

AN ABSTRACT OF THE THESIS OF

Allyn B. Powell for the degree of Doctor of Philosophy
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Title: Life History Patterns of Two Allopatric Clupeids:
Atlantic Menhaden (*Brevoortia tyrannus*) and Gulf Menhaden
(*B. patronus*).

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Dr. Charles E. Warren

Atlantic menhaden, compared to gulf menhaden, exhibit a life history pattern that appears to be adapted to a more unpredictable reproductive environment. From experiments on laboratory-reared eggs and larvae, Atlantic menhaden have larger eggs with larger yolk volume. They are larger at hatching, utilize their yolk faster, begin feeding at an earlier age, and are larger at onset of feeding. Egg size and the rate of morphogenesis from hatching to first feeding appeared to influence future larval size. When given ample food and reared at moderate (20°C) to high (24°C) temperatures, Atlantic menhaden were larger than gulf menhaden at 10-days past first feeding even though growth of both larvae was similar. As Atlantic menhaden undergo their first apparent transformation at a relatively smaller size, they will spend relatively less time in the earliest life history stage.

A synthesis of published adult life histories also indicated that Atlantic menhaden life histories are adapted to a more unpredictable reproductive environment. They have a larger maximum body size and are larger than gulf menhaden at any specific age. They are older than gulf menhaden at the onset of sexual maturity, but have a longer reproductive span. Stock-recruitment models indicated that variations in environmental factors play a major role in determining the number of Atlantic menhaden recruits, whereas environmental factors play a lesser role in gulf menhaden recruitment. Atlantic menhaden populations, unlike gulf menhaden, exhibit density-dependent growth suggesting that food resources for pre-recruit Atlantic menhaden may be limiting when numbers are high.

Exploitation of Atlantic menhaden populations has resulted in a truncation of the population's age structure. This has resulted in: a contraction of spawning in time and space; a truncation of their reproductive span, thus altering the net reproductive rate; a loss in fecundity, as fecundity is age-specific; and if egg size is related to age of fish, a modification of the egg size distribution within the population. Overexploitation of gulf menhaden resulting in alteration of life history traits could have serious consequences because the reproductive span of this menhaden is so brief.

LIFE HISTORY PATTERNS OF TWO ALLOPATRIC CLUPEIDS:
ATLANTIC MENHADEN (Brevoortia tyrannus)
AND GULF MENHADEN (B. patronus)

by

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LIFE HISTORY PATTERNS OF TWO ALLOPATRIC CLUPEIDS:

ATLANTIC MENHADEN (Brevoortia tyrannus) and

GULF MENHADEN (B. patronus)

INTRODUCTION

The Atlantic menhaden (Brevoortia tyrannus) and the gulf menhaden (B. patronus), are schooling, filter-feeding clupeids that are geographically separated, but morphologically similar. The young of both species immigrate into estuaries, which they use for nursery areas during their first growing season. These menhaden dominate United States fishery landings. During 1987, the Atlantic and gulf menhadens constituted 39% of the total fishery landings by weight¹. The fishery utilizes purse-seines and spotter airplanes. Processing provides reduction products in the form of fish meal and oil, used in poultry feed supplements, and refined oil products that are used for human consumption in Canada and Europe. The biological and environmental differences and similarities of these two species make a comparative study of their life histories interesting while the intensive fishery makes an evaluation of their life histories important to fisheries management.

¹ J.W. Smith, National Marine Fisheries Service, Beaufort Laboratory, Beaufort, N.C. 28516-9777, pers. commun. May 1988.

Life History Theory

Interest in the adaptive/significance of life history reproductive strategies was stimulated by Cole (1954), who reminded ecologists of the adaptive values of life history phenomena. Cole believed that organisms exhibit great variability in their patterns of life history characteristics (total fecundity, maximum age, and age-specific schedules of reproduction and mortality). Consequences of these patterns are population birth rates, death rates, age compositions, and potentials for populations to increase their numbers. These individual and population phenomena, Cole suggested, favor population persistence in changing environments. Cole concluded that the study of the adaptive value of reproductive life histories was the most neglected aspect of biological studies.

Cole's (1954) paper stimulated numerous life history studies. Many of these studies have been aptly reviewed by Stearns (1976), who considered key life history traits to be fecundity, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult mortality, and the variation of these traits among an individual's progeny. Such traits are variable within populations and, through natural selection, conspecific individuals belonging to different populations adapt to different circumstances. There is interest in

predicting and explaining the suites of traits that will evolve in organisms living in different kinds of environments.

Life history theory, models and hypotheses are here defined in terms of Endler's (1986) definition of natural selection and the framework of Warren et al. (1979) (Fig. 1). Basically two models have been deduced from life history theory (\underline{r} - and \underline{K} - selection, and bet-hedging) and generally are employed in prediction and explanation of life history traits in different kinds of environments. The \underline{r} - and \underline{K} - selection model predicts \underline{r} -selection will operate when populations encounter variable and unpredictable environments on evolutionary time scales. Here, selection favors rapid growth and development, early age at sexual maturity, small body size, and semelparity. This is accompanied by so-called density-independent mortality, frequent colonizing episodes, lax competition, and short life span. \underline{K} - selection, on the other hand, will operate when populations encounter constant and predictable environments. Here selection favors slow development, delayed reproduction, larger body size, and iteroparity (Pianka 1970). Then density-dependent mortality, saturated communities, keen competition, and long length of life tend to occur. This model should be visualized as an \underline{r} - \underline{K} continuum in that no organism is completely \underline{r} - or \underline{K} -selected, but through trade-offs falls between the two

LIFE HISTORY THEORY

DEVELOPMENTAL, MOVEMENT AND REPRODUCTIVE
LIFE HISTORY PERFORMANCES ARE:

1. VARIABLE AMONG INDIVIDUALS
2. RELATED TO REPRODUCTIVE SUCCESS
AND/OR SURVIVORSHIP (FITNESS)
3. INHERITABLE



LIFE HISTORY MODELS

PREDICT WHAT SUITE OF TRAITS WILL EVOLVE IN
DIFFERENT KINDS OF ENVIRONMENTS

1. r -K SELECTION
2. BET - HEDGING



LIFE HISTORY HYPOTHESES

PROVIDE GENERALIZATIONS ABOUT SPECIFIC LIFE
HISTORY PATTERNS



LIFE HISTORY OBSERVATIONS

- | | |
|------------------------------------|---------------------------------------|
| • EGG SIZE | • NUMBER OF SPAWNINGS
PER LIFETIME |
| • SIZE AT HATCHING | • AGE AT FIRST SPAWNING |
| • SIZE AT FIRST FEEDING | • FECUNDITY |
| • SCOPE FOR GROWTH | • MIGRATION PATTERNS |
| • AGE AND SIZE AT
METAMORPHOSIS | • REPRODUCTIVE PATTERNS |

Figure 1. Life history theory and other components that have been deduced from the theory. Empirical observations include both early life history and adult characteristics.

extremes. An organism can be thought of as an r-strategist or K-strategist only relative to similar organisms in other populations and species (Pianka 1970). This model has been useful to fishery scientists in developing management strategies (Adams 1980), and to estimate natural mortality rates (Gunderson 1980).

The bet-hedging model tends to contradict the r- and K-selection model. Using simulation models, Murphy (1968) advanced the argument that long life, late maturity, and many reproductions are selected for in an environment in which density-independent factors cause wide variation in larval and juvenile survival or in an environment in which intense competition exists between pre-reproductives and reproductives. Murphy also argued that early reproduction, high fecundity, and few reproductions per lifetime will be selected for in environments where adult mortality is high and variable.

Schaffer (1974) mathematically deduced a bet-hedging model in support of Murphy's (1968) arguments. Schaffer's model suggests that when environmentally induced variation in reproduction occurs, the best adapted reproductive strategy would be reduction in per capita reproductive output. Variation in adult survival, on the other hand, should result in greater investments in reproduction. Schaffer (1974) argued that this contradicts the generalizations that fluctuating environments favor greater

reproductive efforts, while stable environments favor small litter size and increased longevity (i.e., r - and K -selection). The principle issue, Schaffer (1974) argues, is the age specificity of the environmental fluctuation, i.e., are juveniles or adults principally affected. The bet-hedging model, then, emphasizes variability and unpredictability in the juvenile stage. As most marine fishes have a relatively high degree of variable and unpredictable mortality during the larval/juvenile stage, the bet-hedging model appears to be the most useful in explaining how life history strategies have allowed fish populations to persist. But Stearns (1976) argues that both models (r - and K -selection, and bet-hedging) could lead to the same predictions for the same environments. In a stable environment where competition is strong and resources limited, the variation in juvenile survival may be much greater than the variation in adult survival. Likewise, in an environment where colonizing episodes are frequent, the variation in adult survival may be much greater than juvenile survival. The different models, then, could be illuminating only different aspects of life history theory.

Stearns (1980), although a proponent of life history theory, questions whether life history strategies are predictable from extant models. Stearns' (1980) work suggested that physiological constraints may prevent evolution and development of characteristics predicted by

r- and K- selection and bet-hedging models. In like manner, biological constraints (e.g., size of brood may be limited by body cavity space), developmental canalization (same phenotype produced under a wide range of genetic and environmental conditions), and evolutionary constraints by lineage may also prevent the evolution and development of characteristics predicted by models deduced from life history theory (Hines 1986). Leggett (1985) argues that difficulties noted by Stearns (1980) are not sufficient to abandon life history theory. I strongly agree with Leggett (1985) and believe that life history theory is robust in that it is far-reaching, provides a good foundation for the deduction of models, and has heuristic power. Many of the inconsistencies discussed -- for example, by Stearns (1980), Leggett (1985), and Hines (1986) -- are more a result of the models deduced from the theory rather than of the theory itself. Hines (1986) suggests that models based on multivariable approaches rather than uni-dimensional approaches should enhance our understanding of life history strategies. A broader understanding of life history strategies, in my opinion, can best be attained by studies that integrate reproductive, movement, and developmental life history traits.

Developmental, movement, and reproductive life history traits together and in interaction with their coextensive environment in large part determine the success of a

genotype. Reproductive life history traits apparently have received the most attention in life history studies (Stearns 1976). But most populations exhibit phenotypic variations, so developmental trait divergences (e.g., tolerance, behavior, preference) enable populations to persist. This is especially true for populations that live in highly variable environments where phenotypic variation dampens, to some degree, effects of fluctuations (Den Boer 1968).

Movement life history traits (e.g., dispersal, local movement, diel migrations, and seasonal migrations) help to spread risks spatially (Den Boer 1968). Leggett (1985) demonstrated that both microscale and macroscale migration of fishes can operate to reduce environmental variation. Environments that appear to be totally unpredictable in respect to reproductive success can, through movement life history traits, be made highly predictable.

A tentative study of the early life histories of the Atlantic menhaden and gulf menhaden (Powell and Phonlor 1986) suggested to me that a more complete and detailed study of the life histories of these two menhadens could provide insight into how life history strategies have allowed fishes to adapt to their coextensive environments. The major objective of this study, then, is to compare the life histories of these menhadens and interpret my observations within the context of life history theory.

Organismic Approach to Life History Theory

The essence of natural systems is their spacial and temporal complexity and variability. Because of this, fishery scientists and managers are required to deal with problems that have a high degree of uncertainty. This can, and does in many instances, lead to management crises. Because of these circumstances, it may be advantageous to view these problems through diverse perspectives.

Fishery problems are usually approached through a mechanistic perspective. Populations are considered on the basis of numerical properties. Within this context, the interest of the fishery scientist is stock and recruitment, yield-per-recruit, surplus production models, and yield calculations. Harvesting and habitat perturbations are generally evaluated as to their effects on population size or yield.

Another approach is possible through an organismic perspective. Here harvesting and habitat perturbations are evaluated in terms of their effects on life history characteristics that enable populations to adapt to their environments. This perspective has been adopted by Murphy (1968), Shaffer and Elson (1975), Leggett and Carscadden (1978), Warren and Liss (1980), Beacham (1983), and Beacham and Murray (1987). It is within this organismic context that this study was conducted.

The interpretation of life history phenomena in this study involves the conceptual framework of Warren et al. (1979) and more general philosophical structures (Pepper 1942). My interest is in entire developing life history patterns of the Atlantic and gulf menhadens, not simply any particular stage of the developmental event. This is in accord with Dobzhansky's (1956) caution that adaptive "traits have no adaptive significance in isolation from the whole developmental pattern of the organism which exhibits them at certain stages of its life cycle." Stearns (1976) also cautions against isolating life history traits (e.g., fecundity, size of young, age distribution, and reproductive effort, etc.) to look for ecological interactions that will explain observed variation. He suggests that we consider "organisms as systems of interacting co-adapted traits, with trade-offs among them." Failure to heed these warnings may severely limit the generalizations and applicability of any life history study.

Fundamental to any organism is its potential capacity (roughly, genotype) that along with an environmental system determines the realized capacity (roughly, phenotype). Any performance of an organism (e.g., growth or reproduction) is, in turn, an outcome of the realized capacity and the environmental system at that time. A well-adapted life history can be understood to be in concordance (harmonious and rule-like relation) with a coextensive environmental

system. For an organism to be adapted requires not only present but also probable future concordance of its capacity as well as its performances with its environmental system (Warren and Liss 1980).

In turn, the life history and evolutionary adaptive capacities of a population of fishes are based on its incorporation of the different life history strategies of its individuals and potential individuals, each having a capacity to adapt (phenotypic plasticity) to somewhat different kinds of habitats. For the population to persist, it must maintain and evolve a variety of life history types that can adapt to diverse habitats. Individuals can persist only in an environment that provides them with suitable conditions. The strategy of a population, then, is to keep its individuals in suitable habitats through space and time (Warren and Liss 1980). All this is roughly in accord with William's (1966) argument that a habitat is fit when an organism has a "near-optimum soma" for existence in that specific habitat, and that at any life history stage an organism must not only be in concordance to its immediate environment, but must retain the ability to adapt to future environments. This concept is further elaborated by Den Boer (1968), who states (p. 191) that "Variation within natural populations as well as in their environments may result naturally in a spreading (diminution) of the risk of

extinction to which these populations are exposed under the influence of variable environmental factors."

Fishery scientists and managers, I believe, should strive to understand and protect the life history and evolutionary adaptive capacities of the fish populations with which they work.

METHODS AND MATERIALS

Adult gulf menhaden were captured by cast net in Pensacola Bay, FL, during the early fall in 1983, 1984, and 1985 and transported to Beaufort, NC, by methods described by Hettler (1983). Adult Atlantic menhaden were collected from a commercial purse seine in Core Sound, NC, during the summers of 1983 and 1985. Menhaden were held in the laboratory at ambient temperatures until water temperatures began falling below 20°C. At this time, sea water controlled at ca. 20° was used. For each spawning, ten menhaden were induced to spawn by methods described by Hettler (1981, 1983). In general, spawning occurred in 20°C water at night, and eggs were collected in the morning. Eggs were placed either in 10-L black-sided tanks immersed in a temperature-controlled water bath or in 100-L black-sided rearing tanks for future use. Temperatures in the 100-L tanks were dependent upon room temperature that was maintained at 19-20°C. Two 40-W fluorescent lamps were placed 90 cm above each large rearing tank, and 40 cm above each small tank. The tanks were illuminated for 12 h daily. The rotifer Brachionus plicatilis was used as the sole food source. Nineteen spawnings were performed to provide eggs and larvae for numerous empirical observations (Table 1).

Table 1. Summary of egg and larval experiments conducted in the laboratory.

Eggs					
Year	Experiment number	Egg size	Yolk size	Oil globule size	Dry weight
Gulf Menhaden					
1984	1	x	x		
	2	x	x		
	3				
1985	1	x			x
	2	x	x		
	3	x			x
1986	1	x	x	x	
	2	x	x		
	3	x	x	x	
	4	x	x	x	
Atlantic Menhaden					
1984	1	x	x		
	2	x	x		
	3	x	x		
1986	1	x	x	x	
	2	x	x	x	
	3	x	x	x	
	4	x	x	x	x
	5	x	x	x	
	6	x	x	x	

Table 1 (contd)

Larvae									
Year	Experiment number	Starvation	Size at hatching	Weight at hatching	Size at first feeding	Weight at first feeding	Yolk absorption rates	Growth vs food & temp.	Growth vs. temp.
Gulf Menhaden									
1984	1	x							
	2				x			x	
	3							x	
1985	1							x	
	2	x			x				
	3	x			x			x	
1986	1		x	x	x	x	x	x	x
	2		x	x	x	x	x		
	3		x	x	x	x	x		x
	4		x	x	x	x	x		x
Atlantic Menhaden									
1984	1	x							
	2	x			x			x	
	3	x			x			x	
1986	1	x							
	2	x			x		x		x
	3	x	x	x	x	x	x	x	x
	4		x	x	x	x	x	x	
	5		x	x	x	x	x	x	
	6		x	x	x	x	x	x	

Eggs

To compare egg, yolk, and oil globule sizes, measurements were made of approximately 50 eggs at 50x magnification for each experiment (Table 1). Yolk and oil measurements were used to calculate volumes. Because the spheroidal oil globule is embedded in the prolate spheroidal yolk mass, oil volumes were subtracted from initial yolk volume estimates to give a more accurate measurement of yolk volume. Analysis of variance (ANOVA) was used to test the differences between species.

Based on the collection of Atlantic menhaden eggs from eight cruises from 1979 to 1981 by the Northeast Fisheries Center (National Marine Fisheries Service, Sandy Hook Laboratory), I investigated the relationship between egg size and the latitudes where eggs were collected. Only the diameters of eggs preserved in 5% formalin could be obtained, because yolk shrinks and deforms from preservation, whereas egg diameter is not affected (Table 2).

Larvae

Starvation experiments were conducted at 16, 20, and 24°C. I chose experimental temperatures that I believe at least one of the menhaden species encounters during its early life history. Approximately 20-25 larvae were randomly placed in 1-L fingerbowls just prior to the day

Table 2. The effects of preservation (5% buffered formalin) on 50 gulf menhaden egg and yolk measurements.

	Egg Diameter (mm) ± SE	Yolk Diameter (mm) ± SE
Live	1.19 ± 0.01018	0.98 ± 0.01016
Preserved	1.21 ± 0.00490	0.75 ± 0.00865

when the larvae would have begun feeding on exogenous food sources (first feeding). Food was withheld from all experimental groups. Mortalities were recorded at least every morning and the results of repeated experiments (Table 1) were averaged.

The lengths and dry weights of menhaden larvae at hatching and at first feeding were determined from larvae reared at 16, 20, and 24°C in 10-L tanks. Standard lengths (SL) and dry weights were obtained from larvae that had been preserved in 5% buffered formalin. To determine when first feeding occurred, 10 larvae at each experimental temperature were sampled daily, starting at 1-d posthatch. Guts were analyzed for the presence or absence of rotifers. The presence of rotifers in any of the 10 larvae was used to signify first feeding. Ancillary first-feeding observations were also made. I observed when the eyes became fully pigmented, when the mouth appeared functional, and when the foregut and midgut were differentiated. These observations as well as all measurements were made at 50x magnification.

Comparative yolk absorption rates were determined at 16, 20, and 24°C, from time of hatching to time of first feeding. Because preservation has a significant effect on the size and condition of the yolk sac and its contents, measurements were made only on live material. Menhaden yolk sacs are elliptically shaped, hence yolk volumes were calculated using the formula for a prolate spheroid:

$$\underline{V} = (\pi/6) \underline{l} \underline{h}^2$$

where \underline{l} is length and \underline{h} is the height of the yolk mass (Blaxter and Hempel 1963; Powell and Phonlor 1986). Because the spheroidal oil globule is embedded in the yolk mass, oil volumes were calculated and subtracted from the calculated yolk volumes to give a better estimate of yolk volume. Yolk and oil globule dry weights were calculated from Eldridge et al. (1982) data on striped bass eggs. Here 1 mm^3 of yolk = $202 \text{ } \mu\text{g}$; 1 mm^3 of oil = $853 \text{ } \mu\text{g}$.

Two types of growth experiments were conducted (Table 1). In one series of experiments, I investigated the growth of young menhaden larvae in relation to two environmental factors. Following Fry (1947), I chose temperature as the controlling factor and food density as a limiting factor. Fifty larvae, approximately 6-d old, were randomly transferred from 100-L rearing tanks to each 10-L experimental tank. The larvae were slowly acclimated to the treatment temperatures (16, 20, and 24°C). Food levels were designed to examine the performance of menhaden larvae at high, moderate, and low food levels. Food densities the first year (1984) were 50, 25, and 5 rotifers ml^{-1} . These densities proved to not limit growth. All three densities could be considered high food levels. Food densities of 10.0, 1.0, 0.1 and 0.025 rotifers ml^{-1} were employed the following years (1985 and 1986). Food densities were monitored each morning. In 1984, three 1 ml samples per

experimental tank were taken. In 1985 and 1986, three samples per experimental tank were taken, but size of the samples varied. Samples for treatments at food densities of 10.0, 1.0, 0.1, and 0.025 rotifers ml^{-1} were 1, 10, 100, and 200 ml, respectively. Treatments were adjusted on the basis of the average of these samples. The duration of the experiment was 7 d. To determine growth, 50 larvae were randomly sampled from the 100-L tank at the beginning of the experiment and preserved in 5% buffered formalin. The survivors at the end of the experiment were also preserved in 5% buffered formalin. Because a treatment is an experimental unit, larvae in each treatment were combined, dry weights obtained, and values expressed as mean dry weight fish^{-1} .

Gain in biomass (B) was calculated as follows:

$$B = (W_t - W_{t-7}) (S)$$

where W = mean dry weight fish^{-1}

t = age in days

S = number of survivors. ANOVA (factorial design) was used in interpreting the data.

Another series of growth experiments was conducted to examine size of larvae 10 d past first feeding. Eggs and larvae were reared in 10-L tanks at temperatures of 16, 20, and 24°C. Larvae were maintained on high food densities (ca > 25 rotifers ml^{-1}). For each experiment, 10 larvae were sampled 10 d past first feeding. Standard length, dry

weight, and mouth width was obtained from larvae preserved in 5% buffered formalin. ANOVA (factorial design) was used in interpreting the data.

Length-weight relationships were derived to estimate sizes that separate early life history events (Balon 1984). Larvae were measured alive and dry weights were obtained from larvae that were preserved by freezing. Larvae used to determine the length-weight relationships were obtained from fish developing from eggs spawned in the laboratory. An analysis of covariance was used to assist in comparing interspecific relationships.

Statistical Analysis

The use of analysis of variance and analysis of covariance in this study was to aid in the interpretation of data influenced by what were probably variable and unidentified factors. I have avoided the use of statistical notation in this paper. When the null hypothesis is rejected at the 0.05 level of significance, differences are referred to as significantly different.

SUMMARY OF ADULT LIFE HISTORIES

The Atlantic menhaden ranges from Nova Scotia to Florida. From May to October, age-1 and older fish are distributed by age and size along the coast, while young-of-the-year fish occur in estuaries. During the fall, fish north of Chesapeake Bay begin a southward movement, and by early winter there is a concentration of fish of all ages south of Cape Hatteras, NC. During late winter and early spring, a northward movement occurs along the coast. Fish from Chesapeake Bay northward continue to move northward during the summer. Atlantic menhaden, south of Cape Hatteras, N.C., make little movement either north or south from June to November (June and Reintjes 1959; Roithmayr 1963; Nicholson 1971, 1978).

The spawning period for Atlantic menhaden is protracted, and a seasonal shift in the area of spawning occurs. Nelson et al. (1977) summarized the spawning cycle of this menhaden, based in large part on gonad maturation studies (Highman and Nicholson 1964) and systematic ichthyoplankton cruises (Reintjes 1961; Kendall and Reintjes 1975). Limited spawning occurs during the spring northward migration off New Jersey and New York. Limited spawning also occurs during the summer as far north as Cape Cod and occasionally in the Gulf of Maine. At this time, spawning occurs well inshore and in bays and sounds from Long Island northward. During the early fall, spawning is widespread from southern

New England to Virginia. Spawning intensity increases during the fall southward migration. By late fall and early winter, spawning is limited to areas between Delaware and North Carolina. Intensive spawning occurs during the winter in the South Atlantic Bight. At this time the stocks move offshore, the only time during the year that Atlantic menhaden schools are not available in coastal waters (Kendall and Reintjes 1975). Atlantic menhaden may spawn as far south as Florida, but at a low intensity in this extreme southern portion of their range.

The gulf menhaden ranges along the Gulf of Mexico coast from Cape Sable, FL, to Veracruz, Mexico (Reintjes 1969). The fishery for this species is most intense off Louisiana and Mississippi (Nelson and Ahrenholz 1986), which suggests that this area is the center of distribution for gulf menhaden. Data from tagging studies (Kroger and Pristas 1975; Ahrenholz 1981) and exploratory fishing cruises (Roithmayr and Waller 1963) showed that there is little to no movement of fish between areas east and west of the Mississippi River Delta. As these fish age, there is a gradual movement towards the Delta. Gulf menhaden overwinter on the inner and middle continental shelf just off the Delta, relatively close to the summer fishing area.

The spawning area of gulf menhaden appears to be from Sabine Pass, TX, to western Florida, based on the analysis of archived egg collections taken throughout the Gulf

(Christmas and Waller 1975) and eggs collected off the west coast of Louisiana (Shaw et al. 1985). The center of spawning is from the Mississippi River Delta west to the Atchafalaya River Delta. Spawning occurs in nearshore coastal waters in depths ranging from 2 to 110 m (Christmas and Waller 1975).

Gulf menhaden spawn mainly from October to March, with a peak in December (Christmas and Waller 1975; Shaw et al. 1985). Christmas and Waller's (1975) analysis of egg collections from throughout the Gulf of Mexico show that spawning begins in the north central portion during October. Spawning occurs throughout the north central area in November, and begins along the Texas coast. By December, spawning peaks along the north-central Gulf of Mexico and begins along western Florida. There is a slight decrease in January, but spawning is still intense in the northwest sector of the central Gulf. A second spawning peak throughout February was noted in the eastern sector of the central Gulf. Spawning becomes less intense during March, and by April spawning has mainly ceased. At this time, adults return to inshore and nearshore waters and the commercial fishery commences.

Compared to the gulf menhaden, the Atlantic menhaden attains a larger maximum body size (L_{∞}), delays sexual maturity, has a lower rate of natural mortality (M), and lives longer (Table 3). The Atlantic menhaden reaches its

Table 3. Summary of life history characteristics for Atlantic and gulf menhadens. Data from Nelson and Ahrenholz (1986) and Ahrenholz et al. (1987).

Characteristic	Species	
	Atlantic menhaden	Gulf menhaden
Maximum body size (L_{∞})	363 - 373 mm ¹	253 mm
Growth rate (k)	0.3637 - 0.4539 ¹	0.4748
Natural mortality rate (M)	0.45	1.1
Age at sexual maturity	2+ years	1 + years
Maximum age	10 years	4 years

¹ Ranges from strong (1958) to weak (1967) year classes. The first value is from a strong year class.

maximum body size at a slower rate (k), but at any age it is larger than the gulf menhaden (Nelson and Ahrenholz 1986; Ahrenholz, et al. 1987).

RESULTS

Atlantic menhaden eggs weigh nearly twice as much as gulf menhaden eggs. The volume of yolk was significantly greater for Atlantic menhaden, but oil globule volumes are similar (Table 4).

I examined ancillary data for possible reasons for intraspecific variation in menhaden egg sizes. Intraspecific differences in egg size have been attributed to maternal size (Beacham and Murray 1985; Hankin and McKelvey 1985; Mann and Mills 1985), adaptations to incubation temperature (Southward and Demir 1974; Ware 1975; Tanasichuk and Ware 1987), seasonal change in the production cycle (Ware 1977), or seasonal change in egg size during the spawning season (Houghton et al. 1985).

Greater variation in egg size occurred in laboratory spawned Atlantic menhaden than in laboratory spawned gulf menhaden (Table 4). This variation could not be related to maternal size, as the mean size of females used for spawning ranged from only 204 to 212 mm TL. There was no discernible change in egg size during the laboratory spawning season (Fig. 2). But when I examined field-collected Atlantic menhaden eggs, egg diameter was positively related to latitude of capture (Fig. 3). This suggested two possibilities. Atlantic menhaden are distributed by age and size (see Summary of Adult Life Histories above) and larger menhaden may produce larger eggs or temperature may be

Table 4. Summary of menhaden egg data. Values in parenthesis indicate the number of experiments.

Species	Eggs				Yolk		Oil Globule	
	Mean diameter (mm)	Range of means (mm)	Mean dry weight (μg)	Range of means (μg)	Mean volume (mm^3)	Range of means (mm^3)	Mean volume (mm^3)	Range of means (mm^3)
Atlantic menhaden	1.61 (9)	1.54- 1.70	78 (2)	77-79	0.5832 (6)	0.4749- 0.6266	0.0028 (6)	0.0019- 0.0037
Gulf menhaden	1.22 (7)	1.19- 1.24	43 (2)	40-47	0.4832 (4)	0.4431- 0.5290	0.0032 (4)	0.0028- 0.0034

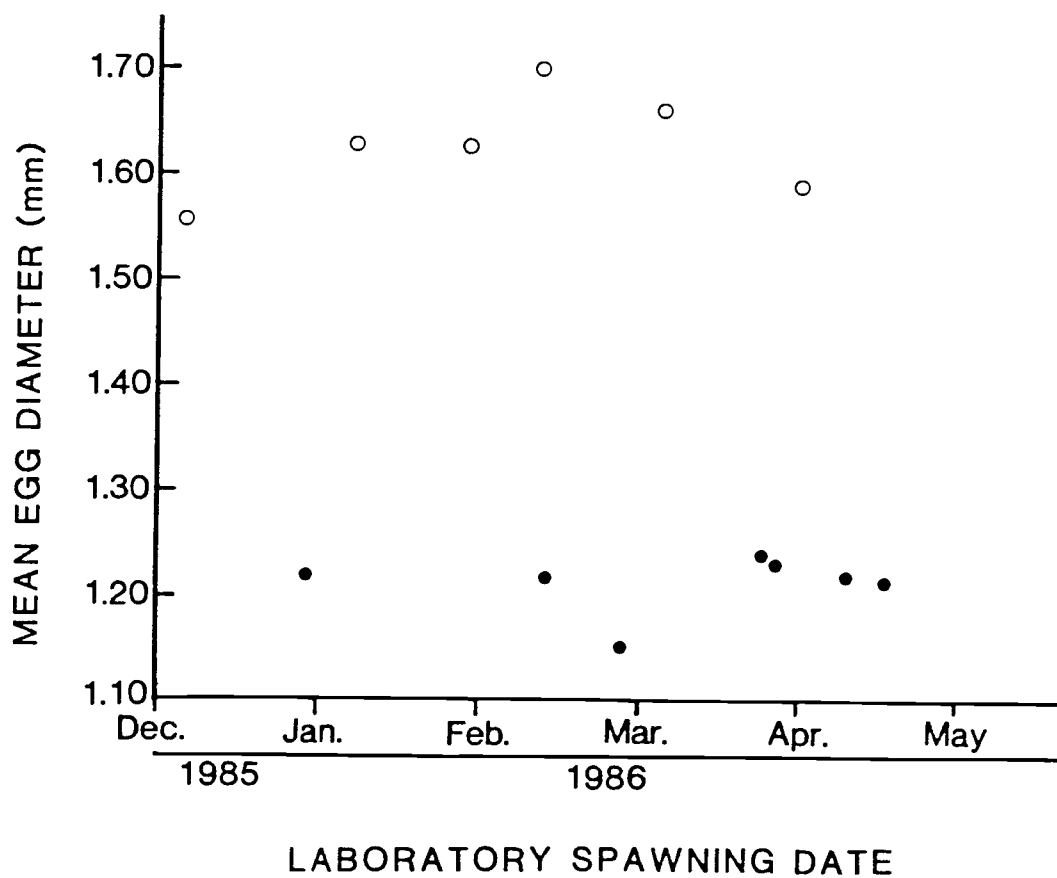


Figure 2. Relationship between mean egg size and laboratory spawning date for gulf (●) and Atlantic (○) menhadens. Means are derived from approximately 50 eggs.

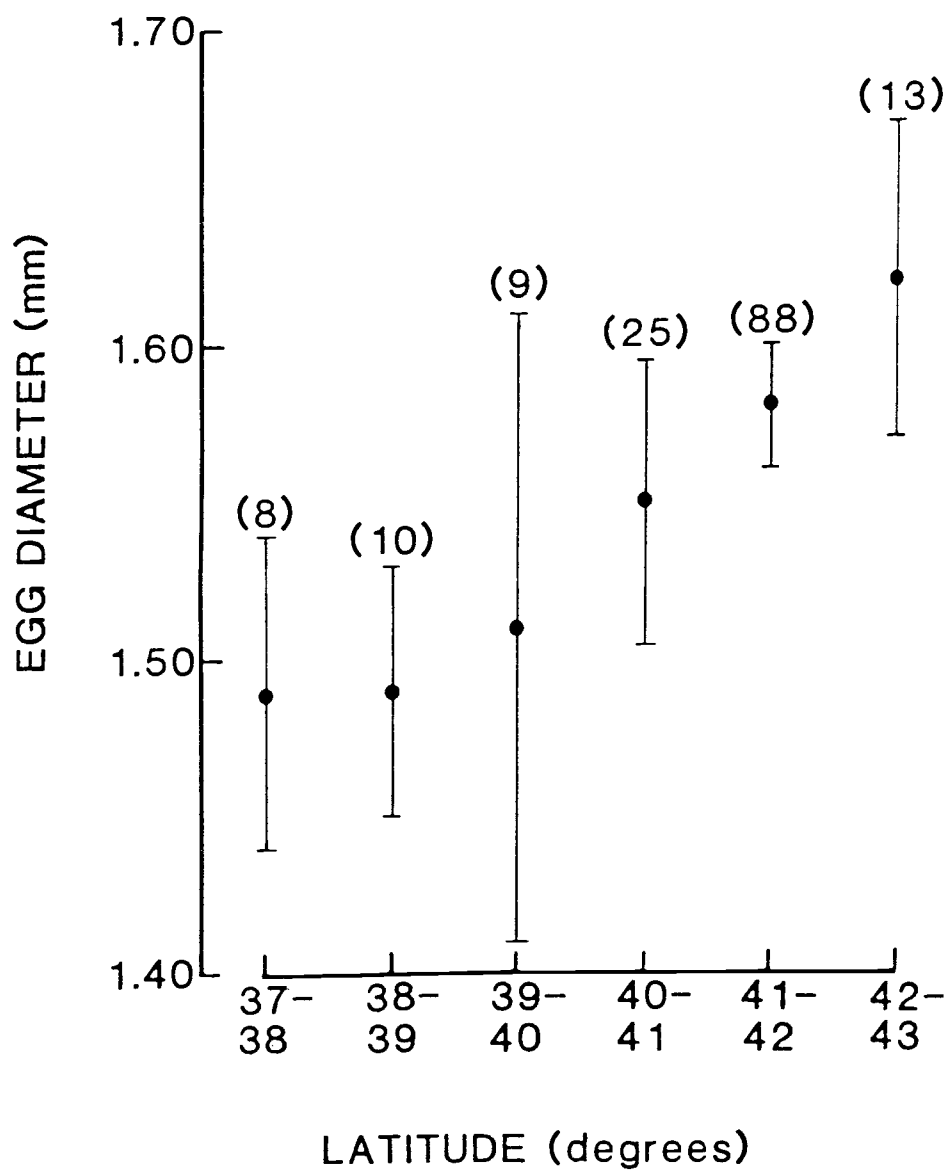


Figure 3. Relationship between mean egg size (± 2 SE) and latitude of capture for Atlantic menhaden. Numbers in parentheses indicate the number of eggs measured.

controlling egg size. Neither of these factors can be isolated with these data.

Newly hatched Atlantic menhaden, in the laboratory, were significantly larger in length and weight than were gulf menhaden (Fig. 4). Temperature appeared to affect length at hatching, as larvae were longer at relatively low incubation temperatures. On the other hand, incubation temperatures in the laboratory did not affect the weight of larvae at hatching.

Yolk reserves were significantly larger for Atlantic menhaden at hatching (as they were for their eggs), but oil reserves were significantly larger for gulf menhaden (Table 5). Temperature did not affect the amount of oil or yolk reserves for recently hatched Atlantic or gulf menhadens. After hatching both the Atlantic and gulf menhadens utilized their yolk and oil reserves at an exponential rate as they aged (Table 6 and 7). Atlantic menhaden utilize their yolk reserves at a significantly higher rate than gulf menhaden, but the rates at which oil was utilized by the two species were not significantly different (Fig. 5). Rates of yolk and oil utilization increased significantly with increasing temperature. When larvae began feeding on exogenous food sources (first feeding), the oil reserve was virtually depleted and very little yolk remained (Table 4). Yolk reserves at this time were similar for the two species and were independent of the rearing temperature. The average

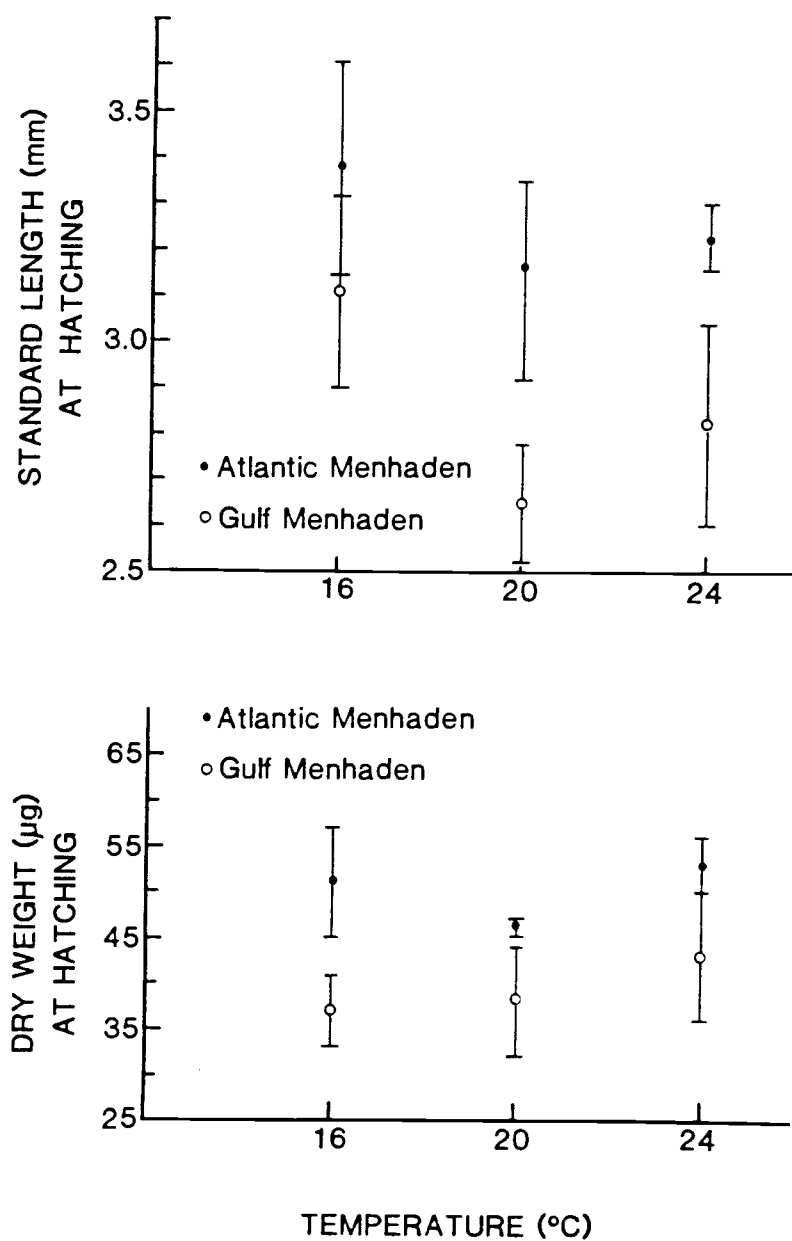


Figure 4. Size of Atlantic and gulf menhadens (± 2 SE) at hatching at various temperatures. Values are means of four experiments.

Table 5. Mean yolk and oil reserves of Atlantic and gulf menhadens at hatching and time of first feeding¹. N indicates the number of experiments.

Species	°C	N	Yolk dry weight (μg) at hatching	Oil dry weight (μg) at hatching	Yolk dry weight (μg) at first feeding
Gulf menhaden	16	3	21.50	2.30	0.05
	20	4	27.89	2.56	0.04
	24	4	22.95	2.50	0.04
Atlantic menhaden	16	5	28.93	1.95	0.04
	20	5	32.05	1.98	0.04
	24	5	30.65	2.02	0.05

¹ Mean oil dry weights (μg) for both species at all temperatures were zero at first feeding.

Table 6. Linear regression equations ($Y = B_0 + B_1X_1$) between \log_e yolk volume in mm^3 (Y) and age in days (X_1) for gulf and Atlantic menhaden.

Species	°C	N	Slope (B_1)	Intercept (B_0)	r^2
Gulf menhaden	16	22	-1.220	-2.089	0.96
	20	17	-1.734	-1.733	0.97
	24	16	-2.228	-2.118	0.98
Atlantic menhaden	16	34	-1.270	-1.765	0.97
	20	21	-2.065	-1.712	0.96
	24	17	-2.595	-1.723	0.97

Table 7. Linear regression equations ($Y = B_0 + B_1X_1$) between \log_e oil volume in mm^3 (Y) and age in days (X_1) for gulf and Atlantic menhadens.

Species	°C	N	Slope (B_1)	Intercept (B_0)	r^2
Gulf menhaden	16	22	-1.432	-5.082	0.81
	20	17	-1.819	-4.985	0.86
	24	16	-2.834	-4.814	0.81
Atlantic menhaden	16	34	-1.222	-5.392	0.92
	20	21	-2.041	-5.232	0.83
	24	17	-2.017	-5.714	0.84

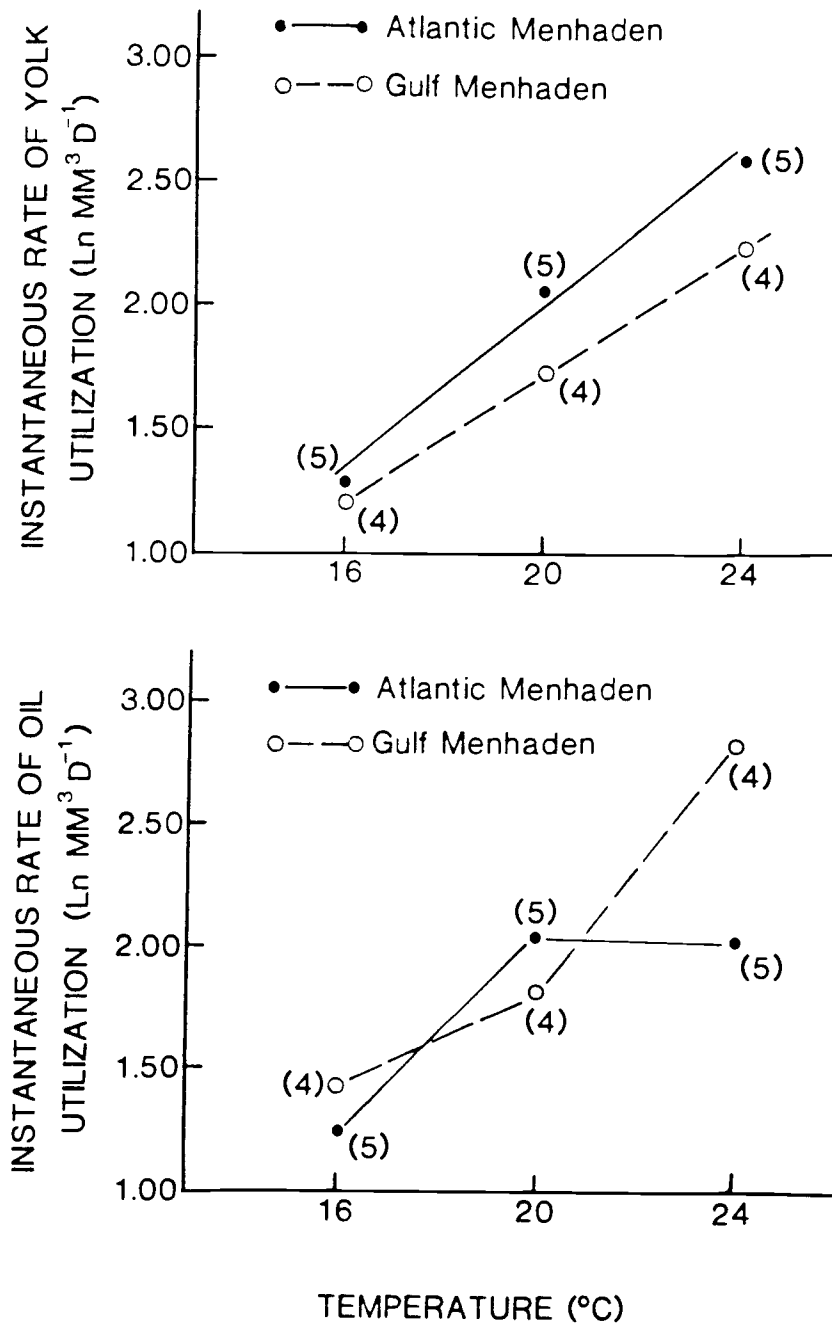


Figure 5. Rates of yolk and oil utilization at various temperatures for Atlantic and gulf menhadens. Values in parentheses denote the number of experiments.

age when these menhadens develop anatomical features associated with feeding is similar, but the time between when these features become discernible and first feeding is less for Atlantic menhaden (Table 8).

Atlantic menhaden were significantly longer and younger than gulf menhaden at the time of first feeding (Figs. 6 and 7). The weights of these two menhadens were, however, similar at this time. Although there was a trend for larvae to be slightly longer as rearing temperature decreased, temperature had no significant influence on size of larvae at first feeding (Fig. 6). On the other hand, there was an exponential decrease in the age at first feeding with increasing temperatures (Fig. 7).

First-feeding Atlantic menhaden, which are longer than first-feeding gulf menhaden, may be slightly more resistant to starvation (Fig. 8). At all temperatures, Atlantic menhaden lived for one (20 and 24°C) to two (16°C) days more than gulf menhaden. The survivorship curves of the two species had similar shapes at the same temperature (Fig. 8). At the highest temperature (24°C) survivorship declined rapidly after the third day, while at the lowest temperature (16°C) it was nearly linear with time.

Growth of the early stages of both menhadens was similar. In a series of experiments in which food concentrations did not limit growth, the biomass (i.e., growth and survival) of both menhadens was relatively low

Table 8. The mean time (days) before first feeding when $\geq 80\%$ of menhaden larvae attained eye pigment (EYE), fore-and mid-gut (FG/MG), and a functional mouth (MOUTH) in relation to temperature. Values are the means of three experiments. Values in parentheses indicate average age (days).

Species	Temperature (°)								
	16°			20°			24°		
	FG/ MG	EYE	MOUTH	FG/ MG	EYE	MOUTH	FG/ MG	EYE	MOUTH
Gulf menhaden	1.0 (4.7)	1.3 (4.4)	1.3 (4.4)	0.7 (3.2)	0.7 (3.2)	0.7 (3.2)	0.3 (2.6)	0.3 (2.6)	0.7 (2.2)
Atlantic menhaden	0.3 (4.9)	0.7 (4.5)	0.7 (4.5)	0.3 (2.9)	0.3 (2.9)	0.3 (2.9)	0 (2.4)	0 (2.4)	0 (2.4)

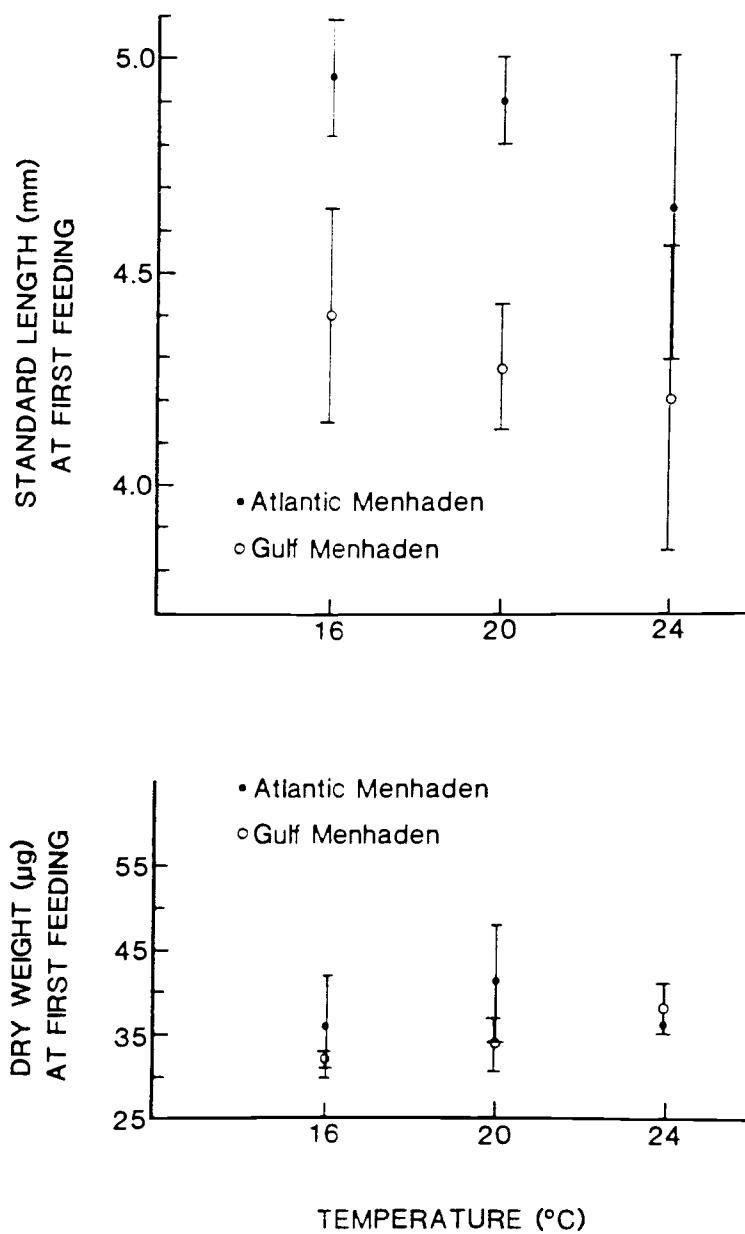


Figure 6. Size of Atlantic and gulf menhadens (± 2 SE) at time of first feeding at various temperatures. Values are means of four experiments.

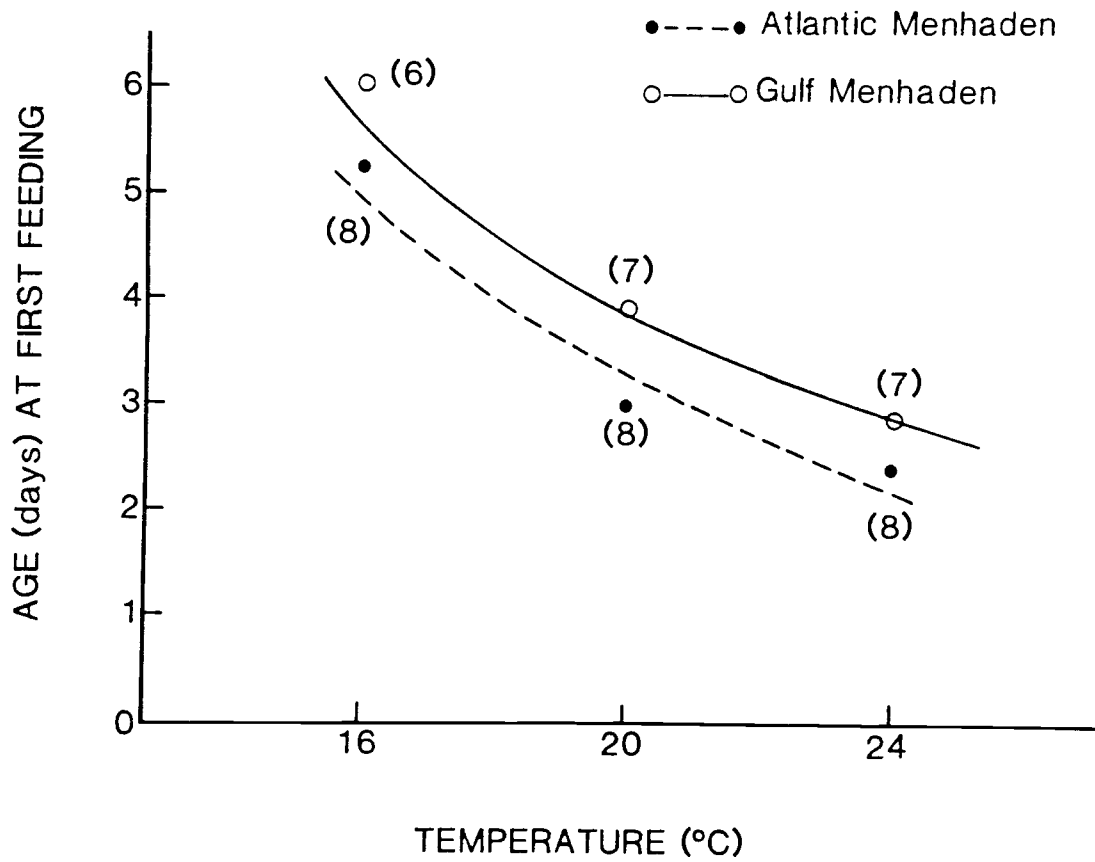


Figure 7. Age when Atlantic and gulf menhadens begin feeding on exogenous food at various temperatures.

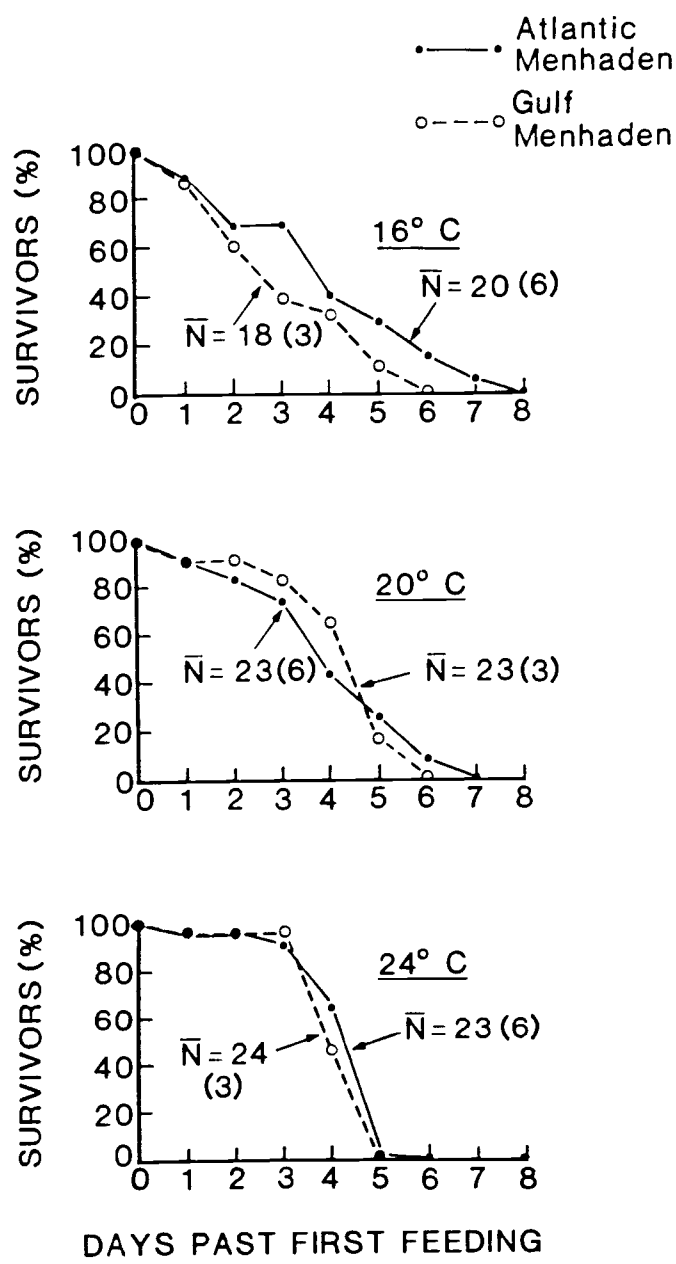


Figure 8. Time to starvation of unfed Atlantic and gulf menhadens at various temperatures. Values in parentheses denote the number of experiments.

at the lowest temperature (16°C) as compared to moderate (20°C) and high temperatures (24°C) (Table 9, Fig. 9). When food was provided in concentrations that ranged from high to very low, food concentrations of 1.0 rotifers ml⁻¹ and below limited the growth and survival of both species similarly (Table 9, Fig. 10). As in the above experiments, low temperatures (i.e., 16°C) significantly affected biomass gained by larval menhaden during this 7-d feeding and growth study.

Egg size (a reproductive trait) along with the rate of morphogenesis from hatching to first feeding (a developmental trait) may influence future larval size even though growth rates are similar. For example, when given unlimited food, Atlantic menhaden were significantly larger than gulf menhaden 10 days past first feeding at moderate to high temperatures (20 and 24°C) (Fig. 11). At the lowest temperature, (16°C) growth was significantly limited for the Atlantic menhaden, the more northern occurring species. On the other hand, there were no significant differences in growth for the gulf menhaden at low, moderate, and high temperatures.

Atlantic menhaden potentially can proceed through the earliest threshold of metamorphosis (i.e., Balon's (1984) concept) more rapidly than can gulf menhaden (Figs. 12 and 13). Based on a comparison of length-weight relationships of the early life history stages of these two menhadens,

Table 9. Mean gain in biomass (dry weight in μg over 7 d for a cohort (50 larvae)) of gulf menhaden and Atlantic menhaden larvae in relation to temperature and food level. Numbers in parentheses denote the number of experiments.

Food level (no. rotifers per ml.) ¹	SPECIES					
	Atlantic menhaden			Gulf menhaden		
	Temperature ($^{\circ}\text{C}$)			Temperature ($^{\circ}\text{C}$)		
	16	20	24	16	20	24
5.0	114 (2)	2296 (2)	1786 (2)	329 (2)	1294 (2)	2092 (2)
25.0	573 (2)	1512 (2)	2711 (2)	229 (2)	1570 (2)	2604 (2)
50.0	164 (2)	2218 (2)	2153 (2)	58 (2)	1922 (2)	1620 (2)
0.025	24 (2)	-65 (3)	12 (3)	42 (3)	41 (3)	8 (3)
0.1	37 (3)	25 (3)	12 (3)	15 (3)	163 (3)	146 (3)
1.0	83 (3)	661 (3)	823 (3)	133 (3)	373 (3)	1562 (3)
10.0	454 (3)	1418 (3)	2594 (2)	302 (3)	1796 (3)	1577 (3)

¹ Food levels are separated into two groups due to experimental design. See text (Methods and Materials, and Results) for explanation.

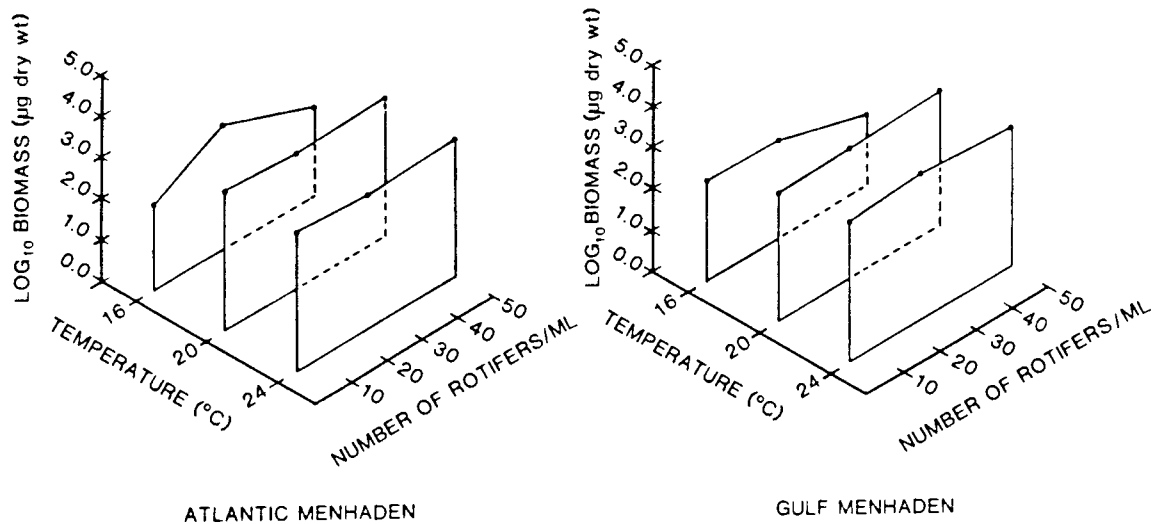


Figure 9. Amount of biomass gained over a 7-d period for early larval Atlantic and gulf menhadens at various environmental conditions. Prey concentrations range from 10 to 50 rotifers ml⁻¹.

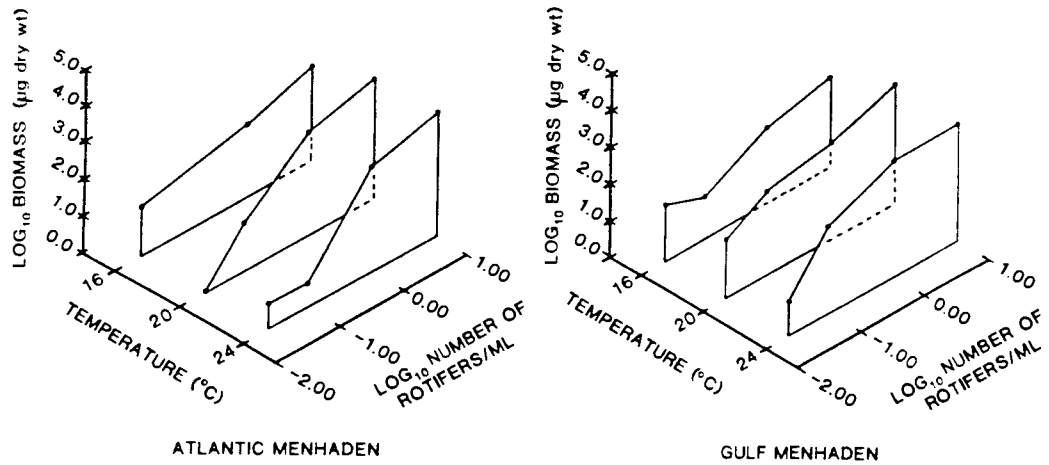


Figure 10. Amount of biomass gained over a 7-d period for early larval Atlantic and gulf menhadens at various environmental conditions. Prey concentrations range from 0.025 to 10 rotifers ml⁻¹.

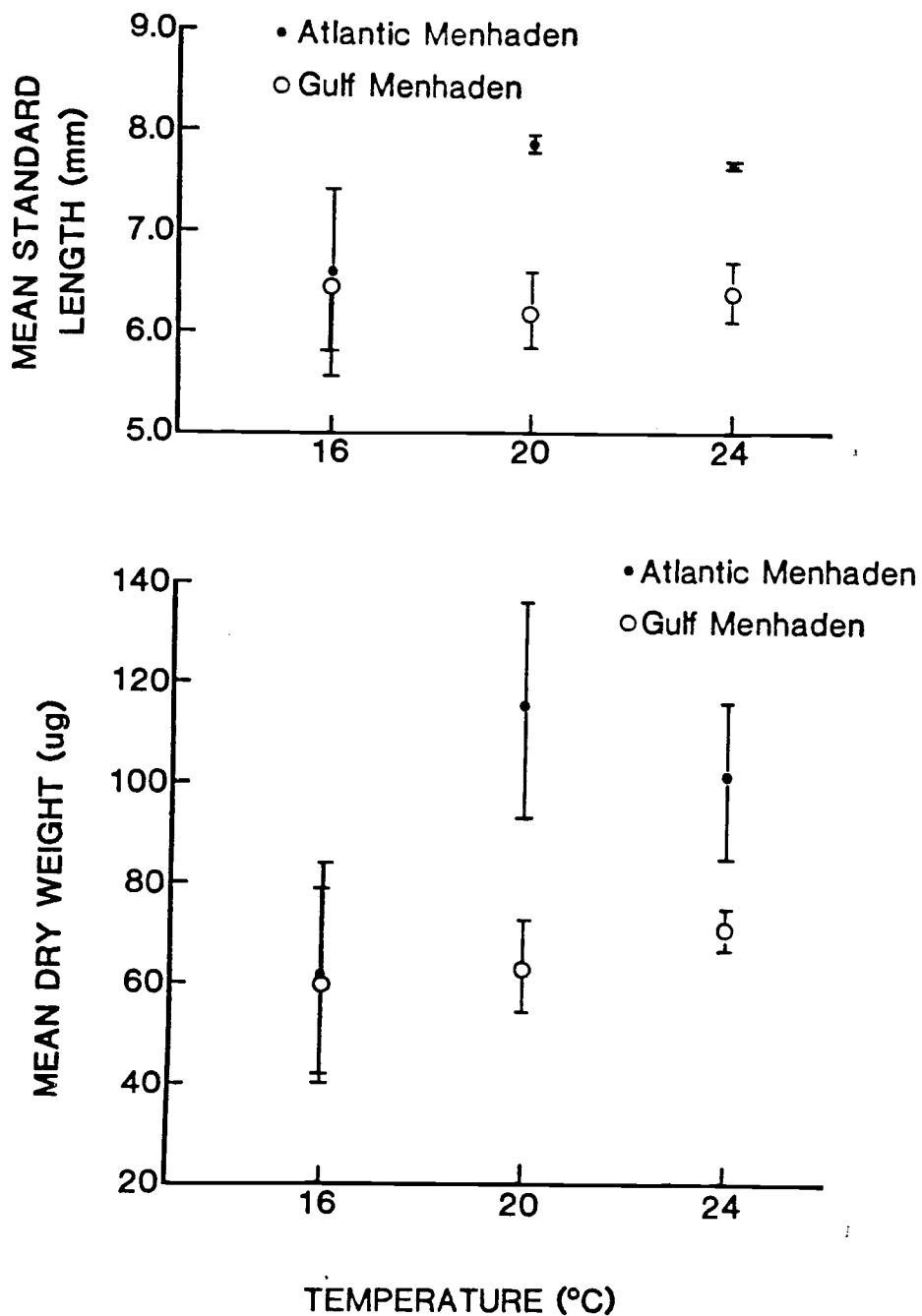


Figure 11. Size of Atlantic and gulf menhadens (± 2 SE) at 10-d past first feeding at various temperatures. Values are means of four experiments.

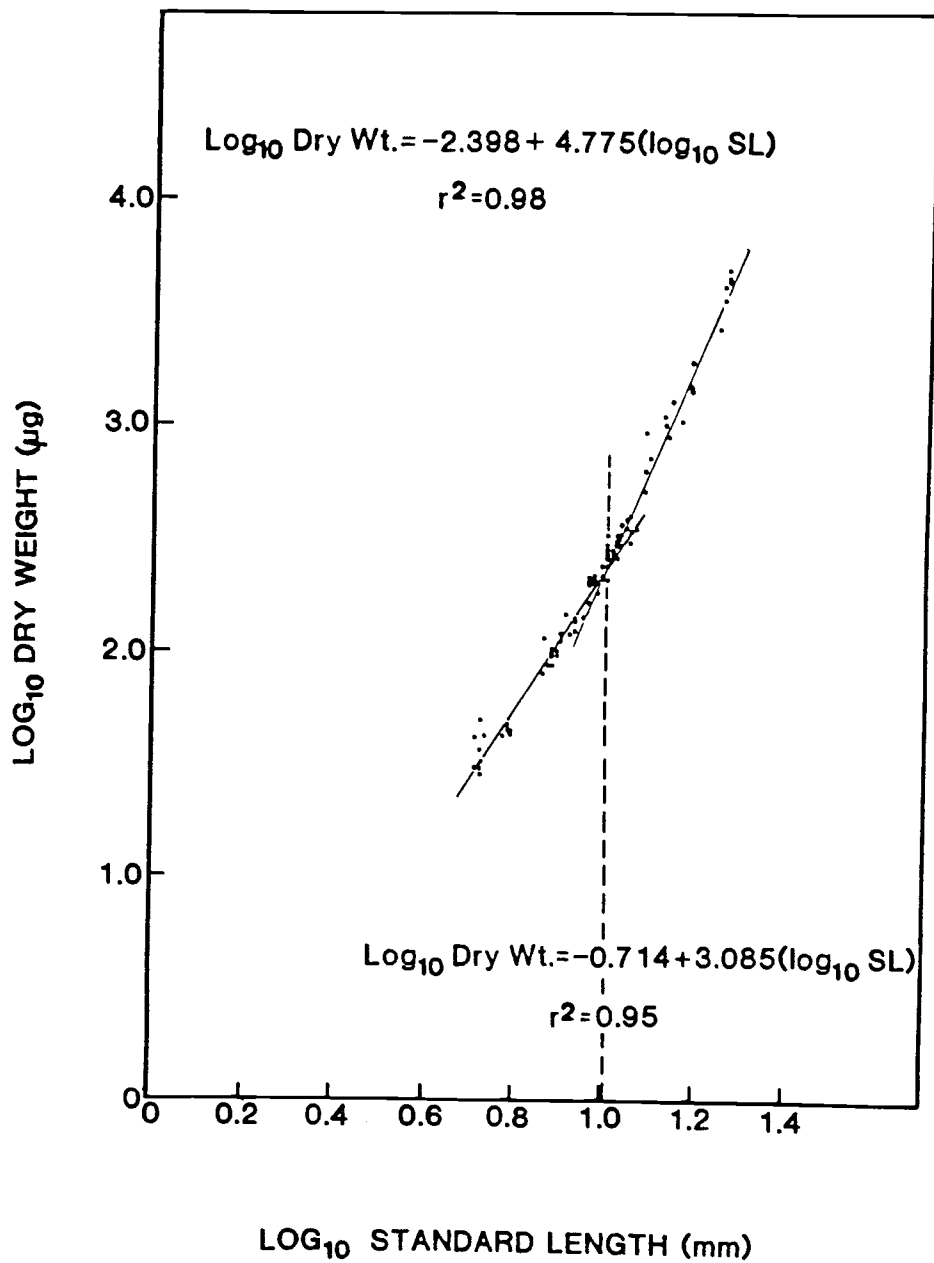


Figure 12. Length-weight relationship of larval Atlantic menhaden showing a change in body stanza at 10 mm SL.

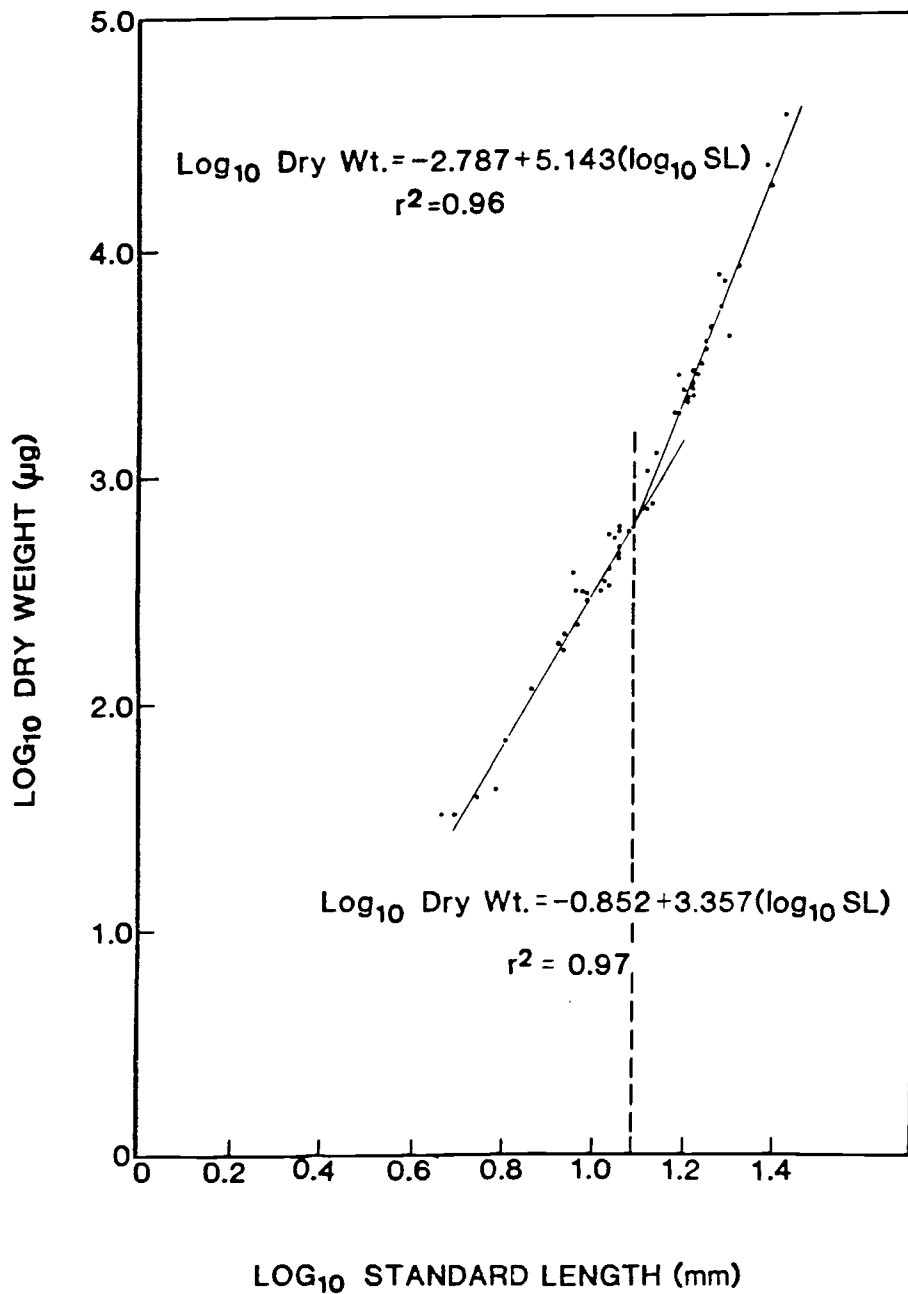


Figure 13. Length-weight relationship of larval gulf menhaden showing a change in body stanza at 12 mm SL.

Atlantic menhaden reach the next body stanza at a smaller size than gulf menhaden. Beginning at this threshold, there is a relatively larger change in weight for a given change in length.

DISCUSSION

Atlantic menhaden, compared to gulf menhaden, exhibit a life history pattern that, within the context of a bet-hedging model with variable juvenile mortality, appears to be adapted to a more unpredictable environment. Relative to gulf menhaden, Atlantic menhaden have larger eggs with larger yolk volume. They are larger at hatching, utilize their yolk at a faster rate, begin feeding at an earlier age, but are larger at this time, and undergo their first apparent transformation at a smaller size. As adults they have a larger maximum body size, are larger than gulf menhaden at any specific age, and adult mortality rates are lower. They are older at sexual maturity but they have a longer reproductive span. The Atlantic menhaden spawning period is prolonged and their age-specific distributions result in spatial and temporal variation in spawning. But, as Leggett (1985) cautions, "correlation between measures of environmental variability and reproductive success," to assess life history theory models, "has too often been assumed rather than measured."

Numerous environmental processes related to larval survival have been described, but their influence on recruitment (\approx reproductive success) is difficult to establish. Such processes that could influence early Atlantic menhaden survival are episodic intrusions of Gulf Stream nutrient rich water into the outer Continental Shelf

(i.e., spawning area) (Atkinson 1985), Ekman transport of larval Atlantic menhaden from their offshore spawning grounds to estuaries (Nelson et al. 1977), storm-induced upwelling on the outer continental shelf, and a density-driven circulation influenced by the passage of winter storms that permit rapid development and shoreward transport of larvae (Checkley et al. 1988). Meteorological and/or hydrological processes that may influence survival of late larval and juvenile Atlantic menhaden within estuaries have not been identified.

A process that could influence early gulf menhaden larval survival is the dynamics of the Mississippi River plume, where notable concentrations of menhaden larvae aggregate (Govoni et al. 1989). This system can, in turn, retain larvae, and the westward veering frontal region interacting with a west-northwest longshore current may aid in the transport of larvae into estuarine nursery areas (Shaw et al. 1985; Kiorboe et al. 1988; Govoni et al. 1989). Still the causal factors that drive these meteorological and hydrological processes are difficult to measure. To compare the environments of the two species of menhaden as they may affect larval/juvenile survival becomes an even more improbable task, as it requires long-term data series for multi-causal factors.

Insight into the predictability of the environments of the Atlantic and gulf menhadens, as they may affect larval

and juvenile survival, was obtained by examining adult population characteristics. Atlantic menhaden exhibit a relatively high degree of variation in spawning success (Table 10) that is not attributable to stock size. Stock-recruitment analyses of these two menhadens (Nelson and Ahrenholz 1986; Ahrenholz et al. 1987) strongly suggest that there is no relationship between the number of Atlantic menhaden spawners and the number of recruits. This could indicate that variation in environmental factors plays a major role in determining the number of recruits to Atlantic menhaden populations. On the other hand, the curve describing the relationship between number of gulf menhaden recruits and numbers of spawners fits a Ricker model well considering the variability inherent in clupeoid recruitment (Nelson and Ahrenholz 1986). This could indicate that variation in environmental factors plays a relatively lesser role in recruitment variability (i.e., larval/juvenile survival) in gulf menhaden populations.

Density-dependent growth is another characteristic that I used to characterize the environments of these allopatric menhadens. It has been well documented that Atlantic menhaden populations exhibit density-dependent growth of individuals (Ahrenholz et al. 1987). Results of two studies (Reish et al. 1985; Ahrenholz et al. in press) suggest that this phenomenon occurs prior to recruitment to the fishery (i.e., during the larval and/or juvenile period). I

Table 10. The estimated fraction (S) of Atlantic and gulf menhadens surviving from egg to recruit from 1964 to 1976. Data from Nelson and Ahrenholz (1986) and Ahrenholz et al. (1987).

Species	\bar{S}	Range of S	High S: Low S
Gulf menhaden	0.00056	0.00021-0.00138	7: 1
Atlantic menhden	0.00034	0.00007-0.00109	16: 1

interpret this to mean that Atlantic menhaden larvae and/or juveniles can be food limited and that this environmental variability in food resources may be a factor influencing recruitment variability. On the other hand, density-dependent growth of individuals has not been detected for gulf menhaden populations (Nelson and Ahrenholz 1986).

Egg size and its adaptive significance has received considerable attention. In general, my results are in accord with other studies of diverse fishes and other organisms. Larger eggs are positively correlated with size of larvae at hatching, yolk reserves, and resistance to starvation (e.g., Blaxter and Hempel 1963, clupeoid stocks; Crump 1984 (amphibia); Wallace and Aasjord 1984 (salmonids); Knutsen and Tilseth 1985 (gadoids); Marsh 1986 (percids); and Goulden et al. 1987 (cladocerans)). Large eggs may result in larger larvae. This could result in increases in mouth sizes (Shirota 1970) and in swimming speeds (Hunter 1981) that broadens the range of prey sizes available and enhance feeding opportunities. Large egg size would appear to have a selective advantage in a food-limited environment, which may be so for Atlantic menhaden.

There is a cost to producing large eggs as fecundity is generally minimized with increased egg size (Bagenal 1973). Furthermore, because larger eggs may have longer incubation times, they may undergo greater mortality (Chambers et al. 1988). With salmonids, which have relatively large eggs and

long incubation times, any resultant decrease in embryo survival may be balanced by higher survival of the fry (Beacham and Murray 1985). Ware (1975) argued that species that spawn at low temperatures, where eggs experience long incubation, produce larger eggs. Selection advantage could shift to smaller eggs as incubation time shortens because the number of eggs hatching could offset the greater mortality of larvae due to relatively small size. This argument is based on the premise that mortality in the open sea is inversely related to particle size. Empirical evidence supports Ware's arguments (e.g., Blaxter and Hempel 1963; Southward and Demir 1974; Hislop 1984; and Ware 1977). These studies, however, were intraspecific and deal with seasonal changes in egg size. Atlantic and gulf menhaden have similar incubation times (personal observation) and spawn at similar temperatures (Shaw et al. 1985; Checkley et al. 1988). Thus it would seem that egg size differences between these congeners cannot be explained by the intraspecific studies on the adaptive significance of egg size discussed above. Furthermore, the often cited trade-off between fecundity and egg size may not hold when comparisons between these two menhadens are made. If these menhadens are determinant spawners, i.e., the number of maturing ova indicate potential fecundity, gulf menhaden do not appear to be more fecund than Atlantic menhaden (Fig. 14).

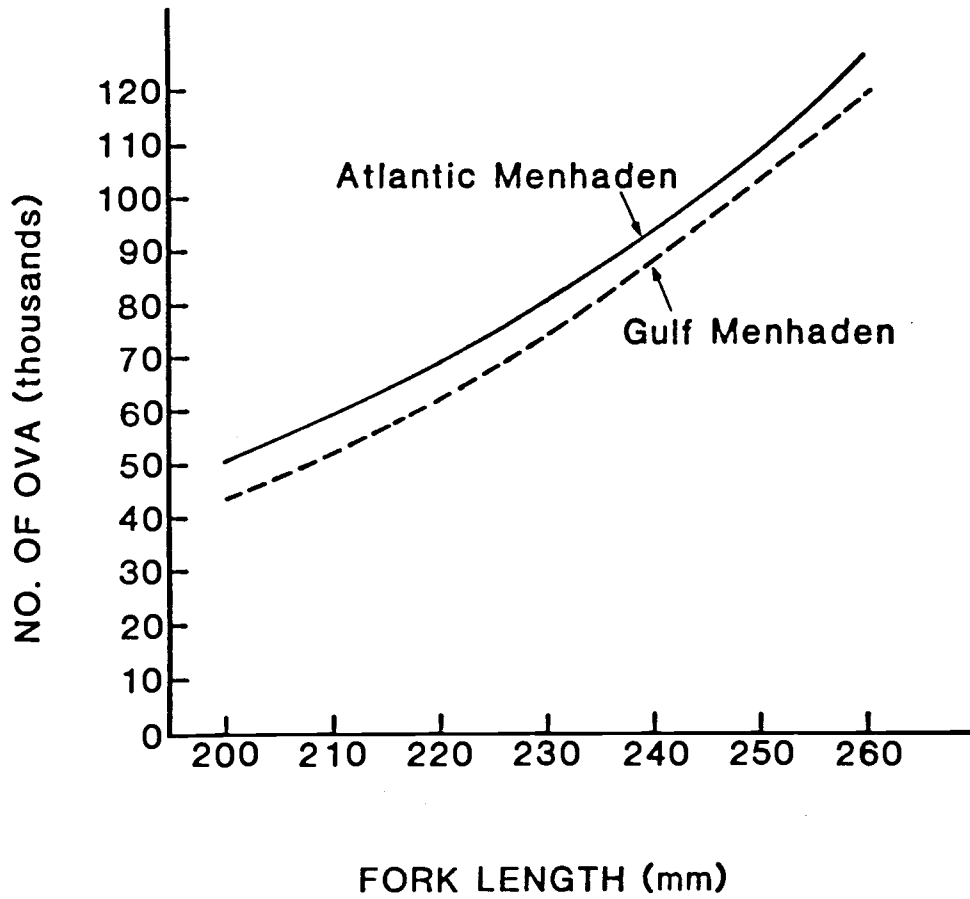


Figure 14. The number of maturing ova in relation to body length for Atlantic and gulf menhadens. Data from Lewis and Roithmayr (1981) and Lewis et al. (1987).

When egg size is assessed in conjunction with other reproductive and developmental traits, a more meaningful insight into menhaden life history patterns can be attained, especially for Atlantic menhaden. Atlantic menhaden not only produce relatively larger eggs that result in a relatively larger larvae at the onset of feeding than do gulf menhaden, but they also have relatively higher rates of yolk utilization and, apparently, relatively higher rates of development (i.e., digestive and sensory systems). Hence, Atlantic menhaden larvae are not only larger, but also younger than gulf menhaden at first feeding. This could result in a relatively larger larval size shortly after first-feeding (e.g., 10d), given that some larvae encounter suitable conditions (e.g., ample food and moderate temperatures). Moreover, Atlantic menhaden appear to enter a new body stage (based on the relationship between length and weight) at a relatively smaller size, thus spending relatively less time in the early larval stage. Williams (1966) argues that acceleration of development will occur in those developmental stanzas in which mortality rates are high. It can be argued from a comparative standpoint that early-larval gulf menhaden may encounter relatively less mortality during the early larval stage. This argument is strengthened when the spatial and temporal spawning habits of these menhadens are considered. Atlantic menhaden populations exhibit more variability in their spawning

habits. This adaptation could allow them to minimize the risk of reproductive failure, as the effects of extreme environmental conditions in one place or time will be dampened by less extreme environmental conditions in others (Den Boer 1968).

The relatively longer length of the juvenile stage (i.e., a delay in the age at sexual maturity) in Atlantic menhaden could be favored if loss of fitness for lengthening the juvenile period leads to gains for some other important development trait (Williams 1966). Age at sexual maturity appears to be a significant life history trait, the tradeoff for a prolonged juvenile period being reduced adult mortality and higher subsequent fecundity (Harvey and Zammuto 1985). Bell (1980) argues that selection for delayed maturity will be selected for if an increase in age-specific fecundity is greater than a decrease in age-specific survivorship. Although age-specific mortality rates have not been reported for either the gulf or Atlantic menhadens, the high rate of adult mortality exhibited by gulf menhaden lends credibility to Bell's (1980) argument. A relatively lower age at sexual maturity in gulf menhaden could be a response to these high mortality rates, if increased fecundity with age does not dampen the high adult mortality rates. Because of the apparent evolutionary significance of age at sexual maturity, this trait should be considered in the analysis

of exploited fish population, and will be discussed in more detail below.

Atlantic and gulf menhaden populations exhibit markedly different reproductive life spans. This trait has received considerable attention from ecologists studying a wide array of organisms (see Stearns 1976 for review). Murphy (1968) argues that when there is uncertainty in larval and juvenile survival, there will be selection pressure for iteroparity. Murphy supports his argument by illustrating the positive relationship between recruitment variability (ratio of maximum recruitment to minimum recruitment) and reproductive span (Fig. 15). The Peruvian anchovy (Engraulis ringens), which reproduces during winter in a stable oceanographic environment (El Niño occurs in summer), has low variation in spawning success (2x) and a short reproduction span (2 years). On the other hand, Atlantic-Scandian herring populations (Clupea harengus) which reproduce in an unpredictable physical environment have high variation in spawning success (25x) and a long reproductive span (18 years). Atlantic and gulf menhadens appear to fit the trend of Murphy's (1968) relationship between reproductive uncertainty and reproductive span in clupeoid fishes, except menhaden have a shorter reproductive span for a given variation in spawning success (Fig. 15). Roff (1981) examined the reproductive span of numerous pleuronectiforms and concluded that variation in reproductive life span of

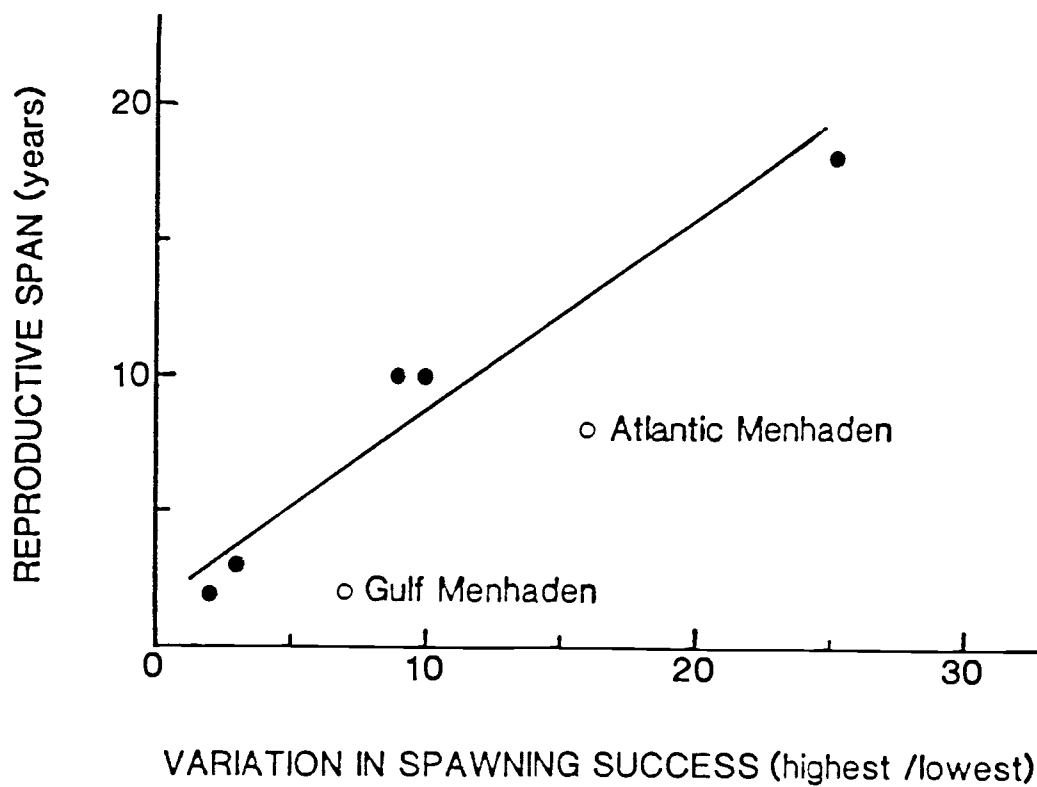


Figure 15. The number of reproductive years as related to variation in spawning success for clupeoid fishes. Data from Murphy (1968), Nelson and Ahrenholz (1986) and Ahrenholz et al. (1987).

flatfishes is not an adaptation to variable reproductive success, but that reproductive life span is correlated with the age at maturity. Roff (1981) argues that the intrinsic rate of population growth, which depends upon age-specific survival and reproduction, will decrease with a delay in sexual maturity. According to this theoretical argument, which disregards environmental conditions, for populations to persist with a change in the age at sexual maturity, there must be an increase in reproductive output per spawning episode or an increase in reproductive life span. Nevertheless, arguments such as Roff's (1981) should be considered in fishery management, especially for Atlantic menhaden populations.

Life history theory should play a major role in fisheries biology and management. Studies that have been linked to life history theory have provided a valuable insight into how fishes have adapted to their environments (e.g., Schaffer and Elson 1975; Leggett and Carscadden 1978; Healey and Heard 1984; Mann et al. 1984; Miller 1984; Chambers et al. 1988). Studies that examine the effects of exploitation on life history traits should alert fishery managers to the importance of maintaining the life history and evolutionary adaptive capacities of fish populations. Murphy (1967) demonstrated, through simulation models, that a high rate of fishing mortality on the Pacific sardine (Sardinops caerulea) greatly reduced the number of

reproductive, adult, age groups. This coupled with two consecutive spawning failures brought about the collapse of the sardine fishery. Failure of the sardine population to recover has been attributed to a build-up of northern anchovy (Engraulis mordax) populations, which share similar ecological requirements. Leaman and Beamish (1984) linked life history theory to the management of long-lived groundfishes. They argue that the truncation of the age structure reduces reproductive span and increases the risk that a long period of unfavorable environmental conditions will result in the loss of a stock. Where there is a high degree of variation in year class strength with strong year classes occurring infrequently, repeated spawnings become more important. Leaman and Beamish (1984) concluded that harvesting strategies must consider life history characteristics to prevent permanent decline in long-lived species.

Atlantic menhaden populations exhibit relatively high variation in larval and juvenile survival (Table 10), and the age classes in the population appear to have evolved to offset this variability. Historically, the population was comprised of 10-11 age groups with, therefore, a high degree of repeated spawnings. But overexploitation has resulted in a dramatic truncation of the population age structure (Fig. 16). I argue that this has reduced migrations of Atlantic menhaden and resulted in a contraction of their

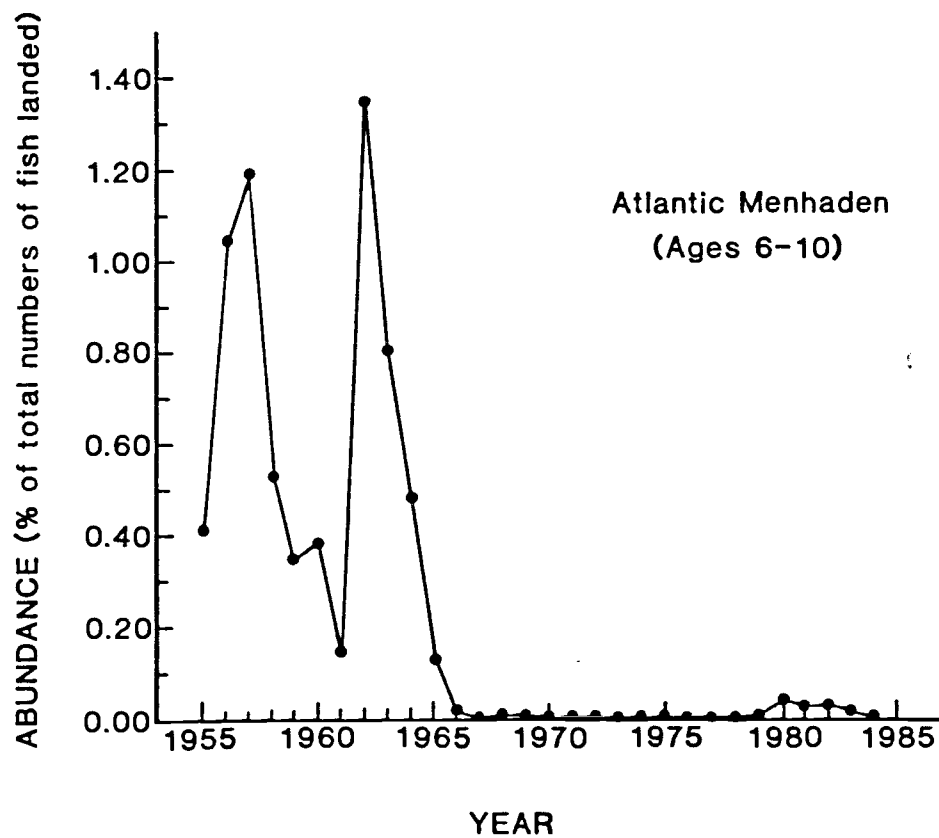


Figure 16. The abundance of older Atlantic menhaden from 1955 to 1985. Data from Smith et al. (1987).

range. This has diminished the population's ability to minimize the risk of reproductive failure by reducing reproductive episodes in time and space (Den Boer 1968). The truncation of the age structure has, in turn, truncated the reproductive span and altered the net reproductive rate -- the average number of age class zero offspring produced by an average newborn organism during its entire lifetime (Pianka 1983). This has been further compounded by a loss in fecundity, as fecundity is age related for these species (Lewis and Roithmayr 1981; Lewis et al. 1987). Moreover, a modification of egg size distribution within the population may have occurred if egg size and age of fish are correlated (Fig. 3). Overexploitation of Atlantic menhaden populations has thus altered their yields as well as their capacities to adapt to their environment, the latter no doubt affecting probabilities of long-term persistence of these populations. On the other hand, the exploitation of gulf menhaden populations has not altered the number of age classes (Fig. 17) and the population appears to be maintaining itself near historic levels (Nelson and Ahrenholz 1986). Overexploitation of this species resulting in alteration of life history traits could have serious consequences as the reproductive span of this menhaden is relatively short.

In conclusion, because fishery scientists must deal with problems that have a high degree of uncertainty, it is

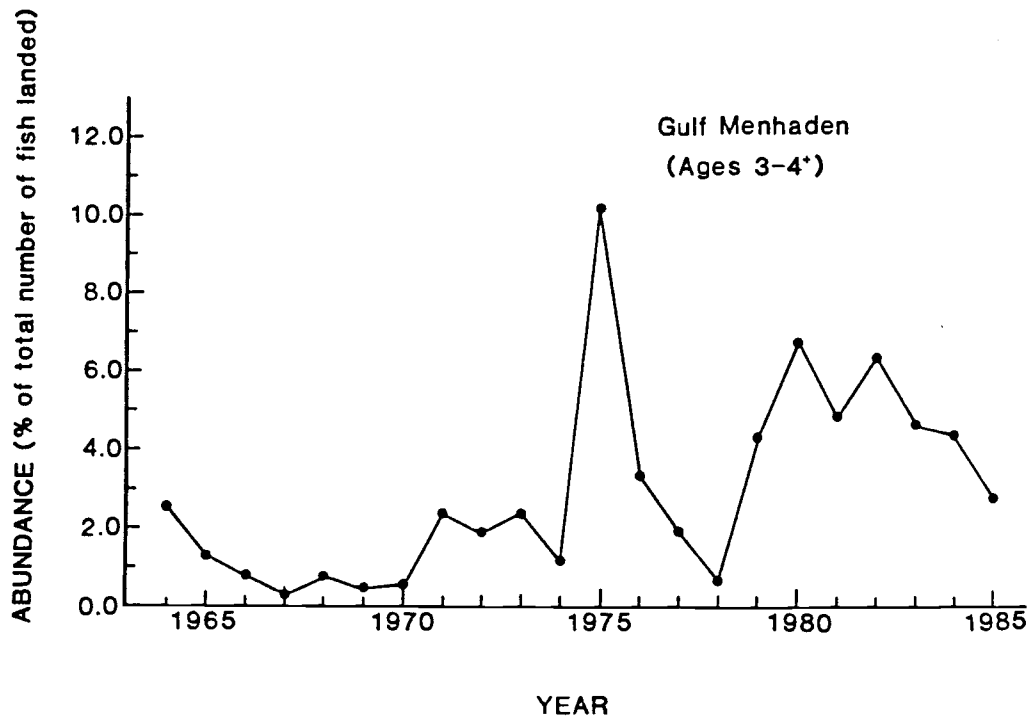


Figure 17. The abundance of older gulf menhaden from 1964 to 1985. Data from Smith et al. (1987).

advantageous to approach fishery problems from both a mechanistic and organismic approach. Biologists should strive to design fishery programs that result in a well-documented fishery that lends itself to both population dynamics and life history approaches. To apply an organismic perspective, I believe, fishery biologists must realize that fish species have the "potential capacity" to evolve in various ways in varying environments. This "capacity" of a species is a result of its organization and involves the integration of local populations (Warren et al. 1979; Warren and Liss 1980). The "adaptive capacity" of the local population, in turn, is a result of its organization that involves the integration of individual life history types. These life history types have a genetically determined "potential capacity", and developmental plasticity exhibiting various life history patterns in different environments. The persistence of a population depends upon the ability of a population or species to maintain a diversity of life history types. We, as fishery biologists and managers, should strive to maintain this diversity and thus the life history as well as evolutionary adaptive capabilities of fish populations.

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