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Author(s): Katharine L. Leigh , Jed P. Sparks , and William E. Bemis
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Food Preferences of Atlantic Hagfish, *Myxine glutinosa*, Assessed by Experimental Baiting of Traps

Katharine L. Leigh[1], Jed P. Sparks[1], and William E. Bemis[1]

We investigated food preferences of Atlantic Hagfish (*Myxine glutinosa*) in Bigelow Bight in the Gulf of Maine by deploying traps at three moderate depths (ranging from 61 m to 132 m) using different types of bait (fish, crabs, and clams) singly and in mixtures. We counted the numbers of specimens caught in each trap, recorded their individual weights and lengths, and noted the presence of eggs. Bait containing fish consistently attracted the greatest number of hagfish, while invertebrate based baits were less effective: there was a nine fold increase in catch rate for traps containing fish bait compared to traps containing only clam bait, and no hagfish were caught using only crab bait. Atlantic Hagfish appear to be adept at detecting even small quantities of fish because baits consisting of 10% fish and 100% fish were equally effective. Even at the relatively shallow and closely adjacent depths sampled we found longer and heavier hagfish at the deepest sampling sites, and individuals from those sites had larger eggs than those from shallower depths.

ACCOUNTS on the Atlantic Hagfish (*Myxine glutinosa*) from the Gulf of Maine describe many aspects of morphology, physiology, systematics, and biogeography (Bigelow and Schroeder, 1948, 1953; Lesser et al., 1997; Martini et al., 1997a, 1997b, 1998; Martini, 1998a, 1998b; Jørgensen et al., 1999; Martini and Flescher, 2002; Clark and Summers, 2007; Cavalcanti and Gallo, 2008). Basic ecological questions remain, including the relative importance of vertebrates and invertebrates in the diet. Atlantic Hagfish engage in opportunistic scavenging and prey stealing (Auster and Barber, 2006), but scavenging alone may not be able to support observed population densities of hagfishes. Field studies and stable isotope data show that some species of New Zealand hagfishes (*Eptatretus* sp.) feed at high trophic levels (Zintzen et al., 2011, 2013, 2015). Atlantic Hagfish prey on invertebrates such as polychaetes, nemerteans, shrimps, and crabs, and scavenge larger vertebrate prey including fishes, birds, and whales, but diet is generally thought to emphasize invertebrates (Shelton, 1978; Lesser et al., 1997; Martini, 1998b). The role that hagfishes play in substrate turnover, nutrient cycling, and detritus feeding, as well as their important direct and indirect effects on commercial fisheries, provide additional motives for investigating feeding preference (Martini, 1998a, 1998b; Powell et al., 2005; Knapp et al., 2011). Thus, we conducted a series of experiments in Bigelow Bight in the Gulf of Maine using invertebrate and vertebrate baits.

A mark recapture study (Walvig, 1967) suggested that Atlantic Hagfish may have extensive home ranges. Apart from reports that specimens are rarely caught at depths shallower than 70 m (Martini, 1998a, 1998b) and a comment by Bigelow and Schroeder (1948) that the depth range extends from a minimum of 15 fathoms (27 m), the relative abundance of Atlantic Hagfish has only been investigated in detail for depths >140 m (Grant, 2006). The average total lengths of individuals increased with depth over a 146 664 m range studied by Grant (2006). Known for their low fecundity, the relationship between depth and reproductive condition is also of interest (e.g., for *Eptatretus cirrhatus*, see Martini and Beulig, 2013). Thus, we also examined size and reproductive differences for individuals caught at depths <140 m and expected hagfish to be more abundant, have larger body sizes, and possess larger eggs at deeper depths.

MATERIALS AND METHODS

Atlantic Hagfish were collected using procedures approved under Cornell IACUC Protocol 2013-17. We performed three experiments, which varied in bait type and trap design. In Experiment 1, we tested hagfish preferences for three different bait types (fish, crabs, and clams). Experiment 2 tested fish and mixed baits consisting of sea clams + fish or crabs + fish. Experiment 3 focused on depth preferences using a different trap design and only fish as bait.

Experiments were conducted southeast of Shoals Marine Laboratory (Appledore Island, ME) in the Isles of Shoals during June and July 2013 (Fig. 1). Sea surface temperatures ranged between 12.2° and 20°C during the seven weeks of our study. Nine sampling sites near a feature known as Old Scantum were chosen because of previous work on hagfish near this area (Bigelow and Schroeder, 1948; Lesser et al., 1997; Martini et al., 1997a, 1997b, 1998). The seafloor consists of mud and pebbles.

For Experiments 1 and 2, three traps were attached at 7 m intervals to line (0.95 cm pot warp), weighted at each end with a cinderblock (13 kg), and connected to a floating buoy to form one trap set. Each individual trap consisted of a 61 cm length of 10.2 cm PVC pipe, with 6.4 mm ventilation holes drilled along its length, a PVC coupling and screw-on cap affixed to one end, and a flexible plastic funnel known as an eel trigger (Neptune Marine Products, Port Townsend, WA) glued to the other end. The trigger allowed hagfish to enter but not leave the trap. Based on Harada et al. (2007), ventilation holes 6.4 mm in diameter would retain almost all hagfish with a body diameter ≥9.6 mm. We drilled a 5.5 cm hole in the side of the pipe and covered it with biodegradable cloth to prevent ghost fishing should a trap be lost at sea.

For Experiments 1 and 2, we set traps overnight in locations at three pre-selected depths. The shallowest depth was targeted to be near 61 m, the intermediate depth to be near 91 m, and the deepest to be near 122 m (Fig. 1; Tables 1, 2). To find our sampling stations, we plotted approximate locations by hand on the chart, measured and recorded the actual depths at sea using vessel sonar (Raymarine ST60), and returned to stations using vessel GPS (Furuno GP-33). Traps were deployed immediately under the vessel; actual depth measurements by vessel sonar are estimated to be accurate

[1] Department of Ecology and Evolutionary Biology, 215 Tower Road, Cornell University, Ithaca, New York 14853; Email: (WEB) web24@cornell.edu. Send reprint requests to WEB.
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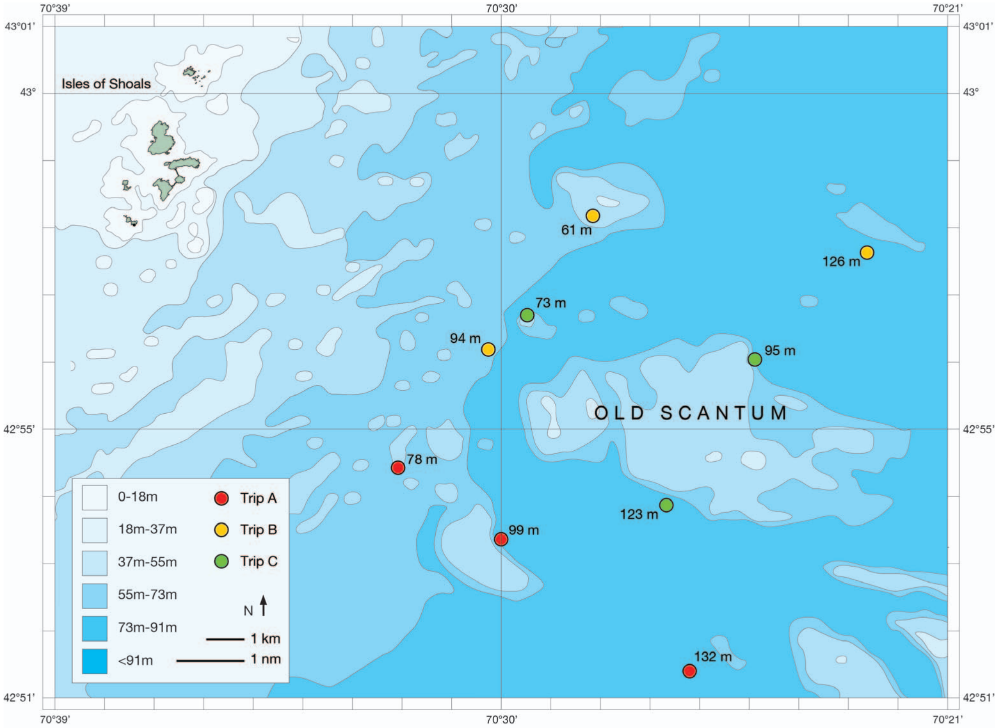

Fig. 1. Locations of sampling sites in Bigelow Bight. Chart based on NOAA 13278. For Experiments 1 and 2, we set traps at sites indicated for Trip A, Trip B, and Trip C. For Experiment 3, traps were set at sites indicated for Trip C. See Tables 1–3.

within ±5 m. In cases where we successfully recovered traps, we had no direct evidence that the traps had moved during the set. Stations were grouped into three separate trips, A, B, and C. Each trip was conducted once a week, in consecutive order as a cycle, once for Experiment 1 and once for Experiment 2. During a single trip, a trap set was deployed at each station using small vessels (7.6 m R/V *Acipenser* or 10 m R/V *John B. Heiser*) and retrieved either by small winch or by hand. Total soak time for each set in Experiments 1 and 2 was recorded to allow calculation of captures/trap/hour (Tables 1, 2).

For Experiment 1, each trap in a set was baited with one of three bait types: fish (Atlantic Herring, *Clupea harengus*), sea clams (*Spisula solidissima*), or crabs (*Hemigrapsus sanguineus*, *Carcinus maenas*, *Cancer borealis,* or *C. irroratus*). We chose to use Atlantic Herring as bait because this species is abundant in the Gulf of Maine; it may not be representative of other types of fishes in terms of nutritional values, such as lipid content. We used sea clams as a proxy for molluscs. We chose crabs because the diet of Atlantic Hagfish includes crabs and because they are specifically known to overlap in their micro-distribution with *Cancer borealis* (Auster and Barber, 2006). Frozen fish were ground using a hand-crank meat grinder on the day of deployment; frozen clams were thawed and removed from their shells; and fresh crabs were smashed into fragments with a hammer. We placed 227 g of bait inside each trap just before deployment. We measured the length and weight of all hagfish collected and dissected the largest hagfish from each trap in order to measure the length of three of its eggs, selected at random.

To assess the impact of fish on bait effectiveness, we incorporated fish into the invertebrate baits of Experiment 2 to yield three bait types: 100% fish; 90% crab and 10% fish; or 90% sea clams and 10% fish.

We could not report data from all traps deployed in Experiments 1 and 2 due to trap loss (Tables 1, 2).

Trip C's shallow, intermediate, and deep stations were used for Experiment 3. We built traps for Experiment 3 from 19 L buckets weighted with cement, fitted with an eel trigger on each side, and with clamp-on lids designed to rust-out over time to prevent ghost fishing. One of these bucket-style traps was deployed at each of the three depths and baited with 680

Table 1. Summary of Experiment 1, Trips 1A–1C.

Depth	Bait	# of hagfish
Trip 1A 6/12/2013 to 6/13/2013; 23-hour soak		
Shallow	Fish	6
	Crab	0
	Clam	3
Intermediate	Fish	9
	Crab	0
	Clam	0
Deep	Fish	24
	Crab	0
	Clam	0
Trip 1B 6/18/2013 to 6/19/2013; 24-hour soak		
Shallow	Fish	5
	Crab	0
	Clam	0
Intermediate	Fish	15
	Crab	TRAP LOST
	Clam	0
Deep	Fish	TRAP LOST
	Crab	TRAP LOST
	Clam	TRAP LOST
Trip 1C (6/12/2013 to 6/13/2013); 24-hour soak		
Shallow	Fish	0
	Crab	0
	Clam	0
Intermediate	Fish	17
	Crab	0
	Clam	7
Deep	Fish	8
	Crab	0
	Clam	TRAP LOST

Table 2. Summary of Experiment 2, Trips 2A–2C.

Depth	Bait	# of hagfish
Trip 2A (7/1/2013 to 7/2/2013); 19-hour soak		
Shallow	100% Fish	0
	90% Crab, 10% Fish	0
	90% Clam, 10% Fish	0
Intermediate	100% Fish	TRAP LOST
	90% Crab, 10% Fish	25
	90% Clam, 10% Fish	19
Deep	100% Fish	6
	90% Crab, 10% Fish	2
	90% Clam, 10% Fish	0
Trip 2B (7/10/2013 to 7/11/2013); 24-hour soak		
Shallow	100% Fish	4
	90% Crab, 10% Fish	TRAP LOST
	90% Clam, 10% Fish	TRAP LOST
Intermediate	100% Fish	0
	90% Crab, 10% Fish	0
	90% Clam, 10% Fish	0
Deep	100% Fish	TRAP LOST
	90% Crab, 10% Fish	38
	90% Clam, 10% Fish	16
Trip 2C (7/16/2013 to 7/17/2013); 24-hour soak		
Shallow	100% Fish	0
	90% Crab, 10% Fish	3
	90% Clam, 10% Fish	13
Intermediate	100% Fish	13
	90% Crab, 10% Fish	0
	90% Clam, 10% Fish	0
Deep	100% Fish	17
	90% Crab, 10% Fish	0
	90% Clam, 10% Fish	11

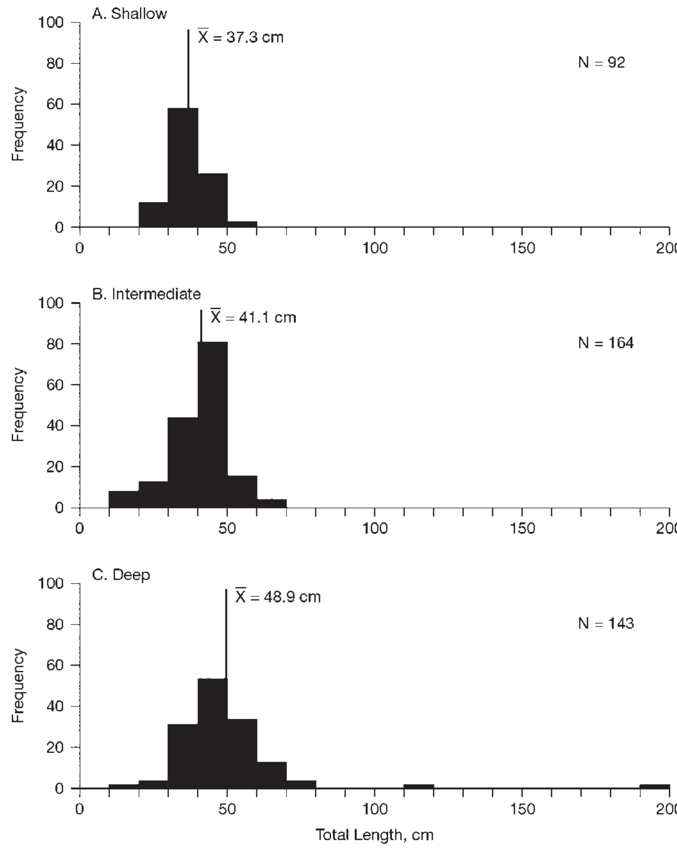

Fig. 2. Length frequency histograms for three depths. The mean total length of hagfish from shallow and intermediate depths did not differ from each other, but both are different from the mean total length of specimens from deep stations ($P < 0.05$).

g of fish. Poor weather prevented overnight retrieval, and traps were not recovered until one week later.

Hagfish length, weight, and frequency by bait type, depth, or trip day were analyzed using a linear model that accounted for potential interactions as well as data loss due to gear damage. We transformed the frequency data with a square root transformation to meet assumptions of linear modeling using R 3.1.2 (R Core Team, 2014). Significance was determined using ANOVA and a least squares means pairwise comparison (Tukey's method for *P*-value adjustment). We compared our results with average lengths obtained from analyses of Northeast Fisheries Science Center (NEFSC) bottom trawl data on hagfish (collected at NEFSC survey stations in the Gulf of Maine provided by Nancy McHugh, pers. comm., 2014).

RESULTS

We caught 399 hagfish during the three experiments (Fig. 2, Tables 1 3). No hagfish were caught with any baits for Experiment 1 at trip C's shallow station (Table 1) or for Experiment 2 at trip A's shallow or trip B's intermediate station (Table 2), but hagfish were caught at all deep stations (Tables 1 3).

Bait type correlations. The number of hagfish captured/trap/hour varied significantly across bait types (Fig. 3). In Experiment 1, no hagfish were collected with crab-baited traps, there was no significant difference between the frequencies of specimens caught using either of the invertebrate baits, and hagfish preferred fish-baited traps over those baited with crabs or clams ($P = 0.002$ and 0.02, respectively).

Experiment 2's addition of fish to invertebrate baits equalized catch rates across all bait types; as long as baits contained fish, hagfish were caught (Fig. 3).

Correlations with catch depths. Lengths and weights of specimens varied across all catch depths (*P*-values < 0.006) with longer and heavier specimens caught at the deepest stations (Fig. 2).

Egg size also demonstrated a positive correlation with respect to specimen length, weight, and catch depth (Fig. 4). No specimens caught at shallow stations had eggs. Of the selected specimens examined from intermediate depth stations, only two of five had eggs, and these were smaller than the eggs in specimens from deep stations. More data are needed to confirm this trend.

DISCUSSION

Hagfish appear to be sensitive to the presence of fish as bait. Fish not only proved to be the most effective bait, but the

Table 3. Summary of Experiment 3, 7/23/2013 to 7/30/2013.

Depth	Bait	# of hagfish
Shallow	Fish	58
Intermediate	Fish	59
Deep	Fish	21

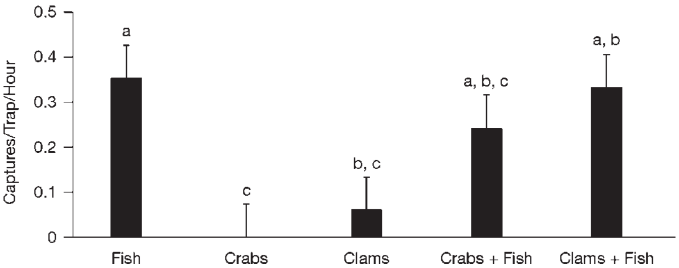

Fig. 3. Comparison of captures/trap/hour in Experiments 1 and 2. Hagfish were caught most frequently with fish baited traps or with mixed baits (crabs + fish or clams + fish). Statistical significance ($P < 0.05$) indicated by letters a, b, and c. Bars sharing a letter are not significantly different from each other.

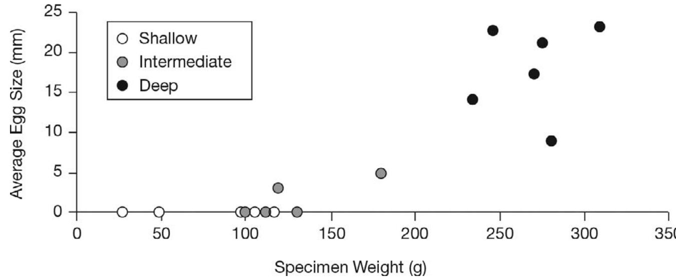

Fig. 4. Average egg size in relation to weight and catch depth based on the length of three eggs (selected randomly) from the largest hagfish in each trap.

incorporation of fish into clam or crab baits increased catch rates and equalized these rates between pure fish and mixed bait types. Our findings may reflect a preference for fish or that fish is easy to detect. Hagfish identify food through smell and touch, so the relative odor potency of baits is important (Clark and Summers, 2007). It is possible that remnants of exoskeleton might have slowed the release of odors or other cues from the crushed crab bait, or that the different lipid content of the baits contributed differently to odor dispersal. Perhaps fish bait provides a stronger scent than the other baits, and thus attracts more hagfish. But if this sensitivity to, and preference for, fish is more than a mere reflection of signal potency, then our findings could indicate hagfish inhabit a more refined ecological niche than previously assumed.

Feeding habits of several species of hagfishes have been studied using stable isotopes (Zintzen et al., 2013). Some evidence suggests that terrestrial carbon inputs may be important for some species (McLeod and Wing, 2007). It will be important to make future stable isotope studies of the population at Old Scantum, including corrections for interpreting $\delta^{15}N$ (because of the unusual osmoregulatory physiology of hagfishes; Churchill et al., 2015). Atlantic Hagfish are linked to higher trophic levels as prey for Atlantic Cod, White Hake, Atlantic Halibut, and pinnipeds.

A dietary preference for fish could be an energy trade-off decision, i.e., a case of optimal foraging. Hagfish may be less likely to encounter opportunities to eat fishes compared with invertebrates, so when opportunities manifest, it may be more energetically efficient to consume fish. Fish consumption should yield relatively more calories per unit of energy invested as compared with invertebrates, which are usually small and may have shells that impede access and provide no calories. According to the Nutrient Data Laboratory (USDA, 2016), Atlantic Herring has 158 kcal and 9.05 g of total lipid per 100 g samples. In contrast, clams (a mixed species category in the Nutrient Data Laboratory database) have 87 kcal and 1.08 g of total lipid per 100 g; blue crab (a proxy for other species of crabs, which are not listed in the Nutrient Data Laboratory database) has 86 kcal and 0.96 g of total lipid per 100 g sample. Based on these data, Atlantic Herring has nearly twice the caloric value of clam or crab baits and nearly ten times as much lipid. Immersion in a fish carcass also might optimize direct nutrient absorption through a hagfish's skin (Glover et al., 2011). It would be interesting to compare hagfish preferences for fish versus whales. The mobile-scavenger stage of whalefalls is a prime opportunity for hagfishes to obtain many calories efficiently (Smith and Baco, 2003; Smith, 2006). Refining hagfish baits based on dietary preferences also might improve the efficiency of studies using Baited Remote Underwater Video Systems (McLean et al., 2015).

Our data suggest that larger hagfish (longer and heavier specimens) occur at deeper depths. Whether the relative abundance of larger hagfish further increases with depth is unclear, but this pattern is not evident in other data sets such as those collected by NEFSC. NEFSC surveys found an average length of 42 cm at all three of our sampling depths that did not vary with catch depth (McHugh, pers. comm., 2014). Perhaps NEFSC did not detect size variation because their capture method (trawling) differed from ours (trapping). Our findings generally agree with those of Grant (2006), although all of our stations were shallower.

Our positive correlations between egg-size and: 1) body size and, 2) catch depth mirror results from the Grand Banks of Newfoundland for *Myxine glutinosa* (Grant, 2006) and from New Zealand for *Eptatretus cirrhatus* (Martini and Beulig, 2013). If mature hagfishes actively migrate to deeper water, then the individuals most responsible for population replacement may be concentrated at depth. Hagfishes are targets for some specialty markets (Ota et al., 2007). Because individuals produce relatively few eggs per adult, the populations of hagfishes have a limited ability to respond to overfishing (Ellis et al., 2015). Further studies with larger sample sizes should be conducted to assess the depth distribution of reproductively active Atlantic Hagfish and such data should be used to inform the fishery.

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