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An Overview of the Biology, Ecology, and Fisheries of the Clupeoid Fishes Occurring in the Gulf of Maine

by

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ABSTRACT

Clupeoid species are important ecological components within marine and riverine ecosystems of the Gulf of Maine. This report summarizes information (1953-1995) for eight species of clupeid fishes (Clupeidae) and two species of anchovy (Engraulidae) occurring in the Gulf of Maine. Accounts are presented for Atlantic herring (*Clupea harengus*), Atlantic thread herring (*Opisthonema oglinum*), Atlantic round herring (*Etrumeus teres*), Atlantic menhaden (*Brevoortia tyrannus*), Hickory shad (*Alosa mediocris*), American shad (*A. sapidissima*), Alewife (*A. pseudoharengus*), Blueback herring (*A. aestivalis*), Bay anchovy (*Anchoa mitchilli*) and Striped anchovy (*Anchoa hepsetus*). Identification keys to families, genera and species are provided. Systematic, biological, ecological, distributional and fisheries data are summarized for each species, with emphasis on data derived from populations in the Gulf of Maine. Whenever possible, natural and human-induced environmental factors affecting populations of clupeoid species in the Gulf are discussed. An extensive bibliography of the literature on these species is also provided, with special concentration on populations occurring in the western Atlantic. Recent declines in abundance, especially of anadromous species and the Atlantic herring, are discussed relative to environmental and fishery practices, as well as the conservation measures being afforded these species. Although considerable information is available for most clupeoid species occurring in the Gulf of Maine, significant gaps in our information remain for some species. Information needs should be addressed to improve understanding of the population biology and ecological interactions of these species within Gulf of Maine communities.

INTRODUCTION

Because of the relative size of their populations and their position within trophic food webs, clupeoid fishes play significant roles in many ecosystems in which they occur. The Gulf of Maine is no exception. Here, as elsewhere, clupeoid fishes serve important roles both as predator and prey species. Eight species of the Family Clupeidae, including the Atlantic herring (*Clupea harengus*), Atlantic thread herring (*Opisthonema oglinum*), Atlantic round herring (*Etrumeus teres*), Atlantic menhaden (*Brevoortia tyrannus*), Hickory shad (*Alosa mediocris*), American shad (*A. sapidissima*), Alewife (*A. pseudoharengus*) and Blueback herring (*A. aestivalis*), and two species of anchovies (Engraulidae), the Bay anchovy (*Anchoa mitchilli*) and Striped anchovy (*Anchoa hepsetus*), occur in the Gulf of Maine.

Large population sizes (historically, at least, for some species) and general availability to fishing gears have subjected many of these fishes to heavy exploitation in commercial, industrial and recreational fisheries in the Gulf and elsewhere. Populations of most commercially important Gulf of Maine clupeoid fishes have undergone considerable fluctuations, with most species, especially the anadromous alosines, presently represented by much smaller populations than those recorded historically. Smaller population sizes have resulted from a number of factors, including such anthropogenic activities as overfishing and habitat loss and destruction.

Because of their ecological and commercial value, clupeoid fishes in the Gulf of Maine such as the Atlantic herring, Atlantic menhaden, American shad, Alewife and Blueback herring, have been the subject material for much detailed research. This report compiles and summarizes available information on the systematics, identification, biology, ecology and fisheries of species of the Family Clupeidae, as well as, two species of anchovies (Engraulidae), occurring in the Gulf of Maine. This report was conducted while preparing chapters summarizing available information for species accounts for a forthcoming revised edition of Bigelow and Schroeder's *Fishes of the Gulf of Maine*, edited by B.B. Collette and G. Klein-McPhee. However, after preliminary review of the literature on Atlantic herring, American shad and Atlantic menhaden, it became apparent that a large volume of information had been published on these species since Bigelow and Schroeder's work in 1953. In fact, Whitehead (1985a, 1985b) estimated that perhaps as many as a hundred or more papers appear annually on various aspects of herring biology and fisheries and that perhaps more information has been published on *C. harengus* than on any other fish species. Given that more information was available than could be included in accounts prepared for the new edition of *Fishes of the Gulf of Maine*, it was determined that summarized information should be made available in another format, which resulted in the production of this work.

The research summarized in this report largely represents information published from 1953 to 1995. It builds upon literature summarized in Bigelow and Schroeder (1953); and for Atlantic herring (*C. harengus*), it also builds upon and expands the detailed account prepared by Sindermann (1979). Other important review articles on Atlantic herring biology and fisheries are found in Blaxter and Hunter (1982), Whitehead (1985a, 1985b), and Blaxter (1985, 1990). Literature of particular interest on herring in Western Atlantic regions includes that of Bigelow and Schroeder (1953), Sindermann (1979), Anthony and Fogarty (1985), Scott and Scott (1988), and Townsend (1992). A bibliography of earlier studies on Atlantic herring in the Northwest Atlantic was compiled by Messieh (1980). The present compilation does not represent a complete summary of all available information for the species. Primarily, it consists of a summary of general life history information available for each species, with particular emphasis on literature originating from studies conducted on the species in the Gulf of Maine and nearby locations. Other references on populations occurring outside the Gulf of Maine were included whenever these sources provided new information on a species that was not available elsewhere. Detailed accounts were prepared only for species occurring regularly, and in abundance, in the Gulf of Maine. For species rarely occurring in the Gulf, or occurring in low abundances, only a general profile of the biology is presented. Recent declines in abundances, especially of anadromous species and the Atlantic herring, are also discussed relative to environmental and fishery practices. Conservation measures being afforded anadromous species whose populations have been reduced are presented. Information summarized in this report is primarily that appearing in peer-reviewed, published scientific literature. Secondary (non-peer reviewed) literature and unpublished theses were examined whenever available to the author, however, no attempt was made to systematically locate all unpublished literature sources for these species.

Given their relative value as fishery resources, and the significant ecological position of these fishes in various ecosystems of the Gulf of Maine, clupeoid fishes will continue to form the basis for continued ecological and fisheries research. This report can serve as a basic guide to information resources for researchers interested in a general survey of the biology and ecology of clupeoid fishes in the Gulf of Maine region. In this capacity, it can also serve as a guideline for areas where quality information is lacking or inadequate. Those also interested in constructing fishery management plans or habitat evaluations for fishery resources will find information in this document useful as a basic reference source. Although considerable information is available for most clupeoid species occurring in the Gulf of Maine, significant gaps in information remain for some species. Information needs should be addressed to improve understanding of the biology and population biology of individual species, and the ecological interactions of these species within Gulf of Maine communities.

Chapter 2. ORDER CLUPEIFORMES
Herring and herring-like fishes

The order Clupeiformes constitutes a part of the Clupeomorpha, a group of fossil and Recent fishes commonly known as the herring and herring-like fishes (Grande 1985; Whitehead 1985a). As Grande (1985) pointed out, in earlier literature the Clupeomorpha (and Clupeiformes) were an artificial assemblage construed to contain any primitive teleost that did not fit into another, better-characterized teleost subgroup. This concept was evident in Bigelow and Schroeder (1953), where Clupeiformes were allied with tenpounders and tarpons (Elopidae). Other earlier systematic treatments also allied the Clupeiformes with tarpons, ladyfishes (Albulidae), milkfishes (Chanidae), and certain other "lower" (i.e. primitive) bony fishes and relegated all of these fishes to the order Isospondyli. Greenwood *et al.* (1966) defined the Clupeomorpha more rigorously, based on uniquely-shared characters, and demonstrated that there was no common ancestry to any of these other groups and the Clupeomorpha. For example, tenpounders and tarpons (*Elops*, *Megalops*) and the ladyfishes (*Albula*) have a leptocephalus larva, which allies them with the eels in the Elopomorpha.

Additional study (Whitehead 1963; Patterson and Rosen 1977; Grande 1985; Whitehead 1985a, 1985b) now defines the Clupeomorpha as those fishes sharing several uniquely derived features including the presence of one or more abdominal scutes, each primitively consisting of a single (unpaired) element which crosses the ventral midline of the fish; an otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and then expands to form ossified bullae in the prootic and usually also the pterotic; and a supratemporal commissural sensory canal primitively passing through the parietals and supraoccipital. A membrane within each prootic bulla separates gas from the swimbladder from perilymphatic liquid surrounding the inner ear (Whitehead 1985a). This system, together with the head canal system and the recessus lateralis, probably functions in detecting and analyzing small vibrational pressures and displacements (Hoss and Blaxter 1982), thereby monitoring information necessary for schooling and other swimming activities, and also the detection of predators and hazards.

Within the Clupeiformes, are two distinct suborders (Grande 1985), the Denticipitoidei (comprised of two monotypic genera, one fossil and the extant African freshwater genus *Denticeps*) and the suborder Clupeoidei, containing the rest of the Clupeiformes. Of the clupeiform fishes, only members of the Clupeoidei are found in the Gulf of Maine.

SUBORDER CLUPEOIDEI

The Clupeoidei comprises a rather large group of fishes with roughly four families, 80 genera, and some 300 species. Most species are marine, coastal and schooling fishes, but some enter brackish or freshwaters and some live permanently in freshwaters (rivers or lakes).

Grande (1985) listed five shared-derived features that characterize members belonging to this suborder including four characters of the caudal skeleton and the loss of most or all lateral line scale canals. This suborder contains three subgroups of clupeiform fishes (Grande 1985), of which only two superfamilies, the Clupeoidea and the Engrauloidea, occur in the Gulf of Maine.

All clupeoid fishes commonly encountered in the western North Atlantic, such as the herrings, sardines, sprats, shads, and menhadens, belong to this subgroup of herring-like clupeoids. These fishes are usually easily recognized externally by their keel of scutes along the belly, the small and often poorly toothed mouths, and their silvery appearance. Round herrings (subfamily Dussumieriinae) differ from other clupeids chiefly in their rounded abdomens, less deep bodies, and terminal position of the mouth. The anchovy-like clupeoids (Engrauloidea) are usually distinctive because of their projecting, pig-like snout, large mouth, and "underslung" lower jaw (which reflects externally the backward obliquely inclined suspensorium).

Clupeoid fishes are of prime importance to fisheries (Blaxter and Hunter 1982). In fact, they represent the largest suborder, in terms of weight landings, of non-domesticated vertebrates harvested by man (Whitehead 1985a, 1985b). Half the world catch of fishes comes from about 60 species of various groups, but a third of those prime species are clupeoids. More clupeid fishes are caught (by weight, but presumably also by number) than members of any other single group of fishes. The size of clupeoid fisheries result from two main factors (Whitehead 1985a). First, the majority of clupeoids feed close to the base of the food chain and thus benefit more directly from nutrient-rich areas where there are strong seasonal or more continuous blooms of plankton. Second, clupeoids are almost always schooling pelagic fishes and thus extremely vulnerable to nets (especially purse seines), which can catch a large volume of fish in a short time. Since it is cooler high latitude seas and areas of upwelling that are richest in plankton, it is here that the major clupeoid fisheries exist. Characteristic of those clupeoid species which dominate these fisheries, however, is a tendency towards rather drastic oscillations in their abundance. Although the production of good or bad year-classes (which may vary by a factor of

10 or more) can be related to ecological factors including recruitment success, the precise role played by fisheries is still not clear (Whitehead 1985a).

Description and Diagnosis (from Whitehead 1985a).--Moderate-sized, small, or very small fishes (2-100 cm SL) without spines in the fins; dorsal fin single and short (11-23 finrays), usually near midpoint of body; pelvic fins with 6-10 finrays, slightly before, under, or slightly behind point equal with vertical through dorsal-fin base; anal fin usually short or moderate (10-36 finrays); caudal fin forked. Body usually fusiform, sometimes almost round in cross-section (*Etrumeus*), but more often compressed, sometimes highly compressed. Typically, with pelvic scute with ascending arms just anterior to pelvic fins (W-shaped in Dussumieriinae and *Engraulis*); a series of similar scutes anterior and posterior to pelvic fins (absent in Dussumieriinae and all New World Engraulidae).

Mouth small, with lower jaw deep and triangular in the Clupeidae, but slender and long in most Engraulidae. Premaxillae triangular (rectangular in Dussumieriinae); maxillae usually with an anterior (first) and posterior (second) supra-maxilla along dorsal margin. Small conical teeth typically present in jaws and on vomer, palatines, and endo- and ectopterygoids (i.e. roof of mouth), but some or all may be absent. Gut short (carnivores), or long and coiled (phytoplankton feeders, filter feeders); some species with muscular stomach like a gizzard (Dorosomatinae; partially so in some Clupeinae); food is collected in a bolus by pharyngeal pouches in Dorosomatinae and some Clupeinae. Swimbladder present, sometimes double-chambered (some Engraulidae), with pneumatic duct joined to esophagus or stomach.

Almost all species with complete covering of cycloid scales on body, scales frequently deciduous; small scales occasionally cover bases of dorsal, anal and/or caudal fins, and one or sometimes several axillary scales lie above bases of first pectoral and pelvic finrays. No lateral line canal with pored scales along sides (occasionally one or two behind gill opening). A branching, mainly cutaneous, sensory canal system covering top and sides of head; supraorbital, infraorbital, preopercular and pterotic canals all meet in the *recessus lateralis*, a special chamber characteristic of clupeiform fishes, its inner wall being a membrane sealing perilymphatic space surrounding inner ear.

KEY TO FAMILIES OF CLUPEOID FISHES IN THE GULF OF MAINE

1a. Articulation of lower jaw under or only just slightly posterior to vertical line through posterior margin of eye; lower jaw deep; snout not pig-like and projecting, lower jaw not underslung .... Clupeidae, p. 5

1b. Articulation of lower jaw located well posterior to vertical line through posterior margin of eye; lower jaw narrow and elongate, usually very slender; snout pig-like and projecting, lower jaw underslung .... Engraulidae, p. 164

Chapter 3. FAMILY CLUPEIDAE

Herrings

Description and Diagnosis.--Typically, oval in cross-section, often deep-bodied and flattened sidewise; with moderately large (about 40-50 in lateral series) deciduous scales on the body (usually absent on head region); with complete series of scutes along abdomen (pelvic scute always present); all fins soft-rayed, entirely lacking spines. Dorsal fin short and near midpoint of body; no dorsal adipose fin; pelvic fins abdominal and located far behind pectoral fins, just in front of, below, or just behind point equal with vertical through dorsal-fin base; anal fin short, its origin well behind last dorsal-fin ray; caudal fin deeply forked. Mouth terminal, with two supramaxillae, with small or minute jaw teeth. Eye moderate, usually with distinct adipose eyelids. Gill rakers long and numerous. Branchiostegals usually 5-10, but 6-20 in the Dussumieriinae. Vertebrae numerous and serially alike. Color silvery.

Within the family, great variation occurs in body shape and depth (round bodied to strongly compressed and deep), development of ventral scutes (some or all absent along abdomen, but some species with a few or complete series of pre-dorsal scutes occasionally present), size and shape of the mouth (lower jaw prominent to mouth fully inferior), number of supramaxillae (one or both absent), tooth development (absent in some, canines in others), and scales (deciduous in some, minute in others).

The Clupeidae is unique among clupeomorphs in having two rodlike postcleithra (Grande 1985). This is a rather large family of mostly marine fishes comprising some 180 species placed in 56 genera, with estimates of as many as 200 species (Whitehead 1985a, 1985b). Whitehead (1985a) stated that clupeids could be conveniently placed in five subfamilies, although he indicated that this arrangement was probably artificial and not reflective of true evolutionary relationships within the family. Grande (1985) also was unable to fully resolve relationships within the family based on his osteological study of the group. He found that the Dussumieriinae, which includes the round herring *Etrumeus*, is unique in having a peculiar unkeeled, W-shaped, pelvic scute. Resolution of relationships among other traditional subdivisional groupings within the family (Alosinae, Clupeinae, and Dorosomatinae of earlier authors), however, are problematical and in need of further study. Although subfamily designations proposed by earlier authors have not been defined by shared derived characters and may merely represent phenetic assemblages, use of conventional subfamily distinctions will be retained in the present work for organizational purposes.

Habits.--A surprising diversity in biologies and ecologies are represented among the clupeids (Whitehead 1985a, 1985b). Some species enter freshwater only to feed (amphidromy), some are anadromous (shads), some live permanently in freshwater or marine ecosystems, some are partial or full-time filter-feeders (gizzard shads), some are predators on fishes, and some produce only small numbers of eggs or attach their eggs to the substrate, while others are prolific, pelagic serial spawners. Typically, clupeids are marine coastal and schooling fishes found in all seas from 70°N to about 60°S, which feed on small planktonic animals (mainly crustaceans,), often form large schools at or near the surface and scatter large numbers of pelagic eggs from which planktonic larvae hatch. Adults are usually 10-20 cm standard length. Members of the Clupeidae are among the most familiar of northern sea fishes and certainly are among the most abundant in terms of number of individuals.

Eight species of clupeids occur in the Gulf of Maine: Atlantic herring, alewife, blueback herring, and American shad are regular components of the Gulf of Maine fauna; the Atlantic menhaden has an irregular occurrence in the Gulf of Maine, but may be abundant periodically; the hickory shad, Atlantic round herring, and Atlantic thread herring occur much less commonly and generally only in low abundance. The American shad, Atlantic menhaden, Atlantic herring, round herring, and Atlantic thread herring are more easily identified; but alewife and blueback resemble one another so closely that they are often confused, even by fishermen who handle them constantly.

KEY TO GULF OF MAINE HERRINGS

1a. Last dorsal-fin ray prolonged .... Atlantic thread herring, p. 70.
1b. Last dorsal-fin ray not prolonged 2
2a. Abdomen rounded, without scutes; mouth relatively small, upper jaw bone extending posteriorly to point anterior to, or under, anterior margin of eye; pelvic fins located posterior to vertical line through posterior base of dorsal fin .... Atlantic round herring, p. 161.
2b. Abdomen sharp-edged, with prominent scutes; mouth relatively large, upper jaw bone extending posteriorly to point at least equal with, but usually extending beyond, vertical through mid-point of eye; pelvic fins located at point equal with verticals between anterior and mid-regions of dorsal fin 3
3a. Predorsal scales forming ridge on either side of midline; head, especially gill cover, very large, about equal with ⅓ standard length; pelvic-fin rays i, 6; free edges of scales on body serrate or pectinate .... Atlantic menhaden, p. 143.
3b. Predorsal scales not forming ridge on either side of body midline; head and gill cover relatively smaller, equal to approximately ¼ of standard length; pelvic-fin rays i, 8; free edges of scales rounded 4
4a. Distance from dorsal-fin origin to tip of lower jaw (mouth closed) nearly equal to distance from dorsal-fin origin to base of central rays of caudal fin; cluster of small teeth present on roof of mouth; ventral edge of abdomen weakly saw-toothed, though sharp; body comparatively shallow .... Atlantic herring, p. 8.
4b. Distance from dorsal-fin origin to tip of lower jaw (mouth closed) considerably shorter than distance from dorsal-fin origin to base of central rays of caudal fin; no teeth on roof of mouth; ventral edge of abdomen more or less strongly saw-toothed, especially between pelvic and anal fins; body comparatively deep 5
5a. Tip of lower jaw extending noticeably beyond upper when mouth is closed .... Hickory shad, p. 139.
5b. Tip of lower jaw not extending appreciably beyond upper when mouth is closed 6
6a. Upper outline of forward part of lower jaw (visible if mouth is opened) nearly straight, and not showing a pronounced angle; upper jaw extending posteriorly to point about equal with vertical through posterior margin of eye .... American Shad, p. 105.
6b. Upper outline of forward part of lower jaw concave with pronounced angle; upper jaw reaching posteriorly only to point about equal with vertical through center of eye 7

7a. Eye diameter relatively large, greater than distance from anterior margin of eye to tip of snout; dorsal region of body distinctly grey-green; peritoneum pale grey .... Alewife, p. 73.

7b. Eye diameter relatively small, only about as great as distance from anterior margin of eye to tip of snout; dorsal region of body distinctly blue-green; peritoneum sooty or black .... Blueback herring, p. 93.

Chapter 4. SUBFAMILY CLUPEINAE

Herrings, Sardines, and Sprats

Description and Diagnosis (Based on Whitehead 1985a).--Small or moderate-sized herring-like fishes with pelvic scute with ascending arms and scutes present before and behind pelvic fins. Upper jaw rounded and not notched when seen from the front; two supramaxillae present, anterior one usually elongate and posterior one paddle-shaped. Mouth terminal, with lower jaw sometimes projecting slightly. Teeth small and conical. Dorsal fin short (13-21 finrays), its origin about at mid-body length; anal fin short (12-23 finrays), its origin usually well posterior of vertical through posteriormost dorsal finray; pelvic finrays 7-10 (mostly 7 or 8).

Habits.--The Clupeinae are mainly marine coastal and schooling fishes, although some species enter or are confined to brackish or freshwater. Species in this group occur in the Indo-Pacific region, on both sides of the Atlantic and in the eastern Pacific. Genera such as *Clupea*, *Sprattus*, *Sardina* and *Sardinops* occur in cool waters and high latitudes extending into waters to approximately 70°N latitude. There are 15 genera and 72 species, making this the largest subfamily in the Clupeidae. Of this subfamily, only *Clupea harengus* and *Opisthonema oglinum* are found in the Gulf of Maine.

Chapter 5. *Clupea* Linnaeus 1758

Herrings

Description.--(Based on Whitehead 1985a). Moderately slender fishes, with abdomen fairly rounded and with scutes not forming a strong keel; mainly characterized by lacking various specialized features of other clupeid genera. Operculum smooth, without bony radiating striae. Posterior border of gill opening smooth and without pair of fleshy outgrowths. Pelvic finrays i 8; pelvic fin insertion posterior to vertical through dorsal-fin origin. No dark spots along sides, at dorsal-fin origin, on gill cover or on tips of caudal fin.

Two morphologically-similar, but genetically distinct, species, the Atlantic herring *Clupea harengus* and the Pacific herring *C. pallasi*, with different life history patterns and different otolith shapes (Bird *et al.* 1986) are currently recognized in the genus (Grant 1986). Only the Atlantic herring occurs in the Gulf of Maine.

Distinctions.--Distinguished from other clupeid genera mainly by lacking specialized features of other genera (Whitehead 1985a). *Clupea* differs from *Sardinella* in having the posterior border of the gill opening smooth and without a pair of fleshy outgrowths (vs. outgrowths present in gill opening of *Sardinella*). From *Alosa*, *Clupea* differs in lacking a strong median notch in the upper jaw and has shorter upper gillrakers. From *Brevoortia* and *Opisthonema*, *Clupea* is easily distinguished in lacking two rows of modified scales on the dorsum anterior to the dorsal fin (present in *Brevoortia*) and *Clupea* species lack a filamentous last dorsal-fin ray (present in *Opisthonema*).

Chapter 6. ATLANTIC HERRING *Clupea harengus* Linnaeus 1758
Herring; Sea Herring; Labrador herring; Sardine

Description.--Body elongate, strongly compressed laterally; ventral margin of abdomen slightly rounded, scutes without prominent keel; caudal peduncle slender. Head relatively small; snout pointed; mouth terminal, relatively large, without median notch in upper jaw; lower jaw projecting slightly beyond upper when mouth is closed; maxilla extending posteriorly almost to vertical through middle of eye; teeth absent on upper jaw, but with minute teeth on maxilla, small teeth on lower jaw, elongate patch of teeth on middle of tongue, and elongate patch of a few stronger teeth on vomer; eye moderate. Fins soft-rayed; dorsal-fin origin approximately at body midlength, directly dorsal to origin of much smaller pelvic fins; height of anal fin relatively low compared with that of dorsal fin; pelvic fins relatively small, abdominal, with distinct axillary process; caudal fin deeply forked. Scales large, cycloid, deciduous, with rounded posterior margin.

Meristics.--Dorsal-fin rays 17-22, mean approximately 19. Anal-fin rays 12-21, mean approximately 17-18. Pectoral-fin rays 14-22, mean 17-18. Vertebrae 51-60 (usually 55-57). Scales approximately 57 in lateral series. Abdominal scutes 26-33 anterior to, and 11-17 posterior to, pelvic fins. Gill rakers long, 40-49, fewer on fish <100 mm SL. Branchiostegals 8-9. (Data from Bigelow and Schroeder 1953; Hildebrand 1963; Whitehead 1985a; Scott and Scott 1988; See Scott (1975) for additional information on meristic features.).

Color.--Color greenish blue to steel blue on dorsum; sides with green reflections; abdomen and lower sides silvery; the change from dark back to pale sides often marked by greenish band; gill covers sometimes golden or brassy; freshly-caught fish generally iridescent with shades of blue, green, or violet; these colors fading soon after capture, leaving only dark coloration on back and silvery pigment on sides. Pelvic and anal fins translucent; pectoral fins dark at bases and along upper margins; caudal and dorsal fins dark grayish or shading into green or blue. No distinctive dark spots on body or fins. Peritoneum dusky.

Size.--To about 43 cm TL (usually 20-25 cm) and 0.68 kg.

Distinctions.--The Atlantic herring lacks an adipose fin, which at once distinguishes it from members of the Salmonidae. Primary characters separating herring from shads and other river herrings (*Alosa* spp.) are the oval patch of small teeth on the vomer (absent in *Alosa*) and absence of a median notch in the upper jaw (present in *Alosa*). Conspicuous field characters separating Atlantic herring from American shad, hickory shad, and alewife are that the dorsal-fin origin in herring is about at the body midlength (vs. considerably farther forward in these others); its shallower body depth (deeper in these other species); and the weakly saw-toothed scutes compared with the usually strongly saw-toothed (especially those on abdomen between pelvic and anal fins) ventral scutes in *Alosa*.

GENERAL BIOLOGY

Habitat.--The herring is a marine, coastal pelagic species often occurring in shallow inshore waters or taken offshore from the surface to depths of ca. 200 m (Whitehead 1985a, 1985b). It is a strongly schooling species that undertakes complex feeding and spawning migrations, whose times and extent correlate with the various more or less distinct spawning populations (Whitehead 1985a). Juveniles and mature fish prior to spawning may form huge schools. Although found primarily in coastal and neritic locations, some populations may enter, or even be confined to, brackish water in bays or saline lakes.

Habits.--The herring is a fish of open waters, traveling as a rule in schools of hundreds or thousands; single fish or even small schools are seldom seen. The magnitude of some of these schools is evidenced in perceptible small-scale ecological changes in the water column through which a school has passed. It is sometimes possible to plot passage of herring schools through an area because the water downstream from the school can be depleted of oxygen and food items, is heavy with feces and mucous, and has even been reported to have a characteristic cucumber odor (Blaxter 1990).

Schooling is one of the most important behavioral attributes of herrings, and this behavior develops very early in the life of these fishes. Schooling begins at about the onset of metamorphosis, usually when fishes are between 35 and 40 mm SL, is well established by the end of metamorphosis, and persists throughout the lifetime of the individual (Sindermann 1979; Gallego and Heath 1994a). Herring are obligate schoolers (Breder 1967) that are always found in polarized schools (Blaxter and Parrish 1965; Shaw 1970), and individuals become extremely agitated if isolated from conspecifics (Parr 1927). Schools are usually comprised of similar-sized fish (Pitcher *et al.* 1985; Pitcher and Parrish 1993), which to a large extent are fishes of the same year-class, although in any school there may be some representation of other sizes and year-classes (Sindermann 1979). Schools may subdivide or coalesce, and it is unknown how long any given school may preserve its identity as such.

School formation and maintenance are influenced by a combination of factors. Individuals are initially attracted to each other by vision and space themselves using information obtained through mechanoreceptors, especially those of the lateral line (Pitcher 1979; Partridge and Pitcher 1980). A study of 3-dimensional structuring of herring schools (Partridge *et al.* 1980) revealed that within a school, herring tended to swim at nearly, but not exactly at, the same depth as their neighbors. Herring were more likely to have as their nearest neighbor fish that were located either above or below them. When compared with cod and saithe, herring exhibited larger interfish distances, which may be related to their body structure (relatively stiff-bodied) and their relatively lesser maneuverability as compared with that of the other species studied.

Individual positioning within a school is also influenced by a variety of factors, including the state of hunger experienced by school members (Robinson and Arenas 1991). In experimental situations, when all fish were well fed or all were hungry, the fish did not swim randomly, but assumed particular positions within the school. When only a single fish was well fed and the rest were hungry, the appearance of the well-fed individual at the front of the school increased significantly. Interfish distances may also increase with increasing hunger experienced by the schooling herring (Robinson 1995). Exposure to schooling juveniles will also encourage pre-metamorphic larvae to opt for schooling prematurely, regardless of any associated disadvantages, such as competition for food (Gallego *et al.* 1995).

Movements of schools are to some extent determined by ocean currents, which is particularly true for juveniles in coastal areas. Purposeful movements of schools seem to be responsive to visual cues, although other environmental and physiological stimuli are undoubtedly involved. Movements of schools are also clearly influenced by seasonal environmental cycles, principally those of temperature, salinity, and food abundance (Sindermann 1979). A school is likely to be more or less stationary when feeding, its members swimming slowly to and fro and drifting as a whole with the current (Huntsman 1934). At other times, schools can be seen traveling rapidly with individual fish swimming side by side, rank below rank, as far down in the water as can be seen, all heading in one direction. There seems no indication that herring swim against the current unless the water is somewhat turbulent (Huntsman 1934). Herring, held in live-nets, swam constantly at a rate of about 6-8 m/min when undisturbed (Fridriksson and Aasen 1950).

Herring are capable of making extensive journeys. Tagging studies have demonstrated the existence of annual migratory patterns, such as movements to spawning grounds, to overwintering areas, and to feeding areas. Some populations have a more persistent migratory pattern than others, and some populations also intermingle more than do others. Adults, have generally been recovered from a wider range of locations than juveniles, indicating that they are apparently capable of covering greater distances in their seasonal movements than are younger stages (Creaser *et al.* 1984; Creaser and Libby 1988). Some adults tagged in the southwestern Gulf of Maine have been found at least as far east as Mount Desert Island on the Maine coast, while others from this spawning population may possibly overwinter in the Mid-Atlantic Bight intermingled with fish from the Georges Bank population (Ridgway 1975). Adults from the Gulf of Maine that overwinter south of Cape Cod may move through Great South Channel and Cape Cod Canal to summer feeding grounds along the Maine coast (NERFMC 1978). Seasonal movements of herring within the Gulf of Maine are discussed in greater detail below.

Circumstantial evidence and data based on tagging studies indicate that progeny of a spawning component of herring have a homing tendency and return to the parental spawning ground (Messieh and Tibbo 1971; Wheeler and Winters 1984b). Analysis of tagging data from Newfoundland waters supported the hypothesis that the majority of herring return to that same area to spawn in successive years. Average annual homing rates, defined as the number of fish returning to the same area to spawn in successive years, was estimated at about 73%.

Little is known of causal mechanisms or environmental cues responsible for herring migration and homing. Herring may not directly recognize a particular spawning ground, but innately recognize it as a place suitable for spawning (Harden-Jones 1968). However, some cue must exist to aid the fish in returning to this general area. Current direction may serve as a general cue allowing herring populations to return to an area of olfactory sensitivity, which then permits return to the parental spawning ground. In the Newfoundland area, herring indicate a general denatant migration to overwintering areas, followed by a contranatant migration during the pre-spawning period (Pinhorn 1976).

Next to schooling, probably the most important behavioral response of herring is vertical movement in response to changing light intensity (Sindermann 1979). Atlantic herring generally undertake diurnal vertical migrations, rising towards the surface at dusk and sinking towards the sea bed at dawn (Blaxter 1990). Herring schools are sometimes visible at the water's surface during the daytime, especially on calm days, where the school can often be detected by a fine rippling of the water (Bigelow and Schroeder 1953). Atlantic herring reportedly do not "fin" or lift their noses above the surface as menhaden often do, and they do not jump unless frightened, but smaller-sized fish are often seen jumping when pursued from below by larger predatory fishes, such as silver hake or striped bass.

The behavior of herring and other clupeids during the night is less well known (Blaxter and Holliday 1963; Blaxter and Hunter 1982). They are often active at the surface at night, where their presence may be betrayed by the trails of luminescence left in their wake. Experimental work with juveniles clearly demonstrated that herring activity had a diurnal pattern, with maxima just after sunrise and just before sunset; and that vertical diurnal movements occur at all seasons, except that depths occupied by herring increase in winter (Brawn 1960a, 1960b; Tibbo 1964; Stickney 1972). Juveniles generally move up in the water column at twilight and remain near the surface if light intensity is low enough. Field observations and catch information also attest to the importance of light intensity, especially with respect to behavior of juveniles. Moonlight, and phase of the moon, are important determinants of the success of the juvenile fishery, so much so, that Anthony (1971) was able to demonstrate successive monthly peaks in the sardine fishery (consisting of juveniles 12-15 cm long that are usually age-1 and age-2), coinciding with dark cycles of the moon.

There is no convincing evidence that herring school in complete darkness, a conclusion borne out by findings presented in a study by Blaxter and Batty (1987). In that study, herring which were schooling in the light, became less active in the dark, their swimming speed decreased, they tended to disperse, and the proportion of gliding compared with swimming fish increased. Also, those herring that were not schooling in the light responded by increasing their swimming speed in the dark. Stronger evidence that herring are much less active and may be orientated at a wide range of angles to the horizontal at night come also from submarine observations (Radakov and Solov'ev 1959; Radakov 1960). Foote and Ona (1987) also reported that tilt angles of herring were above horizontal and very variable at night. A decline in activity in darkness was reported by Batty *et al.* (1986), who found lower swimming speeds and lower food-filtration rates in herring held in the dark. Since vision plays such an important role in schooling behavior, it is expected that herring schools would tend to disperse once light intensity falls below the visual threshold necessary to maintain school structure. Reports of herring schooling at night are rarely accompanied by measurements of ambient light intensity or extent of bioluminescence present in the surrounding water. Only Craig and Priestley (1961) reported herring orientated near the sea bed at night in light intensities below the visual threshold, but strong tidal currents were running in their study area and it is possible that fish were orientated to currents rather than to each other.

Activity of herring is also controlled in great part by water temperatures. Early research showed that adult herring could distinguish between temperatures varying by as little as 0.2° to 0.6°C (Shelford and Powers 1915). Field studies (Zinkevich 1967) of seasonal distribution of adult herring on Georges Bank suggested a preferred temperature range of 5-9°C. Juvenile herring were found to prefer temperatures from 8 to 12°C (Stickney 1969), and Brawn's work (1960a) demonstrated that physiological stress occurred below 4°C and above 16°C, while temperatures below about -1.1°C and above 20°C were generally lethal for this species. When given a choice, herring larvae demonstrated a preference for warmer temperatures, to a maximum of ca. 13°C, than those to which they were acclimated (Batty 1994). High environmental temperatures are detrimental to developing larvae. For Pacific herring (*C. pallasi*), exposure to high temperatures during development results in abnormal jaw development, thereby impairing feeding performance of these larvae (Alderdice and Velsen 1971).

Herring activity in the field during wintertime generally support experimental findings of temperature related activity patterns. For example, observations of herring in Passamaquoddy Bay, indicated that they moved very sluggishly when the water was coldest in February and March (Huntsman 1934). Bigelow and Schroeder (1953) noted that this probably applied to herring all around the periphery of the Gulf, because the upper 40 m of the water column ordinarily cools to about 1-3 °C during those months, with surface waters often approaching the freezing point of saltwater in shallow bays and harbors. When waters warm to about 4-5 °C, herring once again become active.

Temperature preferences of juvenile herring are demonstrated by major activity in weir and stop seine fisheries for juveniles on the Maine coast, which coincides with the period when nearshore water temperatures range from 10 to 13 °C (Sindermann 1979). Activity declines during mid-summer on the western coast of the Gulf, when nearshore temperatures may exceed 13 °C, and during colder months (November to March) schools of juveniles disappear from nearshore waters in the Gulf of Maine. Observations of juvenile herring movements in one Maine estuary (Recksieck and McCleave 1973) also support experimental findings of temperature optima for this stage in the life history.

Atlantic herring have been observed to survive winter temperatures to at least -1.1 °C (Brawn 1960a). One adaptation allowing these fish to withstand such cold temperatures is the production of antifreeze proteins (AFPs) in the blood. Serum of herring taken off Nova Scotia contained antifreeze proteins that were similar to those found in smelt and sea raven (Ewart and Fletcher 1990). Presence of AFPs in herring indicates they have the capacity to survive in icy seawater. Herring off Newfoundland, particularly those caught in the under-ice fishery off northeast Newfoundland, also appear to be quite freeze tolerant, judging by low water temperatures in which they are found and their substantial plasma hysteresis. Fish in these populations may also generate AFPs as adults.

Plasma freezing points are significantly lower and antifreeze activity significantly higher in juvenile than adult herring (Chadwick *et al.* 1990). Mean thermal hysteresis of juveniles was found to be nearly three times higher than that of adults, and juveniles were also more prepared to overwinter under freezing conditions at an earlier date than were adults. The significantly higher levels of antifreeze in juveniles as compared with that of adults suggest that juveniles are better adapted to overwinter in colder water, which is more typically found near the coast in habitats occupied by juveniles. By migrating offshore during wintertime, adults avoid the severely low winter temperatures found closer inshore. Capacity for antifreeze production, or the level of activity of AFPs, may also be related to the population from which the herring originates (Chadwick *et al.* 1990). Accordingly, herring from Brown's Bank where water is relatively warmer during wintertime (ca. 7 °C) showed no evidence of AFP production, which directly contrasts with the situation found in herrings from colder areas within the region.

Salinity is probably a less critical factor than temperature in influencing overall movements and distribution of herring. With increasing age of herring, there is an increasing preference for higher salinities. Larval and 0-age group herring can frequently be found in inshore coves and estuaries where salinities are markedly reduced (Townsend 1992). However, older juveniles reportedly avoid these brackish estuarine conditions (Recksieck and McCleave 1973). Some experimental evidence suggests that juveniles respond to salinity changes, and that they can tolerate changes in salinity (Brawn 1960c, 1960d). Juveniles preferred 28-32 ppt salinity, although salinities as low as 5 ppt could be tolerated for brief periods. In another study

(Stickney 1969), juveniles were found to exhibit a salinity preference in excess of 29 ppt at temperatures under 10°C, but no preference was demonstrated when environmental temperatures exceeded 10°C. Although adult herring regularly enter bays and estuaries in the Gulf, they are not usually reported from water that is appreciably brackish. Bigelow and Schroeder (1953) suggested that salinities of ca. 28 ppt were probably the lower limit of occurrence for adult herring.

Seasonal distributions of adults and juveniles may also be related to availability of food, although isolating individual environmental factors and demonstrating clear relationships for any one variable among the many possible is difficult (Sindermann 1979). Seasonal abundance of zooplankton, the preferred food of adult and juvenile herring, in coastal waters of the Gulf of Maine during warmer months of the year (May-November) is undoubtedly an important determinant affecting herring distribution. Seasonal phytoplankton blooms can act also to exclude schools from localized areas, as was demonstrated for herring in European waters (Savage and Wimpenny 1936), particularly during blooms of *Phaeocystis*, and to some extent on Georges Bank, where Bryantsev (1966) noted that adults avoided shoal areas during summer phytoplankton maxima.

Feeding.--Atlantic herring are facultative, zooplanktivorous, filterfeeders (Blaxter 1990). Food items in the diet vary markedly with fish and prey size, season, and geography (in terms of what food organisms may be present in abundance in a specific location). Larvae, juveniles, and adult herrings are selective opportunistic feeders, taking advantage of concentrations of whatever prey of appropriate size is available in their immediate environment (Sherman and Honey 1971; Sherman and Perkins 1971). Thus, in early spring, dense swarms of barnacle larvae or cladocerans will constitute the principal prey, while later in the season copepods and euphausiids may dominate. Herring are primarily visual particulate feeders that consume a variety of planktivorous organisms, especially crustaceans, during daylight and twilight hours (Battle 1934; Blaxter 1966), although little feeding may occur during the day when the fish are in tight schools at depth or near the sea bed. As the herring grows, its eyes become increasingly adapted to twilight vision (Blaxter 1964, 1966, 1968). James (1988) stated that herring are primarily a twilight forager whose peak feeding activity occurs at dusk and dawn in the upper water layers, with feeding intensity decreasing during the darkest hours.

Herring display a diversity of feeding behaviors, with fish size, light intensity, biting, filtering, prey size, and prey density having interacting roles (Batty *et al.* 1990). Until recently, it was thought that herring were obliged to feed by biting. Biting was observed to cease at low light intensities, with a visual threshold of 0.007 lx when fish were feeding singly and 0.036 lx when fish were feeding as a group (Blaxter 1964). Herring will, however, switch to filterfeeding in the light if food particles of a suitable size and concentration exceed a critical level (Gibson and Ezzi 1985, 1990). Juvenile herring, in the light, have been observed to use two modes of feeding, particle biting and filtering, but in the dark only filtering was observed (Batty *et al.* 1986). When offered wild-caught zooplankton, juvenile herring consumed the larger organisms first, by biting, but only when light intensities were above a threshold of 0.001 lx. Biting was possible at lower light intensities, but only when prey were large.

In darkness, herring apparently are not able to feed by biting, but if conditions are appropriate they can filterfeed during nighttime. Filtering commences in the dark at high prey densities when prey are small, but at low prey densities when prey are large. In the light, fish continued to school while feeding in both modes, however, in darkness, juvenile herring stopped schooling, the fish swam slower in tight circular paths and fed only by filtering. Possibly, this circling behavior was in response to a chemical stimulus. Herring larvae respond to chemical stimuli, including extracts of food organisms such as barnacle nauplii and *Artemia* spp., by increasing their activity and swimming up a concentration gradient (Dempsey 1978). If this behavior persists throughout the life of the fish, it might enable herring to remain within food patches and exploit them in the darkness (Batty *et al.* 1986). In the dark, filtering fish swam faster (0.11 m/s) than non-filtering fish (0.07 m/s). In the light, no difference in speed was measured between filtering and non-filtering fish (0.34 m/s). Owing to the lower filtering speeds in the dark, the removal rate of nauplii from the water was much lower than in the light, except at the highest prey concentrations. This suggests that if nighttime filterfeeding takes place in the sea, it will be of importance only when exploiting dense patches of food.

When filterfeeding, herring utilize their gillrakers as the menhaden does (Moore 1898), although this species does not include smaller microscopic plants (i.e., diatoms or peridinians) beyond fish sizes of more than 15-20 mm long, probably because microstructure of the gillrakers in larger fish is not fine enough to retain these small plankters. Gillrakers first appear on gill arches of herring at a total length of about 16 mm (Gibson 1988). Their number then increases rapidly until the fish are about 50 mm TL, when the rate of addition becomes much slower. Rakers on the first gill arch account for almost 60% of the entire filtering area. Particle retention capabilities of herring when filterfeeding were lower than those expected on the basis of the estimated spaces between the rakers (Gibson 1988). Length of individual rakers and spacing between them continues to increase throughout the life of the fish. Change in filtration area with increasing fish length is thus due mainly to increasing length of the rakers, with increase in filtration area accompanied by an increase in mesh size of the filter.

Ontogenetic Changes in Diet Composition.--Larvae begin exogenous feeding before the yolk sac disappears. Copepod eggs, nauplii, copepodids, mollusk larvae, peridinians, diatoms and other algae constitute much of the diet of early life history stages (Sindermann 1979). Seasonal differences occur in diet composition of larvae. For example, during winter, small copepods such as *Pseudocalanus minutus* and copepodid stages are primary food items for larvae, whereas in spring, somewhat larger copepods (especially small *Pseudocalanus elongatus*) and copepodid stages, cirriped larvae, crustacean eggs, and tintinnids are principal food organisms (Bigelow and Schroeder 1953; Sherman and Honey 1971; Checkley 1982; Cohen and Lough 1983; Munk and Kiorboe 1985; Kiorboe and Munk 1986). As larvae grow, copepods constitute a large proportion of the items eaten.

As juveniles grow they feed mainly on larger copepods (especially *Calanus finmarchicus* and *Temora longicornis*), but will also feed opportunistically on hyperiid amphipods, euphausiids, mysids, cladocerans, barnacle larvae, bivalve larvae, small fishes, arrow-worms, ctenophores, pteropods, and decapod crustacean larvae (Battle *et al.* 1936; Bigelow and Schroeder 1953; Legaré and McClellan 1960; Sherman and Perkins 1971; Maurer 1976). In Maine coastal waters, diets of juvenile herring are varied, but copepods are often the dominant prey, especially in summer (Sherman and Perkins 1971). Legaré and MacLellan (1960) found copepods of the following genera, *Calanus, Pseudocalanus, Eurytemora, Acartia*, and *Tortanus*, to be important dietary items for herring from the Quoddy region of New Brunswick.

Between age-2 and age-3, herring change from a predominantly copepod diet to a predominantly euphausiid diet (Sherman and Perkins 1971; Maurer 1976). Adult herring feed principally on euphausiids (*Meganyctiphanes norvegica*), chaetognaths (Maurer and Bowman

1975; Maurer 1976), and to a lesser degree copepods, particularly *Calanus finmarchicus*. Stomachs of adult herring off the Maine coast (Moore 1898) contained copepods and pelagic euphausiid shrimps (*Meganyctiphanes norvegica*). Fish <10 cm long depended on the former alone, while larger herring had consumed both types of prey organisms. A few larger fish, however, fed almost entirely on copepods, even when both shrimp and copepods were abundant. Shrimp are an important prey item of larger herring, for even in winter, when shrimp are rarely seen at the surface, they can be an important component of the herring's diet (Moore 1898). Preference for this prey organism was such to suggest to Bigelow and Schroeder (1953) that local appearances and disappearances of schools of large herring in the open Gulf were likely related to presence or absence of euphausiid shrimps.

When shrimp are absent copepods are the chief prey item for herring of all sizes. Relatively large-sized amphipods of the genus *Euthemisto* are an important food for herring in European seas, but are not found in stomachs of herring from the western Atlantic (Moore 1898; Bigelow and Schroeder 1953), undoubtedly due to the comparative scarcity of this large active crustacean in coastal waters of the Gulf of Maine.

In addition to consuming a variety of Crustacea, herring also feed on molluscan larvae, fish eggs, annelids and even on such microscopic prey as small as tintinnids and Halosphaera. Although herring are not usually piscivorous, larvae of sand lances, silversides, and young herrings have been found in stomachs. Templeman (1948) also reported that off Newfoundland during wintertime, herring consumed quantities of small capelin. Principal prey organisms of over 5700 herring from the North Sea (Last 1989) were copepods (*Calanus, Temora*), but Euphausiacea and postlarval stages of *Ammodytes* spp. and clupeoids contributed a large percentage of the weight. Fish eggs, chiefly those of plaice (*Pleuronectes platessa*), were also consumed, but not in large numbers.

Spring and summer are the most intensive feeding times for juveniles and adults. Adults cease feeding when spawning begins (Pankratov and Sigajev 1973). Off New Brunswick, the most active feeding period for herrings occurs during September to November (Legaré and MacLellan 1960). Off Newfoundland, herring eat very little during winter (December to April), apparently living on their accumulated fat (Hodder 1972) during this season.

Larval, juvenile, and adult herring have been shown to select the larger prey organisms from those available in the plankton (Sandström 1980; Checkley 1982; Batty *et al.* 1986). Herring ordinarily target individual food objects (Battle 1934) during feeding in daylight. When feeding on euphausiids, herring have often been seen pursuing individual shrimps, which frequently leap clear of the water in an effort to escape being eaten (Bigelow and Schroeder 1953).

Using saturation diving techniques, Cooper (cited in Sindermann 1979) provided additional information on elective feeding behavior of adult herring during different environmental conditions. During late afternoon with no current, at a depth of 33-40 m, adult herring were layered horizontally to obliquely 3-6 m off the bottom. Individuals were spaced from each other and would, every 5-20 seconds, dart 0.3 to 0.6 m after a visually sensed "food item." This behavior lasted for ca. 1 hr during slack waters. During another observation period, with a current of 1.8 km/hr at a depth of 40-45 m, tightly-schooled adult herring (less than one body length separating individuals in the school) were observed for 0.5 hr. Fish appeared to be feeding selectively, but maintained a tight school formation. School speed over the bottom was ca. 1.0-1.5 km/hr.

Studies of metabolic activity have well established that lipid content of herring undergoes a marked seasonal cycle. For spring-spawning herring off Newfoundland, lipid content declined from a high of 15% in January to a low of 6% for spent fish in May and June, which represented a 60% loss in lipid reserves (Hodder *et al.* 1973; McGurk *et al.* 1980). For herring from waters around the British Isles and Ireland, lipid content was highest during the summer months of active feeding and lowest after a winter fast (Henderson and Almatar 1989). In spring-spawning herring from this region, minimum lipid content coincided with the spawning period (Lovern and Wood 1937). Depletion of lipid reserves in these herring during the winter corresponded with development of the gonads.

Earlier studies on energy utilization in herring considered only seasonal changes in total lipid content (Wood 1958; Iles and Wood 1965; Wallace 1986), while that of Henderson and Almatar (1989) examined lipid contents of herring in relation to stage of sexual maturation. This latter study found that somatic lipid content was highest in stage III fish captured in summer and lowest in spent fish sampled after spawning in March. Otherwise, little change in content and class composition of lipid in gonads of both males and females occurred relative to stage of maturity.

Seasonal metabolic activities of North Sea herring have a specific time structure not easily related to environmental variables (Iles 1974a, 1974b). Feeding began in the absence of anabolic growth, and, as a result, both fat and protein stores were accumulated, but in very different ways. Fat was assimilated and deposited almost unchanged; it is metabolically inactive (Lovern 1951). Protein metabolism, however, was very active. Protein was ingested, digested, assimilated, catabolized and anabolized. Both catabolism and anabolism resulted in build up of a metabolic pool. Protein catabolism releases free energy and it is this that supplied all metabolic energy needs, including those generated by increased activity in the search and capture of food. Shortly after feeding and protein metabolism began, somatic growth was initiated as an anabolic process. Preparation of protein subunits for subsequent gonad maturation continued. Thus, somatic growth and gonadal growth differed only in timing of use of material prepared at the same time by the same metabolic processes. Later in the season, there was a fairly short period over which anabolic growth decelerated to zero, and translocation of protein to the gonad began. This coincided with a marked reduction in appetite resulting in cessation of feeding (Iles 1974a, 1974b). The cessation of feeding and somatic growth represented a switch from protein catabolism to fat catabolism and also mobilization of fat reserves for all energy requirements. The largest non-reproductive source of protein loss, represented by maintenance of an active epithelium in the alimentary canal, was thus avoided by cessation of feeding. Other activities involving protein synthesis (e.g., hemoglobin synthesis; Wilkins and Iles 1966) were also curtailed at this time. Iles (1974a) noted, however, that the process of gonad maturation, leading to the ripe, competent gonad was quite distinct from that of spawning, with the two stages being separated by the event of ovulation.

Predators.--In general, herring are preyed upon by nearly all pelagic predators and are considered to be an extremely important forage species because of their numerical abundance and schooling behavior. Herring are a basic food for many fishes, marine birds (Gaskin and Smith 1979; Braune and Gaskin 1982; Hislop and MacDonald 1989), short-finned squid (Lidster *et al.* 1994), and seals, porpoises, and whales (Watkins and Schevill 1979; Hain *et al.* 1982; Wallace and Lavigne 1992; Lawson *et al.* 1994).

Herring of all sizes are preyed upon by a wide variety of predaceous fishes including codfish, pollock, haddock, silver hake, white hake, striped bass, mackerel, sword fish, tuna, billfish, salmon, sculpins, winter flounder, dogfish, porbeagle shark, and skates. For most of their larval stage, herring are solitary, pelagic and vulnerable to planktonic predators which include visual and non-visual feeders, such as jellyfish, chaetognaths, larger copepods, euphausiids, and juveniles and adults of many fish species (Theilacker and Lasker 1974; Langsdale 1993). Predation by fishes can be a significant mortality factor for adult herring, with particular pressure at spawning time. Diver observations (Cooper *et al.* 1975) disclosed that bluefish, cod, and pollock were voracious predators on spawning concentrations in the southwestern Gulf of Maine, with maximum predation activity occurring at night. Silver hake, in particular, are reported to drive schools of herring up onto beaches in the Gulf, where pursued and pursuers alike strand in the shallow waters (Bigelow and Schroeder 1953). One such feeding frenzy occurring on an October morning at Cohasset in Massachusetts Bay many years ago was described in which hake and herring were so intermingled in shallow water that at the height of the carnage that Bigelow and Schroeder filled a dory with both species of fish, using only their bare hands to capture them.

Finback whales also devour herring in great quantities. Hain *et al.* (1982) described an interesting method of prey capture used by humpback whales when feeding on herring and other schooling fishes. In the West Quoddy Head area, they observed humpbacks occasionally feeding on herring close inshore and in coves using a bubble cloud and lunge feeding method. In this feeding behavior, whales dive underwater and swim in a circle beneath the schooling fishes. While swimming in this manner approximately 15 bubble bursts are released, which rise to the surface as columns and appear to form an effective corral. As the bubble corral nears completion, the whale pivots on the axis of its flippers and then banks to the inside and turns sharply into and through the center of the corral below the surface of the water. With mouth agape and lower jaw region distended, the whale then feeds on fishes that have been concentrated into a tight school within the bubble curtain.

The short-finned squid (*Illex*) consumes multitudes of young sardines. On one occasion near Provincetown, in June 1925, Bigelow and Schroeder (1953) reported that packs of perhaps 10 to 50 squid were circling around a school of juvenile herring, bunching them into a compact mass. Individual squid then darted into the school, seized one or two herring, ate only a small part, then darted back for more. A silvery streak of fragments of dead herring remaining along the beach bore witness to the extent of that carnage.

Herring eggs and larvae are also cannibalized by adult herring. Spent herring on spawning grounds have been observed with eggs in their stomachs, as have adult herring with larvae in their stomachs (Sindermann 1979). Herring eggs and spawn are also subject to predation by a variety of bottom predators. Winter flounder are a major predator (Tibbo *et al.* 1963; Pottle *et al.* 1981; Messieh *et al.* 1985), but other species also take their toll including cod, haddock, and red hake (Caddy and Iles 1973), sand lance (Fuiman and Gamble 1988; Rankine and Morrison 1989), sculpins, skates, and smelt (Messieh *et al.* 1985; Scott and Scott 1988), tomcod, pollock, cunner, mackerel, and even herring themselves (Messieh 1988; Fuiman and Gamble 1988). In one particular area, fish predation rates varied with estimates of between 45 and 69% of the initial herring spawn being consumed by these predators (Messieh 1988). These estimates were conservative and represented only a portion of the total predation on the eggs, because predation mortality exerted by invertebrate predators such as lobsters and starfish were not included. On Georges Bank, ca. 8% of the herring spawn was estimated to have been removed by predation within 1-2 d after spawning occurred (Caddy and Iles 1973). Sand lance are clearly a most effective predator on early life stages of herring, with up to as many as 400 eggs and larval herring possibly being consumed per individual sand lance (Rankine and Morrison 1989). Since sand lance are associated with the coarse sublittoral sediments actively selected as spawning sites by herring, they could easily be present in the same areas as herring egg masses (Rankine and Morrison 1989). In one study, sand lance actively hunted herring larvae in preference to more numerous copepods, which, as identified from stomach analysis, provided their usual staple food (Christensen 1983). Additionally, the scyphozoan medusa *Aurelia aurita* has also been shown to be an important predator on larval herring (Möller 1984; Bailey 1984; Bailey and Batty 1984).

Anti-Predator Devices.--Despite incurring heavy predation pressure from a diverse array of predators throughout all life history stages, the herring is not completely defenseless. This species employs a series of effective means to avoid being eaten. Of the array of defenses used by herring (Blaxter 1990), schooling is perhaps one of the most important behaviors in avoiding predator attacks. An aggregation of fish, continually changing position, rapidly responding to noxious stimuli, and with a powerful motivation to remain as a group, is a major problem for visual predators (Blaxter 1990). It is particularly difficult for a visual predator to fixate on an individual within a large school, a prerequisite for successful prey capture. Herring, along with other clupeoids, also have reflecting silvery sides, which is a clever camouflage device to reduce contrast with the background. Among morphological traits effective for predator avoidance, herring have Mauthner cells, giant nerve fibers in the spinal column, that allow extremely fast muscle contractions and provide rapid escape responses to harmful stimuli. These cells can be fired by visual or auditory stimuli and provide the well known and researched "startle response." Backing up the startle response is a unique and very complex auditory system that confers to the herring outstanding hearing ability, both in terms of sound frequency range and auditory threshold. A sound amplification device within the skull is coupled to the head lateral line system via a further membrane, the lateral recess membrane located in the wall of the skull (Blaxter 1990). Movements of the pro-otic membrane are thus transmitted to the lateral line neuromasts. These are stimulated both by sound pressure stimuli from within the skull as well as directly by particle motion stimuli from the same sound source. The auditory system and lateral line thus provide information on the range and direction of sound sources and also play a vital role in the schooling behavior and predator avoidance tactics utilized by this species.

During ontogeny, the timing of development of anatomical structures and sensory modalities used in predator avoidance are important and are closely coupled with life history events accompanying development. Since herring larvae are themselves visual feeders, and consequently must spend some time in sufficiently illuminated layers of the water column, it is likely that initially they rely mainly on their transparency and vertical migratory behavior to minimize visual predation. Early in their ontogeny herring larvae respond with C-starts to either flash or looming visual stimuli (Batty 1989), but are unable to respond to sound stimuli with C-starts at this stage (Blaxter and Batty 1985). At this time, however, they are particularly prone to predation by non-visual predators such as the medusa *Aurelia aurita* (Möller 1980). Neither visual nor sound detection capabilities would be effective in sensing a slow-moving, transparent predator of this type. Swimming ability is also a critical factor in evading predators. Formation of the caudal fin, at about 15 mm, greatly increases swimming performance (Blaxter 1962), and hence the ability to escape weakly-swimming predators.

Herring larvae appear to obtain information used for initiating and timing an evasive response from the speed and distance of the attacking predator (Fuiman 1993). Small larvae (< 20 mm) probably perceive this information through the mechanosensory system, but visual cues may be important to larger larvae. In experimental studies where vulnerability of herring larvae to predation and the ontogeny of evasive capabilities were studied (Fuiman 1989, 1993), response rate of larvae to predatory attack was generally low (ca. 6%) during most of the larval period. At lengths of 26-30 mm, larval responsiveness increased 10-fold, coinciding with major advances in the acoustico-lateralis and visual sensory systems, including development of auditory bullae and cephalic lateral line canals. Gallego and Heath (1994b) also found that in laboratory experiments pre-metamorphic herring (<50 mm) failed to react to about 50% of the attacks of a visual predator (young whiting), but this was reduced to about 20% of the attacks on postmetamorphic fish, when schooling behavior was better developed. These morphological changes are also accompanied by sharp increases in accoustically (Blaxter and Batty 1985; Blaxter and Fuiman 1990) and visually (Batty 1989) stimulated startle responses. On hatching, herring larvae have a pure cone retina (Blaxter and Staines 1980). The presence of rods in the retina is believed to be important for detection of movement (Blaxter 1986). Rods first appear in the ventral retina when the larva is about 22 mm long, but the dorsal retina does not have fully developed rods until the larva is 28 mm long (Sandy and Blaxter 1980). Timing in development of rods is in accord with the onset of startle responses of larvae to visual stimuli.

Increases in responsiveness, response effectiveness, and predator error rate contribute to declines in capture probability as larvae grow (Fuiman 1989). Herring larvae develop startle-response behavior to visual and auditory stimuli at the same time that they become increasingly conspicuous due to increased size, pigmentation and activity (Batty 1987). At this stage in their development, therefore, they become more susceptible to fish predators, but due to their increased size and escape speed, much less susceptible to invertebrate predators (Bailey and Batty 1983, 1984). In mesocosm systems, number of larvae consumed by predators increased with larval length, suggesting that predator encounter rate and possibly attack rate increased with larval length, probably due to increased conspicuousness of the larvae (Fuiman 1989).

Transparency aids visual background matching by transmitting light with minimum interference. Herring larvae display three features which particularly compromise their transparency (Langsdale 1993): (1) the eye; (2) body pigmentation; and (3) opaque gut contents. The eyes of herring become fully pigmented several days before hatching. The proportion of lateral body area occupied by pigment increases significantly during development. Opacity of herring larvae also increases with size due to increasing area of the eyes (which are densely pigmented behind the retina to prevent penetration of light from directions other than through the lens), increasing complexity of the internal body structures, longer light path through the body and the appearance and proliferation of opaque pigment cells (melanophores). An additional factor is the variable amount of food in the gut. The vulnerability of opaque plankters to visual predators generally increases with prey body size (O'Brien *et al.* 1976). Therefore, a critical period in the life history of herring in terms of vulnerability to predation can be expected between the end of the larval and beginning of the juvenile stages, as pigmentation patterns change and before schooling behavior is fully developed (Gallego and Heath 1994b). Langsdale (1993) found that at a body length of ca. 40 mm, "pre-juvenile" herring begin to develop reflective scales. Scales of post-metamorphic juveniles and adult fish reflect underwater background light, minimizing their visual contrast in open water (Denton and Nicol 1965). This metamorphosis also marks the end of the solitary phase of their history, since schooling behavior is first observed in reared larvae around this time (Blaxter and Jones 1967).

Mass Mortalities.--The herring is susceptible to wholesale destruction by stranding on beaches during storms and in its attempts to evade predators, by ingestion of toxic dinoflagellates, and by anthropogenic sources such as water pollution and impacts associated with electric power generation. Instances of mass mortalities, especially of young herring, have been reported in several Gulf of Maine harbors. Bigelow and Schroeder (1953), for example, reported a mass mortality of herring that took place at Cohasset, on the south shore of Massachusetts Bay, in October 1920. On October 5, a large school of juveniles (10-13 cm in length) ran up the nearly landlocked harbor. According to local fishermen, these fishes were driven into the harbor by silver hake. Once in the harbor, the herring were trapped there by the falling tide, and stranded on the mud flats. So numerous were the herring, that the flats were entirely covered with them, and an estimated 20,000 barrels of fish perished. During the next few days, the fish (alternately covered and uncovered by the tide) decayed, and despite tidal circulation, so fouled the water that lobsters impounded in floating cars nearby also died. On October 10 there was a second, smaller run of herring, and on October 15 there occurred a third run as numerous as the first. The newcomers died soon after they entered the harbor. Altogether, approximately 50,000 barrels of fish perished during these events, of which more than 90% were "sperling", 5 to 10% were large adults. A few small mackerel and silver hake, and a large number of smelt were also among the dead fish. So many herring died in this area that tidal flats exposed at low tide were silvery with herring scales even into the last half of October. Residents about the harbor found the stench from the decaying fish almost unbearable. During the ensuing winter, the fish decomposed and the water purified itself.

Mass-mortalities of herring sometimes also occur when they feed on herbivorous pteropods and other zooplankton (cladocerans) which have been grazing on toxic dinoflagellates (*Gonyaulax excavata*) that produce paralytic shellfish (PSP) toxins (White 1977, 1980, 1981). Larval herring are also susceptible to PSP toxins when they feed directly on PSP-producing dinoflagellates (e.g., *Alexandrium* sp). Toxic blooms of *Gonyaulax excavata* (*tamarensis*) have a long history in the Bay of Fundy (White 1980), and since 1972 this organism has spread southward along the New England coast causing annual red tides as far south as Cape Cod (Anderson and Wall 1978).

Scott and Scott (1988) reported that a series of extensive herring mortalities occurred in the Placentia Bay region of Newfoundland during the winter of 1969. The dead herring were red in color (fins and body) and attracted much publicity. Mortality was first thought to be caused by a disease, but was later shown to be the result of industrial pollution, mainly phosphorus, from a nearby industrial plant (Jangaard 1970).

Herring are also impacted by operations associated with coastal electric power generating plants. At the Pilgrim Nuclear Power Station in western Cape Cod Bay (Lawton *et al.* 1984), herring represented 49% of the fishes impinged on intake screens. Induced stress and debilitation in the narrow confines of the Pilgrim Power station's intake forebay were also implicated as potential causative agents for a mass mortality (tubular necrosis of the kidneys) of herring in this area.

Species Associates.--The complexity of food web interactions of herring, especially those highlighting its ecological role as an important forage item for many predatory fishes, aquatic mammals, and fish-eating birds, as a significant predator on the zooplankton community, and as a potential competitor to other planktivorous fishes, is well known and was schematically represented by Hardy (1959).

Alternating cycles of population abundances for herring and mackerel have been hypothesized as reflecting possible interactions between these species (Lett and Kohler 1976, Winters 1976). However, Grosslein *et al.* (1978) examined feeding relationships of herring and mackerel and other western North Atlantic pelagic fishes and found no evidence that adult mackerel or herring had fed on larvae of the other species. They suggested that factors other than the mackerel-herring predation interrelationship were more influential to changes in biomass and abundance cycles previously noted for these species. In another study (Skud 1982), mackerel and herring apparently experienced some level of trophic competition, and each species was found to have preyed upon the young of the other. Messieh (1988) also reported that mackerel may directly impact herring populations because they feed on herring eggs. Skud hypothesized that population size of which ever species (mackerel or herring) happened to be dominant (i.e., most abundant) during a particular period of time would increase during years of higher water temperature and that the abundance of the non-dominant species would simultaneously decline. Increased water temperature enhanced growth and survival, and thus biomass and abundance, of the dominant species; the resulting increased competitive pressures between the species would cause a decline in abundance of the non-dominant one. When dominance changed from one species to the other, the manner in which the biomass of each species responded to temperature would change accordingly. Shifts in dominance could also be stimulated by fishing pressure, thus creating a competitive edge for the species that was fished less heavily.

Parasites and Diseases.--Atlantic herring are host to a diverse parasite fauna, with over 81 species of parasitic organisms infecting this species (Appy and Dadswell 1981; Arthur and Arai 1984; MacKenzie 1987; Bray and MacKenzie 1990). Of these, only about five species, all with direct life cycles (Protozoa and Monogenea), are wholly dependent on the herring for their survival (Mackenzie 1987). The herring serves as a host species (MacKenzie 1987) for the following groups of parasitic organisms (number of species in parentheses): Protozoa (11); Monogenea (17); Digenea (18); Cestoda (9); Nematoda (12); Acanthocephala (10); Hirudinea (1); Branchiura (2); and Copepoda (7). Not only do adult herring serve as hosts, but larval herring are also utilized as intermediate hosts in life cycles of cestodes and digenetic trematodes (Courtois and Dodson 1986; Heath and Nicoll 1991).

Parasites utilizing herring as an intermediate host include the larval nematodes, *Anisakis simplex* (larvae were grown in culture medium to adult stage for accurate identification) recovered from herring taken off Newfoundland (Pippy and Van Banning 1975; Threlfall 1982) and *Contracaecum osculatum*, commonly reported from herring in the eastern Atlantic (Smith and Wootton 1978; Valtonen *et al.* 1988). Although *A. simplex* is a species potentially pathogenic to man (Van Thiel *et al.* 1960), infection rates in herring from the western Atlantic are relatively low, especially among coastal migratory herring, and McGladdery (1986) concluded that raw, salted, smoked, or pickled fillets of most Canadian Atlantic herring were safe for human consumption.

MacKenzie (1987) summarized information on, and detailed relationships of Atlantic herring and its parasites. Noteworthy is his comment that parasites have been used more as biological tags for herring than for any other marine fish. Because they tend to have longer life spans, larval and preadult stages of helminths for which the herring serves as a second intermediate host have proved to be more useful for this purpose than have adult helminths.

Differences in prevalence of a protozoan parasite and an anisakid nematode larvae between consecutive age groups of young herring in the Gulf of Maine were interpreted in terms of age-dependent migrations of young herring within the Gulf (Sindermann 1957a, 1961). Trypanorhynch metacestodes have also been used in attempts to separate stocks of adult herring from a wider area of the Northwest Atlantic. Variations in prevalence and intensity of *Anisakis* spp. larvae were employed to separate stocks of herring in Canadian and U.S. Atlantic waters (Parsons and Hodder 1971; Lubieniecki 1973; Beverley-Burton and Pippy 1977; Chenoweth *et al.* 1986). The potential usefulness of seven parasite species as biological indicators of different aspects of herring biology were also demonstrated (McGladdery and Burt 1985). Among these species, four were found to be potentially useful to reflect changes in seasonal migrations of hosts between different parts of a study area comprising the Bay of Fundy, Nova Scotian shelf, and Gulf of St. Lawrence. Biological information from these parasites suggested that seasonal variation in prevalences could be better explained by changes in herring stock composition than by changes within parasite populations in the same stock of herring.

The life cycle of the sporozoan, *Eimeria sardinae*, is closely linked to reproductive dynamics of male herring (McGladdery 1987). The infective oocyst stage is released with sperm during spawning, and subsequent infection occurs directly via ingestion of these oocysts by other herring on and around the spawning grounds (Lom 1970). Infections with *E. sardinae* may prove useful in separating groups of herring that spawn at different times of the year (McGladdery and Burt 1985; McGladdery 1987), but infection levels are not useful for distinguishing between first- and repeat-spawning herring (McGladdery 1987).

Some parasites cause mass mortalities in herring (Hodder and Parsons 1971; Morrison and Hawkins 1984). Outbreaks of the systemic fungus pathogen *Ichthyosporidium hoferi* caused large-scale mortalities of herring in the Gulf of Maine in 1932 and 1947, and in the Gulf of St. Lawrence in 1898, 1916, 1940, and 1955 (Sindermann 1958, 1963, 1965, 1970, 1979). From disease prevalences in 1955 and 1956, Sindermann estimated that at least one-half of the herring stock of the Gulf of St. Lawrence was killed, an estimate supported by reduction in herring catches in the years immediately following these mortalities. Later examination of herring in the Gulf of St. Lawrence (Tibbo and Graham 1963) indicated that spring-spawning stocks were more severely affected than autumn-spawning stocks. Herring may also be infected by the piscine erythrocytic necrosis virus (PEN) (Reno *et al.* 1978).

Parasitic disease is undoubtedly an important factor contributing to natural mortality in herring and, as MacKenzie (1987) noted, ignorance of the nature of this contribution represents a major gap in our knowledge of herring biology. Heath and Nicoll (1991), for example, noted that despite a number of studies on feeding biology of herring larvae, few of these noted the occurrences of parasites. They found that the incidence of feeding for larval herring infected with cestode larvae was reduced by as much as 50% when compared with levels of prey consumption for non-infected larvae. They also discussed the implications of reduced feeding by larvae, and host and parasite distributions relative to recruitment success.

General Range.--Atlantic herring are confined to cold-temperate and boreal waters of the Northern Hemisphere on both sides of the Atlantic (Whitehead 1985a). In the western North Atlantic, herring range from southwestern Greenland and northern Labrador, south to Cape Cod and Block Island, and are occasionally seen in winter in small numbers as far south as Cape Hatteras and South Carolina. In the eastern Atlantic, herring are found from the northern Bay of Biscay northward to Iceland and southern Greenland, eastward to Spitzbergen and Novaya

Zemlya, and south to the Straits of Gibraltar. In the Baltic Sea, this species occurs to the Gulf of Bothnia and Gulf of Finland. It is presently much less abundant in European waters than previously reported (Scott and Scott 1988). In the North Pacific, there occurs a morphologically similar, closely-related species, *C. pallasi* (Whitehead 1985a).

Occurrence and Seasonal Distribution in the Gulf of Maine.--Atlantic herring appear at one season or another along nearly the entire coastline of the Gulf, as well as on the offshore fishing banks. All stages in the herring's life history occur in Gulf of Maine waters, and this species is one of the most common and abundant elements of the Gulf of Maine fish fauna. In fact, one outstanding feature of the distribution of fishes in the Gulf of Maine is the seasonal abundance of juvenile herring, especially in the Passamaquoddy-Grand Manan region. Historically, herring were much more regular in occurrence from year to year in the Passamaquoddy-Grand Manan region than they were in regions off western Nova Scotia or along the Maine coast (Bigelow and Schroeder 1953). Passing southward around the western periphery of the Gulf, Bigelow and Schroeder (1953) reported that herring were more sporadic in appearances, from place to place, week to week, and from year to year. Very few herring, for example, were seen on the southern side of Massachusetts Bay in some years, while in other years many schools were present. In the northeastern Gulf, herring also appeared to be far less plentiful and less regular in their occurrences on offshore banks than they were in inshore areas.

In most coastal regions of the Gulf of Maine, appearance of schools of large herring, or of small juveniles, is distinctly a seasonal event, with migration patterns varying with season and region in which fish were tagged (Creaser *et al.* 1984; Creaser and Libby 1988). Extremes of movements for adult fish tagged in the Gulf of Maine are Point Judith, RI, and Sydney Bight, NS. Occurrence of a relatively large percentage of prespawning and postspawning adult herring in eastern Maine supports the belief that this area is an important spawning ground for herring (Creaser *et al.* 1984; Creaser and Libby 1988). By October, mature fish are in full force on all spawning areas along the shores of the Gulf, from Grand Manan to Cape Cod. Although less abundant, they are equally widespread inshore in November, and occasionally they are reported from this region in December and even later. It is probable that as the fish spawn, most then move out promptly from the spawning grounds into deeper water given that recently spent fish are not often taken in weirs fished inshore (Bigelow and Schroeder 1953).

For herring larger than sardines, the peak seasonal occurrence inshore in the northeastern part of the Gulf is ordinarily from July through October, which is some two months less than that for sardines. Based on the fact that considerably greater catches of large herring are made in winter than are those of sardines, it appears that a greater proportion of larger fish continue to be available there throughout the colder months than do younger fish. Abundance of euphausiid shrimp (a favorite food of herring) in deeper waters of the northeastern Gulf suggests this may be a rich winter feeding ground for herring (Bigelow and Schroeder 1953). Herring of all ages remain in the open Bay of Fundy throughout the cold season. This is true also for the passages between inner and outer divisions of Passamaquoddy Bay, even when water temperatures there are as low as 0°C. Juveniles remain in Passamaquoddy Bay all winter, and are thought to overwinter mostly on or near the bottom, but apparently they do not move about much during this time.

In the southeastern Gulf, seasonal appearance of large herring inshore has a bimodal distribution. The greatest numbers of large herring occur there from early spring to about June, and then reappear again inshore in autumn, with very few (and not many sardines either) appearing inshore during the summertime. Earliest catches of sardines occurred there sometime in April or May, the latest recorded occurrence for this size group was in mid-November. Howe and Germano (1982) indicated that it is only during summer, and then only in deeper waters in Cape Cod Bay, that abundance of juvenile herring surpasses that of other species taken in trawl catches. Many herring tagged as summer-feeding adults in eastern Maine overwinter in Massachusetts Bay (Creaser and Libby 1988). Tagging studies of herring captured on Jeffreys Ledge and in the Great South Channel also showed that adults moved from tagging sites to coastal waters of Maine and the Bay of Fundy during summer and early autumn and returned to Massachusetts and Rhode Island coastal waters in late autumn and winter (Creaser and Libby 1988). Mature fish reportedly are not usually found in the Massachusetts Bay region until the last week in September, and in most years, large herring vanish from coastal inshore waters of Massachusetts during December. Creaser *et al.* (1984) reported that the majority of herring taken in Massachusetts Bay in winter were adults. This finding is supported by other studies in western Cape Cod Bay, where herring (78-350 mm FL) were among the top four dominant fish species taken in gillnets, with peak numbers occurring there during winter (Lawton *et al.* 1984). Although herring were taken in this area throughout the year, they were far less abundant during summer and early autumn than at other times. Apparently, during late spring and summer these fish moved offshore and northward. The southward winter migration of herring is also indicated by catches in Narragansett Bay, RI, where only during wintertime are herring commonly taken (Jeffries and Johnson 1974).

Seasonal movements of adult herring on Georges Bank (Sindermann 1979) are comprised of three apparent phases: (1) a late summer-early autumn spawning migration of ripening fish on Georges Bank; (2) a rapid post-spawning migration to warmer waters to the south for overwintering; and (3) a spring-early summer northward feeding migration back to Georges Bank. Post-spawning adult herring from Georges Bank move southwest to off Chesapeake Bay in November, and overwinter there, with the larger and older fish moving furthest south. A feeding migration back to Georges Bank begins in May or early June, and continues to shallower spawning sites on the northern edge of the Bank in September. The waters off Cape Cod seem to constitute a mixing area, with different groups passing at different times of the year.

Stock intermixture is a seasonal phenomenon. Anthony (1977) summarized general information about movements of adult stocks in the Gulf of Maine. Based on results from tagging studies, Wheeler and Winters (1984a, 1984b) and Moores and Winters (1984) found that for fish off southeast Newfoundland there is substantial intermingling of local populations from different bays. This intermingling is mainly due to the northward feeding migrations in summer and southward migrations in autumn to overwintering areas. Populations of these various bays, however, tend to be very discrete in the spring, when movement to spawning grounds occurs. Relationships of populations outside the spawning season are dynamic, with degree of intermingling being partially dependent on size of the population. Off the coast of Nova Scotia, herring begin spawning in August and continue to October. Post-spawners migrate offshore, then move northward or southward (even to Cape Cod). Nova Scotia spawners that move south undoubtedly form part of the mixed stocks taken in the U.S. winter-early spring adult fishery in southern New England. A return migration begins in the spring, and some adults reach the Bay of Fundy by June.

Seasonal distribution of juveniles in the Gulf of Maine have been well studied. Seasonal variations in abundance of juvenile herring in this area are simply a matter of local availability.

During springtime (March-May), juveniles 30-50 mm long become widely distributed in the lower Bay of Fundy, around the entire periphery of the open Gulf (east as well as west), out over the basin, and on the northern and eastern parts of Georges Bank (Bigelow and Schroeder 1953). Sardine-size herring, 12-15 cm long and usually 1- and 2-yr olds, occur in abundance usually all summer east of Penobscot Bay, and particularly in the Passamaquoddy Bay region, where they support the famous sardine fishery. Summer concentrations of juveniles along coastal southwestern New Brunswick and eastern Maine are a mixture of Nova Scotia and Gulf of Maine stocks (Sindermann 1979). Age-1 herring, tagged in western and central waters of Maine during the 3rd and 4th calendar quarters (Creaser and Libby 1986), contributed to commercial catches of age-2 fish during the 2nd and 3rd quarters of the following year east of the area where they were tagged. Age-1 herring tagged in easternmost Maine and western New Brunswick waters during the 3rd and 4th quarters, remained in the same area where they contributed to the commercial fishery for age-2 fish during the 2nd and 3rd quarters of the following year.

Bigelow and Schroeder (1953) and others (Creaser and Libby 1986) have noted that juveniles apparently overwinter along the entire coasts of Maine, New Hampshire, and Massachusetts. The relative quantity of fish overwintering in these areas is unknown because tag recovery information is available only from regions where winter fisheries presently exist. Herring tagged as overwintering juveniles in eastern and western Maine remained in close proximity to the area where they were tagged throughout the following summer. Some herring tagged as summer-feeding juveniles in southwestern Maine overwintered in the region of Massachusetts Bay and off New Hampshire, whereas juveniles tagged at the same time in eastern Maine had a greater tendency to overwinter in eastern Maine.

Reproductive Biology

General Description.--Atlantic herring are unusual among clupeoid fishes in that they are synchronous spawners producing a single batch of eggs (Blaxter and Hunter 1982). Herring, as a species, are also quite unusual in the wide range of seasonality exhibited in time of spawning for different populations. Some populations spawn in spring, others in summer or autumn, or according to locality, populations of both spring- and autumn-spawning herring may occur in the same area. The evolutionary origin and ecological significance of multiplicity of herring spawning locations and spawning times, and relationships of variations in reproductive biology to larval production, have been the focus for much interesting discussion (Cushing 1975; Blaxter and Hunter 1982 for eastern Atlantic herring; Graham 1982; Lambert 1984; Lambert and Ware 1984; Sinclair 1988; and Townsend 1992 for western Atlantic herring).

Spawning Location.--Throughout its range, herring spawn in a variety of water depths from 0-5 m off Greenland to 200-300 m for some populations living in the North Sea. In general, spring spawning takes place in inshore shallows, while summer and fall spawning occur in deeper, offshore waters (Messieh 1980, 1988). In the Gulf of Maine (including Bay of Fundy), spawning takes place in water from about 4-6 m down to about 90 m. Spawning does not usually occur in the littoral zone, nor has herring spawn ever been reported as cast up by the surf onto beaches of New England, a fate that often overtakes it in the Gulf of St. Lawrence. Spawning by herring in deep waters (i.e., as deep as 300 m) has not been observed in western Atlantic localities. In the Gulf of Maine, Bigelow and Schroeder (1953) suggested that deep-water spawning would probably be possible only in the eastern basin where the sea floor is hard, but it was not likely to take place in basins on the western side of the Gulf, where soft, muddy substrates predominate.

Herring spawning has occurred at many places in coastal and near-coastal waters around the periphery of the Gulf of Maine to various shoals and ledges located 5-25 miles off the coast, although there is considerable inter-annual variation in precise location and intensity (Sindermann 1979). Spawning has been inferred at several locations from capture of fully ripe females (Boyar *et al.* 1973a), from egg-bed and larval surveys (Boyar *et al.* 1973a; Cooper *et al.* 1975; Iles and Sinclair 1982; Graham 1982; Townsend *et al.* 1986) and from the presence of eggs on lobster traps (Stevenson, 1984). Spawning occurs from the Canada-United States boundary to about Jonesport (44°32'N), in Canadian waters south of Grand Manan Island, on various shoals and ledges off central Maine, on Jeffreys Ledge, in coastal waters of western Maine, New Hampshire, and Massachusetts, and the west side of Passamaquoddy Bay, and a number of locations on the Nova Scotia coast from Yarmouth to Halifax (Ridgeway 1975). Long-term trends indicate a reduction in spawning sites along the immediate New England coast. Historical locations of spawning grounds in the Gulf and nearby environs were discussed in Bigelow and Schroeder (1953). Present major spawning sites in the Gulf (Graham 1982; Stevenson 1989) are Lurcher Shoal and Trinity Ledges, Jeffrey's Ledge (Boyar *et al.* 1973a) and Stellwagen Bank, Georges Bank and Nantucket Shoals. Minor sites such as Grand Manan, Martinicus, and Pumpkin Ledges, have been reported, but their relative contribution is probably small.

In western Cape Cod Bay, Scherer (1984) reported catching larval herring from October to May, but he thought that larvae collected in this region may have originated primarily from outside Cape Cod Bay. He argued that their long larval period (e.g., 100 or more days) and slow growth rates (e.g., 1.5-2.1 mm/wk; Townsend and Graham 1981) can allow for dispersion over relatively long distances (Boyar *et al.* 1973b). Rocky, pebbly, or gravely bottoms, preferred spawning substrates for herring, are found only in small isolated patches in Cape Cod Bay, particularly off Duxbury Beach, Billingsgate, at Provincetown, and at the southern tip of Stellwagen Bank, which was identified as a major spawning area for herring (Graham *et al.* 1972).

On Georges Bank, spawning centers have shifted from historic sites on the northeastern side, where 86% of the total spawning occurred in 1974, to Nantucket Shoals, where in 1976, 97% of the spawning took place (Cohen and Lough 1983). Several reasons possibly accounting for this apparent shift in distribution were discussed by Lough *et al.* (1980) and Anthony and Waring (1980).

Spawning Substrate.--After eggs are released by the female they sink to the bottom, where they are fertilized and remain until hatching. Eggs are spawned on rock, pebble, gravel or shell substrates, to some extent on clay, and probably never, on soft mud substrates. No eggs were found on sandy bottoms in the spawning area studied by Messieh (1988). Eggs are adhesive and will stick in layers or clumps to sand or clay, seaweeds, stones, or to any other objects on which they chance to settle. They are often found massed on net warps, anchors, and anchor ropes.

Direct observations of spawning sites reveal that herring choose a shell, gravel or bedrock substrate which ensures stability of deposited eggs (Messieh 1988). Using a submersible, Caddy and Iles (1973) examined sites used by autumn-spawning herring on Georges Bank in water averaging about 40 m in depth (Drapeau 1973). Spawn was observed on gravel patches devoid of sand, and tidal currents were relatively intense (1.2 m/s). The high energy environment of spawning beds with strong currents prevented silt accumulation that could smother eggs and provided better circulation to supply oxygen and remove accumulated metabolites (Hempel 1971). Three of six grounds used by autumn-spawning herring on Jeffrey's Ledge were characterized by very rough boulder-rock substrate, with slope gradients ranging from 0-40° (Cooper *et al.* 1975). Bottom water currents throughout a tidal cycle at the ledge ranged from 0-2 km/hr, with the average about 0.3-0.5 km/hr. Off southwest Wales (Clarke and King 1985), herring deposited eggs on substrates comprised of nearly equal amounts of coarse shell and stone gravel 2-5 mm in diameter. Shell substrate was composed of broken pieces of topshell, oysters, and other bivalves. Finer shell gravel and sand also received some spawn, but amounts deposited on these were substantially less dense than what occurred on the coarser substrate.

Egg deposition sites of spring-spawning herring in Canadian waters examined by divers indicated a direct relationship between intensity of egg deposition and degree of algal cover. (Tibbo *et al.* 1963; Pottle *et al.* 1980, 1981; Messieh *et al.* 1985). Messieh (1988) reported that correlations between egg densities and macrophyte abundances were not statistically significant for three of four cases he examined. Most eggs were found attached to bottom vegetation at depths of 0.9-4.3 m with greatest egg concentrations occurring at 1.4-4.0 m. In some areas, proportionally larger concentrations of eggs were found on *Phyllophorus* sp. and *Fucus* sp., than on Irish moss *Chondrus crispus* found in the same area, suggesting a preference for these algae. Whereas, in other areas, a high proportion of eggs were attached to Irish moss, which was probably due to widespread distribution of the plant rather than to any behavioral preference by herring (Messieh 1988).

A spawning area used by spring-spawning herring in the southwestern Gulf of St. Lawrence (Messieh *et al.* 1985) was extensive and covered some 2,200 m of bottom area along the shore with a mean width of 400 m (estimated total area 880,000 m^2). The seaward boundary of the bed corresponded approximately to the offshore limit of macrophyte cover. Herring eggs were densely distributed over a depth range of 0.8-3.3 m (mean low water). Substrates within the area consisted of sandstone bedrock and rubble with patches of sand. Irish moss (*Chondrus crispus*) and, to a lesser extent, rockweed (*Fucus* sp.) were the major macrophytes in this area. Only about 54% of the eggs were attached to macrophytes. Intensity of egg deposition varied from a few scattered eggs to patches that were 4-5 layers deep, and was significantly correlated with algal abundance. Mean density of eggs over the entire bed about 10 d after spawning was nearly 25,000 eggs/m^2. Combining estimates of egg deposition with fecundity estimates, these authors calculated that the total number of eggs on the spawning bed were produced by ca. 930,400 mature herring with an estimated weight of about 190 MT.

Spawning Seasonality.--Throughout its range, at least one population of herring is spawning during any one month of the year, with each population having a different spawning time and place. Off the Atlantic coast of the United States, the major herring spawning event occurs from late August through November (Boyar *et al.* 1973b; Colton *et al.* 1979). Neither Scattergood (1952) nor Bigelow and Schroeder (1953) found evidence of spring spawners in the Gulf of Maine. Subsequent studies (Watson 1964; Anthony and Waring 1980; Kornfield *et al.* 1982) supported their conclusion, although others (Tibbo *et al.* 1958; Boyar 1968; Boyar *et al.* 1973b) suggested some indication of minor spring spawning occurring in the Gulf of Maine, but that its contribution was probably negligible compared with the vast volumes of eggs and larvae produced during late summer and autumn spawning in this region. Throughout the Canadian Atlantic area, herring are probably spawning somewhere every month from April to November, with each stock having its own characteristic spawning time (Scott and Scott 1988). Both spring-spawning and summer-fall spawning schools of herring were reported formerly in the Bay of Fundy (Scott and Scott 1988). Spring spawners were present in the south (Nova Scotia) side of the bay from Bier Island at the mouth in as far as Digby Gut, and also in the Parrsboro region on the New Brunswick shore near the head of the bay, with spawning occurring during April and May. But spring spawners never seem to have been very numerous, and it is not known whether any herring now spawn in the bay before summer (Scott and Scott 1988). Spring-spawning as well as autumn-spawning herring have also been reported by fishermen along the west coast of Nova Scotia, although springtime spawning activity in this region has not been verified (Scott and Scott 1988).

Kelly and Stevenson (1985) noted that a major distinguishing feature of herring populations that spawn at extreme ends of the U.S. Gulf of Maine coast is the difference in their spawning times. There is a generally southwest progression of the onset of spawning time, from late August off Nova Scotia to September-October on Georges Bank. Spawning begins in eastern Maine waters during middle to late August and apparently continues into October (Moore 1898; Stevenson 1984; Graham and Sherman 1984), with the heaviest runs of summer-autumn spawners usually arriving in July, August, and September. Spawning begins on Jeffreys Ledge in middle to late September (Cooper *et al.* 1975; McCarthy *et al.* 1979) and, judging from the presence of fully mature fish in October, continues at least into November. Further south in Ipswich and Massachusetts Bays spawning occurs chiefly during October (Allen 1916); while in the vicinity of Woods Hole spawning takes place in late October and early November.

Larval surveys to define location, timing, and extent of spawning, and distribution of larvae in the coastal transboundary areas (from Mt. Desert Isle, eastern Maine, to New Brunswick) reported that there has always been some spawning along the Maine coast and around Grand Manan Island, NB, and this spawning undoubtedly supplies part of the recruitment to the juvenile fishery (Chenoweth *et al.* 1989). The widespread spawning south of Grand Manan and along the Maine coast previously reported (Moore 1898; Bigelow and Schroeder 1953; Huntsman 1953) has since been confined to smaller areas in eastern Maine, but still occurs there in a constant and predictable manner (Stevenson 1984). Surveys showed two separate areas of larval dispersal. Easternmost stations contained low densities of large larvae that were assumed to be part of the annually occurring larval aggregation off Nova Scotia. High densities of small larvae west of Grand Manan indicated spawning in this region was confined to a small area southwest of Grand Manan and along the eastern Maine coast. Larvae west of Grand Manan clearly originated from spawning beds in the shoals southwest of Grand Manan and in Maine's coastal waters off Machias Bay and Cutler Harbor. The abrupt eastern margin characteristic of the coastal Maine larval aggregation persisted for the two months of the survey. The same eastern discontinuity has been shown in larger scale surveys (Iles *et al.* 1985) to co-occur annually and to persist until November. There does not appear to be immigration of herring larvae into eastern Maine waters from spawning in the Bay of Fundy and off southwest Nova Scotia. This evidence supports the view of Graham *et al.* (1984) that herring larvae in coastal Maine waters result from local spawning. This unique larval distribution confirms that the eastern Maine-Grand Manan spawning group is autonomous and has its own separate larval distribution. Observations on spawning areas southwest of Nova Scotia led Iles and Sinclair (1982) to the conclusion that larvae remain in the area of spawning beds for considerable lengths of time, however, studies of herring larvae in eastern Maine waters have concluded that there is transport of larvae in a westerly direction away from the spawning areas (Graham 1982; Townsend *et al.* 1986). Larvae from these spawning grounds of eastern Maine are known to be transported at least as far south as the mid-coast of Maine by the prevailing southwesterly surface current (Graham 1982; Townsend *et al.* 1986; Graham and Townsend 1985), and are distributed along the coast and overwinter in inshore estuaries, embayments and coastal waters (Graham 1982) and in offshore waters of the Gulf (Townsend 1992). However, dispersal from the spawning ground seems more complex than a simple stream of larvae drifting westward into waters where a greater density of food organisms occur (Townsend *et al.* 1986). Chenoweth *et al.* (1989) indicated changing patterns of larval dispersal ranging from persistence within the general vicinity of spawning to a rapid westward movement away from the spawning area. Larvae appeared to remain aggregated during this dispersal period and did not spread out like a plume from a point source. Dispersal of larvae from spawning grounds is discussed further under Recruitment Dynamics.

Although overall sex ratios of spawning herring in samples from Georges Bank and southern Nova Scotia were ca. 1:1 (Pankratov and Sigajev 1973; McKenzie 1964). Early arrivals at spawning grounds are reported to be predominantly male fish. Therefore, the fact that males mature earlier in the season than females (Blaxter and Holliday 1963; Hay 1985) suggests a link between annual maturation cycle and arrival at the spawning grounds. Lambert (1987) suggested that a "fine tuning", that is, age-specific annual ripening of the gonad, determines duration and pattern of spawning around the mean day of arrival. Timing of initiation of spawning in herring seems to be, in a general sense, governed by physical factors, with temperature perhaps being the most important (Berenbeim and Sigaev 1977; Ware and Henriksen 1978; Messieh 1978; Lambert 1987). Warmer temperatures experienced by pre-spawning herring lead to early spawning, whereas cooler temperatures delay spawning. The relationship between bottom temperatures and arrival time on spawning grounds was demonstrated for herring in the Gulf of St. Lawrence (Messieh 1987, 1988) and for herring on the Georges Bank and Nantucket Shoals areas (Grimm 1983).

Relative size and age, and previous spawning experience also influence the timing of spawning by herring participating in a spawning event. In years when average length of spawning fish is relatively larger, spawning tends to occur earlier than in years when fish are smaller. For most herring stocks, the largest (and oldest) fish arrive on the spawning grounds to spawn first and the smallest, first-time spawners, arrive last (Hodgson 1927; Lea 1929; Smith 1938; Runnström 1941a, 1941b; Tibbo 1949; Jean 1956; Day 1957; Blaxter and Hempel 1963; Boyar 1968; Dragesund *et al.* 1980; Lambert 1987). Although temperature was found to explain about 63% of the variability of the mean day of arrival on the spawning ground for fish spawning in the Gulf of St. Lawrence (Lambert 1987), fish length accounted for an additional 1-5% of the variation. For both spring- and autumn-spawning herring in the Gulf of St. Lawrence, herring arrived and deposited eggs on spawning grounds in decreasing order of age and length (Lambert and Messieh 1989).

Spring spawners in the Gulf of St. Lawrence (Messieh 1988) arrived on spawning grounds in late April or early May, and autumn spawners arrived in August. Ware and Henriksen (1978) examined spawning runs off Escuminac, NB, in the Gulf of St. Lawrence, where some fishermen believed the biggest runs occurred on full moons. Instead, results of that study found that herring could occur on the spawning grounds at any phase of the moon. High catches and full moons coincided with no more frequency than by chance alone.

How different spawning times for herring populations have evolved has been the source of much speculation and study (Iles 1964; Cushing 1967, 1969, 1973, 1975; Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair 1988). Initially, timing was thought to be linked to primary production cycles (Iles 1964; Cushing 1967) but, because time of spawning tended to be less variable than timing of primary production blooms, Cushing (1975) postulated that larval survival and subsequent extent of recruitment might depend on closeness of the match between the two events (the "match-mismatch" theory). This attractive "match-mismatch" theory of Cushing was challenged by Sinclair and Tremblay (1984) who, developing further the larval retention hypothesis of Iles and Sinclair (1982), suggested that timing of spawning of herring is determined by two other constraints. These are that herring larvae of a particular population develop within a discrete retention area at a rate attuned to the particular oceanographic situation of that area, and secondly that metamorphosis only takes place within a specific period of the year. Timing of spawning and size of eggs are thus geared to achieve metamorphosis at the appropriate time under certain specific and reasonably predictable environmental circumstances. Sinclair (1988) further discussed these topics in presenting his member/vagrant hypothesis.

Spawning Behavior.--Direct observations of herring behavior during spawning in the North Atlantic are limited (Blaxter and Hunter 1982). Haegele and Schweigert (1985) reviewed the subject for both Atlantic and Pacific herring. Hay (1985), using a beach seine, took small samples on the spawning grounds as fish were spawning. Almost all males were totally spent, but most females were partially spent, suggesting that males probably initiated the spawning act, after which females deposited their eggs on the substrate. Direct observations of spawning *in situ* provided evidence that female herring do not release their eggs until males have released their milt (Messieh 1988). This sequence in the spawning act ensures proper fertilization of the eggs before they adhere to the substrate. Using underwater video to study spawning behavior, Messieh (1988) observed milt on the spawning bed prior to deposition of eggs, thereby providing evidence that females do not release their eggs until the milt is released. A few hours after the milt was discovered, the school of spawning fish was seen moving in a highly organized manner about 30 cm above the bottom. The school was watched swimming in the milt for about 4 hr while the research vessel was still in the center of the milt patch. The vessel was allowed to drift at about 4 km/h so that the substrate could be searched, but no spawn was detected during this time. Deposition of eggs was observed the next day, however, and spawning was completed. For the first time during spawning bed surveys, spawning by herring was observed during daytime.

Spring-spawning herring often arrive at the spawning grounds in runs or waves. Discrete batches of eggs deposited by these waves of spawning herring give rise to a succession of larval cohorts (Hourston 1958; Lambert *et al.* 1982; Dempsey and Bamber 1983). No pattern of rhythmicity has been discerned in autumn-spawning fish (Lambert 1984), and, in contrast to spring-spawning fish, it has been suggested (Bigelow and Schroeder 1953; Jean 1956) that fall spawners leave the spawning grounds and move to deeper water as soon as they have spawned. Lambert (1984) suggested that segregation into runs or spawning waves was probably more commonplace in herring spawning groups (i.e., spring, summer, and autumn spawners) than has been observed.

Spawning Temperatures and Salinities.--In the Gulf of Maine region, autumn-spawning herring usually reproduce at relatively high temperatures (10° to 15°C) and at high salinities. Around Grand Manan and in the northern part of the Gulf, practically all spawning is carried out in waters of about 8-12°C (Bigelow and Schroeder 1953). Spawning in southern Massachusetts Bay and along Cape Cod, where autumnal cooling of surface waters is not as rapid as it is farther north, may take place in slightly warmer waters (12°-14°C). Temperatures of 17.5°C at which autumn spawning occurred in the Gulf of St. Lawrence (Messieh 1988) appear to be near the optimal temperature known for herring (Blaxter and Hunter 1982), whereas spring temperatures of 3.7°C in the same area are near the lower end of the range of spawning temperatures (Jean 1956).

In the Gulf of Maine, herring spawn at salinities ranging from ca. 31.9-33.0 ppt. They do not spawn in brackish water within the limits of the Gulf, although other populations are known to do so at the mouths of certain European rivers in water that is nearly fresh (Bigelow and Schroeder 1953).

Fecundity.--Fecundity of individual female herring varies according to age and size of the female, as well as to the stock to which the female belongs. At the population level, there is a generally positive relationship between adult stock biomass and egg production (Hempel 1971). Fecundity values for individual females range from about 12,000 to upwards of 260,000 eggs per spawning. In sexually mature fish, gonads just prior to commencement of spawning may represent about one-fifth of the total fish weight.

In general, larger females produce more eggs, up to a maximum age (varying with population), and then egg number declines with increased age (Scott and Scott 1988). Fecundity among Georges Bank, southwestern Gulf of Maine, and Nova Scotia autumn-spawning populations are approximately similar (Perkins and Anthony 1969). Eggs per female from this region ranged from 17,000 to 141,000 for 25-33 cm fish respectively. No significant differences in fecundity or egg size were found among the three stock complexes studied. A length-specific fecundity estimate (Kelly and Stevenson 1985) for herring from three spawning areas in the Gulf of Maine indicated that, in general, mean fecundities increased with fish size, ranging from ca. 35,000 eggs in 24 cm females to nearly 191,000 in fish measuring 35 cm. For spring, summer, and fall spawners in the Gulf of St. Lawrence region, egg numbers per female ranged from 23,000 to 261,000 (Messieh 1976). In the Newfoundland area, number of eggs was estimated at 12,750 for females 27.8 cm TL to 241,630 eggs for those 37.0 cm TL (Hodder 1972). Other studies on fecundity of western Atlantic herring include those by Yudanov (1966) and Draganik and Rast (1970).

Variations in fecundity among spawning populations of herring have been attributed to both genetic and environmental factors (Blaxter and Holliday 1963; Parrish and Saville 1965; Hodder 1972; Messieh 1976). Comparative fecundity data, by lengths, for females from different spawning populations in the Gulf of St. Lawrence and Nova Scotia waters indicate that in general, spring spawners produce fewer eggs (up to 50% less) than do autumn-spawning females of comparable size (Hodder 1972; Messieh 1976). Herring fecundity also varies inversely with egg size, which is related to egg weight and number (Hempel and Blaxter 1967; Parrish and Saville 1965; Messieh 1976; Blaxter and Hunter 1982). Lower fecundity of spring spawners, for example, is related to an increase in egg weight due to an increase in yolk size. Possibly, increase in yolk size is an adaptation for more energy in order for young to survive the lower water temperatures of spring (Messieh 1976).

Significance of seasonal egg size differences in herring stocks has been a source of speculation for many years (Gamble *et al.* 1985). The most obvious direct effect is on the fecundity of the various stocks (Hempel and Blaxter 1967; Burd and Howlett 1974).

Explanations have tended to center on the particular ecological advantages of producing fewer but larger eggs in the winter-spring period as opposed to the more abundant small eggs spawned in late summer-autumn (Blaxter and Hempel 1963; Hempel 1965; Mann and Mills 1979). It is believed that large eggs produce larvae able to survive longer in the poorer feeding conditions of the spring season, while greater fecundity in autumn-spawning populations serves to counteract greater predation pressure on larvae at that time. Gamble *et al.* (1985) could not refute any of the hypotheses relating egg size differences to ecological advantage in terms of larval survival at low food levels (Blaxter and Hempel 1963) or predation and fecundity (Ware 1975b). The spring-spawned herring larva grows rapidly and achieves metamorphosis quickly, while the autumn larva remains as a larva for a prolonged period. Results of the study by Gamble *et al.* (1985), however, suggested that there is selection for a check in development in autumn larvae. Autumn spawners producing small eggs may therefore have a selective advantage, since early development is prolonged and pre-winter metamorphosis is thus precluded. This hypothesis tends to support the suggestion by Sinclair and Tremblay (1984) that size of eggs at a particular spawning time is determined by the need for herring larvae to metamorphose within a more limited period of the year. Sinclair and Tremblay (1984) concluded that a simple interpretation consistent with their larval-retention hypothesis was that a "poor" larval retention area and concomitant long larval phase results in a greater accumulative population mortality for the larval phase. Thus, autumn-spawning populations have higher fecundity.

Inter-annual variations in the size-fecundity relationship of herring occur within a spawning population. Annual variations in fecundity at a given length have been noted for female herring in the Dogger and Downs spawning populations in the eastern Atlantic (Bridger 1961). Lett (1976) reported an increase in relative fecundity of herring from the Gulf of St. Lawrence between 1967 and 1970. In the eastern North Atlantic, low fat content of pre-spawning females was thought responsible for reduced number of eggs produced in a given size group of females, indicating that poor food production not only affects growth rate, but it also has the potential to lower fecundity as well (Hempel 1971).

Variations in relative fecundity of a spawning population may also respond to density-dependent factors (Kelly and Stevenson 1985; Bailey and Almatar 1989). Increased fecundity at a given size for females within populations drastically reduced by fishing and other causes of mortalities may represent a way by which herring respond to reduced population size. Density dependence has also been invoked to explain observed changes in fecundity of herring on Georges Bank between 1963-64 and 1968 (Anthony and Waring 1980) and before and after 1973 in the Gulf of St. Lawrence, the Scotian shelf and Georges Bank (Messieh *et al.* 1985). As Kelly and Stevenson (1985) noted, absence of temporal stability in fecundity estimates of spawning populations of herring underscores the importance of obtaining current data for stock discrimination and assessment purposes.

Size and Age at Maturity.--A median size at maturity of 25.4 and 25.3 cm TL, respectively, was recorded for female and male herring taken off the northeastern coast of the United States during recent autumn trawl surveys (O'Brien *et al.* 1993). Median age at maturity was 3.0 yr for females and 2.9 yr for males. Maturity at age (NEFC 1990) is similar to that obtained for Gulf of Maine herring from monthly commercial sampling during 1985-89 (0.39 of age-3 fish, 0.98 of age-4 fish, 1.00 of fish age-5+). Extensive examinations of adult herring from Georges Bank, the Gulf of Maine, and southern Nova Scotia during the 1960s, led Boyar (1968) to the conclusion that herring in those areas spawned at age-4 and at an average total length of

27.5 cm. Fewer herring in that study spawned at age-3 and at sizes around 26.0 cm. Sinclair *et al.* (1982b) noted a positive relationship between juvenile growth rates and L_{50}. Winters (1976) reported decreases in age at 50% maturity with decreasing adult biomass for herring in the Gulf of St. Lawrence, suggesting that density-dependent processes may influence maturation rates of herring.

The percent contribution of age-3 fish to spawning stocks is variable from year to year (probably related to abundance of the particular year-class being recruited). In 1960 for example, age-3 fish represented 62% of the Georges Bank stock. Livingstone and Hamer (1978) reviewed data on age at maturity, and found that from 1960 to 1965 about 29% of age-3 herring on Georges Bank and about 9% of Gulf of Maine age-3 herring were mature. For the period 1966 to 1970, 34% of age-3 herring from these areas were mature. Early maturation (at age-3) of the 1970 year-class was also reported by Dornheim (1975). Samples available to Livingstone and Hamer (1978) during the period 1973-77 were too small to calculate meaningful percentages, but from the limited data available, they were unable to detect any change in age and length at which 50% of herring were mature (M_{50}). However, they did find a decrease in relative numbers of age-3 herring in samples, and also an increase in the mean age and length of fishes in the spawning population.

Eggs.--Eggs are demersal, adhesive, and 1.0-1.4 mm in diameter depending on size of parent fish and also, perhaps, on the population of the fish involved. Eggs have a segmented yolk, a wide perivitelline space, and lack oil globules (Fahay 1983).

Development (From Bigelow and Schroeder 1953; Fahay 1983).--Development of herring embryos can occur over a wide range of salinities (Holliday and Blaxter 1960; McQuinn *et al.* 1983). Developmental rate is governed predominantly by, and is inversely related to, temperature (Messieh 1988). Time to hatching may require as long as 40 d at 4-5°C, 15 d at 6-8°C, 11 d at 10-12°C, and 6-8 d at 14.4-16.0°C, with 10-15 d being an average incubation period for autumn-spawned herring in the Gulf of Maine (Bigelow and Schroeder 1953; Messieh 1988). Hatching success is also temperature dependent. In experimental situations all eggs maintained at 15°C hatched, but none hatched at 0-5°C, and all eggs held at 20°C died (MacFarland 1931).

In the Gulf of St. Lawrence, spring-spawned eggs required about 30 d at 5°C to hatch. Incubation times measured *in situ* indicated that spring-spawned eggs at bottom temperatures of 6.5-9.3°C in the southwestern Gulf of St. Lawrence required 14-16 d (Messieh *et al.* 1985) to hatch, and 17-20 d to hatch at temperatures of 6.0-7.5°C (Messieh 1988). Fall-spawned eggs develop more quickly in the warmer waters present during this spawning season. Estimates of time to hatching range from about 10 d at 15°C (Scott and Scott 1988) to 11 d at 10°C in waters off Nova Scotia (Jean 1956).

The pelagic larval phase is relatively long in herring, varying from 3-11 mo (commonly six) for different populations (Sinclair and Tremblay 1984). Herring are about 5-10 mm total length at hatching, and have a small yolk sac and pigmented eyes. Yolk-sac absorption occurs at ca. 10 mm. Autumn-spawned herring larvae in the southern Gulf of St. Lawrence (Messieh *et al.* 1987) require an estimated 15-17 d from time of yolk-sac absorption to the exogenous feeding stage. Larvae are elongate and have a long straight gut, with the vent always situated posterior to the vertical through the dorsal-fin base. Preanal length is ca. 80% of total length. There are 47 preanal myomeres until larvae reach sizes >20 mm TL, when preanal myomere numbers are reduced to 41-46. Flexion occurs at 16-17 mm, and transformation takes place at about 30 mm.

An air bladder forms at 10-15 mm, but is not noticeable until larvae are about 30 mm. Sequence of fin formation in developing fishes is: pectoral fins form first as bud, but are not completely formed until transformation; dorsal fin forms at about 10 mm; anal fin at about 16 mm; and both are complete by transformation; principal caudal rays complete at about 20 mm; pelvic fins form between 20-30 mm, and migrate posteriorly at transformation.

Metamorphosis into juveniles is a gradual transition to adult characteristics. This is generally achieved by the time fish are 45-55 mm, although some studies report metamorphosis occurring at lengths as small as 30-35 mm (Blaxter and Staines 1971; Boyar *et al.* 1973b; Ehrlich *et al.* 1976; Doyle 1977; Saila and Lough 1981). At metamorphosis, the developing fish resembles a juvenile herring, the body deepens, scales and pigment appear in the skin, and hemoglobin is present in the blood. While spawning of various populations of herring in the North Atlantic can occur throughout the year, metamorphosis from larval to juvenile stage is restricted to a period from April to October (Sinclair and Tremblay 1984). Consequently, relative lengths of developmental periods of larvae are dependent upon spawning time. In the northwest Atlantic, herring larvae from large winter-spring spawned eggs metamorphose within 3-6 mo, while those from smaller summer-winter eggs overwinter as larvae and metamorphosis does not occur until 7-8 mo later.

Pronounced behavioral and physiological changes accompany metamorphosis. The most obvious change in behavior is the development of schooling responses (Sindermann 1979; Gallego and Heath 1994a). In herring, metamorphosis appears to be a physiologically demanding event accompanied by an increase in hemoglobin synthesis as a result of increased activity (De Silva 1974). Fat levels also increase prior to this life history transformation (Marshall *et al.* 1937). These and other related growth processes perhaps explain the seasonal restriction of metamorphosis to the productive period of the year (Sinclair and Tremblay 1984).

Distinctive Characteristics of Larvae.--Atlantic herring larvae are unique among clupeid larvae occurring in the Gulf of Maine in that their myomere count is much higher and the anal fin forms relatively late in development (Fahay 1983). Clupeid larvae are very slender and can easily be distinguished from larvae of all other Gulf of Maine fish of similar form (e.g., sand lance, smelt, or rock eel) by location of the vent, which is situated more posteriorly and closer to the caudal-fin base.

Larval Ecology and Behavior.--In the Gulf of Maine, larvae of autumn-spawned herring are planktonic for about 7 mo. Results of extensive surveys of distribution and abundance of herring larvae in U.S. and Canadian waters were summarized in Sindermann (1979). Larvae from spawning in the southwestern Gulf of Maine (Cape Elizabeth, Jeffrey's Ledge, and Stellwagen Bank) were first seen in late September and early October. Larvae from an undetermined spawning source were also detected off Mount Desert Island in early September. Dispersal was shoreward and southwestward along the coast. Larvae from spawning at Trinity Ledges and Lurcher Shoals appeared during the latter part of September, and early drift was generally northward along the eastern side of the Bay of Fundy. Dispersal was almost entirely shoreward (Graham *et al.* 1972).

On the northern edge of Georges Bank, larvae were first detected during the latter part of September. By December they were widely dispersed over the Bank, with some indication of southwesterly drift. Larvae from spawning on Nantucket Shoals west of Great South Channel were detected in early November. Dispersal was southwestward, and also northeastward to Georges Bank. Overwintering concentrations of larvae exist on Georges Bank until April (and even May in some years), and metamorphose into juveniles at that time (Sindermann 1979). Postlarval movements are uncertain. Boyar *et al.* (1973b) summarized opinions about the movement of larvae spawned on Georges Bank noting that several earlier authors (Tibbo *et al.* 1958; Bumpus 1960) thought that progeny from Georges Bank spawners could contribute to coastal Gulf of Maine stocks, while others (Colton and Temple 1961) felt that this would be unlikely. Both groups mostly agreed that progeny of Georges Bank spawners were unlikely to be carried northward into the Bay of Fundy (Bigelow 1927; Day 1958a, 1958b; Tibbo and Legaré 1960; Bumpus 1960). Boyar *et al.* (1973b) suggested strongly that the major distribution of larvae resulting from Georges Bank spawning most probably remained in the area of the Bank and its contiguous waters. They also concluded that larvae from spawning in western and central parts of the Gulf of Maine appear to be restricted to those waters; the majority of larvae from Nova Scotia spawning either remain near spawning sites or are carried into the Bay of Fundy; and some larvae from the Bay of Fundy drift to eastern coastal Maine, and may even be carried as far south as Cape Cod.

In the Gulf of Maine, larvae are initially concentrated in the upper water column immediately over the spawning areas (Lough 1975), but then are dispersed by surface and near-surface water currents. Circulation of water masses with subsequent distribution of larvae is also partially influenced by bottom topography (Graham *et al.* 1972). In open waters of the Gulf, larval movements depend principally on existing currents, and some larvae are transported from the spawning-grounds to coastal estuaries. Transport times to estuaries can be rapid. Comparison of spawning dates and arrival times for predominant cohorts suggested that larvae reached Sullivan Harbor about 3 wk after hatching (following an egg incubation time of about a week) and to the Sheepscot River in about 5 wk (Stevenson *et al.* 1989). These transport times represent approximate straight line velocities of 5.2 and 6.9 km/d over distances of 110 and 240 km. Previous estimates of larval transport times to Sullivan Harbor (Graham and Townsend 1985) for seven cohorts averaged 14 d (range 5-30 d); a single cohort reached the Sheepscot in 35 d.

Iles and Sinclair (1982) developed the "Larval retention hypothesis" to explain stock structure for herring using information on larval distribution patterns. This hypothesis was based, to a large degree, on repeated observations in the western Atlantic that larvae of herring populations do not drift passively in response to the residual surface layer circulation, but rather they retain themselves for at least several months in relatively limited geographical areas having specific oceanographic characteristics. According to the hypothesis, existence of discrete herring stocks (= populations), the location of spawning sites to which they home, and the relative (maximum) stock size are determined by number, location, and extent of geographically stable retention areas in which larvae can remain aggregated for the first few months of life (Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair and Iles 1985). Iles and Sinclair (1982) argued that well mixed zones and fronts acted as the physical basis for the retention of larvae and a focus for the homing instinct in adult herring. They proposed that retention was not passively maintained by circulation features, but rather it was achieved actively probably through behavioral responses of the larvae, such as vertical migration in relation to tidal currents. Stephenson and Power (1988, 1989) tested aspects of the larval retention hypothesis using the area of high larval density off southwest Nova Scotia, which encompasses the major spawning areas of herring in the Gulf of Maine (particularly off Trinity Ledge, German Bank, Seal Island), and from which most of the larvae are presumed to be derived. Spawning in this area has traditionally peaked about the end of August (Sinclair and Tremblay 1984). The patch edge corresponded loosely with the margin of vertically stratified water; larvae remained within the well-mixed, uniform water mass to the east of what is presumed to be a tidally induced front. Diel patterns of vertical movements of the larvae were evident. Larval densities were sometimes highest in upper layers by day, but differences in patterns occurred between years at the same site indicating that behavior at one location may vary temporally. Larvae occurred throughout the water column, including considerable numbers close to the bottom. Concentration of larvae near the bottom would result in a great reduction in, and possibly avoidance of, the influence of major tide-induced currents that diminish with depth. This pattern of depth distribution would provide a mechanism for retention in the area. If these movements were made primarily to achieve or maintain position (as proposed by Iles and Sochasky 1985), it would have conformed to a tidal schedule. Stephenson and Power (1988, 1989) instead concluded that the migratory pattern followed a diel rather than a tidal cycle, which indicated that it was undertaken in relation to some factor (such as prey availability) other than in response to tidal cycles. Chenoweth *et al.* (1989) further modified the larval retention hypothesis by suggesting that although a significant portion of those larvae spawned in the eastern Gulf of Maine may be retained in the vicinity of the spawning grounds at least until October, retention near the spawning ground is incomplete because around this time the hydrographic structure delineating the frontal boundary between the tidally-mixed and stratified areas disappears, and larvae are then able to disperse.

Throughout the fall (September-November) and shortly after hatching occurs in the various coastal spawning areas (Townsend *et al.* 1989), some portion of the population of summer- and autumn-spawned herring larvae congregate in inshore estuaries and embayments along the Maine coast. Here, herring larvae are among the dominant species of ichthyoplankton collected in the estuaries (Chenoweth 1973). Studies of localized movements of larvae in coastal and estuarine waters of Maine indicated that larvae sampled within 10 miles of shore (50 fathoms) generally moved shoreward all along the coast (Graham *et al.* 1972). Coastal circulation, coupled with diel migrations of the larvae that are counter to existing near-surface current systems, transport larvae during their shoreward migration into the estuaries during fall, winter and spring. Populations of larvae overwinter in the Gulf of Maine, with principal concentrations occurring close to shore and in the estuaries (Townsend *et al.* 1989; Townsend 1992). In some years, inshore catch rates are initially high in the fall, but decline rapidly, presumably due to high mortality, and remain low through February. Several cohorts (up to as many as seven), spawned primarily from late July through October, enter inshore locations in waves during the fall. Some larvae derived from this spawning event remained in coastal waters in the fall and entered the estuary later in winter, at the same time as smaller (10-25 mm) larvae from a previous cohort were dying (Stevenson *et al.* 1989).

Lambert (1984) noted that spacing of larval cohorts has some interesting ecological consequences that may enhance spawning success by increasing chances for larval survival. For example, at any particular moment cohorts are distinct or separated on the basis of size, which can be thought of as separation in space. Also, there is a separation in time between release or origin of each cohort. This confers the advantage of temporal spacing of the larvae thereby avoiding subjection to the same predation levels, or to exploitation of the same food supply.

Densities of larvae inshore following the fall peak in abundance drop off to very low levels in mid-winter (late December and January), before a second group of fall-spawned larvae appears inshore in the spring (February through April), thus giving a bimodal abundance distribution with time (Shaw 1981). During springtime, larvae are abundant in all coastal and inshore sections along the coast of Maine (Stevenson *et al.* 1989). Employing strontium and calcium ratios to infer temperatures experienced by individual fish during development, Townsend *et al.* (1989) determined that the peak of herring larvae occurring inshore during spring represented larvae that had overwintered offshore in the Gulf of Maine. Apparently, larvae that had entered the inshore nursery areas in the previous fall did not survive through the winter. Causes of winter mortality for larvae occurring inshore are not known definitely, but may include exposure to lethal temperatures, predation by any of a suite of invertebrates (Bailey 1982, 1984; Bailey and Batty 1983; Bailey and Yen 1983; Brewer *et al.* 1984; Möller 1984), as well as limitations in food supply. Interestingly, springtime aggregation of older larvae in inshore waters of Maine often occurs coincident with the time of intense inshore phytoplankton and zooplankton blooms (Townsend 1984). Shortly after the onset of springtime, larvae metamorphose to juveniles. It has been suggested that the number of larvae surviving to this important life history transition may be closely coupled to annual recruitment success (Sinclair and Tremblay 1984).

Vertical Migration of Larvae.--Although vertical distribution of herring larvae has been extensively studied since the mid 1920s (Wallace 1924; Johansen 1924), migratory behavior of this species is still poorly understood (Munk *et al.* 1989). Larval herring are light sensitive and generally exhibit diurnal vertical migratory behavior, rising closer to the water surface by night than by day (Blaxter and Hunter 1982). On bright days, herring larvae also tend to seek deeper waters than on dull days (Graham and Sampson 1982). The overall pattern of vertical migration for herring larvae has been described as one which appears to be a semidiurnal migration to the surface at dawn and dusk with larvae dispersed, but concentrated, above the thermocline at night, and at a depth of 20-40 m during the day (Batty 1987, 1994).

The response to light is clearly an important and complex aspect of larval herring behavior (Wales 1984), and it has long been recognized that light plays an important role in directing migratory behavior of these larvae (Woodhead and Woodhead 1955; Wood 1971). In the laboratory, larvae remain at the water surface of a vertical tube in darkness and, as light intensity is increased, they move away from the surface (Blaxter 1973). Replicate experiments (Wales 1975a, 1975b) with eyeless larvae found the same migration, indicating that responses of larval herring to light is controlled by the interaction of more than one type of photoreceptor. Woodhead and Woodhead (1955) showed that changing light intensity may control vertical migration by changing the orientation of swimming movements of larvae from mainly vertical in low-light intensities, to horizontal in high-light intensities. Intermittent vertical swimming in response to incident light levels allows larvae to move vertically through a large depth range, with the possibility of searching or testing water chemically for presence of prey. This mechanism together with the negative buoyancy of the larvae would cause them to move downward during daytime until they reached a depth at which sufficient vertical swimming is stimulated to allow them to hold station. This behavior continues in complete darkness, and as a result, larvae may occur at greater density near the surface at night, but they are also dispersed throughout a wide range of depths (Batty 1987). A fact borne out by the observation that herring larvae in the sea are not always found at the surface at night, but sometimes are distributed evenly over a wide range of depths (Zijlstra 1970; Wood 1971).

As larval size increases, vertical displacements are known to increase and take on a diel character (Wood 1971; Seliverstov 1974). Some researchers have reported that larger larvae were concentrated near the surface at night, whereas in other instances, the same distribution was observed in the daytime (Graham and Sampson 1982; Courtois *et al.* 1982). Furthermore, in some situations, these two behaviors (concentrating at the surface or concentrating at depth during the day or night) could alternate (Sjöblom and Parmanne 1978). The confusing results reported in these studies indicate that light does not influence herring larvae distribution in a straightforward fashion, and that the light cycle alone cannot explain the various patterns of diel migration exhibited by this species. Other environmental and behavioral factors, including turbulence, local conditions of turbidity, size-dependent shifts in diet, and vertical movements of preferred food items probably all contribute to trigger vertical migrations of herring larvae (Graham and Sampson 1982; Munk *et al.* 1989). For example, herring larvae were found to partially compensate for changes in pressure by undertaking vertical movements (Colby *et al.* 1982). Recent field experiments (Fortier and Leggett 1983; Stephenson and Power 1988; Munk *et al.* 1989) have also demonstrated a semidiurnal vertical migration where larvae move to depths occupied by their prey during the day, but the maximum depth to which they go may be restricted by the light intensity threshold for feeding. Munk *et al.* (1989) reported that daytime vertical distribution of larvae in calm weather is mainly determined by feeding conditions: the larvae move to depths where light is sufficient for feeding, and refinement within that zone is made according to a compromise between optimal light conditions for feeding and optimal prey densities.

Although feeding condition and fish size apparently were principal determinators of vertical migrations of herring larvae in their study, Munk *et al.* (1989) also concluded that the pattern was at times more complex. Wind induced mixing of the upper water column or local hydrographic conditions could interact with, or even override the effects of feeding condition and size related behaviors of the larvae. Strong winds, which produce turbulent mixing of surface waters, can prevent concentration of larvae at the water's surface, can facilitate dispersion of larvae throughout the water column, and can lead to a deeper distribution of herring larvae at night (Heath *et al.* 1988). Laboratory experiments (Batty 1987) revealed that turbulence near the surface indeed drives larvae downwards and thus eliminates the accumulation of larvae near the surface.

A number of studies reported finding herring larvae in maximum daytime abundance just above the thermocline (Fossum and Johannesen 1979; Bjorke *et al.* 1986), in regions where copepod prey were expected to concentrate (Batty 1994). Also, herring larvae are sometimes found concentrated along a front between thermally mixed and stratified water (Richardson *et al.* 1986). Batty (1994) pointed out that earlier work (Shelford and Powers 1915) showed that adult herring were sensitive to small scale changes in temperature and that these fish could distinguish between temperatures varying only by 0.6°-0.2°C. When given a choice, herring larvae are also selective for certain temperatures. Since copepod prey are expected to concentrate just above the thermocline, any behavior that would lead larvae to this part of the water column would be advantageous as a mechanism for locating maximum food density. When light is available for feeding, larvae may follow their prey down through the water column. But larvae would be limited by the depth corresponding to the minimum light intensity threshold for feeding. Batty (1994) concluded that it might be conceivable for larvae to move below the thermocline and their preferred temperature, if prey and suitable light were available at these depths.

Other studies have noted differences in vertical distribution relative to ontogenetic stage of developing larvae. Henri *et al.* (1985) reported that the greatest concentration of yolk-sac larvae were found near the bottom. Several others have also either observed or suggested this phenomenon (Tibbo *et al.* 1963; Schnack and Hempel 1971; Caddy and Iles 1973; Colton and Green 1975). Graham and Chenoweth (1973), on the other hand, found no relationship between relative abundance of yolk-sac larvae and depth.

In areas less affected by tide, vertical movements of first-feeding herring do not follow a tidal cycle (Graham and Sampson 1982). In estuaries, however, migrations of herring larvae are related, at least partially, to tidal currents (Graham 1972; Fortier and Leggett 1982). Retention of postlarval herring within the upper estuary apparently results from the tendency for this developmental stage to avoid the strong surface ebb (Able 1978), and to maintain an average vertical position close to the depth of null longitudinal velocity. Thus, net horizontal displacement is reduced. Vertical migrants above this average null velocity level followed a semidiurnal cycle which brought the postlarvae toward the surface during flood tide stages. This synchronization minimized seaward tidal drift linked to incursions within the surface layer. The large-scale cyclonic circulation prevailing at depth appeared responsible for the maintenance of early postlarval herring in the upper estuary.

Variations in vertical position of herring larvae in the St. Lawrence estuary were dominated by a semidiurnal cycle of active migration (Fortier and Leggett 1982, 1983), where larvae followed semidiurnal vertical displacements of their prey (copepods) over distances of a few tens of meters. Both prey and predator undertook vertical co-migrations, so that the two taxa were concentrated in the same depth interval on a given phase of the tidal cycle. Both average depth and semidiurnal migrations of this species were closely related to the vertical distribution of prey. Fortier and Leggett (1983) found that the semi-diurnal migrations of feeding herring larvae therefore did not constitute an active response to changes in the nature of tidal flow (Graham 1972), nor a passive response to vertical mixing (Fortier and Leggett 1982), but rather, they occurred as a behavioral response to fluctuations in the vertical distribution of their prey (copepods). The initial semidiurnal migration apparently followed the passive response of nauplii to tidal mixing. With increasing size, the larval diet included larger and larger items and herring migrations had a circadian character similar to that of copepodid migrations. In another study, Henri *et al.* (1985) concluded that vertical transport of herring larvae in the St. Lawrence estuary was greatest for larvae with low specific gravities. Specific gravity is at a maximum at hatching and decreases to a minimum at yolk-sac absorption. Larval specific gravity, current velocity, and the two-layer residual circulation of the estuary were major factors causing retention and aggregation of the larvae. Thus, they concluded that although yolk-sac larvae were not characterized by strong directed swimming powers, neither were they strictly comparable with passive components of the estuarine environment. The presence of a negatively buoyant yolk sac, whose effect decreases with larval development, combines with the intersection of the level of no net motion relative to the bottom to contribute to strong spatial structuring of larval populations, rather than to random dispersal of yolk-sac larvae. Their data suggested that the degree of retention was least for immediate post-yolk-sac larvae with increased dispersal possibly resulting from minimal specific gravity of these larvae, and because swimming capabilities of the larvae are relatively little developed at this stage.

Larval Feeding Biology.--Although herring larvae begin feeding before total yolk-sac depletion (Heath and MacLachlan 1987; Heath *et al.* 1989), gut content does not increase significantly until after yolk-sac reserves are fully absorbed (Bjorke 1978). Yolk-sac larvae are generally unsuccessful in catching prey organisms, due to the larvae's inexperience and limited mobility associated with presence of the yolk sac (Rosenthal and Hempel 1970). Additionally, lower jaw mobility, which does not occur before yolk absorption, is necessary for successful snapping action during prey capture. Diets of herring larvae broaden as larvae increase in age and as they became increasingly able to capture larger organisms (Blaxter 1965; Blaxter and Hunter 1982; Gamble *et al.* 1985; Heath *et al.* 1989). Small larvae consume naupliar stages and eggs of copepods; larger larvae have a more diverse diet including copepodid stages and nauplii of several species of copepods (Heath *et al.* 1989). Cyclopoid copepodids were a major component in diets of herring larvae during both spring and autumn, but were perhaps more prevalent in diets of autumn-spawned larvae (Gamble *et al.* 1985). In the St. Lawrence estuary, stomach contents of herring larvae included copepods, *Tintinnopsis* sp., phytoplankton, and barnacle nauplii (Courtois and Dodson 1986).

Herring larvae feed selectively (Blaxter 1965; Checkley 1982). Predator-prey relationships of 8000 herring larvae collected on the spawning area on Georges Bank-Nantucket Shoals during three autumn-winter spawning seasons revealed that copepods were the major prey item. With increasing fish size, larval preference moved from egg and nauplii to the larger copepodids (Cohen and Lough 1983). Larvae preyed on synchronously developing juvenile and adult stages of dominant copepods of this area (*Pseudocalanus* sp., *Paracalanus parvus, Centropages typicus, C. hamatus, Oithona* spp., and *Calanus finmarchicus*). No plant material was found in guts of these larvae, but none smaller than ca. 10 mm were examined. Cohen and Lough (1983) compared their results with other studies of larval herring feeding patterns and found that, in general, it appeared that herring larvae usually selected the most abundant prey of a suitable size range. Herring larvae do not, however, consume polychaete larvae, even when these represent a significant amount of the microzooplankton available (Marshall *et al.* 1937; Bainbridge and Forsyth 1971; Fortier and Leggett 1984).

Larval herring feed visually. A 10 mm herring larvae can perceive prey at an average maximum distance of only 10 mm (Rosenthal and Hempel 1970). The light threshold for feeding is about 0.1 lux (Blaxter 1968; Batty 1987), with search rates most effective at around 5 lux (Batty 1987). Earlier measurements of food-searching potential (Rosenthal and Hempel 1970; Blaxter and Staines 1971), made at light intensities (500-1500 lux) considerably higher than this threshold, reported searching values of only about one-half that estimated by Batty. However, since herring larvae usually migrate away from the surface during the day, it is doubtful that they would be subjected to such light intensities in the sea, and estimates provided by Batty (1987) may better reflect conditions encountered in the plankton. Field data on gut fullness of herring larvae suggests a diel periodicity in feeding with maximum contents occurring at dusk (Blaxter 1965; Bainbridge and Forsyth 1971). Cohen and Lough (1983) reported that, for larvae on Georges Bank, feeding was concentrated into two peaks during the daylight hours, one shortly after sunrise and another 6 to 8 hr later. In other studies, peaks in feeding seemed to be related to twilight periods associated with sunrise and sunset (Bhattacharyya 1957; Bjorke 1978; Last 1980). In experimental situations, the proportion of herring larvae swimming was found to be considerably reduced during darkness and at light intensities below the feeding threshold, with yolk-sac and first-feeding larvae active only for 6% of the time (Batty 1987). The amount of time larvae spent swimming, which was minimal in complete darkness, increased with increasing light intensity and as the larvae grew. Maximum swimming speeds for feeding larvae were recorded at light intensities between 10 and 100 lux. Presence of food organisms at light intensities below the feeding threshold (0.1 lux) caused an increase in the proportion of time spent active, but light intensities above the threshold had different effects, depending on developmental stage. Larvae of 12 mm increased swimming speed, but 21 mm larvae decreased speed. In darkness, larvae displayed inactive periods wherein they sank head first, interspersed with periods of upward swimming. As light intensity increased, vertical swimming was replaced by horizontal swimming. The presence of prey also increased the proportion of time that larvae over 12 mm in length spent swimming in the dark.

Swimming speed is important in determining the attainable search rate and to a large extent is responsible for the higher absolute search rate of larger larvae (at a given prey size). The more attacks, the slower the swimming speed. In studies of larval herring foraging behavior, from 40 to 90% of perceptions of prey items were followed by an attack (Munk and Kiorboe 1985), and the smaller the relative prey size, the larger the probability of attack by the larvae (Munk 1992). Larval swimming and attack behavior changes with prey size (six size groups of copepods) and are related to the ratio between prey length and larval length. Attack success is directly related to relative prey size, irrespective of larval size. In experiments using prey of similar size, Rosenthal (1969) also found a direct relationship between larval herring attack success, age, and length. They estimated that effective search rate showed a maximum when prey length was about 0.027 of larval length. Thus, larval foraging was, to a large extent, determined by relative size of prey, with significant selection for preferred sizes. The implication of this finding is that only a restricted part of the potential prey (biomass of size fractions) is of value in larval foraging and consumption, and that coincidence between prey size spectra and peaks in biomass spectra in the environment is important to larval growth and survival.

Larval Growth.--In a general summary regarding herring larval growth, Sinclair and Tremblay (1984) noted that all herring populations whose larval distributions are coincident with tidally well-mixed waters have relatively long larval phases. Shorter phase durations are associated with populations having larval retention areas in calmer, well-stratified water columns. The very rapid and linear growth of progeny of spring-spawning populations contrasts with the sigmoid growth curve of autumn-spawned larvae. Growth rates of spring- and autumn-spawned herring larvae reared under similar conditions in mesocosms were shown to vary widely, with slowest growth for both groups in autumn (Gable *et al.* 1985). Significant differences were apparent between length/weight relations of larvae from seasonally different spawning populations. Most importantly, developmental patterns of larvae from the two seasons were different; autumn-spawned larvae were characterized by a prolonged immediate post-yolk sac period that was not observed in spring-spawned larvae. Whether these differences were caused by extrinsic factors, or reflected intrinsic features of the larvae themselves was not determined.

Over-wintering larvae of several populations have a period of no growth in midwinter that suggests they may be physiologically inactive during this time (Townsend and Graham 1981). Midwinter is a time when food densities are lowest (Sherman and Honey 1970), when water temperatures in the inshore waters of the Gulf of Maine-Georges Bank region approach the lethal limit (0°C) for herring larvae (Chenoweth 1970; Graham and Davis 1971), and when larval feeding activity is also at its lowest (Sherman and Honey 1971). In February and late January, relative condition of herring larvae in these regions is poorest (Chenoweth 1970), and these periods are coincident with periods of high mortality (Graham and Davis 1971).

In estuaries along the Gulf of Maine coast, such as the Sheepscot River, changes in modal lengths of larvae during autumn and winter indicate that larval cohorts enter the estuary and subsequently lose their identities through differential mortality and growth, since larvae are not known to depart the estuary once established there (Graham *et al.* 1972). There appeared to be only one major age group of larvae occupying the estuary through November, but a second age-group of younger larvae was apparent in the estuary by January. Growth rates of 2 mm/wk, excluding the winter period of retarded growth were recorded (Townsend and Graham 1981). Both age groups of larvae in the Sheepscot estuary experienced approximately a 2-3 wk period of retarded growth. The first group of larvae showed retarded growth beginning at a length of ca. 35 mm and about 80-100 d after the mean date of the first growth ring was formed. This period of retarded growth began during the latter half of January and continued until early February. The second major group to enter the estuary showed retarded growth beginning at a length of ca. 26 mm, and 50-60 d after November, the mean date of the first otolith daily growth ring for group 2. This period of retarded growth also began during the latter half of January and continued until early February. Apparently, the environment at this time is not conducive to growth for either group of larvae. The winter slowing of growth reported by Townsend and Graham (1981) was more brief (2-3 wk) than the general slowing down of growth throughout the winter reported by others (Tibbo *et al.* 1958; Das 1968, 1972; Graham *et al.* 1972; Boyar *et al.* 1973b).

Temperature histories inferred from the analysis of strontium and calcium concentration ratios (Radtke *et al.* 1990) in otoliths of the 1986 year-class herring larvae collected between October and April in the Sheepscot River (Townsend *et al.* 1989) demonstrated the usefulness of these ratios as indicators of environmental histories of the larvae. Elemental ratios in the otoliths indicated that larvae entering the estuary in the fall did not survive through the winter, but were replaced by larvae which had remained offshore in the winter and entered the estuary some time later in the spring.

Growth estimates of herring larvae from the Gulf of Maine-Bay of Fundy region based on length frequencies are numerous (Tibbo *et al.* 1958; Tibbo and Legaré 1960; Das 1968, 1972; Sameoto 1972; Graham *et al.* 1972; Messieh and Kohler 1972; Boyar *et al.* 1973b). Estimated overall growth rates of larval herring in the Gulf of Maine based on these studies are 0.13-0.17 mm/d (Graham and Davis 1971; Boyar *et al.* 1973b). For Bay of Fundy larvae, Das (1968) estimated growth rates of 0.29 mm/d in September, 0.21 mm/d in October, and 0.14 mm/d over the winter period. Using length-frequency histograms and cohort mean sizes over time, Lambert (1984) estimated seasonal mean growth rates for herring larvae from the Georges Bank-Nantucket Shoals area of 0.22 mm/d during September-October, decreasing to 0.08 in November, with minimal values of 0.06 mm/d occurring during winter (December-February). For larvae in the Gulf of St. Lawrence, estimated rates were 0.27 mm/d during early larval growth stages and decreasing to 0.09 mm/d near winter (Messieh and Kohler 1972).

Length frequency estimates of growth may be of limited value, however, because in some years more than one mode may be present in the length-frequency distributions of herring larvae for a particular time and geographical area. These polymodal data could indicate mixture of larval cohorts from different spawning populations, or different temporal segments of the same spawning population. Thus, growth rate estimates for larvae based on length-frequency distributions may not be accurate, since individual samples may not represent a single homogeneous group of larvae.

An alternative method to estimate growth rates and age structure of larval herring uses daily growth increments in otoliths (Townsend and Graham 1981; Lough *et al.* 1982). Larvae reared in the laboratory at 10°C begin initial increment deposition in the otoliths, on average, 4.5 d from hatching, which coincides with time of yolk-sac absorption, while the second increment is deposited an average 12 d post-hatching (Lough *et al.* 1982). These results agree closely with those made from field estimates (Lough *et al.* 1982). Jones (1985) reported that otolith increments were formed daily in herring larvae, at least during the early part of the spawning season. Geffen (1982), however, challenged the concept that daily growth increments in otoliths of young fishes provided an accurate index of age (growth rate limitation hypothesis). Data collected in that study from known-age larval herring suggested that frequency of increment formation was less than daily in larvae with a suboptimal growth rate. Non-daily increment formation has subsequently been reported in both larval Atlantic and Pacific herring (Lough *et al.* 1982; McGurk 1984). Campana *et al.* (1987) examined increment formation on otoliths of herring of known age and concluded that increment counts, when assessed with light microscopy, underestimated age in all herring larvae studied, and that previous reports of growth-rate limited increment formation also appeared to provide an empirical description of this same phenomenon. They suggested that resolution-limited increment visibility could equally as well explain problems associated with increment formation (Campana *et al.* 1987), and that a growth-limited hypothesis need not be invoked to explain instances of apparent non-daily increment formation in slow-growing pelagic larvae, such as those of Atlantic herring.

Daily growth increments on otoliths used to estimate growth rates of larval herring in the Gulf of Maine-Georges Bank region (Lough *et al.* 1982) indicated that average growth rates increased from 0.25 mm/d at hatch to 0.30 mm/d at 20 d post-hatch, with an upper rate limit of about 0.35 mm/d, which then declined to <0.15 mm/d after 75 d of age during the winter period (Lough *et al.* 1982). Overall average increase in size for autumn-spawned herring was about 5 mm/mo from time of hatching (6 mm SL) to metamorphosis in the spring (Lough *et al.* 1982). Larvae with a mean size at hatching of 5.7 mm SL were estimated to grow to a mean length of ca. 30.9 mm at 175 d. This estimated size at metamorphosis (30.9 mm) is considerably lower than that reported elsewhere for pre-metamorphic herring larvae in Maine waters, which reach 40.0-40.5 mm in length (Graham *et al.* 1972; Boyar *et al.* 1972b), and is also lower than the estimated maximum length of 42.5 mm for herring larvae from the same area (Saila and Lough 1981).

Estimated growth rates for larval herring in the St. Lawrence estuary range from 0.15 to 0.27 mm/d (Able 1978; Fortier and Leggett 1982). Daily rings on otoliths of autumn-spawned herring larvae in the southern Gulf of St. Lawrence indicated that growth rates increased from 0.28 mm/d to 0.38 mm/d by 20 d age, and declined to 0.05 mm/d at the end of winter shortly before metamorphosis (Messieh *et al.* 1987) at estimated lengths of 38.9-39.4 mm.

Evidence from Gulf of Maine studies shows that growth rates are variable for individual larvae hatched during different portions of the same season (Jones 1985). For autumn-spawned herring larvae hatched early in the season, increase in length was greater than that for larvae hatched later in the season. The most plausible explanation for differences in length-at-increment count was an actual difference in larval growth rate over the spawning season (Jones 1985). Growth estimates for larvae during different years were also variable. For example, an early-hatched larva in one year was estimated to require, on average, 80 d to reach 30 mm, compared with 88 d for a late-hatched larva, while in another year, it would take, on average, 63 d for an early-hatched larva to reach 30 mm compared with 157 d for a late-hatched larva to reach this size. Munk *et al.* (1991) also reported regional and seasonal differences in growth of herring larvae using otolith aging methods.

Larval Growth Energetics.--Yolk-sac utilization in herring larvae is directly related to water temperature (Blaxter 1956; Blaxter and Hempel 1963, 1966; Blaxter and Ehrlich 1974). Gut clearance times for food items in exogenous-feeding larvae depends on the initial amount of food in the guts, and digestion times depend on size and type of prey item ingested (Rosenthal and Hempel 1970). Experimentally, temperature also affected clearance times, with values of 4-10 hr having been recorded (Blaxter 1965) or used to construct energetic models (Beyer and Laurence 1981).

In laboratory experiments, threshold prey densities for larval Atlantic herring to initiate feeding were estimated at ca. 0.17 artemia/mL (Werner and Blaxter 1980). Estimated daily rations from field caught larvae are about 19.6 μg dry weight (Cohen and Lough 1983). These values were a little less than one-third the literature estimates of daily ration (Beyer 1980; Beyer and Christensen 1980; Beyer and Laurence 1981). Larvae averaged 1-7 prey (0.5-48 μg dry weight) per gut. Using calculated rates of digestion, Rosenthal and Hempel (1970) estimated that early postlarval herring could digest 35-40 artemia nauplii daily. Heath (1989) modeled prey ingestion by herring larvae subjected to cross gradients of light intensity and prey concentration in laboratory experiments. Data on otolith ring deposition and condition factors of field-caught larvae showed variations that were consistent with day-to-day differences in the modeled ingestion rate.

A preliminary bioenergetics model based on published data for five larval herring cohorts from each of two different years (Kerr and Dickie 1985) found that interactions between temperature and body size with apparent availability of suitable prey resulted in quite different metabolic environments which supported relatively uniform growth among the different cohorts. During spawning and growing seasons, herring cohorts were found to occupy quite different metabolic niches, although the resultant growth appeared quite uniform. Apparently, advantages of early spawning, resulting in early attainment of relatively larger body size, were offset by superior feeding conditions for cohorts spawned later in the season. Therefore, timing of development in the later cohort resulted in a much more rapid increase in realization of their metabolic potential despite the rapidly falling ambient temperatures they experienced.

Juvenile Biology.--In early spring, herring larvae about 45-50 mm in length metamorphose into young juveniles, which form large schools in coastal waters throughout the Gulf of Maine. Use of coastal and estuarine waters as nursery areas has been observed for herring in the Gulf of Maine and North Sea, but universality of this phenomenon is uncertain, particularly for progeny of herring spawning on offshore banks. Juvenile feeding aggregations occur in shallow coastal waters throughout the warmer months. In coastal waters, early stage juveniles suffer high levels of mortality during their 1st yr of life (Gulland 1965; Cushing 1974; Ware 1975b), when they are preyed upon by other fishes, particularly pollock, cod, silver hake, and dogfish, by marine mammals (seals and whales), and by fish-eating birds. Schools of juveniles in shallow waters are often literally driven ashore and stranded by predator pressure. This phenomenon is particularly common when the year-class is abundant.

In late autumn, juveniles move out of nearshore waters, and results of tagging studies (Speirs 1977) suggest a southwestward movement of at least a part of the population in winter. Tagging results (Stobo *et al.* 1975) indicated that a large part of the Bay of Fundy juvenile population overwintered off the mouth of the Bay. Earlier results of parasitological surveys

(Sindermann 1957a, 1957b) indicated little eastward movement of juveniles from the western coastal sector, but indicated a possibility of greater westward movement for fish having spent their 1st yr in the eastern and central coastal sectors. Spawning populations in the Gulf of Maine (Jeffrey's Ledge, Stellwagen Bank, Isles of Shoals, Martinicus) are logical sources of juveniles from the Gulf of Maine coast and the western Bay of Fundy, but they may not be the only contributors. Some juveniles tagged in Canadian waters have also been recovered in the Gulf of Maine, and even at Cape Cod.

It has been suggested that the offshore banks are overwintering areas for juvenile herring, but as Sindermann (1979) pointed out, the evidence is not substantial. Boyar (1968) had reported juvenile herring on Georges Shoals, an extensive area avoided by commercial and research vessel operations. Indeed, this area may be a limited nursery for juvenile herring. But in general, it would only be in exceptional years that juveniles would be expected to occur in deeper areas of the Bank that are normally fished. There is still great uncertainty about the location of extensive nursery grounds necessary for the large Georges Bank-Nantucket Shoals herring stocks. Coastal waters of southern New England are another possibility, although it seems that juvenile herring occurring in abundance in such inshore waters in earlier years would have been observed and reported. The possible existence of an isolated or unsampled group of juveniles on Georges Bank or elsewhere was not considered a likely possibility by Sissenwine (cited in Sindermann 1979), who determined mortality rates and found them inconsistent with the concept of an unsampled population somewhere in the area (Sindermann 1979).

The source of the New Brunswick juvenile stock remains an enigma. There is some evidence that the Nova Scotia spawning stock does not contribute significantly to the New Brunswick juvenile population. Based on limited evidence, Iles (1971) concluded that late larval stages from Nova Scotia spawning occurred only in the eastern Bay of Fundy. Also, there were differences in vertebral counts between juvenile aggregations on the Nova Scotia and New Brunswick sides of the Bay of Fundy (Tibbo 1968). On the basis of vertebral numbers, New Brunswick juveniles were more like the Georges Bank spawning stock than the Nova Scotia stock, and Iles (1970) suggested a transport mechanism for larval and post-larval drift from Georges Bank in the Gulf of Maine counterclockwise eddy across the mouth of the Bay of Fundy. Earlier studies had concluded that juveniles caught on the western side of the Bay of Fundy and along the Maine coast were derived from, and contributed to, stocks other than the Nova Scotia stock (probably the Gulf of Maine stock complex). However, recoveries made in New Brunswick and Nova Scotia of fishes tagged in eastern Maine as well as those from the western Gulf of Maine have raised some questions about this statement (Sindermann 1979).

One- and 2-yr-old fish move inshore in the Gulf of Maine during the following spring, and are fully recruited to the sardine fishery (Sindermann 1979). Peak catches in western and central sectors of the Maine coast occur in June and September and in the eastern sector in July. During summer, little lateral movement occurs along the coast; movements of schools seem random within any localized area.

Next to schooling, probably the most important behavioral response of juvenile herring is vertical movement in response to changing light intensity (Sindermann 1979). Juveniles move up in the water column at twilight and remain near the surface if light intensity is low enough. Experimental work has demonstrated clearly that herring move toward the surface when light intensity is low; that activity of juveniles has a diurnal pattern, with maximum just after sunrise and just before sunset; and that vertical diurnal movements occur at all seasons, except that median depths increase in winter (Brawn 1960b; Tibbo 1964; Stickney 1972). Moonlight, and phase of the moon, are important determinants of success of the juvenile fishery to the extent that Anthony (1971) demonstrated successive monthly peaks in the sardine fishery which coincided with dark phases of the moon.

Although purposeful movements of schools seem to be responsive to visual cues, other environmental and physiological stimuli are undoubtedly involved (Sindermann 1979). Schools of juveniles in coastal areas move to some extent in response to ocean currents. Movements are also clearly influenced by seasonal environmental cycles, principally those of temperature, salinity, and food abundance. Major activity in weir and stop seine fisheries for juveniles on the Maine coast coincides with the period when nearshore water temperatures are in the 10-13°C range. Activity declines during mid-summer on the western coast, when nearshore water temperatures may exceed 13°C; and during colder months (November-March) schools of juveniles disappear from nearshore waters of the Gulf of Maine. These observations support experimental findings of temperature optima.

Population Dynamics

Growth Parameters.--Growth has been well studied in Atlantic herring. Growth rates among and within populations are variable depending on a number of factors, including temperature (Day 1957; Saville 1978; Moores and Winters 1982), food availability, and population size. Historically, scales were used to age this species (Huntsman 1919; Lea 1919), but since the 1960s otoliths have been used (Hunt *et al.* 1973). Use of otoliths to age young herring from the Gulf of Maine was validated by Watson (1964), but difficulties with ageing older fish persisted through the mid-1970s (Dery and Chenoweth 1979; Dery 1988), with poor agreement between estimates of fish aged by scales and otoliths (Messieh and Tibbo 1970), and between otolith age readings by different age readers (Parsons and Winters 1972). Otoliths of postlarvae as small as 0.31 mm are discoid, but adopt the shape of those from adults at about 1.0 mm otolith length (Harkonen 1986). A description of otolith shape and an otolith length-fish length relationship for herring taken off Newfoundland was described by Lidster *et al.* (1994). Otolith nuclei have also been found useful in discriminating individuals between spring- and autumn-spawning populations (Einarsson 1951).

In U.S. waters, herring attain a maximum length of about 39 cm TL and an age of about 15-18 yr (Anthony 1972), although some reports list herring as old as 20 yr, and older. Male and female herring grow at about the same rate and become sexually mature beginning at age-3, with most maturing by age-4 or age-5. Beverton (1963) and Anthony and Waring (1980) tabulated von Bertalanffy growth parameters for many Atlantic herring stocks. All showed rapid growth in the first years of life, with a marked slowing at the onset of maturity, normally at age-4. Estimated K values for the Georges Bank population were 0.35-0.36, while those for Canadian Atlantic herring populations were between 0.17 and 0.30 (Anthony and Waring 1980). In all cases, 50% maturity occurred at lengths near 80% of the asymptotic length L_∞. During periods of low population levels, herring may mature at smaller sizes. In the western Atlantic, growth rates in several studies were found to increase progressively in a gradient from Nova Scotia to western Maine and to Georges Bank, but with only slight differences between fish from different locations (summarized in Sindermann 1979). Georges Bank herring grew more rapidly, but the maximum size attained was only 35 cm at 14 yr; Nova Scotia and eastern Maine herring grew slower, but reached a greater maximum size (39 cm in 16-18 yr).

Juveniles grow to about 90-125 mm by the end of their 1st yr in the Bay of Fundy and in coastal waters of Maine. Juveniles, 50-65 mm in length, predominate among small herring at Provincetown at the end of June, and juveniles are 54-100 mm on Nantucket Shoals in mid-July. At Woods Hole, herring spawned in October and early November are 76-125 mm long by the following autumn. Growth of juveniles is very rapid at age-1 and age-2 (Anthony 1972). In western Maine, age-1 herring grew as much as 10 cm from early spring to November, and age-2 herring as much as 8 cm. When herring reach about age-2 and lengths of 190-200 mm they accumulate large amounts of fat among the body tissues and viscera during warmer months of the year when growth is rapid. They lose this fat in winter and also at the approach of sexual maturity. This "fat" stage is characteristic of herring in American as well as in European waters, where "fat" herring are the targets of extensive fisheries.

There is great variation in growth between year-classes; with size of age-2 herring varying in one area by as much as six cm between year-classes (Anthony 1971). Herring in western Maine grew faster than those in eastern Maine and averaged nearly 3 cm longer at the end of their 2nd yr. Although herring in eastern Maine grew very slowly at age-1, they increased their rate of growth at age-3 and were the same lengths as western Maine herring at age-5 (Anthony 1972). Because growth varies significantly between year-classes, composition of age groups entering the juvenile fishery is not the same each year. Since the fishery is selective for 17 cm fish, fast growing age-1 fish will enter the fishery in late summer, while slow growing age-3 fish will enter the fishery in early summer.

Density-dependent growth in herring has been observed by a number of authors (Iles 1967; Anthony 1971; Saville and Jackson 1974; Lett and Kohler 1976; Burd 1984; Molloy 1984). Although there is some evidence of density-dependent growth of young herring, the literature regarding density-dependent growth of mature herring is contradictory (Sinclair *et al.* 1982b). Anthony (1971) concluded that growth of juvenile herring along the Maine coast during the first 2 yr of life was density-mediated by regional differences in plankton abundance and water temperature. Growth appeared to be related to both abundance of age-2 fish and water temperature. When abundance was great, its effect overcame positive effects of temperature (or other factors indicated by temperature). Anthony and Waring (1978) reported that while density-dependent growth was exhibited by Gulf of Maine juveniles during some years, in other years this density-dependent relationship completely disappeared. Lett and Kohler (1976) also suggested that growth in herring was density-dependent during the 1st yr, and that this influence determined subsequent growth rates. Any such density dependence must be weak, however, since, as Doubleday (1985) pointed out, even a doubling of growth rates would, in most cases, imply less than 20% annual growth in weight for older fishes. An apparent increase in growth rate in juvenile and adult fish from Georges Bank and the Gulf of Maine was observed beginning with the 1968 year-class (Anthony and Waring 1978). It was hypothesized that increases in growth rate for all year-classes was in response to declines in overall biomass in that population. There was no change in maximum size attained.

Recruitment Dynamics.--Herring populations are subject to extreme year-to-year fluctuations in year-class strength, and considerable attention has been devoted to determining factors that influence recruitment success in this species. Recruitment predictions and understanding causes of fluctuations in recruitment are extremely important, since it is the strong year-classes that traditionally have sustained herring fisheries in the Gulf of Maine, and elsewhere. A striking characteristic of clupeoid stocks in general is their high interannual variability in recruitment levels, which Cushing (1971) attributed to the lack of strong density-dependent regulatory mechanisms. Variability in annual recruitment was clearly evident in herring populations of the Gulf of Maine region, where recruitment from 1947 to the early 1980s has varied by a ratio of 20 to 1 (Anthony and Fogarty 1985). Heavy fishing pressure began there in the mid-1960s, and during this period recruitment fluctuated by only a factor of 9 to 1. Therefore, Anthony and Fogarty concluded that historically, the greatest fluctuations in recruitment for populations in this region occurred in the absence of high fishing mortality, indicating that factors in addition to stock size strongly influenced recruitment success. Indices of abundance of herring in the Gulf of Maine were calculated for three time periods using three different procedures (Anthony and Fogarty 1985). Indices of abundance for the periods of 1915-67 and 1951-81 indicated that productivity, or amount of recruitment per amount of spawning stock, was positively related to either temperature or temperature-related factors (e.g. food availability) at intermediate to high levels of spawning stock biomass. For the time period 1965-81, abundance was calculated by virtual population analysis. Temperature effects during several periods in the 1st yr were related to recruitment levels at age-2. The mean, maximum, and minimum water temperatures during (1) September-December (spawning-early larval development), (2) January-April (overwintering and late larval development, and (3) May-August (postlarval) periods were correlated with abundance. Results of these analyses indicated that effects of environmental influences (temperature) on determination of year-class strength occurred during late larval and early juvenile phases.

Historically, indices of year-class strength in herring populations have been related to water temperature (Postuma and Zijlstra 1974; Lett and Kohler 1976; Dow 1977; Sutcliffe *et al.* 1977; Sinclair *et al.* 1982b), wind strength and/or direction (Carruthers 1951; Sinclair *et al.* 1982a), winter phosphorus concentrations (Cushing and Dickson 1976), salinity (Bowers and Brand 1973), sea level (Sinclair *et al.* 1982a), and interactions with mackerel (Winters 1976; Lett and Kohler 1976; Skud 1982). Dragesund (1970) thought duration and geographical extent of spawning were two important factors contributing to year-class strength in herring. He reasoned that the longer the spawning season and more widespread the deposition of eggs, the greater was the likelihood for good recruitment. Since different age groups of herring tend to spawn at different times and in different areas, Lambert (1987) also suggested that the more age classes actually involved in spawning, the longer would be the spawning season, and hence the more widespread the spawning. Thus, he argued that maintenance of a well-balanced age structure in a herring population would tend to promote a resilient or more stable population, whereas, the converse (reduction of age classes) would render a population more vulnerable to recruitment failure. Others have argued that relative size of the population of adult fishes involved in spawning was the strongest influence on the abundance of eggs and larvae produced. The implication was that a greater number of spawners would translate into a greater probability of survival for a larger amount of larvae. Large differences in quantitative estimates of larvae produced in spawning regions on the Georges Bank-Nantucket Shoals area compared with coastal waters of the Gulf of Maine for the same year were attributed to differences in stock sizes of spawning herring between the two areas (Sindermann 1979).

Since herring undergo little growth after reaching maturity (Blaxter 1990), growth of older year-classes can do little to compensate for overfishing of the stocks. Recovery and maintenance of herring stocks, therefore, depends very much on the recruitment of good year-classes. Recruitment success for herring is believed to be fixed during the 1st yr of life (Anthony and Waring 1980; Lough *et al.* 1985), although some studies questioned the relative importance of mortality events during early life history stages in relation to year-class strength in this species. Stevenson *et al.* (1989) noted that larval herring research in the Gulf of Maine (Graham and Sherman 1987) has been directed at understanding the dynamics of larval production, growth, transport, and survival in order to determine mechanisms affecting recruitment variability for the coastal herring stock and to forecast catch at age-2 in the sardine fishery. Since no positive correlation was evident for 10 previous yr of data between spring larval abundance and catch at age-2, Stevenson *et al.* (1989) believed that there was no basis on which to forecast catch from spring larval survey data. Instead, it appeared that survival of young juveniles during the period following metamorphosis until their recruitment to the fishery a year later was a critical factor affecting year-class size. This life history segment was not addressed by an assessment program that focused solely on the larval stage.

Significant mortality can occur during egg deposition and early development of embryos in the spawning beds. Hatching success of eggs deposited in shallow water may be particularly susceptible to disruption by wave action (Messieh *et al.* 1985; Messieh 1988) with subsequent high egg mortalities. In some areas, eggs are detached from the substrate, or macrophytes with eggs attached are dislodged from the substrate and washed ashore by strong winds causing high egg mortalities (Prince 1907; Tibbo *et al.* 1963; Messieh 1988). The magnitude of these events is evidenced by early reports from the beginning of this century (Prince 1907), which indicated that, in some years after severe gales, herring eggs were heaped knee high for kilometers along the New Brunswick shore. Fishermen in the Escuminac-area reported that enough eggs were washed ashore to be collected for fertilizer as recently as the early 1960s (Messieh 1988). The negligible amounts of beached material reported during more recent surveys (Messieh 1988) were attributed to more recent declines in herring stocks, with concomitant small amounts of spawn in recent years compared with the huge amounts of eggs deposited in previous years.

Natural mortalities of eggs observed over the course of several years on a shallow-water spawning ground of spring-spawning herring in the Gulf of St. Lawrence were estimated to be relatively low (Messieh 1988). The highest mortality (9.6%) was among loose eggs not attached to the substrate; while the lowest (1.2%) was for eggs attached to kelp (*Laminaria* sp.) and seaweeds (*Phyllophora* spp.). Eggs attached to bare rock substrate did not suffer a high mortality. In contrast, in another area where eggs of autumn-spawning herring were deposited on substrates in deeper water without algal cover, mass mortalities were incurred (Messieh and Rosenthal 1989). At this spawning site, eggs were laid in dense mats sometimes reaching 20-30 layers and sometimes these deep-layered egg masses were covered with fungus. The authors hypothesized that after a mass spawning in a relatively restricted area, embryos were developing where oxygen concentrations were insufficient, which triggered the heavy mortalities.

Predation on herring eggs by fishes and invertebrates can also cause heavy mortalities. A minimum of ca. 30% of the total loss of spawned eggs occurring during the incubation period (14-16 d) at a herring spawning bed in the Gulf of St. Lawrence was estimated to be due to predation by fishes (Messieh *et al.* 1985; see detailed discussion under Predator section). In another area, predation on herring eggs by haddock caused significant mortality (Hempel and Hempel 1971), with daily estimates of one haddock consuming the total egg production of one herring (Hempel 1971).

Annual mortality of larval stages can also be significant for herring populations and is an important factor in determining year-class strength in this species. Field estimates of instantaneous mortality rates for populations of herring larvae are highly variable (summarized in Fuiman and Gamble 1988) with a mean reported rate of 0.12/d, and values ranging from a minimum of 0.02 to a maximum of 0.46/d. Age-specific mortality rates of larvae for autumn-winter periods over a 3-yr span during the mid 1970s (Lough *et al.* 1981) indicated interannual differences in estimated mortality rates of 2.2%/d, 2.7%/d, and 3.2%/d, respectively. Graham (1982) described heavy fall mortality of herring larvae in inshore and coastal waters of Maine resulting from density-dependent factors. Mortalities ranging as high as 94% were estimated for herring larvae at the yolk-sac resorption stage sampled off Norway (Dragesund and Nakken 1971).

Five variables identified as important to survival success of early life history stages of marine fishes and most likely to determine recruitment levels are temperature, turbulence, transport, food, and predation (Sullivan 1982). Gallego and Heath (1994b) noted also that, for herring, metamorphosis itself would be associated with high predation risk, since conspicuousness of the larvae is enhanced at this stage, but reactivity and schooling behavior are still not fully developed. Grosslein (1987) provided a synopsis of knowledge on recruitment processes for herring, with special reference to the spawning population on Georges Bank, and Houde (1987) discussed early life history dynamics and recruitment variability in herring.

Several general hypotheses have been developed to explain the link between survival success of early life history stages of fishes and future recruitment to stocks (and fisheries) as juveniles or adults. Hjort (1914) proposed the "critical time period" hypothesis that suggested catastrophic mortality among post-yolk sac larvae, such as those of herring, may occur due to lack of suitable prey at time of first feeding, predation pressures, or passive transport to locations unfavorable for continued survival or recruitment to the parent stock. The first part of Hjort's hypothesis stressing importance of larval survival to future biomass of adult stocks was modified and refined by Cushing (1975) and Cushing and Dickson (1976), who pointed out that survival of larvae, such as first-feeding herring, is largely dependent on synchrony between spawning periodicity and availability of potential prey. Since spawning periods of fishes were shown to be relatively fixed, it was hypothesized that annual variation in timing of plankton blooms may result in a "match-mismatch" between larvae and their principal prey, thus causing wide-scale density-independent variability in recruitment success. In the St. Lawrence estuary, relative survival success of spring- and fall-spawned larval cohorts of herring were found to be quite different (Fortier and Gagné 1990). Development of the spring cohort matched (remarkably well) the timing of development of suitable prey, and larval abundance within the estuary decreased relatively slowly (7.8%/d). The fall cohort, in contrast, hatched in a period of low food availability and dwindled rapidly (28.9%/d). Blaxter (1990), too, thought it likely that match and mismatch between fishes and their prey and predators at various life stages was of dominating importance factoring into year-class strength, and therefore it is the relative timing of trophic events during the long planktonic stage of species such as herring that is paramount to their recruitment success.

Iles and Sinclair (1982) developed the "larval retention hypothesis" to explain several features of herring biology, including a mechanism for the existence of discrete populations and factors affecting recruitment processes in these populations. These authors noted a remarkable correlation between locations of tidally-mixed continental shelf waters and spawning grounds of herring. Thermal fronts delimiting the tidally-mixed areas act as boundaries to dispersal for herring larvae. Thus, larvae are retained in the mixed regime and stock discreteness is maintained. They further suggested that size of retention areas also determined size of the stock.

Later work by Sinclair and Tremblay (1984) discussed timing of spawning of herring populations in light of the match-mismatch theory and found that this theory was inconsistent with the larval retention stock hypothesis. They pointed out that larvae of a discrete herring population develop within, and are thus adapted to, the specific oceanographic conditions of their larval retention area. Secondly, metamorphosis from larval to juvenile stage occurs primarily within a restricted period of the year (April-October). Given these two constraints, they hypothesized that timing of spawning of a herring population is a function of the time necessary to complete the larval phase and yet metamorphose within the acceptable seasonal envelope. Populations that had "good" larval retention areas were able to spawn in the spring and still metamorphose within the seasonal envelope. Populations with larval retention areas that were less "good" for larval growth would have to spawn earlier to satisfy the two constraints.

Another important idea in Sinclair and Iles (1985) was their conclusion that maintenance of the reproductive unit was probably the reason why herring spawned in tidally mixed areas, and that was why it was advantageous for larvae to be retained within these areas for a number of months following hatching. As Townsend (1992) pointed out, food resources, predators, or low temperatures in such tidally-mixed retention areas were possibly deleterious to larval survival but were considered by Sinclair and Iles to be of secondary importance. Sinclair and Iles suggested that the slowed growth resulting from low food supplies in retention areas helped to delay metamorphosis until an optimal time the following spring. Since herring migrate to nursery areas following metamorphosis and not during the larval drift period, the amount of larvae that may be advected away from the retention area prior to metamorphosis was considered, by them, to be relatively insignificant compared with the magnitude of juveniles migrating to nursery areas following metamorphosis. This point regarding relative significance or insignificance of larval drift from the retention area was considered perhaps the most controversial of their contentions (Cushing 1986; Townsend 1992). Heath and Richardson (1989) studied variation in survival of herring between egg stage and age of recruitment to the spawning population for seven populations in northern European areas. They concluded that spawning strategies of some populations were adapted to oceanographic conditions that maximized the probability of a particular larval transport pattern, but that others showed no apparent relationship. No single model, therefore, could account for all spawning strategies observed in the populations studied. They further contended that it was unrealistic to expect a single hypothesis, such as the larval retention hypothesis, to account for the diverse spawning strategies of herring.

Recruitment variability of larval herring in the Gulf of Maine has been the focus of much study. Earlier work by Graham (1982) found significant correlations among winter survival, spring abundance and recruitment, but only poor correlations between fall abundance of young larvae and recruitment success. He suggested that the primary mechanism fixing year-class strength of larvae before metamorphosis into juveniles in the spring was related to the distribution of larvae among the many inshore nursery areas in the fall. He argued that density dependent mortality operated to reduce the numbers of larvae in inshore areas in the fall, and this was followed by density independent winter mortality.

In synthesizing information relevant to factors affecting recruitment of herring larvae in the Gulf of Maine, an important point noted by Townsend (1992) was that while most fishes in temperate and higher latitudes spawn in spring during a time of increasing plankton abundance and warming temperature, autumn-spawning herring do just the opposite. Therefore, larvae of these herring must deal with relatively harsh conditions including extremely low winter temperatures and the lowest food abundances of the year prior to their metamorphosis to juveniles in spring (Graham *et al.* 1990; Campbell and Graham 1991). Thus, processes operating during the fall and winter period following spawning and prior to metamorphosis of larvae to the juvenile stage in spring are the likely factors critical to recruitment success in this species (Townsend 1992). Relatively slight changes in survival during this period could be amplified into much larger changes in survival to the juvenile stage (Houde 1987).

In estuaries along the Maine coast, larvae often accumulate in large numbers in October and November, but shortly after this peak in abundance, their numbers diminish to very low levels during winter. Age composition for a fall larval year-class clearly showed successive replacement of entire cohorts by those spawned progressively later in the year, either as a result of mortality or emigration of earlier cohorts (Stevenson *et al.* 1989; Townsend *et al.* 1989). Mortality seemed the more probable explanation, especially in estuaries where larvae are retained despite a net surface outflow (Graham 1972). During the following March and April, there is a second, sometimes even larger, peak in abundance of herring larvae inshore just prior to metamorphosis. These larvae appear to represent survivors from the previous fall spawning. The exact nature of the origin of the second pulse of larvae, and in particular, their overwintering distribution during the period of low larval abundance inshore, were uncertain (Townsend *et al.* 1989). Townsend (1992) noted that the fate of larvae from spawning on the Jeffreys Ledge area is virtually unknown, although it would appear that they remained in the general western Gulf of Maine area into the winter. He suggested that perhaps these larvae may be significant to the recruitment of pre-juvenile fish entering the Maine coastal and inshore waters in spring, and that this group was certainly in need further study. Graham (1982) concluded that a predominance of late spawned, and hence younger overwintering larvae, may increase the number of larvae surviving into more favorable conditions in the spring and thereby influence year-class strength. It would appear then that the origins of larvae comprising the spring abundance peak inshore on the Maine coast may be from either those larvae released in late fall from retention areas, or larvae that had escaped earlier and overwintered offshore in the Gulf (Townsend 1992).

Recruitment variation in herring as it related to features of the physical oceanography of the Gulf of Maine and adjoining waters were discussed by Townsend *et al.* (1989) and Townsend (1992). Of the many factors affecting recruitment success, larval drift between spawning and nursery areas was thought perhaps the least understood. Townsend (1992) noted that the issue of larval retention vs. larval transport from spawning area to nursery area in the Gulf was not easily resolved, especially given the various accounts of both processes for the same spawning areas. This is the case for the eastern Maine-Grand Manan spawning area and in the eastern Atlantic where evidence of both scenarios, larval retention in the vicinity of spawning areas and larval transport to other areas, is present.

Townsend suggested that if oceanography of the region is considered then some insights into the causes of the apparent discrepancies become apparent. That both retention and transport processes operate in the eastern Maine-Grand Manan region might be due to the particular locations of spawning relative to the frontal region, where geostrophic flow is at a maximum. For this spawning population, a large proportion of the larvae are retained (even into January) in the tidally-mixed spawning area, and a significant proportion of larvae drift away in a westerly direction along the coast of Maine, where some, in turn, are advected out over the open Gulf of Maine. Chenoweth *et al.* (1989) suggested that advection of the larvae may occur when seasonal cooling of the surface waters breaks down the frontal boundary between tidally-mixed and stratified areas. Model results pointed to the likely importance of wind events in breaking up the hydrographic structure surrounding the tidally mixed spawning areas, resulting in release of the larvae (Campbell and Graham 1991). Once the boundary breaks down, the larvae can then disperse. This observation is in keeping with the Iles and Sinclair retention hypothesis (Townsend 1992).

Processes affecting larval survival during this time period are uncertain, although larvae are believed to depend a great deal on being transported to productive inshore nursery areas (Graham 1972; Graham *et al.* 1972, 1984, 1990; Stevenson *et al.* 1989; Townsend 1992). The nature of transport is believed to be the coastal current that moves larvae along the Maine coast southwestward away from the eastern Maine spawning ground (Townsend *et al.* 1986). Chance interactions of larvae from the eastern Maine-Grand Manan spawning group with the frontal region at the edge of this tidally mixed area could result in some larvae being advected away from the mixed area. Therefore, spawning location relative to location of the tidal front (or core of the coastal current) would be an important factor to the numbers of larvae being entrained. This relationship would be analogous to findings by Heath and Rankine (1988), in that larvae hatching nearer the frontal region between mixed and thermally stratified waters (i.e., where geostrophic flow along the front would be greatest) would be more likely to be entrained in the plume of coastal water advected offshore. Alternatively, a greater proportion of larvae hatching nearer the shore would likely result in greater retention of larvae within the mixed region, because significant alongshore transport of those larvae hatching nearer the coast might be less likely.

Therefore, there exists the possibility for larvae from this spawning ground to be carried along two drift routes: one is along the coast where they are made available to inshore nursery areas, and the second path is to be transported offshore over the central Gulf of Maine. Larvae moving along the coast eventually enter inshore nursery areas in estuaries and embayments in fall, perhaps utilizing selective tidal transport (Townsend 1992). Chenoweth *et al.* (1989) found that approximately half of the larvae were retained in the mixing area and moved along the coast, while the remainder appeared to be advected to the west as was suggested by Townsend *et al.* (1986).

At a point downstream along the coast of Maine, part of the eastern Maine coastal current becomes a cold plume as it turns offshore to become part of the Jordan Basin cyclonic gyre system. These waters appear to carry at least some larvae offshore. In order for larvae to be carried offshore with cold water plume, however, they would first have to escape the tidally mixed spawning areas. The exact trajectory of the coastal current/plume system is quite variable, particularly in terms of the point where it leaves the coast as the coastal plume. Because the coastal current results primarily from density contrasts between tidally mixed coastal waters and the more dense, slope-origin, waters in Jordan Basin, the baroclinicity, or intensity of geostrophic current that results, is a direct function of the relative volume of slope water in the basin, which in turn is highly variable (Townsend 1992). Thus, the fate of larvae transported within this current is also potentially variable.

Intrusions of slope water in the Gulf of Maine occur in variable pulse-like events that may be related to storms or interactions of Gulf Stream warm core eddies with the shelf edge in the vicinity of the northeast channel (Townsend and Spinrad 1986; Brooks 1987). One effect of slope water intrusion events is an increase or decrease in volume of dense slope water in Jordan

Basin, and thus in sea surface slope between coastal waters and offshore waters in the basin. This translates into variable baroclinicity, which can, during periods of greater slope water volume in Jordan Basin, spin up the cyclonic circulation over the basin and thus entrain more coastal waters and redirect the coastal current/plume system offshore (Brooks and Townsend 1989). This causes a more energetic coastal current, as well as a more tightly turning circulation around the topographic low over Jordan Basin (Brooks and Townsend 1989). This phenomenon has been hypothesized to result in a greater proportion of herring larvae emanating from the eastern Maine-Grand Manan spawning group overwintering offshore in the Gulf rather than in inshore nursery areas (Townsend *et al.* 1989). This would be especially significant for larvae when these episodes of slope water intrusions coincided with the period of larval drift shortly after spawning. The variability in trajectory of the coastal current/plume system also could result in important interannual variability in both the relative and absolute numbers of larvae that overwinter offshore in the Gulf of Maine. Townsend (1992) pointed out that processes that could influence the spawning grounds in the western Gulf of Maine might be similarly influenced, since waters in the eastern and western sectors of the inner Gulf of Maine appear to be tightly coupled by a mesoscale anticyclonic eddy in the center of the Gulf.

Townsend *et al.* (1986) argued that it was more advantageous for larvae to drift with residual coastal currents, which effectively bring them into contact with a greater food supply, than to be retained in the tidally mixed waters of the spawning areas, which exhibited relatively low plankton production because of light limitations. Initially, larval feeding conditions would generally be better for those larvae that are transported along with the coastal current/plume system, since this system is quite productive and important to the biological productivity of the Gulf of Maine in general (Townsend *et al.* 1987). Drift of the larvae with this current results in their being present in the greatest density of zooplankton food items at just the right time, as they become dependent on exogenous feeding following yolk-sac absorption (Sherman 1976, 1980). With increasing distance away from areas of high energy and vertical mixing in the east, the water column begins to stratify. Increasing stratification leads to increased phytoplankton production and biomass, followed closely by increases in early developmental stages of copepods, which appear to propagate in response to phytoplankton increases. The coastal current (mean speed ca. 17 km/d) is unidirectional and does not reverse with tide. It transports larvae along with developing food resources that peak 8-10 d later in a region about 150 km downstream. Larval condition factors increase to a maximum at this point (Townsend *et al.* 1986). These findings contrast with those of the Iles and Sinclair (1982) larval retention hypothesis. Kiorbøe *et al.* (1988) found a similar pattern for larvae in a frontal region in the northwest North Sea.

It is conceivable that episodes of greater offshore transport of larvae, at least from the eastern Gulf of Maine, result in better survival through the winter. Townsend *et al.* (1989) offered a number of possible explanations for enhanced survival of herring larvae overwintering in offshore waters of the Gulf. The higher temperatures offshore (by 2-4°C compared with inshore areas), especially at depth, might favor more rapid development and hence reduce the time when larvae are most susceptible to predation. Larvae in offshore waters of the Gulf of Maine in winter months could derive some benefit should they reside near the bottom, where the warmest waters in the Gulf are at this time (Bigelow 1927), and where zooplankton populations associated with the bottom nepheloid layer could enhance their feeding environment (Townsend *et al.* 1992).

Since water temperatures can vary by as much as 5 °C between inshore waters along coastal areas of both Maine and Nova Scotia and offshore waters in winter, growth rates of larvae could thus be dependent on where the larvae overwinter. In the Georges Bank-Nantucket Shoals area, evidence suggested that differential overwintering mortality of autumn-spawned herring larvae residing there might have been caused by starvation, because zooplankton levels were at their lowest during this time of year (Chenoweth 1970; Graham and Davis 1971; Sherman and Honey 1971; Dubé *et al.* 1977; Lough *et al.* 1980).

Having survived the winter, inshore migration by the larvae may be related to the intense spring bloom of potential food items in inshore Gulf waters that occurs in February and March (Townsend and Spinrad 1986). Appearance of the springtime peak in herring larvae is coincident with the peak in total annual abundance of all species of fish larvae in coastal Maine waters, which is believed to be related to the production cycle of their zooplankton food (Townsend 1984). If Townsend *et al.* (1989) are correct in concluding that larvae transported offshore under such circumstances are more likely to survive the winter, then enhanced larval survival and perhaps a strong year-class would be expected under these conditions.

It is possible that the relative proportion of larvae that is advected away from the eastern Maine-Grand Manan spawning area differs between years. Should the exact locations of spawning vary between years in relation to the position of the tidal front, we might expect to see corresponding interannual differences in the proportions of herring larvae retained in the area or transported away. It is possible that in some years larvae hatch closer to the frontal region, which would facilitate their being entrained in the eastern Maine coastal current. In addition, and perhaps more importantly, the position of the tidal front varies in its onshore-offshore position depending on the lunar tidal phase. This lunar period, in concert with variable egg bed locations, could produce a periodic release of larval cohorts from the spawning areas, which have been reported to arrive in a series of waves along the coast of Maine (Graham and Townsend 1985). Thus, it is possible that these two processes, variable egg-bed locations and variations in tidal mixing on a lunar cycle, could interact to affect the relative proportion of larvae retained versus transported. Further variability in larval transport could be explained by the above processes interacting with the episodic nature of slope water intrusions into the Gulf of Maine and corresponding changes in the coastal current plume system.

Campbell and Graham (1991) developed a numerical simulation model that underscored the complexity of herring recruitment. This model suggested that interacting processes including larval food supply, winter temperatures, and longshore transport, may influence larval survival following hatching in the coastal, tidally-mixed areas of the Gulf of Maine as larvae face the overwintering period prior to metamorphosis. Add to this list of factors the variability in the timing and nature of impacts of episodic hydrographic events, such as warm core eddies, storms and other features discussed in Townsend (1992), and the emerging picture for comprehending year-class success in Atlantic herring is one of great complexity, highlighted by the interaction of a large number of unpredictable, interacting events. It is little wonder that Townsend *et al.* (1989) concluded that the state of knowledge of how herring early life history dynamics and recruitment processes might exert an important influence on year-class strength remains at only a rudimentary level.

Stocks, Population Structure, and Fisheries Management Issues.

No other teleost species has such a complex population structure or exploits such a wide range of reproductive environments in space and time as does the Atlantic herring (Blaxter 1990). Different populations have colonized environments ranging from high salinity-long migration-oceanic niches in the Atlantic to low salinity-local migration-inshore niches such as those in the Baltic Sea. Each population seems to have preferred spawning grounds and feeding and wintering areas. Fluctuations in biomass occurring in many populations, resulting from natural conditions as well as from increased fishing efforts, have created a need for accurate information on the population biology of this species (Kornfield *et al.* 1982).

The most interesting biological differences between the various populations of Atlantic herring relate to reproduction (Blaxter 1990). In general, herring, at the time of spawning, can be separated into populations which have a characteristic spawning time and place. Historically, throughout the western Atlantic and other regions, a number of specific and subspecific categories have been described to recognize the spawning populations of herring including sibling species, subspecies, populations, stocks, sub-stocks, or races, with little distinction being drawn between these categories (Parrish and Saville 1965; Haegele and Schweigert 1985; Smith and Jamieson 1986). (Throughout the remainder of this discussion subspecific biological categories will be referred to as populations and population segments for fishery management purposes will be referred to as stocks.) Biologists have attempted to use a variety of techniques to discriminate herring populations and stocks including differences in morphology, morphometrics and meristic features (Svetovidov 1952; Anthony 1981b; Lough 1976; Parsons 1972, 1973; Parsons and Hodder 1974; Bird *et al.* 1986), tagging (Anthony 1981a; Stobo 1983; Waring 1981), biological tags (McGladdery and Burt 1985), electrophoretic studies (Ridgway *et al.* 1970; Odense 1980; Odense and Annand 1980; Truveller 1971; Kornfield *et al.* 1982; Grant 1984), mtDNA studies (Kornfield and Bogdanowicz 1987) and life history patterns (Côté *et al.* 1980; Iles and Sinclair 1982; King 1985).

Of all commercially important species, the herring is central to the stock question in fisheries management. Attempts to define populations and stocks of herring have had a long and controversial history (Kornfield *et al.* 1982). Since large numbers of mature adults spawn at relatively discrete geographic locations (Boyar *et al.* 1973a), individual spawning aggregations were historically considered by fisheries managers to be distinct populations or stocks. Parrish and Saville (1965) subdivided Atlantic herring into five groups (without taxonomic status): three groups occurred in the northeastern Atlantic, and two in the northwestern Atlantic. Western Atlantic groups were distinguished by times and locations of spawning, which geographically overlapped in the Gulf of St. Lawrence. These groups, however, were not distinguishable by differences in body size and vertebral number (Parsons and Hodder 1981; Messieh and Tibbo 1971; but see Côté *et al.* 1980). A southern group extended from Virginia to the southern portion of the Gulf of St. Lawrence. These herring spawned in autumn on offshore banks (Anthony and Waring 1980). A northern group of herring spawned in spring, but did not make extensive migrations (Day 1957a, 1957b; Tibbo 1956).

In the northwest Atlantic, there is a mixture of spawning seasons occurring in the populations, with a general clinal trend of spring spawners predominating in the north and autumn spawners predominating in the south (Haegele and Schweigert 1985). These two seasonal spawning groups also differ in a number of other biological parameters. Winter- and spring-spawning populations have large eggs and low fecundity, whereas summer and autumn spawners have small eggs and high fecundity. A simplistic explanation for these differences are poor food supply and low predator pressure in winter and spring, whereas production of more, smaller eggs is related to good food supply and large predator population present during summer and autumn (Blaxter 1990). Additional to differences in spawning time, members of these two broad seasonal groups also differ in age-frequency distributions, growth rates, otolith morphologies, and mean numbers of pectoral-fin rays and dorsal-fin rays.

Intermixing of seasonal spawners from different spawning areas has been the point of repeated speculation (Vernberg 1977). Tagging studies in the western North Atlantic have shown extensive migration and mixing of stocks during nonreproductive periods (Creaser *et al.* 1984). Fish tagged in the Gulf of Maine, Georges Bank, and Nova Scotia mix during non-spawning migratory periods (Speirs 1977; Stobo 1976). Earlier investigations reported that members of different populations of herring in the western Atlantic could sometimes be separated outside the spawning season by anatomical characteristics such as counts of vertebrae, finrays, gillrakers, and scales, or by length or age at first maturity, or by asymptotic (theoretical maximum) length. Herring spawning on Jeffreys Ledge and along the U.S. coast of the Gulf of Maine were recognized as a single stock (Kelley and Stevenson 1985) distinguished from the Georges Bank and southwest Nova Scotia stocks on the basis of differences in phenotypic characters such as growth rates and numbers of finrays and vertebrae, as well as differences in sizes of spawning populations, larval drift patterns, seasonal adult migrations, and parasite occurrences (see Sindermann 1979, for summary). Anthony and Boyar (1968), noting significant differences in number of pectoral-fin rays and vertebrae among samples of herring from the northwest Atlantic, concluded that two general complexes of herring existed within the Gulf of Maine. Meristic differences were interpreted as indicating a change in the distribution of herring. Stevenson *et al.* (1989) considered there to be three stocks of herring that spawn in the summer and fall: 1) the Gulf of Maine off southwest Nova Scotia; 2) Georges Bank; and 3) various locations along the U.S.-Canadian coast between Cape Cod and Grand Manan Island.

Earlier researchers had considered spring- and fall-spawning herring to represent a single population (Jean 1956; Tibbo and Graham 1963), while others strongly supported the idea of separate populations (Messieh and Tibbo 1971; Messieh 1975; Côté *et al.* 1980) for herring spawning in different seasons. Clinal trends indicate an environmental trigger to spawning, and there is firmer evidence that the spawning period is not genetically fixed (Smith and Jamieson 1986). For example, in the northwest Atlantic, autumn- and spring-born fish, identified by otolith characteristics, have been found spawning in their opposite seasons (Messieh 1972). These results suggest that the spawning period is not highly heritable and that fish born in one season do not necessarily spawn in the same season upon reaching maturity. A group of herring within an area may also change its spawning pattern in response to changes in environmental conditions. Thus, apparent differences in spawning times between populations do not necessarily provide evidence for discrete stocks. Although adults concentrate annually at specific locations to spawn, fidelity of particular stocks to specific spawning areas is not absolute. Tagging studies in the northwest Atlantic indicate a homing rate of 66-93% (Wheeler and Winters 1984b), with movement rates to neighboring stocks of 7-34%. These movements between neighboring stocks are small in relation to the range of the entire distribution, but they demonstrate a significant gene flow between neighboring spawning sites.

Meristic characters have been employed to discriminate populations with varying results, and otoliths have been successfully used to demonstrate significant differences between spring- and fall-spawning populations (Côté *et al.* 1980; Messieh and MacDougall 1984). None of these techniques, however, have clearly differentiated one spawning group from the other. Despite characterization of some stocks by these methods, variation in meristic and morphological characters may be induced by different thermal regimes during development (Kornfield *et al.* 1982). Kornfield *et al.* (1982) suggested that the absence of temporal consistency in meristic data does not support a multipopulation model for Atlantic herring.

Iles and Sinclair (1982) proposed the "larval retention hypothesis," as a basis for understanding reasons for the existence of genetically discrete herring stocks (= populations), locations of spawning sites to which they home, and relative (maximum) stock size of individual populations. All of these factors were determined by the number, location, and extent of geographically stable retention areas in which larvae can remain aggregated for the first few months of life (Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair and Iles 1985). Iles and Sinclair (1982) argued that well mixed zones and fronts acted as the physical basis for retention of larvae and a focus for the homing instinct in adult herring. Retention was not passively maintained by circulation features, but rather it was achieved actively probably through behavioral responses of the larvae, such as vertical migration in relation to tidal currents. The geographically discontinuous character of the larval retention areas was thought to reinforce the genetic isolation produced by aggregation into discrete spawning populations. Under this hypothesis, the tandem effect of these two processes should produce a complex genetic population structure in Atlantic herring. Stephenson and Kornfield (1990) noted that the reappearance of spawning herring on Georges Bank was due to a resurgence of the population found there and not recolonization from other areas. They argued that the persistence of this population, in spite of considerable potential for recolonization by herring from other areas, supported the discrete population concept in herring.

Smith and Jamieson (1986) in discussing the larval drift hypothesis noted that the geographical identity of each stock is based on the larval drift from the spawning area to the nursery area (Iles and Sinclair 1982). For those individuals which spawn in unsuitable areas, the larvae will not arrive at a suitable nursery site and so will be lost to the stock. Thus, natural selection must favor the progenies of those adults which home to suitable spawning grounds. This discrete stock model was built up from, and supported by, independent observations on tag returns (Tester 1949; Cushing and Burd 1957; Hourston 1982; Wheeler and Winters 1984a, 1984b), hydrographic phenomena (Iles and Sinclair 1982), spawning times (Haegele and Schweigert 1985), morphometrics (Postuma 1974; Parsons 1975; Rosenberg and Palmer 1982; King 1985), and rates of growth, recruitment and mortality (Burd 1985).

Stephenson and Power (1988, 1989) tested aspects of the larval retention hypothesis using the area of high larval density during autumn off southwest Nova Scotia. They concluded that larvae were retained in the area and the pattern of migration by the larvae was diel rather than tidal indicating that it was being undertaken in relation to some factor (such as prey availability) other than circulation. Chenoweth *et al.* (1989) further modified the retention hypothesis by suggesting that larval retention in the eastern Gulf of Maine spawning ground was incomplete. They suggested that a significant portion of those larvae spawned in the eastern Gulf of Maine may be retained in the vicinity of the spawning grounds, only until October when the hydrographic structure delineating the frontal boundary between the tidally-mixed and stratified areas disappeared.

Fortier and Gagné (1990) also favored a modification of the retention hypothesis. They concluded that spawning times and locations in herring populations may have evolved to favor the initial cohesion of larval fish cohorts by limiting seaward dispersion during early planktonic life. But once initial retention was achieved, early survival within the dispersion area would then be determined by the spatio-temporal match between early postlarvae and their food resources. Therefore, both transport and energetic processes could influence success of a population at colonizing its dispersion area.

Evidence for genetic differentiation among North Atlantic herring populations is weak. For over 20 yr, biologists have studied biochemical variation in Atlantic herring in attempts to define population structure (Kornfield *et al.* 1982). Although allozyme differences between Atlantic and Pacific herring were found to be great enough to recognize both as distinct species (Altukhov and Salmenkova 1981; Grant and Utter 1984; Grant 1986), genetic differences between herring populations from eastern and western regions of the Atlantic are minimal (Odense *et al.* 1973; Odense and Annand 1980; Andersson *et al.* 1981; Grant 1984). Much more of the gene diversity of Atlantic herring is found contained within populations (98.9%), with much less due to population differences (1.2%) (Grant 1984).

Preliminary electrophoretic studies on herring, based on few loci and small sample size, tended to support the hypothesis of complex genetic structure in populations of this species. Previous studies have identified a portion of the biochemical genetic variation in Atlantic herring (Mairs and Sindermann 1962; Sindermann and Honey 1963; Odense *et al.* 1966; Wilkins and Iles 1966; Klose *et al.* 1968; Lush 1969; Naevdal 1969a, 1969b; Simonarson and Watts 1969; Engel *et al.* 1971; DeLigny 1972; Schmidtke *et al.* 1975; Zenkin 1978; Andersson *et al.* 1981). Genetic heterogeneity among populations of western Atlantic herring were reported within the northern American spring spawners (Kornfield *et al.* 1982) and within American autumn spawners in the southern part of the species range (Ridgway *et al.* 1971; Lewis and Ridgway 1972; Kornfield *et al.* 1982).

Among autumn-spawning stocks in the Gulf of Maine, loci showing significant differences were not temporally stable and the magnitude of differentiation between these groups is small implying that they are probably of relatively recent common origin. Rivière *et al.* (1985) also found little differentiation between populations of herring sampled at Isle-Verte, St. Lawrence estuary, using electrophoretic analysis of 10 loci.

Kornfield and Bogdanowicz (1987) using mtDNA did not find a single stock identifier among three spawning groups they examined. Spawning groups were not fully distinguishable by composite mtDNA digestion patterns; no absolute stock markers were present. They concluded that despite the availability of a larger number of polymorphic markers and adequate sample sizes, significant genetic heterogeneity among Atlantic herring stocks has not been demonstrated (Anderson *et al.* 1981; Kornfield *et al.* 1981; Grant 1984; Riviere *et al.* 1985). The magnitude of differentiation between groups is small and implies that they are probably of relatively recent common origin. Statistically significant differences in genetic markers between seasonal spawners do not provide suitable biochemical markers for accurate discrimination of individual fish. Safford and Brook (1992) also found little genetic variation using starch-gel electrophoresis and morphometric analysis of herring in the western North Atlantic. They concluded that Atlantic herring there form a single panmictic population.

Evidence from other sources also suggests that the time of spawning is not genetically fixed. Messieh (1972) found "leakage" of individuals between spawning times; fish of spring-spawning parents (identified by otolith morphology) were found in spawning condition in autumn. In addition, changes within a population in the predominance of spawning times in an area were observed in the Gulf of St. Lawrence following reductions in stock size (Moores

1980).

Current evidence suggests that despite the existence of discrete, defined spawning groups and apparent high homing fidelity, enough gene flow exists between spawning groups to prevent northwest Atlantic herring from evolving into genetically distinct stocks. It is therefore not possible to conclude that populations of each spawning type are genetically isolated from each other. Grant (1984) calculated that it required only 60 fish per generation migrating into each subpopulation to explain the amount of genetic divergence measured within groups of Atlantic herring. This remarkably small number of migrants may account for the lack of genetic divergence between adjacent areas, but he concluded that it is unreasonable to postulate regular gene exchange across the Atlantic Ocean.

Alternatively, he offered another hypothesis for the lack of transoceanic genetic divergence in herring that suggested herring populations may have only begun to diverge in recent geographic time (Grant 1984). In this scenario, a single population, or a few genetically undifferentiated populations, radiated into several widely scattered populations that do not now exchange genes. Under this model, the radiated populations have not yet begun to diverge in response to genetic drift or selection. In support of this hypothesis, Grant indicated that in addition to the genetic information, the model is supported by a mechanism of population contraction (i.e., the Pleistocene glaciation events) as well as the biology of herring. Herring are migratory in character and easily could have recolonized vacated post-glacial areas in the western North Atlantic Ocean. The rate of genetic change due to genetic drift would have been exceedingly slow at population sizes characteristic of Atlantic herring. Estimates of spawning stocks (Iles and Sinclair 1982), which range from 100 to 10^7 MT, translate into population sizes of 20,000 to 2×10^{10} fish, assuming that an average fish has a mass of 500 g. At these population sizes the average time to fixation for a neutral mutation, 4N generations (Nei 1975), is on the order of tens of millions of years. Clearly, very little divergence between populations would be expected in the 18,000 yr since the last glacial maximum in the North Atlantic Ocean.

In spite of the wealth of data, the taxonomic and evolutionary status of herring populations remain problematical, and continue to intrigue biologists and perplex fisheries managers (Smith and Jamieson 1986; Kornfield and Bogdanowicz 1987). Regularity of spawning (both geographic and temporal) (Sinclair and Tremblay 1984), tag evidence for homing (Harden-Jones 1968; Wheeler and Winters 1984b), differential population dynamics of neighboring groups (Sinclair and Iles 1985), and discrete larval distributions (Iles and Sinclair 1982) all suggest that herring spawning units are distinct populations, i.e. self-sustaining, and geographically and genetically discrete. Conversely, much traditional evidence for discrete stocks, based on morphometrics, spawning times and tag returns, is shown to be weak and based on a typological concept. The lack of demonstrable differences in traditional stock identification methods and genetic (particularly isozyme) characteristics have been interpreted as indicating significant gene flow among neighboring spawning aggregations. Results of allozyme surveys have shown little or no genetic divergence between herring stocks (Kornfield *et al.* 1982; Grant 1984; Grant and Utter 1984; Ryman *et al.* 1984; Safford and Brook 1992). Because of the weight of established opinion on herring stocks, allozyme markers have been interpreted as being insensitive to stock events (Kornfield *et al.* 1982; Grant 1984; Grant and Utter 1984; Ryman *et al.* 1984; Cushing 1985). Nor is there a genetic basis to the discrete stock model based on larval retention areas (Iles and Sinclair 1982), although this remains an important model of abundance and recruitment.

Lack of genetic differentiation among populations of Atlantic herring also means that observed phenotypic differences are most likely due primarily to differences in environmental conditions during development, and therefore will not be reliable indicators of stock identity. Results show that individuals from discrete spawning groups cannot be reliably identified off the spawning grounds. Therefore, the contribution of each spawning group to various fisheries cannot be estimated. These results also suggest that the demise of a single spawning ground will not adversely affect the underlying genetic structure of the herring population, as few unique genes should be found exclusively within a spawning location. However, small discrete spawning grounds are apparently necessary to support a large population. Small spawning grounds may be necessary for appropriate spawning behavior or to ensure proper conditions for the larvae. Therefore, until the relationship between discrete spawning grounds and healthy herring populations is understood, management policy should include the maintenance of existing spawning grounds.

Smith and Jamieson (1986) have argued that the lack of genetic divergence among Atlantic herring populations, coupled with the change in spawning season of some of the major stocks, the movements revealed by tagging, and the re-appearance of some "extinct" stocks point to a dynamic balance rather than a discrete stock structure. Therefore, a re-appraisal of the discrete-stock concept is needed for this species. They suggested that herring populations are artificial and transient sub-divisions of a larger gene pool and consequently these have no taxonomic or evolutionary status. That is not to say that the dynamic nature of the herring populations has no evolutionary importance. The spawning populations do not have racial continuity, but their ability to respond and adapt to changing environmental conditions may contribute to the abundance and wide range inhabited by the species. The *Clupea* distributions appear as “sausage shapes” along the continental margins of the North Pacific and North Atlantic oceans. Environmental and seasonal changes, and more recently fishing activities, have exerted irregular pressures, causing contraction of the species in some areas and expansion in others. The stocks appear where the pressures are relaxed and contract where squeezed, but gene-flow is sufficient to maintain the genetic identity of the species.

Smith and Jamieson further pointed out that eliminating the discrete stock concept may appear to simplify management of the species, but the dynamic population concept will demand more careful biological monitoring to determine the changing effects of environment and fishing activities on the species, which for the pragmatic fisheries manager, means there are no easy solutions. One of the great problems in managing stocks of this species is the inability to assess the effects of fishing effort on mixed populations outside their spawning season.

Kornfield and Bogdanowicz (1987) concluded that consistent, significant, genetic differences among spawning groups of Atlantic herring are sufficient, but not necessary, conditions to regard populations as discrete stocks. Their results did not support the hypothesis that discrete Atlantic herring stocks exist throughout the Gulf of Maine, however, the absence of such differences did not allow them to rigorously conclude that there was gene flow among the populations in question. They recommended that, for the sake of preserving variability, resources like the Atlantic herring should be managed under the assumption that every spawning group is a semi-discrete genetic entity.

As a postscript to this discussion on population structure of Atlantic herring, in an important recent paper on herring population dynamics McQuinn (1997) proposed unifying divergent views (discrete population concept and dynamic balance concept) of herring population structure under the metapopulation concept. He concluded that available information suggests that Atlantic herring population structure and dynamics are well described within the metapopulation concept. He uses the example of sympatric seasonal-spawning populations to illustrate the strategy, opportunity and mechanism by which local population integrity and persistence are maintained within the adopted-migrant hypothesis. Local population integrity is maintained through behavioral isolation, i.e. repeat rather than natal homing to spawning areas, while local population persistence is ensured through the social transmission of migration patterns and spawning areas from adults to recruiting individuals.

Importance and Utilization.--Atlantic herring are a significant resource along the eastern coast of the United States and Canada (Kornfield *et al.* 1982), where both spring- and autumn-spawning herring populations support major fisheries (Messieh 1988). Herring usually occur in commercial quantities along the coast of southern Labrador, around the coast of Newfoundland and the offshore banks, in the Gulf of St. Lawrence, along the coast of Nova Scotia and the offshore banks, the Bay of Fundy, including Passamaquoddy Bay, Gulf of Maine, Georges Bank, and during wintertime to coastal waters of Rhode Island, and south to Virginia. The waters of southwest Nova Scotia support a herring population estimated to be on the order of 453,550 MT, which is the basis of the largest herring fishery in the western Atlantic (Total Allowable Catch in excess of 90,710 MT) (Stephenson *et al.* 1987). The larval patch which results from spawning of this population is the largest and best defined of those in the Bay of Fundy and Gulf of Maine (Stephenson and Power 1989). Annual surveys of this larval area are used as an index of abundance in stock assessment (Iles *et al.* 1985; Stephenson *et al.* 1987).

The herring has been continuously exploited since pre-colonial times when prodigious populations were commonly observed by coastal communities. At one time, herring populations were considered inexhaustible, but in recent years stocks in both Atlantic and Pacific waters have declined due to over-exploitation (Whitehead 1985a, 1985b; Scott and Scott 1988). Although stocks have been badly over-fished and depleted in recent years, *Clupea harengus* still ranks as the third most heavily exploited clupeid fish in the world (Whitehead 1985a).

Historical trends and locations of commercial catches within the Gulf of Maine were discussed by Bigelow and Schroeder (1953). A detailed account of fishing activity and fisheries exploitation for *C. harengus* in the western Atlantic was provided by Sindermann (1979), and is presented below.

The earliest organized fishery for herring in the western North Atlantic was probably conducted by Indians using brush weirs (Earll 1887). Captain John Smith's account of the herring in the Gulf of Maine provides some indication of the former abundance of this species: "The savages compare the store in the sea with the hair of their heads, and surely there are an incredible abundance upon this coast." With the appearance of Europeans on American shores and in American waters, herring fisheries developed in a series of phases, with a number of critical motivating factors: (1) European vessels fishing for cod visited waters of the western North Atlantic beginning about 1500 AD. The Europeans discovered very early that herring for bait could be taken near the cod grounds by gillnets fished at night. (2) Beginning with the earliest permanent settlement, herring were used as food by the colonists, as well as for cod bait. Following the Indian example, the Plymouth Colony built and operated a herring weir as early as 1641. (3) During the 19th century, salt herring, either as food or bait, was much in demand, and substantial fisheries developed off Newfoundland, in the Gulf of St. Lawrence, and off New England. (4) With the introduction of trawling for cod and other groundfish, demand for herring as bait declined in the later part of the 19th century, but at about that time (the 1870s) canning juveniles as sardines began and prospered on the Maine and New Brunswick coasts. Additionally, the lobster fishery expanded after 1860, and herring was a major source of bait for this activity. The sardine fishery for juveniles was the principal herring fishery during the first half of the 20th century. (5) Beginning in 1961, exploitation of offshore adult herring stocks by foreign distant water fleets began, and increased annually until 1969, when the combined catch by all nations fishing in waters of the western North Atlantic was almost 907,000 MT. (6) During the 1970s, concern about over-exploitation led to imposition of international catch limitations of increasing severity as herring stocks continued to decline. Almost total failure of the autumn 1977 adult herring fishery on Georges Bank was the most disturbing event during this period of intensive fishing and resultant decline in stock size.

In terms of relative impact on herring stocks, the entire history of the fishery can be divided into two phases representing periods of pre- and post-1961. Before 1961, exploitation by man was minimal, with some stocks (such as Georges Bank) untouched, and other stocks (such as those off southwest Nova Scotia and in the Gulf of St. Lawrence) harvested minimally and inefficiently by gillnets and other fixed gear. The only herring fishery that could be described as intensive prior to 1961 was the sardine fishery for juveniles on the Maine and New Brunswick coasts, and even this fishery was conducted principally with fixed gear. After 1961, fishing pressure on all stocks increased enormously, with mobile gear (otter trawls, paired trawls, mid-water trawls, and especially purse seines) accounting for dramatic increases in annual landings from all known herring stocks of the Northwest Atlantic region.

Landings in the northwest Atlantic from 1920 to 1940 were relatively stable at about 80-100,000 MT, then increased gradually through the 1940s to a peak of 242,000 MT in 1948. During the 1950s catches stabilized at about 160-200,000 MT. The decade of the 1960s saw an unprecedented increase in catches to 967,000 MT in 1969. This dramatic increase occurred because of almost simultaneous developments in several areas: the intensive Georges Bank fishery by several foreign fishing nations (notably the former USSR, Poland, the Federal Republic of Germany, and the former German Democratic Republic) beginning in 1961; the Nova Scotia purse seine fishery for adults, beginning in 1964; the Gulf of St. Lawrence purse seine fishery, which intensified after 1965; and the western Gulf of Maine adult fishery, which began in 1967. An extreme level of exploitation developed quickly during the late 1960s, and was followed in the 1970s with rapidly declining stocks and restrictions on total catches from those much reduced stocks. Increased demand for herring, combined with constantly expanding fishing capacity, led to greater and greater pressure on existing stocks in international waters through vigorous exploitation.

HISTORY OF THE FISHERY IN THE GULF OF MAINE REGION IN RECENT DECADES

1950-1960. Herring fisheries of New England and southeastern Canada were primarily for sardines (juveniles in their 1st, 2nd and 3rd yr of life) using weirs and stop seines. Many fish less than 1-yr old were taken for pearl essence and reduction in the Bay of Fundy. Some adults were taken for lobster bait, reduction, and pickling, by trawlers in Block Island Sound, by floating traps in New Jersey in spring, by purse seining near outer islands (Isles of Shoals, Martinicus, and Grand Manan), and by gill nets off southern Nova Scotia.

From the late 1940s to the early 1960s the annual Maine sardine catch averaged about

58,962 MT (1.8 billion fish) of which age-2 herring constituted about 25,399 MT. Landings in the Gulf of Maine were usually categorized as juvenile ("sardine") and adult fisheries. The division is not precise, however, since some adults may be mixed in with juvenile catches, and some juveniles may be taken in the adult fisheries. The division is particularly indistinct when age-3 fish are considered. They may represent a significant proportion of adult stocks in certain years, but they may also be purse-seined as juvenile schools several miles off the coast.

Throughout the 1950s, and until 1967, most Gulf of Maine catches were of juveniles in the sardine fishery. Large annual variations in catches have occurred during the period since World War II, with peak catches in 1950 of 90,000 MT and in 1958 of 81,000 MT. Decline in sardine catches began in the early 1950s on the eastern Maine coast, while the greatest decline in the central and western sectors of the coast occurred in the 1960s, reaching a low ebb in 1971, with some slight resurgence in the later 1970s.

1960-1970. The Soviet distant water fleet appeared on Georges Bank in force in the autumn of 1961, after several years of exploratory fishing by research vessels. Gillnets and bottom trawls were used first, then later mid-water trawls and finally purse seines of large dimensions. After initial success by the Soviets, vessels from other countries (notably East Germany, Poland, and West Germany) began to appear in increasing numbers. The Georges Bank herring fishery, non-existent in 1960, had reached a production of 373,000 MT by 1968. Initial concentration on spawning aggregations was broadened and expanded to include fisheries on over-wintering grounds from southern New England to Cape Hatteras and on spawning and overwintering groups in the Gulf of Maine.

Failure of the Pacific herring fishery off British Columbia in the 1960s, combined with increased demand for fish meal, diverted Canadian purse seine efforts to the Atlantic. Catches in the Gulf of St. Lawrence, off Newfoundland, and off Nova Scotia increased enormously. This, combined with the increasing foreign catches on Georges Bank and in the Gulf of Maine, resulted in an enormous increase in total herring landings in the Northwest Atlantic during the decade, from a catch of 180,000 MT in 1960 to 300,000 MT in 1964, to 600,000 MT in 1967, then to a phenomenal 967,000 MT in 1969.

During the 1960s, the Maine sardine fishery, which is largely dependent on annual recruitment of 2-yr-old herring, continued a decline that began in eastern Maine in the 1950s and was hastened by a succession of weak year-classes (1963-1965, and 1967-1969). These years of repeated poor recruitment were interspersed with years in which recruitment was good, but the overall decline continued, and included central and western Maine juvenile stocks. The 1960 and 1961 year-classes were excellent, that of 1966 was good, the 1970 year-class was excellent, and the 1974 year-class was good (in terms of relative catches in the juvenile fishery); all other year-classes up to 1974 were poor to very poor.

Declines in juvenile catches on the Maine coast preceded the intensive fisheries on adult stocks on Georges Bank and Jeffrey's Ledge by a number of years. Obvious decline began after 1969 on Georges Bank and after 1971 for Jeffrey's Ledge, and may have begun a few years prior to these dates. Thus, there seems to be little obvious relationship between reduction in adult stock size on Georges Bank and Jeffrey's Ledge, and the decline in juvenile catches on the Maine coast; the decline in the juvenile fishery clearly preceded the increase in exploitation of adult herring in the Gulf of Maine and on Georges Bank.

Significant events also occurred in Canadian waters during the 1960s. A new fishery started in the Banquereau area late in 1968, and by the end of the first full year of exploitation, more than 250,000 MT of herring had been taken. Landings from southwest Newfoundland increased from 6,000 MT in 1961 to 145,000 MT in 1968, and there were five-fold increases in Canadian catches from the Gulf of St. Lawrence and the Bay of Fundy during this same period.

The fishery for juveniles on the western side of the Bay of Fundy took an average of 39,005 MT annually during 1963-65; 56,240 MT during 1966-69; and 20,863 MT in 1970-71. Of these catches, the winter purse-seine fishery took about 54%, principally very small fish less than 1.5 yr.

During the 1960s, three distinct kinds of Canadian fisheries existed in southern Nova Scotian waters: the inshore gillnet fishery for adults; the weir fishery for juveniles; and the purse seine fishery for pre-spawning fish. Catches from traditional weir and gillnet fisheries fluctuated very little from 1960-1970, each accounting for about 9,071 MT annually. Catches by purse seiners, however, increased dramatically in the mid-1960s, reaching a peak of about 108,852 MT in 1967 and 1968.

1970-1979. Several major events took place during this time period. (1) Intensive fishing pressure on all stocks continued until (and even after) national quotas and total allowable catches were imposed by the International Committee on North Atlantic Fisheries (ICNAF) in 1972. (2) The Georges Bank stock continued a decline which began before 1969, and the fishery failed almost completely in 1977, despite imposition of severe catch restrictions (Total Allowable Catch- 60,000 MT) in 1976. (3) The U.S. withdrew from ICNAF and extended its fishery jurisdiction to 200 miles in March 1977. Fishing on U.S. herring stocks in 1977 was limited. Quotas (TAC) were 7,000 MT (Gulf of Maine), with allocations to Canada and others, and 33,000 MT (Georges Bank) with allocations to Canada, Cuba, France, FRG, GDR, Poland, Romania, USSR, and others. (4) During the early 1970s, juvenile catches were low, with an average of less than 20,000 MT, except for 1976, when the catch reached 26,000 MT. The 1971 catch of juveniles in the Maine sardine fishery was only 12,000 MT, the lowest in the history of the fishery. Good year-classes occurred in 1970 and probably in 1974 (based on relative catches in the juvenile fishery). (5) By the end of 1971, the winter purse seine fishery for very small juveniles on the west side of the Bay of Fundy was virtually eliminated by a size restriction imposed as a conservation measure. (6) The Gulf of Maine fishery for adult herring, mainly in the Cape Ann-Jeffrey's Ledge area, began in 1967 and reached a peak period in 1970-72 with catches of 34-39,000 MT. Catches then leveled off at 14-20,000 MT during 1973-76. Beginning in 1975 the catch has been taken principally by the United States. (7) Canadian catches which had begun at about 20,000 MT in the early 1960s (total catches including juveniles and gillnetted fish) rose to 114,000 MT in 1971, 116,000 MT in 1972, 136,000 MT in 1973, 140,000 MT in 1974, and 145,000 MT in 1975.

1980s. A fishery for the Atlantic herring on Georges Bank began in 1961 and yielded 2.45 million MT before crashing in 1977 after a classic "boom and bust" pattern (Stephenson and Kornfield 1990). Demise of the Georges Bank population is thought to have been the result of overfishing, combined with a series of poor recruitment years (Anthony and Waring 1980; Grosslein 1987). The period directly after the collapse, when the Georges Bank population showed no evidence of recovery, coincided with several years of low or average recruitment in neighboring populations (Anthony and Fogarty 1985; Stephenson *et al.* 1987). During that time, variables which influenced recruitment were negatively impacting all herring in the Gulf of Maine. For several years, there was virtually no sign of either adults or larvae from a spawning population that had once been estimated at 1.03 million MT in size (Anthony and Waring 1980; Hennemuth and Rockwell 1987). Virtually no spawning activity was recorded over the years 1977-1984. Only recently has there been generally good recruitment that provided a chance for the Georges Bank population to recover.

The commercial loss was felt not only in the collapse of the large adult fishery, but also in the decrease of the coastal weir fishery in Maine and New Brunswick, which is assumed to have been partially dependent on juveniles from Georges Bank (Sinclair *et al.* 1985). The socio-economic implications of the collapse prompted international meetings to examine the possibility of re-establishing herring on Georges Bank (Graham 1988). The absence of herring after collapse of the Georges Bank fishery was confirmed in a number of research surveys by both Canada and the United States (Stephenson and Kornfield 1990). Sampling during autumn between 1977 and 1984 recorded almost no herring (Smith and Johnson 1986; Azarowitz and Grosslein 1987). More recent surveys indicated reappearance of the herring on Georges Bank, including documentation of spawning in 1986-1987. The reappearance was first noted with captures of postlarval herring in the spring of 1984. Research surveys began detecting prespawning adult herring in the spring of 1986 and first spawning adults in the fall of 1986. These fish were almost exclusively 3-yr olds. Greater numbers of spawning adults were documented again in the fall of 1987, as were also substantial numbers of larvae. Recent evidence (NEFSC 1993) indicates that herring spawning is once again extensive on Georges Bank; herring have now substantially recolonized their historic spawning grounds on eastern Georges Bank. The abundance level of herring has recovered to, and even exceeded, the levels of the mid-1960s, the period prior to foreign overfishing of this species. The population has several strong year-classes, and it is now possible to consider the herring recovery "complete."

The reappearance, almost a decade after collapse of the fishery, raised the question of whether it was the result of resurgence of some remnant of the original Georges Bank spawning population, or recolonization of the Bank by neighboring populations. Three independent lines of evidence suggest that the reappearance of herring on Georges Bank was due to resurgence of the extant Georges Bank population rather than to recolonization from elsewhere. First, reappearance was by a single year-class. Second, isozyme analysis of tissues from adult Georges Bank herring revealed differences from other stocks in the Gulf of Maine. Third, the reappearance of Georges Bank herring did not occur for several years during a time when neighboring populations supported substantial fisheries. Additionally, the group that reappeared exhibited characteristics (location and timing of spawning) which matched those of the historical Georges Bank population and differed from those of neighboring populations.

Maine-New Brunswick Juvenile Fishery

The Maine juvenile fishery for sardines began in the mid-1870s and has been characterized by great annual variations in supply, but by longer-term trends in production. These trends were reviewed by Anthony (1972) and Anthony and Waring (1978). Periods of abundance and scarcity seem apparent: from 1896 to 1916 catches averaged 60,000 MT, then dropped drastically during the period 1917-1940 to an average of 25,000 MT. From the late 1940s through the early 1960s production increased to earlier levels (ca. 60,000 MT average, with large annual fluctuations). During the late 1960s production decreased again to an average of 28,000 MT, and decreased further still during the early 1970s to an average of only 17,400 MT. Some resurgence was seen in 1976 and 1977, however, when catches were 26,400 MT and 27,800 MT, respectively. Whether early periods of low catches (such as the period 1917-1940) were reflections of biological events or merely economic events is not completely understood.

The sardine fishery concentrates on age-2 fish, but will use age-3 fish early in the season and age-1 fish late in the season, to an extent determined by relative availability of age-2 fish. The history of the Maine sardine industry has been one of reduction in production since the early 1950s. Operating canneries have decreased from 50 in the early 1950s to 15 in 1977, and production during that period declined from 2-3 million cases/yr in the early 1950s to about 1 million cases in recent years. The harvest of 2-yr-olds in the Maine sardine fishery has fluctuated from < 4,536 to > 54,426 MT/yr since 1960, reflecting, to a large degree, variations in year-class strength (Stevenson *et al.* 1989).

Exploitation.--A common characteristic of nearly all herring fisheries that have collapsed was their abrupt demise without evident symptoms of distress (Winters and Wheeler 1987). A classic example of this phenomenon was the Georges Bank herring stock that once represented the largest herring population in the Northwest Atlantic (Anthony and Waring 1980), and which sustained catches in excess of 126,994 MT for the period 1966-1975 and then collapsed to less than 1,814 MT by 1977 (Anthony and Fogarty 1985). Analyses showed that recruitment levels plummeted due to catches exceeding surplus production and standing stock biomass declined precipitously from near record levels for the 1979 year-class to virtually nil for the 1981 and subsequent year-classes (Anthony and Fogarty 1985). Stock assessments failed to detect this trend (Anthony and Waring 1980). Such rapid recruitment failures suggest a stock-recruit curve with a very steep left-hand limb and a relatively low threshold (i.e. critical) spawning biomass. This kind of stock-recruit relationship is probably associated with an over abundant egg production, and therefore, recruitment success will be largely determined by density-independent factors. Townsend *et al.* (1989) and Townsend (1992) discussed these factors in light of larval survival and potential recruitment success in the Gulf of Maine.

In the Gulf of St. Lawrence (Moores and Winters 1982; Winters *et al.* 1986) and Newfoundland (Winters and Wheeler 1987), temperature variability was shown to be the main factor associated with variations in the annual growth of several stocks.

Doubleday (1985) reviewed implications of biological characteristics of herring on fishery management strategies, noting that growth patterns and recruitment fluctuations limit opportunities to stabilize catches and stock biomasses without substantial loss of yield-per-recruit. Adult herring stocks under exploitation lack resilience. Stock dynamics, therefore, are much more dependent on recruitment strength than to growth of recruited fish. Under fishing pressure, herring stocks tend to narrow their geographical range (Blaxter 1990). Being a schooling species, the declining stock aggregates in an ever-reduced area, thereby decreasing the diversity of spawning times and locations of the population. Potential effectiveness of fishery management plans is also constrained by tendencies of herring populations to school. Aggregation of fish into schools reduces self-regulatory possibilities in the fishery by allowing catch rates to remain high when overall fish abundance is low (why stocks collapse). Also, at times of low abundance, herrings of different stocks may mix during school formation, complicating estimations of catch-at-age and abundance indices for individual stocks. Given the vulnerability of herring to exploitation and the imprecision of abundance indices, achievement of relative stability of spawning stocks and catches requires adoption of fishing mortality rates near or below 0.2 in adult herring fisheries. If exploitation rate exceeds 0.3, decline of the spawning stock size to a level equal to less than one average recruiting year-class must be expected more than once every 10 yr.

Intensive fishing of adult herring was cited by the sardine industry as the principal cause of the reduced abundance of juveniles in coastal waters of Maine. The industry was well-organized, and had spoken vigorously for effective management of adult herring stocks, both within state territorial waters and in the fishery conservation zone. Conversely, though product prices may be higher for this life-history stage, fisheries on immature herring may also reduce, and even destabilize recruitment, thereby providing lower yield-per-recruit levels than for fisheries on mature herring..

Consumption.--Herring, especially smaller fishes, fresh from the water, are among the most delicious of fishes. The only drawback to eating these fish is that they do not keep well, being rich-meated and oily, and larger-sized fish have many hair-like bones that are troublesome. Atlantic herring have been prized as human food for centuries, and herring fisheries have been the cause of much human conflict (Whitehead 1985b; Scott and Scott 1988). Herring are especially rich in oil, with seasonal values of oil content of raw herring averaging 5-9% for spring-caught fish and 10-15% for summer-caught fish (Leim 1957). Nutritional values for herring are: fat 5-12% (varies seasonally); moisture 67-73%; protein 20-22%; and ash 1-2% (Krzynowek *et al.* 1989). Braune (1987) found significant positive correlations between mercury concentrations in herring and age, weight and length of the fish.

Herring are fished commercially by gillnets, trap nets, weirs, and more recently, purse seines. Introduction of the efficient purse seine changed many traditional fisheries. Weirs are one of the major means of catching small, young, or juvenile herring (2-3 yr olds), known worldwide as "sardines" when canned.

Herring seldom take a baited hook. Although, it seems likely that large ones, when feeding on shrimp, would take an artificial fly, as do spent and hungry alewives (see below) on their return to saltwater following spawning, and shad on their upstream migration to spawning grounds (see below).

Herring represent the primary raw material for the Maine sardine industry, which is centered in the Bay of Fundy, particularly in the Passamaquoddy Bay region, where the largest sardine cannery in the world was once located. The Maine sardine industry peaked in the late 1940s with total production exceeding 3 million standard cases. In 1980, production fell to less than 1 million standard cases and in 1990 the total pack was only 820,000 cases. Fish 10-20 cm long are packed as Maine Sardines. The larger fish are prepared as canned steaks, with a variety of flavoring sauces.

Mature herring are sold fresh, frozen, smoked, salted, pickled, and canned. Small herring are packed as sardines, while larger herring are canned as kipper snacks and fillets. Probably the most important products are frozen fillets, sardines, and pickled and cured dressed herring and fillets. Smoked herring are sold as kippers or bloaters. The roe of herring has recently found a ready market as a delicacy in Japan, where the final product is called "kazunoko" (Scott and Scott 1988). The market for herring roe arose because of the decline of Japanese herring stocks. Large fish are usually exported to Europe for production of smoked and marinated products.

Herring are sometimes canned for pet food, and there is a market for adult herring as bait and feed for zoo and aquarium animals. During the 1950s and 1960s, the use of raw herring for reduction to oil and fish meal grew steadily, until by 1968-1969 most landings of Canadian herring were being processed for this market (Scott and Scott 1988). With decline in world landings of herring, use of herring for fish meal and oil production ceased and catches increased markedly in value. Herring scales are processed for the production of "pearlessence" which is used in paints and cosmetics to provide "glitter." During the 1940s there was a high demand for pearl essence derived from herring scales in making high-quality paints for aircraft.

Chapter 7. *Opisthonema* Gill 1861
Thread herrings

Description (from Whitehead 1985a).--Small or moderate-size herring-like fishes. Pelvic scute without ascending arms. Abdominal scutes present before and behind the pelvic fins. Mouth terminal, lower jaw sometimes projecting slightly. Upper jaw rounded and not notched in anterior view; two supramaxilla present, the anterior usually elongate and posterior paddle-shaped. Teeth small, conical. Dorsal fin about at midpoint of body, short (13-21 finrays); anal fin short (12-23 finrays), its origin usually well posterior to vertical through base of posteriormost dorsal-fin ray; pelvic-fin rays 7-10 (mostly 7 or 8). Bony capsule (bulla) present in pterotic bone. Opercle smooth; gillrakers usually present on posterior face of third epibranchial; upper margin of ceratohyal smooth. Posterior border of gill opening with two distinct fleshy outgrowths. No hypo-maxillary bone. Posteriormost dorsal-fin ray prolonged into long filament.

Five species found only in the New World (one western Atlantic and four eastern Pacific species), mainly in tropical and subtropical waters. These are nearshore, marine pelagic, schooling fishes comprising moderate commercial catches. Much of the catch is reduced to fish meal and fish oil, although minor quantities are used for human consumption (Smith 1994, and references therein). Ecologically, thread herrings form an important forage base for many large, predatory fishes (Finucane and Vaught 1986).

Distinctions.--The filamentous last dorsal-fin ray distinguishes *Opisthonema* from all other clupeoids occurring in the Gulf of Maine. A filamentous last dorsal-fin ray occurs in *Dorosoma* and other gizzard shads, but in these species the mouth is inferior (Whitehead 1985a).

Chapter 8.

ATLANTIC THREAD HERRING *Opisthonema oglinum* (LeSueur 1817)

Description.--A rather thin fish; body depth ca. 32-37% SL; belly sharp and saw-edged. Dorsal-fin rays 19-22; posteriormost ray filamentous. Anal-fin rays 22-25. Pelvic finrays i 7; pelvic fins on abdomen under mid-point of dorsal fin. Scales in longitudinal series 32-35. Caudal fin deeply forked. Lower gill rakers increasing with size, but stable at 28-46 (usually 30-37) after 8 cm standard length (Whitehead 1985a).

Color.--Bluish above, silvery on sides and belly. Scales along dorsum with dark centers, forming longitudinal streaks; with faint dark spot just posterior to dorsal margin of gill cover. Dorsal and caudal fins with black tips.

Distinctions.--The thread herring is distinguishable at a glance from all other herrings inhabiting the Gulf of Maine by the prolonged last dorsal-fin ray (usually about as long or longer than the body is deep). It resembles the gizzard shad (*Dorosoma cepedianum*) of fresh and brackish waters in this respect, but the two differ rather conspicuously. In Atlantic thread herring, the mouth is terminal and the upper edge of the caudal fin is about 1.5 times as long as the head (vs. mouth inferior and caudal fin only about as long as head in gizzard shad); the dorsal-fin origin is slightly anterior to a vertical through the pelvic-fin origin (vs. slightly posterior to this vertical in gizzard shad); distance from pelvic-fin origin to anal-fin origin is at least 1.5 times as long as the anal-fin base (vs. only about 0.75-0.80 in the gizzard shad); and the anal fin in this species is very low, with its first few rays slightly shorter than the diameter of the eye (vs. about 1.5 times as long as eye diameter in gizzard shad). There is little possibility of confusing an Atlantic thread herring with young tarpon although both have a prolonged dorsal-fin ray. The easiest way to distinguish these species is that the dorsal-fin origin of Atlantic thread herring is anterior to the vertical through the anterior base of the pelvic fins, while in tarpon the dorsal-fin origin is situated well posterior to this vertical through the pelvic-fin origin.

Size.--Maximum length about 31 cm.

Habits and Biology.--Aspects of ecology, life history, and reproductive biology of this species can be found in Hildebrand (1963), Finucane and Vaught (1986), and Smith (1994). A coastal, pelagic, schooling species that forms dense, surface schools (but solitary individuals also reported) that probably does not enter low salinity waters. Studies in the Gulf of Mexico report that Atlantic thread herring prefer "bluer" water, higher salinities, and higher water temperatures than menhaden (Finucane and Vaught 1986). Schools of Atlantic thread herring are exceptionally fast and agile (Butler 1961), and are more difficult to catch in purse seines than menhaden.

Thread herring feed by filterfeeding plankton (copepods), but this species also includes small fishes, crabs, and shrimps in its diet. Spawning occurs in May-June off North Carolina (Hildebrand 1963; Smith 1994), while spawning in the eastern Gulf of Mexico is protracted from April through September (Houde 1977). Richards *et al.* (1974) described egg and larval development, and Houde (1977) described aspects of early life history for this species in the eastern Gulf of Mexico.

During summer along the southeastern Atlantic coast, they are distributed ubiquitously in coastal waters from North Carolina to northern Florida to depths of about 9 m, while they concentrate off Georgia and north Florida during spring, fall, and winter (Wenner and Sedberry 1989). Tag recoveries indicate schools of thread herring migrate south along the southeastern

Atlantic coast of the U.S. during fall at up to 11 km/d.

Atlantic thread herring represent an important food source for several coastal pelagic fishes including king mackerel, bluefish, crevalle jack and Spanish mackerel (Smith 1994). In ocean inlet areas of North Carolina, juveniles leaving estuarine waters in fall are fed upon voraciously by bluefish and Spanish mackerels (Smith 1994).

Age estimates using sagittal otoliths indicated that off North Carolina this species reaches ages to 8 yr, with most fishes being 4 yr or younger (Smith 1994). Mean fork lengths (in mm) at age were: 76 at 0+; 155 at age-1; 172 at age-2; 178 at age-3; 180 at age-4; 183 at age-5; 180 at age-6; 186 at age-7; and 175 at age-8.

General Range.--Western Atlantic primarily in tropical and subtropical latitudes, including Bermuda, the Gulf of Mexico, Caribbean and West Indies, straying northward to Chesapeake Bay and occasionally to southern Massachusetts, and only rarely in the Gulf of Maine. They are not numerous north of Cape Hatteras (Hildebrand 1963). This species occurs in the south Atlantic to about Santa Catarina, Brazil.

Occurrence in Gulf of Maine.--An Atlantic thread herring is caught off southern New England occasionally, and they were even reported as rather common in Buzzards Bay and Vineyard Sound during the summer of 1885 (Bigelow and Schroeder 1953). The only record within the Gulf of Maine is that of a single specimen ca. 17 cm long, taken off Monomoy Point, Cape Cod, August 1931 (MacCoy 1931). This is a warm-temperate and tropical species that is not likely to reach the Gulf, except as the rarest of strays.

Commercial Importance.--Along the northern Gulf of Mexico and southeastern Atlantic coasts of the U.S., Atlantic thread herring are mainly harvested with purse seines (Smith 1994). Most of the catch of coastal herrings, including this species, are sold as bait or processed into pet food (Finucane and Vaught 1986). Small amounts of thread herring are harvested off Florida as bait, and at present commercial landings of thread herring for reduction to fish meal and fish oil are restricted to coastal waters between Cape Hatteras and Cape Fear, NC, during late summer and fall (Smith 1994). Landings between 1965-1994 have fluctuated widely, with an average of 1.9 million kg harvested annually. During fall, the visceral cavity of Atlantic thread herring is heavily lined with fat deposits (Smith 1994). Accordingly, yields of fish oil from this species in fall are exceptional, averaging about 37.8 l of fish oil per 304.5 kg of fish, while yields of 56.7-60.6 l are common. Proximate analyses have shown that the protein content of Atlantic thread herring (20.65%; Hale 1984) is slightly higher than that of Atlantic menhaden. The Atlantic thread herring resource, especially the stock in the eastern Gulf of Mexico (Houde 1976) has been extolled as a latent fishery resource with estimates of population size off the southeastern U.S. ranging between 22,000 and 92,000 MT.

Chapter 9. SUBFAMILY ALOSINAE
Shads, Alewives, Menhadens

Description (from Whitehead 1985a).--Moderate to large or (for clupeoids) very large herring-like fishes (to 60 cm length, usually about 20-30 cm); fully scuted along abdomen. Upper jaw not evenly rounded in front, but with distinct notch into which fits symphysis of lower jaw; jaw teeth reduced or absent. Dorsal fin about at midpoint of body, pelvic fins below, anal fin short and well behind dorsal-fin base; pelvic finrays i 6 to 8. Scales usually well attached. Stomach muscular in some. Often with dark spot on side posterior to gill opening; some species with series of similar spots (or even a second row below this) along sides.

Habits.--The Alosinae are marine, pelagic, estuarine, or freshwater fishes, with some species anadromous, semi-anadromous or totally freshwater (rivers and lakes). All are schooling fishes, and most or all are migratory (except where landlocked). Food includes fishes and various invertebrates, but a few are filterfeeders on phytoplankton. A number of shads contribute significantly to fisheries, especially species of *Brevoortia* and *Alosa*.

There are 7 genera and 31 species. Two genera, *Brevoortia* and *Alosa*, occur in the western Atlantic.

Chapter 10. *Alosa* Linck 1790
Shads, River herrings

Description.--Moderate or large herring-like fishes (to 60 cm SL), somewhat compressed, with fairly prominent keel of scutes along abdomen. Upper jaw not evenly rounded in front, with distinct median notch into which fits symphysis of lower jaw; jaw teeth reduced or absent. Upper gillrakers, when numerous, folding down over lower gillrakers at angle of first arch; total gillrakers (upper plus lower) 30-130. Dorsal fin at about midpoint of body; pelvic fins directly below dorsal, pelvic finrays i 6 to 8; anal fin short and situated well posterior to dorsal-fin base. Scales cycloid, with smooth posterior borders, usually well attached; no enlarged and fringed scales along dorsum anterior to dorsal fin. Stomach muscular in some. Often with dark spot on side posterior to gill opening; some species with a series (or even a second row below this) of similar spots along sides.

Distinctions.--The notched upper jaw and long upper gillrakers separates *Alosa* from similar sympatric genera (*Clupea, Sardinella, Sardina*, etc.). Species of *Alosa* also lack the enlarged and fringed scales along the dorsum anterior to the dorsal fin that are characteristic of *Brevoortia*. Members of *Alosa* are easily distinguished from *Opisthonema* in lacking the filamentous last dorsal-fin ray characteristic of species of that genus.

Chapter 11. ALEWIFE *Alosa pseudoharengus* (Wilson 1811)

Gaspereau; Sawbelly; Kyak; Branch herring; Freshwater herring;
Grayback; River herring

Description.--Body relatively deep, moderately laterally compressed, ventral margin of abdomen with distinct keel of sharp, saw-toothed, scutes; caudal peduncle slender. Head relatively small, pointed; mouth terminal, lower jaw rising steeply, rather thick at end, projecting slightly beyond upper jaw when mouth closed and not fitting into a groove in upper jaw; maxilla extending to below middle of eye; a few, minute teeth present on mandible and premaxilla (disappearing with age), no teeth on vomer. Eye large, adipose eyelid well developed. Fins soft rayed; caudal forked; pelvic fins small, abdominal; pectorals low on sides. Scales cycloid, large, deciduous (Bigelow and Schroeder 1953; Hildebrand 1963; Whitehead 1985a; Scott and Scott 1988).

Meristics.--Dorsal-fin rays 12-18 (usually 13-16); anal-fin rays 15-20 (usually 16-18); pelvic-fin rays 10; pectoral-fin rays 14-16. Vertebrae 46-50. Lateral scale rows about 42-50. Ventral scutes strong, 17-21 anterior to pelvic fins, 13-16 posteriorly. Gillrakers on lower limb of first gill arch 38-44, increasing in number with age. Branchiostegals 7, rarely 6. Pyloric caecae numerous.

Color.--Grayish green above, darkest on back, paler and silvery on sides and abdomen. Usually with dusky spot on either side of body just posterior to margin of gill cover at eye level; sometimes with evident longitudinal lines on sides above midline in larger fish. Sides iridescent in life, with shades of green and violet. Colors changing in shade to some extent from darker to paler, or vice versa, to match the bottom below, as fish migrate upstream into shallow water; a golden or brassy cast evident on sea-run fish. Peritoneum pale to dusky.

Size.--To a length of ca. 38 cm SL (usually 25-30 cm), and to ca. 225-250 g in weight.

Distinctions.--The alewife is distinguishable from the Atlantic herring by the greater maximum depth of its body, which is 3⅓ times as long as deep (an alewife of ca. 34.0 cm is about 10 cm deep; an Atlantic herring that long has a depth of only about 7.6 cm); also by the point of origin of its dorsal fin, which is considerably nearer to the snout tip than to the point of origin of the central rays of the caudal fin. Usually there is a dusky spot on either side of the body just behind the margin of the gill cover, and the upper side may be faintly striped with dark longitudinal lines in large fish (both lacking in Atlantic herring). Furthermore, the alewife is much more heavily built forward than the herring, and serrations on the ventral midline are much stronger and sharper (hence the local name "sawbelly") than those of the Atlantic herring. The alewife differs further from the Atlantic herring in lacking teeth on the roof of the mouth.

Alewives are distinguishable from young Atlantic shad by their smaller mouths with shorter upper jaws; also by the fact that the lower jaw of the alewife projects slightly beyond the upper when the mouth is closed, and by the outline of the lower jaw margin, the forward part of which is deeply concave in the alewife, but nearly straight in the shad. Other differences between alewife and the other Gulf of Maine *Alosa* are that these other species have a gently rising lower jaw and more (59-73) or fewer (18-24) lower gillrakers. Chapman *et al.* (1994) also reported distinct differences in mtDNA composition between alewife and American shad.

Adult alewife can be distinguished at capture from blueback herring by differences in eye diameter, body depth, and peritoneum color (Loesch 1987). Eye diameter in the alewife is generally greater than the distance from the snout tip to the anterior margin of the eye, whereas the two measurements are about equal in the blueback herring. The peritoneum of the alewife is generally pale (pearl gray to pinkish white), sometimes with small dark spots (melanophores), while that of the blueback is generally uniformly dark brown or blackish, or sooty gray with darker spots. In fresh specimens, the dorsum is generally dark green in alewife (dark blue in blueback), although coloration fades soon after capture and there is substantial variation in dorsal coloration with ambient light changes (MacLellan *et al.* 1981). Dorsal pigmentation features are associated with differences in vertical distribution between the two species (Neves 1981). Scale patterns also differ in the two species (O'Neill 1980; MacLellan *et al.* 1981). Under magnification, the two species can be separated by scale imbrication patterns and positioning of the scale baseline and dividing line. The baseline is anterior of the dividing line in blueback herring, but the lines coincide in alewife. Other characteristics reflecting differences between these species occur in meristic features (Messieh 1977) and otolith shapes (Scott and Crossman 1973; Price 1978). The alewife also differs from blueback herring in having <45 gillrakers on the lower arch (vs. 45 or more in blueback herring), fewer vertebrae, and more dorsal- and anal-fin rays than does the blueback herring (Messieh 1977). Except for lower gillraker counts, however, differences in meristic features between the two species are small and overlap occurs in the ranges of each characteristic (Hildebrand 1963; Messieh 1977). Interspecific differences between alewife and blueback herring have been shown in electrophoretic patterns of muscle myogen (McKenzie 1973).

Habitat.--The alewife is an anadromous, highly migratory, euryhaline, pelagic, schooling species that spends most of its life at sea and enters freshwater areas to spawn. Some alewife populations are landlocked in freshwater systems, including the Great Lakes and some of the Finger Lakes of New York (Scott and Crossman 1973). Along the U.S. Atlantic seaboard, alewives were taken most frequently in coastal waters ranging between 56 and 110 m and in waters of 3-17°C (Neves 1981). Adult and immature alewives are also taken in abundance in weirs set in shallow coastal waters along the shoreline. Most catches of alewives in offshore locations are made at depths usually <100 m. However, one offshore catch in the Gulf (Vladykov 1936) recorded up to 1800 kg per haul made by otter trawlers fishing between 111-148 m off Emerald Bank, NS (125 km offshore ca. 43°15'N, 63°W), in March 1936. Capture of adult alewives have also been reported at other offshore areas, such as Georges Bank and in the South Channel. Off the Atlantic coast of Nova Scotia, Bay of Fundy and Gulf of Maine (Stone and Jessop 1992), most catches of river herring (alewife principally, but catches may have included some blueback herring) occurred at bottom temperatures of 7-11°C offshore at mid-depths (101-183 m) during spring, in shallower nearshore waters in summer (46-82 m), and in deeper offshore waters in fall (119-192 m).

While in the ocean, the alewife undertakes seasonal migrations, possibly in conjunction with changing patterns of water temperature (Neves 1981). Seasonal movement of alewives along the coast is generally inshore and northwards during springtime from overwintering areas (Stone and Jessop 1992). Spring catches are widespread along the Atlantic coast and occur most frequently over the continental shelf area between Nova Scotia and Cape Hatteras, NC, as alewives migrate toward their spawning rivers. Offshore catches of alewives made during this time suggest a northward progression with season, with catches of fish 25-28 cm in length occurring ca. 113 km off Barnegat, NJ, in early March, about 40-96 km off southern New England in May, and at the 41-m line off Martha's Vineyard by late June (Bigelow and Schroeder 1953). During summer and fall, catches are confined to three general areas in the region north of 40°N latitude: Nantucket Shoals, Georges Bank, and the perimeter of the Gulf of Maine. In the fall, river herrings (including alewife) generally move offshore and southward (Stone and Jessop 1992). Winter catches in the northwest Atlantic are made between 40-43°N latitude.

Catches of alewife in specific areas in the Gulf of Maine, and elsewhere, may also be related to zooplankton abundance in these regions, although direct evidence is lacking (Neves 1981; Stone and Jessop 1992). The temporal and spatial distribution of river herring off the coast of Nova Scotia was thought most likely influenced by the combination of zooplankton concentrations and occurrence of bottom temperatures >5°C (Stone and Jessop 1992).

Habits.--The alewife congregates in schools of thousands of individuals of similar size. Apparently a given school holds together during most of its sojourn in saltwater. Sometimes alewives form mixed schools with blueback herring, Atlantic menhaden or with Atlantic herring.

Light levels play a major role in the daily behavior of alosine fishes, including alewives (Loesch *et al.* 1982). Alewives are light sensitive and tend to be found in the water column rather than at the surface during daylight hours. Diel migratory activities are evident also in YOY alewife as well (Loesch *et al.* 1982; Jessop and Anderson 1989). Bottom catches of juvenile alewives are significantly greater during the day than at night; alewives taken at night occur mostly at the surface. Adult alewives in the sea may undertake vertical migrations corresponding with diel movements of zooplankton in the water column (Neves 1981). Concentration of alewives in bottom water during the day and their upward migration at night, possibly coinciding with extent and timing of vertical migrations of their major food item, *Mysis relicta*, has been reported for landlocked stocks (Lindenberg 1976).

For nearly its entire life, the alewife is in the sea where most of its growth takes place, but upon reaching sexual maturity the alewife enters freshwater rivers and streams to spawn. Adults migrate up rivers and even small tributary streams, spawning in lakes and quiet stretches of rivers during late April or May in Maine and Canada, and somewhat earlier in more southern regions (March in Chesapeake Bay area). Landlocked populations also ascend affluent rivers and streams on spawning migrations (Scott and Crossman 1973).

Temperature.--Along the U.S. Atlantic continental shelf, alewives were taken in coastal waters in temperatures ranging between 3 and 17°C, but were most frequently captured at bottom temperatures of 4-7°C (Neves 1981). Stone and Jessop (1992) reported that the majority of catches of alewife in the Gulf of Maine and off Nova Scotia were in waters warmer than 5°C, with most occurring within the 7-11°C range regardless of season, and with maximum catches within waters of 9-11°C from spring through fall. In the Bay of Fundy, alewife were present in waters of lower temperature. Moderate captures occurred at bottom temperatures < 2°C during spring surveys.

In summarizing spatial and temporal patterns of distribution, Stone and Jessop (1992) noted that these patterns were greatly influenced by oceanographic features. In all seasons, river herring occurred in the Bay of Fundy and off southwestern Nova Scotia, regions characterized by strong tidal mixing and upwelling, but were rarely present on the Scotian Shelf. In spring, alewife were most abundant in the warmer, deeper waters of the Scotian Gulf, particularly along the edges of Emerald and Western Banks and within the channel separating them, and in regions of warm slope water intrusion along the Scotian Slope, the western and southern edges of Georges Bank, and the eastern Gulf of Maine. River herring were not present in colder regions on the eastern and western Scotian Shelf.

Alewives, as compared with blueback herring, may prefer (Klauda *et al.* 1991), and be better adapted to, cooler water temperatures (Loesch 1987). Members of more northern populations may exhibit more tolerance to cold temperatures, and flexibility to thermal selection might be expected of a migratory anadromous fish (Stone and Jessop 1992). Antifreeze activity was detected in blood serum of an alewife collected off Nova Scotia (Duman and DeVries 1974), and alewife from Nova Scotia have a much lower serum freezing point than do those from Virginia (no antifreeze detected in their serum).

In fresh water, adults cannot survive temperatures over 25°C for prolonged periods (Graham 1956; Otto *et al.* 1976), but YOY have an ultimate upper incipient lethal temperature slightly above 30°C (McCauley and Binkowski 1982). Sensitivity to temperature change increases as the upper lethal limit is approached. Although some individuals survive, most alewives acclimated to 27-28°C water died when they were forced to move rapidly into 33.3°C water (Tremblay 1960). Marcy (1976a) collected young alewives in the Connecticut River over a temperature range of 5.7-31.0°C.

Seasonality of Occurrence.--Based on summaries from trawl survey data and fishery observer records, Stone and Jessop (1992) detailed seasonal occurrence for alewife off Nova Scotia and in the Gulf of Maine. In this region during spring, alewives are found predominately in three areas: the Scotian Gulf, southern Gulf of Maine, and off southwestern Nova Scotia from the northeast channel north to the central Bay of Fundy. Some catches also occur along the southern edge of Georges Bank and in the canyon between Banquereau and Sable Island Banks. Relative abundance was highest in the Scotian Gulf between Emerald and Western Banks, and on the southern slope of Georges Bank. Summer distributions were less extensive than in spring and were limited mainly to the eastern Gulf of Maine (off southwestern Nova Scotia) and the Bay of Fundy, with few occurrences nearshore in the central Shelf region. Catches were highest along the northern shore of the Bay of Fundy, with very few fish captured in the Scotian Gulf and on the eastern Scotian Shelf. Fall distributions were more extensive than those in summer. Moderate to large catches were obtained from southwestern Nova Scotia to the Bay of Fundy, the central Scotian Shelf, and Sydney Bight. Very few fish were collected on the eastern half of the Scotian shelf.

Spawning migrations of alewives ordinarily appear inshore early in April in streams tributary to Massachusetts Bay, and equally early (March or April) in the St. John River, NB (McKenzie 1932). Few are seen in the streams of Maine until late April or early May. Arrival times of spawning migrants varies considerably from stream to stream, according to local conditions. The earliest good runs on the Nova Scotia shores of the open Gulf and of the Bay of Fundy may come as early as April (streams of Yarmouth, Annapolis, Hants, and Colchester counties), in May (Digby and King's County streams), or not until June (Cumberland County) (McKenzie 1932). Successive runs within a system follow thereafter, all around the Gulf, until well into June, with later runs going up, and passing, earlier spawners moving downriver. Adult alewives have been seen descending downstream as late as August 20 in some Massachusetts streams (Bigelow and Schroeder 1953).

Feeding.--The alewife is chiefly a particulate-feeding planktivore that consumes a wide variety of zooplankton, including euphausiids, copepods, amphipods, mysids, ostracods, and appendicularians (Bigelow and Schroeder 1953). However, in the sea they also take small fishes, such as Atlantic herring, eels, sand lance, cunners, and their own species, as well as a variety of other fish eggs and larvae. During the spawning season, adult alewives may also ingest their own eggs (Edsall 1964; Carlander 1969), though most are reportedly eaten by immature alewives.

Alewives can feed on zooplankton either selectively, by particulate-feeding on individual prey, or non-selectively by filtering water through their gillrakers (Janssen 1976). The choice of feeding mode depends mostly on prey density, prey size, and visibility (turbidity), as well as predator size (Janssen 1976, 1978a, 1978b).

During the ontogeny of alewife, gillraker morphology changes along with prey capture efficiency (MacNeill and Brandt 1990). As they grow, alewives switch from feeding primarily on microzooplankton to ingesting large quantities of macrozooplankton. This switch likely occurs at sizes smaller than 95 mm FL (Stone and Jessop 1993). Even adult alewives, unlike Atlantic herring, will often contain diatoms in their diets.

Alewives generally feed most heavily during the day (Jessop 1990a). Nighttime predation (Janssen 1978b; Janssen and Brandt 1980) may be affected by ambient light levels. Predation using vision is restricted to larger macrozooplankton, being the only items producing detectable silhouettes. During night feeding, alewives can also utilize the lateral line sense (Janssen *et al.* 1995). Day and night differences in diet composition of alewives collected off Nova Scotia indicated that alewives may particulate-feed on macrozooplankton when prey visibility is high and filter-feed on microzooplankton when prey visibility is low (Stone and Jessop 1993). Diets of anadromous alewife in Minas Basin, NS, a turbid macrotidal estuary (Stone and Daborn 1987) favored larger, more benthic prey (amphipods, mysids and crangonids), while that of co-occurring blueback herring included microzooplankton (calanoid copepods, cypris larvae, and molluscan veligers). Differences in prey selected in this area suggested that alewives utilize a particulate feeding strategy, while blueback herring are predominantly filter-feeders.

At sea, alewives consume a variety of zooplanktonic prey, including euphausiids, calanoid copepods, mysids, and hyperiid amphipods, chaetognaths pteropods, decapod larvae, and salps (Edwards and Bowman 1979; Neves 1981; Vinogradov 1984; Stone and Daborn 1987). Diets of alewives collected during summer and winter cruises off Nova Scotia revealed that euphausiids, particularly *Meganyctiphanes norvegica*, were the most important prey item and represented more than 82% by volume of total stomach contents seasonally and geographically (Stone and Jessop 1993). Contributions by other prey groups (hyperiid amphipods, calanoid copepods, crustacean larvae, polychaetes, chaetognaths, mysids, pteropods, and fish larvae) were small and varied temporally and spatially. The proportion of euphausiids in diets of alewives from the Scotian shelf (winter) and Bay of Fundy (summer) reported by Stone and Jessop (1993) are much higher than the contributions (37-56% by weight) that were reported for alewives collected off the Atlantic seaboard of the United States (Edwards and Bowman 1979; Vinogradov 1984; Stone and Jessop 1993).

The proportion of euphausiids in diets of alewives from the Scotian shelf (winter) and Bay of Fundy (summer) tended to increase with increasing depth. In all areas, feeding activity and the proportion of feeding fish was highest in regions where bottom depths exceeded 200 m. The increased proportion of euphausiids in diets of alewives, as pointed out by Stone and Jessop (1993), coincides with an increased relative abundance of euphausiids with increasing depth. In the Scotian Shelf Basins, *M. norvegica* occur between 170 m and the bottom, with highest concentrations generally below 200 m. In the Bay of Fundy, *M. norvegica* is most abundant where bottom depths are between 165 and 200 m. Stone and Jessop concluded that the greater proportion and number of other prey categories in diets of alewives taken at depths less than 101 m on the Scotian Shelf and Bay of Fundy likely resulted from decreased euphausiid abundance (thereby increasing the relative contribution of other prey) rather than an absolute increase in the abundance of other zooplankters. Depth-related euphausiid species composition in alewife diets closely matched differences in depth preferences of the two major euphausiid species consumed.

Diet composition among alewife of different size groups (95-305 mm) was relatively homogeneous, with euphausiids comprising most of the total food volume (Stone and Jessop 1993). Irrespective of fish size, diets of alewives among all size groups examined were similar in that the average size of *M. norvegica* consumed were similar. Alewives greater than 200 mm FL generally consumed the largest-sized *M. norvegica* that were available. Slight seasonal and geographic differences in the average size of *M. norvegica* ingested likely reflect size differences in euphausiid populations rather than selective feeding by alewives (Stone and Jessop 1993).

Differences in the feeding activity of alewives at sea, as evidenced by stomach fullness, varies on both a diel and seasonal basis (Stone and Jessop 1993). Consistent with observations on other visual particulate feeders, feeding activity during the summer peaks at midday, and occurs during mid-afternoon for fishes captured during winter. Feeding activity in all areas was reduced at night, and was more apparent for fish taken during winter than summer. Daily ration was estimated at 1.2% of body weight during winter and 1.9% during summer (Stone and Jessop 1993).

Alewives do not feed when they are migrating upstream to spawn. However, when spent fish reach brackish water on their return downriver they feed ravenously on small mysids that abound in tidal estuaries.

Much is known about food of alewives in fresh water. Cladocerans (mainly *Cyclops* and *Limnocalanus*) represent 75% or more of the organisms eaten by larval alewives (Norden 1968; Johnson 1983), which also demonstrate a high degree of selectivity in the items eaten. Juvenile alewives tend to eat zooplankton until about 12 cm TL, but larger fish eat increasing amounts of the more benthic amphipod *Pontoporeia* (Morsell and Norden 1968). Juvenile anadromous alewives are opportunistic feeders, rather than determined planktivores (Gregory *et al.* 1983). The cladocerans, *Bosmina* spp. and *Daphnia retrocurva,* along with the copepod *Diaptomus minutus*, were principal food items of young alewives until August, when zooplankton densities decreased and alewives then included more insects in their diets. Rotifers were present in the diets during May and June, but were not eaten when most abundant in the plankton. Rotifers and copepod nauplii were strongly selected by smaller larvae and juveniles, but negatively selected by larger fish. Diet breadth increased with predator body size, generally in accordance with availability of prey. Organisms preyed upon included both planktonic and benthic species, and presence of adult insects indicated a propensity for surface feeding as well.

Predators.--Alewives are eaten by a variety of predators commonly occurring in the Gulf of Maine, particularly schooling species such as the bluefish, weakfish, and striped bass (Bigelow and Schroeder 1953; Ross 1991), and several other marine fishes, such as silver hake and salmon, although little quantitative information is available for predation rates on alewives in the sea. Juvenile bluefish (81-197 mm FL), from the Marsh River estuary, ME, actively fed on alewives and other clupeids (Creaser and Perkins 1994). Young alewives in freshwater fall prey to a variety of predators such as eels, yellow perch, and white perch (Loesch 1987). Predators on anadromous and landlocked river herring are diverse, including ca. 18 species of fishes, as well as turtles, snakes, birds, and mink (Loesch 1987).

Parasites.--Parasites from alewives taken near Woods Hole, MA (Sumner *et al.* 1913), include an acanthocephalan (*Echinorhynchus acus*), cestode *(Rhynchobothrium imparispine*), digenetic trematodes (*Distomum appendiculatum, D. bothryophoron, D. vitellosum, Monostomum* sp.), argulid (*Argulus alosae*), and copepods (*Caligus rapax, Lepeophtheirus edwardsi*). Nematodes (*Anisakis simplex, Thymnascaris adunca*) were reported from alewives taken in western North Atlantic localities (Gaevskaya and Umnova 1977). The parasitic copepod, *Clavellisa cordata*, has also been reported to parasitize the gills of this host species (Wilson 1915; Rubec and Hogans 1987). Landry *et al.* (1992) recovered 12 species of parasites from alewives in the Miramichi River, NB. Among these were one species of monogenetic trematode, four species of digenetic trematodes, one cestode larva, three nematode species, and one species each of annelid, copepod, and glochidia of a freshwater mussel (*Glochidia*). The alewife is also the sole host species for glochidia of the mussel, *Anodonta implicata*, which has disappeared where alewives have disappeared (Davenport and Warmuth 1965). Piscine erythrocytic necrosis (PEN), a blood disease of fishes, was reported from anadromous alewives from Maine coastal waters (Sherburne 1977).

Species Associates.--Alewives and blueback herring co-occur throughout much of their geographic range (Loesch 1987). Although the species are separated by spatial and temporal attributes in their life histories (Loesch *et al.* 1982; Loesch 1987), they were often referred to collectively. Collective reference to the two species stems from similarities in their appearances, times of spawning, methods of capture, and the frequent juxtaposition of spawning grounds (Loesch 1987). Any potential trophic competition in estuarine nursery areas is probably minimized through differences in diet composition and feeding locations utilized by the species. Differences in biologies that serve to reduce any potential competition between alewife and co-occurring American shad and blueback herring were discussed in Schmidt *et al.* (1988). In a study analyzing areas of co-occurrence, juvenile alewife were found not to be directly associated with juvenile blueback herring, in the sense that the presence of one species makes the presence of the other more or less likely (Jessop and Anderson 1989), even though both species co-occurred throughout the pond utilized as a spawning and nursery area. Association between these two species was therefore passive and occurred simply because environmental conditions were suitable for exploitation by these sympatric species. Significant differences found in the parasite faunas of these two species occurring in sympatry were thought to reflect underlying differences in the physiology and ecologies of these two species (Landry *et al.* 1992).

Alewives have significant impacts on the planktonic communities in the ecosystems in which they occur. Efficiency and effectiveness of alewife predation on zooplankton communities is well documented for freshwater areas (Brooks and Dodson 1965). Presence of a population of alewives in lakes and other freshwater habitats can significantly alter zooplankton community structure through predation effects (Hutchinson 1971; references in Loesch 1987). Changes in the zooplankton composition of a small New England reservoir were thought to have possibly resulted from the predation activities of the anadromous alewife population occurring there (Vigerstad and Cobb 1978). The presence of alewife populations in freshwater ecosystems can also contribute to nutrient cycling within these habitats (Loesch 1987). For example, in addition to providing a forage base for predatory consumers, post-spawning alewife mortalities indirectly contribute to nutrient inputs to freshwater systems (Durbin *et al.* 1979; Garman 1992). In some cases, this nutrient input per lake volume amounts to a value comparable with that of mortalities observed during salmon migrations in Alaska. From an *in situ* incubation of autumn leaf litter, it was shown (Durbin *et al.* 1979) that alewife mortality and decomposition provided the N and P that stimulates the microbial breakdown of leaf litter in spawning ponds utilized by alewives. Energy released from leaf litter breakdown, for the most part, passed into the detrital food chain rather than into the planktonic food chain. By hastening breakdown of the leaf litter, alewife mortality and decomposition may even reduce the sedimentation rate of lakes (Durbin *et al.* 1979). In other tidal freshwater streams, increased ammonium concentrations occur coincident with times of peak residence of migratory clupeid fishes, including alewives (Browder and Garman 1994). In these environments, metabolic activities of anadromous clupeid fishes could substantially alter the chemical environment of the streams, with ammonia inputs potentially influencing biotic interactions and nutrient dynamics.

General Range.--Northwest Atlantic and tributary waters along the coast from Labrador and northeastern Newfoundland (Winters *et al.* 1973), southward in the Gulf of St. Lawrence, south to South Carolina (Loesch 1987). It is an anadromous species entering freshwater to spawn, and subsequently has become landlocked in many parts of eastern North America, including the Great Lakes, lakes Seneca and Cayuga in the Finger Lakes of New York, and in certain other freshwater lakes (Scott and Crossman 1973).

Occurrence in Gulf of Maine.--Prior to European settlement, there probably was no stream from Cape Sable to Cape Cod that did not see its annual run of alewives unless they were barred by impassable falls near the mouth. Seasonality of occurrence in this region is March-December, with peak abundance of alewives occurring during summer. Although the alewife is still a familiar fish throughout the Gulf of Maine, stocks have declined substantially during the past two centuries and the range of spawning sites utilized by this species have been severely restricted due to overfishing, pollution of river waters by discharge of manufacturing wastes, and erection of dams prohibiting fish from reaching suitable spawning grounds. By about 1920 (Belding 1921), alewives migrated into only 9 or 10 of the 27 or so streams on the Gulf of Maine coast of Massachusetts that had formerly supported considerable fisheries. In a recent study, alewife represented only 11% of the gillnet and 10.5% of the impingement catch of fishes occurring in shallow coastal waters of southwestern Cape Cod Bay (Lawton *et al.* 1984). Presently, alewives still enter larger river systems throughout the Gulf of Maine including those of the Bay of Fundy, coastal Maine, New Hampshire, and Massachusetts. They utilize many smaller streams in this region as well, provided that these lead to ponds or other areas suitable for spawning, and are not polluted or obstructed by dams or falls that the alewives cannot surmount. Most spawning areas in the Gulf of Maine region are in restoration.

Historically, many more coastal streams in the Gulf of Maine yielded an abundant catch of alewives than do so today (Belding 1921; Bigelow and Schroeder 1953). Recorded landings of alewives in Maine peaked in 1956 when 2,085,420 kg valued at $41,800 were reported (State of Maine 1982). Alewife landings for commercial and recreational fisheries in the State of Maine for recent years are summarized by Squiers and Stahlnecker (1994). Landings were 238,311 kg for 1992; 195,390 kg in 1991; 356,052 kg in 1990; 376,998 kg in 1989; and 399,167 kg in 1988. The amount of annual landings from 1980 through 1988 averaged 629,094 kg. These reductions are reflected in landings for many of the individual rivers. For example, landings for the Damariscotta River stock, formerly the largest alewife run in the state, averaged 324,057 kg from 1970-1979. In comparison, the average annual landing for this run was only 40,638 kg for the period 1982-1991. Because of the drastic reduction occurring in the Damariscotta River stock, the alewife fishery of this river has been closed to fishing since 1993.

In 1993, only 347 MT were landed, which is the lowest level of recorded landings since 1946. Preliminary landings data for 1994 are lower yet and indicate that alewife stocks remain in a depressed state. To understand the magnitude of the loss of this potential resource consider the following comparison. If all potential spawning areas in the State of Maine (State of Maine 1982), including the Penobscot River, were fully utilized, projected alewife landings in excess of 18,182,000 kg annually could be achieved in Maine waters. This level of production and harvest are estimated to potentially provide ca. 80% of the total annual bait requirements for the entire Maine lobster fishery.

Reproductive biology

Spawning Location.--Alewives usually spawn in quiet waters of ponds and coves, including those behind barrier beaches (if there are openings to the sea, natural or artificial), and in sluggish stretches of streams above the head of tide (Smith 1907; Belding 1921; Bigelow and Schroeder 1953; Marcy 1976b). Where further upstream migration is barred by dams, alewives favor shore-bank eddies or deep pools for spawning (Loesch and Lund 1977). Landlocked freshwater populations of alewives also spawn in streams or in shallow-water areas along shore on sand or gravel bottoms (Galligan 1962), and often in areas with some vegetation. Usually, alewives do not spawn in swift-running water, but large quantities of alewife eggs were found in rapids on the Miramichi River (McKenzie 1959), implying that spawning occurred there in swift-moving water.

In the Gulf of Maine (as elsewhere), alewives are decidedly general in their choice of streams, running indifferently up rivers as large as the St. John or Merrimac, or into small tributary streams only a few centimeters deep (Bigelow and Schroeder 1953). In some large rivers they run far upstream to reach spawning grounds. For example, they occur at the Mactaquac Dam, 148 km from the mouth of the St. John River, and some fish passed upstream of the dam proceed another 100 km upriver (Messieh 1977; Jessop *et al.* 1982). In other environments, their journey may be only a few meters, as it is in the artificial cuts that are kept open through barrier beaches to allow fish access to freshwater ponds immediately behind the beach. The shortest alewife stream known to Bigelow and Schroeder (1953) was at Boothbay Harbor, where a considerable number of alewives annually migrated upstream to spawn in Campbell's Pond, a small body of water that is dammed off from the harbor, and reached by a fishway only 5 m long.

During their spawning migration, alewives are much more successful than Atlantic shad in surmounting fishways of suitable design. Generally, alewives, when on a spawning run, do not jump over obstructions although they can negotiate whitewater in rapids and fishways easily. Negotiating swift water does not apparently stress them. Increases in blood lactic acid levels were not extremely high in alewives tested during spawning runs in a fishway in Gaspereau River, NS (Dominy 1973).

Most alewives are believed to return to spawn in their probable stream of origin (Bigelow and Schroeder 1953; Loesch 1987). This theory has been supported by data gathered in meristic studies (Messieh 1977), by the establishment or re-establishment of spawning runs by stocking gravid adults in ancestral or new systems lacking runs (Belding 1920, 1921; Bigelow and Schroeder 1953; Havey 1961), and olfaction experiments (Thunberg 1971).

Since gonads of pre-spawning alewife are near full maturation when fish first enter river systems, little energy is required for gonadal maturation during the freshwater phase of migration

(Crawford *et al.* 1986). During the spawning migration adult alewives may lose a substantial portion of their body weight. Weight loss is attributed to a combination of factors including physiological demands of the migration, extended time of feeding cessation during freshwater migration, increase in metabolic demands associated with the warmer environment encountered during freshwater phases of the migration (compared with colder temperatures in coastal and estuarine waters), and the energy demands directly associated with spawning itself. To reach spawning grounds in Pausacaco Pond, CT (Cooper 1961), adult alewife were estimated to lose on average about 50 g in body weight for females and 36 g for males. During prespawning migration in the alewife, lipid depletion, and not protein utilization, apparently serves as the sole source of energy (Crawford *et al.* 1986). Lipid content in alewives is dependent on a number of factors including reproductive maturity, with lipid levels of 14.4, 8.7, and 5.4% reported for immature, prespawning, and spent alewife. Immature fish are characterized by a very high lipid content associated with the visceral organs. For spent alewife in the Margaree River, NS, a 38% loss of lipid was noted before their re-entry into seawater (migration distance ca. 90 km). In other systems, lipid content declined 22% and 18% in fish completing spawning migrations estimated to cover distances of 31 and 32 km, respectively. Lipid composition and utilization in migrating alewives appears also to be temperature dependent, as late migrants encountering higher temperatures in freshwater phases of the migration had a significantly lower lipid content than those fish arriving earlier (seasonally) in the migration. Relationships between bioenergetics and spawning migration in alewives were compared with those of other anadromous fishes in Bernatchez and Dodson (1987).

After spawning, alewives are noticeably thin, but they apparently recover body weight rapidly upon reaching saltwater. Spent alewives taken near Provincetown as early in the season as July 16 reportedly had already regained a considerable amount of the lipid reserves lost during their spawning migration.

Spawning Seasonality.--Onset of spawning runs in alewife is related to water temperature, thus it varies with latitude, and it may vary annually by 3-4 wk in a given locality (Loesch 1987). Alewives generally initiate spawning runs when water temperatures reach ca. 5-10°C (Loesch 1987). Temperatures below 8°C and above 18°C (24-hr average) generally result in little adult movement into spawning streams (Richkus 1974).

Spawning runs start in late March or early April south of Cape Cod (Hildebrand and Schroeder 1928; Cooper 1961; Marcy 1969), but usually not until early to mid-April in Massachusetts (Belding 1921), and late April to mid-May in Maine (Rounsefell and Stringer 1943; Bigelow and Schroeder 1953). Alewife spawning runs in tributaries in the Bay of Fundy begin in late April or early May and may last for 2 mo, while those in the Gulf of St. Lawrence occur about a month later (Scott and Scott 1988). In the Miramichi River system, spawning usually occurs in June (McKenzie 1959).

Alewife spawning generally precedes that of blueback herring using the same watershed by about 3-4 wk. There is considerable overlap in the spawning seasons of the two species (Loesch 1987), and their peaks of spawning may only differ by 2-3 wk (Hildebrand and Schroeder 1928).

Spawning has been reported to occur at temperatures ranging from 10-22°C (Rounsefell and Stringer 1943; Carlander 1969). The bulk of alewife spawning in the Gulf of Maine reportedly takes place when water temperatures are about 12°-15°C (Bigelow and Schroeder 1953). In the Connecticut River, the majority of alewives were thought to have probably spawned between 7.0 and 10.9°C (Marcy 1976b). The extreme range of temperature within which eggs are spawned in Gulf of Maine tributaries is not known (Bigelow and Schroeder 1953), but spawning in the Connecticut River ceased when waters warmed to 27.2°C (Kissil 1974), and Cooper (1961) reported that upstream migration of alewives in a Rhode Island spawning stream stopped at 21°C.

Spawning Behavior.--Each year males arrive in spawning streams before females. Males usually outnumber females on spawning grounds early in the spawning season, but the ratio decreases as the spawning season progresses. Early male alewife predominance is attributed to males maturing 1 yr earlier than females (Havey 1961; Kissil 1974) and males ripening earlier in the season, thus beginning the spawning run sooner (Cooper 1961). Sex ratios of fish spawning in Damariscotta Lake, ME, were skewed towards males originally, but became more nearly equal later in the spawning season (Libby 1981). Walton (1987) also reported sex ratios ranging from 1.2:1 to 2.7:1 males to females for alewives spawning in this lake, but he attributed the skewed ratios to poor passage in the fishways. The structural configuration of the fishway was selective against the largest or heaviest fish, which were mostly females, thereby decreasing the proportion of adult females that could reach the lake. As size of females decreased with progression of the spawning season, sex ratios became more nearly 1:1. It would appear then that skewed sex ratios in this lake system were apparently artificially affected by physical aspects of the fishway and not necessarily resulting from factors associated with this species' reproductive biology. Estimates of sex ratios of alewives in spawning rivers are also readily affected by spatiotemporal differences in sampling and sampling effort (Loesch 1987). For example, samples collected in the lower portion of an estuary may contain immature females that do not migrate to the spawning grounds (Loesch and Lund 1977). Also, presence of females in spawning condition bias samples because females in the process of spawning attract several males (Loesch 1987). Other physiological aspects of the migration could also influence sex ratios observed on the spawning grounds (Libby 1981).

Upstream movements onto spawning grounds are influenced by light intensity (most movement occurring during daylight hours), water flow (more movement during higher flows), and temperature (Collins 1952; Richkus 1974). Crossing salinity gradients in spawning rivers does not seem to impose difficulties on migrating alewives. Adults, when entering streams to spawn, change from salt to freshwater within a short period of time apparently without damage, and this is equally true of spent fish returning to the estuaries. However, adult alewives appear unable to endure repeated changes between saltwater and fresh, and great numbers are reported to be killed in this way under certain tidal conditions in estuaries (Bigelow and Schroeder 1953).

Several groups or waves of adult alewives arrive at the spawning sites during a spawning season. Spawning lasts only a few days for each group of fish and then spent fish emigrate rapidly downstream after spawning, passing later migrants on their way upstream to spawning grounds (Bigelow and Schroeder 1953; Cooper 1961; Kissil 1974). Fish on their return journey to saltwater are familiar sights in every alewife stream (Bigelow and Schroeder 1953).

Alewife spawn during the day or night, but spawning is apparently greater at night (Graham 1956). During the spawning act, usually a solitary female alewife swims close to shore accompanied by many males (McKenzie 1959; Cooper 1961). As many as 25 males may be attracted to one female (Belding 1921). Groups of spawning fish are often seen swimming rapidly in a circle 1-2 m wide just below the surface. In a matter of seconds this so-called nuptial dance or swim results in the simultaneous extrusion of eggs and sperm that are randomly broadcast into the water column and over the substrate by the mating fishes. Spawning ends abruptly with the fish creating a large splash, and discontinuing the circling swimming behavior.

Characteristically, larger and older fish spawn first, while smaller and younger fish spawn progressively later (Libby 1981). Decreasing trends in mean fork length for each sex during the spawning run were shown by Cooper (1961), Kissil (1974), Rideout (1974), and Libby (1981). In the St. John River system, early spawners are older fish and repeat spawners, with some 9- and 10-yr-old fish that may have spawned as many as five or more times (Jessop *et al.* 1983). However, alewives age-3 to age-5 appeared to dominate age groups on the spawning grounds.

There is considerable variation in the amount of repeat spawning that occurs in the different populations of anadromous alewives. In some populations, fish spawn only once during their lifetimes, while in other populations spawning occurs in several years (up to seven or eight; Jessop *et al.* 1982). The amount of repeat spawners in alewife populations may display a clinal trend in percentage of repeat spawners increasing from south to north (Klauda *et al.* 1991). Repeat spawners may constitute as many as 60% of spawning fish in populations occurring in Nova Scotian waters (O'Neill 1980), Virginia (Joseph and Davis 1965), and Maryland (Howell *et al.* 1990; Weinrich *et al.* 1987), while less than 10% of spawning fish in North Carolina were estimated to be repeat spawners (Tyus 1974). Others (Richkus and DiNardo 1984) disagree with the hypothesis of a clinal trend in the frequency of repeat spawning, and estimate that typical average values may be in the range of 30-40% repeat spawners for alewife populations spawning throughout the geographic range.

Fecundity.--Female alewives are prolific and may produce 60,000 to 467,000 eggs annually (Loesch 1987). Fecundities for Maine alewives reportedly range from 60,000-100,000 eggs/female (Havey 1950), for alewives in Nova Scotia estimates are from 68,000 to 457,000 eggs/female, while average fecundities of ca. 102,800 eggs/female have been reported for other populations (Smith 1907; Hildebrand and Schroeder 1928; Breder and Nigrelli 1936). Total fecundity of anadromous alewives generally exceeds fertility by the extent of postspawning, unripe egg retention (Jessop 1993). Spent alewives from the Parker River, MA, were estimated to retain less than 1% of total ripe eggs (Huber 1978), implying that virtually all ripe eggs were spawned, while unripe eggs represented 30% of the total fecundity. Jessop (1993) estimated that 38-52% of the total fecundity of alewives in his Nova Scotia study was attributable to unripe eggs. He also indicated that egg retention estimates in river herrings are influenced by the method of estimation, and that an overall egg retention estimate of ca. 48% retention for alewives obtained from the fecundities of similarly-sized unspawned and spent fish is probably the most accurate.

Fecundity in alewives is related to age and size of females, but is highly variable (Loesch 1987; Jessop 1993). With increasing latitude, there is also a corresponding decline in fecundity for similar-sized fish (Jessop 1993). However, total lifetime fecundity of alewives in northern populations may be higher because a greater proportion of females in these populations spawn more than once (Jessop 1993). The relationship of fecundity to female length probably best describes egg production in this species (Jessop 1993), with larger females in a population generally producing more eggs than smaller females. Age-based estimates indicate that maximal fecundity for alewife reportedly occurs in females between age-5 and age-7, and purportedly declines with age in older fish (Mayo 1974; Loesch and Lund 1977; Huber 1978). However, for alewives collected in Nova Scotia areas (Jessop 1993), age was found to be a nonsignificant predictor of fecundity, and no fecundal senility was evident in these populations. Based on these findings and re-analysis of other published data, Jessop concluded that the concept of fecundal senility as reported for other alewife populations is questionable. Spawning history (virgin, one or two previous spawns) also does not affect length-adjusted fecundity estimates for alewives in Nova Scotian spawning populations (Jessop 1993).

Eggs.--Fertilized eggs are 0.80-1.27 mm in diameter, pink, semi-demersal to pelagic, and slightly adhesive, but adhesive properties are lost after several hours (Mansueti 1956; Jones *et al.* 1978). When spawned in flowing streams, alewife eggs (after loss of adhesion) are transported downstream (Wang and Kernehan 1979). Marcy (1976b) noted that in the Connecticut River alewife eggs generally were more abundant nearer the bottom than at the surface.

External characteristics of the chorion of alewife eggs are distinctive from those of other fishes co-occurring in the same region (Johnson and Werner 1986). Alewife eggs are slightly larger than those of blueback herring, and do not contain oil globules (Kuntz and Radcliffe 1917; Norden 1967; Wang and Kernehan 1979).

Development.--Incubation takes 2-3 d at 22.0°C, 3-5 d at 20.0°C, and about 6 d at 15.6°C (Rounsefell and Stringer 1943; Mansueti 1956; Jones *et al.* 1978). Optimal temperatures for alewife development are ca. 17-21°C. Maximum hatching success occurs at 20.8°C, but declines significantly at higher temperatures, and ceases entirely at 29.7°C (Kellogg 1982). Minimal survival of river herring larvae has also been reported for those occurring in water temperatures above 28°C (Edsall 1970; Marcy 1971, 1973). Alewife eggs can tolerate a range of temperatures (7-30°C), but a high proportion (69%) of deformed larvae are produced from eggs incubated below 11°C (Edsall 1970; Kellogg 1982). Even though alewife eggs hatch and larvae survive for a short time at 7°C, development of a functional jaw does not occur at temperatures below 10°C (Edsall 1970).

At hatching, alewife yolk-sac larvae are about 2.5-5.6 mm TL (Mansueti 1956; Jones *et al.* 1978), and begin exogenous feeding at 3-5 d posthatch (Jones *et al.* 1978). Yolk-sac absorption (Cianci 1969) occurs in 72 hr at 11.7°C. Alewife larvae are estimated to be about 9.8 mm in length at yolk-sac absorption (Marcy 1976b). Post-yolksac larvae are positively phototropic and exhibit alternate active vertical movements toward the surface and passive vertical descents (Odell 1934; Cianci 1969). Larvae form schools within about 2 wk post-hatching (Cooper 1961). Larval alewives in Gulf of Maine tributaries are estimated to grow to about 15 mm when a month old (Bigelow and Schroeder 1953). Crecco *et al.* (1984) and Essig and Cole (1986) estimated age of larval herring from daily growth rings on otoliths. Larvae transform gradually to a juvenile stage at about 20 mm TL, and are usually fully covered with scales by about 45 mm TL (Norden 1967).

Distinctions of Larvae.--At some stages, alewife larvae can be distinguished morphologically from those of blueback herring using the number of myomeres between insertion of the dorsal fin and the anus (7-9 myomeres for alewives vs. 11-13 for blueback herring; Chambers *et al.* 1976). Alewife larvae can also be separated from those of American shad using myomere numbers (Marcy 1976b).

Larval Ecology and Behavior.--Upon hatching, larvae continue to be transported downstream. In some habitats, such as the Connecticut River, river herring eggs and larvae are the dominant species of ichthyoplankton collected (Marcy 1976b), and their seasonal appearance and abundance are significant features of the fish fauna inhabiting these areas. Larvae in some systems are collected more frequently in water nearer the bottom than in surface layers (Marcy 1976b). River herring larvae nearer the bottom may be younger than those at the surface, suggesting that larvae become more pelagic as they drift downstream. Feeding studies (Norden 1968; Heinrich 1981) show that larvae of all sizes are selective planktivores feeding mostly on cladocerans and copepods, and largely ignoring rotifers.

Juvenile Biology.--Schools of juvenile alewives are widely distributed in ponds, streams or tributaries in which they were spawned. In some systems, such as the Connecticut River, juvenile alosids represent significant proportions of the juvenile fishes occurring in lentic habitats (Marcy 1976b). Juvenile alewives in tidal freshwater systems undergo diel migratory activities (Loesch *et al.* 1982), with a greater concentration in bottom water during the day and an upward movement at night. A similar diel migration has also been noted for alewives in landlocked systems (Janssen and Brandt 1980).

Feeding chronology in juvenile alewives (Weaver 1975) is diurnal, but activity peaks are bimodal. Peak feeding occurs from about 1 to 3 hr before sunset, with a minor increase in feeding activity taking place about 2 hr after sunrise. Predation rates of juvenile alewives can have significant impacts on zooplankton community structure (Brooks and Dodson 1965). For example, juvenile river herring in the Mactaquac impoundment were estimated to have consumed about 73% of the total zooplankton produced from July to October (Watt and Duerden 1974). Zooplankton density and alewife growth in two Rhode Island ponds were also inversely related to juvenile alewife abundance (Richkus 1975).

Growth of juveniles in freshwater nursery habitats is relatively fast. In Nova Scotia, daily growth rate for juvenile alewives declined significantly with increasing summer temperatures (Jessop 1994). Growth rates for juvenile alewife in the James River, VA, ranged from 4-20 mg/d (Weaver 1975). Growth of juvenile alewife from hatching to fall emigration was 113 mm TL in the Connecticut River (Marcy 1969) and Richkus and DiNardo (1984) reported daily growth rates for juvenile alewife of 0.625 mm (NJ population) and 0.820-0.966 mm (MA population).

In the Annapolis River, NS, juvenile river herring utilize nursery areas from August to October, but schools apparently remain offshore and catchability with seines in nearshore areas is low except during twilight and early evening (Stokesbury and Dadswell 1989). About the time of peak downstream emigration, the fish make a short-lived, rapid onshore movement; sizable catches can then be made in shallow waters if a school is encountered. In the Hudson River, juvenile alewives remained in the shallows, or near mouths of tributary streams where they were spawned, for several weeks and then moved offshore as they grew (Schmidt *et al.* 1988). Similar behaviors (general offshore distribution with short-lived onshore rushes) have also been noted among YOY American shad during their downstream emigration in the Connecticut River (O'Leary and Kynard 1986).

In the Gulf of Maine, most juvenile alewives descend their natal rivers in summer (mid-July) or early autumn, with some not leaving until much later in November or December. In streams along the southern Gulf of Maine, downstream movement occurs as early as 1 mo after spawning (ca. June 15), and throughout the summer successive cohorts of juveniles move out of ponds and are carried downstream by river currents. Juvenile alewives tend to emigrate from freshwater nursery areas to more brackish areas about a month earlier than do juvenile blueback herring (Kissil 1974; Loesch 1969; Schmidt *et al.* 1988). By autumn, young alewives, ca. 5 to 10 cm long, have nearly completed their emigration downstream to coastal, saline areas. Young alewives, 102-115 mm, were seined in saltwater near Seguin Island, ME, at the end of July (Bigelow and Schroeder 1953), but others, only 78-92 mm long, occurred near Mt. Desert Island as late as the first of October. Juveniles have been taken around Campobello Island as deep as ca. 92.5 m (Bigelow and Schroeder 1953). Larger and older juveniles (aged as 1-3 yr-old fish) have also been taken in estuarine and inshore waters, but their movements outside the river system are poorly known (State of Maine 1982). In more southern areas, such as the Hudson River, most juveniles have left the upper and middle zones of the river before water temperatures dropped to 7°C in late November (Schmidt *et al.* 1988), although some juveniles remained in that study area until mid-December. Further south, overwintering by juveniles in lower reaches of rivers and estuaries has been observed for juveniles in locations such as Chesapeake Bay (Hildebrand and Schroeder 1928; Pacheco 1973) and in the lower Connecticut River estuary, juveniles (age-1+ fish) have been found in early spring, suggesting that many juveniles probably spend their first winter close to the mouth of that river (Marcy 1969).

Downstream emigration of juveniles undoubtedly is influenced by interacting roles of intrinsic and extrinsic factors. The particular combination of extrinsic factors triggering seaward migration of juvenile alewives from estuaries and other nursery areas is uncertain. Studies concerning the riverine phase of the life cycle suggest that increased precipitation and river flow, decreasing water temperature, or a combination of these factors during autumn are key factors for initiating migration by juveniles (Sykes and Lehman 1957; Walburg and Nichols 1967; Moss 1970; Richkus 1975). In the Connecticut River, decreased temperature occurring during a new or quarter moon was considered to be the major stimulus for downstream emigration of juveniles, rather than increased water flow (O'Leary and Kynard 1986). Low food resources in nursery habitats have also been suggested as a contributing factor initiating downstream emigration of juvenile alewives (Richkus 1975; Vigerstad and Cobb 1978).

Seaward migration in estuaries seems to be a rather slow process for river herrings (Stokesbury and Dadswell 1989). In some areas, juveniles were distributed widely throughout tidal freshwater nursery areas in spring and early summer, but subsequently moved upstream in summer with the encroachment of saline water (Warinner *et al.* 1970). The virtual absence of river herrings from inshore regions of the Annapolis River (NS) estuary for almost a month before a final seaward migration suggests they school offshore in the estuary until the correct migration stimulus occurs. Peak seaward emigration observed during 2 yr of study occurred during new to quarter moon periods (dark nights). Coincident with the dark nights was a sharp decline in water temperature below 12°C. River input appeared to play little role in stimulating seaward movement. Decreasing water temperature and the new moon period rather than river flow have been shown to be the most important factors for downstream migration of juvenile alosids under riverine conditions (Marcy 1976c; O'Leary and Kynard 1986). Seaward movement of juvenile river herring occurs predominantly at night. The documented negative phototrophic response of river herrings appears to keep them relatively immobile during daylight hours (Loesch *et al.* 1982). Although larger individuals have been reported to move downstream first (Chittenden 1969; Marcy 1976c; Loesch *et al.* 1982; Schmidt *et al.* 1988), size at emigration may not be important for alewives, as large interannual variations in size were apparent for juvenile fishes occurring in the Annapolis River (Stokesbury and Dadswell 1989). Juvenile blueback herring and alewife began downstream migration within the headpond from about late July, in conjunction with decreasing water temperatures, through early September until at least late October (Jessop and Anderson 1989). Migration from the headpond probably began about mid-August and increased rapidly through early September. Juvenile alewives and blueback herring exited the headpond in a manner consistent with steady seasonal growth rather than early departure of larger fish (Jessop 1994).

Age and Growth.--Growth rates, age at sexual maturity, and longevity vary greatly for alewife across the geographic range. Different methods have been used to back-calculate lengths-at-age derived from analysis of scale annuli for alewives creating problems associated with subsequent comparisons between studies (Loesch 1987). Some generalizations from studies cited in Loesch (1987) are that females may grow slightly faster and live longer than males (Rounsefell and Stringer 1943; Havey 1961), and that growth in both length and weight continues for most alewife populations after sexual maturation, but at a rate decreasing with age. A maximum total length of 38 cm was reported by Hildebrand and Schroeder (1928), but few individuals exceed 30 cm in length or about 1 kg in weight (Ross 1991).

Walton (1983) examined growth parameters for several Maine alewife stocks and found they were similar to those reported by Havey (1961). No significant differences in length at age were reported for alewives from 21 coastal watersheds of Maine (Walton and Smith 1974). Mean lengths and weights at ages 4-10 for alewives caught during the spring spawning run on the St. John River at the Mactaquac Dam in 1981 were provided by Jessop *et al.* (1983). Lengths-at-age of 4-7 yr old Connecticut River specimens are 26.4 cm at age-4, 27.7 cm at age-5, 29.0 cm at age-6, and 30.2 cm at age-7. Juvenile alewives in Chesapeake Bay are estimated to grow to about 11.5-12.5 cm by the time they are age-1 (Hildebrand and Schroeder 1928).

Adults of a dwarf population of alewives in Walker Pond, ME, were smaller than those of other areas, and young also had a slower growth rate and a more delayed larval to juvenile metamorphosis (Walton 1983). Another distinctive difference in this population is that juveniles emigrated to the sea in their 2nd yr.

Anadromous alewives generally grow faster and attain larger sizes (to 38 cm) than do those in landlocked freshwater environments (to 21.6 cm). Alewives in landlocked freshwater populations usually mature 1 yr earlier than do members of anadromous populations, and this may contribute to the average smaller size of those landlocked alewives (Graham 1956).

Age at sexual maturity is generally higher in populations spawning in the northern portions of the species range. Maturity for alewives is reached in 3 yr in populations spawning in Massachusetts tributaries, and ranges from 3-5 yr for fish spawning in Maine rivers, with the majority reaching maturity at about 4 yr (Rounsefell and Stringer 1943; State of Maine 1982). In Long Pond, ME, some fish matured as early as age-3, others not until age-4, and some females spawned as many as three different years (Havey 1961). Experiments in which adult alewives were stocked in previously uninhabited ponds, led to the conclusion that alewives generally mature sexually at age-3 or age-4, for none of their progeny returned until 3-4 yr after the original stocking (Belding 1921). Sexual maturity of alewife populations in the St. John River, NB, is reached usually at ages 3, 4, or 5, with males tending to mature earlier than females (Jessop *et al.* 1983). Only about 5% of males in this region mature at age-2. Loesch (1987) summarized information on age at spawning, noting that first spawning generally occurs between ages 3 to 6, but the composition of virgin spawners is strongly dominated by age-4 fish. Modal age for spawning alewife across the geographic range of anadromous populations is generally 4 or 5, but the modality is readily affected by the presence of a strong year-class or by recruitment failure. Annual mean lengths of fish entering Damariscotta Lake to spawn were between 30 and 30.9 cm TL (Walton 1987). Alewives caught during spawning runs in Atlantic Canada average 25.4-30.5 cm FL, and occasionally to 35.6 cm FL (Scott and Scott 1988).

Little data are available on age composition of sea-caught alewives (Scott and Scott 1988). Netzel and Stanek (1966) reported average lengths and weights of alewives comprising a subsample from some 13 MT of alewives and blueback caught by otter trawl in October off Georges Bank.

Mortality.--This species suffers high mortality throughout all phases of its life cycle (Kissil 1974). Fewer than 1% of all eggs are estimated to survive through early life stages to become juveniles that migrate to sea. In the Connecticut River, it was estimated that one young fish survived to leave the spawning ground for every 80,000 eggs spawned, which translates to a survival rate of only ca. 0.0014% during the freshwater phase from egg to emigrating juvenile (Kissil 1974). Richkus (1974) reported a 75% mortality rate for juvenile alewives in a 6-wk period prior to emigration from freshwater habitats. In addition to natural mortality events, juvenile alewives (and other species of river herring) can also suffer high mortality due to impacts associated with power-generating facilities. River herrings accounted for 97% of the fish entrained at a nuclear power plant in the Connecticut River (Marcy 1976b).

Total annual mortality of adults is also estimated to be high, with about 70% of adult members dying in a given year. Spawning mortality of adults is highly variable from area to area and from year to year. In Long Pond, ME, annual mortalities in fish between ages 5-6 and 7-8 were estimated to be 78.6% and 74.7% (Havey 1961). Depending on location, 32-90% of adults are estimated to die annually, due to population demographics, and during rigors of spawning migrations and energetic costs associated with reproductive activities. Adaptations in members of northern populations that maximize individual reproductive potential for those fishes living in these highly variable environments are similar to those occurring in northern American shad populations (Jessop 1993). For example, alewife populations at the northern end of the species range ensure higher postspawning adult survival by: 1) completing gonad development prior to river entry; 2) having a higher percentage of, and a higher maximum age of, previously spawning members; 3) having smaller gonad weight relative to body size; 4) a lower fecundity; and 5) having a higher egg weight than do members from more southern populations, where spawning environments are presumably less variable.

Stock Recruitment.--The abundance of alewives returning to freshwater areas to spawn generally is positively correlated with surface area of the spawning grounds and nursery habitats (Walton 1987). Havey (1973) reported a mean relationship value of 0.7 female spawners and 407 juvenile emigrants/ha of freshwater habitat, while Walton (1987) calculated a much higher value of 1.3 female spawners and 8,157 emigrants/ha of lake surface.

For anadromous alewife populations in Maine lakes, no significant relationships have been found between brood stock size and numbers of progeny produced (Havey 1973; Walton 1987). During one study in Damariscotta Lake (Walton 1987), annual harvests of alewives decreased by an order of magnitude, yet reproductive success was not affected by this apparent stock decline. Although a positive and significant relation between the numbers of females entering the lake and the estimated egg deposition was recorded, no significant relationship between estimated egg deposition and number of juvenile emigrants was found. Despite annual variability in estimated egg deposition, the number of juveniles emigrating from the lake remained relatively constant and independent of spawning escapements of adult fish (11-38 fish/ha) throughout the study period (1977-1984). It was concluded from this study that these data supported the hypothesis that number of spawning females and number of juvenile emigrants are asymptotically related over the observed range of adult escapement from the Lake.

Growth of juvenile alewives can be influenced both by intraspecific competition and abiotic factors (Crecco and Savoy 1984; 1985; Jessop 1990C, 1994). Year-class abundance of anadromous populations of alewives which spawn in Maine lakes appears to be established prior to emigration of juveniles from freshwater nursery areas (Havey 1973; Walton 1983, 1987). It has been suggested (Walton 1983) that intraspecific competition for zooplankton during the freshwater growth phase may be a major factor affecting growth, survival and eventual reproductive success in established populations of anadromous alewives in Maine (i.e., Damariscotta Lake) as well as other Gulf of Maine populations. Juvenile alewife abundance from Mactaquac Lake, a headpond environment of the St. John River system, was significantly and negatively correlated with spring discharge (May-June) from the lake (Jessop 1990c, 1994). However, as Jessop pointed out, the relative importance of biotic and abiotic factors in controlling growth and mortality rates of juvenile alewives is uncertain. A high co-linearity among environmental factors such as water temperature and discharge may obscure the mechanisms by which hydrographic fluctuations influence larval and juvenile growth and mortality rates (Crecco and Savoy 1984, 1985). Overall effects of urbanization on spawning and subsequent recruitment success were analyzed in a study on patterns of fish spawning in tributaries of the Hudson River, NY, in relation to effects of urbanization (Limburg and Schmidt 1990). Here, estuarine areas used by anadromous fishes are environmentally sensitive and there exists a strong threshold effect of urbanization (i.e., land use patterns) on spawning success of anadromous fishes at the confluence of streams and estuary.

Historical Fisheries.--Alewife populations along the east coast started to decline in colonial times (Belding 1920, 1921). Combined effects of overfishing, pollution, and damming of spawning rivers and streams have had drastic long-term effects upon this species. Indicative of these problems is that only nine of an original 27 streams along the Gulf of Maine coast of Massachusetts that once held major river herring spawning runs still did so by 1920 (Belding 1921). Bigelow and Schroeder (1953) provided historical information on the extent and amount of fisheries landings of alewife in the Gulf of Maine. Of particular interest are their comments noting the long history of continued decline in abundance of alewife populations of the Gulf. They estimated that in 1896 the total catch for the Gulf of Maine was more than 22 million fish and that by around 1953 populations in the Gulf were much smaller than those of half a century ago (only about ½ as great for the Bay of Fundy in 1945 and 1946 as it had been in 1896, and only about ⅓ as great for Maine rivers). Despite their concerns regarding this downward trend, disruption of spawning habitats and increasing pollution levels associated with human activities has continued to the present day. Reflecting these trends, coastwide commercial harvests have steadily declined during the 20th century. In the New England region, coastal Maine and Merrimac River catches declined by over 76% and 99%, respectively, between the turn of the century and 1950 (Bigelow and Schroeder 1953; Ross 1991). By the late 1980s, North Carolina remained the only state with a substantial commercial fishery, accounting for ca. 80% of the total coastwide catch.

River herrings have traditionally supported a modest commercial bait industry in New England (Bigelow and Schroeder 1953; Ross 1991). Offshore landings are typically by-catch of harvesting other species, and inshore and river harvests are directed specifically toward herring spawning runs. Large catches of river herring were taken offshore by foreign fishing vessels (Neves 1981, and references therein). By far the greatest catches of alewives are made in lower reaches of spawning streams. Alewives are caught commercially in weirs, traps, gillnets, and dip nets (Scott and Scott 1988; Jessop 1990b) set in harbors, river mouths, or in upriver lakes. They are considered one of the easiest fish to catch. Today, recreational fishing accounts for modest harvests, with the greatest effort occurring in the mid-Atlantic states. Much of this harvest is used as bait for predatory sport fishes. Ross (1991) presented a detailed discussion of recreational angling for alewives.

In part due to the prolonged depletion of river herring and shad stocks in the Middle and southeastern Atlantic states, the Atlantic States Marine Fisheries Commission established a coastal management plan for river herring and American shad in 1985. Objectives of this plan include regulating harvests, improving habitat quality and accessibility, and initiating stocking programs to restore populations in rivers where they historically, but do not presently occur. Since most of the alewife harvest of New England traditionally occurred adjacent to, or in estuaries and river mouths, management of these species has been focused upon small geographic areas (Ross 1991). The State of Maine has a management plan that sets regulations on a county-by-county basis (State of Maine 1982). There are presently 34 coastal municipalities in Maine which have vested rights to alewife fisheries within their respective town boundaries. These municipalities operate fisheries on 35 rivers and streams annually and use the income acquired to defray costs of municipal government. These fisheries are managed under joint cooperative management plans approved by the Department of Marine Resources. All other alewife fisheries in the state are under the general jurisdiction of the Department of Marine Resources and Inland Fisheries and Wildlife which coordinates management of these resources on a watershed basis. In Massachusetts, each town may petition the director of marine fisheries to establish local control of management of anadromous herrings. The state manages runs not overseen by local townships.

Current management methods in Maine waters include control of commercial fishing effort, maintenance and improvement of water quality in spawning and nursery areas, and construction of fish passage facilities (State of Maine 1982). Alewives readily utilize most types of fishways such as the vertical slot, pool and weir (overflow and chute type), and denil. In recent years, emphasis has been placed on construction of fish passage facilities in coastal streams and rivers to restore commercial runs of alewives (State of Maine 1982).

Long-term efforts to restore depleted stocks (Belding 1921; Rounsefell and Stringer 1943) have led to significant recovery of alewife stocks in some New England watersheds. Recent efforts to restore, enhance, and monitor alosid populations in Maine systems were summarized by Squiers and Stahlnecker (1994). Alewife restoration is being attempted at several locations within Maine and New Hampshire (Grout and Smith 1994). A total of 58,701 adult alewives were stocked in seven lakes in the Kennebec River drainage during 1994. Permanent downstream passage facilities should be present in all dams during the next several years. The Androscoggin River anadromous fish restoration program commenced in 1982, when 2,326 prespawner adult alewife were stocked into Sabattus Pond. A new vertical slot fishway began operating at the head-of-tide dam in Brunswick in May 1983. River herring passage there has increased from 601 fish to a high of 100,895 in 1989. However, the number of fish ascending the river through the fishway has continued to decline since 1989. In 1990, 95,483 alewives ascended the river, in 1991 about 77,711 fish were counted, in 1992 there were 45,051 fish; in 1993 only 5,202 fish were counted, while in 1994 an estimated 19,190 fish ascended the fishway.

In 1987, a study was begun by the Maine's Departments of Marine Resources (DMR) and Environmental Protection and Inland Fisheries and Wildlife to explore the interaction of anadromous alewives and resident freshwater species in Lake George. In 1991, DMR stocked

2,030 adult alewives in Lake George, 2,005 in 1992, and 2021 in 1993. A weir on the outlet stream was installed prior to adult alewife stocking each spring and remained in place until the third week in November in 1991 and 1992 and into December in 1993 to monitor emigration of postspawning adults and juveniles. A table of juvenile and adult alewife passage through the weir follows:

	adults stocked	adults	juveniles
1991	2,030	1,435	1,035,393
1992	2,005	1,420	1,359,354
1993	2,021	341	420,784

The total number of adults passed out of the lake or gillnetted in the lake represents 71% of the total number stocked in 1991 and 1992. In 1992, the majority (77%) of juveniles emigrated between July 15 and August 1. Juvenile emigration was more gradual in 1991 with less than 40% leaving before August 1. Emigration of juveniles in 1993 began on August 10 and lasted until November 19, with peak levels occurring in October. Delayed juvenile emigration and reduced numbers of both adult and juvenile alewives appeared to be due to very low lake levels and stream outflow in 1993. Juvenile alewives were found in stomachs of brown trout as late as early February during 1993. During 1994, no alewives were captured using a variety of collecting gears.

The juvenile alosid survey in the lower Kennebec River has been conducted since 1979. The survey is conducted to evaluate the rate of increase of the alosid population following the improvement of water quality in the Kennebec River. The 1993 juvenile alewife index for the Androscoggin River and the Upper Kennebec River was the second highest on record and the highest since 1983. Preliminary analysis of 1994 data indicates that the indices for juvenile alewives in the Kennebec and Androscoggin rivers were lower in 1994 than in 1993, but were higher than that estimated for Merrymeeting Bay.

There are about 100 different runs of anadromous fishes in Massachusetts waters. The largest of these occur in the Connecticut and Merrimac rivers (P. Brady, person. commun.[1]). Overall, there has been a decline in fish abundance in the better runs in the state's waters, with large interannual fluctuations noted for fish returning to spawning streams. Some streams are reportedly doing well, some are maintaining, while others show marked declines in spawning fish. Restoration attempts, including construction of fishways and other procedures, are being made at many of these locations.

Importance and Utilization.--Historically, alewives have been harvested for food, bait and fertilizer. Their scales commanded a high price for use in the manufacture of artificial pearls for a brief period during the first world war and for a few years afterward. Currently alewives have little commercial value except as bait. They are good bait for cod, haddock, pollock, striped bass, and are also used as bait in lobster and snow crab fisheries (Scott and Scott 1988). In some regions alewives are also used in the production of fish meal and oil (Scott and Scott 1988). In Maine, the alewife has little recreational value although they are occasionally taken by rod and line (State of Maine 1982). The major use of this resource (State of Maine 1982) is by commercial fishermen who harvest and sell them for lobster and trawl bait, and to reduction plants for processing into fish protein. The fishery takes place in the spring from late April through late June as the fish ascend rivers to spawn. Over 90% of the current annual harvest is used for lobster bait. In recent years, mean annual landings of 1,363,636 kg have provided about

6% of the annual bait needs for Maine's 10,000 licensed lobster fishermen. However, as a seasonal bait source for the spring lobster fishery, the alewife resource provides 30-50% of the total bait needs for the coastwide lobster fishery.

Alewives are an excellent food fish and are preferred by many consumers over the Atlantic herring (Bigelow and Schroeder 1953). Alewives may be marketed for human consumption as fresh, frozen, smoked, salted or pickled product. They are also canned for pet food (Scott and Scott 1988). The flesh is white and sweet, but bony. Only a very small part of the total catch is smoked or pickled and sold for human consumption in Maine (State of Maine 1982). Ross (1991) provided an excellent discussion of preparing alewives as tablefare. Nutritional values for alewives are: fat 3-15% (varies seasonally); protein 12-20%; moisture 66-80%; and ash 1-3% (Sidwell 1981).

Chapter 12. BLUEBACK HERRING *Alosa aestivalis* (Mitchill 1814)

Glut herring; Summer herring; Blackbelly; River herring

Description.--Body deep, moderately laterally compressed, moderately elongate, ventral margin of abdomen saw-toothed with distinct keel of sharp scutes; caudal peduncle slender. Head relatively small, pointed; mouth terminal, lower jaw projecting slightly, rather thick at end, extending beyond upper jaw when mouth closed and not fitting into groove in upper jaw. Lower jaw rising steeply within mouth; minute teeth present at front of jaws (disappearing with age), no teeth on vomer. Maxilla extending posteriorly to below middle of eye. Eye relatively large. Fins soft-rayed; dorsal fin small, distal margin concave; anal fin slightly longer than dorsal; pectoral fin moderate; pelvic fins small, abdominal; caudal fin forked. Scales cycloid, large, deciduous; ventral scutes strong.

Meristics.--Dorsal-fin rays 15-19. Anal-fin rays 15-21. Pelvic-fin rays 8-11. Pectoral-fin rays 12-18. Vertebrae 49-51. Lateral scale rows about 41-54. Ventral scutes anterior to pelvic fins 18-22, posterior ventral scutes 12-17. Total scutes 31-27. Gillrakers on lower limb of first gill arch 41-52 in adults (fewer in fishes under 10 cm SL). Branchiostegals 7. Pyloric caeca numerous. (Bigelow and Schroeder 1953; Whitehead 1985a; Scott and Scott 1988).

Color.--Freshly-caught fish dark blue, bluish-green or sometimes bluish-gray above, sides and abdomen silvery and iridescent; olive-black longitudinal lines above midline of sides sometimes evident on adults and a dark or black spot posterior to gill cover at eye level. Fins pale yellow to green. Peritoneum usually sooty, brown, or black.

Size.--To about 38 cm SL (usually 25-30 cm) and about 220 g in weight. Scherer (1972) reported sexual dimorphism in size of adults, with females being longer than males.

Distinctions.--Blueback herring resemble the alewife in shape and general appearance, and these species are difficult to distinguish, especially as juveniles, even by experienced fishermen who regularly handle large numbers of each species. At capture, adult blueback herring can be distinguished from alewife by differences in eye diameter, body depth, and peritoneum color (Bigelow and Schroeder 1953; Loesch 1987). Eye diameter in the blueback is generally about equal to the distance from snout tip to anterior margin of the eye, whereas eye diameter is larger than snout length in the alewife. The peritoneum of blueback herring is generally uniformly dark brown or blackish, or sooty gray sometimes with darker spots (melanophores), while that of alewife is pale (pearly gray to pinkish white). In fresh specimens, the dorsum of the blueback is generally dark blue (vs. dark green in alewife), although coloration fades soon after capture, and there is substantial variation in dorsal coloration with ambient light changes (MacLellan *et al.* 1981). Dorsal pigmentation features are associated with differences in vertical distribution between the two species (Neves 1981). Under magnification, scale imbrication patterns and positioning of the scale baseline and dividing line will separate the two species (O'Neill 1980; MacLellan *et al.* 1981). In blueback herring, the baseline is anterior to the dividing line, whereas these lines coincide in alewife. These species also differ in otolith shape (Scott and Crossman 1973; Price 1978). Blueback herring have more than 45 gillrakers on the lower arch (vs. fewer than 45 in alewife), have more vertebrae, and have fewer dorsal- and anal-fin rays than do the alewife (Messieh 1977). Except for higher gill raker counts, however, meristic differences between these two species are small and ranges of each characteristic overlap (Hildebrand 1963; Messieh 1977). Interspecific differences between alewife and blueback herring occur in electrophoretic patterns of muscle myogen (McKenzie 1973).

Blueback herring are distinguishable from young Atlantic shad by their smaller mouths with shorter upper jaws; the lower jaw of the blueback projects slightly beyond the upper when the mouth is closed, and the anterior outline of the lower jaw margin is deeply concave in the blueback, but nearly straight in the shad. Blueback herring have more (59-73) gillrakers on the lower arch than do American shad. Chapman *et al.* (1994) reported distinct differences in mtDNA composition between blueback herring and American shad.

The blueback herring is readily distinguished from Atlantic herring by position of the dorsal-fin origin, which is considerably nearer to the snout tip than to the origin of the central caudal-fin rays than it is in Atlantic herring. Usually the blueback herring has a lateral dusky spot just behind the gill cover margin (lacking in Atlantic herring) and the upper sides of the body may have faint stripes or dark olive-black longitudinal lines in large fish (no lateral stripes in Atlantic herring). The blueback also differs from Atlantic herring in lacking teeth on the roof of the mouth. The anterior part of the body in blueback herring is much more heavily built than is that of the Atlantic herring, and serrations on the abdominal midline scutes are considerably stronger and sharper, so much so that "a practiced hand" should easily separate Atlantic herring from alewives (Bigelow and Schroeder 1953).

GENERAL BIOLOGY

(Recent syntheses of blueback herring biology are Loesch 1987; Scott and Scott 1988; Klauda *et al.* 1991; and DesFosse *et al.* 1994).

Habitat.--The blueback herring, like the alewife, is an anadromous, euryhaline, schooling, coastal pelagic species that spends most of its adult life in the sea, approaching the shore and returning to freshwater only to spawn late in spring. Spent fish return to sea shortly after spawning. Bigelow and Schroeder (1953) commented that practically nothing was known of blueback herring movements in the sea, except that they were schooling fishes. They noted occurrences of this species at locations offshore of Cape May, NJ, and suggested that perhaps the blueback moved away from the coast and overwintered near the bottom offshore.

Little information is available on life history aspects for subadult blueback herring after they emigrate to the sea as YOY or yearlings, and before they mature and return to freshwater to spawn (Klauda *et al.* 1991). Like other anadromous river herrings, they exhibit seasonal migrations and movements in conjunction with changes in temperature and photoperiod, but direct evidence as to the relative importance of extrinsic factors in directing migrations is unavailable. New Jersey inshore waters to at least 8 km offshore appear to be an important overwintering area for juveniles (<120 mm SL) originating from rivers in that region (Milstein 1981).

Based on trawl data, in summer and fall blueback herring are confined to areas on the continental shelf north of 40°N, such as Nantucket Shoals, Georges Bank, and the perimeter of the Gulf of Maine, usually in water temperatures less than 13°C (Neves 1981). In the fall, catches occur especially along the northwestern edge of the Gulf of Maine. Winter catches of this species were between 40 and 43°N, and spring catches were distributed over most of the continental shelf between Cape Hatteras and Nova Scotia as fish began their migration toward their spawning rivers. Catches of blueback herring in specific areas in the Gulf of Maine may be related to zooplankton abundance, although direct evidence is lacking (Neves 1981). On the continental shelf between Cape Hatteras and Nova Scotia, bluebacks occupied water shallower (27-55 m) than that (56-110 m) inhabited by alewives collected during the same periods (Neves 1981).

Bluebacks usually enter freshwater only to spawn, but unlike alewives do not readily become landlocked. Juvenile blueback herring collected in Lake Champlain, NY, are of uncertain origin, and it is unknown whether they represent a landlocked population in this system (Plosila and LaBar 1981). A landlocked population occurs in Kerr Reservoir, VA (DesFosse *et al.* 1994).

Habits.--Blueback herring, like alewives, are vertical migrators at sea and follow the upward (night) and downward (day) movements of their planktonic food supply (Neves 1981). Juvenile blueback herring in tidal freshwaters of Virginia also undertake diel migrations (Loesch *et al.* 1982). In this system, a high proportion (90%) of surface trawl catches at night consisted of blueback herring while relatively few (1%) contained alewives. More than three times as many juvenile bluebacks were taken at the surface than were collected in bottom waters. Inverse associations between catches and opacity index values indicates that changes in blueback herring availability were due to negative phototropic behavior by the fish, or perhaps, in response to the planktonic prey they follow.

Temperature.--Several investigators have noted the effects of temperature on behavior of blueback herring (Bigelow and Welch 1925; Collins 1952; Loesch and Lund 1977). Collins (1952) reported that adult blueback herring respond to temperature differentials of about 0.5°C. Marcy (1976a) collected blueback herring in the Connecticut River over a temperature range from 6.7-32.5°C. Mass mortalities of adult blueback herring in the Connecticut River were correlated with a lethal combination of low dissolved-oxygen content and high water temperatures (Moss *et al.* 1976).

Feeding.--The blueback herring is a plankton feeder, subsisting chiefly on copepods, amphipods, mysids and other pelagic shrimps, and small fishes while in the sea (Bigelow and Schroeder 1953; Brooks and Dodson 1965; Scott and Scott 1988). Stomach contents of adult blueback herring captured at sea indicated that calanoid copepods, mysids, and other zooplankters were important food items (Neves 1981). Alewives taken at the same time also fed on similar prey items. Microzooplankton, including calanoid copepods, was determined to be the most important food category of adult blueback herring in Nova Scotian waters (Stone 1986). In contrast, alewives taken during that study consumed larger and more benthic-oriented prey. It is of interest that feeding efficiency of blueback herring is strongly inhibited even by the presence of small amounts of weed (Janssen 1982). Adult blueback herring on the spawning migration continue to feed on a variety of planktonic organisms, as well as terrestrial insects (Creed 1985). In Minas Basin, NS (Stone and Daborn 1987), a turbid macrotidal estuary, blueback herring appeared to concentrate their feeding on microzooplankton (calanoid copepods, cypris larvae, and molluscan veligers). Diet composition suggested that blueback herring were primarily filter-feeding to capture prey when foraging in this environment (Stone and Daborn 1987).

Diets of juvenile bluebacks inhabiting nursery areas in the Holyoke Dam region of the Connecticut River indicated that they fed predominantly below the surface and consumed primarily copepods and cladocerans (Domermuth and Reed 1980). Electivity indices indicated moderate selection for daphnids and strong selection for bosminid cladocerans. Only small amounts of benthic prey were included in diets of juveniles, indicating that feeding was mostly in the water column. Diets of blueback herring were found to be somewhat restricted compared with those of co-occurring American shad. Food habits studies on bluebacks from the James River, VA, also found a low diversity of prey items consumed by juvenile bluebacks, with copepods comprising the major prey items (Burbidge 1974).

In the feeding process, a blueback herring searches as it swims, sighting most prey above its horizontal course, and swims upwards to take the prey (Janssen 1982). Blueback herring apparently do not distinguish between motile and nonmotile prey, perhaps because any prey's image is moving across its retina as the herring swims (Janssen 1982).

Feeding activity of juvenile blueback herring was found to vary directly with, but lag behind (6-8 h), the illumination level (Jessop 1990a). Feeding begins after dawn, increases during the day to a maximum near dusk, then declines or ceases overnight, at which time stomachs empty (Burbidge 1974; Weaver 1975; Jessop 1990a); illumination increased during the forenoon, decreased during the afternoon, and was essentially constant overnight.

Predators.--Little is known of predation rates on bluebacks in the sea (Scott and Scott 1988). Blueback herring are important forage species for a variety of predators, including eels, and many larger species of schooling predators such as bluefish, weakfish, and striped bass (Dadswell 1985; Ross 1991). They are also preyed upon by seals and avian predators such as gulls and terns. During spawning runs, undoubtedly bluebacks are also eaten by large predaceous fishes, ospreys, and seabirds, but data on actual predation rates are unavailable. In freshwater systems, the young fall prey to a variety of predators such as eels, yellow perch, and white perch. A large variety of predators are listed for anadromous and landlocked river herring (Loesch 1987), including ca. 18 species of fishes, turtles, snakes, birds, and mink. Included in this list were species of marine fishes commonly found in the Gulf of Maine, such as silver hake, striped bass, bluefish, and salmon. Juvenile blueback herring in estuaries, such as the Hudson River (Juanes *et al.* 1993), are common items in diets of young bluefish (101-150 mm).

Parasites.--Little is known about parasites or diseases of blueback herring (Scott and Scott 1988). In the Woods Hole region, the acanthocephalan *Echinorhynchus acus* was listed as a parasite of the blueback (Sumner *et al.* 1913), and the parasitic copepod, *Clavellisa cordata*, also infects the gills of this species (Rubec and Hogans 1987). Landry *et al.* (1992) recovered 13 species of parasites from blueback herring occurring in the Miramichi River, NB. Among these were one species of monogenetic trematode, four species of digenetic trematode, one species each of Cestoda, Acanthocephala, Annelida, Copepoda, and Mollusca (glochidia), and three species of nematodes.

Species Associates.--Since diets of co-occurring blueback herring and alewives are similar, potential competition for trophic resources could result, especially in freshwater nursery habitats. However, differences in temporal and spatial distributions of spawning activity between the two species would serve to separate alewife and blueback herring stocks, thereby reducing any potential competition (Loesch *et al.* 1982; Loesch 1987). Blueback herring and American shad larvae coexisting in the Connecticut River avoided any potential competition by utilizing different prey items, or when consuming the same prey taxa, these predators selected different size components of the available prey items (Crecco and Blake 1983). Differences in life history aspects of blueback herring compared with those of American shad and alewife that could serve to reduce any potential competition were discussed by Schmidt *et al.* (1988). Landry *et al.* (1992) found significant differences in prevalence of parasites between sympatric alewife and blueback herring and concluded that these differences reflected underlying differences in the ecologies and physiology of the two species.

Predation by blueback herring could change community structure of zooplankton occurring in lakes (Brooks and Dodson 1965; Hutchinson 1971; references in Loesch 1987). Presence of large schools of migrating bluebacks in small tidal streams may also affect ammonium concentrations (Browder and Garman 1994) in these areas, potentially influencing biotic interactions and nutrient dynamics in these habitats.

General Range.--Blueback herring occur in northwest Atlantic coastal waters and tributary freshwaters from Cape Breton, NS, to the St. John's River, FL (Bigelow and Schroeder 1953; Scott and Scott 1988). In northern regions of its range, it occurs from the southern Gulf of St. Lawrence, southward along the coast of Nova Scotia to the New Brunswick watershed in the Bay of Fundy (Scott and Scott 1988). Though widespread in the Gulf of Maine (Bigelow and Schroeder 1953), it not as abundant there as it is in southern New England. Overall, the blueback herring has a more southern distribution than does the alewife, and is more numerous in southern portions of its range.

Occurrence in Gulf of Maine.--Because of similarities in morphology and associated difficulties in identifying alewife and blueback herring, these species have not always been correctly identified or handled separately, although fishermen have recognized the existence of two distinct species since at least 1816 (Bigelow and Schroeder 1953). The alewife occurs more commonly and abundantly in the Gulf of Maine than does the blueback herring (Bigelow and Schroeder 1953), and most information regarding *Alosa* from this region probably pertains to the alewife. Consequently, little reliable information regarding historical patterns of temporal occurrence and abundance for blueback herring is available for Gulf of Maine localities. Nor is there any definite information available on blueback herring as to how regularly they enter streams in the Gulf of Maine for spawning (Bigelow and Schroeder 1953).

Bigelow and Schroeder (1953) speculated that schools of bluebacks could be expected anywhere between Cape Sable and Cape Cod. Scott and Scott (1988) reported this species as occurring in many rivers along the Nova Scotia coast, in the St. John and Kennebecassis rivers, and probably in other rivers of the Bay of Fundy drainage of New Brunswick as well. Gulf of Maine localities for blueback herring based on specimens or reliable citations (Bigelow and Schroeder 1953) included Yarmouth, NS; St. John Harbor and Shubenacadie River; the St. Croix River; Dennys River, Eastport; Bucksport; Casco Bay; Small Point; Freeport; Sheepscot River; and other localities along coastal Maine; as well as Massachusetts Bay; Gloucester; and Cape Cod. A few fish reported from Georges Bank in 1913 may also have been bluebacks. Bigelow and Schroeder (1953) identified 10 blueback herring that were trawled at about 83 m off southern

New England, indicating that this species may occur as far offshore as do alewives.

Spawning Location.--In portions of the geographic range where blueback herring and alewife co-occur, the two species, to a large degree, are spatially isolated with respect to their spawning grounds (Loesch 1987). Blueback herring in the sympatric range prefer to spawn over hard substrates where the flow is relatively swift, and actively avoid lentic sites (Bigelow and Welsh 1925; Marcy 1976b; Loesch and Lund 1987; Johnston and Cheverie 1988). The two species may occur together where further upstream migration is prohibited (Loesch 1987). At such sites, blueback herring concentrate and spawn in the main stream flow, while alewife favor shorebank eddies or deep pools for spawning (Loesch and Lund 1977). Although the northern stocks usually do not spawn in ponds, they have the ability to do so (Loesch 1987). For example, blueback herring captured at the base of the Mactaquac Dam in the St. John River system spawned successfully after being released into the head pond.

In the Carolinas, where alewives are few, and further south where they are absent, blueback herring exhibit more variety in selection of spawning grounds (references in Loesch 1987). In South Carolina, blueback herring choose seasonally-flooded rice fields, cypress swamps, and oxbows in preference to adjoining streams. This clinal change in habitat preference reflects the blueback herring's ability to adapt to the substantial environmental changes encountered from the Canadian maritime provinces and New England southward to the broad coastal plains of the southern United States (Loesch 1987). Furthermore, selection of lotic spawning sites in the north by blueback herring, but lentic sites in the south suggests a clinal spawning pattern that reduces competition with alewives for spawning grounds where the two species are sympatric (Loesch 1987).

Blueback herring spawn in freshwater or brackish habitats above the head of tide (Nichols and Breder 1926; Hildebrand 1963), and can undergo extensive migrations to reach upstream spawning habitats. In a coastal stream in the Gulf of St. Lawrence, blueback herring have also been observed to spawn above the head of tide in fast-flowing waters. There, eggs were spread over the bottom where they adhered to sticks, stones, gravel and aquatic vegetation (Johnston and Cheverie 1988). Blueback herring larvae are highly tolerant of salinity early in life, allowing the species to utilize both freshwater and marine nurseries (Chittenden 1972b). Even fish as small as 34-47 mm reportedly tolerate water of 28 ppt salinity.

Earlier reports (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Hildebrand 1963) that blueback herring do not ascend rivers as far as the alewife during its spawning migration are not entirely accurate. Studies in the Connecticut River (Crecco 1982) indicate that it is the blueback herring, not the alewife, that migrates farther upriver. Both species occur at the Mactaquac Dam, 148 km from the mouth of the St. John River (Messieh 1977; Jessop *et al.* 1982), and some fish passed above the dam proceed another 100 km upstream. Distributions of YOY fish further substantiate that blueback herring migrate far upstream (references in Loesch 1987). The upstream distribution of gravid blueback herring may only be a function of habitat suitability and hydrological conditions permitting access to such sites (Loesch and Lund 1987). The premise of a shorter spawning migration by blueback herring developed because early studies were conducted primarily in northern areas, where only alewives entered the head ponds (Loesch 1987).

Blueback herring, like alewife, presumably return to spawn in natal streams (Messieh 1977; Loesch 1987), but some individuals can stray to adjacent streams. Olfaction appears to be the major sensory mechanism used by alewife, and perhaps blueback herring, to find and migrate into natal watersheds (Thunberg 1971). Meristic differences among fish from different river systems supports the theory that blueback herring home to natal streams (Messieh 1977). Other evidence comes from the establishment or reestablishment of spawning runs after gravid fish are placed in ancestral or new systems lacking runs (Bigelow and Welsh 1925). Blueback herring will also occupy new systems or increase in abundance within systems when changes in physical or hydrological conditions permit or enhance entry (Loesch 1987). A huge increase in numbers of blueback herring passed above the Holyoke Dam on the Connecticut River was observed after improvements to the lift facilities (Moffitt *et al.* 1982).

The lipid content of blueback herring migrating into streams of Nova Scotia was neither size nor sex specific, and overall, was either similar to that of alewife co-occurring in one system, or somewhat lower than that of alewife from another system (Crawford *et al.* 1986). The difference in lipid levels between alewife and blueback herring appeared not due to genetic factors, but was a consequence of migration under different temperature regimes. Late migrants of this species had a significantly lower lipid content than earlier arrivals. Significant lipid depletion was noted in blueback herring spawning in the Margaree River, with lipid declining from 7.3% to 5.4% in fish sampled over a distance of 15 km.

Upon entering freshwater, gonads of blueback herring are nearly fully mature and little energy is required for full maturation during the freshwater phase of the spawning migration. Adult blueback herring, which feed during their freshwater migration (Creed 1985), swim at midwater depths, not in deeper water in the Connecticut River (Witherell and Kynard 1990).

Populations of blueback herring spawning in northern extents of the geographic range display a variety of adaptations for successful reproduction in these northern environments. For example, there are latitudinal trends from south to north of increasing length at age (Richkus and DiNardo 1984). There is an increased proportion of, and maximum age of, previously-spawning blueback herring in these northern populations (Jessop 1993). Fish in northern populations also have a smaller gonad weight relative to body size, a lower fecundity, and higher egg weight, which are components of a life history strategy that serve to maximize individual reproductive potential in these highly variable northern environments (Glebe and Leggett 1981a, 1981b; Jessop 1993).

Spawning Seasonality.--Onset of spawning in blueback herring is related to water temperature (Loesch 1987), thus it varies with latitude, and it may vary annually by 3-4 wk in a given locality. Spawning by blueback herring generally begins between 10 and 15 °C (Loesch 1987). Optimal spawning temperatures are 21-25 °C (Cianci 1969; Marcy 1976b; Klauda *et al.* 1991). The minimum temperature in which spawning has been reported to occur is 14 °C, whereas spawning ceases when temperatures exceed 27 °C (Loesch 1968). Coincident with this observation, Edsall (1970) and Marcy (1971, 1973) have recorded minimal survival of river herring larvae held at temperatures above 28 °C. In rivers of Nova Scotia, blueback spawning migrations occur primarily in June at 13-21 °C, but spawning does not occur until the water warms to 20° or 22 °C (Crawford *et al.* 1986). In the southwest Margaree River, NS, the blueback herring run began when water temperature was 13.3 °C, which was 21 d later and some 4.4 °C higher than the alewife run that had occurred earlier in that river. This difference in seasonal timing (about a month or so) in peak spawning activity between alewives and blueback herring appears to take place wherever these species occur sympatrically. Several authors have noted that although the blueback herring spawns about a month or so later than does the alewife, their spawning peaks differ only by 2-3 wk (Hildebrand and Schroeder 1928; Loesch 1987).

In northern sections of its distribution, blueback herring reproduce from April to as late as August (Bigelow and Schroeder 1953; Marcy 1976b). In tributaries to the St. John River, NB, blueback herring are present as early as May (Messieh 1977; Jessop *et al.* 1982), but do not spawn until June when water temperatures have increased (Scott and Scott 1988). Blueback herring were collected in mid-April in the lower Connecticut River in water temperatures as low as 4.7°C, but spawning did not commence until about mid-May (Loesch and Lund 1977) and may have continued until August (Marcy 1976b). Spawning occurs much earlier in the year in populations reproducing in the southern portions of this species geographic range.

Spawning Behavior.--Males generally arrive in the spawning streams before females and tend to dominate in the early runs, but the proportion of females increases (sometimes significantly) in the later runs (Loesch and Lund 1977; Loesch 1987). Spawning time for a wave of migrants is about 4-5 d (Klauda *et al.* 1991). Estimates of sex ratios are affected by spatiotemporal differences in the occurrence of the different sexes, and through sampling location and effort (Loesch and Lund 1977). Samples collected in the lower portion of an estuary may contain immature females that do not migrate to the spawning grounds. The proportion of male blueback herring on the spawning grounds after the day of arrival can change because males tend to remain longer than females and, after exiting, some males may actually return with the succeeding wave of upstream migrants (Loesch 1969). Additionally, during the process of spawning, female bluebacks attract several males (Loesch and Lund 1977).

In the Connecticut River, blueback herring are reported to spawn in the late afternoon (Loesch and Lund 1977). Blueback herring were observed spawning in a coastal stream on Prince Edward Island usually between dusk and 0100 hrs (Johnston and Cheverie 1988). During spawning, a female and two or more males swim circularly at about 1 m from the surface. Swimming speed gradually increases and the group dives to the bottom and releases gametes (Loesch and Lund 1977). Eggs and sperm are broadcast over the substrate. Spent adults migrate rapidly downstream after spawning.

Repeat spawning occurs in blueback herring at an average rate of about 30-40% (Richkus and DiNardo 1984). About 75% of blueback herring spawning in Nova Scotia were repeat spawners (O'Neill 1980), whereas in Chesapeake Bay tributaries (Joseph and Davis 1965), 44-65% of bluebacks had spawned previously. In the Fishing Bay area of Maryland, 45% of the blueback herring had spawned once, 21% had spawned twice, 7% three times, and 1% four times (Krauthamer and Richkus 1987).

Fecundity.--Fecundity is relatively high in the blueback herring and is related to age and size of the female, but is highly variable (Loesch 1987). Total fecundity estimates for anadromous blueback herring range from about 30,000-400,000 eggs (Loesch 1981; Jessop 1993). However, total fecundity exceeds fertility because postspawning females often retain substantial residual fecundity (Loesch and Lund 1977; Jessop 1993). Estimates of retained unripe eggs for various populations of blueback herring range from 23-44% of the total fecundity (Loesch and Lund 1977; Jessop 1993).

Total fecundity generally increases with length of females (Loesch 1981; Jessop 1993), and length may be the best predictor of fecundity for this species. In Nova Scotian waters (Jessop 1993), total fecundity for fish 205-280 mm FL ranged from 52,300 to 363,500 eggs/female. In the Connecticut River, the number of eggs per individual female in blueback herring ranged from 45,800 to 349,700 for females 23.8-31.0 cm long, respectively (Loesch 1981). In this population, weights of spawned and unspawned eggs increased with total fish

length through the 296-305-mm length interval, then declined.

Although fecundity is also positively correlated with age in some populations **(Jessop 1993), age was found to be a statistically nonsignificant predictor of fecundity for blueback herring in Canadian Maritime rivers. A maximum fecundity at about age-6 was reported by Loesch and Lund (1977), who also reported that fecundal senility may occur in chronologically or physiologically older blueback herring. Jessop (1993), however, did not find any evidence of fecundal senility in blueback herring spawning in Nova Scotian waters.**

Early Life History

Eggs.--Eggs are yellowish, semi-transparent, and 0.87-1.11 mm in diameter. Eggs are pelagic, or semi-demersal, like those of the alewife, and adhesive during the water-hardening stage, becoming less so afterwards (Johnston and Cheverie 1988). Both unfertilized and fertilized eggs of blueback herring differ from those of alewife (Kuntz and Radcliffe 1917; Norden 1967).

Development.--Incubation requires only about 3-4 d at 20-21 °C (Kuntz and Radcliffe 1918; Jones *et al.* 1978) and 58-55 hr at 22.2-23.7 °C (Cianci 1969; Klauda *et al.* 1991). Young bluebacks are about 3.1-5.0 mm TL at hatching (Jones *et al.* 1978). Eggs and larvae can tolerate salinities as high as 18-22 ppt (Johnston and Cheverie 1988), and small juveniles (34-47 mm) reportedly tolerate water of 28 ppt salinity. Cianci (1969) calculated that yolk absorption for blueback herring required 72 hr at 23.6 °C. Yolk absorption occurs between about 5.0-9.8 mm (Marcy 1976b), and exogenous feeding takes place 3-4 d posthatch (Klauda *et al.* 1991). Larval transformation to the juvenile stage is usually completed by about 20 mm TL (Klauda *et al.* 1991). Growth is fairly rapid; young are 30-50 mm long within a month and already show most diagnostic characters of the adult (Bigelow and Schroeder 1953). Essig and Cole (1986) used daily growth rings on otoliths to estimate lengths-at-age for larvae.

Distinction of larvae.--Larvae of blueback herring and alewife are difficult to distinguish. Chambers *et al.* (1976) studied both species in Chesapeake Bay and noted several differences useful in distinguishing larvae of these species including number of myomeres between insertion of the dorsal fin and position of the anus (11-13 for blueback herring vs. 7-9 myomeres for alewives).

Larval ecology and behavior.--Early life history stages are found in brackish and tidal freshwaters of their natal streams. In some riverine locations, such as the Connecticut River, river herring eggs and larvae may represent the dominant species taken in ichthyoplankton collections (Marcy 1976b). Marcy (1976b) found that blueback herring larvae occurred more frequently in bottom waters than in surface waters. He estimated that larvae nearer the bottom were younger than those occurring at the surface, suggesting that larvae become more pelagic with downstream drift. Yolk-sac larvae have limited swimming ability and are therefore carried passively by currents and swept downstream to slower moving water where they grow and develop into juveniles (Johnston and Cheverie 1988). Larval blueback herring are photosensitive. Density of larval blueback herring at the surface gradually increased from day through dusk and night with maximum density occurring in surface waters at dawn (Meador 1982).

First-feeding (5-12 mm) larvae in the Connecticut River consumed mostly rotifers (67% of the diet), while larger larvae fed extensively (27% of the diet) on cladocerans (*Bosmina* spp.; Crecco and Blake 1983). Blueback herring larvae have a smaller mouth gape at length compared with that of American shad, and tended to select smaller prey sizes at length compared with those consumed by shad larvae (Crecco and Blake 1983). Prey widths were also consistently smaller for blueback herring than for shad. Temporal changes in prey selection among blueback larvae generally followed changes in river zooplankton. Rotifers (*Keratella* spp.) were the most selected prey among all length groups of larvae during the period when they were the most abundant zooplankton; somewhat later, a second group of rotifers became abundant and were consumed in large quantities. There was a linear relationship between mouth gape and body length among blueback herring larvae. Prey width increased with length of the larvae, but prey selected by bluebacks were always smaller than those selected by shad larvae. Diet-breadth values for blueback larvae varied considerably among collection periods and appeared to be partially governed by prey-switching. Diet-breadth values for this species were always higher than those for co-occurring shad larvae. It was suggested that the ability of blueback herring larvae to utilize the abundant rotifer community may be instrumental in their numerical dominance over American shad in the Connecticut River (Marcy 1976c), as well as in other east coast rivers (Loesch and Kriete 1980).

Juvenile Biology.--Juvenile blueback herring can constitute significant portions of the fish fauna seasonally inhabiting rivers and streams. In the Connecticut River, Marcy (1976a) estimated that anadromous fishes and marine fishes utilizing the river as a nursery area constituted about 67% of the young fishes in the river, and of these blueback herring were the most abundant. Juvenile blueback herring undergo diel migratory activities (Loesch *et al.* 1982). Bottom catches of blueback herring were significantly greater during the day than night, and conversely, surface catches were significantly greater at night than during the day. This inverse association between blueback herring abundance at the surface and opacity index values indicates that the diel activity of blueback herring is an expression of a general negative phototropic behavior by the fish or the prey they followed. Also, juvenile bluebacks occur much shallower in the water column and are spatially separated from co-occurring alewives which live deeper in the water column. Feeding by blueback juveniles in the Potomac River began at dawn, increased through the day to a maximum at dusk, and then declined from dusk to dawn (Burbidge 1974).

Young blueback herring apparently grow slower than alewives, at least in Chesapeake Bay (Hildebrand and Schroeder 1928). Growth estimates for juveniles in the Connecticut River were 0.657 mm/d (Krauthamer and Richkus 1987).

In autumn, juvenile blueback herring at around 50 mm begin migrating downstream to the estuary. Compared with the migration schedule of juvenile alewives, juvenile blueback herring tend to remain in their natal rivers about a month longer into the fall before returning to the sea (Kissil 1969; Loesch 1969; Marcy 1976b). Downstream migration in Gulf of Maine tributaries reportedly takes place rapidly during October (Bigelow and Schroeder 1953).

Increased river flow, decreasing water temperature, or a combination of both factors during autumn, are key stimuli for this migration (Sykes and Lehman 1957; Walburg and Nichols 1967; Moss 1970), although the particular combination of extrinsic factors triggering seaward migration of juvenile blueback herring is uncertain.

Virtual absence of river herrings from inshore regions of the Annapolis estuary (NS) for almost a month before a final seaward migration suggested that they school offshore in the estuary until the correct migration stimulus occurs (Stokesbury and Dadswell 1989). Peak seaward emigration during 2 yr occurred during new to quarter moon periods (dark nights). Since a negative phototrophic response would tend to keep them relatively immobile during daylight hours (Loesch *et al.* 1982), perhaps, decreasing light levels play some role in stimulating this migration. However, coincident with these dark nights was a sharp decline in water temperature below 12°C. River input appeared to play little role in stimulating seaward movement. In the Connecticut River, decreased temperature (and not increased water flow) occurring during a new or quarter moon was also found to be the major stimulus for the beginning and ending of downstream migration of juvenile blueback herring (Marcy 1976c; O'Leary and Kynard 1986). Migration began in September as water temperature declined to 21°C, peaked at 15-14°C, and ended in late October or early November at 10°C (O'Leary and Kynard 1986). Migration of blueback herring lasted 42 d in 1981 and 67 d in 1982. Most movement peaks were centered on quarter moon periods; none was centered on a full moon. Sex ratios of migrating juveniles were 1:1 in two out of three yr. Seasonal and daily patterns of outmigration in blueback herring may be related to changes in behavioral response due to decrease in water temperature below a threshold of 21°C. However, O'Leary and Kynard (1986) noted that light intensity could also affect daily activity patterns in this species during migration, but little is known about this aspect of their biology. They reported that in their study area blueback herring were active throughout the 24-hr period (peak activity at 1800 hr during 1 yr; 2400 hr another year), with large catches occurring during daytime. Daily movement patterns changed during the migration; fish were most nocturnal early in the run and daytime movement increased in the peak and late portions of the run. They hypothesized that migration of blueback herring may be triggered on a daily (but not a seasonal) basis by increasing (not decreasing) light intensity, because their movements began at about 0600 hr each morning.

In the Hudson River, bluebacks were among the dominant nearshore fishes collected in seines and the distribution and movements of blueback juveniles were different from those of alewife and American shad (Schmidt *et al.* 1988). Recruitment to the juvenile stage begins later (in early July) in blueback herring, because they spawn later than the other two species. Low abundance of blueback juveniles in the lower zone of the river through the end of September suggested that, unlike the other two *Alosa* species, juvenile blueback herring remain in the vicinity of their natal areas throughout the summer. By the end of November, virtually all juvenile blueback herring had left the study area. The few that remained in December may have been individuals that would have overwintered in the estuary as Davis and Cheek (1973) reported for blueback herring in Chesapeake Bay. Marcy (1969) noted that juvenile blueback herring (aged as 1+) have been found in the lower Connecticut River in early spring, indicating that many probably spend their first winter close to the mouth of that river.

Size at emigration may not be important for river herrings, since large interannual variations in size of migrating juveniles have been reported. No size-related downstream movements of blueback herring were observed by Schmidt *et al.* (1988) in the Hudson River, but in the Connecticut River blueback herring segregated by size prior to emigration (Loesch 1969).

Age and Growth.--Growth rates, age at sexual maturity, and longevity vary greatly for this species geographically. Some of this variation is undoubtedly natural, but part is due to different methods of measuring fish lengths and back-calculating lengths at age from scale annuli (Loesch 1987). Hildebrand (1963) reported a maximum length to 38 cm, but generally, few individuals exceed 30 cm or about 1 kg in weight (Ross 1991). A 30.4 cm FL female blueback was listed from the St. John River (Jessop *et al.* 1983).

In general, female bluebacks are larger and heavier, and grow somewhat faster, than males of the same age (Loesch 1987). Bluebacks are generally smaller and shorter than alewives of the same age. Males and females reach a maximum age of about 11 yr (Jessop *et al.* 1983). Some comparative growth data on bluebacks from the St. John River system, NB, is available in Messieh (1977).

Data available for bluebacks caught by otter trawl in July 1964 off Georges Bank (Netzel and Stanek 1966) had mean lengths at age (otoliths used for aging) as follows: 24.0 cm at age-3, 26.9 cm at age-4, 28.1 cm at age-5, 29.2 cm at age-6, 30.2 cm at age-7, and 31.3 cm at age-8. Mean lengths and weights at age-4 through age-10 (scales used for aging) for bluebacks caught during the spring-spawning run on the St. John River at the Mactaquac Dam in 1981 were provided by Jessop *et al.* (1983). Lengths of male and female Connecticut River bluebacks at age are: age-3 males 25.9 cm, females 26.2; age-4 males 26.7 cm, females 27.7 cm; age-5 males 27.9 cm, females 29.2; age-6 males 28.7 cm, females 30.2; and age-7 males 29.7 cm, females 31.0 cm (Loesch 1987).

First spawning by blueback herring generally occurs from age-3 to age-6, but the composition of virgin spawners is strongly dominated by age-4 fish (Loesch 1987). In general, spawning stocks of river herring are consist primarily of 3-8-yr-old fish. Scale examination of age-10 and age-11 male and female fish indicated up to eight previous spawnings. Males tend to dominate age-classes 3-5; females live longer and, thus dominate older age-classes. Recruitment to the matured population is essentially completed by age-5. From information synthesized by Loesch (1987), essentially 54-99% of male blueback herring and 41-98% of the females mature by age-4. Sexual maturity of bluebacks in St. John River is attained mainly between age-3 and age-5; 5% or less of both males and females matured at age-2 or age-5 (Messieh 1977).

Mortality.--Blueback herring undoubtedly suffer high mortalities throughout their life cycles, but little information is available on rates of mortality. Estimates are that fewer than 1% of all river herring eggs survive early life stages to migrate to the sea (Kissil 1974). Anthropogenic sources of mortality can also be significant (Taylor and Kynard 1985). Marcy (1976b) found that juvenile blueback herring and alewives represented about 97% of fish entrained at a nuclear power plant in the Connecticut River. A stock-recruitment relationship for blueback herring returning to the Mactaquac Dam, St. John River, was discussed by Jessop (1990c).

Importance and Utilization.--No commercial distinction is made between blueback herring and the more abundant alewife; both species are equally useful for bait and for food. It is usually harvested with the alewife and marketed similarly. Ross (1991) provided a discussion of management strategies being used to restore spawning populations of bluebacks and alewives (see alewife account), and presented an excellent discussion of preparing blueback herring as tablefare.

Chapter 13. AMERICAN SHAD *Alosa sapidissima* (Wilson 1811)

Description.--Body relatively deep, body depth variable and increasing with age (30.2-36.8% SL); body moderately laterally compressed, its greatest thickness generally about one-half of its depth, and elongate; ventral margin of abdomen saw-toothed with sharp scutes forming distinct keel; caudal peduncle slender. Head relatively small (23-28% SL), broadly triangular; snout length 4.8-7.1% SL; mouth terminal and relatively large; lower jaw not excessively thickened and not rising steeply within mouth, fitting into deep notch in upper jaw so that jaws about equal when mouth closed; maxilla extending to vertical through posterior margin of eye. Teeth small (missing in adults, minute in juveniles to 15 cm SL), weak, few in number on premaxilla and mandible, and median line of tongue; no teeth on vomer. Eye relatively small (4.0-5.9 HL), adipose eyelid well developed. Lateral line absent on body. Dorsal and anal fins soft-rayed, moderately-sized; dorsal fin somewhat elevated anteriorly, its margin slightly concave, situated above pelvic fins and anterior to body mid-point. Pelvic fins abdominal, with axillary scale equal to, or sightly larger than one-half length of fin; pectoral fins low on sides. Caudal fin deeply forked, lobes of nearly equal width and somewhat shorter than head. Scales cycloid, large, deciduous, crenulate on posterior margin. (Bigelow and Schroeder 1953; Hildebrand 1963; Whitehead 1985a; Scott and Scott 1988; DesFosse *et al.* 1994).

Meristics.-- Dorsal-fin rays 15-20, usually 17 or 18. Anal-fin rays 18-25, usually 20-22; pelvic-fin rays 8-10, usually 9; pectoral-fin rays 14-20 (usually 16). Vertebrae 53-59. Lateral scale rows 50-64; prepelvic ventral scutes strong, 18-24 (usually 20-22); postpelvic scutes 12-19, usually 15-17; total scutes 34-39, usually 35-38. Lower gillrakers numerous, 59-76 in adults (fewer in young, 26-43 in specimens smaller than 125 mm), long and slender. Branchiostegal rays 7, rarely 6. Pyloric caecae numerous, usually clustered on right side. Additional meristic data for hatchery-reared larvae (Johnson and Loesch 1983) and comparisons of finray counts for several populations of juvenile American shad are also available (Nichols 1966; Carscadden and Leggett 1975a; DesFosse and Loesch 1985).

Color.--Dark blue or blue-green metallic luster on dorsum, gradually shading to white and silvery on lower sides and abdomen; large black spot on shoulder immediately posterior to gill cover, followed by several (4-27) smaller dark or indistinctly dusky spots in an irregular longitudinal row, with second row of spots (1-16) occasionally below first, and rarely with third row of spots (2-9) ventral to second row. No dark lines along rows of scales. Fins pale to greenish; dorsal and caudal somewhat dusky in large specimens; tips of lobes of caudal dark in some specimens. Peritoneum pale to silvery.

Size.--American shad is the largest clupeid species occurring in the Gulf of Maine. Historically at the height of their abundance (DesFosse *et al.* 1994, and references therein), more large American shad were evident in the various spawning populations with some reaching 5.4-6.3 kg. Presently, specimens reach about 50 cm SL, with Atlantic males typically ranging to 0.9-1.4 kg, and females 1.4-1.8 kg (DesFosse *et al.* 1994). The sportfishing world record is 5.1 kg fish taken in the Connecticut River, MA, in 1986 (IGFA 1994). Hildebrand (1963) cited a 600 mm fish, but did not indicate whether this measurement referred to SL or TL (DesFosse *et al.* 1994). Carlander (1969) reported a 658 mm FL fish and Burgess (1980) listed 584 mm as the maximum SL. Adult shad are sexually dimorphic with respect to size (Walburg and Nichols 1967), with females being longer and heavier than males at all ages.

Distinctions.--American shad differs from Atlantic herring in lacking teeth on the vomer; adult shad have only weak teeth on the jaws, although young shad have small jaw teeth that may persist until the fish is ca. 30 cm or so long. American shad is similar to hickory shad, alewife, and blueback herring in its deep body and sharply saw-edged abdomen. It differs from hickory shad in having a longer mouth with upper jaw reaching posteriorly to a vertical through the posterior margin of the eye, and when the mouth is closed, the lower jaw tip is entirely enclosed within the tip of the upper jaw (whereas in hickory shad the posterior extent of lower jaw only reaches a vertical through the mid-eye region and the lower jaw projects farther forward than upper jaw when the mouth is closed). American shad also have many more lower gillrakers (59-73) than do hickory shad (18-23).

American shad differs distinctively from alewife and blueback herring in that the upper outline of the shad's lower jaw is very slightly concave, without a sharp angle, while in these others, the lower jaw outline is deeply concave with a pronounced angle. The shad differs from these other species in having more lower gillrakers (59-73 vs. 38-43 in alewife and 41-51 in blueback herring). Additionally, shad has a smaller eye than that of the alewife (ca. equal to snout length), and the American shad has a larger mouth than either of these other species (posterior extent of jaws reaching posteriorly only to vertical through mid-point of eye in alewife and blueback herring). The American shad differs further from alewife by its lower jaw which projects slightly beyond the upper when the mouth is closed. American shad differs further from blueback herring in its very pale peritoneal lining (vs. dusky or dark black in blueback herring). Chapman *et al.* (1994) reported distinct differences in mtDNA composition between American shad and alewife and blueback herring.

GENERAL BIOLOGY

Habitat.--American shad is an anadromous, highly migratory, coastal pelagic, schooling species, spending most of its adult life in the sea and returning to freshwater only to spawn. Length of time of ocean residence varies depending on the fish's sex and latitude of the home river (Leggett 1976). Adult fish apparently never re-enter freshwater until they return to their natal rivers in spring or early summer to spawn, though they may sometimes be found in lower reaches of estuaries at other times of the year. A fall run that occurred in September and October into the St. John River estuary, NB, was not a feeding or fall-spawning migration (Gabriel *et al.* 1976), but resulted from aggregation of fish there that had strayed from adjacent feeding areas. In the ocean, shad are found from the surface to about 220 m (Walburg and Nichols 1967). Bottom trawl catches in the Atlantic indicate that American shad occur at bottom temperatures of 3-13 °C (Neves and Depres 1979). In the Gulf of Maine, American shad are commonly taken in surface waters near coastlines (in spring, summer, and early fall), but in late fall and winter fish move deeper and can be found far offshore. Catch records include captures of this species up to 80-96 km offshore of eastern Nova Scotia (Vladykov 1936), 64-80 km off the coast of Maine, 40-145 km off southern New England, and even as far as the southern part of Georges Bank (40°52'N, 67°40'W), ca. 193 km from the nearest land (Bigelow and Schroeder 1953; Dadswell *et al.* 1987).

During spawning runs, American shad ascend rivers and migrate considerable distances upstream, but usually they do not ascend as far upstream as do alewives or blueback herring. After spawning, adult fish return to oceanic waters, followed thereafter by juvenile fish emigrating seaward from spawning grounds and nursery areas. Postspawning fish up to 4.5 kg and averaging about 2.2 kg have been reported in the Gulf of Maine and Bay of Fundy (Hildebrand 1963), and schools of them have been seined occasionally in summer and autumn, even into December, at various places along the Maine coast, where they have been the object of a frozen-fish industry in some years. Immature fish (0.2-1.2 kg) sometimes congregate along the Maine coast and are more or less common in the Massachusetts Bay region during late summer and fall. By winter, adults and immature fish move offshore and out of the Gulf of Maine. Probably, YOY American shad overwinter near mouths of their parent streams.

Habits.--While in the sea, American shad form relatively large schools, sometimes numbering in the thousands. Shad are vertical migrators that follow the daily upward (night) and downward (day) movement of large zooplankters on which they feed (Neves and Depres 1979).

One of the most significant features of the life cycle of American shad is the pronounced seasonal migration undertaken by this species (McDonald 1884; Talbot and Sykes 1958; Leggett 1976; Dadswell *et al.* 1987). American shad are long distance, coastal migrants. Each spring some young adults and those adults that survive spawning (see Reproduction section below) leave offshore wintering grounds and take part in extensive seasonal migrations north along the Atlantic coast, returning generally southward in the fall (Talbot and Sykes 1958). Tagging studies indicate a general northward migration of American shad in springtime, generally in the direction of the river in which fish were spawned (Leggett 1973, 1976). One migration route leads to the head of the Bay of Fundy, where fish arrive in June (Dadswell *et al.* 1983, 1987). Large migratory schools in the spring consist not only of spawning adults but also of non-spawning younger fish. The extreme endpoints of the coastal migration of shad are Florida (Williams and Bruger 1972) and Labrador (Dempson *et al.* 1983). During seasonal migrations, shad may travel great distances. For example, shad tagged in Cumberland and Minas basins of the inner Bay of Fundy have been recaptured in coastal and river waters from Labrador to the St. John's River, FL, which is ca. 3000 km from the original tagging site (Dadswell *et al.* 1987). During a mean life span of ca. 5 yr at sea, an American shad could migrate up to 20,000 km (Dadswell *et al.* 1987). Seasonal migrations are thought to occur mainly in surface waters, but American shad have been caught at depths to 220 m (Walburg and Nichols 1967).

Historically, the timing of American shad migrations were believed to be regulated by water temperature, both at sea and in the rivers (Leggett and Whitney 1972). Indeed, as early as 1884, Marshall McDonald developed the theory that shad were restricted to a narrow range of temperatures and that timing of runs depended on when water temperatures in individual rivers warmed to an optimum. Later migration models (Leggett and Whitney 1972; Leggett 1976; Neves and Depres 1979) maintained that seasonal movements of American shad were broadly controlled by climate and that fish maintained themselves within migration corridors or oceanic paths of "preferred" isotherms.

Direct evidence from tag returns, however, suggests that American shad cross thermal barriers, remain for extended periods in temperatures outside their "preferred" range, and migrate rapidly between regions regardless of currents and temperatures (Dadswell *et al.* 1987; Melvin *et al.* 1986). Dadswell *et al.* (1987) analyzed return information from 50 yr of tagging studies that included information from American shad tagged throughout almost their entire Atlantic coastal range. These data and that of population discrimination studies suggest that origin, life history, and chance play a role in the seasonal migrations of American shad. This evidence also indicates that American shad alternate between extrinsic and intrinsic cues to direct migration, depending on their physiological state, and at times during migration shad may use a bicoordinate navigation system with map (geographic contours), compass (magnetic capabilities), and clock (timing of tides) (Dadswell *et al.* 1987). The following information regarding shad migrations in the Atlantic was summarized from Dadswell *et al.* (1987). Two general conclusions are evident from analysis of tag returns. Shad tagged in or near spawning streams are recaptured over a wide area of the Atlantic coast, however, the majority of returns are in or near the river of tagging and few returns are from other freshwater sites. These data indicate that fish spawning in a stream represent a relatively homogeneous aggregation from a single river population. Shad tagged at ocean sites were also recaptured over wide areas of coast but, in contrast, returns were distributed evenly over several freshwater sites. Ocean aggregations, therefore, represent a heterogeneous mixture of American shad from many rivers.

Although American shad populations mix while in the sea over most of the range (at least from Chesapeake Bay to the St. Lawrence River) discrete aggregations exist seasonally at widely separated marine locations. During winter, aggregations were observed off Florida, the mid-Atlantic Bight (MAB), and on the Scotian shelf. During summer, aggregations occur in the upper Bay of Fundy, St. Lawrence estuary, and off Newfoundland and Labrador. Seasonal aggregations in the MAB and Bay of Fundy are well documented (Perley 1852; Leim 1924; Talbot and Sykes 1958; Neves and Depres 1979; Dadswell *et al.* 1983). Aggregations at the other sites, however, are poorly known, but records of occurrence and tag returns from these areas are persistent through time. Summer records off Newfoundland and Labrador were first reported in the 1930s, and although the total number of records is small, they are persistent. Since shad tagged in the inner Bay of Fundy were recaptured in subsequent years in the Newfoundland-Labrador region at times coinciding with maximum abundance of American shad in the inner Bay of Fundy (Dadswell *et al.* 1983), these must represent separate groups. Similarly, American shad tagged in the inner Bay of Fundy 1-3 yr previously had a mean recapture date of 180.5 d in the St. Lawrence estuary. It appears that aggregations occurring in the St. Lawrence River and St. Lawrence estuary are from two different groups. The annual occurrence of American shad in summer at the Isle Verte site and the similarity of oceanographic conditions there to those of the inner Bay of Fundy suggest that this site is another marine terminus for American shad migrations.

Occurrence of American shad on the Scotian shelf in winter is known from catch records (Vladykov 1936) and tag returns (Vladykov 1956). Persistent annual patterns of seasonal occurrence were also evident in data analyzed by Dadswell *et al.* (1987). Oceanographic conditions at 100-200 m on the Scotian shelf during winter (9-10°C; McClellan 1954) are within the preferred temperature range of American shad. Fish tagged in the Bay of Fundy during summer were recaptured annually off Florida in the winter. This aggregation off the Florida coast is probably different than that overwintering in the mid-Atlantic Bight.

The next stage in analysis of tag return information was to address the question as to the origin of fish comprising seasonal aggregations. Tag returns indicate that American shad overwintering in the MAB represent populations spawning in streams from Quebec to Georgia. Fish tagged in Delaware Bay in spring were recaptured in rivers of the Bay of Fundy and Gulf of St. Lawrence a few weeks later (White *et al.* 1969; Miller *et al.* 1982), and spawners tagged in Bay of Fundy rivers were recaptured the succeeding winter in the MAB (Melvin *et al.* 1986). Those shad tagged in Chesapeake Bay and Pamlico Sound in winter and early spring were recaptured in rivers to the south (to Georgia), during the same or subsequent years (Talbot and Sykes 1958).

The regional composition of the winter aggregation occurring off Florida is unknown. No evidence is available to suggest that American shad from populations north of Cape Hatteras overwinter with this group. Tag return information from the Bay of Fundy are ambivalent. Mean day of recapture was earliest for Florida and North Carolina south of Cape Hatteras, suggesting that American shad migrated onshore, then moved both north and south towards rivers in Georgia and South Carolina.

American shad overwintering on the Scotian shelf appear to be mostly fish from northern populations. Fish tagged in Canadian rivers migrate to the Scotian shelf in winter. Otolith analysis (Williams 1985) indicated that ca. 73% of fish overwintering on the Scotian shelf came from Canadian locations, while ca. 27% were thought to have originated from rivers in the MAB.

Summer aggregations occurring in the Bay of Fundy include individuals from populations along the entire Atlantic coast. The majority of fish arriving during June and July when water temperatures are ca. 10-16°C are of northern origin (Bay of Fundy and Gulf of St. Lawrence). American shad originating from rivers south of Cape Cod are present throughout the summer, but constitute the majority during July-August when water temperatures are 16-20°C. Population discrimination studies conducted in the upper Bay of Fundy coincident with a tagging study corroborate the seasonal representation of American shad from different regions (Melvin *et al.* 1992).

Origins of shad in the summer aggregation in the St. Lawrence estuary and off Labrador are unknown. Tag information (Vladykov 1956) suggests that some fish in the St. Lawrence aggregation may originate from as far away as Chesapeake Bay, but more information is needed to properly assess this group.

The northward, inshore coastal migration each spring of American shad was postulated over a century ago (McDonald 1884), but not demonstrated until the 1950s (Talbot and Sykes 1958). While at sea, fish from all Atlantic coast populations were previously thought to move together as a single group (Hollis 1948; Vladykov 1936, 1956; Talbot and Sykes 1958) along a coastal corridor in areas of preferred temperature range (13-18°C) (Leggett and Whitney 1972). However, Neves and Depres (1979) demonstrated that while some fish were migrating north within a few km of the coast, another group was offshore along the continental shelf over depths of 50-200 m in temperatures of 3-15°C. Tag returns indicate that major American shad migrations north alongshore in the mid-Atlantic region were probably pre-spawning adults, since most tag returns later during the same year were from rivers (Talbot and Sykes 1958; Miller *et al.* 1982). Offshore migrants were probably juveniles and non-spawning adults. Inshore migrations of ripe adults is bioenergetically inefficient because migration in the mid-Atlantic region is against countervailing currents. Nevertheless, inshore migrations would be required in this area to facilitate recognition of homing cues, especially olfactory ones (Dodson and Dohse 1986).

Dadswell *et al.* (1987) noted that data are unavailable to calculate migration rates of fishes in offshore areas. However, inshore migration rates could be determined with tag return information. Pre-spawning American shad moved north rapidly, some traversing 2500 km from Delaware Bay to the Gulf of St. Lawrence in 60 d. Prespawning migrants traveled at speeds estimated to be ca. 30.2 km/d, which, as noted by Dadswell *et al.*, were similar to the theoretical optimal migration rate of 29 km/d (Leggett and Trump 1978). In contrast, post-spawning adults had a mean migration rate of only about 8.8 km/d.

South of Cape Cod, prespawning shad migrate close inshore (Leggett and Whitney 1972; Dadswell *et al.* 1987), but north of there, tag returns are fewer and the migration corridor is less clear. Some fish perhaps migrate along the coast of Maine, while others may migrate offshore around the edges of Georges Bank (Dadswell *et al.* 1987). Prespawning fish arrive at rivers south of Cape Cod at water temperatures of ca. 13-18°C (Leggett and Whitney 1972), but shad move to northern rivers almost as quickly before ocean temperatures are above 10°C (Melvin *et al.* 1986). Dadswell *et al.* (1987) note that non-reproductive shad migrating from wintering sites in the MAB must cross the Gulf of Maine during May-June where constant subsurface temperature of 6°C prevails, to arrive annually in the Bay of Fundy during June-July.

A counter-clockwise migration pattern was evident in shad in the Bay of Fundy. Fish entered the Bay during April-May on the Nova Scotian side and later departed on the New Brunswick side from August-October. In the inner Bay, the shad run appeared to divide by chance, with portions going to both Minas and Cumberland basins. Once fish had committed to either route, however, their migration pathway was rigid. American shad that migrated first to Cumberland Basin moved along the northern shore (NB) and left the Bay during August-September on either side of Grand Manan Island. Fish that moved first to Minas Basin, however, migrated through Cumberland Basin before leaving the Bay of Fundy by the same route as those migrating into Cumberland Basin only. Migration rates of all recaptured Bay of Fundy shad during summer were similar, ca. 3.6 km/d, and direction of movement was the same as direction of residual current flow in the Bay of Fundy (Dadswell *et al.* 1987).

American shad departed from the Bay of Fundy through the Gulf of Maine by two routes. One contingent followed the Maine coastline at ca. 100 m depth and passed the Portland-Cape Ann region in October-November. Lack of returns from inshore during fall and results of trawl surveys (Neves and Depres 1979) indicated that migration southward was largely offshore. Some of these fish, however, arrived off Florida and Georgia in inshore waters during November-December. The other contingent left the Bay along the eastern shore of Grand Manan Island, passing Brier Island and southwest Nova Scotia. This second contingent, which may have consisted largely of Bay of Fundy or northern fish, occupied the Scotian shelf during winter. They were probably joined by fish migrating south from the Gulf of St. Lawrence (Vladykov 1956) and Labrador.

The migration pattern of the Scotian shelf winter aggregation is as follows. After wintering on the shelf, fish moved inshore along eastern Nova Scotia. Some probably migrated back to the Bay of Fundy and others moved north to the Gulf of St. Lawrence around Cape Breton. The pathway for inward migration is not well documented, but shad were off the northern shore of the St. Lawrence estuary in June. Those fish departed the Gulf of St. Lawrence via its southern shore, in the same direction and route as the main residual current flow.

Summary by season of tag returns, occurrence records, and trawl survey information illustrate a pattern consistent with three winter sites and three summer terminus points for American shad during their annual migration along the Atlantic coast. During January-February, American shad are off Florida, the mid-Atlantic Bight, and Nova Scotia, and are entering rivers to spawn from Florida to South Carolina. In March-April, movement is onshore and northward, both in the MAB and off Nova Scotia, and spawning runs are underway from North Carolina to the Bay of Fundy. By late June, American shad are concentrated in the inner Bay of Fundy, inner Gulf of St. Lawrence, and off Newfoundland, but spawning fish are still upstream in coastal rivers from the Delaware River north to the St. Lawrence River. During autumn, American shad leaving the St. Lawrence estuary are captured across the southern Gulf of St. Lawrence, but at the same time, those departing the Bay of Fundy are found from Maine to Long

Island and some already have arrived off Florida and Georgia.

Based on historical records, a null hypothesis that American shad in the sea are concentrated into a relatively small geographic area at any one time and that adults and juveniles are migrating together could have been constructed. McDonald (1884) was first to state this hypothesis and empirical justification was provided by Talbot and Sykes (1958) and Leggett and Whitney (1972). Temperature was thought to provide the migration cue (McDonald 1884; Leggett and Whitney 1972) and to regulate ocean swimming speeds (Leggett 1977a). Neves and Depres (1979) questioned this hypothesis, stating that it would be energetically wasteful for North Atlantic populations to follow the same shoreward route as do shad in mid-Atlantic and South Atlantic aggregations. However, these authors still proposed temperature as the controlling factor for migrations and postulated a range in which migration purportedly occurred.

Results of the analysis of 50 yr of tagging studies (Dadswell *et al.* 1987) clearly indicate that shad are not all concentrated into a relatively small geographic area at any one time, nor do they migrate together at the same rate. Instead, discrete aggregations occur in the sea at the same time at widely separated geographic locations. These aggregations move north and south along the Atlantic coast on a seasonal basis with considerable mixing.

Questions remain as to what cues or clues fish are using to regulate where or when they move in the sea. Although there is no doubt that shad move north or south seasonally, evidence does not suggest that certain temperature levels provide the major cue; migrating fish off Virginia experience a totally different suite of temperature stimuli from those wintering on the Scotian shelf. However, fish from both these sites arrive at the Annapolis River (NS) to spawn during the same time period (Melvin *et al.* 1986).

Fish migrating from Delaware Bay in April to spawn in the Miramichi River in June will encounter ocean temperature ranges from 10-12°C to 4°C. Similarly fish leaving the Bay of Fundy in September and entering the St. John's River, FL, to spawn in December would leave 18°C water, migrate through waters of 10-12°C in the Gulf of Maine, and traverse water as warm as 20°C before arriving in Florida. In each case, the same behavioral response occurs under different and diverse temperature stimuli. Temperature change with an additional stimulus such as photoperiod may initiate migratory behavior, but timing of such behavior by different fish appears related to their origin or life history stage.

Temperature is generally a poor cue for migratory direction among fishes (Smith 1985). A shad selecting a broad temperature preference range of 13-18°C (Leggett and Whitney 1972) or 3-15°C (Neves and Depres 1979) cannot perceive which way to turn within this preferendum for directional movements. Therefore, Dadswell *et al.* (1987) could not accept the hypothesis that temperature plays a keystone role in American shad migration.

This raised the question of what factors then are important to the migration route. If populations of fish are reproductively isolated to a sufficient degree and accumulate genetic adaptations to local situations, then genetic control over migration may be under active selection. Recent work has suggested that origin may control migration of homing salmon (Thorpe and Mitchill 1981; Quinn 1982; Brannon 1984; Healey and Groot 1987). It has been demonstrated that American shad have a high degree of homing to their probable stream of origin (Hollis 1948; Carscadden and Leggett 1975a, 1975b; Melvin *et al.* 1986). Although all shad populations are mixed together at sea, different populations demonstrate behavior that suggests there is some intrinsic control of migration. The early and rapid migration of some fish south to Florida in the fall suggests that individuals know where they should go and when to arrive. Shad spawning in the Annapolis River (NS) home from southern (Virginia) and eastern (Scotian shelf) wintering grounds. Homing from these two areas to the same locality implies navigation ability that overrides different temperature and current conditions encountered along the two routes. Origin, then, appears to provide both the cues and the clues for migration.

Life history stage of shad also appears to have some control over migration. Ripe fish migrate close to shore in spring, which may be a strategy to improve recognition of homing clues (Dodson and Dohse 1986), but non-reproductive fish apparently remain offshore (Neves and Depres 1979). Ripe fish migrate at a much faster rate than postspawning or feeding ones. Slower migration rate during feeding is one strategy that optimizes growth (Ware 1975a). Offshore residence of non-reproductive shad could result from ontogenetic changes in preference for temperature (McCauley and Huggins 1979) or light intensity (Loesch *et al.* 1982). Movements of tagged American shad in the Bay of Fundy indicated there was an element of chance involved in migration, at least within confined coastal areas. The role of chance in offshore migrations of shad is unknown.

In general, genetic or life history characteristics of American shad appear to influence behavior and to provide many cues for migration. Alternatively, when intrinsic factors do not influence or override external ones, some similar migration patterns are obvious suggesting the use of external stimuli. Temperature change or some aspect of seasonality strongly influences migratory direction. During increasing temperatures and day length, fish move north; when these decrease, shad move south. However, when shad are within large semi-enclosed coastal regions, they follow the direction of residual currents and the coastline.

Whether fish can use the much more subtle residual currents for guidance clues is unproven, but general observations are that they may (Dadswell *et al.* 1987). Lateral line systems may provide sensory ability to distinguish current or water movement direction in the absence of visual cues (Sutterlin and Waddy 1975). Migration information for American shad suggests this species may use a physiological optimizing strategy (Leggett 1977a) while it is non-reproductive, but uses a bicoordinate system (Quinn 1982) when it must reach a specific goal at a certain time. Extrinsic factors related to ocean climate, seasonality, and currents may provide cues and clues for portions of non-goal oriented migration. Intrinsic cues and bicoordinate navigation appear to be important during goal-oriented migration.

Temperature.--Young shad are temperature sensitive and are behaviorally capable of avoiding temperature changes of a kind that otherwise could prove lethal (Moss 1970). Lower lethal temperatures for American shad are estimated to occur at about 4-6°C (Tagatz 1961; Chittenden 1972a). Few, if any, American shad were found to enter estuaries, such as the Connecticut river, during springtime spawning migrations when water temperatures were below 4°C (Leggett 1973). Temperatures above 22°C approach the upper limit of temperature tolerance estimated for adult shad in the Connecticut River (Marcy 1976a). Minimal survival for river herring larvae (including American shad) was noted at temperatures above 28°C (Edsall 1970; Marcy 1971, 1973). Occurrence of juvenile shad in rivers is also influenced strongly by temperature. Marcy (1976c) caught juvenile shad in the Connecticut River between 10 and 31°C, but noted that only one fish occurred in water warmer than 30°C.

Feeding.--American shad are opportunistic predators that tend to eat whatever is most readily available (Willey 1923; Leim 1924; Bigelow and Schroeder 1953; Maxfield 1953; Massman 1963; Levesque and Reed 1972; Marcy 1976c). In the ocean, they feed primarily on zooplankton. Shad taken in the Gulf of Maine in summer were full of copepods (chiefly

Calanus), whereas stomach contents of fish from the Nova Scotia coast of the Bay of Fundy (Willey 1923) consisted chiefly of copepods (*Arcatia, Temora*, and other smaller species), mysid shrimps, and larval stages of barnacles. In the open Bay of Fundy, American shad feed chiefly on copepods and mysids, but ostracods, amphipods, isopods, insects, and small fishes also contribute to diets of these fishes (Leim 1924). Although copepods and mysids are eaten by shad of all sizes, diets of fish over 40 cm usually consist of larger zooplankters, predominantly mysids. American shad will occasionally feed on pelagic euphausiid shrimps, fish eggs, and even bottom-dwelling amphipods, indicating that foraging sometimes also occurs near the substrate. Occasionally, shad eat small fishes, such as smelt, or sandlances (Leidy 1868), but generally fishes are only a minor dietary component. While enroute to spawning grounds in freshwater reaches of rivers, adults seldom feed, although they will often strike an artificial fly, lure or live minnow. Juvenile fish during their residency in rivers also have a broad diet in which they consume copepods, cladocerans, aquatic insect larvae, especially chironomid larvae, and adult aquatic and terrestrial insects (Leim 1924; Maxfield 1953; Massman 1963; Levesque and Reed 1972; Marcy 1976c).

Generally, shad are particle feeding planktivores that select individual food items during prey capture. However, shad will switch to filterfeeding (Dadswell *et al.* 1983) when in turbid waters (e.g., inner Bay of Fundy), which may be advantageous to finding food in turbid areas.

Predators.--A variety of predators include American shad in their diets. Seals feed on shad (Melvin *et al.* 1985; Scott and Scott 1988), and monkfish caught in weirs will also eat adult shad. It is likely that young shad, as with other juvenile river herring, fall prey to predators in freshwaters, but Leim (1924) found no evidence of predation by eels or striped bass in the Shubenacadie River. In lower reaches of estuaries, such as the Hudson River (Juanes *et al.* 1993), juvenile shad are common dietary items of young bluefish (101-150 mm), and undoubtedly they are consumed by other predaceous fishes that normally include clupeoids in their diets (Creaser and Perkins 1994). American shad are also attacked and preyed upon by sea lampreys *Petromyzon marinus* (Melvin *et al.* 1985; Warner and Katkansky 1970).

Parasites.--Early information on parasites infecting shad included the acanthocephalan, *Echinorhynchus acus*, the nematodes *Ascaris adunca, Ascaris* sp., and the copepod *Caligus radiatus* (Sumner *et al.* 1913). Of 110 American shad Leim (1924) examined, infection rates of 35%, 51%, and 7% for nematodes, trematodes, and acanthocephalans, respectively, were noted. Twenty-six species of parasites were identified in a recent study of 695 fish examined from seven Atlantic localities ranging from the St. John's River, FL, to Cumberland Basin, Bay of Fundy (Hogans *et al.* 1993). Only three of these parasites had previously been reported from American shad. Species identified were predominantly boreal marine forms that have low host specificities and widespread distributions. The greatest species diversity within shad parasite assemblages was found among fish from the Cumberland Basin and the spawning population of the Shubenacadie River. The seven most abundant parasites occurring in American shad from all areas included the monogenetic trematode *Mazocreoides georgei*, digenetic trematodes *Lecithaster confusus* and *Genitocotyle atlantica*, the cestodes *Diplostomum spathaceum*, *Scolex pleuronectis*, and an unidentified pseudophyllidean plerocercoid, as well as the nematode *Hysterothylacium aduncum*. That no parasite species occurred in shad from only one area undoubtedly reflects the migratory habits of this species. High prevalence levels of parasites and the incidence of exotic, southern parasite species, such as *Genitocotyle atlantica*, in shad from the Cumberland Basin and most or all river populations were thought to indicate that all individual shad spend some portion of their life at or near the southern extent of their reported range (i.e., the Cape Hatteras region or further south; Hogans *et al.* 1993). The copepod *Clavellisa cordata* has also been reported parasitizing gills of shad (Rubec and Hogans 1987). The leech, *Calliobdella vivida* also has been reported from this host (Appy and Dadswell 1981). Additional information on parasites of American shad was provided in Hoffman (1967).

Species Associates.--In riverine situations, shad larvae and juveniles co-occur seasonally with those of several other river herring species. Because of some similarities in life histories and morphology, and overlap in spawning biologies, there is potential for these species to compete if resources become limiting. Sympatric populations of shad and blueback herring larvae in the Connecticut River apparently coexist within the same habitat without competition by utilizing different prey taxa, or by selecting different size components within the same prey taxon (Crecco and Blake 1983). Differences in ecologies of shad, alewife and blueback herring that could serve to reduce potential competition among these co-occurring species were discussed in Schmidt *et al.* (1988). Predation impacts of juvenile shad, as well as those of other anadromous river herrings, may alter structure of zooplankton communities occurring in nursery areas (Brooks and Dodson 1965; Vigerstad and Cobb 1978). Large schools of migrating shad in small tidal streams could also have effects on ammonium concentrations, potentially influencing biotic interactions and nutrient dynamics in these habitats (Browder and Garman 1994).

General Range.--American shad occur in Atlantic coastal waters and in streams and rivers of North America from northern Labrador at South Aulatsivik Island (56°45'N, 61°41'W) near Nain (Dempson *et al.* 1983), southward to the St. John's River, FL (Bigelow and Schroeder 1953). Historically, shad were believed to be most abundant in central portions of the Atlantic coast range (Leim 1924). American shad were introduced in 1871 into the Sacramento and Columbia rivers of the Pacific coastal system and are now successfully established from Kamchatka Peninsula (Asia) and Cook Inlet, Alaska, to Baja California. Introductions in the Gulf of Mexico apparently failed (Bigelow and Schroeder 1953; Whitehead 1985a; Scott and Scott 1988).

In the Canadian Atlantic region (Scott and Scott 1988), shad occur from southern Labrador (few isolated collections near Nain and at Sand Hill River) (Hare and Murphy 1974), and from Newfoundland (few collections), but apparently there are no spawning populations north of the St. Lawrence River (Leggett 1976). This species is more commonly taken in spring, summer, and fall in the Gulf of St. Lawrence. Reproductive populations are reported in the St. Lawrence River (Vladykov 1950), tributaries in Quebec, and in many rivers of all the Maritime Provinces.

Occurrence and Abundance in the Gulf of Maine.--When the first settlers arrived in New England they found seemingly inexhaustible multitudes of American shad annually migrating in all larger rivers and many of the smaller streams, with the tributaries of the Gulf of Maine hardly less productive than those of the Hudson or Delaware rivers (Bigelow and Schroeder 1953). With increases in human populations and industrial development along watersheds, one stream after another was rendered impassable through construction of dams near the mouth, degradation of spawning areas, and/or diminished water quality through pollution. From the Canada-U.S. border to Cape Cod, access to river spawning areas used by shad was almost completely denied through construction of dams during the early part of the last century (Walburg and Nichols 1967). These activities resulted in the extirpation of many native spawning populations between these two points (Bigelow and Welsh 1925; Taylor 1951;

Mansueti and Kolb 1953). Consequently, abundance of American shad stocks in the Gulf of Maine is merely a remnant in comparison with that of colonial days (Taylor 1951; Bigelow and Schroeder 1953).

American shad seasonally occurring in the Gulf of Maine are far too numerous to be accounted for by the small production that still takes place in the rivers of Maine and Bay of Fundy. Extensive tagging experiments (summarized in Dadswell *et al.* 1987) have shown that most medium-sized and larger American shad found in the Gulf are immigrants from the south, some from as far as the Altamaha River, GA. Others come from as far north as the St. Lawrence estuary. Shad migrating to the Gulf of Maine during summertime feed and grow on the rich supply of plankton they find there. By the end of December, however, they leave this area, not to reappear anywhere on the Gulf of Maine coast until the onset of the next spawning season, when maturing fish again return to rivers of their native watersheds.

The history of shad distribution and occurrence in Maine's waterways was compiled recently (State of Maine 1982) and information from that document follows. Historically, shad were abundant in all major rivers and along the entire coast of Maine. Commercial landings in the late 1800s and early 1900s provided some insight into the magnitude of the fishery. However, these landings do not reflect the true magnitude of the resource. Many upriver production areas of major shad rivers had already been denied to spawning adults for at least 60 yr prior to systematic recording of commercial shad landings. In addition, commercial catches recorded along the coast outside the river systems are not entirely fish of Maine origin. In fact, many fish taken in the commercial shad fishery of the late 1940s were believed to have originated in rivers to the south and possibly north of Maine.

From the beginning of recorded landings in 1887, the fishery remained relatively stable at about 464,545 kg annually until 1911, rose to a peak of 1.45 million kg in 1912, dropped to an average of about 51,364 kg annually from 1928-1933, essentially were commercially extinct from 1934-1940, increased to a high of 500,000 kg in 1946, and have remained at a relatively low level from 1948 through 1976. The directed river fishery for American shad occurred from colonial days until about 1920. Subsequent to 1920, most catches were taken along the coast and incidental to other fisheries, although a very small inriver fishery persisted in the lower Kennebec until the early 1930s.

Excluding the New Hampshire portion of the Androscoggin and Saco River drainages, the total land area of Maine that drains into Maine coastal waters approximates 62,162 km^2. Historically, ca. 33,153 km^2 or 50% of this drainage area was accessible to American shad. According to Atkins (1887), construction of the Augusta dam resulted in an approximate 50% decline in the shad catch in the lower Kennebec River. Therefore, the 8,236 km^2 of the upper Kennebec River previously accessible to shad apparently produced about 50% of the commercial harvest. During the 12-yr period from 1903-1914, the lower Kennebec River yielded an average annual catch of 311,485 kg. Assuming this represented 50% of the former yield of the Kennebec, a value of 8,236 km^2 of drainage would be represented by this yield. Since the total historically accessible area for shad in the Kennebec drainage was 31,080 km^2, a reasonable estimate of potential historical yield would be approximately 1,227,273 kg of Maine produced fish. Assuming harvest of 30-80% of the total run, which is characteristic of commercial shad fisheries in southern New England areas, the total Maine historical production would range from 368,167 kg to 981,778 kg. Assuming the average size fish would weigh ca. 1.82 kg, the total production would range from ca. 202,300 to 539,400 adult fish.

The current resident shad runs in Maine have been reduced to only a remnant of their former abundance. Because of dams and pollution, the presently suitable and accessible watershed area in Maine has been reduced from 31,080+ km^2 to 1787 km^2, which represents a mere 5% of the former habitat. Of the 1787 km^2 of watershed currently utilized by shad, less than optimum fish passage, low levels of spawning adults, and incidental capture of spawning shad by commercial fisheries have slowed the reestablishment of significant shad runs in these limited areas. At present, the total shad runs in Maine are estimated at no more than several thousand fish annually. The current offshore catches landed in Maine are a mixture of fish from Maine and river systems to the north or south.

Although a small sportfishery harvests an estimated 100-600 adult shad/yr, the current supply of Maine shad is incapable of supporting a directed commercial fishery. Incidental commercial catches are taken by trawlers and gill net fishermen along the coast of Maine. The total available supply of Maine-produced shad is probably no more than a few thousand fish annually and this does not constitute a commercially attractive resource.

Presently, there are small runs of American shad (usually <100 fish) in the following rivers (T. Squiers, person. commun.[2]): Salmon Falls, Mousam, Kennebunk, Saco, and the Nonesuch rivers. In the Kennebec-Androscoggin complex there still exists some remnant stocks. There is an active restoration program in the Medomak River with stocking taking place during 1992-94. Small numbers of fish still return to the St. George and Penobscot rivers. The Pleasant River has a few shad returning to spawn there, while a small run also occurs in the East Machias and Narraguagus rivers. There is a restoration program initiated for the Saco River system. In the Presumpscot River, a fish passage has been provided at Smelt Hill and Highland Lake, which has resulted in the reestablishment of an alewife run. The Kennebec River has an interim trap and truck program that was initiated in 1985. Fishways have been built on the first three dams of the Androscoggin River, and there has been an ongoing restoration program since 1983. In the Medomak, fish passage has been improved, and there is an ongoing restoration program for both alewives and American shad in this system. In the Penobscot system, the Marsh stream fish passage has been provided. The Souadabscook Stream run of alewives is maintained by dipping adults over the head of the tide dam. A new fishway was destroyed by a flood. Blackman stream has two impassable dams still present. Hydroelectric dams at the head of tide on the Pleasant River were removed. A few American shad may enter other Gulf of Maine streams in some years if not yearly, but these runs are not of substantial size.

In the northern Gulf of Maine and Bay of Fundy, Leim (1924) noted that shad were found mainly near the mouths of the Miramichi River, NB (Gulf of St. Lawrence drainage), and the Saint John, Petitcodiac, Shubenacadie, and Annapolis rivers (emptying into the Bay of Fundy), including the Cumberland Basin. Spawning populations also occur in the inner basins of the Bay of Fundy (Dadswell *et al.* 1983, 1987).

In New Hampshire, attempts are also being made to establish spawning runs of shad in several river systems (Grout and Smith 1994; Grout pers. commun.[3]). Earlier stocking of streams with eggs began in 1972, but yielded poor results (returns of less than a dozen shad/yr). From 1980-1988, between 600 and 1300 spawning shad were transported and distributed into the Lamprey, Cocheco and Exeter rivers. Gravid American shad were transported from the Holyoke fish lift on the Connecticut River in Massachusetts and released into the rivers to spawn naturally. Juvenile surveys in the rivers indicate that spawning was successful, although numbers of juveniles sampled annually varied considerably. Confirmed returns to the Exeter

River, as well as to the Lamprey and Cocheco rivers (from previous releases of adult shad) continued to be low, with exception of the Lamprey River, which experienced returns of at least 200 shad in 1993. Other recommendations include consideration of dams that allow migrating shad access to a larger section of the Lamprey River with increased potential for spawning and nursery habitats.

In southern Gulf of Maine, a shad run occurs in the Merrimack River. Along Massachusetts Bay's southern shore, small runs of American shad also occur in South River, Marshfield, Indianhead River (part of North River system), Pembroke, and Mill Creek, Sandwich (P. Brady, person. commun.[1]). In summer and autumn, immature American shad, as large as 0.9-1.1 kg, may be relatively common in Cape Cod Bay near Provincetown and in inner portions of Massachusetts Bay (sometimes in traps at Beverly or Manchester), and off Cape Ann.

Reproductive Biology

Spawning Location.--American shad migrate from the sea into coastal rivers in spring to spawn in freshwater (Leim 1924; Massmann 1952; Walburg 1960; Marcy 1976c; Williams and Daborn 1984), when water temperatures range from 16.5 to 19.0°C (Leggett and Whitney 1972). American shad spawn in river areas dominated by broad flats with relatively shallow water (1-6 m) with moderate (0.3-1.0 m/s) current (Smith 1907; Bigelow and Welsh 1925; Massmann 1952; Marcy 1972; Leggett 1976; State of Maine 1982). In the Connecticut River, shad eggs were found from 0.6 to 7.3 m deep (Marcy 1976c). Walburg and Nichols (1967) reported that ca. 40% of spawned eggs occurred in water less than 3 m deep. Unlike alewife, American shad seems always to spawn in rivers, seldom if ever in lakes. In Gulf of Maine tributaries, viable eggs may be found on river bottom types ranging from fine sand to coarse rubble to ledge, but never on silty or muddy bottom areas (State of Maine 1982). Highest survival rates of shad eggs reportedly occur in those settling over gravel and rubble substrates (Layzer 1974). In the Annapolis River, NS, spawning occurred in the more slowly flowing section of the river (Williams and Daborn 1984) where fish selected sandy or pebbly shallows for spawning grounds.

Shad spawn in freshwater, but there does not appear to be any required distance above brackish water for spawning locations (Massmann 1952). In larger rivers, shad may migrate far upstream to reach favorable spawning grounds. For example, in the St. John River, NB, they ascend about 322 km to Grand Falls, and they run up 483 km (or did so historically) in the Altamaha River, GA, and for 603 km in the St. John's River, FL. Presently (though few enter either of these rivers now), they can run up only about 56 km in the Penobscot, where they formerly ascended some 145 km, or 71 km (to Augusta) in the Kennebec, which they formerly ascended 174 km (to Carratuk Falls). The dams at Lawrence, only ca. 32 km upstream, now stop any stray American shad that may still enter the Merrimack, which they formerly ascended for 201 km to Lake Winnepesaukee (Stevenson 1899). In the Connecticut River, shad spawn in areas up to 174 km from the river mouth (Marcy 1976c).

During migration from the sea into estuaries and freshwater systems, shad experience dramatic changes in both salinity and temperature. For example, in the Connecticut River, fish experience a range of salinities from ca. 27 o/oo to 0 o/oo; and temperature differentials of up to 10°C because of the more rapid warming of river water compared with that of Long Island Sound (Leggett 1976).

Males arrive on spawning grounds first, followed by females (Leim 1924). Spawning takes place in the evening after sundown and may continue to midnight or later (Leim 1924;

Massmann 1952; Walburg and Nichols 1967; Chittenden 1969; Williams and Daborn 1984). Spawning may also occur on dark afternoons, as was observed for shad in the Connecticut River (Marcy 1976c). During spawning, the female is accompanied by one or several males, and spawning fish swim close to the surface, sometimes with their backs exposed leaving a visible wake (Medcof 1957). Spawning fish may splash at the surface while forming a closely-packed circle (Marcy 1976c). Eggs are released in open water, where they are fertilized by the males.

During upriver migrations individual American shad apparently spawn repeatedly as they progress upriver thereby producing a gradual reduction both in weight and energy content of testes and ovaries (Glebe and Leggett 1981b). This spawning mode may be necessary to facilitate the high fecundity of American shad. An estimated two- to four-fold increase in body cavity volume would be required in American shad to accommodate an equivalent number of eggs if all eggs reached full volume and were spawned at one time (Shoubridge and Leggett 1978). Late run migrants may spawn earlier in the upriver migration (Chittenden 1969; Glebe and Leggett 1981b). Gonad weight and energy reductions measured in these fish (captured nearer the river mouth) suggested that higher water temperatures encountered by these fish may have induced spawning sooner in the upriver migration and before the spawning grounds used by earlier-running fish.

Spent and very emaciated fish begin their return journey to the sea immediately after spawning. In the Kennebec River, they were first seen on their way downstream about June 20 and constantly thereafter throughout July, while in the St. John River, spent fish migrated downstream in July and August (Bigelow and Schroeder 1953). Fish migrating downstream may begin feeding before reaching saltwater and recover a good deal of fat before moving out to sea (Atkins 1887). The young descend downriver in autumn of their 1st yr of life.

Spawning Seasonality.--Water temperature controls the timing of migration of American shad into natal rivers, as well as the spawning activity and survival of eggs and larvae (Walburg 1957; Massmann and Pacheco 1957; Leggett and Whitney 1972; Leggett 1976). Throughout their geographic range, adult shad enter streams in their home river in spring or early summer when water temperatures have reached about 10°-12°C. Consequently, American shad spawning runs occur at correspondingly later times in the year passing from south to north along the coast. For Gulf of Maine localities (Atkins 1887), such as the Kennebec River, the first American shad appear late in April, with the main run occurring in May and June. The first ripe females are caught during the last week in May, and spawning begins in early June, with most fish doing so during that month. A few shad spawn as late as July, and in some years, there may be an occasional shad spawning as late as August. These dates probably applied equally well to timing of spawning in the Merrimack River in days when American shad were plentiful there (Bigelow and Schroeder 1953), but the season was somewhat later in the St. John River (Leim 1924), and also in the Shubenacadie River, N.S. (i.e., from mid-May until end of June). In Canadian rivers, spawning normally occurs in May, June, or even July (Scott and Scott 1988). Spawning fish enter rivers as early as November in Florida, with peak migration occurring in January (Leggett 1976); peak migration occurs in January in Georgia; in March in waters tributary to Pamlico and Albemarle sounds, NC; in April in the Potomac River; and generally in May and June in streams from Delaware to Canada (Walburg 1957; Leggett and Whitney 1972).

American shad usually enter rivers at temperatures around 10-16°C and cease to migrate when water temperatures reach about 20°C. Initiation of spawning depends on water temperatures. Peak runs of fishes on the upstream spawning migration usually occur at about

18.5 °C. Mansueti and Kolb (1953) reported that shad ovaries developed more slowly at 12.8° than at 20-25 °C. Temperatures below ca. 16 °C prolong the developmental period and reduce survival (Leim 1924; Leach 1925; Mansueti and Kolb 1953; Bradford *et al.* 1968). In the Annapolis River, NS, spawning was monitored by collecting eggs (Williams and Daborn 1984). Although eggs were collected at temperatures from 10.5 to 22.7 °C, most were taken at water temperatures of 13-18 °C. Spawning apparently ceased when water temperature dropped below 13 °C. In the Shubenacadie River, NS, American shad spawn mostly in temperatures higher than about 12 °C, and spawning is temporarily interrupted if water chills below this temperature (Leim 1924). In the Connecticut River, Marcy (1976c) collected eggs at temperatures ranging from 7.5 to 24 °C, with peak spawning occurring at 22 °C in 1968, and at 14.8 °C in 1969. Onset of American shad spawning in the Connecticut River begins at temperatures of 13-18 °C (Leggett and Whitney 1972). Based on records at fish lifts, peak movement in east coast rivers occurs in temperatures between 16.5 and 21.5 °C (Leggett 1976). Temperatures for maximum hatch and survival of eggs ranges from 15.5-26.5 °C (Leim 1924; Massmann 1952; Walburg 1960; Bradford *et al.* 1968; Marcy 1972).

Depression of water temperatures retards the onset and duration of spawning (Leggett and Whitney 1972). Spawning of American shad below 16 °C has been reported by Marcy (1972) and Schmidt *et al.* (1988), and Carscadden and Leggett (1975a) reported consistent American shad spawning at temperatures below 16 °C in a tributary of the St. John River, NB. In the Connecticut River, Marcy (1976c) reported that eggs were not found in abundance below 12 °C.

Synychrony between shad spawning and temperature is believed to be under strong selective pressure (Leggett 1969), because it insures that egg development coincides with rising water temperatures, which have been shown to be beneficial for development and survival (Crecco and Savoy 1987). Egg incubation time for American shad declines from 15 d at 14 °C to 3 d at 22 °C (Watson 1970; Marcy 1976b). This may be a further adaptation by which larvae hatch at water temperatures most conducive to successful feeding and survival.

Levels of dissolved oxygen also strongly influence the location and success of spawning by shad (Ellis *et al.* 1947; Sykes and Lehman 1957; Bradford *et al.* 1968; Chittenden 1969, 1973; Thurston-Rodgers and Baren 1978; Miller *et al.* 1982; Maurice *et al.* 1987). Dissolved oxygen levels of 4-5 mg/L are suitable for juveniles (Burdick 1954), and result in the successful hatch of healthy larvae (Bradford *et al.* 1968). However, DO values less than 4 mg/L result in deformed larvae being hatched. Adult shad undergo rapid respiratory movements as DO decreases below 4 mg/L (Tagatz 1961); DO levels of ca. 3.5 mg/L cause sublethal effects (Chittenden 1973), levels at 2-3 mg/L result in about a 33% mortality (Dorfman 1970), and high moralities occur at DO levels less than 2 mg/L (Tagatz 1961; Chittenden 1969). Rapid declines in size of shad runs in the Delaware River, for example, were attributed to severe pollution levels with concomitant decreased DO levels in the river between Wilmington, DE, and Philadelphia, PA (Ellis *et al.* 1947). Low DO values (< 3 mg/L) in the Delaware River were thought to make tidal freshwaters unsuitable as spawning grounds for shad, and to actually block the spawning migration of late migrants into this region of the river (Sykes and Lehman 1957; Chittenden 1969; Miller *et al.* 1971; Thurston-Rogders and Brown 1978; Maurice *et al.* 1987). In fact, in some years during low DO levels in the Delaware River, large numbers of shad were killed (Sykes and Lehman 1957; Chittenden 1969) or blocked from migrating. Therefore, shad were forced to spawn in less favorable habitats located downstream, or to leave the river altogether and spawn in other systems (Chittenden 1969; Miller *et al.* 1971). With improved water quality, including higher

DO levels, shad once again have returned and now successfully spawn in this region of the Delaware River (Maurice *et al.* 1987).

Homing Behavior.--American shad return to their natal rivers and streams to spawn (Hollis 1948; Mansueti and Kolb 1953; Dodson and Leggett 1973, 1974; Carscadden and Leggett 1975a, 1975b; Williams and Daborn 1984; Melvin *et al.* 1986). Olfactory and rheotactic cues guide their homing migration. American shad probably learn these cues during their initial migration to the ocean as young fish. Mark-recapture studies (Hollis 1948; Mansueti and Kolb 1953; Williams and Daborn 1984; Melvin *et al.* 1986) have shown that American shad have relatively low straying rates (about 3%). Studies of meristic variation have also suggested that American shad not only home to their natal rivers, but even to tributaries at least within some of the major northern spawning rivers (Carscadden and Leggett 1975a, 1975b).

Much has been learned about migratory movements of shad both as they approach coastal spawning rivers and their movements within the river systems (Dodson and Leggett 1973). Three distinct phases to migration were defined by Dodson and Leggett (1974). The first phase is the approach to the home river, however, shad do not enter it immediately. Temporal restriction is perhaps related to gonadal development and modulated by the endocrine system which delays entry into the river until conditions, both physiologically and hydrographically, are optimum. The second phase is characterized by reduced swimming speeds compared with those of saltwater and freshwater phases and occurs in saline parts of the estuary. These delays are related to adaptation to the freshwater environment, which apparently requires considerable time. In the last phase, the freshwater phase, migration is clearly more direct and executed at high swim speeds with over-riding upriver orientation independent of current flow.

Sonic-tagged fish in Long Island Sound exhibited a well-defined behavior pattern highly correlated to tidal conditions. American shad tended to orient into the current at all times, but the precision and directivity of the countercurrent orientation differed depending on direction of tidal current. The precision of countercurrent orientation was greater and magnitude of angular changes in bearing less during ebb than flood tide. Shad also demonstrated a significant positive correlation between swimming speed and tidal current speed. Shad swam west at a speed significantly greater than the ebb tide current speed, but during flood tide, they swam at a speed about equal with the tidal speed. Combination of orientational and kinetic components of this rheotactic behavior resulted in active westerly displacement during the ebb and a tendency to drift to the west during the flood. This rheotactic behavior caused most shad to move west beyond the Connecticut River (Dodson and Leggett 1973). The fact that tagged fish were subsequently captured in the Connecticut River, however, indicated that this westerly bias was reversed at some point in western Long Island Sound. Olfactory-occluded American shad (Dodson and Leggett 1974) demonstrated that this westerly bias was significantly impaired when the fish were unable to detect odors. Although tide-specific behavior cannot be related to a tide-specific olfactory cue, loss of directional bias following occlusion of the nares, nevertheless, implicates an olfactory-rheotactic mechanism. A model of olfactory-mediated directional bias for migrating shad in reversing tidal currents hypothesized that fish can learn tide-specific rheotactic behavior that increases migration rate (Dodson and Dohse 1986). This model also suggested that behavioral modifications, leading to synchrony of tidal and natal-river olfactory cues at the detectable edge of the diffuse olfactory field, could determine the mechanism by which migrating shad approached the Connecticut River.

In tidal regions of the river, under conditions of reverse and 0-flow, shad generally stop migrating, meander or hold position, or undergo some down-river movement (Leggett 1976). In the region of the saltwater/freshwater interface, upriver migration rates of American shad were reduced for periods ranging from 17-71 hrs (Dodson *et al.* 1972). The fish exhibited extensive meandering which resulted from a combination of passive drift and relatively inactive swimming that retained them near the leading edge of saltwater intrusion. Meandering was apparently due to the obvious physiological stress associated with adaptation to freshwater; shad must adapt slowly to freshwater (Leggett 1976). Tagatz (1961), for example, showed that an abrupt transfer of shad from salt to freshwater of similar temperature resulted in some mortality. Once shad leave the interface zone and enter freshwater, upstream migration was continuous, though not necessarily direct. Shad move through conditions of zero and reverse flow and show no obvious changes in behavior related to tidal conditions. Swimming speeds were greater in freshwater (63 cm/s) than in brackish water (39 cm/s). The average rate of upriver migration of Connecticut River shad was estimated to be between 5-8 km/d in freshwater, with time of migration from saltwater interface to spawning area requiring 10-16 d. Females swam somewhat faster than males. Later migrants entering the river moved faster than earlier migrants. There was a diel cycle in swimming speeds in freshwater. Maximum speeds occurred at ca. 0400 and 1800 hr, perhaps associated with sunrise and sunset; minimum values occurred at ca. 1100 and 2400 hr. Swimming speeds in brackish water were more uniform throughout the daily cycle, except for distinct reductions at 0300 and 1600 ca. 1-2 hr before sunrise and sunset. Swimming speeds increased when shad oriented into the currents and especially so when fish oriented upriver, thereby suggesting that rheotaxis directs upriver migration.

Although shad migrating upriver orient into flowing water (Katz 1986), little is known of how they react to differing currents, or of any preferences for particular velocities. Precise adjustment of swimming speeds to changes in current velocity, both at sea (Dodson and Leggett 1973, 1974) and again in freshwater, indicate shad are able to detect slight changes in current velocity and may employ these in orienting to the river channel (Leggett 1976). Shad that were sonically tagged and followed upriver to their spawning grounds (Leggett and Jones 1973; Katz 1986) swam upstream individually and moved independently with no schooling. In pools below Holyoke Dam on the Connecticut River, groups of up to 75 American shad schooled and swam in large circles, moving neither upstream nor downstream. Leggett and Jones (1973) reported a linear relationship between shad absolute swimming speed and river water velocity. However, their data were limited to a maximum current speed of ca. 60 cm/s. A curvilinear form to this relationship became apparent when currents in excess of 60 cm/s were measured (Katz 1986). Swimming speeds during daylight hours ranged from 11 to 93 cm/s when water temperatures were below 20°C and from 9.8 to 64 cm/s when water temperatures exceeded 20°C. Swimming speeds at night ranged from 8 to 53 cm/s. As water velocity increases, shad increase their swimming effort until they reach some upper limit of effort (Katz 1986). Although shad can swim 347 cm/s for at least 20 m (Weaver 1965), it is unlikely that speeds greater than 170 cm/s can be sustained because of aerobic exhaustion (Katz 1986). In fact, during one field study, a major flood produced flows reaching 300 cm/s that flushed all tagged shad downriver from the study site.

Most variations in swimming speeds are associated with the migratory season or have been attributed to changes in water temperature. Speed differences among individual migrating shad appears to be inherent in individual fish, and most likely are associated with physical and physiological differences among fish. Leggett (1976) noted that swimming speeds did not increase with temperature, even though migration rates of individual males and females increased as the spawning run progressed. This indicated that increasing rate of upriver migration later in the spawning run resulted from a more direct course upriver rather than an adjustment in swimming speeds. Males enter rivers later than females, and this may explain their faster swimming speeds compared with those of females. Downriver movements are characterized by less meandering and holding position.

During both upstream and downstream migrations in the Connecticut River, shad were found to follow the river channel (Leggett 1976) with only periodic movement to shallow waters. It was suggested that perhaps migrating shad were using an environmental cue, such as water velocity, to remain in the channel, or that they were simply following the deepest part of the channel. Since shad are capable of detecting small differences in water velocity (Dodson and Leggett 1973, 1974), it was thought possible that the fish may prefer certain velocities and adjust their swimming depth and location accordingly. Analyzing data collected from gillnet captures, Witherell and Kynard (1990) found that most (83%) adult American shad on spawning and postspawning migrations in the Connecticut River were caught in the lower half of the water column, but not on the river bottom (most were caught 2 m off the bottom). Vertical distributions of gravid and spent fish were similar for both sexes. American shad showed no diel, seasonal or yearly changes in depth distributions, however, larger gravid fish swam deeper in the water column than did smaller gravid fish. Depth distributions did not significantly change with changes in turbidity or light intensity. They concluded that since shad swim at about the same speed both day and night, and these fish do not have night-adapted vision (Katz 1978), then shad probably followed the river channel and migrated at a constant rate relative to the bottom. Something besides visual cues are used during upriver migration. Of interest, however, is that Dodson and Leggett (1974) reported blind individuals that failed to adjust swimming speeds relative to tidal current velocity. This suggests that shad adjust their swimming speed in relation to a visual cue, possibly displacement over the bottom.

Once shad reach the spawning grounds they are dispersed throughout the water column. Adults caught at night with floating gill nets have been captured along the top and bottom of the net (Katz 1976), or throughout the net (Layzer 1974).

Repeat Spawning.--South of Cape Hatteras, N.C., American shad are semelparous (they die after spawning), whereas in rivers to the north of this region, they become increasingly iteroparous, with individuals surviving and returning to the ocean, living to spawn in subsequent years (Leggett and Carscadden 1978; Glebe and Leggett 1981a, 1981b). In the northern part of their range and especially in Canadian waters, shad may return to spawn in the same river, or even the same tributary, as many as five times (Carscadden and Leggett 1975b). The percentage of adults that live to be repeat spawners increases as one progresses northward along the Atlantic coast. For example, in the York River, VA, 24% of shad are repeat spawners, while American shad in the Connecticut River have a 63% incidence of repeat spawning (Leggett and Carscadden 1978), and 73% and 64% of American shad in the St. John and Miramichi rivers, NB, respectively, are estimated to be repeat spawners.

It has been hypothesized that this shift from semelparity in the south to iteroparity in the north represents adaptive variation occurring among genetically discrete populations (Carscadden and Leggett 1975a; Leggett and Carscadden 1978; Glebe and Leggett 1981a). The capability of spawning more than once conveys to a population a greater degree of stability and reduces the probability of extinction under fluctuating environments characteristic of north temperate regions

(Ricker 1954, 1975; Beverton and Holt 1957; Holgate 1967; Murphy 1968). Postspawning mortality among anadromous stocks may be strongly linked to energetic demands of migration (Leggett and Trump 1978; Glebe and Leggett 1981a, 1981b), and migration distance may limit the proportion of repeat-spawning American shad within and between rivers (Shoubridge and Leggett 1978). Studies on bioenergetics of American shad during the spawning migration in the Connecticut River (Glebe and Leggett 1981a, 1981b) found that somatic weight loss and associated energy depletion were extreme (45-60%), with up to 50% and 70% of available body protein and lipid, respectively, being used to fuel the migration. Extent of reserve depletion was sex- and size-specific. Small individuals and males suffered the greatest tissue depletion. Decline in somatic protein was 27% in male fish and 40% in female fish (Glebe and Leggett 1981a). High water temperatures accounted for reduced energy efficiency of late migrant shad, and resulted in greater depletion of total body reserves in these fish. More extensive depletion may contribute to the higher mortality reported among this component of the population. Gonad development was complete prior to entry into the river, which may conserve somatic reserves during the freshwater fast and hence maximize survival. This pattern of energy utilization may also influence demographic parameters, especially the repeat spawning habit. The close relationship between water temperatures during migration, energy use, and mortality also suggests that energy allocation to migration versus reproduction is delicately adjusted with the maximum possible allocation being made to reproduction (Glebe and Leggett 1981b). The relationship between bioenergetic costs and behavior of migrating shad in relationship to strategies employed by other anadromous fishes was studied by Bernatchez and Dodson (1987).

Fecundity.--Annual fecundity is generally highest and several-fold higher in populations reproducing in the southern portion of the species range than in those spawning in rivers at the northern end of the geographic range. Since northern shad spawn more than once and repeat spawning occurs rarely in shad spawning south of Cape Hatteras, reciprocal latitudinal trends in annual fecundity and repeat spawning therefore cause average lifetime fecundity to be roughly constant over the species' Atlantic coast range (Bentzen *et al.* 1989).

American shad are prolific spawners and may produce up to 600,000 eggs per season (Cheek 1968). Within a region, fecundity generally increases with size of female. Shad fecundity in the St. Lawrence River ranges from 58,534 to 390,633 eggs per female, with an average value of 125,166 eggs reported for 48 females (Roy 1969). The female with the most eggs (390,633) was 54.6 cm long, but another 54.1 cm long contained only 73,095 eggs. Carscadden and Leggett (1975a) gave fecundity figures for the Saint John River, NB, populations ranging from 118,929 to 165,776 eggs. Most Canadian shad (Leim and Scott 1966) produce from 20,000 to 150,000 eggs per female, which is probably representative of fecundity of shad spawning in Maine localities (State of Maine 1982). Estimated annual fecundity ranges from 256,000 to 384,000 eggs/female for shad spawning in the Connecticut River (Leggett 1969).

EARLY LIFE HISTORY

Eggs.--Fertilized eggs are 2.5-3.5 mm in diameter, transparent, pale pink or amber, semi-buoyant and not adhesive (like those of other river herrings). After fertilization, single eggs sink to the bottom, and drift with the current (Carlson 1968; Chittenden 1969; Marcy 1976c). Marcy (1976c) reported that shad eggs were nearly equally abundant at the surface and the bottom in areas sampled in the Connecticut River. Water hardening of eggs and their resultant increase in diameter may lodge eggs in bottom rubble (Jones *et al.* 1978). Dense aggregations of eggs may be highly susceptible to fungal infections (Leach 1925). Whitworth and Bennett (1970) followed movement of shad eggs from the time they were broadcast until they sank or lodged on the bottom, which occurred in about 5-35 m downstream. Based on calculations of egg age and current speeds, Marcy (1976c) estimated that most shad eggs had traveled only 1.6-6.4 km downstream from where spawned. Carlson (1968) and Chittenden (1969) made similar observations on shad eggs in other east coast rivers.

Hatching occurs in 12-15 d at 12°C, and in 6-8 d at 17°C. This temperature range is characteristic of Gulf of Maine and Bay of Fundy rivers during the season of incubation. Development of shad eggs in the Connecticut River is prolonged and mortality increases concomitantly when water temperatures decline below 16°C (Marcy 1972). Although larvae are found in the Connecticut River from May to August (Marcy 1976c), June is the month when most larvae emerge, with peak larval emergence occurring at water temperatures of 20-22°C (Marcy 1976c; Crecco *et al.* 1983; Crecco and Savoy 1987). No shad eggs occurred in water with a dissolved oxygen content of less than 5 ppm (Marcy 1976c), and Carlson (1968) reported that the LC_{50} for DO is between 2.0-2.5 ppm. In the Connecticut River, larvae reportedly grow well at pH values between 6.0-7.0 (Crecco and Savoy 1987). Larval development reportedly is more successful in brackish than in pure fresh water, with salinities of about 7.5 ppt being about the most favorable for development (Leim 1924).

Development.--Sequence of egg development for American shad was described by Hildebrand (1963), Watson (1968), and Marcy (1976b). Studies by Watson (1968), Chittenden (1969), and Marcy (1976b) adequately describe development and ontogenetic changes associated with egg and early yolk-sac larvae. More recently, Johnson and Loesch (1983, 1986) described morphological development of shad over the standard length range from yolk-sac absorption to postflexion stage. A complete description of morphological development and body proportion ratios is now available from hatching through adult stage for this species (Mansueti and Hardy 1967; Lippson and Moran 1974; Jones *et al.* 1978; Johnson and Loesch 1983; Howey 1985).

Newly-hatched larvae are about 5.7-10.0 mm TL at hatching (Marcy 1976c), transparent and extremely slender. Some larvae drift into brackish water shortly after hatching, while others remain in freshwater throughout the summer months (State of Maine 1982). Yolk-sac absorption occurs in 3-5 d at 17°C and in about 7 d at 12-14°C, with fish length ranging between 9-15.5 mm TL at the end of this stage (Hildebrand 1963; Watson 1968; Marcy 1976c). During development, the vent moves anteriorly as in other larval Clupeidae. Growth is relatively fast. Median fin formation is completed by 17-21 mm SL (Bigelow and Welch 1925; Johnson and Loesch 1983), while paired fin development is completed between 23-28 mm SL, at about 21-28 d, when metamorphosis is nearly complete. Mean number of preanal myomeres increases during development (Chambers *et al.* 1976), and developmental sequence of various caudal fin components shows a distinction between preflexion, flexion, and postflexion larvae. Development of hypurals and notochord flexure are important in distinguishing larval and early juvenile stages of development. Illustrations and descriptions of larvae and juveniles are provided in Jones *et al.* (1978) and Johnson and Loesch (1983).

During development of hatchery-cultured American shad, morphometrics and body proportion ratios change with ontogeny of larval stages (Johnson and Loesch 1983). Head and snout length, eye diameter, and body depth exhibit a curvilinear relationship with increasing standard length, while preanal and predorsal length show a linear relationship with increasing standard length. Predorsal and preanal myomere counts decrease during ontogeny with corresponding anterior dorsal fin migration and shortening of the gut (Mansueti and Hardy 1967; Johnson and Loesch 1983).

Distinctions of Larvae.--American shad eggs and larvae are readily distinguished from other species of *Alosa* (Mansueti and Hardy 1967). Larvae are extremely slender, with the anus situated almost as far back as the caudal-fin base (Leim 1924). From yolk absorption to about 13 mm SL, ventral pigmentation pattern is one of the most important characteristics for identification of larval American shad (Leim 1924; Hildebrand 1963; Jones *et al.* 1978; Johnson and Loesch 1983). Specimens from freshwater are usually more pigmented than those taken in brackish water (Leim 1924; Jones *et al.* 1978; Johnson and Loesch 1983). Pigmentation pattern sequence for larvae taken in freshwater can compare with that outlined by Johnson and Loesch (1983), while pattern of ventral pigmentation described by Leim (1924) should be used when identifying larvae in the 10-13 mm SL size range. Leim (1924) used ventral pigmentation patterns to separate larval American shad and alewife, and Chambers *et al.* (1976) noted that ventral pigmentation patterns were similar for larval alewife and blueback herring, but distinct from that of American shad. Marcy (1976a) noted that American shad in the Connecticut River had 41 or more myomeres compared with 37-40 myomeres in alewife and blueback herring. A table comparing pigmentation characteristics, and morphometric and meristic information, useful in identifying the three species was prepared by Johnson and Loesch (1983).

Larval Ecology.--Both larval and juvenile American shad are associated with specific littoral habitats such as eddies and backwater areas (Mitchill *et al.* 1925; Watson 1968; Cave 1978; Crecco *et al.* 1983) where river flow is greatly reduced. Yolk-sac larvae and postlarvae of American shad are planktonic (Jones *et al.* 1978) and are therefore vulnerable to passive dispersal and transport downstream (Schmidt *et al.* 1988). In the Connecticut River, river herring (including American shad) larvae nearer the bottom were younger than those at the surface suggesting that larvae become more pelagic as they drift downriver (Marcy 1976b). Larvae lead a solitary life. Schooling behavior is first observed in post-metamorphic shad juveniles at an average size of 25 mm TL (Howey 1985). In circular tanks, juveniles tended to remain oriented into the current. A school of juvenile shad would break up when food was offered and regroup after feeding was completed.

First-feeding shad larvae (10-13 mm) are between 4-9 d old (Crecco *et al.* 1983), and larvae of all sizes eat mostly crustacean zooplankton (cyclopoid copepodids) and immature insects such as chironomid larvae (Leim 1924; Mitchell *et al.* 1925; Maxfield 1953; Crecco and Blake 1983). Chironomid larvae, cyclopoid copepodids, and, to a lesser extent, *Bosmina* sp., constitute up to 95% of the diet in shad of the Connecticut River. Shad larvae exhibit some feeding selectivity, as most in this area fed predominantly on less-abundant crustaceans and immature insects (Crecco and Blake 1983). In fact, the cladoceran, *Bosmina* sp., was utilized extensively by shad of all sizes, while rotifers were seldom encountered. Size of prey items consumed generally increased with size of larvae, and range of prey widths also increased steadily with body length. Mean mouth gape of shad larvae was always greater than that of co-occurring blueback larvae at a given length, and shad larvae of all sizes generally selected the larger cyclopoid copepodids and chironomid larvae. Diet overlap indices varied over time, but were generally higher among length groups within species than between species (vs. blueback), suggesting that any potential competition for food would be more severe from conspecifics than through interspecific competition (Crecco and Blake 1983).

Feeding behavior of larval shad is similar to that described for larvae of other clupeid species (Howey 1985) in that larvae draw their bodies into an S-shape, from which a rapid strike is made at selected prey organisms. Small larvae often fail to capture prey at which they strike, but the proportion of successful strikes quickly increases as larvae grow. At 6 d, larvae strike at *Artemia* using an abrupt swim method (Wiggins *et al.* 1985) in which they undergo a short period of fast swimming to catch prey. Alternatively, the larvae would simply slowly swim through the *Artemia* at the water's surface. These young larvae made an average of 16 orientations, and seven strikes, three of which were successful. In contrast, at 12 d, larvae oriented themselves on an individual *Artemia*, dropped back into an S-strike posture, and struck hard at the prey. Larger larvae averaged 55 orientations, 18 strikes, and nine successful strikes, during the hour-long observation period (Howey 1985). Shad larvae at 12d not only sought food more actively as indicated by increased number of orientations, but additionally were more selective in feeding than younger larvae. Older larvae were also slightly more efficient at feeding, with 50% of strikes resulting in prey capture.

In culture systems, shad larvae are photopositive, especially from 14 d post-hatching until metamorphosis (Howey 1985). Diel variation in feeding intensity occurs, with peak feeding in evening hours (1800-2100) for both 6 d and 12 d larvae (Wiggins *et al.* 1985). At 18 d, there was no obvious peak in feeding activity, rather, feeding occurred more uniformly throughout the daylight hours. Field-caught larvae were also found to have a peak stomach content volume at 2200 hr (Levesque and Reed 1972). In culture systems, feeding intensity for larvae of all ages declined during early morning (0300-0600). Incidence of feeding increased with age of larvae. First-feeding larvae, 6 d of age, had a 30% mean incidence of feeding for the 24-hr period. Mean incidence of feeding increased to 45% at 12 d, and 68% at 18 d (Howey 1985).

American shad larvae 7-10 mm in the Connecticut River exhaust the yolk sac approximately 3-6 d post hatching (Leim 1924; Maxfield 1953; Marcy 1976c; Wiggins *et al.* 1985), suggesting that the first growth ring is deposited shortly after hatching, and just prior to exogenous feeding. Length increments among larval shad determined from daily increments on otoliths (Howey 1985; Savoy and Crecco 1987) followed an asymptotic relationship in which length increments were nearly linear from hatching until about 20-40 d old, followed by a 10-d period of declining growth rates as larvae approached metamorphosis (30-d old).

After metamorphosis, juvenile American shad apparently undergo a second asymptotic growth phase, as indicated by a linear increase in length from 30 to 70 d, with daily length increments declining slowly to a theoretical asymptote (87-106 mm) at about 75-100 d old. In the growth model used, larval shad were estimated to grow 0.7-0.9 mm/d from hatching to about day 20, after which daily length increments diminished to about 0.3-0.5 mm/d. Juvenile shad grew about 1.2-1.4 mm/d between days 30-60, then daily growth in length decreased to about 0.8-0.9 mm/d between 60 and 90 d.

Murai *et al.* (1979) reported that growth rates of larvae are retarded by depressed water temperatures. However, cohort-specific growth rates of larval shad were found to increase linearly with rising zooplankton densities, and asymptotically with rising river temperatures and declining river flows (Crecco and Savoy 1985). By contrast, juvenile growth rates among 5-d cohorts showed no significant linear or nonlinear relationships to water temperatures and river flows. There is convincing evidence that juvenile shad growth rates are mainly governed by intraspecific competition rather than by abiotic factors (Crecco and Savoy 1985). This growth compensation hypothesis is supported by significant inverse correlations between juvenile mean lengths during emigration and adult shad abundance.

Howey (1985) reported on growth and hatching success in intensive culture systems for shad reared from fertilized eggs to fingerlings. Eggs incubated at 17°C averaged 70% hatch. Three-day-old fry were fed *Artemia* nauplii and converted to an open-formula diet when averaging about 25 mm. Growth in length at about 18°C was asymptotic during larval and juvenile development, with one growth period evident from hatch to metamorphosis and another through juvenile development. Initial weight increases were rapid with gains as high as 7.1%/d during metamorphosis. Although increases in length during the initial 40 d post-hatch was slight, weight increase was rapid (Howey 1985) with fish doubling their weight between days 7 and 14 and increasing it more than 12-fold by day 40. Weight increase rates declined slightly for ca. 10 d prior to metamorphosis. The fish experienced another period of rapid weight increase during metamorphosis, gaining as much as 10.3 mg/d (7.1% increase) as their body form changed from thin and elongated to deeper and more robust. Following metamorphosis, daily weight increase began to decline, averaging 4.7, 2.3, and 1.3% for American shad 75, 100, and 150 d old, respectively, and became significantly less (0.3%) between 150-200 d of age (72-89 mm TL). Growth coefficients (K-values) increased steadily from 0.0204 to 0.908 for shad between 7 and 150 d old, but decreased to 0.767 and 0.705 for fish 200 and 250 d old (ca. 89 mm TL). Daily growth rates for both length and weight declined after fish were 75 d old.

Egg mortality of cultured American shad was 30-35% during incubation (Howey 1985). After hatching, mortality rates were highest among first-feeding larvae (7-10 mm) and lowest among fry approaching metamorphosis (20-23 mm). Daily mortality rates among first feeding fry averaged 1.4%/d during the initial 10 d and 2.1%/d for the next 5 d when most nonfeeding fish died. From 16-70 d post-hatch, mortality averaged 0.75%/d, ranging as high as 1.5% during the period when most fish underwent metamorphosis. Following this transformation, juvenile shad continued to exhibit daily mortality rates of up to 0.5%/d. For every 10,000 larvae hatched, ca. 7,100 survived after 3 wk, 6,300 to metamorphosis, and 6,000 were still alive after 10 wk. High mortality during early larval development of cultured shad is similar to that observed in natural populations. For example, Crecco *et al.* (1983) estimated that only 1.86% of 4-d old Connecticut River shad survived to metamorphosis, while Leggett (1969) estimated a 0.001% survival rate from egg to adult for shad completing life cycles in the Connecticut River. Survival rates through metamorphosis of larval and juvenile shad in culture systems were significantly higher than those for feral shad and other laboratory-reared clupeids.

Survivorship curves estimated for larval shad in the Connecticut River were age specific, with mortality rates of 19.8-26.5%/d for first-feeding larvae (10-13 mm), and 4.3-8.7%/d for larvae approaching metamorphosis (Crecco *et al.* 1983). The magnitude of larval mortality between 10 and 25 mm is a declining function of age, demonstrating that probability of surviving to metamorphosis depends largely on whether a larva can survive the first 8-12 d after exogenous feeding begins. Because mortality rates were consistently higher for first-feeding larvae among the 4-yr sampled, mortality during this 5-d period could greatly affect year-class strength. During days 4-9, 70-85% of the losses occurred, thus supporting the concept of a critical period in the life history of this fish. Other researchers also have noted high mortality rates for larvae during the period 3-7 d post-hatching (Bradford *et al.* 1968; Howey 1985; Wiggins *et al.* 1985). Zooplankton densities during larval development suggest that differential larval mortality is due partly to temporal changes in food availability. Short periods of food deprivation among first-feeding larvae could result in death from malnutrition. High and persistent zooplankton densities during shad development can therefore enhance year-class strength.

Crecco and Savoy (1987) found that mortality rates estimated from 35-40,000 larvae were highest (9-11%/d) for cohorts that emerged during late May when river temperatures were below 18 °C and river flows exceeded 800 m^3/s. Mortality rates of larval cohorts were lowest (3-5%/d) after mid-June when temperatures rose above 21 °C and flows diminished below 300 m^3/s. Cohort mortality rates were positively correlated with larval feeding success, but were unrelated to zooplankton abundance. Cohort mortality rates were also positively related to relative abundance of newly-hatched larvae of each cohort, suggesting the presence of density-dependent mortality, which was estimated at 8-11% and 26% of the total larval mortality rate in two different years. Overall results of this study strongly indicated that mortality of larval shad and subsequent production of juveniles were strongly linked to hydrographic and meteorological events mediated by density-dependent processes.

Juvenile Biology.--Juvenile shad spend ca. 4-6 mo in their natal rivers. While in these habitats, they undergo diel migratory activities (Marcy 1976c; Loesch *et al.* 1982). During daylight hours juveniles occur near the bottom, whereas at night, they occur in greater abundance in surface waters. Young shad develop schooling behavior before migrating downstream. Schooling frequency (studied in experimental situations) is group-size dependent (Ross and Backman 1992), with large groups of shad juveniles spending nearly all their time in schools. Polarized schooling, as a final behavioral state, was not predictable in shad until group size reached about 50 fish. Individual survival increased as a function of increasing group size. Larger group sizes promote schooling, which, somehow, in turn, improves the survival of individual shad (Ross and Backman 1992).

Juvenile shad are indiscriminate predators (Walburg 1957) that feed both beneath and at the surface (Levesque and Reed 1972; Domermuth and Reed 1980). Young shad have even been reported to leap from the water to capture insects flying over the water's surface (Massman 1963). Insects and crustaceans (Walburg 1957), planktonic crustacea and chironomid larvae (Leim 1924), adult and larval insects, and ostracods (Hildebrand and Schroeder 1928) are the most important foods consumed by juvenile shad. In the Connecticut River, young shad consumed over 16 different prey types consisting largely of planktonic and drifting cladocerans, some copepods, and small amounts of terrestrial insects (Levesque and Reed 1972; Domermuth and Reed 1980). Virtually no benthic organisms were contained in diets of these fishes. In the Connecticut River, juvenile shad showed strong preference for daphnid cladocerans and selected moderately for bosminid cladocerans. Copepods, macrothricid cladocerans, and chironomid pupae were moderately rejected, while chydorids, sidids, and chironomid larvae were strongly rejected. In two Virginia tributaries of Chesapeake Bay, insects of terrestrial origin represented a larger proportion of food items consumed by juvenile American shad from areas upriver of the spawning grounds, while aquatic insects predominated in diets of fish taken downriver from the spawning grounds (Massman 1963). Feeding began to increase in late afternoon, was most active at dusk, and continued to a lesser extent during the night and almost ceased by midday. Marcy (1976c) also noted that feeding occurred only during late afternoons and early evenings near the shore where fish dimpled the surface while feeding on flying stages of ants. Wind direction and force appeared to be important factors in regulation of insect availability and consequently the amount of surface activity of the fish (Marcy 1976c). Both Massmann (1963) and Maxfield (1953) noted orientation toward terrestrial foods when available. Massmann particulary noted that, in Virginia, important food sources for young shad did not originate in the rivers, but rather, they originated from the wooded areas bordering them.

Young shad grow fast while in natal rivers before moving downriver to lower reaches of the estuary in the fall. By the end of their first summer's growth, they generally range from 37 to 112 mm TL and resemble adult shad in appearance. Shad spawned in Bay of Fundy tributaries reach lengths of 75-155 mm by the end of the first growing season (Leim 1924). Growth increments determined from sagittal otoliths of juvenile shad in the Connecticut River (Crecco *et al.* 1983) followed an asymptotic pattern with age. First summer growth in length of juvenile shad in Chesapeake Bay (Hildebrand 1963) ranged from 20 to 69 mm in June, 30-74 mm in July, 45-79 mm in August, 50-95 mm in September, 45-99 mm in October, and 60-119 mm during November. Larger fish, 150-225 mm, of ca. 7-mo age were also captured along with YOY fishes. Generally, growth rates of juveniles after having entered the sea are not well known because of difficulties associated with capturing specimens at this stage of the life history (Hildebrand 1963).

In culture-reared American shad, following metamorphosis, juveniles undergo a second asymptotic growth phase (Howey 1985). Between 60 and 75 d of age, mean length increased 0.67 mm/d or 1.9%. Daily length increments then declined slowly toward a theoretical asymptote, averaging 0.9, 0.6, 0.2, and 0.2% for shad 100, 150, 200, and 250 d old, respectively. Growth rates of reared shad were similar to reported values of natural populations (Chittenden 1969; Johnson 1980; Crecco *et al.* 1983).

Mortality rates of feral juveniles are much lower than for larvae, ranging from 1.8 to 2.0%/d (Crecco *et al.* 1983). Juvenile shad reared in culture exhibited mortality rates of up to 0.5%/d until they averaged ca. 75-80 mm TL (Howey 1985).

Juvenile shad utilize rivers and streams as a nursery area during their first summer and fall, at which time they begin a downstream migration to the sea. In some systems, such as the Connecticut River, juvenile river herrings, including young shad, represent significant components of the juvenile fish community (Marcy 1976a). In this river, results of a 7-yr study showed that anadromous and marine fishes utilizing the study area constituted 67% of the young fishes, with blueback herring being the most abundant species. Seaward migration in estuaries seems to be a rather slow process for river herrings (Stokesbury and Dadswell 1989). Timing of seaward migration of juvenile shad along the east coast of North America is earliest in rivers at northern latitudes (O'Leary and Kynard 1986), with larger individuals usually moving downstream first (Chittenden 1969; March 1976c; Schmidt *et al.* 1988). Timing of juvenile migration is triggered by temperature (Chittenden 1969; Sykes and Lehman 1957; Leggett and Whitney 1972). In areas such as Chesapeake Bay, young fish (95-154 mm) overwinter in deeper waters (Hildebrand and Schroeder 1928). However, since lower lethal temperatures for shad are about 4°C (Tagatz 1961; Chittenden 1972a) and sublethal effects begin at about 6°C, juveniles in northern estuaries usually cannot overwinter in their natal rivers, and must leave before temperatures decline to this point.

In tributaries of the Gulf, juvenile shad begin seaward migration in late summer or early fall (State of Maine 1982). Seaward movement of river herrings occurs predominantly at night and the negative phototrophic response of these fishes (Loesch *et al.* 1982) appears to keep them relatively immobile during daylight hours. Juvenile river herrings utilize the Annapolis River, NS, as a nursery area from August to October (Stokesbury and Dadswell 1989). In the Connecticut River (Marcy 1976a, 1976c), shad juveniles are present July-November. Downstream movement of juvenile shad in this river does not begin until about mid-August, when water temperatures are highest, or just beginning to decline (Marcy 1976c). Peak migration was reached in September, with the bulk of the population leaving the river in late September and early October. By December most migrants had left the river. Most juveniles have left the Hudson River by mid-November (Schmidt *et al.* 1988), before water temperatures become detrimental to survival at 4-6 °C. Fish migrate downstream in late September and early October in the Delaware River (Sykes and Lehman 1957). Farther south, migration does not begin until late November or early December in the Potomac River, VA (Hildebrand and Schroeder 1928), the Cape Fear River, NC (Davis and Cheek 1967), and the Altamaha River, GA (Goodwin and Adams 1969).

The particular combination of extrinsic factors that triggers seaward migration of juvenile shad from estuaries is uncertain. Key factors influencing timing of downstream migration of juveniles have been identified as either increasing river flow, decreasing water temperature, or a combination of both during autumn (Leach 1925; Hildebrand and Schroeder 1928; Sykes and Lehman 1957; Chittenden and Westman 1967; Davis and Cheek 1967; Walburg and Nichols 1967; Watson 1968, 1970; Moss 1970; Williams and Bruger 1972). Temperatures near 15 °C were thought to be a primary stimulus for juvenile shad to leave Atlantic coastal rivers (Hildebrand and Schroeder 1928; Sykes and Lehman 1957; Leggett and Whitney 1972). Chittenden (1969) reported that declining temperature (i.e., decreases to those slightly above the lethal limit) triggered the final movement of juvenile shad from freshwater, whereas factors associated with body size appeared to initiate earlier stages of seaward emigration. Moss (1970) reported that young shad in laboratory situations respond minimally to a rapid temperature change of ca. 1 °C, but they avoided rapid temperature change of 4 °C. Moss concluded that fish are behaviorally capable of avoiding temperature changes of a kind that otherwise could prove lethal. These observations were later confirmed with a field test by Marcy (1976c).

Temperature has most often been reported as the primary factor triggering downstream migration of juvenile river herrings. Chittenden and Westman (1967) reported that movement of juvenile shad out of the Delaware River was almost complete when temperatures fell to 8.3 °C. Sykes and Lehman (1957) noted that juveniles initiated downstream migration only when the temperature fell below 21 °C. Marcy (1976c) noted that juveniles in the Connecticut River began downstream emigration during mid-August when temperatures were between 26-23 °C. By early September-early October, the bulk of the juveniles had left the study area as temperatures fell from 23-17.8 °C, and only a small portion were left in mid-October and early November when water temperatures declined to 17.8-10.9 °C. No juveniles were left in the river at the end of November when water temperature was <6.6 °C. Watson (1970) also reported that larger juveniles moved downstream prior to the time when declining temperatures became a critical factor.

Decreased temperatures occurring during a new or quarter moon phase, were considered to be the major stimuli for downstream migration of juvenile river herrings in the Connecticut and Annapolis rivers, rather than increased water flows (O'Leary and Kynard 1986; Stokesbury and Dadswell 1989). In the Connecticut river, shad migration began at 19 °C, peaked at 14-9 °C, and ended at 10-8 °C (O'Leary and Kynard 1986). In the Annapolis River, movements of juvenile shad were coincident with the dark nights and a sharp decline in water temperature below 12 °C. In both systems, shad moved in the afternoon and evening (peak activity between 1800 and 2200 hrs); most movement peaks were centered on quarter-moon periods. Peak seaward emigration occurred during new to quarter moon periods (dark nights). In both river systems, schools of juvenile shad apparently remained offshore just prior to downstream migration and catchability with seines was low except during twilight and early evening periods. Onshore movement, just prior to emigration, was rapid and short-lived and sizable catches apparently depended on encountering a school. The virtual absence of river herrings from inshore regions for almost a month before a final seaward migration suggested they schooled offshore in the estuary until the correct migration stimulus occurred (Stokesbury and Dadswell 1989). During seaward migration, shad were concentrated in the upper 2 m of water column (Buckley and Kynard 1985).

River discharge appeared to play little role in stimulating seaward movement in either system. Decreasing water temperature and the new moon period rather than river flow have been shown to be the most important factors stimulating downstream migration of alosids under riverine conditions (Marcy 1976c; O'Leary and Kynard 1986).

Fish size does not appear to be as important in emigration of shad juveniles (O'Leary and Kynard 1986). In the Connecticut River, mean length of migrating shad increased during the course of migration, and large interannual variations in size of downstream migrants were apparent in several other studies (cited in O'Leary and Kynard 1986), which suggests that this parameter may not be important as others in regulating the timing of juvenile shad migration.

A general explanation of the patterns of seasonal and daily migration of juvenile American shad may be that decreasing temperature in the fall acts as a behavioral releaser, allowing existing behavior patterns to be expressed as downstream migration (O'Leary and Kynard 1986). Each day as light decreases, premigratory American shad lose their rheotactic orientation (Fisher 1981). This results in breakdown in schooling behavior beginning in late afternoon and continuing throughout the night (Katz 1976). Both Katz (1976) and Fisher (1981) observed that juvenile American shad were strong swimmers in the daytime, when they schooled, but that in darkness their swimming ability greatly decreased and schooling ceased. Downstream migration of American shad may result from the following sequence: when temperatures are above a threshold of 19°C, juveniles maintain position in the river at night, possibly by using areas of reduced flow or by maintaining contact with the bottom; as temperature decreases below the threshold level, the behavioral tendency to maintain position is lessened and fish begin to drift downstream. This movement appears to be passive. Therefore, decreasing temperature would initiate the migration each year. A daily migration would occur in the late afternoon and at night when temperature decreased below the threshold at which fish maintain position in darkness.

After moving downstream to lower reaches of the estuary, juvenile shad enter the sea. Overwintering of juvenile fish from most Atlantic seaboard rivers is believed to occur in the middle Atlantic area (State of Maine 1982). Juveniles and prespawning adults remain in the ocean where they join with the adults on coastal migrations moving into the Gulf of Maine and Canadian waters in summer and then southward to the Carolinas in fall and winter. When they become sexually mature they form schools with older, larger shad and participate in a spawning migration to their natal streams. Nothing is known about mortality experienced by immature shad (age groups 1-3), or the factors determining it (Leggett 1976).

POPULATION DYNAMICS

Age and Growth.--American shad have been aged using scales and otoliths (Leim 1924; Cating 1953; Lapointe 1957; Judy 1961; Melvin *et al.* 1985). According to Leim's investigation, based on scale studies and length frequencies, shad in the upper Bay of Fundy average about 4.1-4.5 cm in 9-10 wk, 7.5-15.5 cm by end of the first growing season, 12.8-15.0 cm at age-1; 23.0-25.4 cm at age-2; 33-36 cm at age-3; 38-41 cm at age-4; and 47-49 cm at age-5. The two largest American shad he examined, about 62 and 63 cm long, appeared to be 7- and 6-yr old, respectively. In the Bay of Fundy (Leim 1924), American shad weigh about 91 g at 20 cm; about 273 g at 31 cm; about 605 g at 38-42 cm; about 1.14 kg at ca. 52 cm; and 2.04 kg at 59-61 cm, although variations occur according to their condition. Shad may grow somewhat faster in waters of the open Gulf of Maine (Bigelow and Schroeder 1953). American shad are occasionally reported to 5.5 kg, and older literature mentioned American shad of 6.6 kg, but none so large has been credibly reported in the Gulf in recent years. Although shad weighing in excess of 4.5 kg are infrequently captured (Ross 1991), most adult males are typically between 0.7 and 2.7 kg, and females between 1.6 and 3.6 kg. American shad may grow to 76 cm in length, but the largest individuals caught are usually less than 61 cm long. The largest American shad recorded by the International Game Fish Association (1994) was one weighing 5.10 kg, caught in the Connecticut River, in 1986.

Females may reach a greater age than males. Among older fish (ages 7-11 yr) examined by Borodin (1924), only seven were males as compared with 86 females. In the Shubenacadie, and presumably in other Gulf of Maine rivers, the oldest shad are estimated to be age-8 or age-9. However, shad runs in the northeastern United States and Canadian Maritimes are dominated by age-4 and age-5 fish (State of Maine 1982). In the Bay of Fundy, shad may live for 8 or 9 yr, while in the Gulf of St. Lawrence they are somewhat older. Annapolis River (NS) populations are slow-growing, longer-lived, and larger (Melvin *et al.* 1985) than those of surrounding areas. In this system, the oldest male was estimated to be age-12, the oldest female age-13. The largest shad caught was a female 61.7 cm FL, with a weight of 1.92 kg. The usual size was about 50 cm FL, and none were over 60 cm FL. The large individual size and older age of the population was attributable to a very low fishing mortality, about 5%/yr. American shad spawning in New England waters generally do not live beyond 5-7 yr of age, although age-10 and age-11 individuals are infrequently caught.

As fish mature with the approach of the spawning period, they move into their parent streams to deposit their eggs and repeat the life cycle. The average life cycle is from 3-6 yr, but some repeat spawners may live as long as 10-11 yr. Males generally reach sexual maturity 1 yr earlier than females. Mean age at maturity for both sexes occurs earlier in the south and increases with latitude toward the north (Leggett 1969; Carscadden and Leggett 1975a, 1975b).

In the Bay of Fundy, although a few shad spawn at age-4, most are age-5 (45.7-48.3 cm long) at first spawning; maximum age represented among spawning fish was 8 or 9 yr (Leim 1924). In the Shubenacadie, and presumably in other Gulf of Maine rivers most spawning fish are age-5, while the oldest are 8 or 9 yr. In New England waters, spawning males reach sexual maturity between age-3 and age-5, females between age-4 and age-6. Males enter the Connecticut River from the sea in their 4th yr, when 30.0-35.0 cm long. The smallest females returning to the Connecticut River to spawn were 40.0-43.0 cm and were in age-5, age-6 and age-7 (Marcy 1972).

Stock Structure.--Although American shad spawn in Atlantic coastal rivers from Florida to Quebec, juveniles and adults originating throughout this range form seasonal migratory aggregations in the ocean (Talbot and Sykes 1958; Leggett 1977a, 1977b; Dadswell *et al.* 1987; Melvin *et al.* 1992). For example, mark-recapture studies of fish tagged during the summer in the Bay of Fundy have provided recaptures from all major shad spawning rivers along the Atlantic coast of North America including those in Florida and Georgia (Dadswell *et al.* 1987).

Despite intermixing of shad populations in the marine habitat, evidence suggests that fish home to natal rivers to spawn (Melvin *et al.* 1986) and adults ascending particular rivers might form genetically discrete populations. It has been postulated that each major shad-producing river along the Atlantic seaboard has its own distinctive spawning stock (Carscadden and Leggett 1975a, 1975b). A number of local races are known from Atlantic drainages that are distinguishable on basis of morphology (Fishler 1959; Hill 1959; Carscadden and Leggett 1975a).

Previous studies of Atlantic shad have utilized meristic features and, to a lesser extent, morphometrics to investigate the relative contribution of major spawning rivers to specific fisheries (Fischler 1959; Hill 1959), or statistical significance of these characters to identify distinct river populations (Warfel and Olson 1947; Nichols 1966; Carscadden and Leggett 1975b). Multivariate analysis of meristic characters revealed significant differences among spawning shad collected from various rivers along the coast (Carscadden and Leggett 1975b). Melvin *et al.* (1992) used 10 meristic and 16 morphometric characters of shad collected from 14 rivers (Quèbec-Florida) to develop a linear discriminant function. Using this function, they then sampled fish from the mixed-stock occurring in the Cumberland Basin to determine their place of origin. Of the fish sampled, 10.9% were assigned to rivers south of Cape Lookout, NC, 38.1% were determined to have originated from rivers between Cape Lookout and Cape Cod (the area representing the largest spawning areas for American shad on the east coast), 32.5% came from rivers of the Bay of Fundy, and 18.5% came from rivers tributary to the Gulf of St. Lawrence. Interestingly, tag returns of fish tagged in the Cumberland Basin occurred in frequencies corresponding to those determined by the linear discriminant function classification.

Others (Williams 1985; Melvin *et al.* 1992) have used otoliths or multiple meristic and morphometric characters to assign stock origin of shad collected in the mixed summer fishery in the Cumberland Basin, NB, to three broad geographic groups encompassing Canadian Atlantic, mid-U.S.-Atlantic, and south U.S. Atlantic rivers. Large overlaps in scoring, however, hinders applicability of such analyses in assigning individual fish to respective populations. Carscadden and Leggett (1975b) found little difference in meristic features among year-classes of American shad in the St. John River, NB, however, DesFosse and Loesch (1985) reported the occurrence of significant temporal variability in meristic features among year-classes of juvenile shad and other alosids spawned in tributaries of Chesapeake Bay.

The possibility of separate genetic populations (stock, races, or metapopulation) is also suggested by latitudinal variation in phenotypic traits (Leggett 1969; Carscadden and Leggett 1975b; Leggett and Carscadden 1978; Shoubridge 1978; Melvin *et al.* 1992), such as differences in reproductive traits of shad from different regions of the species range. South of Cape Hatteras, NC, shad are semelparous, whereas to the north, they become increasingly iteroparous, frequently spawning repeatedly over several years (Talbot and Sykes 1958; Leggett 1969). Annual fecundity in shad follows the reverse pattern. It is several-fold higher in shad spawning in southern rivers compared with those spawning in rivers at the northern end of the range. These reciprocal latitudinal trends cause average lifetime fecundity to be constant over the species' Atlantic coast range (Bentzen *et al.* 1989). It was hypothesized that this shift from semelparity in the south to iteroparity in the north represented adaptive variation occurring among genetically discrete populations (Carscadden and Leggett 1975a; Leggett and Carscadden

1978; Glebe and Leggett 1981a).

Attempts to examine genetic differentiation of American shad using allozyme electrophoresis (Shoubridge 1978; Sismour and Birdsong 1986) have yielded equivocal results. No significant genetic heterogeneity was revealed among shad collected at several sites in Chesapeake Bay using electrophoretic analysis of proteins (Sismour and Birdsong 1986).

Analysis of mtDNA variation in Atlantic American shad from different river drainages (Bentzen *et al.* 1988, 1989; Nolan *et al.* 1991; Chapman 1993) have suggested that overall levels of mtDNA sequence divergence among shad are low (mean 0.2%). Results of the mtDNA analysis by Bentzen *et al.* (1989) suggested that low level of mtDNA variation in American shad may be a consequence of population bottlenecks that occurred during Pleistocene glacial maxima. Differences in the reproductive traits of northern and southern populations of American shad, if genetically mediated, are likely to have evolved since the Pleistocene. Nolan *et al.* (1991) examined 4-base data of the mtDNA molecule in American shad and found significant differences in distribution of several restriction site polymorphisms among samples analyzed. The fragment they analyzed, however, was coincident with the size polymorphism in the mtDNA molecule noted in different populations (R. Chapman, pers. commun.[4]). Their data, however, generally supported the hypothesis proposed by Bentzen *et al.* (1989), that the Miramichi, Hudson-Delaware, and St. John's (Canada) rivers support separate stocks of American shad. They also found an absence of substantial gene flow among American shad spawning systems which are geographically distant. Based on significant differences of mtDNA frequencies among populations they sampled, they concluded that female shad exhibited accurate region-specific homing behavior, and that it could be postulated that spawning populations or "stocks" of shad could represent geographic regions rather than specific rivers. They pointed out that Williams (1985) had earlier delineated shad into three distinct geographic spawning groups based on otolith analysis, and Melvin *et al.* (1992) also found three stocks based on multiple meristic and morphometric characters. Additionally, Dadswell *et al.* (1987) found three distinct oceanic aggregates of shad within overall mixed groups of Atlantic coast fish. Data of Nolan *et al.* (1991) minimally support this division; however, more samples should be examined before a definitive conclusion can be made.

Chapman (1993) studied shad in the Susquehanna River to determine if it was possible to use mtDNA to identify the source(s) of resurgence of this species, since shad were stocked from a number of different sources. He found that many shad had mtDNA genotypes that were common to several if not all drainages, therefore, most individuals could not be uniquely identified to any one river system. Only a small portion of the Susquehanna stock could be assigned to stocking efforts with some confidence.

Chapman *et al.* (1994) expanded on the mtDNA analysis of shad populations using both 4-base and 6-base fragments and found that 4-base data revealed some differences, while the 6-base data contained homoplasies. They concluded that because the assignment of stock structure is dependent upon unambiguous determination of shared matriarchal ancestry, the present data would not recommend the use of six-base data as a tool for management of *A. sapidissima* populations. While it is possible to make qualitative assessments of statistical differences among populations when genealogical relationships are uncertain, quantitative determinations of the degree of differences would be unwarranted. Therefore, they concluded that assessment of contributions of spawning stocks to mixed populations could be completely misleading for this reason as well (Chapman *et al.* 1994).

Variations in Abundance.--Influence of environment and size of parent stock are important factors influencing recruitment in Atlantic shad (Leggett 1976). Strong year-classes occasionally arise from small parent stocks suggesting that year-class strength is established by differential mortality during the pre-recruitment phase (Crecco *et al.* 1983). Major decreases in year-class strength of alosine populations during one season is common, although these fishes generally have the ability to recover from catastrophic mortality in 1-2 yr (Mansfield and Jude 1986).

Marcy (1976c) found that June river flows and water temperatures in the Connecticut River were significantly correlated with American shad year-class strength. An index of abundance was validated for juvenile shad in the Connecticut River (Crecco *et al.* 1983; Savoy and Crecco 1988). Year-class strength of juveniles was shown to correlate positively with recruitment levels of adult females 4-6 yr later, suggesting that year-class strength is established prior to the juvenile stage (Crecco *et al.* 1983). The stock recruitment relation was environment dependent; stock size was strongly influenced by climatic variability and river hydrography, and weakly related to escapement, with year-class strength established prior to the juvenile stage (Crecco and Savoy 1984, 1987; Crecco *et al.* 1986; Savoy and Crecco 1988).

Crecco and Savoy (1987) found that all survivorship curves calculated on data collected from 1979-1984 demonstrated that mortality rates were highest among first-feeding larvae, then declined steadily through juvenile development. There was a strong inverse correlation between mortality rates of first-feeding larvae and year-class strength, whereas mortality rates of all other life stages showed only weak correlations. Results of this study were consistent with the "critical period" hypothesis (Cushing 1975). Mean monthly river flow, temperature, and mean monthly rainfall correlated significantly with corresponding juvenile indices only for the month of June, when most Connecticut River shad hatch. High June river flows were inversely related to feeding success of first-feeding larvae and year-class strength. Results indicated that temporal change in rainfall, river flow, and temperature, coincident with early larval development, are ultimate regulators of year-class strength of shad in the Connecticut River and probably elsewhere. Models also estimated that 10-25% of recruitment variability is explained by addition of parent stock size. Density-dependent factors (competition and predation) also exert a subtle, but measurable, influence on American shad recruitment (Leggett 1977a; Yoshiyama *et al.* 1981; Crecco and Savoy 1987), although their effects are obscured statistically by climatically induced variability. Lorda and Crecco (1987) developed an environment-dependent stock recruitment model for shad in the Connecticut River. Their model explained over 80% of recruitment variability from the 1966-1980 year-classes. They estimated that shad have a relatively high compensatory mortality ($Z_c = 1.21$).

Leggett (1977a) demonstrated that June temperatures and June river flows were related to deviations from the stock-recruitment relationship of shad for the Connecticut river population. High river flows and low river temperatures in June reduced larval feeding success, survival, and ultimately shad year-class strength, providing a reasonable explanation for the lack of a parent-progeny relationship (Crecco and Savoy 1984).

Differential egg mortality could also account for large fluctuations in year-class strength. American shad eggs and early larvae may experience high mortality (15-40%/d) in the Connecticut River, but the average density-dependent mortality rate during those stages was estimated to represent only a relatively small percentage (18%) of the total pre-recruitment mortality (Savoy and Crecco 1988). This suggested that most annual variability in American shad recruitment is explained by density-independent factors, which is consistent with the significant positive correlation between mean June flow and egg and early larval mortality rates, and with the significant inverse correlations between June river flow and adult recruitment. Most (82%) density-dependent mortality occurs during the egg and early larval stages.

Stock-recruitment models without environmental factors explain less than 3% of the recruitment variability (Crecco *et al.* 1986). Other environment-dependent stock-recruitment models predicted 80-90% of the recruitment variability. The density-dependent exponents of these models were highly significant, indicating that density-dependent regulations exert a subtle but measurable influence on year-class strength of American shad in the presence of climatic variability. Over 62% of the recruitment variability from the 1966-80 year-classes was explained by mean June river flows (Crecco *et al.* 1986; Lorda and Crecco 1987). Cool, wet summers were demonstrated to be a factor in the year-class success of shad in the Connecticut River (Crecco and Savoy 1984).

Juvenile mortality rates, in contrast to those of larvae, appear to be much lower and independent of year-class strength. Crecco and Savoy (1984) did not find a statistically significant stock-recruitment relationship for juvenile shad in the Connecticut River.

American shad populations, as with other river herrings, have been declining throughout the species' range since colonial times. Commercial landings of this species have declined over the past 100 yr, reflecting this major reduction in population size. The decline has been particularly severe in spawning rivers south of Delaware Bay (Cooper 1984). While overall catches of shad along the Atlantic seaboard has decreased, shad stocks in the Connecticut, Hudson, and Delaware rivers appear to have stabilized (Cooper 1984). Anthropogenic influences, such as overfishing, destruction of freshwater habitat, alteration of river flows, construction of barriers prohibiting fish access to return to spawning grounds, industrial pollution, and mortalities associated with electric power generation (Bell and Kynard 1985; Taylor and Kynard 1985) have all had long-term negative impacts on populations. Dam construction appears to be the primary factor causing major declines in anadromous herring, such as the American shad (Chittenden 1976; State of Maine 1982; Moffitt *et al.* 1982).

Intensified fishing efforts combined with effects of pollution and loss of access to spawning and nursery habitat markedly reduced New England shad stocks (Ross 1991). A recent study (Polgar *et al.* 1985) modeled effects of pollutant loadings on shad stocks in northeastern estuaries and found that stock abundance was more strongly influenced by human population levels (but not dredging activities) compared with the climatic factors they incorporated into their model. In another study, historical trends in shad abundance in several mid-Atlantic estuaries were found to be influenced by climatic variables, but fluctuations in abundance of these populations were also strongly correlated with general water quality conditions (i.e., sewage loading or dissolved oxygen level of the estuary) within the fish's spawning habitat (Summers and Rose 1987).

American shad restoration projects, including shad culture, aimed at reversing the declines in tributaries along the east coast, have been underway for some time (Leach 1925; Chittenden 1971; Meinz 1978; St. Pierre 1977; Howey 1985; Wiggins *et al.* 1985, 1986; Barry and Kynard 1986; Ross 1991). In addition to habitat restoration, the number of adult American shad lifted over dams to gain access to additional spawning areas has improved reproductive success and subsequent recruitment (Moffitt *et al.* 1982). The Atlantic States Marine Fisheries Commission established a coastwide management plan in 1985 to address coordinated management activities directly related toward regulating the harvest, improving habitat quality and accessibility, and initiating stocking programs to restore American shad to rivers where they historically existed.

Most river systems feeding into the Gulf of Maine are in restoration, which includes stocking adult shad (from Connecticut River), and raising shad from eggs for stocking purposes. Despite efforts to augment stocks over the last 20 yr, by opening up new habitats for spawning, stocking, and controlling fishery activities, shad runs have continued to decline throughout Gulf of Maine tributaries. Continued reduction in stock abundance despite restoration efforts is troubling, and may reflect an overall decline in water quality in many Gulf of Maine tributaries. Although great potential exists for restoring and vastly improving abundance of shad stocks spawning in Gulf of Maine tributaries, as of yet, this potential has gone unrealized largely because numbers of fish utilizing these areas continues to diminish. Achievement of the 1967 Maine Legislative Mandate for clean water by October 1, 1976, greatly improved the outlook for restoration of diadromous fish resources in that state. In 1982, overall abundance of anadromous fish stocks was estimated at ca. 10% of their historic levels (State of Maine 1982). Present resource management and enhancement programs are directed toward mitigation of the adverse circumstances which caused the decline of these recreationally and commercially valuable anadromous fish resources. Recent progress in water pollution abatement has greatly improved water quality of historical spawning and nursery habitats. Current programs are designed to increase the availability of historical anadromous fish spawning habitat, maintain existing runs at optimal levels, and increase knowledge of habitat requirements, recruitment, and exploitation to enhance fishery management capabilities and identify critical habitat areas. Restriction of commercial and recreational fisheries to provide adequate spawning escapement would also benefit populations. The single most serious remaining obstacle to expansion of anadromous fish runs, however, is the existence of numerous dams which deny fish access to upstream habitat. Removal of obsolete or neglected dams, where possible, allows for the greatest number of species to utilize upriver habitat. Elimination of river impoundments also increases the amount of spawning and nursery habitat for American shad. Although many fishways have been constructed to assist shad and other migrating fishes in reaching their spawning grounds, construction of fishways is only a beginning of restoration efforts for anadromous fishes. Construction of fishways is not a solution unto itself. Fishways also need to be monitored and repaired annually to ensure their continued proper functioning. Many times, fishways are installed, but little money is appropriated for their continued maintenance.

Restoration plans for anadromous fishes in the state of Maine were expected to produce an estimated annual yield of shad harvest of 1,250,000 kg with an estimated value (at 1981 prices) of $275,000. Over a 50-yr period, if values remained the same as in 1981, these resources were estimated to generate over $145,000,000 to the economy of the state. These values were considered minimal because no values for recreationally caught shad were derived, and a hidden value was also recognized in that these species serve as an important forage base for freshwater game fish and commercially important marine species.

Shad restoration efforts for individual river systems in the State of Maine were detailed by Squiers and Stahlnecker (1994). These are discussed to illustrate the magnitude of effort being applied to restore populations of anadromous fishes, and to demonstrate the various levels of results and the disappointments achieved in these efforts. During 1994, 879 adult shad were released at Waterville, upstream of the head-of-tide dam. A total of 47,000-57,000, 30-38 d-old fry were released in the Kennebec River in Waterville. An additional 4,000 fry were released in the Kennebec river at Sidney. Shad were also stocked in the Medomak River drainage (ca. 56,000 fry). In 1994, 706 adult shad were released at Auburn. One fish ascended the fishway in 1994. On the Saco River, new fish passage facilities were completed at the head-of-tide dams in 1993. A fish lift was built and a Denil fishway was constructed in the West Channel dam. A total of 997 shad were lifted in 1993. In 1994, 386 shad were lifted and four were passed in the Denil fishway. In the Kennebec system, the juvenile alosid survey was continued, where the greatest catch per unit of effort for juvenile shad occurred in the Androscoggin River, followed by Merrymeeting Bay. No shad were captured in 1994 in the upper Kennebec River. The index for the Androscoggin River was the highest on record since the survey was initiated in 1979. Conversely, the index for the Kennebec was the lowest since 1982. In the Androscoggin River, the juvenile shad index for 1994 was less than in 1993, while it was about the same for Merrymeeting Bay.

In Massachusetts (P. Brady, person. commun.[1]), efforts are also being made in many areas to restore anadromous fish populations. Over 100 active runs of alewife occur and over 200 fishways have been constructed since the 1930s to facilitate upstream movements by migrating river herrings and other fishes. The largest runs of anadromous clupeids in state waters are in the Connecticut and Merrimac river drainages. Most Massachusetts coastal streams have relatively small headwater ponds compared with those of Maine and areas further south. There is considerable interannual variation in numbers of migrating river herrings in most streams; some streams are doing well with restoration, others are holding their own, and in some the populations of anadromous fishes are declining. Despite restoration efforts, overall, there has been noticeable decline in runs of anadromous fishes in the larger systems. In Herring River, Bourne, which empties into Cape Cod Canal, there was a 43% decline in the adult run between 1993 and 1994.

Despite the efforts being made to restore populations of these fishes, there continues a decline in abundance of anadromous fishes along the entire U.S. east coast. This long term decline in anadromous fishes is difficult to understand. It is unknown if this represents a natural decline in population cycle of these species. Other factors potentially influencing the downward cycle are increased degradation of water quality in natal rivers (as evidenced by declines in other estuarine resident and anadromous fishes such as smelt, Atlantic tomcod and white perch), impacts of coastal intercept fisheries on migrating adult fishes, and impacts from a complex predator-prey interaction with striped bass whose populations have undergone a resurgence in recent years.

Importance and Utilization.--Extensive commercial and recreational fisheries developed for American shad along the entire east coast in the 19th century. Now, the American shad is only of minor commercial importance, with landings occurring chiefly in rivers of the Middle Atlantic region and in the Hudson River (Whitehead 1985a). American shad have little current commercial importance in the Gulf of Maine. Commercial fishing methods for taking shad include pound nets, gill nets, and seines. Small quantities are also taken with fyke nets, otter trawls, purse seines, traps and dip nets.

The shad is a highly regarded game fish in many parts of coastal United States (Ross 1991), but less so in Canada (Scott and Scott 1988). Presently, there is limited participation in sport fisheries for American shad in U.S. Gulf of Maine tributaries. The Annapolis River (NS) has one of the few sport fisheries for American shad in Canada (Scott and Scott 1988).

Historically, substantial quantities of shad were taken in recreational fisheries where migrating fish, enroute to spawning grounds, were especially targeted. Many American shad were caught with flies and lures, and by snagging, by crowds of anglers seeking this species on its migratory journey. Ross (1991) provided a detailed account of sport fishing and preparation methods for enjoying American shad as tablefare. American shad are marketed fresh and salted; the flesh is white, flaky and of fine flavor, but bony. A good-quality caviar can be made from the roe. Shad liver oil contains 500-800 USP of vitamin A and 50-100 IU of vitamin D per gram, but is not as rich in vitamins as is the oil from cod or haddock livers. Nutritional values for shad are: Fat 3-17% (varies seasonally); moisture 65-73%; protein 16-20%; ash 1-2% (Sidwell 1981).

Chapter 14. HICKORY SHAD *Alosa mediocris* (Mitchill 1814)

Fall herring; Shad herring

Description.--Body moderately slender, moderately compressed, with greatest thickness notably less than ½ its depth; body depth (26.7-32.8 SL) rather greater in large than in small specimens, depth usually exceeding length of head, abdomen with distinct keel of scutes. Snout length 5.9-7.5% SL. Maxillary length 10.4-13.4% SL. Lower jaw very prominent, projecting beyond upper when mouth closed; not rising steeply within mouth. Teeth present in jaws, reduced or absent in upper jaw of larger fishes (> 23 cm SL), teeth absent on vomer; teeth on tongue minute, in small elongate patch. Scales only moderately adherent, with definite crenulate membranous margin, preceded by longitudinal striae.

Meristics.-- Dorsal-fin rays 15-20, most frequently 17-18; anal-fin rays 19-23, most frequently 20-21; pectoral-fin rays 15-16; pelvic-fin rays 9. Vertebrae 54-55. Scales ca. 45-50 in lateral series; about 16 longitudinal rows of scales on body between base of pelvic fin and anterior dorsal rays. Ventral scutes moderately developed, 19-23 (usually 20-23) prepelvic ventral scutes, 12-17 (usually 13-16) postpelvic ventral scutes. Lower gillrakers 18-23 (usually 20-21), apparently not increasing in number with age. Branchiostegals 7-8. Pyloric caecae numerous. (Bigelow and Schroeder 1953; Hildebrand 1963; Whitehead 1985a).

Color.--Grayish green on dorsum, shading somewhat gradually into iridescent silver on sides. Nape green; side of head brassy. Tip of lower jaw and snout dusky. Tongue dusky to blackish. Narrow dark lines along rows of scales on upper part of sides (most distinct in large specimens that have lost their scales). Dark spot on shoulder, usually with several obscure dark spots along sides. Peritoneum somewhat pale, but with scattered dusky punctulations (Hildebrand 1963). Dorsal, anal, and caudal fins dusky. Outside margin of pelvic fin dusky or black, inner rays translucent. Pectoral fin dusky to darkly pigmented.

Size.--Hickory shad are relatively large anadromous herrings reaching standard lengths of approximately 46 cm, with most usually 30-38 cm. According to DesFosse *et al.* (1994), the maximum size reported in earlier literature, about 61.0 cm, was not based on an actual specimen and its reliability is questionable.

Distinctions.--Hickory shad differ rather noticeably from Atlantic herring in that the dorsal-fin origin is anterior to the body midpoint (vs. at about body midpoint in Atlantic herring), in lacking teeth on the vomer (vs. cluster of teeth present on vomer of Atlantic herring), the strongly saw-toothed keel along the ventral margin of the abdomen (vs. only weakly saw-toothed keel in Atlantic herring), in its lower jaw projecting much farther beyond the upper jaw when the mouth is closed (vs. only slightly projecting in Atlantic herring), in its much deeper body with more obvious taper toward both snout and tail (vs. more elongate body with more gradual taper in Atlantic herring).

The hickory shad is similar to Atlantic shad, alewife, and blueback herring, and would most likely be confused with these species. It resembles all three in its general body shape, dorsal-fin position, deep body, strongly saw-toothed keel along the abdomen, and lack of vomerine teeth. It is readily distinguished from all three species in having the lower jaw projecting strongly beyond the upper when the mouth is closed (vs. lower jaw not projecting beyond upper when mouth closed in these other species). It has much fewer lower gill rakers (18-23 on first gill arch) than American shad (59-76), alewife (38-44), or blueback herring (41-52). Its upper jaw, which reaches posteriorly only to the vertical through the center of its eye, is shorter than that of the American shad (posterior extent of jaw reaching to vertical through posterior margin of eye). Under favorable circumstances, its color (faint dusky longitudinal stripes on sides, and snout tip dusky) is also characteristic and distinctive from these others (sides without dusky longitudinal stripes and snout pigmentation otherwise).

GENERAL BIOLOGY. The hickory shad is a poorly-studied species and more information is needed about this species, both from the perspective of scientific curiosity and also for practical management considerations.

Habitat.--Coastal waters and tidal freshwaters.

Habits.--The hickory shad is a euryhaline, anadromous, species that spends most of its adult life in the sea, entering brackish and freshwaters only to spawn. Little information is known concerning habits of hickory shad while in the sea or during its spawning migration.

Feeding.--The hickory shad is the most piscivorous member of the genus found in the Gulf of Maine. Small fishes, including sand lance, anchovies, cunners, herring, scup, and silversides, together with squid, fish eggs, small crabs, and a variety of pelagic Crustacea, were significant prey items included in diets of fishes examined at Woods Hole, MA (Bigelow and Schroeder 1953; Hildebrand 1963).

Predators.--Little is known about the enemies of this species (Hildebrand 1963), but no doubt they are eaten by larger fish and are caught in limited quantities by man.

Parasites.--Linton (1901) listed a variety of parasites infecting hickory shad, including nematodes, cestodes, and digenetic trematodes. Wilson (1915) recorded the parasitic copepod, *Clavellisa cordata*, from the gills of this species.

General Range.--Coastal waters and rivers of the northwest Atlantic along North America from the Gulf of Maine (perhaps to mouth of Bay of Fundy) southward to St. John's River, FL (Hildebrand 1963). Most abundant in Chesapeake Bay and coastal waters of North Carolina. This is the least abundant and least common member of *Alosa* on the east coast (DesFosse *et al.* 1994).

Occurrence in Gulf of Maine.--The Gulf of Maine is the extreme northern limit of the geographic range of hickory shad. It is more commonly found and more abundant in the southern regions of its range (Virginia and North Carolina). It occurs uncommonly within the Gulf of Maine, and most captures are during autumn. Bigelow and Schroeder (1953), for example, did not directly observe any specimens from the Gulf, though they noted that in 1932, anglers trolling off the Merrimack River caught hickory shad while fishing for striped bass and mackerel. Historical, documented captures of this species compiled by Bigelow and Schroeder (1953) include those from North Truro, Provincetown, Brewster, Boston Harbor, off Portland, and Casco Bay. These authors noted also that possibly this species occurred as far north as the mouth of the Bay of Fundy. Hildebrand (1963) listed this species from Campobello Island, New Brunswick.

The hickory shad is usually more plentiful west of Cape Cod, where it occurs commonly from spring throughout summer and early autumn at Woods Hole. During this time, as many as 3500 were taken at a single lift of one trap. In 1919, the Massachusetts catch of hickory shad, practically all from the south coast, amounted to 5,818 kg, and none were listed for Massachusetts for any subsequent year.

Reproductive Biology

Spawning location and spawning seasonality.--Hickory shad are anadromous (Mansueti 1972a) and ascend coastal streams during spring spawning runs. In Chesapeake Bay, hickory shad spawn in tidal freshwaters during spring, with peaks in early May and spawning continuing through early June (Mansueti 1972a). In Virginia and more southern parts of its range, hickory shad have been found in rivers as early as February and as late as May (Smith 1898; Davis *et al.* 1970). An adult female taken from the York River system on April 12, 1995, was gravid (VIMS, unpublished data). Little is known about specific spawning locations, times, or spawning behavior (DesFosse *et al.* 1994), although there is evidence of spawning in main channels, flooded swamps, and sloughs (Mansueti 1972a; Davis *et al.* 1970; Pate 1972). The spawning period may be relatively long, as inferred from the large variation in size of young fish captured the same day at one locality (Mansueti 1972a; DesFosse *et al.* 1994).

Fecundity.--Fecundity is estimated to be 43,000-348,000 eggs per female (Pate 1972).

Eggs and Development.--Mansueti (1972a) collected and described eggs, larvae, and early young stages of specimens taken in freshwater systems of Chesapeake Bay. Eggs are slightly adhesive and semi-demersal. Other references on hickory shad larvae are those of Mansueti and Hardy (1967), Lippson and Moran (1974), Jones *et al.* (1978), and Wang and Kernehan (1979).

Population Dynamics

Age and Growth.--Little is known concerning growth rates, age structure, or population dynamics of this species. Bigelow and Schroeder (1953) reported that a hickory shad of about 38 cm weighs slightly less than ca. 0.5 kg, while one of 46 cm weighed ca. 0.91 kg. Adult sizes of 28.7-41.4 cm TL are reported for males, and 32.0-45.2 cm TL for females (Mansueti 1972a; Burgess 1980). Most hickory shad mature at 3-5 yr; a small percentage of each sex matures at age-2 (Mansueti 1958; Pate 1972). In spawning runs on the Patuxent River, males were 28.7-41.4 cm TL, females were 32.0-45.2 cm TL (Mansueti 1972a). Average size in Chesapeake Bay populations (Hildebrand and Schroeder 1928) was 38.1 cm TL and 0.45 kg, maximally 45.7 cm TL and 0.9 kg. Growth of juveniles may be more rapid than in other east coast alosids, with total lengths of 14.0-19.0 cm attained by age-1 fish.

Importance and Utilization.--Overall, of minor importance to commercial and recreational fisheries (Whitehead 1985a), but sometimes may be taken in some abundance locally (e.g., North Carolina). Recorded commercial catch for 1983 was only 30.8 MT (Whitehead 1985a). Commonly taken in seine nets, pound nets, and in lesser quantities in gill and fyke nets.

It has become a popular sport fish in recent years (Burgess 1980), and will strike a small spinner or other artificial lure, and is reported to give a good fight when hooked (Bigelow and Schroeder 1953). In some regions, such as those within Chesapeake Bay, the roe of this species is prized above that of other *Alosa* species.

Chapter 15. *Brevoortia* Gill 1861

Menhadens

Thomas A. Munroe and Joseph W. Smith

Description.--Moderately large herring-like fishes (to 50 cm SL, usually 20-30 cm) characterized by a fairly deep and compressed body, with the abdomen fully keeled with scutes. Head large, prominent, especially the gill cover. Mouth large, with upper jaw distinctly notched in midline and with tip of lower jaw fitting into this notch. Jaws in adult menhaden lack teeth. Gillrakers long, fine, and very numerous; gillraker numbers increasing with size of fish. At angle of upper and lower gill arches, gillrakers of upper arch overlapping those on lower arch. With two rows of modified predorsal scales forming ridge on either side of body midline. Dorsal and anal fins moderately long, with anal-fin origin located at, or posterior to, vertical through base of posteriormost dorsal-fin ray. Pelvic fin with i 6 finrays. (Based on Dahlberg 1970; Whitehead 1985a).

Distinctions.--Species of *Brevoortia* are distinguished from all other clupeids by the modified predorsal scales forming a ridge on either side of the body midline; shape of other scales on the body; and presence of a notched upper jaw. Six species are included in *Brevoortia*, but only the Atlantic menhaden, *B. tyrannus*, is known from Gulf of Maine waters (Bigelow and Schroeder 1953; Dahlberg 1970; Whitehead 1985a). *Brevoortia patronus*, the gulf menhaden, from the northern Gulf of Mexico is closely related to *B. tyrannus*, and has been accorded specific status based on differences in meristic features and life-history characteristics (Hildebrand 1948; Dahlberg 1970). However, genetic distinctness of the gulf menhaden is questionable (Avise *et al.* 1989), as analysis of mtDNA genotype frequencies indicated recent gene flow has occurred between populations of Atlantic and gulf menhadens (Bowen and Avise 1990). Atlantic and gulf menhaden populations are apparently disjunct, with a gap on the Atlantic coast of south Florida and the Florida Keys (Dahlberg 1970). However, at the southern ends of their respective ranges, both species hybridize with the yellowfin menhaden, *B. smithi* (Reintjes 1960; Hettler 1968; Dahlberg 1970), providing a possible avenue of gene flow between Atlantic and Gulf forms (Bowen and Avise 1990).

Chapter 16. ATLANTIC MENHADEN *Brevoortia tyrannus* (Latrobe 1802)

Pogy; Mossbunker; Bunker; Fat back

Thomas A. Munroe and Joseph W. Smith

Description.--Body strongly laterally compressed and deep (ca. 3 times as deep as long), deepest at dorsal-fin origin or at region slightly anterior to this point; ventral margin of abdomen with keel of sharp-edged scutes; caudal peduncle slender. Head large, cheeks deeper than long. Mouth large, oblique; maxilla extending to or beyond point equal with vertical through posterior margin of eye; lower jaw projecting slightly and fitting into notch in upper; teeth absent. Snout blunt. Eye small. Fins soft rayed. Dorsal and anal fins moderately long; dorsal-fin origin at point about midway between snout and caudal-fin base. Anal-fin origin at or slightly posterior to vertical through base of posteriormost dorsal-fin ray. Pelvic fins relatively small, abdominal, axillary process present. Pelvic-fin origin at vertical equal with or slightly posterior to dorsal-fin origin. Pectoral fin slightly falcate, axillary process present. Caudal fin deeply forked. Scales adherent, cycloid, exposed field deeper than long, posterior margin serrate or pectinate. Scales on dorsum, above base of anal fin, and those at base of tail much smaller and irregularly placed. Gillrakers very long and numerous, close-set, forming effective basket-like sieve.

Meristics.--Dorsal-fin rays 19-20. Anal-fin rays 20-24. Pelvic-fin rays i 6. Pectoral-fin rays 16-17. Predorsal scales in two rows (ca. 33-39 specialized scales) on either side of body midline; prepelvic scutes 19-21; postpelvic scutes 11-13. Scales in lateral series 40-58 (usually about 45-52). Vertebrae 45-50, usually 47-49. Gillrakers 100-150 on lower limb of first arch. (Bigelow and Schroeder 1953; Whitehead 1985a; Scott and Scott 1988).

Color.--Dark blue, green, blue gray, or blue-brown above, with silvery sides and abdomen, and with strong yellow or brassy luster. Conspicuous dusky or black spot on each side of body immediately posterior to gill cover, followed along sides by varying number of irregularly arranged smaller dark spots forming up to six approximate lines. Fins usually with yellowish cast, caudal sometimes dusky at base and on free margin of fin. Peritoneum black.

Size.--Adult menhaden usually average 20-30 cm FL and 0.25 to about 0.60 kg in weight. Maximum sizes have been reported to 50-51 cm TL (Whitehead 1985a; Scott and Scott 1988), but the longest menhaden on record (Reintjes 1982) is an 8-yr-old fish, measuring 41.8 cm FL and weighing over 1.36 kg.

Distinctions.--The large scaleless head, nearly one-third the total body length, distinguishes the Atlantic menhaden from any other Gulf of Maine fish. This species is easily distinguished from other clupeids occurring in the Gulf of Maine by the two rows of modified predorsal scales (lacking in other species). It is further distinguished from other family members occurring in the region in having posterior scale margins nearly vertical (not rounded), and pectinate (vs. smooth margins in other clupeids). The upper jaw also has a distinct median notch, and is without teeth.

GENERAL BIOLOGY

Recent overviews of biology, ecology, fishery and utilization of menhadens appear in Ahrenholz (1991), Smith (1991), and Waters (1994).

Habitat.--Menhaden inhabit pelagic, euryhaline waters of estuaries and bays, as well as polyhaline coastal waters on the inner continental shelf. Menhaden seldom are far from land and rarely leave continental shelf waters (Hildebrand 1963; Scott and Scott 1988). Along eastern

North America, Atlantic menhaden stratify by age and size, with older and larger fish ranging farther north (Nicholson 1978).

Habits.--Atlantic menhaden are pelagic, marine, schooling fishes, forming large and compact schools, both as juveniles and adults. Schools are comprised of fish of similar size. In calm weather, schools are often detected by distinctive ripple action on the surface, or by frequent "whips" as the dorsum and caudal fin break the surface of the water. They are occasionally seen with their snouts out of water. These behaviors distinguish menhaden from schools of Atlantic herring and mackerel. Menhaden schools can be visually identified also because the brassy hue of the sides of these fishes are often readily visible to the careful observer who approaches the school cautiously.

Atlantic menhaden are temperate, summer and fall seasonal species in the Gulf of Maine. Adults undergo extensive north-south seasonal migrations along the coast and stratify latitudinally by size and age from late spring to early autumn (Nicholson 1971). Locally, adults undergo frequent movements in and out of bays and inlets depending on tides, season, and weather. Patterns of movement into Narragansett Bay, RI, during spring, summer, and fall were thought to be regulated by local availability of food (Durbin 1976). Generally speaking, throughout their range, Atlantic menhaden move north and inshore in summer and at least some of the population moves south and into deeper water during winter. Juvenile (Kroger *et al.* 1971) and adult menhaden leave northern New England waters by autumn when they migrate southward and winter off Virginia and the Carolinas. The following spring, adults again migrate northward into the Chesapeake Bay area and northward into New England waters (Henry 1971). Seasonal movements of Atlantic menhaden were described by June and Reintjes (1960), June and Nicholson (1964), Nicholson (1971), and Dryfoos *et al.* (1973).

Atlantic menhaden inhabit waters varying substantially in salinity from almost freshwater (3.5 ppt) to full strength ocean salinity (Engel *et al.* 1987; Reintjes 1982). Adult Atlantic menhaden are generally found in meso- and polyhaline estuarine and neritic waters, but juveniles in particular, occur throughout most of the larger estuaries along the coast, including low salinity waters of estuarine tributaries. Juvenile menhaden are estuarine dependent and can tolerate sudden salinity shifts (Engel *et al.* 1987). Larval and juvenile menhaden are frequently found in great abundance in shallow, low salinity, estuarine waters. Juveniles remain within these protected waters throughout summer, moving down-estuary into coastal rivers and open bays, and into nearshore oceanic waters as they grow. Hettler (1976) reported that growth of juveniles in lower salinity waters (5-10 ppt) was faster than that of those maintained at higher salinities (28-34 ppt).

Atlantic menhaden are usually found in waters warmer than about 10°C. Bean (1903) reported that Atlantic menhaden cannot survive in water temperatures much below 10°C. Juveniles have been collected in Narragansett Bay, RI, at temperatures as low as 1.2°C (Herman 1963), although condition of juveniles raised in mesocosms in Rhode Island declined noticeably in January when temperatures dropped below the range at which menhaden normally live (Keller *et al.* 1990). Mortalities during winter cold periods have occurred in Canadian waters, particularly in the Kennebecassis River, where menhaden kills triggered by low winter temperatures reportedly occur nearly annually between December and February (Scott and Scott 1988).

Studies on effects of thermal effluents on juvenile Atlantic menhaden concluded that rapid mortality occurs in effluents with temperatures exceeding 33°C (Lewis and Hettler 1968;

Young and Gibson 1973). Relationships between survival time and various temperatures are presented in Hoss *et al.* (1974) and Lewis (1965).

Feeding.--Atlantic menhaden are pelagic, filterfeeding fish. They feed at or close to the primary production level, where they consume large quantities of phytoplankters, particularly diatoms (Peck 1894). As Atlantic menhaden increase in size, there is a gradation, or trend, in feeding repertoire that changes from a predominantly herbivorous to a more omnivorous diet, with wide overlap in diet between size classes (Friedland *et al.* 1984). Menhaden are an adaptable species capable of grazing on planktonic organisms, including several species of benthic diatoms (Edgar and Hoff 1976), copepods, euphausiids, annelid worms, as well as organic detritus (Bigelow and Schroeder 1953; June and Carlson 1971; Jeffries 1975). Few other adult fishes have the ability to feed directly on phytoplankton. Recent evidence suggests that juvenile Atlantic menhaden readily digest cellulose and other vascular plant material, and that detritus of vascular plant origin forms an important component of their diet (Lewis and Peters 1984). Their digestive system is characteristic of herbivores, with a strong, muscular gizzard-like stomach. However, Friedland *et al.* (1989) noted that the distribution of juvenile menhaden appeared to respond to gradients of phytoplankton cells of sufficient size to be filtered by the fish. A chemosensory preference for plant rather than detrital particles and a foraging strategy patterned by the efficiency of their gillraker feeding structure was suggested.

Atlantic menhaden feed by filtering prey items from the water with a straining apparatus in the shape of successive layers of comb-like gillrakers. They feed by swimming with mouth agape, filtering out the entrapped organisms with the uniquely efficient, feathery gillrakers. No other Gulf of Maine fish has a filtering apparatus comparable to that of the Atlantic menhaden, nor has this species any rival in the Gulf in its utilization of the phytoplanktonic assemblage. Menhaden feed by swimming with their mouth open and gill openings spread. Bigelow and Schroeder (1953) watched small fish in Chesapeake Bay swimming downward as they fed, then turning upward to break the surface with their snouts, still with open mouths. The mouth and pharyngeal sieve act exactly as a tow net, retaining whatever is large enough to enmesh, with no voluntary selection of particular plankton units. The menhaden, parallels baleen whales, the basking shark, and giant manta rays in its mode of feeding, except that its diet consists of smaller organisms because its filter-feeding apparatus is closer meshed.

Atlantic menhaden capture food particles by mechanically sieving food items through their branchial basket as opposed to aerosol entrapment mechanisms; that is, structures that are sticky or mucous covered (Friedland 1985). Food particles are retained at various positions on the gillrakers, then transported to the base of the raker blade before being passed farther back in the buccal cavity for ingestion. Particles larger than the spaces between raker blades tumble along the leading edges of the rakers to the base. Particles smaller than the spaces between blades, but nonetheless filterable, may be transported by a different mechanism. Sites of small particle capture are the branchiospinules, which lack mucous cells, suggesting that food is captured primarily by a mechanical sieving at these sites. Gill arch sections where most filtration takes place have a cutaneous fold over the mesial raker elements. Epithelium on the lateral surface of this cutaneous fold is rich in mucous cells. Positioning of this surface relative to the base of the filtering rakers suggests that particles coming off the raker blades are held in dynamic balance and are transported back into the buccal cavity over, or complexed with, a mucous layer, and then ingested.

Taste buds are located on the tongue and in the fifth branchial arch. Taste seems to be a two-stage process (Friedland 1985). Both food and non-food particles incite gulping and in turn initiate feeding. It is possible that taste buds on the tongue are mechanoreceptors and responsible for initial detection of potential food items. If particles ingested are useable food, then feeding continues; conversely, if particles are not useable, feeding stops. Friedland noted that taste buds located on the gill arch are chemosensory in nature. He hypothesized that information processed by tastebuds enabled fish to determine if ingested particles were food and whether feeding proceeded.

Peck (1894) calculated that an adult menhaden was capable of filtering about 24-28 l of water per minute, while McHugh's (1967) estimate was slightly lower (15.2 l/min). While fish do not feed continuously, this estimate provides some measure of the tremendous amount of water sieved for plankton. Assuming a steady filtering rate over a 6-mo period, an individual fish could filter plankton from more than 3.9 million liters of water in ca. 180 d.

While historically Atlantic menhaden were thought to feed primarily on phytoplankton (Peck 1894; Darnell 1958; June and Carlson 1971), questions have been raised recently as to whether zooplankton, bacteria, and detritus are also important foods (Friedland *et al.* 1984). A widely held conception was that menhaden were unable to filter small phytoplankton and depended mostly on large phytoplankton and zooplankton (Durbin and Durbin 1975, 1981; Durbin *et al.* 1981; Blaxter and Hunter 1982). This view was supported by analyses of stomach contents in which zooplankton was reported as the primary constituent (Richards 1963; Jeffries 1975). Bacteria had been suggested as a potential food resource based on anatomical considerations (Reintjes and Pacheco 1966) and analyses that found anomalously high nitrogen concentrations in stomach contents (Peters and Kjelson 1975). It has been suggested that detritus is an important energy source for menhadens in allochthonous systems (Peters and Schaaf 1981; Lewis and Peters 1984; Deegan *et al.* 1990).

In laboratory studies, minimum particle sizes that adult menhaden (25.7 cm FL) could filter were 13-16 µm, and filtering efficiencies increased with size of food particles (Durbin and Durbin 1975). In the absence of detritus, minimum particle sizes filtered by menhaden (138 mm FL) were between 7 and 9 µm (Friedland *et al.* 1984). Filtration efficiencies also increased with increasing size of prey particles. For example, the dinoflagellate, *Prorocentrum minimum*, was filtered at an average of 16.5% for the 12 µm morph, while an average of 41.5% were filtered for the 17 µm morph.

Detritus in combination with phytoplankton prey resulted in capture of prey particles below the minimum size threshold and enhanced filtration efficiencies of prey particles above the threshold. However, effects of detritus on filtering efficiency were not consistent among various algae tested. For some species, filtering efficiency with detritus present increased, but for others it was slightly lower or unchanged (Friedland *et al.* 1984). Small prey particles (< 25 µm) had enhanced filtration efficiencies at slower swimming speeds, but differences in efficiency for large particles due to swimming speed were indistinguishable. Presence of detritus, probably the rule in nature rather than the exception, should enable grazing fish to retain smaller particles more efficiently than could be retained in clear water, and should enhance their ability to retain larger particles. Friedland *et al.* (1984) showed that 4-µm flagellates, not filtered in the absence of detritus, can be filtered at 10% efficiency if they are part of a natural assemblage containing detritus. These authors inferred that, conceptually, submicron particles, such as bacteria, can also be filtered (retainment efficiencies estimated at ca. 4%).

The smaller minimum size threshold and more rapid increase in filtration efficiency with increased prey size for small menhaden (138 mm FL) suggest differences in functional morphology of the menhaden feeding apparatus as fish increase in size. Perhaps spacing of the branchiospinules is more important than number and size of gillrakers, since it is their spacing that probably determines filtering efficiency (Magnuson and Heitz 1971). The rate of increase in filtering efficiency as prey size increased was greater for smaller menhaden than for larger menhaden, suggesting that raker gaps in juveniles are in a narrower size range. As prey size increases, proportionally more rakers of a smaller fish would be capable of filtering prey. Maximum filtration efficiencies should correspond to prey sizes exceeding most of the raker gap dimensions. The maximum occurs at prey sizes of ca. 100 µm for 138-mm FL menhaden, whereas for larger menhaden, this maximum occurs at a prey size of ca. 200 µm (Durbin and Durbin 1975).

Predators.--The oil-laden menhaden, swimming in schools of closely-ranked individuals, is prey for nearly every piscivorous fish, marine mammal and seabird in the Gulf of Maine. Whales and porpoises devour them in large numbers, and sharks are often seen following schools of Atlantic menhaden. Bluefish, striped bass, bluefin tuna (Crane 1936), and sharks (Medved *et al.* 1985) are primary fishes that prey upon Atlantic menhaden. In Chincoteague Bay, VA (Medved *et al.* 1985), menhaden were found in 13% of stomachs, and represented the second most abundant prey of 40-80 cm FL sandbar sharks (*Carcharhinus plumbeus*). Pollock, cod, silver hake, and swordfish also feed on menhaden in the Gulf of Maine, as do weakfish south of Cape Cod. Tuna allegedly consume great numbers of this species. Bluefish prey heavily on menhaden throughout their range (Grant 1962; Friedland *et al.* 1988), including the Gulf of Maine when both species are abundant there. Menhaden are also important in the diets of seabirds, herons, egrets, ospreys and eagles (Hildebrand 1963).

Yolk-sac and first-feeding larvae of Atlantic menhaden are prey to a variety of predators including adults of the comparatively large-sized copepod *Anomalocera ornata* (Turner *et al.* 1985). Yolk-sac larvae were also consumed by the smaller copepod (*Centropages typicus*), but this crustacean was unable to feed upon larger, and more active, first-feeding larvae.

Parasites.--Menhaden are host to, and play an important role in life cycles of, a variety of parasites including protozoans (Hardcastle 1944), monogenetic (McMahon 1963) and digenetic (Linton 1905) trematodes, nematodes, cestodes, copepods (Wilson 1932), and isopods (Kroger and Guthrie 1972). Westman and Nigrelli (1955) provided a list of 13 species of parasites and Reintjes (1969) listed five more, for menhaden occurring in United States waters. Guthrie and Schwartz (1990) reported the rare occurrence of a barnacle (*Balanus venustus*) on a juvenile menhaden taken off South Carolina. During winter in Chesapeake Bay, newly-metamorphosed sea lampreys also parasitize Atlantic menhaden (Mansueti 1962b).

Mass Mortalities.--Mass mortalities of menhaden have been reported in many parts of the species range along the coastal United States, usually associated with oxygen depletion in semi-enclosed, shallow-water habitats (small coves and heads of tidal creeks) during late summer. Menhaden often strand in myriads in shoal water, either in their attempt to escape their enemies or for other reasons. The teeming numbers of fish milling about in warm shallow waters may literally exhaust the dissolved oxygen, resulting in deaths of hundreds to thousands of fish (Reintjes and Pacheco 1966). Algal blooms and bacterial respiration associated with active or decaying plankton probably contribute to dissolved oxygen depletion and mass mortalities of menhaden. Dissolved oxygen tolerance studies indicated that significant mortalities occurred at a concentration of 1.1 mg/l dissolved oxygen when menhaden were acclimated at 28°C (Burton *et al.* 1980).

In more southern regions, annual menhaden kills or die-offs are well documented (Westman and Nigrelli 1955; Stephens *et al.* 1980; Ahrenholz *et al.* 1987a). During spring, investigators noted mass mortalities of menhaden that apparently had "spinning disease," named for the erratic swimming behavior and disorientation of the infected fish. The causative agent of this disease remained unknown until Stephens *et al.* (1980) isolated a virus from brain and pancreatic tissue of afflicted menhaden.

Noga and Dykstra (1986) noted that in spring 1984, menhaden in the Pamlico Sound area of North Carolina began to display deep, penetrating ulcers on their flanks and near the anus. As the year progressed, an increasing number of fish became affected, until a massive die-off occurred in November. The necrotic ulcers of the diseased menhaden were infected with oomycetes of the fungi genera *Saprolegnia* and *Aphanomyces*. They believed that these fungi were not the primary cause of the disease, however, but only secondary to some other stressor.

The ulcerative syndrome is a regional problem in the U.S., being observed on fish from Delaware to Florida (Hargis 1985; Levine *et al.* 1990). Ulcerative mycosis can be a serious disease of menhaden in the southeastern coastal United States, and at times 100% of the fish collected in trawls are infected with this pathogen (Dykstra *et al.* 1989). Several potentially different (and taxonomically uncertain) species of fungi (*Aphanomyces* and *Saprolegnia*) have been isolated from infected menhaden. These genera are normally associated with freshwater environments and it is uncertain what predisposes menhaden to infection by these fungi. High precipitation levels and subsequent increased run-offs, with its associated low salinities, suspended organic and inorganic materials, and sediment and detritus loads were suggested as possible causative agents altering responses of menhaden to infection with the fungus (Dykstra *et al.* 1989). Shafer *et al.* (1990) found that the suspected fungal pathogen (*Saprolegnia* sp.) recovered from menhaden was more salt tolerant than previously believed, suggesting that the fungus could be pathogenic in menhaden, at least under mesohaline conditions.

Recently, an insidious dinoflagellate was identified by Burkholder *et al.* (1992) as the responsible agent for major kills of Atlantic menhaden (also affecting striped bass, flounder, sciaenids and eels) in the Pamlico Sound system of North Carolina. The so-called "phantom" alga, *Pfiesteria piscida*, requires live finfish excreta for excystment from the bottom sediments and release of its potent exotoxin. Even low algal cell densities cause neurotoxic signs in fish and eventual death. Within hours of the fish's death, the vegetative form of the alga encysts and returns to the sediments. Burkholder *et al.* suggested that this toxic phytoplankter may be an undetected source of fish moralities in nutrient-enriched estuaries.

Another source of mass mortalities of Atlantic menhaden occurs in the vicinity of effluent water from electric generating power plants, where water supersaturated with dissolved gases adversely affects finfishes causing "gas bubble disease." Mass mortalities, involving an estimated 5,000 to 43,000 menhaden were recorded near the Pilgrim Nuclear Power Station in western Cape Cod Bay (Bridges and Anderson 1984).

General Range.--Atlantic menhaden occur in coastal waters along the Atlantic coast of North America from the Gulf of St. Lawrence and Nova Scotia to Indian River, FL. Occurrence of menhaden in Canadian waters is mostly sporadic and unpredictable. Specimens have been taken in the St. John River, NB, as far as 24 km upstream from the mouth (Scott and Scott 1988) and in the Kennebecassis River, a tributary of the lower St. John River (Scott and Scott 1988). In Canadian waters, menhaden sometimes occur in fair numbers. Over 100 were caught in weirs off

Deer Island, Passamaquoddy Bay, NB, in October 1960 (Leim and Scott 1966), and hundreds were caught in Passamaquoddy Bay by weirs and otter trawl in August 1983. Many have been captured from the Gulf of St. Lawrence, off Nova Scotia (off Halifax County in May and June 1970), and in the Bay of Fundy. In the Canadian region, they occur in relatively enclosed or restricted areas such as St. Margarets Bay, NS, and in inland tidal waters such as the Kennebecassis River, NB (Scott and Scott 1988).

Occurrence in Gulf of Maine.--The Atlantic menhaden is a summer seasonal species in the Gulf of Maine, and the Gulf is the northerly limit for commercial quantities of menhaden. Since menhaden tend to stratify along the East Coast of the U.S. by size and age, it is generally accepted that fish taken on the New England coast are larger and fatter than those caught farther south. In years of peak abundance, menhaden occur throughout nearshore waters of the Gulf from Cape Cod to Penobscot Bay and the Mount Desert Isle region. Their chief centers of abundance lie in Massachusetts Bay within 1-2 km or so of land, particularly off Barnstable and in the mouths of Boston and Salem Harbors, in Casco Bay, and among the islands, and northward to Penobscot Bay. Bigelow and Schroeder (1953) noted that in some years menhaden congregated as much as 64-80 km offshore, as happened in 1878, for instance, but generally there are no reports of menhaden from the central part of the Gulf, or from the offshore Banks.

Perhaps, the most interesting aspect of menhaden occurrence in the Gulf of Maine is the tremendous interannual fluctuations in abundance that may be related to variations in water temperatures and fluctuations in year-class strength, as well as other factors. In their account of historical cycles of menhaden abundance in the Gulf of Maine, Bigelow and Schroeder (1953) noted that there were periods of great abundance followed by times when this species was scarce or entirely absent from Gulf of Maine waters. For example, after being absent from the Gulf of Maine for several years, menhaden were plentiful in Maine waters in 1889 (when more than 4.5 million kg were caught). In 1890, they were so numerous that four fertilizer factories were established, and nearly 90 million fish were taken during that season. This period of plenitude was short-lived as less than one-half as many fish were caught in Maine waters (ca. 41 million) in 1891, while few menhaden were taken or seen north of Cape Cod in 1892. Several additional periods of alternating abundance and scarcity for menhaden in Gulf of Maine waters have also occurred and were discussed by Bigelow and Schroeder (1953).

Seasonal Occurrence in the Gulf of Maine.--Seasonal appearance and disappearance of menhaden into and out of the Gulf of Maine in spring and fall, respectively, is a result of migration around Cape Cod and is a well-documented annual event. In years when menhaden are present in the Gulf of Maine, they usually appear in Massachusetts Bay about mid-May; off the Maine coast during the last half of May or first part of June; and usually reach peak abundance between July to early September. Most depart coastal areas of Maine by late September and leave the Massachusetts Bay region by early November. It is unusual to find menhaden along these shores after the middle of November, although juveniles have been taken in the Sheepscot River in early December.

Menhaden are temperate fish, and studies in the Gulf of Maine corroborate earlier observations that menhaden usually do not appear in spring until coastal waters have warmed to 10°C or more, or in abundance until temperatures are several degrees higher (Bigelow and Schroeder 1953). In response to falling temperatures during autumn, menhaden leave coastal regions of northern New England. They may persist later into fall in the southern Gulf of Maine, as Lawton *et al.* (1984) reported catching menhaden (85-349 mm FL) in western Cape Cod Bay from March to December.

Reproductive Biology

General Description.--Atlantic menhaden are prolific spawners that usually reach first maturity as late age-2 fish (Lewis *et al.* 1987). Their reproductive life span may reach 6-7 yr (Higham and Nicholson 1964). Menhaden are probably determinate, multiple spawners that spawn over a broad geographical and temporal range (Lewis *et al.* 1987). Atlantic menhaden probably spawn during every month of the year, although not in all areas at the same time (Lewis *et al.* 1987). North of Long Island, NY, sexually active fish have been collected from May to October, except for July (Lewis *et al.* 1987). During November and December, most menhaden of spawning age occur off Virginia and North Carolina (Nicholson 1971). In late spring, fish from Virginia and the Carolinas move north where they distribute in nearshore localities from Chesapeake Bay to Maine, with the older and larger fish moving farther north.

Eggs, which are spawned in the open ocean, and larvae depend on Ekman transport and ocean and tidal currents for transport into the estuaries (see below) (Nicholson 1972; Nelson *et al.* 1977). Within the estuaries, larvae metamorphose into juveniles. Juveniles spend up to their first full year in the estuaries after which they tend to join the coastal migratory population of the adults.

Spawning Location.--Sexually ripe individuals appear to occur during all months, but at different locales (Nicholson 1972). Spawning occurs over open shelf ocean waters, as well as near major sounds and bays from Long Island northward (Reintjes and Pacheco 1966; Ferraro 1981a, 1981b; Judy and Lewis 1983; Ahrenholz *et al.* 1987b; Ahrenholz 1991). It has been suggested that spawning over a wide range of environmental conditions throughout the year minimizes reproductive failure, since the effects of extreme environmental conditions in one place or time will be dampened by less-extreme environmental conditions in others (Den Boer 1968; Powell 1993).

In the southern Gulf of Maine, menhaden eggs were found throughout Cape Cod Bay during the spawning season (Scherer 1984), but were particularly abundant in the southeast section of the Bay where densities of over 1000 eggs per 100 m^3 of water were occasionally recorded. On a seasonal basis, menhaden larvae can also constitute a significant fraction of the ichthyoplankton occurring in the southern Gulf of Maine, where in Cape Cod Bay, for example, this species ranked 14th in abundance of the 35 categories of larvae taken during one study (Scherer 1984).

Spawning Seasonality.--Menhaden eggs can occur somewhere off the east coast of the United States during almost every month of the year (Judy and Lewis 1983). Spawning probably occurs in every month, but not in all areas at the same time (Lewis *et al.* 1987). Generally, the seasonal distribution of eggs and larvae corresponds with seasonal distribution of adults (Kendall and Reintjes 1975; Higham and Nicholson 1964; Judy and Lewis 1983).

In the south half of their range, the spawning seasonality of menhaden extends from about November to March (Judy and Lewis 1983). At this time, most spawning-age fish are concentrated off the Virginia and North Carolina capes. It is most likely that during this period and in this region that the maximum numbers of menhaden spawn. Apparently, little contribution to the overall stock is made from spawning taking place in areas north of the northern New Jersey-Long Island region. The majority of new recruits are probably produced in the estuaries of the Carolinas, Virginia, and north to New Jersey.

In the South Atlantic Bight, larvae have been collected in abundance between 20 and 75 km offshore. As fish move north in late March, spawning continues, but at a decreasing rate. By May, most spawning is restricted to coastal areas in the northern half of the species range. By about June to July, when fish are stratified by age and size along the coast, spawning falls to a minimum.

In the Gulf of Maine, menhaden probably spawn during July and August. In southeastern Cape Cod Bay, menhaden spawn from about May to early October (Scherer 1984), while in Narragansett Bay, RI, menhaden may spawn as early as April (Oviatt 1977). Larvae are present in southern Cape Cod Bay from May-December (Scherer 1984), and have been reported from several other areas north of Martha's Vineyard (Marak and Colton 1961). There is a paucity of information on menhaden spawning in Canadian waters (Scott and Scott 1988), but ripe males and females were taken in the St. John River as late as August 24, suggesting that some spawning occurs in this vicinity. As large numbers of menhaden again begin to mature sexually in October, spawning increases in ocean waters from about Long Island to Virginia as the population migrates south along the coast.

Spawning Temperatures and Salinities.--Broad seasonal and geographic occurrences of eggs and larvae indicate that spawning probably takes place over a wide range of temperature (Judy and Lewis 1983). A seasonal progression of larval occurrence coincides with adult seasonal movements north and south along the coast. Spawning may be limited by high water temperatures (20.5°C monthly mean maximum). In Peconic Bays, NY, spawning took place at water temperatures ranging from 12.1° to 25.0°C and salinities from 20.0 to 30.0 ppt, but spawning was most intense at water temperatures between 15° and 18°C (Ferraro 1981a, 1981b). Hettler (1981) reported on experimental conditions for artificial spawning and rearing of larvae in captivity.

Fecundity.--Fecundity is related to the size of female menhaden (Higham and Nicholson 1964; Dietrich 1979; Lewis *et al.* 1987), although there is high intra- and inter-year variability in the relationship between length and potential number of ova produced. Fecundity estimates range into the hundreds of thousands of ova per female. Minimum size (FL) at sexual maturity is about 180 mm (Lewis *et al.* 1987). Few age-1 fish were mature, but most late age-2 (just prior to turning age-3) females were mature. On average, fecundity estimates range from ca. 48,000 ova for a 180-mm FL female to over 500,000 ova for females of ca. 360-mm FL. A maximum value of about 6.3×10^5 ova per female was calculated.

Eggs.--Eggs of Atlantic menhaden are buoyant, spherical, and highly transparent. They usually occur in the upper water column to depths of 10 m (Reintjes 1969; Judy and Lewis 1983). They are easily distinguished from eggs of any other Gulf of Maine fish by their large size (1.3-1.9 mm in diameter), broad perivitelline space, small oil globule (0.15-0.17 mm), and very long embryo. Menhaden eggs tend to be larger at higher latitudes (Powell 1993), but there is considerable variation in egg size at any given latitude, and egg size is positively correlated with female size. Incubation is rapid with hatching usually occurring in less than 48 hrs at 15-20°C (Jones *et al.* 1978), and at 66 hrs at 15°C (Hettler 1981).

Estimated rates of daily and total mortality during embryogenesis for menhaden spawned in Peconic Bays, NY, ranged from 3.4 to 94.6%, and 11.1 to 99.8%, respectively (Ferraro 1981a). Embryo mortality was generally lowest early in the spawning season. Survivorship curves through the early post-larval stage ranged between a minimum survivorship of 0.01 to 0.04% for the first 13 d of embryonic and larval life.

Development.--Embryology of Atlantic menhaden was described by Ferraro (1980), who noted temperature and salinity effects on rate of embryonic development of eggs artificially fertilized from one female. Hettler (1981) successfully spawned and reared larvae to the juvenile stage. Larvae are 2.4-4.5 mm SL on hatching, and grow to 5.7 mm in 4 d after hatching (Bigelow and Schroeder 1953; Fahay 1983; Powell 1993). Estimates of yolk utilization, yolk and oil volumes, and growth rates during development were provided by Powell (1993) for Atlantic menhaden reared under laboratory conditions.

Dorsal and caudal fins first become visible at a length of 9 mm; at 23 mm all fins are well developed; scales are present at 33 mm; metamorphosis commences at about 35 mm; and at 41 mm fry have most characters of the adult, except their eyes are proportionately much larger.

The development of sensory systems in menhaden larvae were described by Hoss and Blaxter (1982). At hatching, larvae have unpigmented eyes. In early stages, the larva possesses a row of 8-11 prominent neuromast organs on either side of the body that become less obvious at 12 mm. The anlage of the swimbladder is present at 10 mm and the pro-otic bullae first appear at 12.5 mm. At this stage the bullae are covered dorsally by a melanophore cap and in some precocious fish the bullae may contain gas bubbles. Pterotic bullae develop at about 30 mm. The swimbladder first contains bubbles of gas at a body length of 13 mm. The lateral line first appears in the region of the lateral recess at a body length of about 17 mm. The lateral recess membrane is functional at 18 mm. Three neuromast organs can be identified within the lateral line on each side by 26 mm; by 32 mm the secondary canal system starts to develop.

The youngest menhaden larvae resemble those of Atlantic herring, but in menhaden the fins are formed, the tail becomes forked, and the body deepens at a much smaller size than it does in Atlantic herring. A menhaden of 20 mm is as far advanced in development as is a larval herring of 35 mm, which makes it easy to distinguish the older larvae of these two clupeids.

Larval Ecology and Behavior.--Larval Atlantic menhaden are pelagic and those spawned offshore may spend up to several months in continental shelf waters before being transported to estuaries at lengths of 10-22 mm (Massmann *et al.* 1962; Nelson *et al.* 1977). In the ocean, larvae appear to be most concentrated in the upper water column (Kendall and Reintjes 1975; Nelson *et al.* 1977; Judy and Lewis 1983). With movement inshore, larval menhaden are found closer to the bottom (Kjelson *et al.* 1976). Larval menhaden are transported and move into lower salinity waters in estuarine tributaries. Here they are found in great abundance, and they metamorphose into juveniles, usually at a length of about 34 mm (McHugh 1967; Wilkens and Lewis 1971). Metamorphosis apparently occurs only in the estuary, since no metamorphic larvae or prejuveniles have been collected at sea (Kendall and Reintjes 1975).

Recruitment success of estuarine-dependent fishes such as Atlantic menhaden is believed to depend heavily on transport to nearshore areas by water currents (Nelson *et al.* 1977; Maillet and Checkley 1991). Checkley *et al.* (1988) suggested that Atlantic menhaden has evolved to reproduce under physical conditions optimal for the survival and shoreward transport of its eggs and larvae.

Spawning occurs during winter on the continental shelf south of Cape Hatteras (Judy and Lewis 1983; Checkley *et al.* 1988) and is thought to be maximal during storms in water upwelled near the western edge of the Gulf Stream (Govoni 1993). From offshore areas, eggs and larvae of Atlantic menhaden drift shoreward along with abundant food items in the warm surface stratum of a density-driven circulation maintained by large sea-air heat flux (Checkley *et al.* 1988). Rapid development due to warm temperature and abundant food in the surface stratum shortens the exposure of eggs and larvae to predators and thereby enhances their survival. Thus, this circulation brings menhaden larvae to within ca. 20 km of shore on average and at times much closer. Subsequent movement of menhaden larvae to and through the inlets is believed to result from their vertical movement combined with nearshore and estuarine circulations (Wilkens and Lewis 1971).

Field data from off the North Carolina coast show that menhaden larvae are associated with specific water masses (Govoni and Pietrafesa 1994). Larvae may use such clues as T-S gradients associated with the mid-depth pycnocline or surface layers to avoid offshore-flowing waters. Larval menhaden are considered to have sustainable swimming speeds (1-2 body lengths/s, which roughly equals ca. 0.5-3.0 cm/s) insignificant for transport to nurseries especially as young larvae. De Vries *et al.* (1995a, 1995b) studied behavioral responses of larval Atlantic menhaden to salinity and temperature changes. In the laboratory, larval menhaden undergo an ascent response when exposed to salinity increases. This was corroborated in the field, where larvae would typically experience an increase in salinity upon descent in the water column, which would then cause them to swim upwards. Gradients of decreasing salinity were not found to function as cues affecting larval swimming behavior and vertical distribution (De Vries *et al.* 1995a). Utilizing salinity gradients could maximize larval residence in onshore-flowing water, and minimize transit time across the continental shelf.

In another study (De Vries *et al.* 1995b), laboratory-reared larval menhaden of two different ages were exposed to varying relative rates of temperature increases and decreases, which were presented from both above and below the larvae. Temperature decreases from below caused an ascent response in both age groups, but neither responded to this cue from above. Minimum absolute decreases of 0.1 °C and 0.05 °C must occur before a response occurred for each age group, respectively. Young larvae did not respond to temperature increase, while older larvae ascended regardless of whether the increase was presented from above or below. The authors concluded that, on the continental shelf, detectable temperature gradients appear common, both for temperature decreases that would occur upon descending, and also for temperature increases that would occur upon ascending. However, it is uncommon for larvae to encounter temperature increases upon descending that initiate an ascent response. These results support the hypothesis that larvae are capable of using temperature gradients for depth regulation.

Atlantic menhaden larvae >12 mm SL apparently make vertical migrations to the surface to replenish gas in the swimbladder (Hoss *et al.* 1989). Furthermore, this behavior may also be important in relation to the transport mechanisms that move menhaden from offshore spawning grounds towards estuarine nurseries. Larval menhaden inflate and deflate the swimbladder on a diurnal cycle that appears to be a light-dark function and not endogenous, because it is disrupted in constant light and can be initiated during daylight by darkening. Laboratory experiments show that menhaden larvae rise to the surface at sunset to fill their swimbladders with air (Hoss *et al.* 1989; Forward *et al.* 1993). Inflation occurs rapidly and begins within 5 minutes of onset of darkness. This behavior is believed to increase buoyancy of the larvae at night, allowing them to expend less energy staying in the mid- to upper water column (Hoss *et al.* 1989; Forward *et al.* 1993). At sunrise, air is expelled from the swimbladder, allowing larvae more swimming agility and maintenance of deeper position in the water column. Deflation is less well studied, but appears to be cued by an increase in light intensity (Forward *et al.* 1994). Results of day and night field sampling (Govoni and Pietrafesa 1994) support this observation. Since larvae are relatively transparent, the difference in refractive index between air and water increases the contrast between an inflated swimbladder and the surrounding water. This increase in visibility could lead to increased detection by predators (Forward *et al.* 1994). It has been suggested (Forward *et al.* 1994), therefore, that deflation of the swimbladder at sunrise may be a predator avoidance response.

Transport of larval Atlantic menhaden across the southeastern continental shelf to bays and estuaries is undoubtedly dependent on numerous physical and biological conditions (De Vries *et al.* 1995a, 1995b). Selective pressures to obtain sufficient food, escape predation, and remain in water warm enough for survival combine with those for enhanced shoreward transport to affect that portion of larval depth distribution under behavioral control. For menhaden larvae, salinity and temperature gradients may be cues for electing depth-selective behavior (De Vries *et al.* 1995a, 1995b).

Atlantic menhaden larvae begin feeding on zooplankton about 2-4 d post-hatching (Reintjes 1982; Powell 1993), depending on water temperatures during development. They are size-selective plankton feeders. Although there is no direct evidence of the food they ingest before entering the estuary, it is quite possible that they feed on pteropods and bivalve larval stages, as well as crustacean nauplii which are food sources for other members of the herring family.

Instantaneous growth rates of 0.043 mm/d have been recorded for larvae at 20°C for 21 d with abundant food supply (Powell and Phonlor 1986). In experimental situations (Powell 1993), growth rates at 16°C (0.27 mm/d) are lower than for those at 20°C (0.047 mm/d) and 24°C (0.049 mm/d). Size at first feeding is about 4.8 mm SL (Powell 1993).

Juvenile Biology.--As postlarval menhaden metamorphose into prejuveniles (ca. 30 mm) they develop a functional branchial filtering apparatus, which enhances their ability to graze on phytoplankton and suspended detritus. Late-stage juveniles and adults are primarily herbivores, but they also retain the ability to feed on zooplankton (Edgar and Hoff 1976).

Growth of juvenile menhaden is relatively rapid, but variable depending on a variety of factors, including time of hatching and length of growing season (function of latitude). Growth of juveniles in lower salinity waters (5-10 ppt) was faster than that demonstrated (Hettler 1976) for juveniles maintained at higher salinities (28-34 ppt). For juvenile menhaden raised in mesocosms in Rhode Island, estimated rates of daily growth ranged from 0.85-1.10 mm/d (Keller *et al.* 1990). Reintjes (1969) also reported increases in mean length of juveniles of about 1 mm/d over intervals of 2-3 d. Ahrenholz *et al.* (1995) used known-age fish to provide continuous validation from first feeding through metamorphosis, to juveniles up to 9-mo old. On average, larval and juvenile Atlantic menhaden form one growth increment/d on their sagittal otoliths. Juvenile menhaden up to 200 d old were reliably aged within a confidence interval of 7 d and up to 250 d old within a confidence interval of about 16 d. One experimental group displayed growth rates (0.67-0.95 mm/d) similar to the higher rates observed for juveniles captured from estuarine nursery areas. Menhaden hatched in summer are 6-8 cm long by their first winter, and average about 16 cm by their second winter; fall-hatched fish are 3 cm and about 13 cm long, in their first and second winters, respectively, with every gradation in size between these depending on the precise season when the fish were spawned (Ahrenholz 1991).

Juvenile menhaden are obligate schoolers, sometimes forming schools of large dimensions. Young fish remain in bays and estuaries in the Gulf of Maine throughout summer. In fall, most migrate from these tributaries and bays into the ocean, where they generally undergo a migration to deeper or warmer waters.

POPULATION DYNAMICS

Age and Growth.--Atlantic menhaden, which can normally live to be 8 yr old, are relatively fast growing until at least age-4, at which time growth slows (Henry 1971). During the 1950s and 1960s, Reintjes (1969) noted that of over 100,000 fish examined, fish 8-10 yr old were uncommon and only one 12-yr-old was noted. Cooper (1965) recorded an exceptionally large menhaden (age-8+) taken in a fish trap off Rhode Island, July 7, 1961, weighing 1674 g and measuring 47.0 cm TL. June and Roithmayr (1960) list the following age-size relationships for menhaden (age in yr; size in mm FL): age-1= 135 mm; age-2= 215 mm; age-3=250 mm; age-4=270 mm; ages 5-7=300-350 mm.

Growth rates of Atlantic menhaden vary in different fishing areas as well as from year to year (Reish *et al.* 1985). Fish caught in the North Atlantic are not only older, but also larger for a given age than fish caught in the South Atlantic (Nicholson 1971). During summer, menhaden stratify by age along the coast, with younger fish occurring in the more southern part of the range and older fish predominating in the north. Nicholson (1971) concluded that age-1 menhaden were most abundant from Chesapeake Bay to New Jersey; age-2 from New Jersey to the south shore of Long Island; age-3 from Long Island sound to Nantucket Sound; and age-4+ from Nantucket Sound to Maine. Fish taken by purse seiners in Narragansett Bay, RI (Durbin *et al.* 1983), were predominantly age-2 and age-3. In all age groups represented, the fish from Narragansett Bay were significantly smaller than fish caught from Long Island Sound to the Gulf of Maine during 1955-71. There is no information on growth rates in the Canadian Atlantic area (Scott and Scott 1988). Average size of individuals within each age group also increased with latitude, especially with age-1 and age-2 fish. This size stratification was much less pronounced for age-3 and older menhaden.

Atlantic menhaden are sexually mature at age-2, with all fish being mature by age-3 (Lewis *et al.* 1987). Individuals of a given age class tend to be larger toward the northern half of their range, although they are sexually mature at smaller sizes in more southern areas (Reintjes *et al.* 1979). The minimum FL of potential spawners was 230 mm in the North and Middle Atlantic regions, and 210 mm in the Chesapeake Bay and South Atlantic regions.

The age structure of Atlantic menhaden on the east coast of the U.S., as indicated by changes in age composition of the fishes taken by the commercial fishery, has been dramatically altered by fishing activities and recruitment patterns. Prior to 1966, age-4 and older menhaden contributed significantly in numbers and biomass to the North Atlantic catch (Nicholson 1975). During the 1960s, the stock structure became truncated and fish older than age-3 were uncommon. Older fish virtually disappeared from the Gulf of Maine. The stock rebuilt during the 1970s to where commercial quantities of the older age groups were again available in the Gulf of Maine by the late 1970s to mid-1980s.

On a seasonal basis, growth of individual menhaden has been described as rapid in spring and summer, with a decrease in fall and winter (June and Roithmayr 1960). Durbin *et al.* (1983) also indicated significant variation in menhaden growth rates in Narragansett Bay, RI, perhaps in relation to varying temperature and food conditions. In a mesocosm study, Keller *et al.* (1990) demonstrated differences in growth rates of Atlantic menhaden possibly attributable to food availability. Durbin and Durbin (1983) predicted a linear relation between plankton concentration and growth of adult Atlantic menhaden, but expected that growth rate would approach an asymptote with further increases in ration size. Their studies demonstrated that menhaden regulate their swimming speeds according to the abundance of plankton in the water. They concluded that the swimming speed of menhaden has evolved towards maximizing growth rate rather than growth efficiency. In most circumstances, the growth efficiency for calories and nitrogen were significantly different. Observed swimming speeds in menhaden resulted in higher growth efficiency for nitrogen at low plankton abundance, but higher efficiency for calories at moderate to high plankton abundance. This accounts for the seasonal increase in fat content of menhaden during summer, yet indicates that protein will be conserved when food abundance is low.

Mortality.--Dryfoos *et al.* (1973) reported estimates of natural mortality (M) of 0.52, while Ahrenholz *et al.* (1987) used a value of 0.45. Reish *et al.* (1985) estimated average monthly fishing mortality rates of 0.18 and 0.09 for age-2 fish during summer and fall, respectively. Predators, parasites and disease, fishing pressure, and fluctuating environmental conditions are thought to be the most important factors contributing to mortality in Atlantic menhaden (Reish *et al.* 1985).

Population Structure.--Debates have arisen over whether this species consists of a single panmictic population or two or more subpopulations (Epperly 1989). Certain meristic and morphometric features, growth rates, movements, and the spatio-temporal nature of spawning have suggested the existence of two or more subpopulations (June 1958, 1965; Sutherland 1963; Higham and Nicholson 1964; June and Nicholson 1964; Dahlberg 1970). However, after reviewing available data, Nicholson (1971, 1978) rejected the multiple subpopulation hypothesis and attributed differences in meristic features of fish from different regions to differences in water temperatures during larval development. Juveniles collected north of 40°N have lower numbers of total and trunk vertebrae, ventral scutes and interhaemal spines, and shallower heads, smaller eyes, and shorter predorsal lengths (Epperly 1989). In considering the possibility of at least two subpopulations of Atlantic menhaden, Epperly (1989) noted that meristic and morphometric characteristics of juveniles of a geographic area are homogenous with respect to their parents and are temporally consistent. There is also an accumulation of significant differences in the frequencies of transferrin alleles between juveniles caught north and south of 40°N, which may be consistent with a division of the gene pool. Despite increasing population sizes and numbers of older fish, which migrate farthest north (Smith *et al.* 1987), the numbers of juvenile Atlantic menhaden in estuaries of the northern North Atlantic area declined over 98% in the 1970s (Ahrenholz *et al.* 1986); concomitant declines in yield-per-recruit and size at age (more than can be explained by density-dependent growth) indicate biological changes in characteristics of the stock, or alternatively, in the relative proportions of contributing subpopulations (Ahrenholz *et al.* 1987b). Although evidence is still inconclusive, potential for at least two subpopulations still exists: one which spawns in summer and is responsible for primary recruitment in the northern areas, and one that spawns in autumn through spring and contributes the majority of recruitment in the Middle and Southern Atlantic areas.

Avise *et al.* (1989) reported exceptionally high levels of genetic variation in mitochondrial genotypes among 17 menhaden specimens assayed, all of which had differentiable mtDNA genotypes. With this level of variation, they estimated that mtDNA assays were capable of fingerprinting individual specimens of menhaden.

Importance and Utilization.--Atlantic menhaden is one of the most commercially important fishes occurring along the Atlantic coast of the United States, especially from

Massachusetts to the Carolinas. It is rarely eaten by humans because of the oily and bony flesh, although the roe is highly prized in some areas of coastal North Carolina. The majority of the catch is processed into fish oil, fish solubles, and fish meal. Most menhaden meal is incorporated into poultry, livestock, and aquaculture feeds. Most menhaden oil is exported outside the U.S., and is refined into edible cooking oils. Domestic uses include paints, soaps, pharmaceuticals, and lubricants. Menhaden are an excellent source of polyunsaturated fatty acids, and contain a high percentage of omega-3 fatty acids (Krzynowek and Murphy 1987). Nutritional values for menhaden are: Fat 8-16%; Moisture ca. 71%; Protein ca. 16.5%; and Ash ca. 4%. Considerable amounts are used locally for bait in lobster and crab fisheries, and minor quantities are ground up into "chum," which is used by sport fishermen to attract large game fish. Practically the entire commercial catch of menhaden is taken by purse seines, pound nets, and gillnets; they almost never bite a baited hook.

History of the Fisheries in Recent Decades.--Since 1980, the Atlantic menhaden purse-seine fishery (for reduction to fish meal and oil) has annually accounted for almost 40% of the total fisheries landings by weight along the East Coast of the United States (Fishery statistics, U.S.). Because of migration patterns of Atlantic menhaden, the fishing season along the Atlantic coast varies in accordance with the seasonal arrival of menhaden schools (Reish *et al.* 1985). Fishing usually begins in April or early May south of Cape Hatteras, NC, and extends from Virginia to New Jersey by June. Schools of menhaden usually enter the Gulf of Maine by early June (June and Reintjes 1976), where peak catches are made during July and August. Schools depart the area during September (Nicholson 1971).

The purse-seine fishery for reduction is centered in Chesapeake Bay with 75-80% of the coastwide catch made between Long Island and Cape Hatteras, then landed in Reedville, VA (Smith 1991). The fishery is carried out during daylight and almost exclusively in coastal waters (< 5 km from shore) by spotter aircraft and large carrier vessels called steamers (up to ca. 61 m long) that tender a pair of purse-seine boats (9.2-12.3 m long). Schools of menhaden are encircled with the net by the purse boats, pumped aboard the steamer, and off-loaded at a shoreside factory.

Menhaden undergo a wet reduction process to fish meal, fish oil, and fish solubles. Fish meal is an important ingredient in poultry, swine, and aquaculture feeds. Fish solubles are often re-introduced onto the fish meal to create a "whole meal" product. Menhaden oil produced in the United States is exported to European markets for refining into margarine and cooking oil. In 1989, the U.S. Food and Drug Administration approved use of processed fish oils in margarine and other foods for U.S. human consumption, and new markets in this country are developing (Hale *et al.* 1991).

Along the east coast of the United States, the Atlantic menhaden population is considered a unit stock (Ahrenholz *et al.* 1987b). The fish stratify by age and size during summer, with older and larger fish found farther north. Typical age compositions of commercial port samples in recent years are: age-1 and -2 Atlantic menhaden in Chesapeake Bay catches, age-2 and -3 fish in catches from the Middle Atlantic, and age-3 to age-5 fish in the Gulf of Maine. Contemporary (1993) average fork lengths and weights for coastwide port samples are 178 mm FL and 104 g for age-1 fish, 235 mm FL and 237 g for age-2 fish, 258 mm FL and 325 g for age-3 fish, and 279 mm FL and 393 g for age-4 fish (unpublished data, NMFS, Beaufort, NC).

Since the 1950s, the Atlantic menhaden stock has undergone several periods of expansion and contraction. Coastwide landings peaked during the 1950s (645,855 MT in 1956), and up to

23 plants operated from Florida to Maine. Through the 1960s, structure of the Atlantic menhaden stock changed dramatically. Stock size decreased due to exploitation and poor recruitment (Ahrenholz *et al.* 1987b). The age structure became truncated, and fish became scarce in the northern half of their range (Vaughan 1990). Historically, the annual catch for regions north of Cape Charles, MD, prior to 1963 amounted to 65% of the total catch, but after 1966 only accounted for less than 4% of the total catch (Nicholson 1975). The absence of older and larger menhaden, which constituted the majority of catches in these northern regions, reflected the dramatic decrease in numbers of older fish in the population. From 1955 through 1968 the average age of the catch in northern regions was 3-yr-old menhaden, whereas the bulk of the catch in southern regions during this same period was comprised primarily of age-1 and age-2 fish (Henry 1971). Landings declined during this same period and fell to 146,587 MT in 1969. Most plants north of Chesapeake Bay closed.

Through the 1970s and 1980s recruitment levels increased and the age structure again broadened. During this time, the Atlantic menhaden population supported a large commercial fishery and also managed to steadily increase its size despite dramatic changes in characteristics of its spawning stock (Ahrenholz *et al.* 1987b). Population regrowth in the 1970s occurred during a period when an estimated 80-90% of potential spawners were harvested by the fishery and average size at age was declining. Landings improved to 379,712 MT in 1983. Consequently, several factories in New England reopened (Smith 1991). Other studies reporting on stock structure and management of menhaden stocks are those by Vaughan (1991), Vaughan and Merriner (1991), and Vaughan and Smith (1991).

Fish factories in the Gulf of Maine primarily processed fish offal from the New England groundfisheries, but during summer and early fall reduced Atlantic menhaden when these fish were locally available. Through the 1950s, annual menhaden landings for reduction in the Gulf of Maine averaged 10,885 MT, and at this time up to three factories at Gloucester, MA, and Portland, ME, processed Atlantic menhaden during summer. When the stock contracted during the 1960s, menhaden were scarce in New England waters (Nicholson 1975) (no menhaden landings for reduction were recorded in Massachusetts or Maine from 1963-69). As recruitment improved during the 1970s, up to three factories at Gloucester, MA, and South Portland and Rockland, ME, handled menhaden for reduction (Smith 1991), and annual landings for the period averaged 14,513 MT. Stock rebuilding continued through the 1980s and annual landings for the decade in the Gulf of Maine averaged about 25,399 MT (Vaughan 1990; unpublished data, NMFS, Beaufort, NC).

By the 1980s, the character of the fishery in the Gulf of Maine changed. Despite an abundance of fish in coastal waters, factories at South Portland (in 1983), Gloucester (in 1984), and Rockland (in 1988) closed, primarily due to recurring odor problems associated with fish reduction adjacent to populated urban areas (Smith 1991). Concurrently, a national trend toward "waterfront gentrification" made seaside properties more valuable for condominium and marina development than traditional uses such as boat yards and fish houses (Houlahan 1987). In 1987, a fish factory at Blacks Harbour, NB, began processing menhaden caught in southern Maine, but transported by U.S. steamer to Canada. In 1988, a firm in Portland entered into an agreement (an Internal Waters Processing venture, or IWP) with Russia, which sited a foreign factory ship in Maine territorial waters (< 5 km from shore) for the purpose of processing menhaden caught by American owned and operated vessels. Through 1993 up to three factory ships (under two IWPs) operated along Maine's coast, and in 1992 a second Canadian factory in Saulnierville, NS, processed menhaden caught in Maine. Between 1990-1993 combined menhaden landings for the IWPs and in Canada averaged about 33,563 MT annually, although landings for 1993 declined to about 9,071 MT (unpublished data, NMFS, Beaufort, NC).

Purse seining for menhaden in the Gulf of Maine is primarily a summer fishery, although in recent years landings have occurred as early as June 7, 1991, and as late as October 4, 1990 (unpublished data, NMFS, Beaufort, NC). Small fixed-wing aircraft locate menhaden schools and direct the purse boats to encircle the school. Fish are pumped aboard the steamer, then transported to the factory at the end of the trip, usually one to several days. In a variation of the conventional menhaden steamer method of fishing, small (12-15 m) multi-use craft (often trawlers) are converted during summer to purse seiners with one purse boat. The catch is pumped aboard a third and larger vessel, or "run boat," which carries fish to the factory ship(s). In recent years, about four conventional menhaden steamers and a dozen smaller purse-seine vessels fished in Maine waters. Only conventional steamers laden with fish make the 12-16-hr voyage to Canadian factories.

Most purse-seine sets in Maine coastal waters occur within 5 km of land in coastal rivers and coves and around islands and islets. Generally, the fishery is carried out in the Casco Bay area during June and July, and farther north and east in Penobscot Bay and vicinity during August. Although difficult to quantify, Atlantic menhaden are taken in purse seines and pound nets to be sold as bait to lobster fishermen. Recent landings of Atlantic menhaden for bait in Maine are substantial and are estimated at 8.6 million kg (unpublished data, NMFS statistics office, Portland, ME). Minor quantities of Atlantic menhaden are taken in coastal weirs (and used for bait) as far north as New Brunswick (Conners Bros., pers. commun.[5]), especially during years of peak resource abundance.

Numerous references recount the sporadic nature of Atlantic menhaden abundance in the Gulf of Maine (Bigelow and Schroeder 1953; Conniff 1992). Several years of prodigious numbers of fish in Maine's coastal waters are followed typically by a few years when fish are scarce. This intermittent abundance of menhaden in the Gulf of Maine results from several factors. First, a "dominant year class phenomenon" occurs when above average year-classes of Atlantic menhaden recruit into Maine's fisheries as age-2 fish, and then recur in the catches through the following 2 yr as age-3 and age-4 fish. For example, the 1988 year-class of menhaden was exceptionally good, and the Gulf of Maine supported record landings for reduction from 1990-1991 (> 36,284 MT each yr). By 1992, the 1988 year-class passed through the fishery, and an equally dominant year-class did not follow. By 1993 (when the 1988 year-class was age-5), landings plummeted to about 9,071 MT. Second, the major concentration of fishing effort in the modern Atlantic menhaden fishery occurs in the Chesapeake Bay area. Thus, large numbers of age-1 and age-2 menhaden are harvested by Virginia-based vessels before they recruit into the Maine fishery as age-2 and age-3 fish, and the numbers of fish in average to below average year-classes are pared substantially before they reach the Gulf of Maine. Third, environmental cues may alter migration routes of menhaden into the Gulf of Maine. The literature suggests that the 15 °C isotherm may act as a thermal barrier to the movement of menhaden (Bigelow and Schroeder 1953). Some suggest that below average coastal water temperatures in the Gulf of Maine during summer may displace menhaden schools farther offshore, or up in coastal river systems where purse seiners cannot operate. Inherent foggy weather conditions along the Maine coast in summer often prevent spotter aircraft from locating fish schools. Lastly, unusual conditions occur that alter the normal summer migration of menhaden. For example, summer 1994 was atypical as far as coastal migrations of adult Atlantic menhaden were concerned. Fish were scarce in the Gulf of Maine and coastal waters of Massachusetts and Rhode Island. However, adults of the age (ages 2-5) and size (25-30 cm FL) composition "normally" found in the Gulf of Maine, were abundant in New Jersey coastal waters throughout summer 1994 (unpublished data, NMFS, Beaufort, NC). It is unclear why these adult fish failed to migrate farther north during this summer.

During years of peak abundance (as recent as 1990 and 1991) numerous menhaden fish kills occurred in isolated coves of coastal Maine. Menhaden schools were likely chased into blind coves by schools of predators such as bluefish and striped bass (Conniff 1992), or menhaden schools were feeding on a local bloom of plankters. The large numbers of menhaden in a small area deplete the available dissolved oxygen, then the fish school dies *en masse*. Lobsters held in pounds for future markets may also succumb in affected coves. Periodically, the odor and sight of rotting fish has had local impacts on the coastal resort industry.

Ecological Importance.--The ecological role of menhaden cannot be overstated. Menhaden convert energy derived from phyto- and zooplankters, and possibly also vascular plant detritus, into hundreds of thousands of metric tons of fish flesh. In turn, menhaden are of paramount importance as a prey species for numerous piscivorous fishes, mammals, and seabirds. Larval and juvenile menhaden are seasonally very important components of estuarine fish assemblages (Bozeman and Dean 1980; Pacheco and Grant 1965; Tagatz and Dudley 1961). Given the tremendous numbers of individual menhaden, individual growth rates, filtering and feeding capacity, and seasonal movements, they consume and redistribute significant amounts of energy and biomass on an annual basis, both within and between estuarine and continental shelf waters. In Narragansett Bay, RI, for example, menhaden were shown to have local impacts on plankton communities (Oviatt *et al.* 1971), where notable reductions in chlorophyll *a* levels within menhaden schools were due to consumption of phytoplankton by the menhaden. Also, within the immediate vicinity of schools, dissolved oxygen tended to be lower than ambient levels, and ammonia levels were higher than in areas without schools of menhaden.

Chapter 17. SUBFAMILY DUSSUMIERIINAE
ROUND HERRINGS

Description.--Small, or moderate-sized, herring-like fishes characterized by a peculiar, unkeeled, W-shaped pelvic scute, immediately anterior to pelvic fins, with arms extending laterally around bases of the finrays. Also characterized by absence of scutes along the abdomen, and featuring an extremely high number of branchiostegal rays (14-20), higher than for any other group of clupeomorph fishes (Grande 1985).

Habits.--Round herrings are pelagic inshore fishes, feeding mainly on zooplankton. They scatter pelagic eggs from which planktonic larvae hatch. All are schooling fishes and exploited by fisheries, especially in Japan, South Africa, and Indonesia. The largest species reach 25 cm SL, smaller species are mature at about 5 or 6 cm (Whitehead 1985a).

In earlier works, round herrings were placed in the family Dussumieriidae (Whitehead 1985a). As presently perceived (Grande 1985), there are two pairs of genera, which have been placed in separate tribes, containing about 12 species.

Distinctions.--Members of this subfamily are immediately distinguished from all other clupeids by presence of a W-shaped pelvic scute and absence of any other abdominal scutes.

Chapter 18. *Etrumeus* Bleeker 1853

Description.--Body slender; abdomen rounded, without pre- and post-pelvic scutes. Head triangular. Mouth terminal and relatively small; posterior extent of jaws not extending beyond vertical through anterior margin of eye. Premaxillae rectangular; teeth minute. Isthmus with distinct notch ("shoulders") anteriorly on each side. Fins soft-rayed. Dorsal fin located about at body mid-point. Pelvic fins situated at or posterior to vertical through posterior dorsal-fin base, caudal fin forked. Scales cycloid, relatively large and deciduous. Pelvic scute W-shaped.

Meristic features.--Branchiostegal rays 11-15. Gillrakers 30-39. Dorsal-fin rays 15-22. Anal-fin rays 10-13. Pectoral-fin rays 14-17. Pelvic-fin rays i 8. Vertebrae 49. Lateral scales about 48-55.

Diagnosis.--The W-shaped pelvic scute, numerous branchiostegal rays (11-15), and rectangular premaxillae distinguish *Etrumeus* from all other genera of clupeids occurring in the Gulf of Maine (Whitehead 1985a).

Habits.--Marine, pelagic, primarily inshore schooling fishes of both the New World (Atlantic and Pacific coasts) and Indo-Pacific regions, except those areas between 25°N and 25°S. Two species, *Etrumeus whiteheadi* and *E. teres*, are currently recognized in the genus, although Whitehead (1985a) commented that what are presently recognized as populations may prove on further study to represent valid species or subspecies. Only the Atlantic round herring, *E. teres*, occurs in the Gulf of Maine.

Chapter 19. ATLANTIC ROUND HERRING *Etrumeus teres* (DeKay 1842)

Description.--Body slender, only about one-sixth as deep as long; belly rounded, without pre- and post-pelvic scutes; body depth 16.0-18.5% SL. Head triangular; head length 24.0-29.0% SL. Eye diameter 6.5-8.0% SL. Snout length 6.0-9.5% SL. Mouth terminal and relatively small, posterior extent of jaws not extending posteriorly beyond vertical through anterior margin of eye. Maxilla 7.0-10.5% SL. Premaxillae rectangular, teeth minute. Isthmus with distinct notch ("shoulders") anteriorly on each side. Fins soft-rayed. Dorsal fin located at about body mid-point. Pectoral fins moderately developed, reaching notably less than halfway to base of pelvic fin, with long membranous axillary process present. Pelvic fins situated posterior to vertical through posterior dorsal-fin base. Caudal fin forked. Scales cycloid, relatively large and deciduous. Pelvic scute W-shaped.

Meristic features.--Dorsal-fin rays 15-22, usually 18 or 19. Anal-fin rays 10-13, most frequently 11. Pectoral-fin rays 14-16. Pelvic-fin rays i 8. Vertebrae 49. Lateral scales about 48-55 (usually missing). Gillrakers 30-38 on lower limb, ca. 14 on upper limb. Branchiostegal rays 11-15. Pyloric caecae numerous. (Bigelow and Schroeder 1953; Hildebrand 1963; Fahay 1983; Whitehead 1985a).

Color.--Olive green above with silvery sides and abdomen.

Size.--Adults are 20-25 cm FL. Age estimates for the eastern Atlantic *E. whiteheadi* show that fish smaller than 12 cm are < age-1 and that analysis of growth increments is unreliable for larger fish (Waldron *et al.* 1991).

Distinctions.--The most distinctive feature of Atlantic round herring among Gulf of Maine clupeids is that the abdomen is rounded, without a keel of sharp-edged scutes. It is the most slender of Gulf of Maine clupeids in that its body is only about one-sixth as deep as long, thus suggesting a smelt in its general outline (but round herring lack the adipose fin characteristic of smelt). The Atlantic round herring's dorsal fin is situated entirely anterior to the vertical through the pelvic-fin origin (vs. directly above pelvic-fin origin in all other Gulf of Maine clupeids), and it has fewer anal-fin rays (only ca. 13) compared with those of herring (ca. 17), alewife (ca. 19) and American shad (ca. 21).

GENERAL BIOLOGY

Habitat.--Round herrings are marine, pelagic, fishes that are rarely taken inshore. This is a schooling species found mainly over deeper waters along the continental shelf and slope or deeper, with schools usually concentrated between 37 and 92 m (Shaw and Drullinger 1990, and literature cited therein). On the southeast U.S. continental shelf, adults have been taken between 10 and 366 m. A seasonal shift in depth distribution may also occur, with fish moving offshore (56-183 m) during summer-fall, and inshore (10-27 m) during winter-spring (Barans and Burrell 1976). In southern areas, round herring do not occur in nearshore or estuarine habitats, but are taken only offshore in water of at least several meters in depth (Hildebrand 1963; Shaw and Drullinger 1990). It apparently does not undertake long distance migrations along South Atlantic coasts of the U.S. (Reintjes 1979).

Habits.--The round herring apparently undertakes diurnal vertical migrations (Bullis *et al.* 1971), with fish occurring at the surface at night and 9-37 m off the bottom during the day. Round herring form dense schools, often with other pelagic schooling species, including Spanish sardine, rough scad, and chub mackerel (Bullis *et al.* 1971; Crawford 1981). Bullis *et al.* (1971) reported a mixed school of round herring and Spanish sardine west of Tampa, FL, that was estimated to be 80 km long, 16 km wide, and about 3.7 m thick.

Feeding.--Round herrings feed mainly on zooplankton, although little is known of the diet composition, prey selectivity, or other aspects of the feeding ecology of adult round herrings.

Predators.--Undoubtedly, round herrings are consumed by a wide variety of pelagic predators, including fishes, seabirds and marine mammals that feed on other clupeoid species. However, little quantitative data are available regarding predation rates on these species.

Parasites.--Little information is available concerning host-parasite relationships of round herring. Larval nematodes utilize round herring as an intermediate host (Takao 1990). Langdon *et al.* (1992) reported that specimens of round herring they examined were not host for the myxosporean parasite *Kudoa thyrsites*.

Western Atlantic Distribution.--Round herring occur in waters of the northwest Atlantic from the mouth of the Bay of Fundy southward to Florida, Gulf of Mexico, Venezuela, and Guianas (Whitehead 1985a). Occasionally, this species is common as far north as Woods Hole, MA, but usually occurs only as strays north of about Cape Cod.

Occurrence in Gulf of Maine.--Adults are infrequently recorded from the Gulf of Maine. Specimens have been taken at Provincetown, MA (two specimens deposited in MCZ); one round herring was taken in the Yarmouth River which empties into Casco Bay, and one in Casco Bay itself on September 15, 1924 (Bigelow and Schroeder 1953). It was also reported from Jonesport and Eastport, ME, in 1908 (Bigelow and Schroeder 1953). A number of specimens were taken at Campobello Island, at the mouth of Passamaquoddy Bay in September

1937 and October in weirs at Campobello and Grand Manan islands (Leim 1937; McKenzie 1939). Along the coast of eastern Maine, in August-September 1953, approximately 90,909 kg of round herring were landed (Scattergood 1953). Scott and Scott (1988) also noted that adults are reported infrequently from the Canadian Atlantic region, and these are almost always from the lower Bay of Fundy (including Passamaquoddy Bay) and southern Nova Scotia. Some captures appear to have occurred corresponding with periods of unusual warming.

Reproductive Biology

Spawning Seasonality and Location.--Reproductive biology of the round herring and details relevant to the distribution and population dynamics of this species in the western Atlantic are presently sketchy (Shaw and Drullinger 1990; Chen *et al.* 1992). Off South Africa, the reproductive biology of a related species, *E. whiteheadi*, was reported by Roel and Melo (1990). Larvae of round herring have been collected off the South Atlantic Bight during January and February (Fahay 1975). Spawning occurs during late January to early June in the Gulf of Mexico (Fahay 1983; Shaw and Drullinger 1990). Houde (1977) reported that, in the eastern Gulf of Mexico, round herring spawn from mid-October to the end of May offshore between the 30 and 200 m isobaths. One major spawning area in the Gulf is located about 150 km west-southwest of Tampa Bay, FL, with another minor area located just north of the Dry Tortugas (Houde 1977). Off Texas and Louisiana, round herring spawned in areas from 50 to 200 km offshore, and may also have spawned in habitats at the edge of the continental shelf (Fore 1971). High concentrations of round herring larvae were found on the outer shelf (depths 40-182 m) and near the shelf break during sampling off the Mississippi River delta region (Shaw and Drullinger 1990). Abundance of round herring larvae was lower on the inner shelf, although sampling limitations may have accounted for this finding.

Eggs of round herring have been collected at the surface at temperatures of 18.4-26.9°C and salinities of 34.5-36.5 ppt (Houde 1977). Shaw and Drullinger (1990) collected recently-hatched larvae at surface temperatures and salinities ranging from 16.7-23.8°C and 33.8-36.5 ppt, respectively. For all sizes of larvae collected, temperatures at time of collection ranged from 15.0-30.0°C, while salinities were 28.7-37.5 ppt.

Round herring scatter pelagic eggs during the nighttime, with peak spawning estimated to occur at 2200 hr (Houde 1977). The larvae are planktonic.

Eggs.--Eggs are pelagic, spherical, about 1.17-1.37 mm in diameter (Houde and Fore 1973). The yolk is segmented and there is a small perivitelline space, but the egg lacks oil globules.

Development.--Hatching occurs in about 2.1 d at 21-22°C (Houde 1977). Larvae at hatching are 3.8-4.8 mm TL and have unpigmented eyes. Larvae are elongate with a long straight gut with the vent always posterior to the dorsal fin (Houde and Fore 1973). Flexion occurs at 8-10 mm TL, transformation begins at about 18 mm SL, and is completed at 28-33 mm TL (Hildebrand 1963).

Larval Ecology and Behavior.--In the eastern Gulf of Mexico, greater numbers of larvae are caught at night (daytime net avoidance); larger larvae (13.0-18.0 mm) apparently are also able to avoid nets at night (Houde 1977; Shaw and Drullinger 1990). In one study in the northern Gulf of Mexico, larval round herring were taken most frequently throughout the water column at the offshore stations in water 91 m deep, although one of the largest single collections was made at 18 m (Chen *et al.* 1992).

Larval diets consist primarily of copepod nauplii, copepodids, and adults, with pteropods, tintinnids, invertebrate eggs, and *Eucalanus* nauplii contributing lesser percentages (Chen *et al.* 1992).

Age estimates, based on daily otolith rings, averaged 0.71 mm/d for December (Chen *et al.* 1992). The fastest growth rate (ca. 0.85 mm/d) for round herring larvae occurred at about 15 d. Mortality estimates of larvae were provided by Houde (1977).

Importance and Utilization.--Round herrings are the basis of important fisheries in other regions of the world (primarily Japan, southern Africa, and the Red Sea). An evaluation of the fishery potential of round herring resources in the eastern Gulf of Mexico estimated stocks at 3.3×10^4 to 4.2×10^5 MT (Houde 1977). For the entire Gulf of Mexico, estimates (Reintjes 1980) range from 1.1×10^5 to 1.1×10^6 MT. The total catch worldwide for round herrings (both species) in 1983 was 110,084 MT (Whitehead 1985a), but more recent estimates of round herring (*E. whiteheadi*) biomass in the southern Benguela system are of the order of a million metric tons (Roel and Armstrong, unpublished data, cited in Waldron *et al.* 1991). Annual catches of round herrings are increasing in the region off southern Africa.

Chapter 20. SUBORDER ENGRAULOIDEA
FAMILY ENGRAULIDAE
Anchovies

Description.--Small to moderate-sized, elongate and somewhat moderately laterally compressed, silvery, herring-like fishes (Hildebrand 1963; Scott and Scott 1988; Whitehead *et al.* 1988). Head moderately long. Most species with prominent pig-like snout projecting beyond lower-jaw tip. Eye prominent and located relatively far forward; adults sometimes with adipose eyelid. Mouth large, gaping, horizontal, situated low on head; with long, slender, "underslung" lower jaw with point of articulation located well beyond posterior margin of eye. Typically, with two supramaxillae. Jaw teeth usually small or minute; minute teeth also present on vomer, palatines, tongue, and pterygoids. Gillrakers generally short, slender, 10-50 or more on lower limb of first arch, (but long and up to 100 or more in *Anchovia*). Branchiostegals 7-19. All fins soft rayed; dorsal fin short (12-16 finrays in American genera) and usually near midpoint of body; pectoral fins situated low on body; pelvic fins ventral, with i 6 finrays, located about midbody (before, under, or behind vertical through dorsal-fin base); anal fin usually moderately long (in American genera), about 15-40 finrays in American species; caudal fin deeply forked. Scales moderate in size, cycloid, ca. 30-60 in lateral series, often deciduous. Lateral line absent. Pelvic scute with lateral arms always present; New World anchovies lack pre- and post-pelvic scutes. Vertebrae 40-44 (for species occurring in northwest Atlantic). Size to 50 cm, but most species usually less than 15 cm.

Dorsal portion of body typically blue/green or translucent gray; sides usually silvery (sometimes with distinct silver midlateral stripe); fins hyaline, dusky, or faint yellow, sometimes chrome or orange; also with black markings just behind gill opening or on fin tips or margins of fins in some species; no species with black spots on sides (as in some clupeids).

Approximately 16 genera with about 139 species are currently recognized in the family (Whitehead *et al.* 1988). Anchovies are most closely related to the Clupeidae and have been described as essentially clupeids with a different head (Nelson 1984; Grande 1985; Grande and

Nelson 1985; Whitehead *et al.* 1988).

Habits.--Most species inhabit coastal waters in tropical and temperate (from about 60°N to 50°S) Atlantic, Pacific, and Indian oceans. Some species enter brackish or freshwater to feed or spawn, some live permanently there, and some are found high up the Amazon (Whitehead *et al.* 1988). Most anchovies are strongly schooling species that feed on small planktonic animals (especially crustaceans), either by locating individual prey or by more indiscriminant filterfeeding. Larger anchovies may also include small fishes and other invertebrates in the diet. Most, perhaps all, species scatter relatively large numbers of eggs from which planktonic larvae hatch.

In areas of abundance, anchovies are fished commercially as food fishes and are sold fresh, cured, or canned and are also used for bait and fish meal (Hildebrand 1963; Scott and Scott 1988; Whitehead *et al.* 1988).

Only two species, the bay anchovy, *Anchoa mitchilli*, and striped anchovy, *A. hepsetus*, have been reported from the Gulf of Maine. Larvae of the silver anchovy, *Engraulis eurystole* (Swain and Meek 1885) have been collected on the Scotian shelf (Markle *et al.* 1980), but thus far this species is unknown from the Gulf of Maine. The bay anchovy occurs more frequently in the Gulf of Maine than other anchovies, and there is probably a spawning population in southern Cape Cod Bay (see Scherer 1984). Striped and silver anchovies are more common and abundant in areas south of the Gulf of Maine. Presence of these species in the Gulf or on the Scotian shelf occurs only occasionally, primarily during periods of higher water temperatures.

Distinctions.--Gulf of Maine fishes with which one might possibly confuse an anchovy are juvenile herring, smelt, or silversides. Anchovies are easily distinguished from Atlantic herring by their large, underslung, mouths that articulate well beyond the vertical passing through the posterior margin of the eye (mouth smaller, terminal, and articulation point of jaws located at vertical through anterior or midpoint of eye in herring); in lacking abdominal scutes (vs. scutes present in herring); in having the dorsal-fin origin located entirely posterior to the vertical passing through the pelvic-fin origin (vs. dorsal-fin origin located at vertical line equal with, or slightly anterior to, pelvic-fin origin in herring); in having tips of pectoral-fin rays (when these are laid back against body) nearly reaching pelvic-fin origin (vs. pectoral fins more widely separated from pelvic-fin origin in herring); and the anal fin of anchovies is much longer than that of herring. Anchovies lack a dorsal adipose fin which distinguishes them at a glance from smelt. Silversides (*Menidia* spp.) have two separate dorsal fins instead of the single dorsal fin characteristic of anchovies.

Chapter 21. *Anchoa* Jordan and Evermann 1927
Anchovies

Description (based on Whitehead *et al.* 1988).--Fairly small, slightly or quite strongly compressed anchovies (to ca. 13 cm SL, usually 6-10 cm). Snout fairly pointed (strongly pointed in subgenus *Anchovietta*); maxilla long (reaching beyond anterior margin of pre-operculum), tip pointed, reaching well beyond tip of second supra-maxilla; fine teeth on lower jaw; gillrakers slender, increasing in number in larger fishes in some species (lower gillrakers as few as 12-14 in some species, usually 17-24, but to 28 in others, and to 32 in one species); gillrakers present on posterior face of third epibranchial. Pseudobranch usually short, but longer than eye and extending onto inner face of operculum in several species of subgenus *Anchoa* and all species of subgenus *Anchovietta*. Canals on gill cover with or without a pre-opercular branch passing posteriorly onto operculum and running ventrally parallel to temporal canal. Dorsal-fin origin at about midpoint of body; anal fin short, moderate or long (14-22 branched finrays in some species, usually about 20-27, but up to 34-37 in other species); its origin usually at vertical through dorsal-fin base (occasionally just anterior, and in subgenus *Anchovietta* below or behind base of posteriormost dorsal-fin ray).

Habits.--Members of *Anchoa* occur in marine and estuarine habitats, and some species penetrate into freshwaters. They are found along Atlantic and Pacific coasts and lower parts of rivers of North, Central, and South America. Some species filterfeed on small planktonic organisms, those with few gillrakers feeding on larger animals (shrimps, small fishes, etc.). Approximately 34 species, 16 Atlantic and 17 eastern Pacific. Only two species, *Anchoa mitchilli* and *A. hepsetus*, are known to occur in the Gulf of Maine.

Distinctions.--The rather long maxilla and its pointed tip distinguishes *Anchoa* from *Anchoviella* (maxilla blunt, its tip barely extending beyond tip of second supra-maxilla).

KEY TO ANCHOVIES OCCURRING IN THE GULF OF MAINE

1a. Anal-fin origin at vertical through anterior margin of dorsal fin; silvery lateral band diffuse; 24-30 anal-fin rays .... Bay anchovy, p. 166.

1b. Anal-fin origin at vertical through posterior rays of dorsal fin; silvery lateral band bright and well defined; 16-23 anal-fin rays .... Striped anchovy, p. 172.

Chapter 22. BAY ANCHOVY *Anchoa mitchilli* (Valenciennes 1848)
Whitebait

Description.--Body variable, rather slender, more slender in northern populations; depth ca. 4-5 times in SL, moderately compressed, greatest thickness usually exceeding depth of caudal peduncle. Body depth 16-27% SL. Head 22.0-26.5% SL. Snout short, fairly blunt, slightly over one-half of eye diameter; 3.7-7.2% SL, projecting not more than 1/4 of its length beyond mandible tip. Eye 5.8-8.2% SL. Post-orbital length short, 11.0-13.5% SL. Maxilla long, 17.5-21.0% SL, tip pointed and reaching beyond posterior border of preoperculum, extending nearly to margin of opercle. Mandible 16.5-18.5% SL. Cheek short and broad, about as long as eye, posterior angle approximately 60°. Dorsal fin rather low, with nearly straight margin, posteriormost finray scarcely longer than finray immediately before it; longest dorsal-fin ray failing to reach tip of fin if depressed posteriorly; dorsal-fin origin variable; usually located between point slightly nearer to caudal-fin base than to upper anterior angle of gill opening and the point equidistant between caudal-fin base and posterior margin of eye. Anal fin moderate to long, its origin usually just somewhat posterior to vertical through dorsal-fin origin; anal-fin base 25-30% SL. Anus nearer to pelvic-fin tips than to anal-fin origin. Pelvic fin very small, not quite reaching half-way point to origin of anal fin; inserted nearer to anal-fin origin than to pectoral-fin base by distance equal to diameter of eye. Pectoral-fin length 12-20% SL, somewhat variable, failing to reach base of pelvic fins by distance equal to, or even greater than, diameter of eye in northern specimens; sometimes reaching base of pelvic fins in southern fish. Axillary scale of pectoral fin rather narrow. Caudal fin deeply forked. (Hildebrand 1963; Whitehead *et al.* 1988).

Meristic features.--Dorsal-fin rays 14-16, anal-fin rays iii,20-30; pectoral-fin rays 9-12 (usually 11-12); lateral scales 38-44, relatively large, thin, easily detached; lower gillrakers 21-25 (higher part of range in specimens from northern populations), upper gill rakers 20-26; vertebrae 38-44.

Color.--Whitish silvery to pale along sides of body, abdominal walls translucent; dorsal-most surface greenish with bluish reflections; sides with narrow, ill-defined, silvery band scarcely wider than pupil of eye, extending from gill opening posteriorly to caudal-fin base. Body and fins speckled with many small, rounded melanophores.

Size.--Maximum length about 11.0 cm, but seldom more than 10.0 cm SL and usually only to about 7.5 cm SL (Hildebrand 1963).

Distinctions.--The bay anchovy is readily distinguished from the striped anchovy in having the anal-fin origin located at a vertical passing through the anterior margin or anteriormost (unbranched) dorsal-fin rays (vs. anal-fin origin located at vertical passing through middle or posterior dorsal-fin rays in striped anchovy); in having a more diffuse silvery lateral band (vs. lateral band bright and well developed in striped anchovy); and in having more anal-fin rays (24-30 vs. 16-20 in the striped anchovy); in having fewer pectoral finrays (i,9-12, usually 10 or 11, in bay anchovy vs. 13-16, usually 14-15, in striped anchovy). In bay anchovy, the anus is also nearer the pelvic fins than the anal-fin origin (vs. anus closer to anal-fin origin in striped anchovy).

GENERAL BIOLOGY

Much of the information presented is synthesized from species profiles by Robinette (1983), Morton (1989), and Houde and Zastrow (1991).

Habitat.--Throughout its range, the bay anchovy is pelagic in nearshore coastal marine waters, but is most plentiful in shallow, tidal estuaries with muddy bottoms and brackish water (Hildebrand 1963; Whitehead *et al.* 1988; Houde and Zastrow 1991). The bay anchovy also occurs in the mouths of rivers, along exposed sandy beaches, and in shallow waters of intertidal creeks (Reis and Dean 1981). It seldom occurs in waters deeper than 25 m (Byrne 1982), but has been collected to at least a depth of 36 m (Hildebrand 1963). This species inhabits both clear and turbid waters, and has been collected over all types of substrates, including muddy coves, grassy areas, surf zones, oyster bars, sandy beaches, and sand and silt bottoms (Vouglitois *et al.* 1987; Houde and Zastrow 1991).

Habits.--The bay anchovy is pelagic in all life stages. In upper Chesapeake Bay, larval and juvenile bay anchovy were most abundant near the surface (upper 3 m) from May to October, but apparently moved to deeper waters as winter approached (Dovel 1971). In the York River, Chesapeake Bay, bay anchovy schools break up at night and individual fish are transported by currents, whereas in daylight, bay anchovy schools maintain a relatively fixed location (Luo 1993). Anchovies swim at night, but at slower speeds than in the daytime, and in no fixed directions.

The bay anchovy is euryhaline, tolerant of salinities from virtually freshwater to fully saline, or even hypersaline conditions (Hildebrand 1963; Dovel 1971; Houde and Zastrow 1991). Further south, larvae and small juveniles are distributed throughout low salinity subestuaries, remaining there until fall before dispersing to over-wintering areas. In Virginia tributaries of Chesapeake Bay, juveniles have been collected as much as 64 km above brackish water (Massman 1954).

In the northern parts of its range, bay anchovy occur inshore only during the summer (Hildebrand 1963; Scherer 1984). There is no known substantial north-south seasonal migration, rather the species undergoes seasonal inshore-offshore movements in the temperate parts of its range (Hildebrand 1963; Vouglitois *et al.* 1987); moving out onto the inner continental shelf in fall and winter and returning to estuaries in spring. Further south, the bay anchovy is a year-round resident in the larger estuaries. For example, in Chesapeake Bay, adults migrate to deeper waters in the Bay during winter (Hildebrand and Schroeder 1928; Setzler *et al.* 1981), and may migrate to the lower Bay regions during the coldest winters (Wang and Houde 1995), but are usually collected there throughout the entire year.

Feeding.--Juvenile and adult bay anchovy feed opportunistically primarily on zooplankton, which are selected as individual particles (Cowan and Houde 1990). It is a major consumer of plankton, with copepods comprising the dominant prey (Stevenson 1958; Hildebrand 1963; Din and Gunter 1986; Vasquez 1989; Houde and Zastrow 1991). Larger fish also consume macrozooplankton such as mysids, larval fishes, crab larvae, isopods, other invertebrates including some benthic organisms (e.g., polychaetes and mollusks), and fish larvae (Allen *et al.* 1995). Small particulates (e.g. algae, detritus) may be found in stomachs of all anchovy length classes (Houde and Zastrow 1991). Although copepods are the predominant food consumed, they may be replaced in the diet when other potential foods are abundant (Din and Gunter 1986). Allen *et al.* (1995) noted that the selective preference for larger crustaceans and fish larvae by adult anchovies may be an important factor in the recruitment success of some estuarine macrofauna, especially fiddler crabs. Megalopae were selected for even when their densities were low. Feeding may occur throughout the day, but during summer months in Chesapeake Bay, feeding is most intense from dawn to mid-morning (Vasquez 1989). Daily ration was estimated to be 16.2% of body weight and bay anchovy were able to consume as much as 28% of their own body weight each day with an assimilation efficiency of over 68% (Vasquez 1989). Food consumption and other energetics parameters (Vasquez 1989) were temperature dependent at 19-27°C (range of temperatures studied), with highest consumption and growth at 27°C.

Predators.--Bay anchovy is a major prey item for commercially and recreationally important predatory fishes (Hollis 1952; Merriner 1975; Chao and Musick 1977; Baird and Ulanowicz 1989; Safina and Burger 1989), such as bluefish (Grant 1962; Friedland *et al.* 1988; Juanes *et al.* 1993), striped bass, summer flounder, and weakfish (Houde and Zastrow 1991). In Chesapeake Bay, bay anchovy are estimated to provide more than one-half of the total energy intake of predatory fishes, contributing 70, 90, and 60% to their diets in summer, fall and spring, respectively (Baird and Ulanowicz 1989). In the Hudson River estuary, bay anchovies were the predominant food and were most abundant in stomachs of bluefish smaller than 150 mm. Small bluefish (<120 mm) fed predominantly on bay anchovies, and although prey size generally increased with bluefish size, even the largest bluefish examined had consumed relatively small bay anchovies (Juanes *et al.* 1993). Bay anchovy are also eaten by seabirds, including the common tern (Safina and Burger 1985), and might also be an important food item for other waterfowl and other animals (Dovel 1971). In the laboratory, early life history stages of bay anchovy are preyed upon by the ctenophore, *Mnemiopsis leidyi* (Monteleone and Duguay 1988). This ctenophore predator co-occurs with spawning bay anchovy (Johnson 1987).

Species Associates.--Potential competitors of anchovy are other planktivorous fishes, including sea herring, alewife, blueback herring, menhaden, striped anchovy and silversides. The diet of bay anchovy was demonstrated to overlap with that of blueback herring in the James River, VA (Burbidge 1974). Diets of bay anchovies did not overlap significantly with those of other zooplanktivorous fishes (silversides and striped anchovy) in South Carolina saltmarsh creeks (Allen *et al.* 1995). Instead, these species demonstrated spatial and temporal partitioning of the habitat, with fine scale differences occurring in the composition of diets. In estuarine areas, ctenophores (comb jellies) and other jellyfish are major consumers of zooplankton and may compete with bay anchovy for this trophic resource (Houde and Zastrow 1991). Allen *et al.* (1995) suggested that selective preference for larger crustaceans and fish larvae by adult anchovies may be important in determining recruitment success of some estuarine macrofauna, especially fiddler crabs. Megalopae of fiddler crabs were selected for even when their densities were low.

General Range.--Western North and central Atlantic coastal regions from Maine, and Cape Cod Bay, MA, south to Florida Keys and westward around the Gulf of Mexico south to Yucatan, but not in West Indies (Hildebrand 1963; Scherer 1984; Lawton *et al.* 1984). In coastal waters around Woods Hole and to the west and south of this area, this species occurs in much greater abundance (Hildebrand 1963; Vouglitois *et al.* 1987).

Occurrence in Gulf of Maine.--The bay anchovy has been taken in Casco Bay, ME, at Provincetown, MA (Bigelow and Schroeder 1953), and western Cape Cod Bay (Lawton *et al.* 1984; Scherer 1984). It does not appear to be abundant in the Gulf of Maine, and seldom strays north of Cape Cod Bay. Generally, bay anchovy occur only in low abundance, and only in the western Cape Cod Bay region of the southern Gulf of Maine (Lawton *et al.* 1984). This species is rare in the middle and northern Gulf (Bigelow and Schroeder 1953; Hildebrand 1963). Eggs and larvae of anchovies have also been collected in ichthyoplankton samples taken during June through October in this same region (Scherer 1984). Larvae of *Anchoa* spp. (presumably *A. mitchilli*) were not very abundant in the samples, ranking only 29th of the 35 most abundant species in the study.

Reproductive Biology

General Description.--The bay anchovy, like other clupeiform fishes, is a batch (i.e., serial) spawner (Zastrow *et al.* 1991; Luo and Musick 1991). Individual females in Chesapeake Bay spawned at least 50-55 times each season, producing 442-2026 (mean =1,129) ova per batch (Zastrow *et al.* 1991; Luo and Musick 1991). On average, bay anchovy in lower Chesapeake Bay spawned every 4 d in June, every 1.9 d in the beginning of July, and every 1.3-1.4 d from early July-end of August (Luo and Musick 1991).

Spawning takes place usually in the evening between 1800 and 2400 hr (Hildebrand and Cable 1930; Ferraro 1980; Zastrow *et al.* 1991; Luo and Musick 1991), although some spawning can occur somewhat later (at least until about 0100). Hydrated ova first appear in evening samples, beginning at about 1800 hr (Zastrow *et al.* 1991). Hydration occurred between 1700 and 1800 hr and most females had fully hydrated ova by 1800 hr. Most spawning probably occurred between 2100 and 2400 hr. No fish were found with hydrated ova after 0033 hr, indicating that daily spawning activity was completed by that time. Daily spawning time varied from month to month (Luo and Musick 1991), spawning was delayed as the season progressed. It was estimated (Zastrow *et al.* 1991) that during the peak of the 1987 spawning season in mid-Chesapeake Bay, virtually all mature bay anchovy females spawned each night.

Spawning Seasonality.--The bay anchovy has a protracted spawning season, from May to September in northern areas, and possibly extending throughout the year in southern parts of the range (Houde and Lovdal 1984). In western Cape Cod Bay, eggs were collected from June-August, and anchovy larvae (presumably this species) from July-October (Scherer 1984). In Barnegat Bay, NJ, and Great South Bay, NY, spawning may begin as early as April, peak in June and July, and be essentially completed in August (Vouglitois *et al.* 1987; Monteleone 1992). The spawning season in Great South Bay (late May-early August, with shorter peak season during late June-late July) is among the shortest reported for this species (Castro and Cowen 1991) and comparable only with that reported for anchovies in Long Island Sound (Wheatland 1956). Some spawning begins in April in the lower Chesapeake Bay, with most spawning in this area extending from May to September (Dovel 1971; Olney 1983; Dalton 1987; Zastrow *et al.* 1991; Luo and Musick 1991; E. Houde, pers. commun.[6]). The spawning season in mid-Chesapeake Bay extends from mid-May to mid-August (Zastrow *et al.* 1991). In this area, GSI values were low in March, increased in April and May, and peaked in July, before rapidly decreasing in August toward their lowest levels in fall and winter. At Beaufort, NC, spawning in the bay anchovy was reported (Kuntz 1914) to extend from late April to early September, while in Biscayne Bay, FL, spawning may occur year round (Houde and Lovdal 1984).

Spawning Temperatures and Salinities.--Bay anchovies spawn where water depth is less than 20 m in salinities of 0-32 ppt (Dovel 1971; Olney 1983; Houde and Zastrow 1991). Peak spawning in Chesapeake Bay apparently occurs at 13-15 ppt (Dovel 1971) and at average surface water temperatures of 26.3-27.8°C (Houde and Zastrow 1991). In the Delaware River estuary, Wang and Kernehan (1979) reported peak spawning at 22-27°C.

Fecundity.--Batch fecundity is a linear function of fork length and body weight (Luo and Musick 1991). Overall egg production for the season was estimated at 45,110 eggs per female (55 mm FL fish), equivalent to 346% of a female's body energy. Batch fecundity averaged 643-740 eggs/g of female (Zastrow *et al.* 1991; Luo and Musick 1991). During the peak spawning period, daily spawning output was estimated to be 6.3% of body energy. Most spawning energy in bay anchovy was derived from daily feeding, not from fat reserves (Luo and Musick 1991). In Chesapeake Bay, the somatic weight component increased by 32-33% and total body weight by 26% during spawning season, indicating that feeding not only met energy requirements of daily spawning but also provided surplus energy for growth (Wang and Houde 1994).

Size and Age at Maturity.--Sexual maturity is attained at a relatively early age and small size. In Chesapeake Bay, some YOY anchovies may mature by late summer of their 1st yr (Luo and Musick 1991), although most apparently overwinter before maturing the following year (Zastrow *et al.* 1991). In mid-Chesapeake Bay, male and female bay anchovy matured at 40 to 45 mm FL, corresponding to an average age at first maturity of ca. 10 mo posthatch (Zastrow *et al.* 1991). Luo and Musick (1991) also found some female bay anchovy from the lower Chesapeake Bay that were mature at age-0+ and <40 mm FL, and Stevenson (1958) reported finding some sexually mature bay anchovies in the Delaware Bay region that were 35-40 mm SL. Age-1 females (50-55 mm in length) have been estimated to produce from 92 to >99% of the anchovy eggs spawned in Chesapeake Bay (Zastrow *et al.* 1991).

Early Life History.--An account of the embryology and larval development can be found in Kuntz (1913). Other general references on early life history and development are Lippson and Moran (1974), Mansueti and Hardy (1967), and Fahay (1983). Tucker (1988) reported on energy utilization in eggs and larvae.

Larval anchovies (bay and striped) constituted a major portion of the ichthyoplankton collected throughout Narragansett Bay, RI (Bourne and Govoni 1988). During a 2-yr period in Great South Bay, NY (Monteleone 1992), the bay anchovy was the most abundant ichthyoplankter, comprising >96% of the eggs and >69% of the larvae collected. In several other east coast localities including Long Island Sound (Wheatland 1956), Mystic River estuary (Pearcy and Richards 1962), Barnegat Bay (Vouglitois *et al.* 1987), lower Hudson River (Dovel 1981), and Chesapeake Bay (Dovel 1971; Olney 1983), bay anchovy has been reported as the numerically dominant member of the ichthyoplankton.

Eggs.--Eggs are pelagic and transparent, barely elliptical with a long axis of 0.84-1.11 mm. The shell is smooth and transparent; the yolk segmented. The perivitelline space is narrow and there are no oil globules.

Development.--Hatching occurs at 1.8-2.7 mm. The body is long and slender. The yolk sac is greatly elongate and tapers posteriorly. The larvae are transparent and show no pigmentation. Yolk-sac absorption is completed 15-18 hr post hatching. The mouth is apparently functional 36 hr after hatching. Mouth is large, terminal and extends to the middle of the eye; becoming subterminal as development progresses. Flexion occurs at 7-8 mm, and transformation occurs at about 20 mm. Larvae 7-8 mm in length have developing dorsal and anal fins and some pigmentation in the thoracic region and at the base of the anal fin. Dorsal, caudal, and anal fins develop at the same time; the pectoral fin forms as a bud but is not complete until later. The pelvic fins form late in development. At 12 mm length, the dorsal and anal fins have finrays formed. The projecting snout is not developed until the fish reaches 20-25 mm in length (Hildebrand 1963). Juveniles differ from adults in having a terminal mouth and a short rounded maxilla, which does not reach the margin of the opercle. Juveniles also lack the silvery band of adults. Larval and juvenile stages may be completed in as little as 2.5 mo (Hildebrand 1963; Zastrow *et al.* 1991; Luo and Musick 1991).

Larval Growth.--Growth rates of larvae based on field estimates ranged from 0.25 mm/d (Fives *et al.* 1986), 0.43-0.56 mm/d (Leak and Houde 1987), to 0.60-0.75 mm/d (Rilling 1996). In the laboratory, reported mean growth rates of 0.48-0.54 mm/d were estimated (Saksena and Houde 1972) in direct relationship to prey concentrations. In another study (Houde 1978), growth rates of 0.32-0.63 mm/d were reported. In mesocosm studies (Cowan and Houde 1990), growth rates of 0.39-0.63 mm/d have been recorded. Instantaneous mortality rates of larvae reared in these mesocosms were high (0.08-0.23/d), but were lower than those recorded for bay anchovy larvae from estuaries with gelatinous zooplankton and fish predators present. Larval growth rates tended to be faster in Great South Bay, NY (Castro and Cowen 1991), than for those reported for anchovies occurring further south.

Larval Feeding.--The first food of larval bay anchovy is microzooplankton, including copepod nauplii, rotifers, and tintinnids (Detwyler and Houde 1970; Houde and Lovdal 1984). Older larvae feed upon larger copepodids and adult copepods. In Great South Bay, NY (Castro and Cowen 1991), and in Chesapeake Bay (Rilling 1996) positive correlations between anchovy egg or larval densities and microzooplankton abundances were found, suggesting that larval food availability determines intensity and timing of the peak spawning period in this system.

POPULATION DYNAMICS

Age and Growth.--Adult bay anchovies may live to be slightly more than 3 yr, although few otolith-aged individuals apparently survive to that age (Newberger and Houde 1995). Mean lengths-at-age of adults in mid-Chesapeake Bay (Newberger and Houde 1995) were 55.0 mm FL at age-1, 70.7 mm FL at age-2, and 83.1 mm FL at age-3. For anchovies in lower Chesapeake Bay, size at 50% maturity has been estimated to be 36.9 mm FL with age at 50% maturity occurring at about 80 d (Luo and Musick 1991). Other studies (E. Houde, person. commun.[6]) from this area, however, report that few anchovies <40 mm are mature and very few of these fish mature before they have overwintered, i.e., age at maturity is generally 10 mo or older. Average annual mortality rates for bay anchovy are high, ranging from 89-95%/yr (Newberger 1989).

Within Chesapeake Bay, fish condition and body energy levels fluctuate seasonally, and are related to anchovy size (Wang and Houde 1994). Energy equivalents were highest in December, before the overwintering period. The overwintering loss of energy was estimated to be 33-35% of total body calories, and was primarily derived from fat deposited in somatic and visceral tissues. While overwintering, somatic weight also decreased indicating that visceral lipids did not meet energy demands, and that part of the energy for overwintering survival came from muscle. The amount of lipid required for anchovy to survive a cold winter is not known. Wang (1992) suggested that a size-selective overwintering mortality in this species may selectively kill smaller fish, although it was difficult to conclusively separate possible size-selective mortality from loss of individuals due to migration from the system.

Importance and Utilization.--The bay anchovy is a small, unexploited species of anchovy. It has limited commercial use primarily as a baitfish and has been used to a limited extent in the preparation of anchovy paste (Hildebrand 1963).

In areas where abundant, it is extremely important in estuarine and coastal food webs (Baird and Ulanowicz 1989; Houde and Zastrow 1991). In fact, the bay anchovy may have the largest numbers of any estuarine fish found along the south Atlantic and Gulf coasts of the United States (Baird and Ulanowicz 1989). Its production links secondary plankton production to fisheries output and is very important to the energetic processes of the ecosystem (Luo and Musick 1991).

Chapter 23. STRIPED ANCHOVY *Anchoa hepsetus* (Linnaeus 1758)

Description.--Body somewhat compressed, elongate; depth about 5 times in SL. Snout pointed, about 3/4 eye diameter; maxilla long, tip pointed, reaching beyond posterior border of preoperculum, almost to gill opening. Anal fin short, its origin about at vertical through midpoint, or slightly posterior to mid-point, of dorsal-fin base. Anus nearer to anal-fin origin than to pelvic fin tips. (Hildebrand 1963; Whitehead *et al.* 1988).

Meristic features.--Dorsal-fin rays 13-16; anal-fin rays iii,16-20; pectoral-fin rays 13-15; scales in lateral series about 37-43; lower gillrakers 15-25, usually 16-19; upper gill rakers 19-22; vertebrae 40-44.

Color.--Fresh specimens pale gray and iridescent; upper surface of head with some green and yellow; dorsal regions with dusky dots; with prominent, broad, silver stripe along side (also with dark line above lateral silver stripe) of uniform width, except narrowed immediately behind gill opening; silver stripe equal with about 3/4 eye diameter. Dorsal and caudal fins more or less dusky on some specimens.

Size.--Maximum about 15.0 cm SL, commonly 10.0-13.0 cm SL.

Distinctions.--Striped anchovy closely resembles the bay anchovy, but differs in having fewer anal-fin rays (16-20 vs. 24-30 in bay anchovy) and the anal fin is placed at a vertical through the posterior rays of the dorsal fin.

Habits.--Marine, pelagic, coastal, forming dense schools, often in shallow waters close to shore (but recorded to 70 m); able to tolerate a wide range of salinities, from hypersaline to almost freshwater (Hildebrand 1963; Whitehead *et al.* 1988).

Feeding.--Feeds on copepods (especially when young), mysids, gastropods, foraminifera, and occasionally, ostracods and annelids (Stevenson 1958; Hildebrand 1963). Summer and fall diets of striped anchovy in saltmarsh creeks of South Carolina consisted of a variety of small and large planktonic items (Allen *et al.* 1995), including copepods, crab zoeae and megalopae, shrimp larvae, and fish larvae. Virtually the only adult copepod consumed by striped anchovies was *Acartia tonsa*.

Parasites.--The principal parasites are nematodes, cestode larvae (*Rhyncobothrium* sp.) and digenetic trematodes (Hildebrand 1963).

General Range.--Western North Atlantic north as a stray to Maine (Kendall 1931) and to the outer coast of Nova Scotia (single capture of five specimens, 5.4-5.9 cm TL, taken in Bedford Basin; Vladykov 1935; Scott and Scott 1988), south to Fort Pierce, FL (but not Florida Keys), at least the northern part of the Gulf of Mexico, and western central and South Atlantic (Gulf of Venezuela south to Uruguay). In coastal waters along the eastern United States, the striped anchovy is more abundant from Chesapeake Bay to Florida; overall, this is a more southerly fish than the bay anchovy (Hildebrand 1963).

Occurrence in Gulf of Maine.--Inclusion of this species is based on one record off the mouth of the Penobscot River, near Portland, October 8, 1930 (Kendall 1931). One specimen was saved and identified, and Bigelow and Schroeder (1953) reported that the herring fishermen who brought it in stated that there were "lots of them" on that date.

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