Abstract.—The species *Myxine glutinosa* has long been recognized as encompassing both eastern and western North Atlantic populations. Wisner and McMillan (1995) have proposed splitting the species into *M. limosa* (Girard, 1858; western North Atlantic) and *M. glutinosa* (Linnaeus, 1758; eastern North Atlantic). We examined a variety of morphological characteristics, including cusp counts, slime pore counts (total, prebranchial, trunk, and tail), total length, and body proportions (prebranchial, trunk, and tail length, maximum width and depth, and depth at cloaca). Several western Atlantic populations of varying size were compared with one large sample from the waters between Sweden and Denmark. The results indicate that although specimens from the Gulf of Maine differ significantly from those collected in the eastern North Atlantic, specimens collected from the mid-Atlantic coastal region of the United States and from northern Canadian waters are less distinctive. In addition, there are significant morphological differences among the populations sampled in the western North Atlantic. It is therefore suggested that until and unless molecular data indicate otherwise, the species name *M. glutinosa* be retained as encompassing both eastern and western North Atlantic populations.

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A population profile for hagfish, *Myxine glutinosa*, in the Gulf of Maine. Part 2: Morphological variation in populations of *Myxine* in the North Atlantic Ocean

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Only one hagfish, *Myxine glutinosa* (Linnaeus, 1758), has been found on both sides of the North Atlantic Ocean; this is the only hagfish reported from within the Gulf of Maine. *Myxine glutinosa* are an important species in the Gulf of Maine because 1) they are present in substantial numbers (densities may reach 500,000/km^2), and they may have a considerable impact on the benthic community (Lesser et al., 1996; Martini et al., 1997b), 2) they have direct and indirect effects on commercial fisheries in the Gulf of Maine, through predation on groundfish in fixed gear fisheries and through competition for shrimp, and 3) they have commercial value as the basis for a leather fishery that provided Gulf of Maine fishermen with $1.2 million in 1996.

The first part of this study (Martini et al., 1997a) presents morphological data and a population profile for hagfish in the inner Gulf of Maine. In this report we compare the morphological characteristics of this population with those of *M. glutinosa* populations in other geographical regions. Wisner and McMillan (1995) proposed splitting *M. glutinosa* into *M. glutinosa* (Linnaeus, 1758) for the eastern North Atlantic (ENA) and *Myxine limosa* (Girard, 1858) for the western North Atlantic (WNA). The proposed separation was based on differences in size at sexual maturity, maximum size, and the color of preserved specimens. We undertook this analysis initially to see if there were significant morphometric differences that would support the separation of species. This ultimately led us to perform statistical comparisons among our morphological data, collected in the inner portion of the Gulf of Maine, and the data of other researchers working with eastern and western North Atlantic populations of *M. glutinosa*.

Materials and methods

Wisner and McMillan included morphometric data for *Myxine* collected over a very broad area. The latitudinal limits were 33°46'N to 66°39'N, and the longitudes ranged from 79°42'W to 52°13'W. Of the 138 specimens cited in their report, only 28 (20%) were collected within the boundaries of the Gulf of Maine. Their study provided detailed data

on the numbers of slime pores (prebranchial, trunk, tail, and total) and total cusp counts for *Myxine* in the eastern and western North Atlantic. Through correspondence with Robert L. Wisner,[1] we obtained data and collection information for 73 western North Atlantic (WNA) and 179 eastern North Atlantic (ENA) specimens. These data sets permitted extensive comparisons with our morphological data for 1478 specimens from the inner Gulf of Maine (WNA).

Methods of measuring and counting followed those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). The body axis was divided into prebranchial, trunk, and tail regions. The prebranchial 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 tail region extends from that point to the tip of the tail. The sum of these measurements is equal to the total length (TL). The proportional measurements were recorded in millimeters and converted to percentages of total length. Additional data included body depth, body width, cloacal depth, and tail depth (in mm and %TL); total slime pore count (TP) with prebranchial, trunk, and tail counts (as values and %TP), and total cusp counts.

Morphological data were collected from 306 hagfish from the inner Gulf of Maine during five years of trap surveys at depths of 120–150 m by staff and students of the Shoals Marine Laboratory. Samples were collected from late June to early September. The traps used in this study were comparable to those set by the commercial hagfishing fleet. The trap used on most trips consisted of a weighted garbage can with 5–7.5 cm holes in the side and an inner, baited trap of wire screening. After collection, the animals were transferred to tanks of chilled seawater (2–6°C) at 32–35 ppt salinity for transport to the marine laboratory. All measurements were taken on fresh specimens. Total length data from these samples were combined with length data provided by the New England Fisheries Development Association for 1172 hagfish collected by fishermen within 80 km of the shoreline in the southern Gulf of Maine over the period of June–July 1995. All specimens were collected at depths of 120–180 m.

Samples from elsewhere in the North Atlantic were collected by either trawling or trapping at depths of 30–600 m between 1965 and 1987 (Wisner[1]). Collections in the eastern North Atlantic were from midsummer (August); those from the western North Atlantic were from all seasons. The morphological data from these collections were recorded from preserved specimens by Robert L. Wisner and Charmion McMillan. An analysis of variance was performed on the data with the fixed effect of collection site by using Statview 4.5 (Abacus Concepts Inc., 1995). This analysis consisted of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance.

Results

When plotted out on regional charts (Fig. 1), the data

[1] Wisner, R. L. 1996. Marine Biology Research Division, Univ. California, San Diego, La Jolla, CA 92093-0202. Unpubl. data.

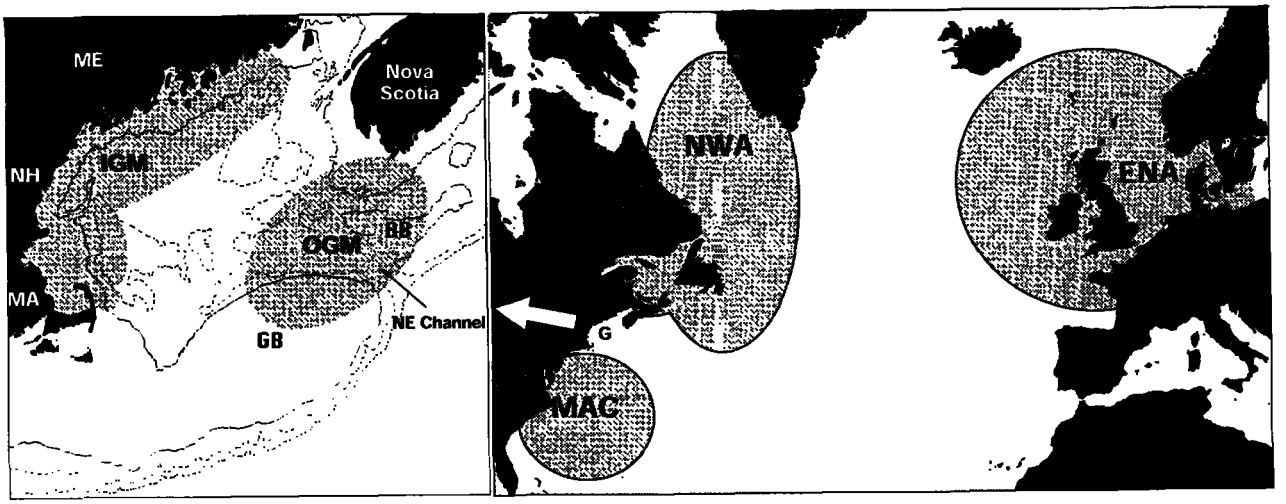

Figure 1

Sampled populations of *M. glutinosa* in the eastern and western North Atlantic. The shaded areas indicate the approximate range of collection sites for each data set. (**Left**) Collection sites within the Gulf of Maine. The 100-m, 200-m, and 300-m depth contour lines are indicated. OGM = outer Gulf of Maine; IGM = inner Gulf of Maine; BB = Brown's Bank; GB = George's Bank (**Right**) Other collection sites in the North Atlantic. ENA = eastern North Atlantic; NWA = Northwest Atlantic; G = Gulf of Maine (see [left]); and MAC = mid-Atlantic coast.

Table 1

Morphological measurements for *Myxine glutinosa* in the eastern and western North Atlantic. Asterisks indicate values significantly different ($P<0.0001$) from the Eastern Atlantic population.

Character	Mean	SD	Range	%TL[1]	SD	Range	*n*
Eastern North Atlantic group (ENA)							
Total length (mm)	299	31	227–387	100			179
Prebranchial (snout:pcd)	82	8	61–101	27.4	1.1	24–31	179
Trunk	174	20	133–227	58.2	1.5	54–62	179
Tail	44	5	33–59	14.9	0.9	12–18	179
Width	14	2	10–21	4.9	0.5	3–6	179
Depth (trunk)	18	3	13–26	6.1	0.6	5–8	179
Depth (cloaca)	14	2	10–20	4.7	0.5	4–7	179
Depth (tail)	15	2	12–20	5.1	0.4	4–6	179
Inner Gulf of Maine group (IGM)							
Total length (mm)[2]	524*	102	170–950	100			1478
Prebranchial (snout:pcd)	135	27	54–200	26.7*	1.6	24–37	143
Trunk	311	72	28–459	61.4	5.9	42–83	143
Tail	64	14	25–106	12.6*	1.2	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

[1] %TL = Percentage of total length. Values were log-transformed before comparison.
[2] Combined data, from Martini et al., 1997a, and Kuenstner, 1996.

collection sites fell into four groups: 1) mid-Atlantic coast (MAC), from the latitude of Charleston, South Carolina, to the southern coast of New England (n=51, with data on total length, slime pore counts, and cusp counts), 2) the outer Gulf of Maine (OGM), from the area of Brown's Bank (n=13, with data on total length, slime pore counts, and cusp counts), 3) the northwestern Atlantic (NWA) off Labrador, including Davis Strait (n=9, with data on total length, slime pore counts, and cusp counts), and 4) the eastern North Atlantic (ENA), from the Skaggerrack, between Sweden and Denmark (n=179, data on total length, proportional lengths, slime pore counts, and cusp counts). Our data set comprised a separate group, 5) the inner Gulf of Maine (IGM), represented by samples from within 80 km of the shoreline (n=1478 for total lengths, n=143 for proportional measurements, n=94–97 for slime pore counts and cusp counts).

Comparisons of morphometric data for the ENA and IGM populations, the two groups for which the greatest number of measurements were available, showed differences in total length and proportional measurements (Table 1). Table 2 presents data on cusp counts and slime pore counts for all groups (NWA, IGM, OGM, MAC, and ENA). The proportional measurements expressed as %TL and %TP were log-transformed before analysis and retransformed for presentation in the tables. Figure 2 illustrates the results of the post-hoc multiple comparison tests (Scheffe F-test) at the 5% level of significance. Table 3 details these results. Table 4 compares the data on total length for the sampled populations.

These results can be briefly summarized as follows:

1 The NWA sample, closest geographically to the ENA population, can be distinguished from the ENA only in terms of the trunk slime pores as a percentage of the total slime pore count. The total length data for the NWA and ENA groups are not significantly different.
2 The NWA sample is distinct from the OGM sample in terms of the total slime pore count and differs from the IGM sample with regard to prebranchial, trunk, and total slime pore counts as well as the total cusp count. The differences in regional slime pore count between the NWA and IGM samples were not significant when compared as percentages of the total slime pore count.
3 The OGM sample differs from the ENA sample in terms of the total slime pore count, and from the IGM sample in terms of the trunk slime pore count (as a value, not as a percentage of total slime pores) and in the total slime pore count. The total length data for the OGM and ENA groups were not significantly different, but the OGM animals were significantly smaller than those of the IGM.
4 The mid-Atlantic coastal group (MAC) has characters that overlap those of other groups. The MAC

Table 2

Tooth cusp counts and slime pore counts for populations of *Myxine glutinosa* L. in the eastern and western North Atlantic. Parenthetical values refer to the data expressed as a percentage of the total number of slime pores.

Character	Population	Mean	SD	Range	*n*
Total cusp count	NWA	32	1	31–34	9
	OGM	35	2	33–39	7
	IGM	35	2	28–40	97
	MAC	35	2	30–38	51
	ENA	34	1	29–38	101
Total slime pore count	NWA	95	2	91–101	9
	OGM	106	4	100–113	13
	IGM	114	7	91–128	94
	MAC	100	4	91–108	51
	ENA	96	5	85–108	143
Prebranchial slime pores (%)	NWA	26 (27)	3 (2)	23–32 (25–29)	9
	OGM	31 (29)	1 (1)	28–32 (28–30)	13
	IGM	33 (29)	4 (3)	20–45 (21–40)	94
	MAC	28 (28)	2 (2)	25–33 (25–33)	51
	ENA	27 (28)	3 (2)	20–36 (24–33)	143
Trunk slime pores (%)	NWA	58 (61)	3 (1)	56–66 (59–62)	9
	OGM	63 (59)	2 (1)	59–67 (57–61)	13
	IGM	67 (59)	4 (3)	51–77 (51–69)	94
	MAC	59 (59)	2 (2)	54–65 (55–64)	51
	ENA	56 (58)	3 (<0.5)	50–63 (57–60)	143
Tail slime pores (%)	NWA	11 (12)	1 (2)	8–13 (8–14)	9
	OGM	13 (12)	1 (1)	11–15 (10–14)	13
	IGM	13 (11)	2 (1)	8–19 (9–15)	94
	MAC	12 (12)	1 (1)	10–14 (10–14)	51
	ENA	12 (13)	1 (1)	8–15 (9–14)	143

data and the NWA sample differ significantly in the total cusp count. The MAC sample differs from the OGM sample in terms of the total slime pore count; it differs from the IGM sample in terms of prebranchial, trunk, tail, and total slime pore counts; the regional differences are not significant when compared as percentages of the total slime pore count. The MAC sample differs from the ENA sample in the trunk slime pore count (as a value, not as a percentage of total slime pores) and total cusp count. The total length data for the MAC, OGM, and ENA groups are not significantly different; all are significantly smaller than the IGM animals.

5 The IGM data is distinct from the ENA group for trunk, tail, and total slime pore and cusp count data. The IGM and ENA groups also differ significantly in prebranchial, trunk, and tail lengths, body width, body depth, tail depth, and cloacal depth (as percentages of total body length).

6 Hagfish from the inner Gulf of Maine were significantly larger than hagfish collected in any other location ($P<0.0001$). The average lengths of the OGM and MAC samples (315 mm and 280 mm respectively) were not significantly different from that of the ENA population (290 mm; see Tables 4 and 5). Further, we are unaware of any records for *M. glutinosa* larger than 450 mm outside of the Gulf of Maine or the adjacent continental slopes. Wisner and McMillan (1995) reported total lengths of 117–501 mm for their WNA sample (n=78). With deletion of the 13 animals known to be from the outer Gulf of Maine, the size range becomes 117–446 mm. This range, which still includes 15 animals from the outer Gulf of Maine,[2] is within the size range reported for eastern North Atlantic *M. glutinosa* (maximum size of 450 mm. It may also be significant that one of the OGM specimens, 350 mm in total length, contained fully mature eggs (SI075-689, from 42°40.5' N, 66°37'W; Wisner[1]). This is above the size of sexual maturity for eastern North Atlantic *M. glutinosa* (200 mm) but below the apparent length at maturity for specimens in the IGM sample (400 mm; Martini et al., 1997a). The large maximum size and large size at maturity

[2] Data forms did not permit determination of individual sizes, only ranges for these collection sites.

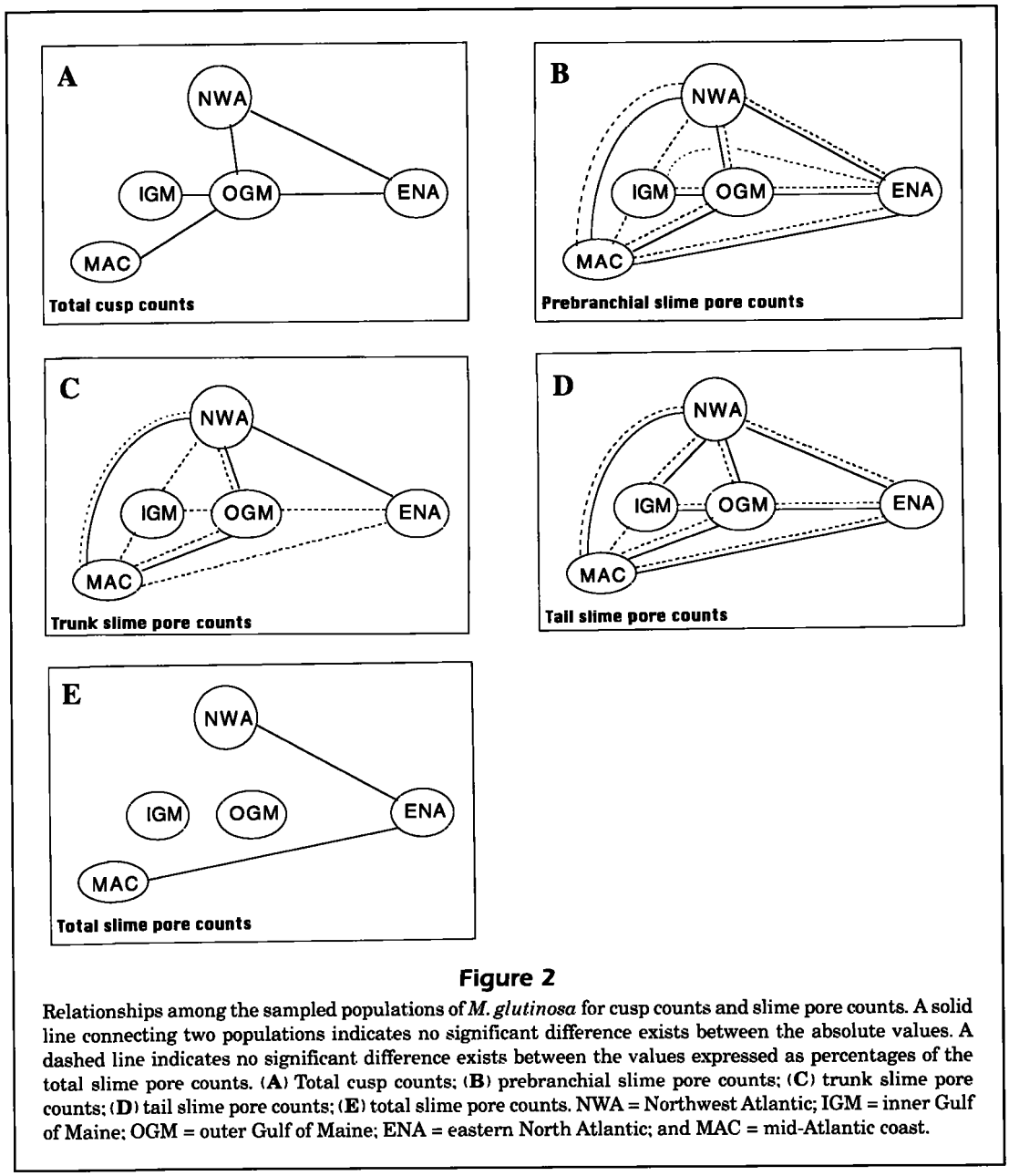

Figure 2

Relationships among the sampled populations of *M. glutinosa* for cusp counts and slime pore counts. A solid line connecting two populations indicates no significant difference exists between the absolute values. A dashed line indicates no significant difference exists between the values expressed as percentages of the total slime pore counts. (**A**) Total cusp counts; (**B**) prebranchial slime pore counts; (**C**) trunk slime pore counts; (**D**) tail slime pore counts; (**E**) total slime pore counts. NWA = Northwest Atlantic; IGM = inner Gulf of Maine; OGM = outer Gulf of Maine; ENA = eastern North Atlantic; and MAC = mid-Atlantic coast.

that has been widely attributed to *M. glutinosa* in the western North Atlantic thus appears to be valid only for the inner Gulf of Maine.

In summary, the IGM group is significantly larger in total length than any other population sampled. Proportional measurements could be compared only between the IGM and ENA samples. In addition to having much greater total length, hagfish from the IGM sample are more slender (both in width and depth) and have shorter prebranchial segments and shorter, narrower tails than ENA specimens. Allometric effects are probably not responsible for these differences, which remain significant even when the IGM data set is restricted to animals of the same size range as that in the ENA sample (<400 mm). Total length, slime pore counts, and total cusp counts could be compared among all groups. The highest variability observed was in the total slime pore count. Specimens from the Gulf of Maine (IGM and OGM) differed from one another and from all other sample groups. In terms of the regional distribution of slime pores, there were significant differences between the IGM and ENA samples when compared as absolute values or as percentages of the total slime pore count. Differences in the regional distribution of slime pores

Table 3

Results of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance. For counts, means, and standard deviations, refer to Table 2. The asterisks (*) indicate values significant at the 5% level (Scheffe *F*-test).

Groups compared	Mean diff.		*P*-value	
Prebranchial slime pore counts, as value and percentage of total (in parentheses)				
IGM vs. MAC	5.216	(0.020)	<0.0001*	(0.4127)
IGM vs. NWA	7.517	(0.033)	<0.0001*	(0.1905)
IGM vs. OGM	2.756	(0.005)	0.2380	(0.9979)
IGM vs. ENA	6.045	(0.014)	<0.0001*	(0.0915)
MAC vs. NWA	2.301	(0.019)	0.7105	(0.8340)
MAC vs. OGM	−2.46	(0.009)	0.4471	(0.9913)
MAC vs. ENA	.828	(−0.010)	0.8798	(>0.9999)
NWA vs. ENA	−1.472	(−0.019)	0.9448	(0.8091)
OGM vs. NWA	4.761	(0.028)	0.0865	(0.6534)
OGM vs. ENA	3.288	(0.009)	0.0661	(0.9849)
Trunk slime pore counts as value and percentage of total (in parentheses)				
IGM vs. MAC	8.550	(0.002)	<0.0001*	(0.9985)
IGM vs. NWA	9.197	(−0.017)	<0.0001*	(0.2559)
IGM vs. OGM	4.838	(0.004)	0.0022*	(0.9985)
IGM vs. ENA	11.170	(0.010)	<0.0001*	(0.0212)*
MAC vs. NWA	0.647	(−0.019)	0.9997	(0.2076)
MAC vs. OGM	−3.712	(0.002)	0.0861	(>0.9999)
MAC vs. ENA	2.619	(0.008)	0.0030*	(0.3125)
NWA vs. ENA	1.972	(0.027)	0.8591	(0.0054)*
NWA vs. OGM	−4.359	(0.022)	0.2478	(0.2986)
OGM vs. ENA	6.331	(0.006)	<0.0001*	(0.9760)
Tail slime pore counts as value and percentage of total (in parentheses)				
IGM vs. MAC	0.995	(−0.006)	0.0166*	(0.0694)
IGM vs. NWA	1.655	(−0.005)	0.1012	(0.9683)
IGM vs. ENA	0.794	(−0.012)	0.0088*	(<.0001)*
IGM vs. OGM	−0.276	(−0.010)	0.9987	(0.0694)
MAC vs. NWA	0.660	(0.001)	0.9538	(0.9995)
MAC vs. OGM	−1.271	(−0.004)	0.2460	(0.9376)
MAC vs. ENA	−0.201	(−0.006)	0.9940	(0.1040)
NWA vs. ENA	−0.861	(−0.007)	0.8116	(0.6125)
NWA vs. OGM	−1.932	(−0.006)	0.1156	(0.9204)
OGM vs. ENA	1.075	(−0.001)	0.3745	(>0.9999)
Total slime pore counts				
IGM vs. MAC	14.227		<0.0001*	
IGM vs. NWA	18.429		<0.0001*	
IGM vs. OGM	7.566		0.0039*	
IGM vs. ENA	17.38		<0.0001*	
MAC vs. NWA	4.203		0.6730	
MAC vs. OGM	−6.661		0.0353*	
MAC vs. ENA	3.154		0.0922	
NWA vs. OGM	−10.863		0.0054*	
NWA vs. ENA	−1.076		0.9995	
OGM vs. ENA	9.787		<0.0001*	
Total cusp counts				
IGM vs. MAC	0.432		0.9625	
IGM vs. NWA	3.409		0.0006*	
IGM vs. OGM	0.235		>0.9999	
IGM vs. ENA	1.883		<0.0001*	
MAC vs. NWA	2.978		0.0109*	
MAC vs. ENA	1.667		0.0003*	
MAC vs. OGM	−0.197		>0.9999	
NWA vs. ENA	−1.310		0.7119	
NWA vs. OGM	−3.175		0.1263	
OGM vs. ENA	1.864		0.4313	

between the groups IGM-MAC, IGM-NWA, IGM-OGM, and MAC-ENA were not significant when compared as percentages of the total slime pore count. Total cusp counts differed significantly between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA.

Discussion

The primary goal of this analysis was to assess the validity of the proposed splitting of *M. glutinosa* L. into two species. With the exception of the IGM data, the proposal by Wisner and McMillan (1995) was based on a general morphological comparison of animals collected from the eastern and western North Atlantic. This study used their data, assigned to the NWA, OGM, MAC, and ENA groups. As is often the case when working with fishes whose lifestyles, habits, and population dynamics are poorly understood, there are a number of potential complicating factors that could bias these data. For example, both the Wisner and McMillan study and our own have compared specimens collected by 1) different methods, 2) at different times, and 3) at different depths. This is not unusual; the majority of the 59 currently recognized species of hagfishes are known from small numbers of animals (often just one) caught accidentally in mobile fisheries gear. The limitations of our data sets are therefore shared not just with Wisner and McMillan (1995) but with many other studies of hagfish systematics. Our goal was to determine if—given the limitations of the available data—the proposed split could be justified on the basis of the available morphological data.

We will now discuss each of these complicating factors as they influence hagfish collections in general, and the data in this study in particular.

The collection method might affect the size range of animals captured

Comparative data on trawl versus trap collection of *Myxine* are unavailable, but it is known that trawl-

Table 4

Size distribution in populations of *Myxine glutinosa* in the eastern and western North Atlantic. Total length measurements (in mm) reported for eastern and western Atlantic populations (all groups). See text for explanation of abbreviations.

	NWA	OGM	IGM	MAC	ENA
		315	509	280	299
Average	190–405	215–510	195–724	220–380	227–392
range	(n=11)[1]	(n=13)[1]	(n=306)[3]	(n=13)[1]	(n=179)[1]
			529		312
		103–405	170–950	220–420	253–362
		(n=8)[2]	(n=1172)[4]	(n=37)[2]	(n=8)[5]
					<450[6]

[1] From Wisner and McMillan (1995).
[2] From raw data provided by R. Wisner (see Footnote 1 in main text).
[3] From Martini et al. (1997a).
[4] From Kuenstner (1996).
[5] From Fernholm (1981).
[6] From Adams and Strahan (1963).

Table 5

Results of post-hoc multiple comparison tests of total lengths; asterisks (*) indicate values significant at the 5% level (Scheffe F-test). See text for explanation of abbreviations.

Groups compared	Mean difference	P-value
IGM vs. MAC	231.490	<0.0001*
IGM vs. NWA	213.798	<0.0001*
IGM vs. OGM	196.381	<0.0001*
IGM vs. ENA	213.099	<0.0001*
MAC vs. NWA	−17.692	0.9996
MAC vs. OGM	35.109	0.9698
MAC vs. ENA	−18.391	0.9943
NWA vs. ENA	−1.217	>0.9999
NWA vs. OGM	−17.417	0.9996
OGM vs. ENA	16.718	0.9904

ing estimates of hagfish population density produce gross underestimates (Wakefield, 1990). Given the maximum swimming rate of adult *Myxine* (<1 m/sec, Foss, 1968), hagfish of any size are probably unable to outrun a trawl. We would predict that trapping would collect smaller individuals that might slip through the trawl mesh, whereas trawling could collect mature animals that might not be attracted to traps (breeding hagfish may not feed; Walvig, 1963). However, because we have no indication of allometric effects of body size on any morphometric character for *M. glutinosa*, the statistical comparisons of slime pore counts, cusp counts, or proportional measurements should be unaffected by variations in total length among the sample populations. Neither traps with large-bore entrances or trawl nets, the collection methods used for these data, should bias the maximum recorded size.

Collections made at different times of the year may produce biased samples owing to seasonal migrations or breeding activities

Although no large-scale tagging studies have been performed, field observations and their relatively inefficient and slow swimming speed suggest that *M. glutinosa* are relatively sedentary animals with small home ranges. Among hagfishes, only *Eptatretus burgeri* is known to have seasonal migrations (Fernholm, 1974), and their migration is related to a specific breeding cycle that is unique among hagfishes. *Myxine glutinosa* has no particular breeding period, and adults at all stages of gonadal development are present throughout the year (Walvig, 1963; Martini et al., 1997b). There were no significant differences in the population profiles for animals collected at our primary study site in June–September from one year to the next, and although weather and sea-state conditions prohibited collection in midwinter, no population differences, in terms of size range or abundance, were apparent in ROV surveys performed in December–January as compared to July–August (Martini, personal obs.).

Collections made at different depths may yield different sex ratios and population profiles

The reported depth range of *M. glutinosa* is extensive (50–1100 m). There are no reports of depth stratification by size or sex for any species of *Myxine*, and only suggestions of unequal depth distribution (by size and sex) for two species of *Eptatretus* (*E. stouti* and *E. deani*) (Johnson, 1994; Wakefield, 1990). All known *M. glutinosa* populations have sex ratios that are highly skewed in favor of females, but above the size at sexual maturity there are males and females of all sizes. Any variations in the sex ratios would not affect the morphological parameters we compared because no sexual dimorphism has been reported for these characters in *M. glutinosa* or any other hagfish species.

The IGM data were collected from fresh, rather than preserved, specimens

Fixation shrinkage of 10–15% may occur in preserved specimens (Wisner[1]). This shrinkage would not affect parameters such as cusp counts or slime pore counts, but it would potentially affect total length. Shrinkage alone, however, could not account for the magnitude of the observed differences in maximum total length (950 mm for IGM, versus a maximum of

510 mm elsewhere in the WNA, and 450 mm in the ENA) or the minimum size at sexual maturity (400 mm for the IGM vs. 200 mm for the ENA). Shrinkage may have affected some of the proportional comparisons between the IGM and ENA samples, but the effect is not straightforward. The IGM hagfish (fresh measurement) have proportionately shorter prebranchial segments and tails than the ENA specimens (preserved measurement), and the IGM specimens are more slender (both in width and depth).

The morphological measurements were made by different groups

We do not believe that the differences observed among these populations reflect variation in protocol between the research groups because differences in slime pore counts and cusp counts among the sampled populations remain if the IGM data are set aside, and a single team (Wisner and McMillan) collected the NWA, OGM, ENA, and MAC data sets.

Conclusions

Our analyses of the available data do not support a clean division between eastern and western North Atlantic populations of *M. glutinosa*. We therefore support retention of the species name *M. glutinosa* for both eastern and western populations pending the results of mtDNA analysis or other molecular comparisons.

Specific arguments against species or subspecies division include the following: 1) Considerable variability exists in the total slime pore count among the WNA groups examined; 2) Although there were significant regional differences in slime pore count between the IGM and ENA samples, when compared as absolute values or as percentages of the total slime pore count, this was not the case for the other WNA groups; 3) Total cusp counts were also variable, with significant differences noted between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA; and 4) The degree of differentiation versus the ENA group, in increasing order, would be NWA (trunk slime pore percentage) → OGM (total slime pore count) → MAC (trunk slime pore count and cusp count) → IGM (total, trunk, and tail slime pore counts and cusp count).

This pattern suggests, but does not prove, the existence of clinal variations that may reflect the degree of relative isolation of the populations. Although on a map the Gulf of Maine appears continuous with the western North Atlantic, in fact it is almost completely isolated from the offshore waters by extensive banks and shoals (Fig. 1A). There is only one deepwater connection (260–270 m) between the Gulf of Maine and the North Atlantic. This narrow connection, the Northeast Channel, extends between Brown's Bank (BB), where the majority of the OGM samples were collected, and a shallow ridge that extends northeast from George's Bank (GB). Oceanographically the Gulf of Maine resembles a landlocked sea, like the Mediterranean, rather than a contiguous portion of the North Atlantic. For example, the salinity, temperature, tides, and current dynamics of the Gulf of Maine are distinct from those of the North Atlantic. This combination of factors could isolate hagfish populations within the Gulf of Maine from those elsewhere in the western North Atlantic. The distinct characteristics of the Gulf of Maine environment may also be linked to physiological differences between *M. glutinosa* in the Gulf of Maine versus the eastern North Atlantic. For example, *M. glutinosa* in the eastern North Atlantic have been maintained at water temperatures as high as 15°C (Palmgren, 1927; Gustafson, 1935), whereas specimens at the Shoals Marine Laboratory (Gulf of Maine) quickly become moribund as temperatures approach 10°C (Martini, personal obs.).

The size difference between the IGM and other sampled populations could be a function of age, with members of the IGM population having longer lifespans. However, this is impossible to evaluate without growth rate or longevity data—which does not presently exist for this or any other species of hagfish. Alternatively, the large total size and large size at maturity for hagfish within the Gulf of Maine may reflect the relative availability of food. It is interesting to note that Kendall described winter flounder (*Pleuronectes americanus* [formerly *Pseudopleuronectes americanus*]) of the George's Bank region as a separate species from those found elsewhere in the western North Atlantic, on the basis of its unusually large size; this proposal was ultimately rejected because there were no other morphological differences. It is not clear, however, that the ecosystem in the inner Gulf of Maine is significantly more productive than that of the Skaggerack in the eastern North Atlantic; both areas support substantial commercial fisheries.

Wisner and McMillan (1995) proposed species separation based on maximum size, size at maturity, and differences in the color of preserved specimens. As indicated above, the large maximum size and large size at maturity appear to be characteristic of the IGM population only, rather than a general characteristic of WNA populations of *Myxine*. We remain unable to evaluate the significance of the color differences in preserved specimens noted by Wisner and McMillan (1995) for eastern versus western North

Atlantic *Myxine*. The patterns they described as typical for the WNA are not found in our preserved specimens from the IGM. Further, our field data, which included ROV and submersible observations and trap collections, indicate that the described color patterns are not characteristic of living members of the inner Gulf of Maine populations. Whether they are characteristic of other WNA populations, or typical of only a few subpopulations, remains to be determined.

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