratio (F:M)
June	216	200	1.08:1
July	177	160	1.11:1
August	79	76	1.04:1
September	20	8	2.5:1
Overall ratio	492	444	1.11:1

Table 2. *Anchoa mitchilli*. Summary statistics and coefficients of the weight-length relationship ($W = aL^b$), and Fulton's condition factor for fish caught in June, July and August in Narragansett Bay. Summary of data from Newberger & Houde (1995) for June, July and August in Chesapeake Bay are shown for comparison

Area	n	$W = aL^b$			Fulton condition factor	
		a ($\times 10^{-6}$)	b	R ²	Mean	SD
Narragansett Bay	1149	1.37	3.40	0.99	7.19	1.20
Chesapeake Bay						
1986	1004	1.99	3.38	0.97	9.26	1.21
1987	1190	4.36	3.18	0.98	8.96	0.79

Morphometrics

The relationship between length and weight was described for all adults collected as $W = (9.70 \times 10^{-6}) \times L^{2.94}$, and for all juveniles collected as $W = (1.54 \times 10^{-6}) \times L^{3.35}$. Mean Fulton's condition factor for all adults (7.61×10^{-6}) was higher than that obtained for juveniles (5.48×10^{-6}). The weight-length relationship derived from all fish collected in June, July and August was $W = (1.37 \times 10^{-6}) \times L^{3.40}$, and the mean Fulton's condition factor for these months was 7.19×10^{-6} (Table 2).

Relative abundance-at-age

Otolith marginal increments were lowest for fish collected in May (Fig. 3), so the annuli were accepted as valid indicators of age to the nearest year. The age composition of the otolith-aged adult fish was 289 Age 1 and 33 Age 2. An additional 43 otoliths were unreadable and could not be aged. The population prior to YOY recruitment was composed primarily of first-year fish which were spawned in 1996 and overwintered successfully (Fig. 4). Second-year fish were not abundant, and no fish were found to have survived

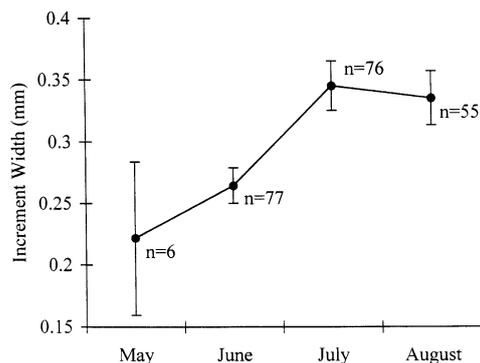


Fig. 3. *Anchoa mitchilli*. Mean monthly marginal increments on otoliths of aged bay anchovy from Narragansett Bay, Rhode Island. Error bars = 95% CI; n = sample size

a third winter. By August, YOY had recruited to the trawl and dominated the population (Fig. 4).

Growth

Growth of first year fish during 1997 is strongly suggested by the modal movement of the monthly length-frequency distributions, such that by August of 1997 no fish spawned in 1996 were smaller than 60 mm fork length (Fig. 4). In June, first-year fish had a mean fork length of 63.7, while mean length was 71.9 mm by August.

Parameters of the TVB growth model were estimated as: $K = 1.15$, $L_{\infty} = 89.87$, and $t_0 = -0.31$. Without constraints, there was not an adequate time-series to obtain a realistic fit from the seasonally oscillating model; therefore, the parameters (K , L_{∞} , t_0) obtained from the traditional model were used to constrain the SOVB model (c and t_s were allowed to vary). The resulting model was then manipulated in the c and t_s parameters to obtain a more realistic visual representation of the growth of the bay anchovy (Fig. 5). The 95% confidence intervals of K and L_{∞} are presented in Table 3.

Growth rates were calculated from observed length-at-age data, and length-at-age data predicted from both the TVB and the manipulated form of the SOVB models (Table 4). Growth rate was calculated in units of mm d^{-1} over different time-steps to elucidate low-resolution changes in growth rate by age and season. Growth per day calculated from observed data was greatest during the first year of growth (Age 0 to Age 1 = 0.111 mm d^{-1}), decreasing by nearly an order of magnitude during the second year (Age 1 to Age 2 = 0.017 mm d^{-1}). Growth rates calculated from both model estimates were close to those calculated from observed data during the first year, while during year 2, model-derived growth rates were greater than the observation-based growth rate (Table 4).

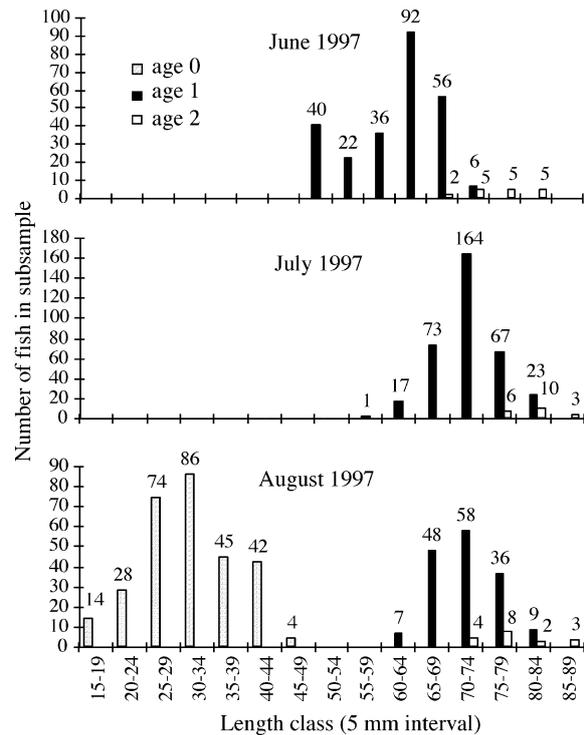


Fig. 4. *Anchoa mitchilli*. Age-frequency distribution of a subsample of the RIFW trawl survey catch of in Narragansett Bay during summer 1997, estimated by age-length keys constructed on a monthly basis

Table 3. *Anchoa mitchilli*. Confidence intervals (CI) of the von Bertalanffy equation parameters growth coefficient (K) and inferred length (L_{∞}), obtained by fitting Narragansett Bay anchovy length-at-age data

	K	L_{∞}
Best fit	1.154	89.87
Upper 95% CI	1.320	94.39
Lower 95% CI	1.003	86.10

Table 4. Growth (in mm d^{-1}) calculated annually and over the growing season, from observed and predicted length-at-age data ($(L_2 - L_1)/\text{time}$; Ricker 1975). Data from Narragansett Bay compared to data obtained for Chesapeake Bay by Newberger and Houde (1995). Hatch date taken as July 15. Age 0 fish in August are juveniles spawned in that year. Age 0 fish in May are fish that have overwintered successfully. TVB, SOVB: traditional and seasonally oscillating versions of von Bertalanffy growth model

Time period over which growth was calculated	This study			Newberger & Houde	
	Observed data	Predicted by TVB	Predicted by SOVB	Predicted by TVB	Predicted by SOVB
Annual growth (Aug to Aug):					
Age 0 to Age 1	0.111	0.103	0.101	0.053	0.063
Age 1 to Age 2	0.017	0.033	0.032	0.043	0.044
Age 0 to Age 2	0.064	0.068	0.067	0.048	0.054
Growing season (May to Aug):					
Age 0 to Age 1	0.148	0.065	0.123	0.050	0.103
Age 1 to Age 2	0.069	0.020	0.039	0.040	0.072

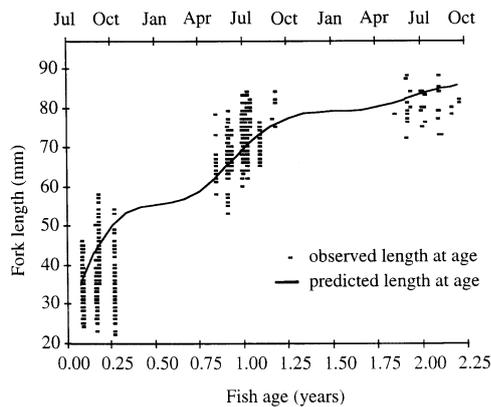


Fig. 5. *Anchoa mitchilli*. Growth in Narragansett Bay as described by seasonally oscillating version of von Bertalanffy growth model, constrained to parameters yielded by the traditional model, and adjusted for appropriate seasonality. Observed lengths-at-age (in years, with corresponding months) are also shown. Model parameters are: $L_{\infty} = 89.87$, $K = 1.15$, $t_0 = -0.31$, $c = -0.90$, $t_s = 0.024$ (see 'Methods' for details)

The TVB model does not reflect the seasonal growing pattern of the bay anchovy at this latitude. This is demonstrated by the apparent underestimate of growth by this model during the growing season (May to August: Table 4). The increased slope of the SOVB model (Fig. 5) during these months provides growth-rate estimates closer to those calculated from observed data (Table 4).

Mortality

Adult mortality (mortality between first spring and death), calculated with 1997 RIFW catch data (excluding YOY) and partitioned by age using the age-length key developed in this study, was estimated to range from 48% yr^{-1} (Robson & Chapman 1961) to 90% yr^{-1} (Heincke 1913; (Table 5). The regression method (Ricker 1975) gave an annual adult mortality of 89%. Mortality including YOY data was estimated to range from approximately 91 to 97% yr^{-1} . Bay anchovy migrate out of Narragansett Bay during the winter months; therefore, the assumption of a closed population is not met and mortality calculations also reflect population losses due to migration.

Alternative mortality estimates not affected by migration losses were obtained by life-history parameter methods. The different methods utilized resulted in annual mortality estimates

ranging from 64 to 97% yr^{-1} (Table 5). The Alverson & Carney (1975) method, which uses all 3 parameters (L_{∞} , K , t_0), gave the highest estimate of 97% annual mortality, while the lowest estimate of 64% was obtained by the Pauly (1981) method.

DISCUSSION

Sex ratio

A sex ratio significantly in favor of females has been found for *Anchoa mitchilli* both in Barnegat Bay, New Jersey (as high as 1.93:1: Vouglitois et al. 1987) and in the Chesapeake Bay (mean of 1.16:1: Newberger & Houde 1995). While the overall mean difference in abundance between females and males was not found to be significant in this study, females were more abundant than males in each monthly set of samples (Table 1). An unbalanced sex ratio favoring females seems to be the common situation for this species, and does not appear to be due to sex-based differences in weight or length (Vouglitois et al. 1987). Unbalanced sex ratios (female- or male-favored) have been found in other engraulid species, although there is no clear explanation for this phenomenon (Klingbeil 1978, Vouglitois et al. 1987, Fernandez & Dvaraj 1989, Giraldez & Abad 1995).

Morphometrics

Comparison of the weight-length relationship obtained in this study for all fish caught in June, July and August (pooled) to the relationships found by

Table 5. *Anchoa mitchilli*. Instantaneous and annual natural mortality rates. All mortality is assumed to be natural mortality or losses to migration, as *A. mitchilli* is not commercially fished

Method	Instantaneous mortality rate (Z)	Annual natural mortality (%) (A)	Standard error (a,b) or confidence interval (c) for A
Ricker (1975) ^a	2.17	89	0
Heincke (1913) ^a	2.27	90	5.41×10^{-4}
Robson & Chapman (1961) ^a	0.65	48	5.38×10^{-4}
Ricker (1975) ^b	2.41	91	1.39×10^{-1}
Heincke (1913) ^b	2.61	93	1.00×10^{-3}
Robson & Chapman (1961) ^b	3.44	97	6.92×10^{-4}
Alverson & Carney (1975) ^c	3.45	97	95–98%
Hoenig (1983) ^c	1.87	85	80–88%
Pauly (1981) ^c	1.02	64	60–68%

^{a,b}Catch-data methods: ^acalculated excluding young-of-the-year (YOY), ^bcalculated including YOY; ^clife-history-based methods

Newberger & Houde (1995) indicates a greater weight-at-length for Chesapeake Bay anchovies during these months (Fig. 6). Furthermore, Fulton's condition factor was found to be significantly lower ($p \ll 0.001$, Student's t -test assuming unequal variance) in Narragansett Bay fish than in Chesapeake Bay fish during the months of comparison (Newberger & Houde 1995) (present Table 2). This lower condition factor indicates that fish in Narragansett Bay may be allocating a greater proportion of their energy resources during the summer months to length increase rather than weight increase in comparison to fish from lower latitudes.

Selective pressures at high latitudes, including a shorter growing season and more pronounced seasonality, may result in a different energy-allocation strategy than that employed at more southern points of a species' range (Schultz & Conover 1997). Close to the northern extent of the range of a species, the adaptive capacity of an individual may be fully extended, i.e. *Anchoa mitchilli* may not be able to grow fast enough/spawn early enough for YOY to gain sufficient length and energy stores for overwinter survival much farther north than Narragansett Bay (Shuter & Post 1990, Conover 1992). The preferential allocation of growth in length as opposed to weight found in this study may be an adaptive strategy of *A. mitchilli* at this latitude (as opposed to a general consequence of the more rapid growth achieved by anchovies in Narragansett Bay; see later subsection 'Growth').

Fish commonly exhibit hyperallometric energy storage, such that an individual will need to become relatively large (in length) in order to reap the benefits of greater energy storage and decreased weight-specific metabolism (Shul'man 1974, Schultz & Conover 1997); that is, small fish may need to attain a minimum length before they will benefit from allocating resources to storage in lipid. The relatively rapid increase in length observed for bay anchovies in this study may enable this fish to gain sufficient pre-winter energy stores coupled with a lower weight-specific metabolic rate (Oliver et al. 1979, Shuter & Post 1990). Also, since muscle tissue has been indicated as the major energy-storage site of the bay anchovy (Wang & Houde 1994), allocation to lean tissue may provide a necessary baseline of energy storage for this fish. It is unknown from these data, however, if condition factor increases once the anchovies have left the Bay in the fall.

As this energy-allocation strategy may be most pertinent to the YOY anchovies, it may be more instructive for purposes of latitudinal comparison to compare the Fulton's condition factors obtained for juveniles separately. These data indicate a greater condition factor in adults than in YOY, and future studies may wish to take this factor into account.

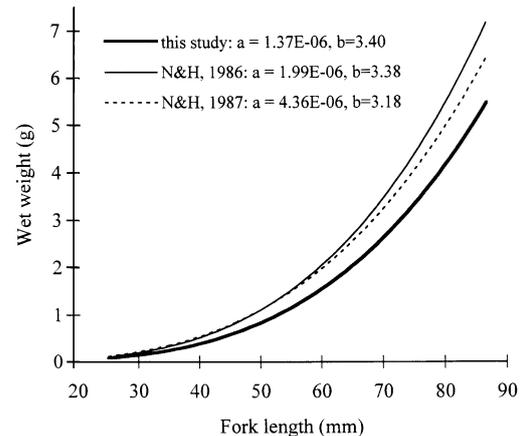


Fig. 6. *Anchoa mitchilli*. Plot of weight-length equation, $W = aL^b$, obtained with weight-length data. Parameters (a,b) obtained by Newberger & Houde (1995) are shown for Chesapeake Bay in 1986 and 1987 in comparison to parameters obtained in this study

Age structure and abundance

The Narragansett Bay population was dominated during June and July by fish spawned the previous year (Fig. 4). The population was dominated by YOY once they recruited to the trawl, beginning in August (Fig. 4). As has been found in other studies (Voughlitois et al. 1987, Newberger & Houde 1995), the bay anchovy is a very short-lived species. Recruitment fluctuations will thus have a tremendous impact on the year-to-year abundance of this species (Newberger & Houde 1995). At more northerly latitudes, however, events outside an estuary during the winter months (i.e. overwintering mortality, change in migration patterns) may also impact the abundance of adult fish that return to a certain estuary or bay during a given year (Voughlitois et al. 1987).

A plot of abundance (on a catch-per-unit-effort, CPUE, basis) of YOY and adults from the RIFW trawl survey from 1990 to 1998 does not suggest a relationship between spawning stock biomass and YOY recruitment (Fig. 7). While the population abundance of adults remained somewhat constant from year to year, there were pronounced fluctuations in YOY abundance. The large fluctuations in YOY abundance hint at the tremendous reproductive capacity of this species (Luo & Musick 1991), and also suggest that interannual variation in YOY abundance may be due less to fluctuations in spawning stock biomass than to other factors, such as competition, predation, and environmental conditions of food and temperature. The discrepancy between abundance patterns of YOY and adults could also suggest that losses due to migration and/or overwintering mortality of young fish are important factors in controlling abundance of adult anchovies within Narragansett Bay.

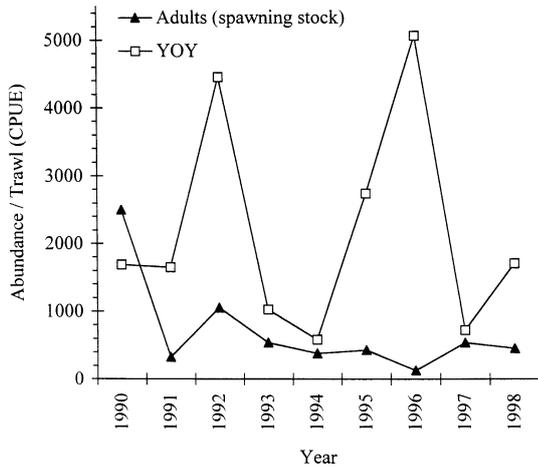


Fig. 7. *Anchoa mitchilli*. Relative abundance (catch-per-unit-effort, CPUE) of young-of-the year (YOY) and adults in RIFW Narragansett Bay trawl survey, 1990–1998

Growth

In Narragansett Bay, growth rate from Age 0 to Age 2 calculated from observed length-at-age data was rapid, 0.064 mm d^{-1} ; similar values with obtained from both the TVB and SOVB model-predicted length-at-age (Table 4). These growth-rate estimates were each higher than those obtained for the same time span using model-predicted values based on parameters found for Chesapeake Bay anchovies (Newberger

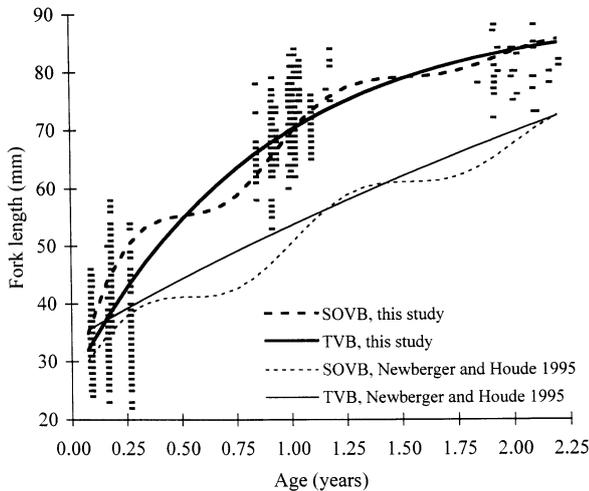


Fig. 8. *Anchoa mitchilli*. Traditional and seasonally oscillating versions of the von Bertalanffy growth model, plotted using parameters obtained for Narragansett Bay anchovies (this study) and parameters obtained by Newberger & Houde (1995) for *A. mitchilli* in Chesapeake Bay. Observed lengths-at-age for Narragansett Bay fish are also shown (short, horizontal data bars)

& Houde 1995) (Table 4). Observation-based and model-prediction-based growth rates found in the present study were most rapid during the first year of life (Age 0 to Age 1), slowing considerably after the second summer (Age 1 to Age 2; Table 4).

Observed and predicted (by both versions of the von Bertalanffy model) length-at-age of Narragansett Bay fish were greater than those predicted from Chesapeake Bay data (Newberger & Houde 1995) (Fig. 8). Mean fork lengths in Narragansett Bay at Ages 1 and 2 predicted by the TVB model were 70.7 and 83.8 mm, respectively, while in Chesapeake Bay they were 50.4 and 67.6 mm, respectively (Newberger & Houde 1995). This contrast is clearly significant, suggesting an intraspecific variation in growth rate, possibly along a latitudinal gradient.

The model parameters K and L_{∞} obtained in this study also differ markedly from those obtained by Newberger & Houde (1995); Narragansett Bay values of $K = 1.15$ and $L_{\infty} = 89.87$ are higher and lower, respectively, than the values ($K = 0.36$ and $L_{\infty} = 107.0$) from Newberger & Houde's best-fitting model (SOVB). The value of L_{∞} obtained in this study may be a more realistic estimate than that given by Newberger & Houde, as it is very rare to observe bay anchovies greater than 100 mm total length (Hildebrand 1963); the largest fish observed in this study was 88 mm fork length.

Rapid initial growth which declines as fish age, so that most growth is completed early in life (see Table 4), is also characteristic of a higher value of K . The Chesapeake Bay data suggest that anchovies there are growing at a more even pace throughout life. This is evidenced by the higher growth-rate values estimated using parameters of Newberger & Houde (1995) for the second year of life (Age 1 to Age 2) in comparison the present study's estimates (Table 4). The fact that Age 3 fish were found in Chesapeake Bay while no fish older than Age 2 were found in the present study suggests that there may be trade-offs associated with the very rapid growth seen in Narragansett Bay anchovies.

As both Narragansett Bay and Chesapeake Bay populations of *Anchoa mitchilli* are dominated by Age 1 and Age 0 individuals (Newberger & Houde 1995), the more rapid growth and greater length-at-age (Fig. 8) seen in the Narragansett fish suggest that the Narragansett Bay population will have a greater average length than that in Chesapeake Bay. While differences in sampling technique are not accounted for, all samples compared were collected during the summer months. A comparison of the present data with published values of mean length from Chesapeake Bay indicates a much higher mean length (>15% difference) of anchovies in Narragansett Bay (Table 6).

Mortality

Mortality was estimated by methods based on both catch data (Heincke 1913, Robson & Chapman 1961, Ricker 1975) and life-history parameters (Alverson & Carney 1975, Pauly 1981, Hoenig 1983). Both sets of estimates have associated flaws: the catch-data techniques suffer from assumption violations (e.g. the population is not closed and recruitment is variable), while the life-history parameter methods are several steps removed from actual data and thus may result in imprecise estimates (Vetter 1988).

The lowest mortality estimates, calculated by the Robson & Chapman (1961) approximation (excluding YOY data), and the Pauly (1981) equation, are probably spurious (Table 5). The abbreviated data series used in calculating adult mortality probably rendered the Robson & Chapman method inappropriate. The Pauly equation does not take the longevity of the fish into account; a maximum observed age of <3 yr is a constraint that should be considered. The Hoenig approximation also seems low: Hoenig (1983) noted that the assumption of constant mortality rate with age in this method is violated in some engraulid stocks (Beverton 1963), so that this may not be the best estimator for this taxa.

The higher values (>90% annual mortality) obtained by both the catch-analysis and life-history-based methods are the best estimates of mortality for the bay anchovy (Table 5). These values are similar to the best estimate range (89 to 95%) specified by Newberger & Houde (1995); the catch-curve estimates (Ricker method) excluding YOY were nearly identical ($Z_{\text{this data}} = 2.17$; $Z_{\text{N \& H (1995)}} = 2.19$).

The high mortality rate of this species is consistent with its other life-history traits: rapid growth and high reproductive capacity. This species is very strongly r-selected, and is well adapted for survival in often unpredictable estuarine environments.

While supporting the conclusions of other authors regarding the major life-history features of this species (e.g. fast growth, short-lifespan, high mortality), the results of this study also suggest some latitudinal differences. Environmental pressures resulting from more pronounced seasonality increase with increasing latitude; a shorter season for growth and reproduction coupled with more severe winter conditions may limit the abundance of this fish at latitudes above Narragansett Bay. My data suggest that bay anchovies at this latitude grow more rapidly than their southern conspecifics, particularly during the first year of life. Selection for rapid growth early in life may arise from over-

Table 6. *Anchoa mitchilli*. Comparison of mean fork length in Narragansett Bay, NB (this study) to that in Chesapeake Bay, CB (Luo & Musick 1991, Newberger & Houde 1995). -: no data

Age class	Bay	Fork length			Source
		Mean	SD	n	
Adults	NB	68.70	7.26	906	This study
	CB	55	-	-	Luo & Musick (1991)
Combined (juvenile + adult fish)	NB	61.26 ^a	15.97	1149	This study
	CB	51.90	8.30	1004	Newberger & Houde (1995)

^aLengths of approximately 100 juveniles and 100 adults from a given catch irrespective of the actual proportion of juveniles to adults in the catch

wintering mortality of smaller fish that do not have adequate energy reserves (Conover 1990, Schultz et al. 1998). These data also suggest that Narragansett Bay fish allocate resources preferentially to length versus weight during the growing season, in contrast to fish from Chesapeake Bay; this may suggest some selective benefit as well.

Future work should include investigation of the bioenergetics of *Anchoa mitchilli* at this latitude to better quantify the energy allocation strategy used by the Narragansett Bay population. Targeted sampling of this species as it moves out of the bay in the fall would be crucial to such a study. More rigorous comparison of anchovies on a latitudinal basis should be undertaken, including investigation of the genetic versus environmental contribution to apparent latitudinal differences in growth rate. Finally, clarifying the question of where these fish overwinter would provide valuable insight into the ecology of the bay anchovy at this latitude.

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