mouth of the Piscataqua River, Gloucester, Marblehead Harbor, Swampscott, Nahant, and Dorchester in Boston Harbor; and in the outer waters of Massachusetts Bay. There are specimens in the Museum of Comparative Zoology from Trenton, Maine, from outer Boston Harbor, and from near Provincetown. Two were taken in the central basin of the Gulf in July 1931 at a depth of 161–174 m; one was trawled by the *Atlantis* in the deep trough west of Jeffreys Ledge at 132–143 m and another in the southwestern basin of the Gulf off Cape Cod at about 183 m, in August 1936; *Albatross II* trawled one on the eastern slope of Nantucket Shoals (40 °05′ N, 69°22′ W) at 95 m in May 1950. One of the crew of the dragger *Eugene H* reported capture of four on the northeastern part of Georges Bank on 12 October 1951.

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WOLFFISHES. FAMILY ANARHICHADIDAE

RODNEY A. ROUNTREE

Wolffishes are large, blennylike fishes of the suborder Zoarcoidei and are most similar to wrymouths (Cryptacanthidae) and gunnels (Pholidae). Lack of pelvic fins distinguishes wolffishes from all other blennylike fishes except wrymouth, but they can be readily separated from the latter by the large canine tusks, deeper, more robust body, and presence of a separate caudal fin. Wolffishes differ from other blennioid fishes, and from most other acanthopterygian fishes, in that the posterior dorsal spines are short and rigid, whereas all anterior spines have flexible tips (Gill 1911). However, the particularly wide separation of the sacculus and lagena from the utriculus of the inner ear is the most distinctive feature of the family (Berg 1940; Barsukov 1959).

Wolffishes are the largest of the blennylike fishes, reaching 1.8 m in the western Atlantic (Robins et al. 1986), and more than 2.5 m worldwide (Nelson 1994). There are five species in the family, two of which occur in the Gulf of Maine; one, Atlantic wolffish (*Anarhichas lupus*), commonly, and the other, spotted wolffish (*A. minor*), only as a stray from the north. Another cold-water species, northern wolffish (*A. denticulatus*), is included in the following key, as it has been recorded repeatedly from nearby Nova Scotian waters; there is one record from the "Gulf of Maine" (MCZ 99513), and it occurs south to Block Canyon. Owing to strong ontogenetic changes, there is currently no reliable key for all sizes of wolffishes. Barsukov (1959) provided separate keys for wolffish 2–6 cm, 7–20 cm, and larger than 20 cm. The following key has been compiled based on information from Barsukov 1959 and Templeman 1984b, 1986c.

Wolffishes are among the most interesting fishes in the Gulf of Maine region. Apart from their impressive physical appearance, aspects of wolffish reproductive biology, including large egg size, prolonged incubation period, egg brooding behavior, probable internal fertilization, and possible spawning migrations, together with the annual loss of their entire set of teeth and the apparently prolonged fasting period associated with spawning and tooth replacement, make wolffishes unique among Gulf of Maine fishes. In addition to arousing our interest and curiosity with their unique biology, wolffish are good eating. In fact, extensive research is under way in Europe and Canada to develop aquaculture of Atlantic and spotted wolffishes because of the relative ease of raising the young and the growing market demand for the species.

KEY TO GULF OF MAINE AND NOVA SCOTIAN WOLFFISHES LARGER THAN 20 CM TL

1a. Bands of molar teeth on vomer and palatine bones about equal length; body distinctly spotted, spots extending well onto sides of head ..... **Spotted wolffish**

1b. Bands of molar teeth on vomer and palatine bones not of equal length; body usually plain-colored, barred, or indistinctly spotted; if spotted, spots not extending onto sides of head 2

2a. Central band of molar teeth much shorter than bands flanking it on the palatines; canine teeth small, not prominent; body usually plain or blotched; if spotted, spots not extending onto sides of head; head pointed, body deepest at the midpoint; dorsal fin rays 76–81; vertebrae 78–82 ..... **Northern wolffish**

2b. Central band of molar teeth much longer than those flanking it on the palatines; canine teeth very large and prominent, forming tusks; body distinctly barred; head blunt, body deepest at head; dorsal fin rays 69–79; vertebrae 72–78 ..... **Atlantic wolffish**

ATLANTIC WOLFFISH / *Anarhichas lupus* Linnaeus 1758 / Catfish, Ocean Whitefish /

Bigelow and Schroeder 1953:503–507

Description. Body deepest close behind heavy, blunt head, tapering back to slender caudal peduncle (Fig. 253). Dentition formidable, a row of about six very large, stout, conical canine tusks in upper jaw, a cluster of five or six smaller canines behind them. Roof of mouth armed with three series of crushing teeth. Central series of vomerine teeth a double row of about four pairs of large, rounded molars united (but not fused) into a solid plate. Each of outer series of palatine teeth

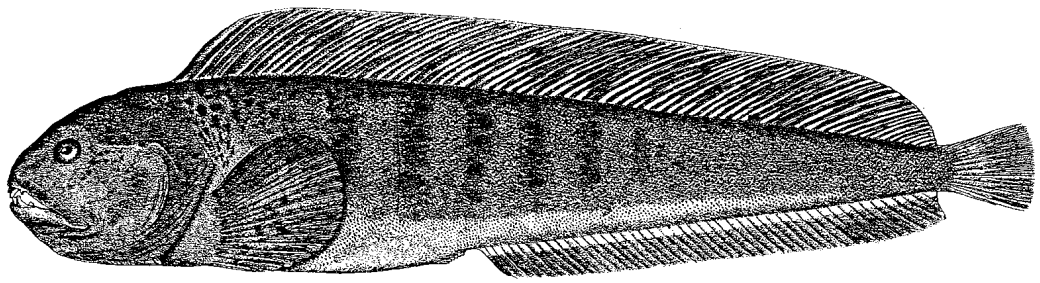


Figure 253. Atlantic wolffish *Anarhichas lupus*. Georges Bank. Drawn by H. L. Todd.

with two alternating rows of blunt conical teeth. Lower jaw with four to six large tusks in front, two longitudinal diverging rows of rounded molars behind. Dorsal fin extends from nape to caudal fin base, uniform in height except for rounded corners. Anal fin about half as high as dorsal, little more than half as long. Pectoral fins large, rounded. Caudal fin small, weak, slightly convex in outline. Head naked but poorly developed scales present on body. Swim bladder absent. Presence of lateral lines previously overlooked in North American literature (e.g., Bigelow and Schroeder; Scott and Scott 1988; Nelson 1994) but two branches of the lateral line present on body (Barsukov 1959). Both branches begin just behind head, at about level of pectoral fins. Dorsal branch extends to about midpoint of body, running approximately one eye diameter below dorsal fin. Lower branch runs laterally down middle of flank to at least caudal fin base. In living specimens, lateral lines clearly visible as two rows of faint black (posteriorly) and white (anteriorly) bicolor spots (R. Rountree, pers. obs.).

Meristics. Dorsal fin spines 69–79; anal fin rays 42–48; pectoral fin rays 18–22; branchiostegal rays 6 or 7; vertebrae 72–78 (Barsukov 1959; Scott and Scott 1988).

Color. Atlantic wolffish are dull-colored and vary widely in tint. Adults are usually marked with a variable number (8–13) of dark bars (formed by numerous irregular patches and spots) that extend onto the dorsal fin. However, early juveniles lack these bars and could be confused with spotted wolffish, which have similar bars until they reach a maximum length of 20 cm (Barsukov 1959). Throat and belly back to the vent are dirty white tinged with the general ground tint of the upper parts. Wolffish vary in color geographically from dull olive green, purplish, brownish, bluish gray, to slate (Bigelow and Schroeder). Bigelow and Schroeder suggested that the color varies with that of the fish's surroundings, purplish and brown tints ruling among red seaweeds and olive gray on clean bottom. Specimens living in aquariums tend to be somewhat lighter than described by Bigelow and Schroeder (R. Rountree, pers. obs.). Lateral line pores on the head, particularly those around the eye, stand out as bright white spots. The margins of the dark bars are often boldly marked off in white above the dorsal branch of the lateral line. These white margins sometimes expand dorsally to form strong white bars on the dorsal fin that alternate with the often fainter black bars. Usually the anterior white margin of the first dark bar forms a bold white patch over the first three spines of the dorsal fin. Another bold white patch occurs on the base of the pectoral fin. Presence of these white markings appears to be behaviorally controlled (R. Rountree, pers. obs.).

Size. Reach 1.5 m and 18 kg (Goode 1884; Idoine 1998b), but wolffish longer than 1.2 m are seldom seen, and the larger fish brought in run less than 1 m (Bigelow and Schroeder). European authors write of Atlantic wolffish of 1.8 m and even longer but lengths over 1.25 m have been disputed (Barsukov 1959). A fish 0.8 m long weighs about 4.5 kg and one of 0.9 m about 7.3 kg. The largest fish recorded from Icelandic waters was 1.16 m (Jonsson 1982). A general north to south increase in wolffish size has been reported for southwestern Greenland (Riget and Messtorff 1988) and in the northwest Atlantic (Templeman 1986b). The all-tackle game fish record is 23.58 kg for a wolffish caught on Georges Bank in June 1986 (IGFA 2001).

Distinctions. The great projecting tusks, blunt snout, massive head, and small eyes give Atlantic wolffish a singularly savage aspect. Wolffish resemble a huge blenny in general makeup, except that the dorsal fin spines are flexible at their tips instead of stiff; pelvic fins are absent; and the mouth is armed with a set of teeth more formidable than those of any other Gulf of Maine fish, except for spotted wolffish.

Habits. Wolffish are widely renowned among fishermen for their ferocious appearance, temperament, and biting ability. They have been known to bite through a broom stick, break steel knives (see comments in Gill 1911), and crush the sides of steel fish baskets (R. Rountree, pers. obs.). Their fierce appearance has inspired many legends over the centuries (Smitt 1892; Barsukov 1959). *Anarhichas* comes from a Greek word meaning "to climb up" because it was believed that they climb up onto rocks and cliffs. Some legends claim that wolffish gnawed scars onto anchor chains on which they had climbed (see, e.g., Smith 1833).

Atlantic wolffish are benthic fish distributed throughout the Gulf of Maine in depths of 40–240 m, but are concentrated between 80–120 m (Nelson and Ross 1992). Bigelow and Schroeder noted reports of the species from tide pools at Eastport,

Maine, but never heard of it in such situations or at low-water mark anywhere else in the Gulf. They have been reported from depths of 0–600 m off western Greenland (Riget and Messtorff 1988) and Newfoundland (Albikovskaya 1982; Templeman 1984a); 8–450 m off Iceland (Jonsson 1982); and 10–215 m off Norway and the Barents Sea (Falk-Petersen and Hansen 1991). They have been collected at depths of less than 2–10 m with seines, gill nets, and pound nets in the White Sea (Pavlov and Novikov 1986, 1993; Pavlov 1994). They were most abundant at depths of 40–180 m in Icelandic waters (Jonsson 1982), and 101–350 m off Newfoundland (Albikovskaya 1982).

Albikovskaya (1982) collected Atlantic wolffish at temperatures of −1.9° to 11.0°C, with the biggest catches between −0.4° and 4.0°C off Newfoundland. In Norwegian waters they are found at temperatures of −1.3° to 11°C (Falk-Petersen and Hansen 1991). Beese and Kandler (1969, cf. Jonsson 1982) suggested a temperature tolerance of −1.3° to 10.2°C for Icelandic and northern European waters. Bigelow and Schroeder reported a similar temperature range for the Gulf of Maine. However, data from laboratory predation experiments indicate survival at temperatures as high as 17°C, although feeding activity was negatively correlated with temperature and appeared to cease by 17°C (Hagen and Mann 1992). Atlantic wolffish can survive temperatures as low as −1.7°C in the laboratory, owing to a high concentration of antifreeze in the blood (King et al. 1989). In the White Sea, some individuals have been collected in water temperatures as high as 15.4°–18°C (Pavlov and Radzikhovskaya 1991).

Atlantic wolffish are usually solitary except during the mating season, when bonded pairs occur. However, some apparent "colonial settlements" have been reported (Pavlov and Novikov 1993), the occurrence of which may be related to limited shelter availability. In a scuba survey of shelter sites Pavlov and Novikov (1993) found that Atlantic wolffish prefer sites with complex bottom relief such as rocks and large stones and were only rarely observed in algae or over sand bottom. The entrance to a shelter was frequently marked by piles of crushed shells that had apparently been evacuated from the gut. They suggest that feeding takes place largely in areas away from the shelter sites. Adults did not occupy permanent shelters and did not display territorial behavior. In fact, they were sometimes observed sharing shelters with other conspecifics and with large cod (Pavlov and Novikov 1993). However, other researchers suggest that shelter sites may be limiting during the breeding season owing to competition with conspecifics (Johannessen et al. 1993) and ocean pout (Keats et al. 1985).

Although scuba observations suggest that wolffish may remain inactive at night and forage only during the day (Bernstein et al. 1981), other researchers consider wolffish to be essentially nocturnal (Gill 1911; Barsukov 1959; Jonsson 1982); Pavlov and Novikov (1986) found that Atlantic wolffish feed most actively at night in large ponds and fish pens. Wolffish may be able to vocalize by grinding their pharyngeal teeth (Barsukov 1959).

Food. The food of Atlantic wolffish was first examined as early as 1772 from Icelandic waters (Ólafsson 1772, cf. Palsson 1983) and 1784 in European waters (Andre 1784). Gill (1911) reviewed other early accounts of wolffish food habits. The best food habits data available for Atlantic wolffish is from the Labrador-Newfoundland region of the northwest Atlantic (Albikovskaya 1983). In this region, all three wolffish species had very similar diets (70% similarity), with northern wolffish exhibiting the greatest differences. Atlantic and spotted wolffish fed primarily on benthic fauna, whereas northern wolffish fed mainly on bathypelagic forms. Diet composition exhibited strong regional variation. The most important food groups were crabs, starfish, brittle stars, sea urchins, and bivalve and gastropod mollusks. In the North Sea (Liao and Lucas 2000a), diet was dominated by decapods (particularly Paguridae), bivalves (particularly Pectinidae), and gastropods (particularly Buccinidae). Although Bigelow and Schroeder reported that the diet of Atlantic wolffish consisted wholly of hard-shelled mollusks, crustaceans, and echinoderms, fishes have also been reported (Smith 1892; Fulton 1903a; Sæmundsson 1949; Barsukov 1959; Albikovskaya 1983; Palsson 1983; Templeman 1985; Keats et al. 1986a,b; Liao and Lucas 2000a,b), and can be important locally (Albikovskaya 1983; Palsson 1983). Even large fishes such as Atlantic cod, cunner, redfishes, and skates have occasionally been found in Atlantic wolffish stomachs (Gill 1911; Jonsson 1982; Albikovskaya 1983; Templeman 1985; Keats et al. 1986b).

More recently, bivalves (including the economically important sea scallop, Icelandic scallop, and ocean quahog), gastropods, decapods, and echinoderms (particularly an ophiuroid *Ophiura sarsi*), were the most frequently observed food items in the Gulf of Maine–Georges Banks area (Nelson and Ross 1992; Bowman et al. 2000). Larger individuals (51–80 cm TL and larger) fed primarily on bivalves; medium-sized individuals (11–50 cm TL) consumed a much larger proportion of echinoderms; and the smallest individuals (1–10 cm TL) ate more amphipods (particularly *Parathemisto* spp.) and euphausiids (Bowman et al. 2000).

Cannibalism of eggs and larvae has been noted under both natural and laboratory conditions (Jonsson 1982; Keats et al. 1986b; Moksness et al. 1989; Moksness and Stefanussen 1990; Pavlov and Radzikhovskaya 1991; Johannessen et al. 1993). A high incidence of fishing boat discards has been reported in stomachs of wolffish (Barsukov 1959).

Feeding by Larval and Juvenile Stages. Food habits of the pelagic larval stage in northern European waters have been described by Baranenkova et al. (1960), Pavlov et al. (1987), Falk-Petersen et al. (1990), and Orlova et al. (1990), and initial feeding and rearing studies have been examined in Europe by Ringø et al. (1987) and Moksness et al. (1989). Off northern Norway, 250 stomachs of larvae 20–40 mm TL were found to contain 1- to 3-mm crustaceans and 6- to 10-mm fish larvae (Falk-Petersen et al. 1990). The diet was dominated by amphipods, particularly *Hypera galba* juveniles (53%), decapod

crustacean larvae (16%), and fish larvae (8%). Similarly, pelagic fry (24–26 mm) fed on pelagic larvae of benthic invertebrates and on fish larvae and eggs, but benthic juveniles (7–19 cm) fed exclusively on benthic forms such as echinoderms and mollusks (Baranenkova et al. 1960).

Feeding Behavior. The behavior of Atlantic wolffish feeding on green sea urchins in Newfoundland has been described by Keats et al. (1986b): "When an urchin is 'sighted' the wolffish generally turns slightly on its side and grasps the urchin with its canine teeth, while its body is at a 45° angle laterally to the bottom. A side-to-side motion is sometimes used to remove the urchin from the substratum. . . . There is a violent dorsoventral jerking of the wolffish as the urchin test is being crushed." Similar observations have been made by Russian scientists from submersibles (Barsukov 1959).

Several studies have examined the highly specialized dental morphology of wolffishes and discussed implications for food habits (Andre 1784; Crisp 1853; Gill 1911; Luhmann 1954; Barsukov 1961; Verigina 1974; Le Cabellec et al. 1978; Albikovskaya 1983). The large hook-shaped teeth are used to tear food from the bottom, whereas the heavy conic and round teeth on the vomer and palate are used to crush hard skeletons and shells of prey. Although these studies imply that the food of wolffishes is completely crushed and macerated before it reaches the stomach (except Crisp 1853), intestines full of small whole crabs and sand dollars have been observed (R. Rountree, pers. obs.). Similar observations were made in early studies (Verrill 1871; Gill 1911).

Wolffish teeth are quickly worn down by the grinding action used for crushing hard-shelled prey and are replaced annually (Luhmann 1954; Barsukov 1959, 1961; Albikovskaya 1983). According to Barsukov (1961), peak shedding of teeth of Barents Sea Atlantic wolffish probably occurs from December to January, but can take place anytime between October and May. Detailed anatomical descriptions of tooth replacement are provided by Luhmann (1954) and Barsukov (1959). Jonsson (1982) provided data from a survey of the tooth replacement stage of Atlantic wolffish from Icelandic waters. Teeth are exchanged from September to December, rarely into January; hence exchange occurs during, or just after, the spawning season. Females appear to undergo tooth replacement shortly before males. New teeth are loose and surrounded by soft gum tissue, but by January or February they have become firm. New and developing teeth are bright red in all three North Atlantic wolffish species (Luhmann 1954; Barsukov 1959), but the color fades within a few weeks in Atlantic wolffish (R. Rountree, pers. obs.). It may take more than 2–3 months after tooth loss before new teeth are fully functional (Barsukov 1959). Nine adult and late juvenile Atlantic wolffish captured on Georges Bank in early December 1994 exhibited a wide range of tooth replacement stages from the presence of scattered old broken teeth, to the absence of all teeth, to the presence of new teeth in various stages of development, including scattered red teeth (R. Rountree, pers. obs.). It appears, therefore, that there is a great deal of individual variation in timing of tooth replacement in Gulf of Maine wolffish.

Wolffish appear to fast for up to several months during the tooth replacement, spawning, and brooding periods. The extent to which these periods overlap is not clear. Male wolffish appear to reduce feeding or fast during up to several months of egg brooding between July and November (Keats et al. 1985; Ringø and Lorentsen 1987). Wild-caught Atlantic wolffish held in captivity during breeding studies stopped feeding 1–2 weeks prior to spawning (Pavlov and Novikov 1986; Johannessen et al. 1993). Gut indices indicate that feeding activity is higher during spring and summer and drops in winter (Albikovskaya 1983; Templeman 1986b; Falk-Petersen and Hansen 1991; Liao and Lucas 2000b). However, in Norwegian waters feeding activity was not correlated with the reproductive cycle or the egg-guarding period (Falk-Petersen and Hansen 1991). Most fish collected in Icelandic waters during September and December had empty stomachs and were in poor condition, suggesting that Atlantic wolffish do not feed during the tooth replacement–spawning period (Jonsson 1982). Baranenkova et al. (1960) also reported that benthic juveniles (7–19 cm) do not feed during the period of tooth replacement. Barsukov (1959) and Luhmann (1954) independently hypothesized that feeding is restricted to soft-bodied animals during the tooth replacement period to prevent damage to the developing new teeth. They further suggest that the nearly simultaneous loss of all teeth is an adaptation to feeding on hard-shelled animals, since a developing individual tooth would not be able to withstand grinding pressures during feeding. The unusually low resting metabolism, among the lowest known, of Atlantic wolffish (Liao and Lucas 2000a) may be an adaptation to extended fasting periods required by tooth replacement and brooding.

A short, large-diameter esophagus empties directly into a small sacklike stomach (13% of body length), and then into an enlarged, but relatively short (52–86% of body length) intestine (Verigina 1974). After crushing and maceration in the oral cavity and pharynx, calcareous exterior material (shells and tests) are evacuated through the large anus (Crisp 1853; Bray 1987). Most digestion occurs in the enlarged intestines, which have an increased surface area resulting from heavy folds in the intestinal wall, rather than in the stomach (Verigina 1974; Bray 1987). Much of the material filling the digestive tract is not digestible, so a large amount of food must be processed to obtain an adequate diet (Orlova et al. 1989). Digestion rates for various prey under different temperatures have been examined in Europe (Orlova et al. 1989). Wolffish have been noted to have an unusually large gall bladder (Crisp 1853).

Predators. Atlantic wolfish have been reported from stomachs of Greenland shark (Bigelow and Schroeder 1948b; Barsukov 1959), Atlantic cod (Sæmundsson 1949; Barsukov 1959; Orlova et al. 1990), haddock (Orlova et al. 1990), and gray seal, *Halichoerus grypus* (Pierce et al. 1989). Eggs are frequently preyed on by spotted wolffish (Jonsson 1982). Atlantic wolffish

were rarely found in an extensive demersal fish food habitats data set collected by the Northeast Fisheries Science Center between 1973 and 1990, occurring only in spiny dogfish, thorny skate, Atlantic cod, red hake, pollock, haddock, and sea raven stomachs, of which spiny dogfish, sea raven, and cod had the most frequent occurrences (Rountree 1999). Most prey were 3- to 10-cm juveniles. Sea raven were the only species to prey on wolffish larger than 25 cm, with prey ranging from 7 to 57 cm TL.

Parasites. Jonsson (1982) reviewed some early accounts. Most notably, a sporozoan parasite infecting wolffish muscle tissue causes a condition referred to as "hairy catfish" and can sometimes significantly adversely affect the marketability of catches in Iceland (Jonsson 1982). Other information on parasites is contained in Margolis and Arthur (1979), Khan et al. (1980), Zubchenko (1980), Appy and Dadswell (1981), Bray (1987), and Bray and Gibson (1991). Wolffish are infected mainly by parasites that have developmental connections with benthic organisms (Zubchenko 1980). Bray (1987) examined the relationship between digestive system physiology and function and parasite location. A parasitic fungoid microorganism *Mycelites ossifragus* has been found to burrow into wolffish teeth (Schmidt 1954; Kerebel et al. 1979) and may play a role in wolffish tooth destruction (Barsukov 1959).

Reproductive Habits. Wolffish ovaries are paired, elongate, and yellowish, located in the dorsal half of the abdominal cavity (Falk-Petersen and Hansen 1991). Males have a pair of elongate testes ventral to the kidneys. Sexually mature males can be distinguished from females by an enlarged urogenital papilla (Falk-Petersen and Hansen 1991), which probably functions in copulation (Johannessen et al. 1993; Pavlov 1994; Pavlov and Moksness 1994). Ripe females have a pronounced pot-bellied appearance up to a few weeks before spawning (Pavlov and Novikov 1986; Johannessen et al. 1993, Pavlov and Moksness 1994). The oral cavity and lower lips of both sexes may become pink, red, or orange 1–2 weeks prior to spawning (Pavlov and Novikov 1986). A few hours before spawning a transverse sickle-shaped genital pore opens into the oviduct.

In Norway gonadosomatic indices (GSI) of females are highest during summer and fall, whereas males show little seasonal variation (Falk-Petersen and Hansen 1991). However, testes contain active spermatozoa through much of the year (Falk-Petersen and Hansen 1991; Johannessen et al. 1993; Pavlov and Moksness 1994). In the western Atlantic, female GSI appear to be negatively correlated with feeding index, with reduced or eliminated feeding during the period of highest GSI (Keats et al. 1985). Male GSI and feeding index were negatively correlated with brooding activity, with lowest GSI and lowest feeding during brooding.

Most individuals are mature by age 6 and about 40 cm TL (Falk-Petersen and Hansen 1991). In the White Sea, males begin to mature at about 40 cm and age 6–7 (Pavlov and Radzikhovskaya 1991). Size at first maturity may vary regionally owing to temperature effects (Templeman 1986b). In the northwest Atlantic females reach sexual maturity at 43 cm off Labrador and northeast Newfoundland and at 58 cm in St. Pierre Bank and southern Grand Bank (Templeman 1986b). Sizes at 50% maturity were 51.4 cm for northern areas and 68.2 cm for southern areas (Templeman 1986b). Mature females have been found as small as 25 cm in the relatively warm waters of Iceland (Jonsson 1982). Some females mature in under 2 years (0.5–1.0 kg) under culture (Moksness and Stefanussen 1990).

Females appear to be group-synchronous, with several egg generations present at any given time (Falk-Petersen and Hansen 1991). Some individuals may not spawn every year (Pavlov and Novikov 1986; Falk-Petersen and Hansen 1991; Pavlov and Moksness 1996). Egg masses vary in size according to the size of the female, but generally are about 10–14 cm in diameter (Jonsson 1982); hence, fecundity increases with fish size from about 5,000 eggs at 60 cm to 12,000 eggs at 80–90 cm (Falk-Petersen and Hansen 1991). Jonsson (1982) reported 338 eggs in a 25-cm (age-7), and 4,900–5,000 eggs in a 59-cm (age-9) Atlantic wolffish from Iceland. In the Canadian Atlantic, the relationship between fecundity and length has been reported as $F = 0.3090L^{2.4239}$ (Templeman 1986b). Individual fecundity ranged from 2,300 eggs in a 44-cm fish to 37,920 eggs in a 117-cm fish. Gusev and Shevelev (1997) recently described and compared fecundity among all three Barents Sea wolffishes. Absolute fecundity increases in all three species with increase in body length and weight. Atlantic wolfish have the lowest absolute fecundity. Dzerzhinskiy and Pavlov (1992), Pavlov and Novikov (1993), Pavlov and Moksness (1994, 1996) have described gonad maturation and reproduction in White Sea populations.

Spawning Season. Information on the spawning period of Atlantic wolffish is somewhat contradictory, partly because of geographic differences (McIntosh and Prince 1890; Barsukov 1959; Beese and Kandler 1969; Jonsson 1982; Templeman 1984a,b; Keats et al. 1985; Pavlov 1986; Falk-Petersen and Hansen 1991; Johannessen et al. 1993, Pavlov and Novikov 1993; Pavlov and Moksness 1994). The long incubation time (4–9 months, depending on temperature) and the tendency for mechanical stimuli to induce late-stage embryos to hatch prematurely (Pavlov and Novikov 1986) are probably major sources of this confusion. Findings that wolffish can spawn over much of the year in the laboratory (Pavlov and Moksness 1994) further complicates interpretation of field evidence. In other words, there is an inadequate distinction between the spawning and hatching periods in most studies.

In the northwest Atlantic eggs have been collected in February (McKenzie and Homans 1938) and March (Powles 1967), whereas early larvae have been collected from January to March (Bigelow and Schroeder). In addition, scuba observations of recently hatched larval wolffish have been reported during October and November from the coast of Nova Scotia (Keats et al. 1986b). In other areas eggs have been collected from

July through April (Barsukov 1959; Jonsson 1982; Falk-Petersen et al. 1990, and citations therein), whereas recently hatched larvae have been collected from January to June (Barsukov 1959; Baranenkova et al. 1960; Falk-Petersen et al. 1990; Pavlov and Novikov 1993; except Collett 1883, cf. Barsukov 1959). A single wolffish larvae was reported in November off Norway (Collett 1883).

Based on egg and larvae collections, a late fall and winter spawning period was suggested for the Gulf of Maine (Bigelow and Schroeder) and Icelandic waters (Sæmundsson 1949). Subsequent studies, however, have concluded this to be in error and that peak spawning occurs in September and October in these regions (Jonsson 1982 and citations below). However, the only indisputable evidence for a spawning period was provided by scuba observations off Nova Scotia (Keats et al 1985). Nested pairs of adults or brooding males, together with eggs, were observed from August to October in 5–15 m of water off Nova Scotia (Keats et al. 1985). Based on egg size, Templeman (1986b) concluded that spawning occurred mainly in autumn off Newfoundland; however, precise identification of the spawning period is uncertain owing to the small sample sizes during this period. A similar July–October spawning period was later reported for Norwegian waters based on back-calculated growth of spring-captured larvae (Falk-Petersen et al. 1990) and on female gonadosomatic indices (Falk-Petersen and Hansen 1991). Jonsson (1982) states that Atlantic wolffish spawn mainly in September and October, but as late as December in Icelandic waters (based on implied captures of ripe females). He further discussed apparent misidentification of the spawning period by earlier researchers based on egg and larval collections. Finally, White Sea populations have also been reported to spawn in late summer and autumn based on laboratory studies (Pavlov and Novikov 1986; Pavlov and Radzikhovskaya 1991), and later on laboratory spawning, larval collections, and scuba observations of pair bonding (Pavlov and Novikov 1993). In direct contradiction to these studies, some of these same authors later concluded from laboratory observations that spawning occurs from October to February (Johannessen et al. 1993; Pavlov and Moksness 1994).

Two different studies found that wolffish are capable of spawning over much of the year in the laboratory (Johannessen et al. 1993; Pavlov and Moksness 1994). In the first, wild brood stock from Norway were spawned under laboratory and seminatural conditions from October to February. In the second, eggs and larvae collected off the coast of Norway and reared to maturity spawned mainly from December through March at 5–8°C, although some spawning occurred from October through July (Pavlov and Moksness 1994). Many males were found to be ripe through most of this period. The authors suggest that the protracted spawning period resulted from the constant photoperiod in the laboratory, since spawning occurred in water temperature too high for the eggs to remain viable, and that timing of maturation and spawning is dependent more on photoperiod than temperature. These observations suggest the intriguing possibility that timing of egg maturation and spawning of Atlantic wolffish may be highly plastic and dependent on local conditions. Reports of apparent seasonal spawning migrations may result from inshore-offshore seasonal migrations related to foraging and tooth replacement episodes, in which some members of the population spawn inshore during the late summer and fall and offshore during late fall and winter.

Spawning Behavior. Male and female pairs form during the spring and summer before spawning (Keats et al. 1985; Pavlov and Novikov 1986, 1993). Data from scuba studies in 5–15 m of water off Newfoundland indicate that wolffish first move into the shallows in mid to late spring, form mated pairs during summer, and spawn from August to October (Keats et al. 1985). Egg masses were observed in nests under rocks from August to November; however, no mated pairs were observed after October. Pavlov and Novikov (1993) made similar observations of prespawning behavior in the White Sea, but noted that prespawning pairs left their shallow-water nesting sites and migrated to deeper water immediately prior to spawning in late July to September.

Johannessen et al. (1993) and Pavlov and Moksness (1994) examined female spawning behavior. The pot-belly appearance of ripe females, which is due to a gradual increase in egg size, begins developing 3–5 months prior to spawning (Johannessen et al. 1993), corresponding to the time of pair-bonding observed in the field (Keats et al. 1985). The pot-belly becomes pronounced 1–2 weeks prior to spawning (Pavlov and Novikov 1986; Johannessen et al. 1993; Pavlov and Moksness 1994). A 12- to 24-h side-laying phase occurs 30–50 h prior to spawning, in which the females rest motionless on the bottom. This is followed by 3- to 6-h "labor" phase, in which females undergo violent twisting and bending motions and convulsive shivering. By the end of the labor phase a 2–10 mm opening into the oviduct has appeared. Copulation probably occurs at this time (Johannessen et al. 1993). An 8- to 15-h resting phase occurs after the labor phase, in which eggs probably become fertilized (Pavlov and Moksness 1994). Extrusion of eggs occurred in 3–7 min at the end of the resting phase. The female then curls up around the eggs, which are embedded in mucus (Pavlov and Radzikhovskaya 1991; Johannessen et al. 1993). After 6–10 h the mucus has dissolved and the eggs are firmly attached to each other in a ball. The female continually turns the eggs, which are not attached to the substrate. The probable internal fertilization of wolffish has been discussed by several authors (Johannessen and Moksness 1990; Kvalsund 1990; Pavlov and Radzikhovskaya 1991; Pavlov et al. 1992; Pavlov 1994; Pavlov and Moksness 1994).

Little is known of male spawning behavior, as they show little interest in spawning in the laboratory (Johannessen et al. 1993; Pavlov and Moksness 1994). Although females initially guard the eggs after spawning in aquariums and under laboratory conditions, they lose interest after a few hours and may cannibalize them (Hognestad 1965; Ringø and Lorentsen 1987; Johannessen et al. 1993; Pavlov and Moksness 1994). The

male is believed to begin brooding the eggs shortly after spawning. Based on sex determination of eight adults guarding eggs in the wild, Keats et al. (1985) suggested that in this species only males brood eggs. Since eggs can take up to 9 months to develop, it is not clear whether parental care always lasts through hatching, although brooding for up to several months has been observed (Keats et al. 1985; Ringø and Lorentsen 1987). Male parental care of eggs has also been suggested for White Sea populations based on sex ratio data from trawl catches (Barsukov 1953, 1959; Pavlov and Novikov 1986). Males appear to reduce or stop feeding during the brooding period (Keats et al. 1985). They become very aggressive during the spawning season, and paired adults must be isolated when held in captivity (Pavlov and Novikov 1986). It has been speculated that males periodically release milt, even prior to the spawning season, as a pheromone to mark territories and attract females to nesting sites (Johannessen et al. 1993).

Early Life History. Egg and larval development are described in detail for Atlantic wolffish from Scotland (McIntosh and Prince 1890) and the White Sea (Pavlov 1986; Pavlov et al. 1992). The effect of temperature on the development of the skeletal system has been described in detail (Pavlov 1997; Pavlov and Moksness 1997). Eggs of Atlantic wolffish are large (5.5–6.8 mm in diameter), yellowish, opaque, and with an oil globule of 1.75 mm (Bigelow and Schroeder; McIntosh and Prince 1890; McKenzie and Homans 1938; Powles 1967). Eggs are laid in large tight clusters in nests guarded by the parental male (Keats et al. 1985; Ringø and Lorensen 1987). They may be confused with the eggs of ocean pout (*Zoarces americanus*), which lay similar egg masses at the same time as wolffish (Keats et al. 1985). However, ocean pout eggs are 8–9 mm in diameter and have a 3.2 mm oil globule (Methven and Brown 1991), distinguishing them from the smaller wolffish eggs. Ringø et al. (1987) described the amino acid and lipid composition of eggs, and Loenning et al. (1988) compared information on Atlantic wolffish egg morphology and physiology with that of several other pelagic and demersal eggs from northern Norway.

Egg and larval development has been described from a series of studies in Europe (Pavlov 1986; Pavlov and Novikov 1986; Pavlov et al. 1987, Ringø et al. 1987; Pavlov and Moksness 1994). Incubation time is highly dependent on water temperature and varies between 3 and 9 months, with 5°–7°C optimal. Larvae hatch at 17–20 mm. Prolarvae (about 22–24 mm) retain remnants of the yolk sac and oil globule and have a large eye with a diameter that is one-half the head depth. Small teeth are present. The finfold is completely differentiated. Melanophores are uniformly distributed over the body, but transverse pigment bands begin to appear on the trunk in some individuals. Narrow longitudinal bands of pigment are located along the base of the dorsal and anal fins, and a third band may be present along the midline of the body. These three pigment bands were also described by McIntosh and Prince (1890) for *Anarhichas lupus* and all three species of Atlantic wolffishes by Baranenkova et al. (1960). A few melanophores are present along the bases of the dorsal and anal fins. Canals of the lateral line appear on the head. The prolarval stage lasts from a few hours to 6 days.

In the larvae (>28 mm) the yolk sac has been reabsorbed and the relative depth of the body has increased. In White Sea populations 9–11 transverse pigment bands (bars) are present at this time (Pavlov et al. 1987). However, in Atlantic populations bars do not begin to develop until 130–150 mm (McIntosh and Prince 1890; Barsukov 1959). The feeding larval stage lasts only about 10–15 days at 5°–7°C. In the laboratory, fingerlings begin settling to the bottom at 25–30 mm, where they appear to defend territories. At this stage fingerlings become deeper bodied, pigment spots appear at the base of the dorsal (9–10) and anal fins (4–5), and conical teeth appear on the premaxillary, palatine, vomer, and dentary bones. The total pelagic stage lasts about 20 days, but might last up to 2 months at colder temperatures (Pavlov 1986).

The descriptions of newly hatched Atlantic wolffish larvae first provided by McIntosh and Prince (1890) and then by Bigelow and Schroeder were probably of individuals that had hatched prematurely owing to disturbance in the trawl and laboratory (Ringø et al. 1987). This would account for the long larval developmental period they reported and bias their description of larval behavior. Bigelow and Schroeder described wolffish 31.8–44.5 mm long as silvery on the sides in life, but the metallic hue fades after preservation, leaving only the dark brown pigment granules with which the sides are thickly dotted.

Fry of all three species of northwest Atlantic *Anarhichas* were described by Baranenkova et al. (1960). Pelagic larvae and juveniles of *A. minor* can be distinguished by presence of six or seven dark transverse stripes (or bars), giving them a somewhat mottled appearance. With growth these bars break up into large spots. *Anarhicas lupus* and *A. denticulatus* are more darkly and evenly pigmented, with vertical bars forming in the largest (over 10 cm) *A. lupus*. Smaller sizes of these two species can be distinguished chiefly by the length of a rayless membrane connecting the anal and caudal fins. In *A. lupus* this membrane is longer than the last anal ray, whereas in *A. denticulatus* it is shorter. The arrangement of teeth, though different from that of the adults, might be a useful for distinguishing among species of pelagic larvae (Barsukov 1959; Baranenkova et al. 1960).

Larval and Juvenile Distribution. In the Gulf of Maine, Atlantic wolffish larvae have been reported from the channel between Browns Bank and Cape Sable, near Seal Island (Nova Scotia), on German Bank and off its slope, off Lurcher Shoal, off Machias (Maine), on Jeffreys Bank (off Penobscot Bay), and in Massachusetts Bay a few miles off Gloucester. Bigelow and Schroeder interpreted this distribution data as indicating that Atlantic wolffish breed in the Gulf wherever they are found. They made similar observations for more northern parts of the American range of wolffish and noted that pelagic young

have been reported off northeastern Newfoundland, in the Strait of Belle Isle, and off Sandwich Bay on the Atlantic coast of Labrador by the Newfoundland Fisheries Research Commission. In the Gulf of Maine, small numbers of pelagic juveniles (30–90 mm TL) were collected from stomachs of groundfishes captured at depths of 54–268 m, primarily during April and May, and which were widely distributed throughout the region (NEFSC, unpubl. data). A notably large number (102) of pelagic juveniles (37–49 mm TL) were found in six Atlantic cod stomachs from a single trawl tow made in 100 m off the western coast of Nova Scotia in the vicinity of Cape St. Mary on 20 April 1984.

Orlova et al. (1990) determined that pelagic juveniles are rare at depths of 0–50 m in the water column throughout northern Europe. Based on data from infrequent catches from various gears and from occurrences in haddock stomachs, they concluded that there is little relationship between juvenile size and depth of capture. Recently hatched larvae (22–26 mm) were collected in near-bottom layers in areas 68–385 m deep. Larger individuals (19–55 mm) have been collected in the upper 100 m over depths of 80–3,100 m. Atlantic wolffish juveniles (27–70 mm) were also found in haddock stomachs from 100 m (Orlova et al. 1990). Falk-Petersen et al. (1990) collected larvae 13–42 mm TL in northern Norway during March, May, and July. They found no significant length relationship with depth, but most larvae were collected in the upper 25 m. An earlier study in the region reported that pelagic larvae occurred mainly in depths of 100–200 m, and juveniles at 68–385 m (Baranenkova et al. 1960). Little is known of the distribution or habitat use of juveniles after settlement (Keats et al. 1986a). Wolffish larger than 50 cm TL have not been collected in shallow water (<30 m) off Newfoundland, where spawning activity has been documented (Keats et al. 1985, 1986a). After a review of distribution records in the literature, Keats et al. (1986a) hypothesized that juveniles probably inhabit deeper offshore waters and move inshore only when they become sexually mature. Atlantic wolffish size-depth distribution data for the Gulf of Maine (Nelson and Ross 1992) support this idea. However, small numbers of juveniles 11–50 cm are consistently collected throughout the Gulf of Maine during spring and fall NEFSC groundfish surveys, with the greatest concentrations occurring in the vicinity of Jeffreys Ledge (NEFSC, unpubl. data). In northern European waters, benthic juveniles (7–19 cm) were most abundant at 100–200 m depths (Baranenkova et al. 1960). However, juvenile wolffish have been reported in shallow kelp beds off Greenland (Fabricius 1780); and Iceland (Sæmundsson 1949).

Larval and Juvenile Habits. Atlantic wolffish larvae and early juveniles are pelagic between 20 and 40 mm TL, with settlement beginning by 50 mm TL (Falk-Petersen and Hansen 1990, 1991). In the laboratory they appear to undergo a transitional period between 50–100 mm TL in which they spend part of their time on the bottom and part in the water column (Moksness et al. 1989). At this time they also become aggressive and show signs of territorial behavior. However, juveniles larger than 100 mm TL were more gregarious and spent most of their time on the bottom. Based on limited trawl data, Bigelow and Schroeder concluded that larvae probably remain near the bottom and do not disperse widely from the hatching locality. Changes in juvenile coloration (Baranenkova et al. 1960; Pavlov 1994) and teeth arrangement may be associated with the shift from a pelagic to a benthic habitat (Baranenkova et al. 1960).

Age and Growth. In the Gulf of Maine, Atlantic wolffish mean length at age has been reported as 4.7 cm TL at age 0 and 98 cm TL at age 22 (Nelson and Ross 1992). In Iceland, fish 10.5–98.5 cm ranged from age 0 to age 20 (Jonsson 1982). Similarly, fish from Norwegian waters of 26–112 cm TL were age 5 to age 23 (Falk-Petersen and Hansen 1991). Data provided by Jonsson (1982) indicate that they reach 10.5 cm during the first year (age 0), and 13.6 cm by age 1. A comparison with other age-growth studies (Jonsson 1982) indicates a size of 21.8–28.7 cm by age 4 (Barsukov 1959; Beese and Kandler 1969, cf. Jonsson 1982). In contrast, growth rates of cultured fish have been much higher (Moksness et al. 1989; Moksness and Stefanussen 1990). Atlantic wolffish fry cultured in Norwegian studies grew 2–3.6% body weight per day over the first 150 days posthatch and grew best below 10°C (Moksness et al. 1989). More recently, larvae reared from 2.6 g at start-feeding grew to 900 g within 34 months, for a growth rate of 0.58% body weight per day (Moksness and Stefanussen 1990). Wolffish raised on dry and moist pellets grew more slowly, 0.16–0.26 $g \cdot day^{-1}$ (Stefanussen et al. 1993).

Atlantic wolffish from the Gulf of Maine apparently grow faster than those from Iceland (Nelson and Ross 1992) but those from the North Sea grow fastest (Liao and Lucas 2000a). The von Bertalanffy parameters for the North Sea population are (Liao and Lucas 2000a) $L_\infty = 111.2$ cm, $t_0 = -0.43$, $K = 0.12$ for males; $L_\infty = 115.1$ cm, $t_0 = -0.39$, $K = 0.11$ for females. Males have been reported to grow faster and reach a larger size than females in Icelandic and Norwegian waters (Jonsson 1982; Falk-Petersen and Hansen 1991), although differences do not become obvious until after age 12 (Jonsson 1982). Nelson and Ross (1992) noted that studies in the western Atlantic have lacked sufficient data to detect growth differences between the sexes. They found that growth begins to slow at about age 5 to age 6, corresponding approximately to the size at maturity (47 cm based on Templeman 1986b), and hypothesized that the decrease in growth rate was due to a diversion of resources to gonadal development.

General Range. Both sides of the North Atlantic; north to Davis Strait in American waters; south regularly to Cape Cod; less often west along southern New England, and exceptionally to New Jersey; also Greenland, Iceland, and northern Europe south to northern France and Ireland (Briggs 1988).

Occurrence in the Gulf of Maine. Atlantic wolffish are widely scattered throughout the Gulf of Maine (Map 30).

West of the Scotian Shelf, abundance is highest in the southwestern portion of the Gulf of Maine from Jeffreys Ledge to the Great South Channel at depths of 80–120 m (Nelson and Ross 1992). High abundances are also found on the northeast peak of Georges Bank and on Browns Bank. Somewhat smaller concentrations appear off of southwestern Nova Scotia in the vicinity of Wedgeport, and throughout the central Gulf. Populations of Atlantic wolffish in the western Gulf of Maine are probably discrete from those on the Browns Bank and Scotian Shelf areas (Idoine 1998b).

Movements. Whether or not wolffish undergo seasonal movements between deep and shallow waters has been argued for some time (see reviews of early accounts in Gill 1911, Jonsson 1982, Templeman 1984a, and Keats et al. 1985). Bigelow and Schroeder considered it a relatively stationary species based on monthly commercial catches and a generalized account of its behavior. Nelson and Ross (1992) reported a weak seasonal shift in the depth distribution between shallow water (<120 m) in spring and deeper water in fall in the Gulf of Maine. They also reported a weak size stratification among depths during spring, but data from less than 40 m are sparse, and they reported no significant corresponding difference during fall. They interpreted these data as an indication of inshore movement by mature adults in spring. However, their own data show that large numbers of wolffish remain in deep water during both seasons. The spatial patterns they observed could alternatively be interpreted as resulting from decreased catchability in the fall owing to behavioral changes (discussed below), compounded by a nonseasonal depth stratification of size classes (i.e., juveniles inhabit deeper water). Keats et al. (1985) also suggested that mature wolffish move inshore during spring, spawn during summer and fall, and move back offshore during late fall after the eggs hatch, based on scuba observations conducted in 5–15 m off Nova Scotia. However, as Keats et al. (1985) themselves recognize, these movements must involve only part of the spawning population since egg masses have been collected in deeper waters (100–130 m) in the region (McKenzie and Homans 1938; Powles 1967). Further, an extensive trawl survey in nearby Newfoundland waters found that Atlantic wolffish were most abundant in depths greater than 100 m during April–July, the time of presumed inshore migrations. A tagging study off Newfoundland (Templeman 1984a) lends little support for a migration hypothesis. Atlantic wolffish were usually recaptured within 8 km of the release site after 5–7 years, although a few individuals migrated as far as 338–853 km (Templeman 1984a).

Inshore-offshore migrations have been suggested in other geographic areas. Strong evidence of short (<185 km) seasonal movements, based on long-term tag recapture and catch data, has been reported in Icelandic waters (Jonsson 1982). Some individuals, however, have been reported to travel distances ranging from about 200 to 670 km within a year of release and up to 925 km within 3 years (Jonsson 1982). It is thought that adults move inshore during January–March to feed after a prolonged fasting period associated with spawning and/or with annual tooth loss (see discussion below). In late summer they begin migrating to offshore spawning grounds in 140–200 m, where they remain between September and January (Jonsson 1982). White Sea populations are thought to make similar movements, with spawning occurring from late July to September (Pavlov and Novikov 1986, 1993). Barsukov (1959) suggests that the seasonal movement pattern may switch between northern and southern populations, with the northern populations moving inshore during summer and offshore during winter, whereas southern populations do the opposite.

Movements may be influenced by local seasonal temperature regimes. For example, Pavlov and Novikov (1986, 1993) suggest that spawning movements in the White Sea may result from temperature requirements for the developing eggs. They hypothesized that mature adults leave inshore feeding grounds, where water temperatures are too high for normal egg development, in late July and move to offshore spawning grounds, where water temperatures range from −1° to 5°C and are more suitable for egg development. Interpretation of distribution data may also be complicated if some members of the adult population skip spawning years (Pavlov and Novikov 1986, 1993).

More extensive tagging data on movements as well as better spatial and temporal data on tooth replacement and spawning are needed to determine to what extent wolffish populations undergo seasonal migrations in all geographic areas and why they do so. It is clear that any presumed inshore-offshore migrations cannot be attributed to spawning activity alone, since eggs are found in both inshore and offshore areas and large segments of the populations are found in deep water during all seasons. At the present time, the data are not sufficient to discount the possibility that spawning occurs in all depths of their distribution and that apparent seasonal movements result from behavioral changes affecting catchability.

Importance. The market demand for wolffish is comparatively recent. It is an excellent table fish, selling readily as "ocean catfish" or as "whitefish." The commercial catch of Atlantic wolffish in the Gulf of Maine–Georges Bank area results mainly as by-catch from demersal otter trawl fisheries (Idoine 1998b). The total nominal catch increased from about 200 mt in 1970 to about 1,200 mt in 1983 (Fig. 254) and then declined steadily to a low of 400 mt in 1996. The NEFSC spring bottom trawl survey biomass index has also shown a consistent downward trend; the 1997 index value of 0.13 kg per tow, is the lowest in the time series (Idoine 1998b). Population dynamics and stock assessment parameters are currently unknown. Although the species is currently not managed, it is clearly overexploited and depleted.

The Icelandic fishery for wolffish has historically been the largest Atlantic wolffish fishery (Jonsson 1982). Catches of wolffish in Iceland and Europe increased greatly after World War II, from about 13,608 mt·year^{-1} to more than 36,287 mt·

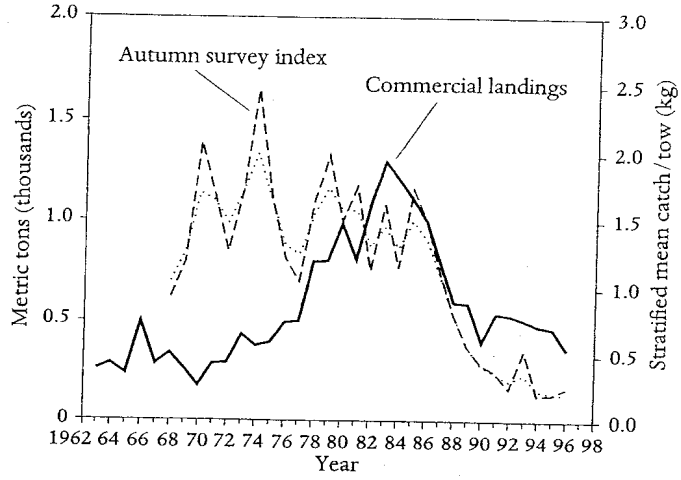


Figure 254. Commercial landings and NEFSC autumn survey index for Atlantic wolffish *Anarhichas lupus*, Gulf of Maine–Georges Bank, 1963–1996. (From Idoine 1998b.)

year^{-1} (Jonsson 1982). Catches in the northwest Atlantic have historically been small compared to Icelandic and European catches, averaging about 7,257 mt·year^{-1} between 1954 and 1973 (Jonsson 1982).

West Greenland waters have supported a local and international fishery for wolffish (including both spotted and Atlantic wolffish) since 1938 (Smidt 1981). The local longline fishery originally targeted spotted wolffish for production of skins. Frozen spotted wolffish fillets were targeted by inshore longliners beginning in 1951. The offshore trawl fishery began to increase substantially in the 1970s owing to declining Atlantic cod catches. Total nominal catches fluctuated between 4,000 and 6,000 tons during the 1950s and 1960s and appeared to be declining by the late 1970s (Smidt 1981).

It has been suggested that wolffish might be important predators on economically important bivalves (Sivertsen and Bjørge 1980, cf. Hawkins and Angus 1986; Nelson and Ross 1992; Stokesbury and Himmelman 1995). Several studies have used Atlantic wolffish as a model species in describing predation on sea urchins and attempt to examine its role in sea urchin population control (Breen and Mann 1976; Bernstein et al. 1981; Keats et al. 1986b; Hagen and Mann 1992). Sea urchin aggregation behavior is strongly influenced by wolffish and American plaice abundance (Bernstein et al. 1981).

Wolffish are the subject of extensive culture efforts in northern Europe (Pavlov and Novikov 1986; Ringø et al. 1987; Moksness et al. 1989; Johannessen et al. 1993; Pavlov and Moksness 1994; Tulloch et al. 1996).

SPOTTED WOLFFISH / *Anarhichas minor* Ólafsen 1772 / Spotted Catfish /

Bigelow and Schroeder 1953:507–508

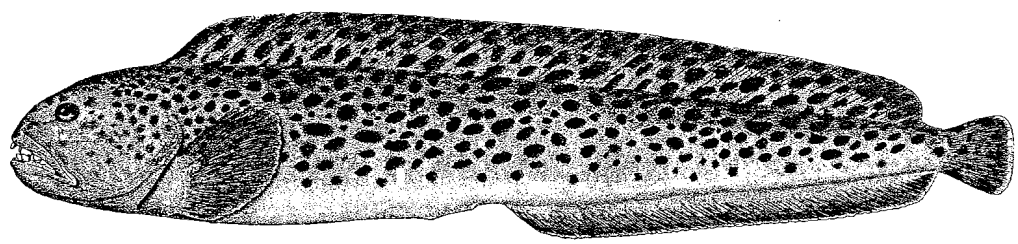


Figure 255. Spotted wolffish *Anarhichas minor*. Off La Have Bank. Drawn by H. L. Todd.

Description. Body stout, moderately compressed (Fig. 255). Head heavy, blunt, profile rounded. Central (vomerine) band of teeth on roof of mouth about equal in length to bands on either side (palatine).

Meristics. Dorsal fin spines 74–80; anal fin rays 44–48; pectoral fin rays 20–23; branchiostegal rays 6 or 7; vertebrae 76–79 (Barsukov 1959; Scott and Scott 1988).

Size. Notwithstanding their Latin name, spotted wolffish are fully as large as Atlantic wolffish and are said to reach 1.83 m, but lengths above 1.35 m have been disputed (Barsukov 1959). One 94-cm-long individual weighed 5.9 kg eviscerated. Spotted wolffish lengths tend to increase along a north to south cline in western Greenland waters (Smidt 1981; Riget and Messtorff 1988). No length differences between males and females have been reported (Templeman 1986a).

Color. Body pale olive to chocolate brown, upper parts including dorsal and caudal fins thickly sprinkled with blackish brown spots of different sizes and irregular shapes (Scott and Scott 1988).

Distinctions. Spotted wolfish resemble Atlantic wolffish closely in general form and in arrangement of fins. The chief difference is that while the central (vomerine) band of teeth on the roof of the mouth is longer than the band on either side (palatine) in Atlantic wolffish, they are of about equal length in spotted wolffish. The red teeth described by Bigelow and Schroeder cannot be taken as a distinctive character since

new teeth developing after the annual tooth loss are red in all wolffish species (Luhmann 1954; Barsukov 1959). Presence of thickly sprinkled irregularly shaped blackish brown spots on the dorsal and caudal fins, as well as on the head and flank, is the most useful field mark for spotted wolffish. A spotted form of northern wolffish (Templeman 1986c) can be distinguished from spotted wolffish by the lack of spots on the sides of the head and by differences in the number of vertebrae and dorsal fin rays. Young spotted wolffish smaller than 20 cm have 7–11 bars on their sides that break up into scattered spots with growth (Barsukov 1959), and hence could be confused with Atlantic wolffish. However, bars are lacking in Atlantic wolffish smaller than 7 cm and are absent or weak in individuals up to 20 cm. If present, bars on Atlantic wolffish are brownish and much longer than wide, whereas in spotted wolffish they are dark gray to black and nearly as wide as long.

Habits. Spotted wolffish were the least abundant species of wolffish collected off Newfoundland by Albikovskaya (1982) during April–July. They occurred at all depths from 1 to 600 m and at temperatures from −1.4° to 9.0°C, but were most common between 101 and 350 m and at temperatures under 5°C. In western Greenland waters, spotted wolffish were evenly distributed across three depth zones (0–200 m, 200–400 m, and 400–600 m) and between northern and southern areas (Riget and Messtorff 1988). Pelagic fry (24–26 mm) of spotted wolffish occur farther offshore and at greater depths (264–455 m) than Atlantic wolffish in the Barents Sea (Baranenkova et al. 1960). Juveniles (9–19 cm) were most frequently captured at depths of 200–250 m. Pelagic larvae (25–43 mm) were abundant in offshore waters in western (Smidt 1981) and eastern Greenland (Hansen 1968, cf. Scott and Scott 1988) during the summer. In the Barents and Norwegian seas, extensive collections have only rarely taken larvae or pelagic juveniles in the upper 100 m (Orlova et al. 1990, and citations therein). Orlova et al. (1990) collected 11 juvenile spotted wolffish (14–22 cm) in 220 m of water off Spitsbergen during August. Seasonal migrations have been suggested based on limited tag return data from the Barents Sea (Konstantinov 1961) and western Greenland (Riget and Messtorff 1988). Most individuals moved less than 100 km from the release site, although the longest migration was 777 km (Konstantinov 1961; Riget and Messtorff 1988). Little movement was noted for spotted wolffish tagged off Newfoundland, based on a limited sample size (Templeman 1984a). The pattern of longline catches of spotted wolffish from coastal, inshore, and fjord areas of Greenland suggests movements inshore and into the fjords during June and July (Riget and Messtorff 1988).

Food. Spotted wolffish from the Labrador-Newfoundland region have diets similar to Atlantic wolffish (Albikovskaya 1983). Both species feed heavily on echinoderms, but spotted wolffish eat fewer mollusks and more fishes, including *Sebastes* and *Gadus morhua*. Diet was highly variable among locations, and consumption was lowest in late fall and winter. Templeman (1986a) reported a similar diet of 52% echinoderms, 23% fish, 15% decapod crustaceans, and 10% other invertebrates, based on more limited data. Fishes preyed on included *Amblyraja radiata, Gadus morhua, Melanogrammus aeglefinus,* and *Sebastes* sp. No significant differences were found among diets of pelagic fry of all three wolffish species, based on limited data (Baranenkova et al. 1960; Orlova et al. 1990). However benthic juveniles had diets similar to adults, with more fishes in spotted wolffish (Baranenkova et al. 1960; Orlova et al. 1990). Frequent collections of Atlantic wolffish eggs in stomachs of spotted wolffish captured on Atlantic wolffishes' Icelandic spawning grounds (Jonsson 1982) suggest strong interspecific interactions. Spotted wolffish have been noted to feed frequently on fish offal discarded from fishing boats (Sæmundsson 1949).

Tooth Replacement. Spotted and Atlantic wolffish have similar dentition; teeth are replaced annually in both species (Albikovskaya 1983), and replacement in the two is similar (Luhmann 1954). Tooth shedding takes place later in the Barents Sea (January–February) for spotted and northern wolffish (February–March), compared with Atlantic wolffish (October–May, peaking December and January) (Barsukov 1961). Juveniles do not feed during tooth replacement (Baranenkova et al. 1960).

Parasites. Eleven species of parasites were reported from spotted wolffish, with heavy infestations of several trematodes (Zubchenko 1980). Many parasites were common to both spotted and Atlantic wolffishes. Heavy infestations of *Acanthopsolus anarhichae* in both wolffishes may be an indication of migrations to shallow waters, since the intermediate gastropod host, *Buccinum undatum,* is only found in depths less than 150 m (Zubchenko 1980).

Predators. Reported from stomachs of Greenland shark, cod, and pollock (Barsukov 1959).

Reproduction. Females mature at 48–62 cm and males at 53–71 cm in western Greenland waters (Smidt 1981). In the Barents Sea, female spotted wolffish first mature at 53 cm and age 7, and 50% of the females are mature at 75 cm and age 9 (Shevelev 1988). Males first mature at 66 cm and age 9, with 50% maturity at 95 cm and age 12. All females larger than 100 cm and males larger than 110 cm are mature (Shevelev 1988). Templeman (1986a) examined trawl data from throughout the northwest Atlantic between 1946 and 1967 and concluded that spawning probably occurs during or soon after July–August based on egg size and ovarian weights. Unusually large catches (11–59,000 kg) of spotted wolffish in 146–192 m of water on the Grand Bank during August and September may be an indication of spawning aggregations (Templeman 1986a). First maturity occurred at 75–80 cm for females, but exhibited some geographic variation. Fecundity varies from 4,200 to 35,200 eggs, averaging 5,504 eggs at an average fish length of 66.2 cm, 9,415 at 75.5 cm, 14,219 at 85.4 cm, 18,867 at 97.1 cm, 24,829 at 104.9 cm, and 33,920 at 117.6 cm (Gusev and Shevelev 1997).

Age and Growth. Spotted wolffish from the Barents Sea average 15.2 cm and 0.03 kg at age 0, 19.4 cm and 0.07 kg at age 1, 46.4 cm and 0.99 kg at age 5, and 118.5 cm at age 17 to age 21, based on analysis of hard parts (Shevelev 1988 and citations therein). Moksness and Stefanussen (1990) observed much higher growth rates for cultured spotted wolffish, with the fry growing faster (0.62% per day) than those of Atlantic wolffish (0.58% per day), increasing from 6.3 g on capture to 3,400 g after 34 months. They predicted that, if raised from start-feeding at an optimal temperature of 6°C, spotted wolffish should reach 6 kg in 2 years. However, an individual tagged in Norwegian waters increased in size from 78 cm to 120 cm in 1 year (Østvedt 1963, cf. Shevelev 1988), corresponding to an increase from 5 to 19 kg (0.21% body weight per day).

General Range. Chiefly north of the Arctic circle; north coast of Russia, White and Barents seas, and Iceland, south to middle Norway (vicinity of Bergen) on the European coast; Greenland; and southward occasionally to the Gulf of Maine on the American coast.

Occurrence in the Gulf of Maine. Goode and Bean's (1879) statement that "the Fish Commission has specimens from off the mouth of Gloucester Harbor and from Eastport, Maine," long remained the only notice of this northern fish for the Gulf of Maine, and fishermen have either never seen it there or have failed to distinguish it from Atlantic wolffish, which is unlikely, so striking is its color pattern. The late Walter Rich, of the U.S. Bureau of Fisheries, obtained a specimen that had been taken in 64 m off Cape Elizabeth (then in the collection of the Portland Society of Natural History); another, weighing 1.5 kg, was caught on a longline off the Portland lightship on 23 April 1927. Evidently spotted wolffish reach the Gulf of Maine only as accidental waifs from their Arctic home, to be watched for but hardly to be expected. They appear to occur regularly on Sable Island Bank and Banquereau Bank off outer Nova Scotia (Bean 1881; Vladykov 1935a; McKenzie and Homans 1938; McKenzie 1939).

Importance. Spotted wolffish are taken as by-catch from trawl and longline fisheries on both sides of the Atlantic, but are not usually reported separately from Atlantic wolffish (Smidt 1981; Jonsson 1982 [see Atlantic wolffish]). A local fishery for spotted wolffish skins off west Greenland began in 1938 and switched to mainly a filet fishery in 1951 (Smidt 1981). It has been found that spotted wolffish off the coast of Greenland in the vicinity of a zinc-lead mine have concentrations of lead in their organs (Bollingberg and Johansen 1979).

Suborder Trachinoidei

Thirteen families with a total of 51 genera are currently placed in this suborder (Nelson 1994), of which one family, the Ammodytidae, occurs in the Gulf of Maine. Systematic placement of this family has persistently plagued researchers studying these fishes. Many years of discussion concerning the phylogenetic placement of ammodytids resulted in proposed affiliations of the Ammodytidae with several different families and family groups (see Pietsch and Zabetian [1990] for historical background), but no completely acceptable conclusions were derived from these earlier studies. The current hypothesis of relationships places Ammodytidae as the sister group to Trachinidae and Uranoscopidae (Pietsch and Zabetian 1990), although Ida et al. (1994) noted inconsistencies in the number of shared characters between Trachinidae and Ammodytidae reported by Pietsch and Zabetian (1990).

SAND LANCES. FAMILY AMMODYTIDAE

MARTHA S. NIZINSKI

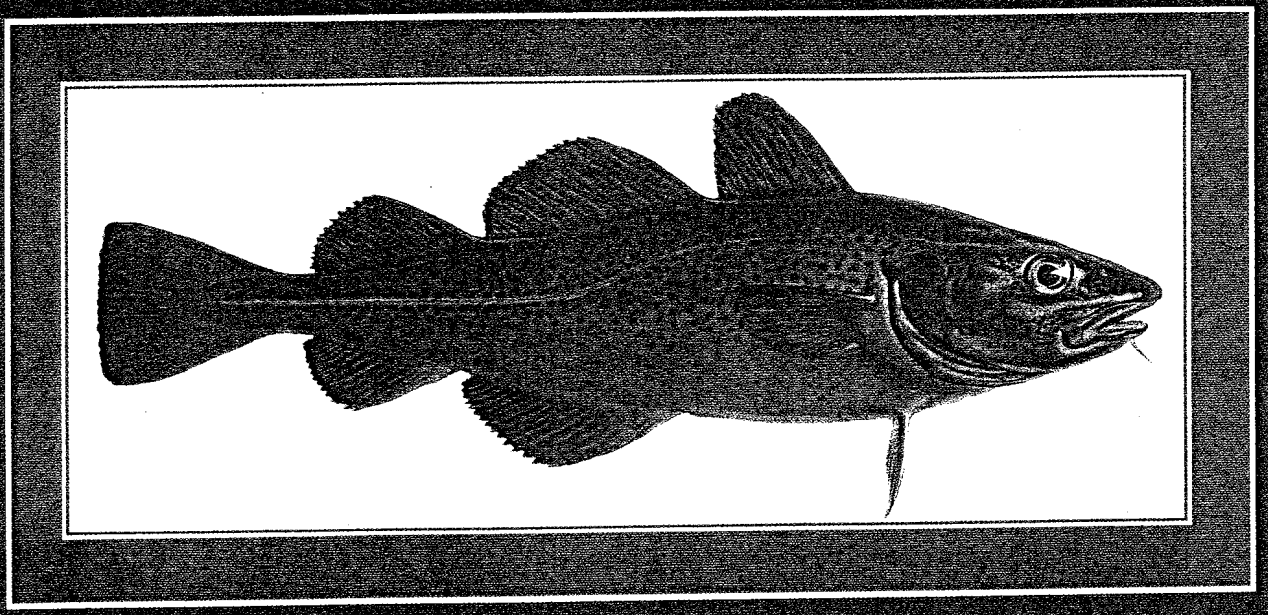
Sand lances are slender, schooling marine fishes found in both littoral and offshore environments in all major oceans and seas. The Ammodytidae currently includes seven genera and approximately 27 species (Ida et al. 1994; Collette and Randall 2000).

Confusion also surrounds species recognition within this group, and much of it can be attributed to morphological similarities and clinal variation, both with latitude and distance offshore, in meristic features among species. For example, 23 nominal species have been described in the genus *Ammodytes*. However, only six species are currently recognized (Reay 1970), two of which occur in the western North Atlantic.

Members of this family are characterized by a narrow, elongate body; small head, with the lower jaw protruding beyond the upper; jaws toothless, no teeth on roof of mouth; more abdominal than caudal vertebrae; a small, deeply forked caudal fin; pelvic fins minute or absent; low ridge of skin present on either side along abdomen; and dorsal and anal fins without spines (Pietsch and Zabetian 1990). Additionally, these fishes possess distinctive rows of oblique folds of skin, called plicae (Fig. 256), which occur on the lateral body surface and are lined on the underside by cycloid scales. Characteristically, plicae run downward and backward in a regular serial arrangement from the area above the pectoral fin base to the caudal peduncle.

BIGELOW AND SCHROEDER'S

FISHES
OF THE GULF OF MAINE



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THIRD EDITION