Abstract.-Populations of Atlantic hagfish, Myxine glutinosa (L.), are found throughout the Gulf of Maine in soft-bottom substrates at depths greater than 50 m. This report presents data on the sizes, weights, morphometric characters, and reproductive states for specimens collected at a study site approximately 50 km offshore in the Gulf of Maine. Limited comparisons with data from specimens collected elsewhere suggest that this data set is representative of hagfish populations within the inner Gulf of Maine. The small number of eggs produced (less than 30 per female), the large number of animals without macroscopically visible gonadal tissue (25% of the population), and the small number of males (<6% of the population), gravid females (<1%), and postovulatory females (<5%) suggest that hagfish have limited reproductive potential. This raises serious questions about the long-term viability of the New England eelskin fishery.

A population profile for Atlantic hagfish, *Myxine glutinosa* (L.), in the Gulf of Maine. Part I: Morphometrics and reproductive state

Frederic Martini* John B. Heiser**
Michael P. Lesser***
Shoals Marine Laboratory, G-14 Stimson Hall Cornell University, Ithaca, New York 14853
*Present address: 5071 Hana Hwy, Haiku, Hawaii 96708 E-mail address: martini@maui.net
**Present address: Section of Ecology and Systematics Cornell University, Ithaca, New York 14853
***Present address: University of New Hampshire Department of Zoology and Center for Marine Biology Durham, New Hampshire 03824

The hagfishes, or Myxinoidea, are worldwide in distribution, with 59 species recognized at present (Fernholm¹). Hagfishes are noteworthy from an evolutionary standpoint because they represent the oldest extant clade among the craniates. A better understanding of their anatomical and physiological characters may thus reveal information about an early stage in vertebrate evolution. Although eel-like in general body form, hagfish lack jaws, paired fins, vertebrae, bone, and a variety of other gnathostome characteristics.

All known species of hagfish live in close association with the bottom, resting on the substrate or occupying burrows within soft sediments (Gustafson, 1935; Adam and Strahan, 1963, a and b; Foss, 1963; Fernholm, 1974; Neira, 1982; Martin and Heiser, 1989; Cailliet et al., 1992; Barss, 1993). They are generally described as predators on invertebrates and as opportunistic scavengers on both invertebrate and vertebrate remains. There are two major groups of living hagfishes united under the family Myxinidae: the Eptatretinae, typified by the genus Eptatretus (30-35 species), and the Myxininae, typified by the genus Myxine (19 species) but also including the genera Nemamyxine, Neomyxine, and Notomyxine (Nelson, 1994). The characteristics of the Myxine appear to be more derived than those of the *Eptatretus*. For example, hagfishes of the genus Eptatretus have multiple efferent gill openings on each side of the pharynx, vestigial eyes beneath a pale skin patch, and traces of a cephalic lateral line complex. In contrast, hagfishes of the genus Myxine have a single common efferent duct opening on each side of the pharynx, even smaller eyes covered by undifferentiated integument, and no traces of any lateral line components. In general, the genus Eptatretus has a more widespread distribution than the genus Myxine, whose center of diversity appears to be the New World, where 14 of 19

¹ Fernholm, B. 1996. Box 50007, S-104 05, Stockholm, Sweden. Personal commun.

species have been identified (Wisner and McMillan, 1995).

Only one myxinid, *Myxine glutinosa* L., is found on both sides of the Atlantic Ocean, and this is the only hagfish reported within the Gulf of Maine. There are several reasons why *Myxine glutinosa* is an important species for the Gulf of Maine:

- 1 The substantial numbers present and their ongoing energetic requirements suggest that they play a significant role in the benthic ecosystem throughout the Gulf of Maine (Lesser et al., in press).
- 2 This species has both direct and indirect effects on commercial fisheries in the Gulf of Maine. In areas of abundance their opportunistic feeding habits can reduce the value of the catches made by longline or fixed gillnet fisheries. Hagfish have been known to feed on restrained or moribund cod, herring, haddock, hake, mackerel, spiny dogfish, and mackerel sharks caught in fisheries gear (Gustafson, 1934; Bigelow and Schroeder, 1953; Strahan, 1963). Equally important, feeding studies by Shelton (1978) suggest that hagfish predation could have a significant impact on *Pandalus borealis* populations within the Gulf of Maine.
- 3 Myxine glutinosa populations are now targeted by American and Canadian fishermen in the Gulf of Maine to meet the South Korean demand for "eelskin" used to manufacture expensive leather goods. In 1990, the sale of eelskin leather goods, all produced from hagfish skin, brought South Korea revenues of approximately US\$100 million (Gorbman et al., 1990). The value of eelskin products imported into the U.S. alone in 1992 was US\$70 million (Melvin and Osborn²). So large is this market that Korean processors, unable to supply the demand from overexploited eastern Asian fisheries, have begun sampling and purchasing hagfish from several other regions, including North and South America (Gorbman et al., 1990). During 1993 and 1994, Gulf of Maine fishermen harvested roughly 1600 metric tons (3.6 million pounds) of hagfish, and there were unknown effects on the ecology of the region (Kuenstner, 1996).

Part 1 of this report presents morphological data and a population profile generated in a study of a hagfish population in the Gulf of Maine. Part 2 of this report, published separately, will relate these and other data to the proposal made by Wisner and McMillan (1995) to reserve *M. glutinosa* for the eastern Atlantic, and to give western Atlantic populations, including those of the Gulf of Maine, separate status as *Myxine limosa*.

Materials and methods

The primary study site was adjacent to a small rock ledge known locally as "the Nipper" (near 42°57'N, 70°17'W). This site is within the Bigelow Bight, approximately 25 km west of Jeffrey's Ledge and 50 km east of the New Hampshire coast. The Bigelow Bight and Jeffrey's Ledge are both important groundfishing areas. Hagfish in the study area inhabit a superficial zone of fine, organic sediment covering a layer of grainy clay that overlies a thick layer of silty clay. Individual hagfish are usually found in shallow, sinusoidal, temporary burrows, with nose and barbels exposed to passing currents. The bottom temperature year-round is 4-6°C, and the salinity is 32 ppt or higher at all times. The superficial biotic community includes representatives from several families of tube worms, Cerianthid anemones, tunicates, sponges, and shrimp (Pandalus borealis). Comparable habitats that could support hagfish populations cover 60-70% of the floor of the Gulf of Maine (National Ocean Service³).

Hagfish were collected with baited traps set on the bottom in depths of 130-150 m. The traps consisted of garbage cans with holes punched in the side and with an internal screen that funneled hagfish toward the enclosed bait. The baited traps were left on the bottom for periods of 30 minutes to 1 hour and then retrieved. The animals were then placed in seawater chilled to approximately 4°C for transport to the Shoals Marine Laboratory on Appledore Island. Maine. After being held in refrigerated aquaria for a period of hours to days, animals were sacrificed and measurements were taken. The aquarium complex was monitored daily, and animals dying in captivity were measured immediately, prior to disposal. Morphometric data were collected from fresh specimens from the primary site between June 1989 and August 1992.

Methods of measuring and counting followed those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). All measurements were recorded in millimeters. For descriptive purposes, after total length (TL) was recorded, the body axis was divided into 3 regions (*snout-pcd*, *trunk*, and *tail* regions; n=143) or 4 regions (*prebranchial*, *branchial*, *trunk*,

² Melvin, E. F., and S. A. Osborn. 1992. Development of the west coast fishery for Pacific hagfish. Seattle, WA. Natl. Mar. Fish. Serv., NOAA. Final Rep. NA90AA-H-SK142.

³ National Ocean Service, Coast and Geodetic Survey. 1995. Gulf of Maine and George's Bank, Chart No. 13009. National Ocean Service, Silver Springs, MD.

Character	Mean	SD	Range	%TL ¹	SD	Range	n
Total length (mm)	509	104	195724	100			202
Snout-pcd ²	135	27	54-200	27.0	1.6	24-37	143
Prebranchial	82	20	34–130	17.0	1.9		67
Branchial	46	14	16-75	9.3	2.1	5-21	67
Trunk	311	72	107-459	61.4	3.8	42-83	143
Tail	64	14	25-106	12.6	1.1	9–17	143
Width	14	7	4–35	2.7	1.1	2–6	91
Depth (trunk)	22	7	8–35	4.2	0.7	2–7	87
Depth (cloaca)	19	5	6–28	3.7	0.5	2–5	198
Depth (tail)	20	5	8–30	4.0	0.5	2–5	97
Weight (g)	136	67	8-290				80
Total cusps	35	2	28-40				97
Multicusps outer	2	0.3	1–3				97
inner	$\frac{1}{2}$	0.1	1-2				97
Unicusps	-	011					
outer	7	0.7	5-9				97
inner	7	0.7	6–9				97
Total slime pores (left side)	114	7	91 –1 2 8	%TL ³	SD	Range	94
Snout-pcd	33	4	20-45	29	3.0	21-40	94
Trunk	67	4	51-77	59	2.9	51-69	94
Tail	13	2	8-19	11	1.3	9-15	94

² pcd = pharyngocutaneous duct.

³ % TP = Percentage of total slime pore counts.

and *tail* regions; n=67). The snout-pcd measurement extends from the tip of the snout to the anterior margin of the pharyngocutaneous duct (pcd), the trunk continues to the anterior margin of the cloaca, and the caudal region extends from that point to the tip of the tail. The sum of these measurements is equal to the total length.

For one series of animals, prebranchial and branchial measurements were taken within the snoutpcd length. The prebranchial region extends from the tip of the snout caudally to the rostral margin of the first gill pouch, the branchial region extends from that point to the anterior margin of the pharyngocutaneous duct.

Width is the maximum width of the trunk; depth (trunk) is the body height, exclusive of fin fold, at that site. Cloacal depth, measured at mid-cloaca, excludes the dorsal fin fold, whereas tail depth spans the entire tail, including dorsal and ventral fin folds. Cusp counts (unicusps and multicusps on outer and inner rows) were recorded for the left side; then the right side was counted to obtain the total cusp count. When slime pores were counted, the first two axial regions were combined and recorded as the snout*pcd* count, which corresponds to the *prebranchial count* of Wisner and McMillan (1995). This distinction was made to maintain consistency with the length data, where prebranchial and branchial lengths together constitute the snout-pcd length. Reproductive state was determined by visual inspection, rather than histological analysis. If present, ova were measured and the maximum length recorded.

Results

Table 1 summarizes pertinent morphometric data for this population of *Myxine glutinosa*. Hagfish species in general show remarkable variation in number of gill pouches. Table 2 presents data on the total number of gill pouches in our sample population. The range of gill pouch data (range:10-14, n=94) is greater than that reported for *M. glutinosa* in the eastern Atlantic by Fernholm and Hubbs (1981) (range: 11-13, n=8).

Despite the size of the landings (over 1,400 metric tons in 1994 [Kuenstner, 1996]), there are relatively few available data concerning the lengths and

Table 2Number of gill pouches in Myxine glutinosa (n=94).								
	No. of gill pouches (total)							
	10	11	12	13	14			
Incidence (%)	1.1	1.1	74.5	7.4	15.9			

weights of the harvested hagfish. This may in part reflect the effort required to immobilize and weigh individual hagfish. To address this problem we reviewed the morphometric data for a relatively quick and reliable method of estimating sizes and weights in the field. The easiest and most accurate method found involved measuring the depth of the body at the cloaca, excluding the dorsal fin fold. The fin fold was excluded to make the measurement easier to perform at sea with unanesthetized animals. (A caliper measurement of cloacal depth can be taken quickly, with minimal stress to the animal.)

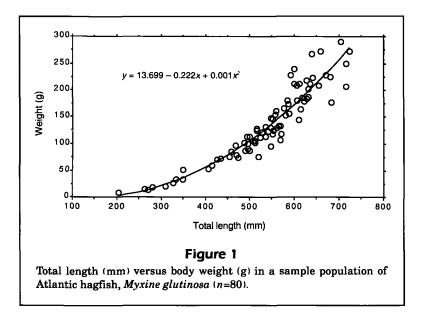
Figure 1 presents the relationship between total length and weight for a sample population of n=83. Figure 2A is a length histogram for the entire sample population (n=306) which comprised 202 animals whose lengths were measured directly (see Table 1) and 104 lengths calculated on the basis of cloacal depth using the formula shown in Figure 2B.

Figure 3A is a weight histogram for the entire sample population which comprised 80 direct measurements (see Table 1), 122 weights calculated on the basis of total length (see Fig. 1), and 104 weights calculated on the basis of cloacal depth with the formula shown in Figure 3B.

Note the preponderance of adult specimens and the absence of juveniles smaller than 195 mm (7.6 in.) at this collection site. No smaller individuals have been seen with ROV's or manned submersibles in this area, either on the soft bottom or over the associated rocky ledges (Martini and Heiser, 1989; 1991). Data on 1,172 animals from other locations in the Gulf of Maine (details below) indicate animals as small as 170 mm TL. However, the size of M. glutinosa at hatching has been estimated to be approximately 50 mm (Fernholm, 1969), and there has long been a general consensus that hagfishes, including Myxine, do not have a larval stage (Putnam, 1874; Dean, 1900; Worthington, 1905; Walvig, 1963). The absence of animals of 50-170 mm TL from traps at widespread locations and in visual surveys of bait stations suggests that newly hatched M. glutinosa may target different feeding resources from those targeted by older animals. Juveniles may, for example, feed solely on invertebrates within the substrate.

No data are available concerning the reproductive cycle and behavior of M. glutinosa. The sampled population contained a mixture of sexually immature and sexually mature individuals (Fig. 4). The following patterns can be recognized:

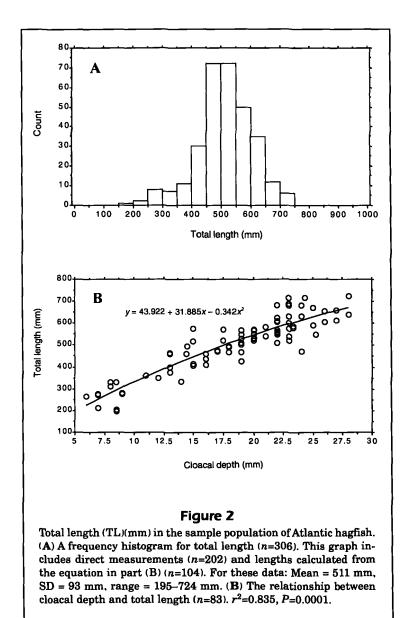
- 1 Individuals shorter than 400 mm TL are sexually immature. These animals either lack macroscopically visible gonads altogether or have granular tissue in the gonadal mesentery that cannot be identified as either testicular or ovarian in nature.
- 2 Approximately 59% of the population is classified as females on the basis of egg development. Testicular tissue is usually rudimentary in these animals.

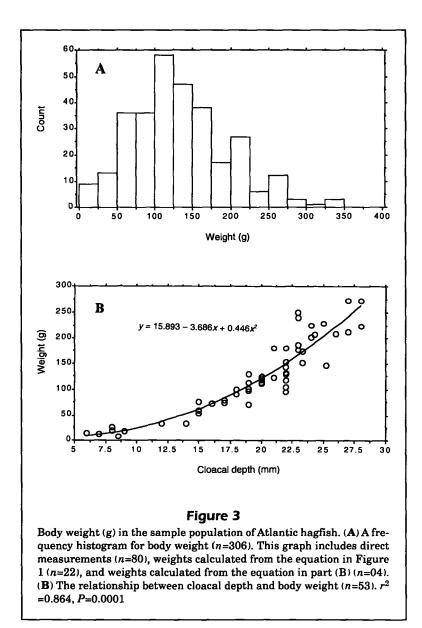


- 3 Males represent a very small percentage of the population (less than 6%).
- 4 Roughly 25% of the adult population does not have macroscopically identifiable gonadal tissue; the presence of large numbers of sterile individuals has also been reported for populations in the eastern North Atlantic (Schreiner, 1955; Jespersen, 1975).
- 5 The overlap in sizes between males and females suggests neither protandry nor protogyny.

Regression analyses were performed on morphological data sets to detect significant trends. No relationships were found between total slime pores, snout-pcd slime pores, or tail slime pores versus total length. This finding indicates that the number of slime pores is fixed for each individual and that additional slime pores are not added as growth occurs. However, with growth, the prebranchial region forms a significantly smaller percentage of the total length. The feeding apparatus, consisting of the tooth cusp plates and the dental muscle complex (Dawson, 1960), is therefore relatively large in smaller individuals. No data are available concerning the life span or growth rates for this species.

To determine whether or not our data were representative of the Gulf of Maine as a whole, we began by comparing the morphological data from our study site with data from eight specimens collected at Stellwagen Bank in Massachusetts Bay (42°20'N, 70°17'W), roughly 36 km from our primary study site. The size range (460–600 mm TL; average: 523 mm





TL) was comparable to that found at the Nipper (range: 195–724 mm TL; average: 509 mm TL). Although the small size of the Stellwagen sample constrains the power of statistical comparison, the only statistically significant differences found between these groups were that the maximum depth and width (in percent of body length) of animals from Stellwagen Bank were greater than those from the original study site. This may reflect differences in the substrate and food availability between the two locations, or it may be an artifact of the small sample size.

We next compared our length distribution data with catch statistics collected between 19 May and 28 July 1994 by the New England Fisheries Development Association (Kuenstner, 1996). The close agreement between the data sets (Fig. 2A vs. Fig. 5) suggests that the sampling reported here is representative of hagfish populations throughout the Gulf of Maine.

Discussion

The gonads in hagfishes develop within a mesenterial fold located to the right of the dorsal mesentery that supports the gut. The anterior 2/3 of the gonad may develop into ovarian tissue, and the posterior 1/3 may develop into testicular tissue. Details of sexual differentiation are known for only a few species, notably the Pacific hagfish, *Eptatretus stouti*. Gorbman (1990) reported that *E. stouti* are protogynous hermaphrodites: sexually immature animals are found at some stage of female differentiation, and mature animals are usually differentiated as either males or females. Mature females are longer than 200 mm TL and males are longer than 280 mm TL. The largest animals are usually females. The incidence of hermaphroditism in animals over 230 mm TL is very low (0.3% [Gorbman, 1990]), but there is evidence that this condition may persist throughout the life of the individual (Johnson, 1994).

In our study of M. glutinosa, animals at any size above 400 mm TL, the minimum size at which gonadal tissues become macroscopically identifiable, may have no discernible gonads or possess an immature ovary and immature testis, a mature ovary and immature testis, an immature ovary and a mature testis, or a mature ovary only. Animals with only mature testes were not seen, and only one animal was observed with what appeared to be a mature ovary and a mature testis. There was no apparent relation between total length and sex of the individual, nor between length and the lack of visible gonadal tissue. An incidence of sterility of 25% in animals over 400 mm TL is higher than the 13% incidence reported by Schreiner (1955) for mature eastern Atlantic M. glutinosa.

The sex ratio of females to males in many *Eptatretus* species has been reported to be skewed, from slightly to strongly in favor of females. For example, Johnson (1994) reported a sex ratio for *E. deani* of 2.58:1 and for *E. stouti* a sex ratio that gradually decreased from 1.8:1 at small sizes to roughly 1:1 for animals near 380 mm TL. Because sizes and sexes are unevenly distributed over the depth range where *E. stouti* is abundant (100-400 m), the sex ratio can vary widely depending on the depth of and season at the collection site. This may explain the broad range of sex ratios (0.58:1 to 4.38:1) reported for

E. stouti above 200 mm TL collected from a single area in British Columbia (Leaman⁴).

The sex ratio of females to males in our sample of *M. glutinosa* was highly skewed, at 9.8:1. This highly

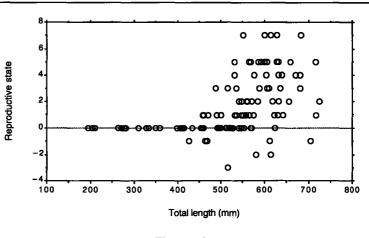
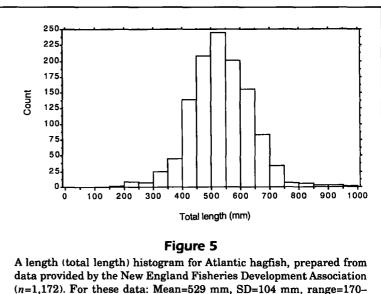


Figure 4

A scattergram of the reproductive state of the population of Atlantic hagfish as a function of total body length (n=122). Key: -3 = male, swollen testicular follicles; -2 = male, testicular follicles containing fluid; -1 = male, testicular tissue present; 0 = no macroscopically visible gonadal tissue; 1 = female, eggs <5 mm; 2 = female, eggs 5–9 mm; 3 = female, eggs 10–14 mm; 4 = female, eggs 15–19 mm; 5 = female, eggs >20 mm; 6 = female, shelled eggs in coelom; and 7 = female, postovulatory follicles.



950 mm. Compare with Figure 2A, P=0.000.

skewed sex ratio is typical for the species as a whole. The paucity of males in populations on both sides of the Atlantic has long been recognized, but it remains unexplained (Schreiner and Schreiner, 1904; Conel, 1931; Holmgren, 1946; Schreiner, 1955; Walvig, 1963; Cunningham, 1886–87). Males whose testes contain mature spermatozoa are even more unusual. Jespersen (1975) collected 1,000 specimens at a fjord

⁴ Leaman, B. M., ed. 1992. Groundfish stock assessments for the west coast of Canada in 1991 and recommended yield options for 1992. Biological Sciences Branch, Dep. Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia.

reputed to contain a relatively high proportion of males. Of 200 animals identified as male, only one contained a testis with motile sperm. Holmgren (1946) suggested that either ripe males may have a different distribution or that the ripe males do not feed. The latter suggestion appears more plausible in view of the broad areas sampled by investigators over the last 100 years.

Among hagfish, only *Eptatretus burgeri* has been shown to have an annual breeding cycle (Fernholm, 1975; Patzner, 1977; Tsuneki et al., 1983). Our data, collected during the summer months (June–August), indicate that there is no correlation between the size of a female and the size of the eggs within the ovary. Thus at any given time, one can collect females with ova at any stage of maturation. This is consistent with the contention that *M. glutinosa*, like most other hagfishes studied, have no specific breeding season (Cunningham, 1886–87; Nansen, 1887; Walvig, 1963).

The location of egg deposition also remains a mystery. Over the last 150 years, fewer than 200 eggs of Myxine glutinosa have been recovered. Only 4 of these eggs were fertilized, and none of the embryos were in an ideal state of preservation when examined. A trawled and damaged embryo, described by Dean (1899), has been the only report of a fertilized hagfish egg recovered in the western Atlantic. The great majority of the Myxine eggs-fertilized or not-described in the literature were collected in the eastern Atlantic, primarily from the nets of trawlers working soft bottom substrates. Three embryos of M. glutinosa, in somewhat better condition than Dean's specimen, served as the basis for papers by Holmgren (1946) and Fernholm (1969). Despite concerted efforts, no egg clusters were seen during winter and summer ROV surveys or summer submersible dives in an area supporting a large hagfish population, nor on the adjacent ledges (Martini and Heiser, 1989).

It is not known where or when mating takes place, nor how males locate females (or vice versa). Although at least one species (*Eptatretus burgeri*) has an annual reproductive season and migrates to reproductive sites that are used year after year (Tsuneki et al., 1983), such is not the case for *M. glutinosa*. The population at our primary study site appears to remain in place throughout the year; ROV work in June–September and December–January did not reveal any obvious differences in abundance at our study site.⁵ However, these observations need to be supported by additional collections and tagging studies.

Although our picture of reproduction in this species remains incomplete, it is clear that the population reproduces very slowly. Of 122 animals surveyed in the summers of 1989-90, only five were females with postovulatory follicles, and only one had fully developed shelled eggs loose in the coelom. In animals with postovulatory follicles, the remaining ovarian tissue did not contain eggs in advanced stages of development; there must therefore be a significant time period between reproductive cycles for a given individual. The time required for a female M. glutinosa to produce a clutch of eggs is not known, but it is probably longer than a year (Patzner and Adam, 1981). This makes good sense because the synthesis of large $(25 \text{ mm} \times 10 \text{ mm})$ yolky eggs is a substantial energetic investment. It appears likely that the reproductive potential of the population as a whole is relatively low, because 1) many of the individuals have no discernible gonads, 2) each mature female produces only 20-30 eggs at a time, and 3) a relatively small proportion of the females contain mature eggs at any given time. This low reproductive potential has obvious implications for the development of a sustainable fishery for these animals.

Given the evidence, there is considerable risk that the Gulf of Maine industry will prove to be another boom-and-bust fishery. The processors accept only fish greater than 350 mm in length (Kuenstner, 1996), which corresponds to a weight of more than 43 g (see Fig. 1). Because the average weight for Gulf of Maine specimens greater than 350 mm was 140 g, the fishing years of 1993–94 probably represented a harvest of roughly 11 million individual hagfish. The actual impact on the population is considerably greater, however, because 1) smaller hagfish are caught in the traps and are discarded into the surface waters and 2) hagfish of all sizes escape from the trap as it ascends. Except in winter, when the fishery is relatively inactive, hagfish released or escaping in this manner are unlikely to survive. The oceanographic conditions where these hagfish are collected are extremely stable, with summer temperatures of 4–6°C and a salinity of 33–34 ppt. Hagfish held in aquaria at the Shoals Marine Laboratory survive at 0-4°C but become increasingly agitated and soon die if the temperature rises above 10°C. Surface temperatures in the inner Gulf of Maine reach 16-18°C or more in the top 25-50 m during July and August, and at least one other warmwater mass covers the cold bottom water (Appollonio and Mann, 1995). When suddenly exposed to salinities below 31 ppt, individuals will struggle violently, produce copious slime, and then become moribund (Martini et al., pers. obs., and Adam and Strahan, 1963a). Surface salinities are often below 30 ppt in

⁵ This conclusion is based on visual surveys only. Weather conditions and equipment problems made it impossible to collect specimens during the winter trips.

surface waters of the Gulf of Maine (Bigelow, 1914). This combination of factors suggests that hagfish released at the surface or escaping from a trap within superficial water layers are unlikely to reach the bottom alive.⁶

On some commercial hagfishing trips, up to 70% of the catch (by weight) was discarded as unmarketable (Gryska⁷; the average for late 1995 was estimated at 41.1% (Kuenstner, 1996). The number of escaping animals cannot be estimated. It is therefore possible that the number of individuals removed from the environment may be twice the number landed onshore. Although the hagfish population present in the Gulf of Maine as a whole might well support such a harvest for a time, this level of fishing pressure could not be sustained. Because the fishing effort is not randomly distributed throughout the Gulf of Maine, the populations at sites targeted by this fishery can be expected to decline much more precipitously. There are already anecdotal reports suggesting that after only two years the catch per trap set has declined, and the average size of caught hagfish is decreasing (Hall-Arber, 1996).

It is not known what effects a decline in hagfish abundance will have on benthic ecology. However, from a regulatory perspective it is obviously difficult to set politically viable quotas or guidelines for a fishery when virtually nothing definitive is known about 1) the size of the population, 2) reproductive potential, 3) individual growth rates, or 4) longevity. There is therefore an urgent need for increased research on the basic biology and ecology of this interesting species.

Acknowledgments

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⁶ For release of live hagfish, the Shoals Marine Laboratory uses special gear that holds the animals in a volume of chilled, fullsalinity sea water until the apparatus contacts the bottom.

⁷ Gryska, A. 1994. New England Fish. Development Assoc., 451 D St., Boston, MA. Personal obs.

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