Herrings and Shads of North America: Diversity, Natural History, Conservation, and Aquarium Care

Christopher Scharpf
1107 Argonne Drive, Baltimore, MD 21218
ichthos@charm.net

"... it is a fish of crowds, not one to strike out much of its own."
— *John Hay*

Silvery, slab-sided, and generically fish-shaped, members of the family Clupeidae—herrings, shads, sardines, pilchards, sprats, and menhaden (collectively called clupeids)—are easily overlooked in favor of more charismatic or distinctively assembled fishes. But their role as an abundant food source for higher predators, including man and fishes eaten by man, makes them impossible to ignore. Pound for pound, clupeids are arguably the most important fishes in the world.

Diversity and Distribution

Nature, recognizing a good thing, wisely made clupeids a cosmopolitan family. Herrings and their allies are found in all seas from 70°N to about 60°S, with anadromous and freshwater species occurring in all continents within their oceanic range. The family comprises 214 described species in 65 genera in six subfamilies: pristigasterids (Pristigasterinae), round herrings (Dussumieriinae), herrings, sardines and sprats (Clupeinae), freshwater herrings (Pellonulinae), shads and river herrings (Alosinae, herein referred to as alosines), and gizzard shads (Dorosomatinae). Ten species from the alosine and gizzard shad subfamilies occur in the fresh waters of North America (see pp. 13-14).

Members of the genus *Alosa* comprise at least 15 species throughout Europe and North America, with four species occurring in Atlantic Coast drainages of the U.S. and Canada, and two species ranging from the Gulf Coast upwards through the Mississippi Basin into Iowa, Wisconsin, and Minnesota. Some Atlantic species occur far outside their native ranges, usually in lakes and reservoirs, either from intentional introductions to provide forage for stocked gamefish, or by passage through manmade waterways.[1] The American shad (*A. sapidissima*) was planted into California's Sacramento River in 1871 and has spread up the Pacific Coast and across the Bering Strait into the Kamchatka Peninsula. Apparently, temperature anomalies and ocean currents caused by El Niños have proven to be conducive to American shad reproduction (Ebbesmeyer and Hinrichsen, 1997), as have the reduced-current areas created by dams (Hinrichsen and Ebbesmeyer, 1998). Today, the largest American shad run occurs in the Columbia River of the Pacific Northwest.

Gizzard shads of *Dorosoma* comprise five species in North and Middle America, with two widespread American species native to fresh and brackish waters east of the Continental Divide, and two species in México. (The fifth species, *D. chavesi*, is endemic to Nicaragua). The two American species have been introduced throughout the U.S. as forage fishes.

[1] Miller (1957) concluded that landlocked alewives (*A. pseudoharengus*) are native to Lake Ontario, but admitted that there was no conclusive evidence to back this up. Daniels (2001) reviewed evidence that alewives either entered Lake Ontario via the Erie Canal, were accidentally stocked with other shad fry, or are native as Miller suggested; stocking appears to be the most likely explanation, although Daniels, like Miller, admits that direct evidence is lacking.

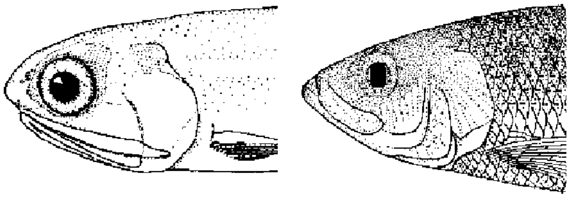


Fig. 1.
Mouths of (left) bay anchovy (*Anchoa mitchilli*) and (right) hickory shad (*Alosa mediocris*), showing how the lower jaw extends farther behind the eye in anchovies than it does in herrings.

General Description

Clupeids are readily distinguished from anchovies (Engraulidae) by their small and terminal (as opposed to large and underslung) mouth (Fig. 1), and by the presence of sharp scutes along the belly (giving some herrings the nickname "sawbelly"). Clupeids are also superficially similar to mooneye and goldeye (Hiodontidae); again, the clupeid's saw-edged belly is a giveaway. Other distinguishing differences between the two families are the clupeid's eyes, which have an anteriorly positioned eyelid of transparent adipose tissue, and the clupeid's absence of lateral line scales.

Adult gizzard shads are easily distinguished from alosines by the presence of a distinctive dorsal fin with the last ray drawn out into a long, whiplike filament (Fig. 2). The two genera also differ in the anatomy of their digestive systems. Gizzard shads get their name from a muscular, thick-walled stomach that's similar to the gizzards of wildfowl. Although generic separation of gizzard shads from alosines may be artificial (a gizzard is found in two other clupeid genera), gizzard shad intestines are unique among the family; like that of a cow and various herbivorous minnows, it is long and looped back upon itself so that it can better digest and assimilate large amounts of planktonic vegetable matter.

Size Range

Smallest: Sanaga pygmy herring (*Thrattidion noctivagus*) of Cameroon, 2.14 cm (4/5 in). The smallest North American species appears to be the Pacific gizzard shad (*Dorosoma smithi*), which reaches at least 14 cm (5.5 in), but more field data is needed to confirm its maximum size.

Largest: Four species are known to reach 60 cm (24 in): Allis shad (*Alosa alosa*) of Europe, Hilsa shad (*Tenualosa ilisha*) of the Indian Ocean, and hickory shad (*Alosa mediocris*) and American shad of North America; however, the Allis shad appears to reach 60 cm more regularly than the other species, so it's regarded as the largest herring here. Of the two

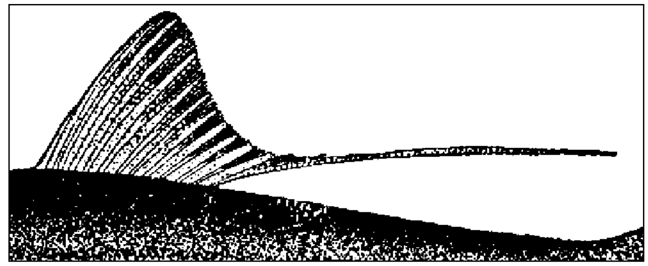


Fig. 2.
Dorsal fin of an adult threadfin shad (*Dorosoma petenense*), showing the whiplike dorsal filament.

American species, American shad is the largest, as it often reaches 50 cm (20 in) and weights of 2-4 kg (4-8 lbs).[2]

Natural History

As the differences in their digestive systems and distributions begin to indicate, *Alosa* and *Dorosoma* live markedly different lives. All but one of North America's six alosine species (except for nonindigenous landlocked populations) are anadromous, living at sea and only entering fresh water to spawn. Gizzard shads, on the other hand, spend most of their lives in fresh water. The two genera also differ in what they eat. *Alosa* are predatory, consuming a variety of invertebrate organisms at each life stage and small fishes as adults. *Dorosoma* are filter-feeders and browsers; their specific feeding mechanisms, described below, are among the most interesting of North America's freshwater fishes.

Anadromous alosines are river-specific, with each major river along the Atlantic Coast appearing to have a discrete spawning stock (ASMFC, 1999). Depending on their location, alosines may spawn once and then die (semelparity), or they may survive to make several spawning runs per lifetime (iteroparity). For American shad, the degree of semelparity decreases the further north the fish lives. Populations in the environmentally benign waters of Florida are entirely semelparous, while populations in the harsher, more environmentally unpredictable waters of New Brunswick are 60-80% iteroparous (Leggett and Carscadden, 1978). Northern stocks of American shad produce fewer eggs than southern stocks, presumably to save energy for their lengthy post-spawn migrations: north to feeding grounds in the summer, then

[2] Size estimates are based on data from Whitehead (1985). The Dorab and whitefin wolf herrings (*Chirocentrus dorab* and *C. nudus*, respectively) of the Indo-Pacific are the largest clupeoids in the world, reaching 100 cm (39 in), but are placed in a separate family (Chirocentidae).

south to warmer waters to overwinter. They also conserve energy by swimming more slowly during their migrations than stocks from the south (Glebe and Leggett, 1981). In addition to saving energy, iteroparity may provide northern stocks a "second chance" should environmental conditions not be to their liking. For example, if a springtime cold snap wiped out a portion of that year's spawn, northern stocks would have an opportunity to try again the next year (K. A. Hattala, pers. comm.). Precisely what controls the direction and path of alosine migrations is the subject of intense investigation and speculation among fishery scientists. Also under investigation are the homing cues that allow many alosines to return to spawn in the very rivers where they were born.[3]

For many coastal residents, the annual return of alosines to their freshwater spawning grounds is a harbinger of spring. In fact, the return of American shad, beginning in April, occurs almost simultaneously with the blooming of a shrubby tree called a serviceberry, or shadbush, and the arrival of a gnat, called a shad fly. When the shadbush blooms and the shad fly buzzes about, American shad are coming up the rivers to spawn. In Cape Cod, the spawning run of the alewife[4] (*A. pseudoharengus*) is a popular event for nature lovers. Alewives prefer to ascend streams during the day, usually in bright, sunny weather, making them easy to see. Sometimes their upstream migrations demonstrate a dramatic, salmon-like persistence. In rapid waters not much deeper than their bodies, alewives will turn on their sides and force themselves up through the current—a spectacular sight for those who are fortunate enough to see it.

Although Atlantic Coast alosines vary in when and where they migrate and spawn, they all follow a pattern similar to that of American shad. Usually the males, called bucks, arrive from the ocean first, followed a few days later by the females, or roe shad. Here they spend 3-5 days getting acclimated to fresh water, slowly swimming back and forth from brackish water into increasingly less brackish water on a daily basis (Leggett, 1976). Once acclimated, they quickly begin to move toward their spawning areas. Neither sex feeds during their upstream journey,[5] but that may be attributable to the fact that larger food items found in the ocean (e.g., krill) are not found in fresh water (K. A. Hattala, pers. comm.). A spawning shad loses up to 40% of its body weight (McPhee, 2002). Water temperature is the primary factor that triggers spawning, but daylength, water current velocity, and turbidity exert some influence as well (ASMFC, 1999). Males pursue females during the night in a series of rapid, fluttering movements at the surface, called "washing" by shad anglers. Then a mass communal spawning takes place, with some individuals spawning in pairs, or in small groups comprising one female and several males. The spawning run can last for 8-10 weeks, with adults spawning with more than one partner. (Details on spawning behavior are given on p. 8, below, in the section on captive propagation.)

By moving far upstream to spawn, shad parents bestow their young with a selective advantage. In the words of biologist Boyd Kynard, they're born "at the head of the chow line" (quoted in McPhee, 2002). Upstream, where tributaries wash zooplankton into the river, there's more food for a large concentration of newly hatched shad to eat than there is downstream. As the shad larvae grow, they drift downstream with the current until they mature into juveniles. Juveniles remain in nursery areas—usually deep pools away from the shoreline in non-tidal areas—feeding on increasingly larger organisms, including copepods, chironomid larvae, and aquatic and terrestrial insects.[6]

By late fall, most juvenile American shad migrate to nearshore coastal wintering areas, then make their way to the ocean, where they presumably join other schools from other

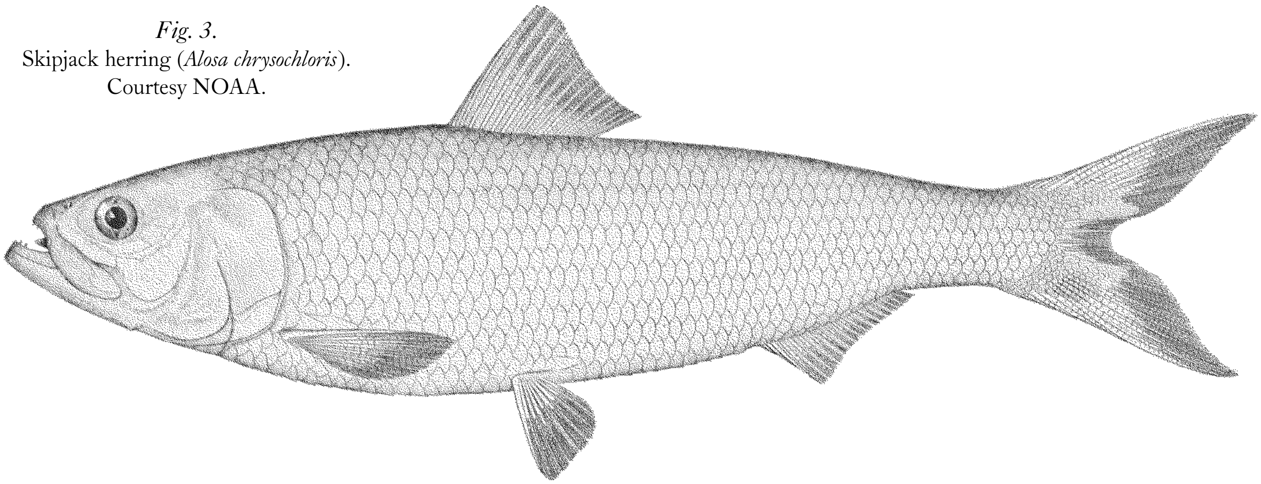
[3] Not all alosines return to their natal rivers; a small percentage stray to other rivers.

[4] The origin of the name "alewife" is not clear. Some say it's a derivation of the Indian word "aloofe," meaning bony fish (alewives, like other alosines, are filled with small bones). Cape Cod naturalist and alewife-watcher John Hay believes the name comes from an English source. Hay notes that alewife is a colonial name for an alehouse keeper. According to one 1675 passage, "The alewife is like a herrin', but it has a bigger bellie, therefore called an alewife." Since an alewife (the fish) has "a deep body and is heavily built forward," Hay writes, "so perhaps a comparison with a hearty alewife of sixteenth- or seventeenth-century England would not be too far-fetched" (Hay, 1959). The species is known by an assortment of other colorful local names, including spring herring, branch herring, bit-eyed herring, ellwife, ellwhip, goggle-eye, sawbelly, grayback, freshwater glut, bang, kyak, mulhaden, racer, seth, and buckeye.

[5] Although migrating shad do not feed, they still strike lures. Why? No one knows. One guess is that the shad may be expressing aggression, irritation, or both. (Migrating Pacific salmon, which also do not feed, strike lures too.) Shad rarely swallow the lures, which usually get snagged on the outer rim of their mouth (McPhee, 2002).

[6] Juveniles can often be seen dimpling the water as they pluck flying insects from the surface. Fisheries ecologist Karin Limburg once examined a 6.3 cm (2.5 in) alosine with its gut full of flying ants. "The amount of food in this fish, relative to its size," Limburg wrote, "would have been the human equivalent to a full Thanksgiving dinner with all the trimmings—turkey and all!" (Limburg, 1997). An alternative explanation of dimpling is juvenile shad at the bottom of the school rushing to the surface to avoid a predator (McPhee, 2002).

Fig. 3.
Skipjack herring (*Alosa chrysochloris*).
Courtesy NOAA.



river systems and spend 3-6 years wandering up and down the coast before returning to their natal streams to spawn. Iteroparous adults return to the sea and migrate northward to their summer feeding grounds. When winter arrives, they migrate southward to the warmer waters of the mid-Atlantic Coast. During an average life span of five years, a single American shad may migrate over 20,000 km (13,670 mi) (Dadswell et al., 1987).

Alewives and blueback herring (*Alosa aestivalis*, front cover, top two fish) represent an example of what scientists called sympatry—when species occur together, and may even appear identical, but do not interbreed. Commercial fishers often catch both alewives and blueback herring together. Since the two species look so much alike, fishers refer to them both as river herring in the U.S., and as alewife or gaspereau in Canada. Yet while these two species may look alike, and live (and often perish in nets!) together, nature has inserted subtle yet significant differences into their life histories in order to keep them separate. In northeastern rivers where alewife and blueback herring co-exist, alewives spawn in more sluggish waters, while blueback herrings seek out swifter flowing channels. In southeastern rivers where alewife are few, the blueback herring is less choosy about water velocity, and will spawn in a wider variety of sites, including shallow areas covered with vegetation, rice fields, and swampy areas. Obviously, if the two species spawned in the same areas, their populations might suffer since their young, which eat the same kinds of food, would be forced to compete (Loesch, 1987). And while the contents of fishermen's nets seem to indicate that the two species school in the ocean together, other evidence suggests that alewives live at a greater depth. The greener dorsal coloration of the alewife and its slightly larger eye may be adaptations to the deeper, dimmer waters of the Continental Shelf, where green light penetrates more so than blue (Desfosse et al., 1994).

Alosines that live in landlocked populations obviously cannot migrate to sea to mature; they do, however, undertake abbreviated "migrations" by moving into shallower waters to spawn. In some lakes, alsoines take advantage of the largely unexploited planktonic food supply and make up a disproportionate and unhealthy percentage of the fish population, crowding out other fishes such as perches and minnows. In the Great Lakes, the alewife has been implicated in the decline of ciscoes (*Coregonus*), plankton-eating relatives of the trout (Smith, 1985). In Lake Michigan, massive die-offs of alewives that litter the beaches have been a common (and smelly) occurrence. Die-offs in the 1960s were caused by an over-abundance of fish that outstripped its food supply. That problem has been mitigated with the introduction of non-native Pacific salmon (*Oncorhynchus*), an efficient alewife predator. More recent die-offs are attributed to the alewife's inability to tolerate the sharp temperature changes between the deep, cold waters of the Great Lakes, and the shallow, warmer waters along its banks and in its tributaries (Moy, 1999).

The only naturally occurring non-anadromous alosine in North America is the skipjack herring (*Alosa chrysochloris*, Fig. 3); with the possible exception of some Mississippi River populations, it completes its entire life cycle in fresh water. Even so, the skipjack herring, like its fellow alosines, migrates upstream to spawn. It's a fast-swimming fish that got its common name from its habit of skipping out of the water while in pursuit of its favorite food, minnows.

In contrast to the predatory *Alosa*, the favorite foods of *Dorosoma* are algae and zooplankton. Juvenile *Dorosoma* do not possess a gizzard; it develops as they mature. Juvenile gizzard shad (*D. cepedianum*, Fig. 4, bottom) feed in schools, filtering protozoans and unicellular algae from the water column through their long gill rakers. As their gizzard forms they become less gregarious and shift to almost total herbivory, browsing through bottom sediment and over the surfaces of logs, plants, and other submerged objects. Unlike gizzard shad, juvenile threadfin shad (*D. petenense*, Fig. 4, top) do not change their diet as they mature, nor do they abandon their mid-water schooling behavior. Their diet consists of small plant and animal matter, especially blue-green bacteria, diatoms, green algae, fish larvae, water mites, and microcrustacean eggs. Threadfin shad only take food from the bottom when pelagic food is not available (Ingram and Ziebell, 1983).

How *Dorosoma* digest their food is unique among North America's fishes. Instead of immediately swallowing their food, *Dorosoma* store it in special sacs at the top of their gill arches called epibranchial organs. Here the food softens into a round mass, or bolus. When the epibranchial organ is full, the bolus is passed down the pharynx into the fish's gizzard-like stomach.[7]

Gizzard shad prefer slower moving waters, while threadfin shad prefer stronger currents. Both species spawn in the spring. Gizzard shad usually spawn at night, as a "group of males and females swimming near the surface begin to roll and tumble about each other in a mass, the eggs and sperm being ejected during this activity" (Miller, 1960). Threadfin shad spawn in the first few hours after sunrise until about noon, with large aggregations of adults swimming toward the surface and parallel to the shore. Smaller groups of one to several females and many more males sometimes split off from the main group and, in very shallow water, scatter their eggs on floating objects and emergent substrate (Shelton et al., 1982). Apparently, darkness is the cue that prompts threadfin shad to ovulate; when researchers squeezed the sides of females caught before and after the brief spawning window, eggs were not in position to be released (McLean et al., 1982). The eggs of both species sink to the bottom and stick to plants and other objects.[8]

[7] The epibranchial organ may explain why some claim that gizzard shad eat mud. True, gizzard shad pick up bottom debris and sort through it looking for food. And true, it's likely that mud is incidentally ingested. But the belief that mud is a staple of their diet is probably due to the fact that by the time the bolus reaches the intestine it has been partially digested into a mud-like consistency (Becker, 1983). It has also been suggested that *Dorosoma* eat sand; though it's never been proven, sand may assist in the grinding of food in the gizzard (Bodola, 1966).

[8] Little is known about the two *Dorosoma* species endemic to México, longfin gizzard shad (*D. anale*) and Pacific gizzard shad (*D. smithi*). Both presumably feed and breed like their counterparts to the north.

The ecological importance of alosines and gizzard shads cannot be emphasized enough. Freshwater ecosystems, by their very nature, lose energy and nutrients to the ocean; they're literally washed downstream. But anadromous fishes like alosines are one way for energy and nutrients from the ocean to transfer back into fresh water. One study has shown that decomposing post-spawning alewives stimulate microbial activity that releases the vast supply of energy stored in the autumn leaves that litter stream bottoms during the spring (Durbin et al., 1979). In addition, alosine eggs and fry provide an abundant food source for freshwater fishes. How abundant? Consider this: One ecologist estimated June abundance of blueback herring larvae in the Hudson River Valley to exceed 85 billion individuals, and American shad larvae at 168 million individuals (Limburg, 1997). In the ocean, alosines are preyed upon by many species including sharks, tunas, seals, and porpoises. And in their respective food webs, *Dorosoma* serve as a short and efficient link between microscopic plant life and larger predators. Occasional massive die-offs of *Dorosoma* provide an important source of food for waterfowl, wading birds, and avian predators such as bald eagles.

Aquarium Care and Captive Propagation

Pelagic, schooling fishes like clupeids are poor subjects for the home aquarium since they're accustomed to swimming across great distances in vast, unimpeded expanses of water. Life in the glassy confines of an aquarium, however, is too confining. Clupeids are extremely nervous unless they are kept in large schools, and overly sensitive to vibrations and the sudden turning on-and-off of lights. Frightened clupeids bash themselves against the aquarium glass as if trying to break through it, and they easily lose their loose-fitting scales, which, for such delicate fishes, is almost always fatal.[9] For these reasons, clupeids are best left in the wild, or to large public or laboratory aquaria that can accommodate their spatial and schooling needs.

But if you're the type of aquarist who enjoys a challenge, then keeping clupeids will pose just that. First, forget about obtaining mature specimens from the wild. Their reputation for immediately dying if you so much as touch them with a net is legendary.[10] And should one survive the net, it will

[9] Although detrimental in captivity, loose-fitting and easily shed scales help clupeids in the wild maintain speed and mobility.

[10] "They're fish with emotional problems," says Boyd Kynard of American shad. "You can lift them out of the water a matter of seconds

Fig. 4.
Top: threadfin shad (*Dorosoma petenense*).
Bottom: gizzard shad (*D. cepedianum*).
Photographs © Garold Sneegas.

almost certainly beat itself to death against the sides of a collecting bucket or transport container unless anesthetized. Instead, the key to maintaining alosines in aquaria is to get them while they're still larvae, or newly post-larval, and let them mature under captive conditions. It's not that *Alosa* juveniles are less delicate than adults—they aren't. (They see a net and die, joked one biologist I spoke with.) Rather, the advantage of keeping juveniles is that their size allows them to be transported without netting or lifting them out of the water. Be mindful, though, that juvenile alosines are sensitive to water turbulence. In fact, hatchery workers are so paranoid about this sensitivy that they take great care to avoid turbulence when pouring juveniles from one container to another (M. L. Hendricks, pers. comm.).[11] Instead, gently corral them into a wide-mouth container and then let them swim out on their own accord. Another, perhaps greater, advantage is that it is easier to maintain a large school of juvenile alosines than a large school of adults. Schooling, even to the point of overcrowding, appears to be the secret to keeping captive alosines happy.[12]

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and they just die, the stress is so great. I've never handled another species like that. It may be that their potassium level goes down. In any case, some sort of chemical imbalance occurs and it's irreversible. They literally die of fright" (quoted in McPhee, 2002). Shad biologist Kathryn A. Hattala tells a slightly different story. She thinks alosine sensitivity to netting is a matter of timing and handling, and may depend on what river system the fish is from. Alosines captured in, say, the Delaware and Connecticut rivers have had a longer and more arduous migration, so they are more stressed and prone to die. In contrast, adult alosines captured in tidal areas of the Hudson River are "lively and feisty . . . [and] will not stay still for a few seconds for us to even measure!" (K. A. Hattala, pers. comm.).

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[11] Juvenile alosines can't be *too* sensitive considering that the 10,000 newly hatched American shad that seeded the Pacific Coast's shad population in 1871 survived their journey from Albany, New York, in four eight-gallon milk cans! Water was changed about eight times during the week-long journey, with water from whatever river or lake that was encountered along the way. Ice-water was used to keep the water temperature below 28°C (82°F). When the shads' yolk sacs were used up after five days, the fish fed on small insects that came in during the water changes (Ebbesmeyer and Hinrichsen, 1997).

According to fisheries ecologist Karin Limburg, laboratory experiments on American shad metabolic rates in response to schooling density show that a good rule for keeping shad is definitely "the more, the merrier" (K. Limburg, pers. comm.). The more shad that were in a tank, the lower their metabolic rates. "I'm sure there's a break-point where oxygen stress and the buildup of ammonia would counteract the benefits of schooling with large numbers of other shad," Dr. Limburg adds, "but we certainly did not reach that threshold." Finally, Dr. Limburg advises that sea salt is a great aid in times of stress. She used a salt solution of 5 ppt when she transferred fish, and found that larvae had the lowest mortality and best growth at 10 ppt (as opposed to 0 and 20 ppt).

Feed juvenile alosines live baby brine shrimp. As they grow they can sometimes be weaned over to fine grain foods, but small live foods, such as adult brine shrimp, should always be part of their diet. Aquaria should be as large as possible, with a large, open swimming area and efficient (but gentle) wet/dry filtration. Other tankmates are not recommended. In the aquarium, alewives are said to be aggressive towards other fish; when food enters the water, they swarm into the food and consume it while the other fish retreat to the side and don't feed (Becker, 1983).

Acquiring larval and juvenile alosines may be as difficult as keeping them. Catching them in the wild seems impractical, since locating juveniles would require knowing when and where the parents spawned, and where the juveniles are feeding. A more reliable source would be hatcheries where alewives are raised for bait. Educators may wish to contact the Chesapeake Bay Foundation, which supplies larval shad and equipment to select Maryland and Virginia schools.

Few public aquaria exhibit alosines, partly because of their difficulty, but mostly because they are not "sexy" fish that sell tickets. One facility that does is the National Aquarium in Baltimore (NAIB), which maintains a circular, 22,000-gallon "schooling" tank with approximately 800 alewives. NAIB aquarists collect the alewives from freshwater ponds in New Jersey, where they are raised commercially. During the night the fish are attracted to lights, which are strategically placed to draw them into small impoundments. In the morning the gates to the impoundents are closed and the fish are easily (but gingerly) collected. The alewives (about 1000 per load) are shipped to NAIB in a special truck outfitted with a 10-foot round tank. Back at NAIB the alewives are slowly conditioned to salt water (31 ppt) during a 30-90 day quarantine period. Once on display, the outflow of the tank's sand filter system forces the fish to swim in one direction. Eventually the fish develop ulcers on one side of their mouths, presumably from rubbing up against the acrylic walls of the tank. This is remedied by reversing the direction of the flow. Since the alewives are constantly swimming, they are fed a high-energy diet of small krill in the morning and Tetramin flakes throughout the day with the use of an automatic feeder. Once the alewives are settled in the aquarium scale loss is minimal. Their life expectancy on display is 1-2 years (R. Bromwell, pers. comm.).

Little has been published on the aquarium care of gizzard and threadfin shads. In one laboratory experiment, threadfin shad were maintained in 40-gallon tanks on a diet of live daphnia, chironomid larvae (bloodworms), and tubifex worms. The fish were quite proficient at digging out food that was buried in the sand (Ingram and Ziebell, 1983). A key to their captive survival, it seems, is light handling and quick transport from the field. (Adding some salt to the water also helps reduce stress.) McLane (1955) reported catching threadfin shad at night with a flashlight; the fish were attracted to the beam and literally jumped out of the water onto dry sand at McLane's feet. Gizzard shad are displayed at the Mississippi Museum of Natural Science in Jackson, but even here aquarists admit that the fish are delicate and that few of the shad they catch—about one in 200—survive the journey from stocking ponds to the aquarium. The few that do survive, however, readily accept prepared food and live a long time (R. Weitzell, pers. comm.).

As with most migratory fishes, alosines will not naturally spawn in aquaria since the environmental cues that induce spawning (as far as they are known) are too complex to be simulated. But alosines are artificially spawned at hatcheries in one of two methods. Most "low-tech" hatcheries are located directly on the rivers where the young are to be released. Hatchery workers collect ripe males and females as they return to spawn. They squeeze the female's eggs into a shallow bowl or bucket and fertilize them by gently stirring in sperm from the males. The eggs are then placed into hatching tanks that are continuously refreshed with water pumped from the river. As the newly hatched fry mature, they make their way through a pipeline that whisks them to their permanent home.

[12] In the wild, schooling has a hydrodynamic advantage, similar to what bikers experience when they ride in packs, or when geese fly in a "V" formation. By riding vortices of water that come from the fish in front of them, shad are able to swim with less energy in a school than they could by themselves. The larger the school, the less oxygen they consume (McPhee, 2002).

A more "hi-tech" hatchery approach allows shad to spawn on their own with the help of hormone injections. Migrating alosines are collected from the wild, dipped into an anesthetic to keep them calm, sexed, and tested to see if their eggs and sperm are sufficiently developed for the hormone to work. A glass pipette is inserted through the vent and into the testes and ovaries and small samples of eggs and sperm are removed, which are then examined under the microscope. If a fish is ready, it's given a hormone injection—a grain of rice-sized pellet with the consistency of an aspirin. Since mortality is high from the rough handling, hatchery workers also mix non-injected specimens in with the injected ones. Hormones released during the induced spawning process cause the non-injected fish to spawn as well. The resulting orgy-like spawning act, described below, is summarized from a hatchery report from the Maine Department of Marine Resources (Chapman and Chapman, 1997):

In June and July 1997, around 30 American shad were injected and released into a 3,030-gallon, naturally lit spawning tank.[13] During the day, the shad swam parallel to each other, usually against the current. But as the hormones took effect and the afternoon waned, the shad got more excited and unpredictable in their movements. First, occasional individuals "changed lanes." Then they began doing U-turns and 360° loops around the tank, now usually with the current. Then this looping turned into sudden high-speed bursts, with individuals racing around the tank one to 1-1/2 times. Now the shad also began to get more aggressive. A male approached a female from the rear and attempted to touch his nose to just in front of her tail. The female didn't seem to like this, and so the two shad, as a pair, chased around for one or two circuits of the tank, often splashing and slapping on the surface (the behavior shad anglers call "washing"). However, the fish had not yet spawned. Instead, the high-speed, pair-swimming behavior apparently serves as a way to get the other shad more excited. As darkness fell, more and more shad seemingly lost their inhibitions and began falling out of their parallel swimming patterns. The number and frequency of aggressive encounters, along with the U-turns and 360° loops, continued to increase as the evening wore on. Eventually, the aggressive pairings became mutually agreeable and spawning occurred. Each pair of spawning shad swam in tight 360° loops, during which they vibrated or jerked spasmodically, with the inside shad pushing against the outside shad's body. During these encounters eggs and sperm were squeezed out. Apparently, the sight (or scent?) of these spawning shad incited unpaired shads to swim in vibrating circles by themselves. Since they do not have a mate to help them release eggs and sperm, they availed themselves of whatever was in the water, pushing, bumping, or vibrating against filter pipes and the tank walls. One individual shad was observed several nights in a row slowly bumping its side against the tank in what seemed like a choreographed manner. It would visit the same several spots on the tank wall, bump it gently several times, then swim to another spot and repeat the ritual. After several stops the shad would reverse direction, swim directly back to the original spot, and begin the pattern again. Hatchery workers who placed their fingers against the tank glass could detect some of these vibrations, which were described as "much like [that of] a low frequency vibrator pad." In this particular tank, the shad produced 0.2-2.3 liters of eggs nightly, at an average of 82,700 eggs per female.

Threadfin shad are cultured in nursery ponds and stocked into reservoirs and lakes to provide forage for gamefish. (Fishery managers prefer threadfin shad over gizzard shad because their smaller size makes them easier for predators to swallow.) Nursery ponds are seeded with a fertilizer, such as fresh cow manure, in order to stimulate a bloom of plankton. Shallow portions of the ponds are stacked with six-inch bales of hay to provide a place to spawn. Since overfertilizing, over-feeding, or too much hay can deplete oxygen levels, especially during the summer, an emergency water supply is recommended. As long as nursery ponds are free of predators, a yield of 50,000-100,000 threadfin shad per acre is possible (Higginbotham, no date).

Importance to Humans

The clupeids' claim to "most important fishes in the world" is based on more than just their ecological importance; combined with their cousins the anchovies, clupeids are the most *economically* important fishes in the world as well. When fishery statistics are reviewed worldwide, no other group of fishes is harvested more, and consumed more, by man.

Among North America's freshwater clupeids, Atlantic Coast alosines have been the most economically significant.

[13] A 7-watt light bulb was placed over the tank so that hatchery workers could observe the shad after dark. The visible level of light did not seem to bother the shad and was just enough to see them as they swam around in the tank. However, additional experiments showed that fewer eggs were produced when the intensity of the light was increased. In brightly lit tanks, the shad gathered in dimmer areas. In the wild, American shad, which spend most of their lives in the dimly lit ocean, avoid bright light during the day.

Alosines provided food and fertilizer for Native Americans and early European settlers. Although shads were initially shunned by New Englanders in favor of Atlantic salmon, colonists eventually discovered the tasty roe of female American shad and learned how to properly fillet and prepare their bone-filled bodies. What's more, salted shad provided an inexpensive staple during the winter when other sources of protein were scarce.[14] Pickled, smoked, salted, canned, or planked (broiled over a charcoal fire), the American shad (Fig. 5) lives up to its scientific name—*Alosa sapidissima* means "most delicious shad." Because of their low price and excellent flavor, shad are sometimes called "poor man's salmon." Their roe is an annual rite of spring for many easterners, while many anglers enjoy shad as a good fighter at the end of a line.

Shad fishing quickly became a large and integral part of the growing economies along the mid-Atlantic Coast, with thousands of fishermen each trapping thousands of migrating shad daily. Over the years, their shad trapping contraptions got bigger and better: gill nets attached to poles driven into the river's bottom, seines (sometimes pulled by horses), pound nets, fyke nets, and shad floats (a floating seine fishery that could house up to a hundred men and pull seines hundreds of yards long). Especially devastating to shad runs were "fish dams" or "fish baskets"—V-shaped stone walls built across narrow streams or river channels that trapped migrating shad into boxes or cages, from which they were easily shoveled into bags or barrels (Gerstell, 1998).

Blueback herring and alewife are less palatable than American shad, and so command only a tiny fishery in which they're converted into fish meal for poultry, cat food, and fertilizer. Along Lake Michigan, residents are encouraged to take as many dead alewives as they want for compost heaps. According to the University of Wisconsin Sea Grant Institute, "Scientists are working on ways to make a smoked or sardine-like food product from Great Lakes alewives" (UWSGI, 1999). Whether a market exists for a fish that grosses people out when it dies and litters the beaches remains to be seen!

In addition to fish meal, humans have found other uses for alewives. In some East Coast water supply reservoirs, alewives have been introduced to control the plankton blooms that cloud drinking water. This practice once caused a minor disturbance in New York City when larval alewives from the Kensico Reservoir passed through the 5/8-inch mesh screens of the reservoir's outlet and flowed out of household faucets (Hay, 1959)! In other reservoirs, carcasses from alewife die-offs have clogged the intakes of power plants and municipal water filtration facilities.

One of the most widespread uses of alewives is to provide forage for sport and commercial fishes such as salmon, steelhead, lake trout, white bass, striped bass, and walleye. Gizzard and threadfin shad are also used for this purpose. But the efficacy and ecological wisdom of stocking clupeids to feed gamefish is questioned by many biologists. Alewives tend to benefit only those gamefishes that live in the middle of the water column, and are seldom eaten by more bottom-dwelling predators such as crappies and black basses. Alewives can also turn the tables on the fishes they're supposed to enhance by preying on gamefish larvae. Gizzard shad are excellent forage when they're small, but often grow too large to be preyed upon. Threadfin shad, by eating zooplankton, can reduce the amount of food available to young gamefish and sometimes cause clear lakes to turn green (Moyle, 2002). And then there are the ecological consequences of the population explosions and massive die-offs to which all landlocked clupeids are prone. Some biologists prefer that lakes not be stocked with forage fish at all; when forage fish are *not* abundant, they say, gamefish are hungrier and more willing to take a lure (Desfosse et al., 1994).

Although few people eat skipjack herring, the fish puts up a good fight when hooked, earning it the nickname of "Tennessee tarpon." The skipjack's importance to humans, however, had little to do with its taste or fighting ability. In the early 1900s, millions of ebony clam (*Fusconia ebena*) shells were harvested to make pearly buttons. The skipjack is the host for the clam's larvae, or glochidia.

The use of clupeids as baitfish is limited due to their fragility, but *Dorosoma* are commonly used as live bait for striped bass even though bait-bucket mortality is high. Dead specimens make excellent trot-line bait, either cut or whole. In Florida, gizzard shad are used raw or cooked for baiting eel and blue crab traps (McLane, 1955). Skipjack herring were once a popular catfish bait, but that practice has declined now that the skipjack is harder to come by.

Conservation

It's hard to imagine how many alosines once returned to the fresh waters of eastern North America. In Colonial times,

[14] Many history books tell the story of how George Washington's starving troops—and perhaps the fledgling American nation—were saved by an early spawning run of American shad in the Schuylkill River at Valley Forge in March 1778. But as John McPhee explained it in his 2002 natural and cultural history of American shad, *The Founding Fish*, the story of the "savior shad" is pure legend.

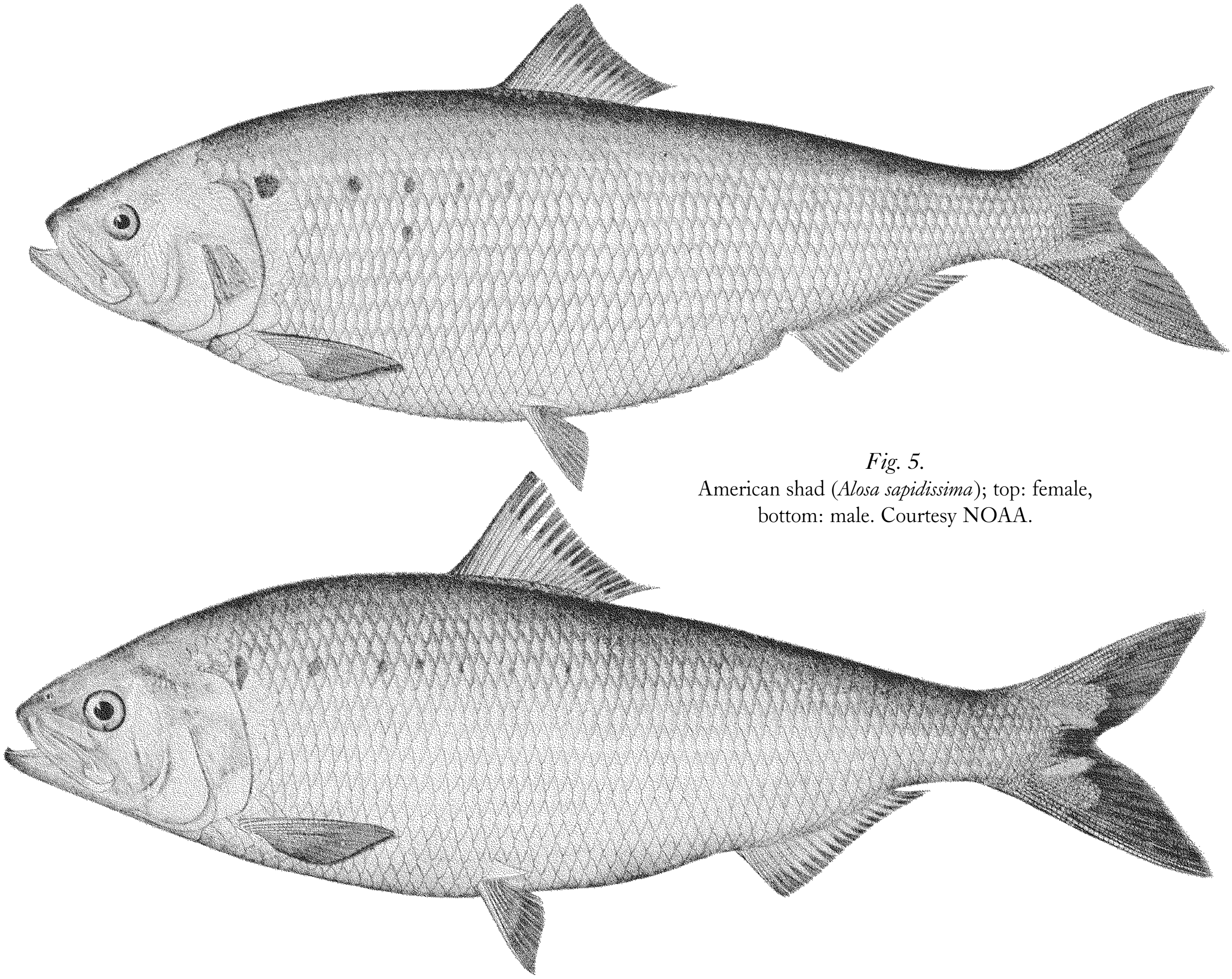

Fig. 5.
American shad (*Alosa sapidissima*); top: female, bottom: male. Courtesy NOAA.

settlers boasted they could catch American shad in frying pans (Anon., 1999b). Wagons crossing the James River by Richmond, it is said, used to squash the fish there were so many (Anon., 1996). By the second half of the 20th century, however, shad were gone from most rivers, or disappearing. In 1979, only 50 shads returned to the Susquehanna, which in the past had seen millions (Anon., 1999b).

The reasons for the declines are the same for other migrating fishes such as salmon and American eel: dams, overfishing, and pollution. Beginning in the 18th century, the construction of dams blocked alosines from reaching their spawning grounds. Three types of dams were involved: mill dams, which blocked smaller tributary streams; canal feeder dams, which, before the advent of railroads, diverted river water into manmade canals to facilitate inland shipping; and power dams, which made their first appearance in 1904. By the time the larger hydroelectric dams blocked off spawning runs for good, the damage had been done.[15] As fishermen developed more efficient ways to harvest more alosines during their upstream migrations, fewer alosines returned to spawn. And since alosines fail to spawn unless there is a large number of other alosines around them, the fewer that returned, the lower their chances of spawning. In recent decades, "intercept fisheries," in which alosines are caught off shore before they reach fresh water, have further depleted stocks. And for the lucky few alosines that manage to evade fishermen's nets, dams, and other obstructions (such as road culverts and

[15] It's ironic that American shad have declined on the East Coast in part because of dams, yet are flourishing while salmon are declining on the West Coast in part because of them. The reason for this seeming contradiction is that shad are adapted to East Coast rivers, which are slower-moving and warmer. Salmon are adapted to the colder, swifter-flowing rivers of the Pacific Northwest. The warmer waters and lake-like conditions that dams create are poor habitat for salmon, but ideal habitat for shad (Hinrichsen and Ebbesmeyer, 1998). Shad also take advantage of salmon ladders to get over the dams, a feature that, until recently, was missing from most dams on the East Coast. In addition, shad will abort spawning attempts if conditions are unfavorable and try again another year. Pacific salmon (except steelhead) die in fresh water whether or not they are able to spawn.

stream gauge stations), there's pollution to contend with. The Delaware River had a "pollution block" for many years because of industrial chemicals and municipal wastes coming from Philadelphia and Wilmington that stopped shad cold.

The decline of Atlantic Coast alosines did not happen recently, or even begin in the increasingly industrialized America of the 20th century. Alosines, especially American shad, began to decline as early as 1830 (Gerstell, 1998). The protection of shad runs dates as far back as 1700, when the Province of Pennsylvania outlawed the construction of fish weirs that completely blocked the passage of fish up rivers and streams. In 1761, Pennsylvania outlawed the use of fish dams or baskets. It should be noted, however, that the objective of such legislation was not conservation per se; instead, these laws were designed to make shad "equally available" to everyone living along the river (Gerstell, 1998). But the dangers of obstructions and the evidence of declining shad numbers made it clear to anglers and politicians alike that some kind of conservation efforts were in order to save the fishery.

Instead of curtailing their own detrimental fishery practices, anglers turned against the construction of canal dams across the Susquehanna River and its tributaries. The Susquehanna, which begins in Cooperstown, New York, travels through Pennsylvania, and empties into Chesapeake Bay in Maryland, was the center of the commercial shad fishing industry in the 18th and 19th centuries. One dam in particular, Columbia Dam, was the subject of a 19th-century anonymous poem called "A Dam Nuisance" (Gerstell, 1998):

> When April comes on the shadfly's wing
> 'Tis a sign that shad are ripe, and Spring,
> The luscious creature, has bared her arms
> To show the world voluptuous charms,
> . . . She hears the fisherman's tale of woe
> From Havre de Grace to Otsego,
> . . . For the savory shad is seen no more
> Above Columbia's smoke-rapt shore.
> . . . Through the centuries we'll sing the psalm,
> "O dam Columbia! Columbia Dam!"

Eventually, increasing public complaints about canal feeder dams prompted legislators to force dam owners to incorporate fishways or sluices for shad to pass through. But according to shad fisheries historian Richard Gerstell (1998), most of these fishways were never built because the law requiring them was rarely enforced.

As alosine harvests continued to drop throughout the 19th and 20th centuries, fisheries managers turned to artificial propagation to enhance stocks. In fact, American shad was the first species cultured by the U.S. government (Desfosse et al., 1994). But some biologists were skeptical that stocking hatchery raised fish would be a successful rehabilatory measure. They pointed out that it would be impossible to provide hatcheries on a scale large enough to replace natural production, especially considering the estimate that it took 100,000 eggs to produce one adult shad for market, and that it would take nearly four billion fry released annually to meet the minimum requirement for Chesapeake Bay alone (Mansueti and Kolb, 1953). Hatcheries were a token measure, skeptics argued, toward appeasing criticism from fishers and politicians who scrutinized the use of public funds in fishery science.

The warnings of shad hatchery skeptics would have proved valid if harvest pressures had continued unabated. Between 1980 and 1982, Maryland shut down the commercial harvest of American shad within its borders. Virginia began a similar moratorium in 1994. Maine, New Hampshire, Massachusetts, and Rhode Island also prohibit the harvest of migrating shad. Without fishers removing alosines as quickly as they return, hatcheries have a chance to begin rebuilding the stocks with the express purpose of bringing back the fishery. The three main states of the Susquehanna and Chesapeake watersheds—Maryland, Virginia and Pennsylvania—began culturing and releasing shad in record numbers. Since 1986, federal, state, and tribal hatcheries released over 320 million fry into Chesapeake Bay tributaries (Anon., 2001). Early results from a decade of intensive stocking appear to show that hatchery shad are helping replenish the annual runs. The number of shad crossing the Conowingo Dam on the Susquehanna have gone up from a low of 50 in 1979 (PFBC, 2000) to over 193,000 fish in 2001 (Anon., 2001). At one point, hatchery fish comprised up to 90% of the returning shad; that number has bounced between 29-55% in recent years (PFBC, 2000).[16]

[16] Hatchery shad can be distinguished from wild shad by the presence of a tetracycline "tag." Recently hatched fry are immersed in a tetracycline solution. At this age, the only skeletal bone in shad is the earbone, or otolith (the rest of the bones are still cartilage). Otoliths grow by adding rings (like the way a tree trunk grows rings) at a rate of one per day. If a three-day-old shad is dipped into tetracycline, the chemical "marks" the third ring. When migrating adults return over a fish ladder or fish lift at a dam, about one of every 100 is caught and sacrificed. The otolith is removed and examined under a microscope. Under ultraviolet light, the tetracycline tag produces a yellow glow. Additional immersions on later days and feed laced with tetracycline produce more marks. Unique combinations of these marks are used to match individual shad to specific hatcheries, broodstock source, stocking sites, and age at stocking (PFBC, 2000).

Hatcheries are not the only factor in shad restoration. In recent years, the construction of large fish lifts, or elevators, has helped migrating shad surmount otherwise insurmountable hydroelectric dams. (For the most part, juvenile shad are able to move downstream through the dams without aid.) In 1991, a $12 million fish elevator system opened at the 100-foot-high Conowingo Dam on the Susquehanna River, the closest dam to Chesapeake Bay. In 1997, $20 million and $16 million fish lifts opened, respectively, at the Holtwood and Safe Harbor Dams upstream from Conowingo. Prior to the opening of these two lifts, shad were collected at Conowingo and trucked 60 miles upstream to their spawning grounds. In 2000, the opening of a $9 million fish lift at York Haven Dam just south of Harrisburg reopened almost all of the Susquehanna's 444 miles and its tributaries—historically the shad's largest East Coast spawning ground—for the first time in nearly a century (Blankenship, 2000). In Virginia, a $1.4 million fish lift at Boshers Dam on the James River has reopened most of that river for the first time since Andrew Jackson was president (Anon., 1999a).

Despite encouraging numbers, American shad are far from being out of the woods. Stocking and fish lifts can only go so far to restore populations. The rivers that hatchery raised shad return to must be healthy if the fish are ever to rebuild and maintain self-sustaining populations. American shad eggs and larvae are especially sensitive to acid and aluminum, which often spike to dangerous levels in poorly buffered streams when storms wash pollutants and nutrients into the water (ASMFC, 1999). Water withdrawals for power plants and other uses also effect shad populations. Eggs and fry can be impinged on intake screens, or sucked into the intake pipes where death—from impeller blades, extreme heat, and pressure changes—is imminent.

Another threat to shad populations is the ocean, or "intercept," fishery. Even though commercial in-river landings of American shad have shown long-term declines, coastal ocean landings have increased more than four-fold since 1978 (ASMFC, 1999). It's unclear whether this increase is the result of intensified fishing efforts, the influx of hatchery raised fish, or a combination of these and other factors. But what is clear is that shad populations cannot be expected to rebound if they never make it back to fresh water. That's why the Atlantic States Marine Fisheries Commission (ASMFC) voted in 1999 to reduce the coastal shad fishery by 40% in three years, and close it completely in five. Critics of the ASMFC decision say there is no scientific evidence that ocean fishing hurts shad stocks. Supporters of the decision say that scientific evidence isn't needed, and that it's unfair that millions of dollars are being spent on fish lifts and hatcheries only to allow fishing fleets to catch the shad at sea (Blankenship, 1998). While there's no guarantee that closing the intercept fishery will improve shad stocks, it certainly can't hurt. It's simply the removal of another obstacle to shad recovery.

So much for American shad. What about other North American clupeids? Blueback herring and alewife—collectively called river herring—are largely overlooked by conservation workers in favor of their tastier and more culturally iconic cousin. Historically, the two species packed streams in such large numbers that settlers called them "glut" fish and complained that even the freshest of rivers stank of fish (Anon., 2000). Today, only small numbers of river herring remain on the East Coast (although large numbers of landlocked alewife persist outside their native range). The collapse of their populations is blamed on foreign fishing fleets. During the 1960s and early 1970s, before the United States restricted foreign fishing within 200 miles of its coast, fleets were often seen harvesting river herring within sight of the beach. A few hatcheries are attempting to stock river herring into headwater streams where they once occurred, but their efforts are hampered by the fact that the mouths of newly hatched fry are too small to feed on brine shrimp (M. L. Hendricks, pers. comm.). To curtail starvation, hatchery workers release river herring when they're still in their larval phase, which only increases their chance of being eaten in the wild (Anon., 2000). Although fish lifts and other conservation measures are directed at American shad, biologists hope that river herring will also benefit from improved passage and begin to rebound on their own.

Hickory shad (*A. mediocris*, front cover, bottom two fish) are also largely overlooked by conservation workers; in Maryland, where they're protected, they're the subject of a small hatchery program. Populations of the Alabama shad (*A. alabamae*) and skipjack herring have suffered significant declines over the last 40 years due to stream impoundments. Other threats include poor water quality and the commercial and navigational dredging of sand bars, over which the shad spawns. Alabama shad are extirpated from Indiana, protected in Kentucky, Missouri, and Tennessee, and a candidate for federal Endangered Species Act protection (NMFS, no date). Skipjack herring are largely gone from the upper Mississippi River, where they were once abundant. They're listed as endangered in Wisconsin. And as for gizzard shad and threadfin shad, it seems their ability to thrive in ponds, reservoirs, and other landlocked areas will ensure their survival should native populations precipitously decline.

Although specific runs may be extinct or nearly so, no North American clupeid species (with the possible exception of Alabama shad) is in any imminent danger of extinction. But in terms of their historical numbers and once great commercial value, some clupeids are functionally wiped out. It will be interesting to see how alosine populations respond over the next dozen or so years. But in our scramble to rebuild the fishery, let's not neglect the fish. At some point we may have to concede that irreparable damage has been done to alosine populations, and that hatchery technology cannot supplant natural selection. Whether alosines can be harvested again is not that important. What is important is that shads and river herrings always be here, so that our children, and all children from now on, can stand along the banks of a shallow stream as the shadbush blooms and the shad fly buzzes about, and witness one of nature's most spectacular rites of spring.

Table 1. Herring and shad genera, subgenera, and species (Clupeidae) native to the fresh waters of North America.

Conservation status key: E = endangered; T = threatened; R = rare; SC = special concern.

Subfamily Alosinae

Genus *Alosa* Linck, 1790

Subgenus *Alosa*

ETYMOLOGY: from the Saxon *allis*, old name of the European shad

alabamae Jordan & Evermann, 1896; Alabama shad
ETYMOLOGY: of Alabama, where type was collected
DISTRIBUTION: Gulf of Mexico from the Mississippi delta east to the Chochtawhatchee R. (FL); north to IA and WI, east to WV
STATUS: vulnerable; E (KY); R (MO); SC (TN); extirpated (IN)

sapidissima (Wilson, 1812); American shad
ETYMOLOGY: most delicious, referring to its being the most delectable of shads
DISTRIBUTION: Atlantic Coast from Sand Hill R. (Labrador) to S. Johns R. (FL); introduced and spreading throughout Pacific Coast into Russia
STATUS: common; SC (MD); extirpated (ON)

Subgenus *Pomolobus* Rafinesque, 1820

ETYMOLOGY: *pomo*, opercle; *lobus*, lobe, referring to the lobed opercles Rafinesque used to distinguish "goldshads" from true herrings

aestivalis (Mitchill, 1814); blueback herring
ETYMOLOGY: of the summer, presumably because it enters coastal waters later than *A. pseudoharengus*
DISTRIBUTION: Atlantic Coast from Cape Breton (NS) to St. Johns R. (FL); introduced into VA reservoirs
STATUS: common

chrysochloris (Rafinesque, 1820); skipjack herring
ETYMOLOGY: *chryso*, gold, *chloris*, green, referring to color of the back
DISTRIBUTION: Red R. drainage and Mississippi R. basin, from MN south to Gulf, and from PA west to SD, NE, KS, OK, TX; Gulf drainages from Apalachicola R. (FL) to Colorado R. (TX)
STATUS: common; E (WI); T (PA)

mediocris (Mitchill, 1814); hickory shad
ETYMOLOGY: mediocre, referring to its taste or food value as compared to *A. sapidissima*
DISTRIBUTION: Atlantic Coast from Kenduskeag R. (ME) to St. Johns R. (FL); possibly Campobello Island (NB)
STATUS: common; E (PA); SC (MD)

pseudoharengus (Wilson, 1811); alewife
ETYMOLOGY: *pseudo*, false; *harengus*, herring
DISTRIBUTION: Atlantic Coast rivers from Red Bay (Labrador) to SC; introduced into Great Lakes and elsewhere
STATUS: common

Subfamily Dorosomatinae

Genus *Dorosoma* Rafinesque, 1820

Subgenus *Dorosoma*

ETYMOLOGY: *dora*, lanceolate; *soma*, body, referring to eel-shaped larvae

anale Meek, 1904; longfin gizzard shad (*sardina del Atlántico*)
ETYMOLOGY: referring to long anal fin
DISTRIBUTION: Río Papaloapan in s. Veracruz and Oaxaza (Méx.), south to n. Guatemala
STATUS: information not available

petenense (Günther, 1868); threadfin shad (*topote*)
ETYMOLOGY: originally described from Lake Peten, Guatemala
DISTRIBUTION: Ohio R. (IN, IL) and Mississippi R. basin from IL to Gulf; Atlantic drainages of FL; Gulf drainages from FL to Guatemala; widely introduced elsewhere

STATUS: common
NOTE: Some authorities recognize two subspecies: *D. p. petenense* and *P. p. atchafalayae* Evermann & Kendall 1898, named after the Atchafayala River (LA), from where it was described. Populations introduced into California are assigned to this nominal subspecies (Moyle, 2002).

smithi Hubbs & Miller, 1941; Pacific gizzard shad (*sardina del Pacifico*)
ETYMOLOGY: in honor of ichthyologist Hugh M. Smith
DISTRIBUTION: Pacific drainage of n.w. Méx. between Sinaloa and Sonora
STATUS: information not available

Subgenus *Signalosa* Evermann & Kendall, 1898
ETYMOLOGY: *signum*, flagstaff or pole; *alosa*, shad; referring to long, whiplike dorsal ray

cepedianum (Lesueur, 1818); gizzard shad (*sardina molleja*)
ETYMOLOGY: "Named for Bernard Germain Étienne de la Ville sur Ilion, Comte de La Cépède (1756-1825), known as Citoyen Lacépède during the French Revolution; a brilliant and most industrious writer, who compiled his great Histoire Naturelle des Poissons under most difficult conditions during the French revolution" (Jordan & Evermann, 1896).
DISTRIBUTION: St. Lawrence-Great Lakes, Mississippi, Atlantic, and Gulf Coast drainages from QU to ND and NM, south to FL and Méx.; widely introduced elsewhere
STATUS: common

MARINE CLUPEIDS that occasionally enter fresh water in North America:

- *Brevoortia patronus* Goode, 1878, Gulf menhaden (AL, MS)
- *Harengula jaguana* (Poey, 1865), scaled sardine (FL, MS)
- *Opisthonema oglinum* (Lesueur, 1818), Atlantic thread herring (FL)

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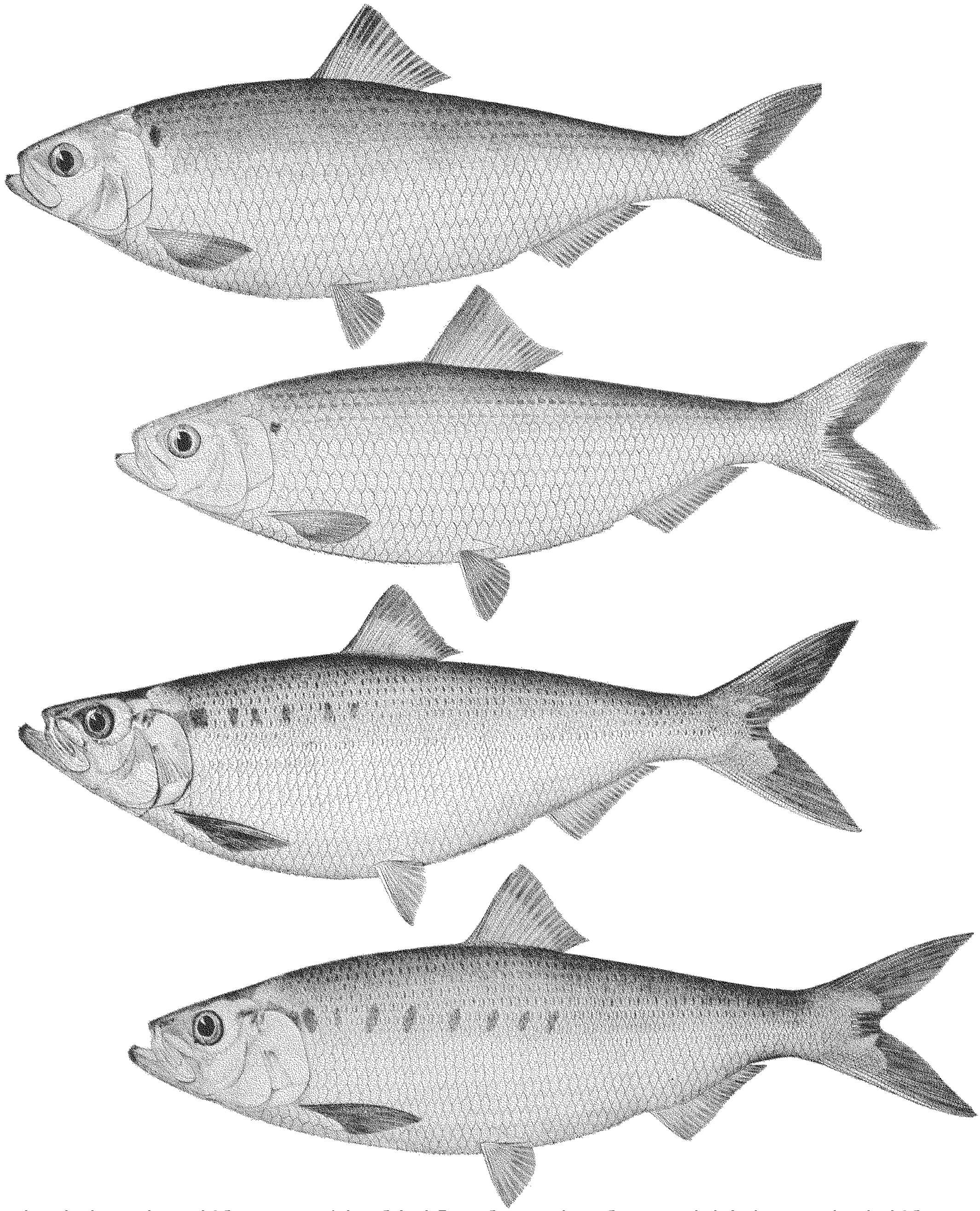

Top to bottom: blueback herring (Alosa aestivalis)female and male, and hickory shad (Alosa mediocris) female and male. Courtesy NOAA.