

ARTICLE

Gastric Evacuation Rates of Spiny Dogfish, Goosefish, and Summer Flounder: Implications for Multispecies Models

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Abstract

The gastric evacuation rates of Spiny Dogfish *Squalus acanthias*, Summer Flounder *Paralichthys dentatus* and Goosefish *Lophius americanus* held at two different temperatures were determined in the laboratory by gastric lavage. Overall, exponential models provided the best fit for the evacuation rates. The Spiny Dogfish, an elasmobranch, evacuated more slowly than the Summer Flounder (a teleost) but the Goosefish, also a teleost, had the slowest evacuation rate of the three species. The Goosefish evacuation rate was nearly ten times slower than that of Summer Flounder. Evacuation was more rapid at the higher temperature tested in all three species. At 15°C, Summer Flounder had the highest average evacuation rate (0.094 exponential rate of decline), followed by Spiny Dogfish (0.063 exponential rate of decline), and then Goosefish (0.018 exponential rate of decline). Among the three species, activity levels and feeding behaviors are also very different, contributing to differences in evacuation rate. Species-specific parameters of evacuation rate should be considered to better inform multispecies and ecosystem models and to more accurately estimate consumption and prey removal rather than using broad taxonomic groupings as in current common practice.

Evacuation rate is a measure of the rate at which food passes out of the stomach to the intestine of an animal. Evacuation rate and stomach contents data are used to estimate consumption rate, which is used in many multi-species and ecosystem models (Durbin et al. 1983; Bromley 1994; Curti 2021). Currently, consumption rates are estimated based on evacuation rate parameterized at a broad taxonomic level based on several well-studied groups (e.g., salmonids, flatfish, and gadoids; Bromley 1994). In the northeastern USA, some food web models

make the assumption that all elasmobranchs have one evacuation rate, and all teleosts have another, higher evacuation rate (Overholtz and Link 2007). Similarly, while evacuation rate is recognized as temperature-dependent, many modeling studies utilize a general temperature-dependent equation (Durbin et al. 1983; Bromley 1994).

In the past few decades, there has been a large shift in dominant predators in the northeastern U.S. shelf ecosystem (Lucey and Nye 2010; Smith and Link 2010). As part of this shift, Spiny Dogfish *Squalus acanthias*, Goosefish

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Lophius americanus, and Summer Flounder *Paralichthys dentatus* are more abundant, and questions have been raised regarding changes in the trophic dynamics in the ecosystem. Spiny Dogfish are thought to compete with other commercially valuable groundfish for resources (Morgan and Sulikowski 2015). Overholtz and Link (2007) indicated that the dominant piscivore has shifted from Atlantic Cod *Gadus morhua* to Spiny Dogfish or Goosefish and that Goosefish are functionally replacing Atlantic Cod as the dominant piscivore within the northwestern Atlantic ecosystem. Curti (2012) found Goosefish to be the dominant predatory species within the Georges Bank fish community across all the years she modelled. Summer Flounder—an important predator on squid, especially during the winter—may be causing an additional stress on the already robust squid fishery (Staudinger 2006). Recognizing that the northeastern U.S. shelf ecosystem is one of the fastest warming in the world (Pershing et al. 2015) raises the importance of understanding the effects of these changes in community structure and on the trophic dynamics and highlights the need to incorporate this understanding into assessments and management (MAFMC 2016).

To better inform multispecies and ecosystem models in the region, we estimated evacuation rates for three common fishery species in the northeastern U.S. shelf ecosystem: Spiny Dogfish, Goosefish, and Summer Flounder. We used gastric lavage methods for estimating evacuation rate and conducted experiments at different temperatures to evaluate the temperature dependence of evacuation. We used the same methods as in a previous study on Clearnose Skate *Raja eglanteria* (Stehlik et al. 2015) and information from the literature to examine two hypotheses: (1) evacuation rates are similar across species in the same taxonomic class or subclass, and (2) evacuation rates in elasmobranchs are lower than evacuation rates in teleosts.

METHODS

Fish collections.—Fish used in this study were collected from coastal New Jersey. Live adult Summer Flounder

were collected by hook and line from waters in outer Raritan Bay using a single barbed hook with bait during September through October 2014. Once unhooked, they were immediately put into 113.6-L coolers and given frequent seawater changes until they were transferred to the laboratory.

Live adult Spiny Dogfish and Goosefish were obtained by a commercial fisherman (Captain Kevin Wark, FV *Dana Christine*, Barnegat, New Jersey), using sink gill nets. Goosefish adults were caught in December 2013 and January, April, and May 2014. Adult Spiny Dogfish were caught from November through December 2015. Live, undamaged fish of both species were transported on the ship in tubs with flowing seawater and then brought to the laboratory within 2 h in live wells containing seawater.

Laboratory holding conditions.—All aquaria at the James J. Howard Marine Sciences Laboratory used for holding fish or in experiments received a continuous flow of filtered ambient seawater from Sandy Hook Bay. Salinities ranged from 22 to 25 psu. Temperature was maintained by adding flowing chilled or heated seawater to the ambient water. Aquaria were maintained at 10, 12, 15, or 20°C ($\pm 1.0^\circ\text{C}$) as required for each experiment. Fish were acclimated to water temperatures that matched desired experimental conditions. The experimental temperatures chosen reflected those that exist within the habitat ranges of the species in the mid-Atlantic region (Packer et al. 1999; Steimle et al. 1999; Stehlik 2007). The first experimental temperature used for each species was closest to the field collection temperature and then was raised or lowered based on the anticipated natural seasonal change. We chose not to use temperatures above 20°C because based on experience, fish in captivity tend to succumb to disease at these temperatures. The light regime in the laboratory was programmed to give 12 h of light and 12 h of dark. Aquaria were round with diameter of 2.5 or 1.8 m, with depths of 0.5 m, and with no sediment on the bottom.

Spiny Dogfish ($N = 15$; all females; length range = 81–93 cm; Table 1) were held in small groups and acclimated

TABLE 1. Spiny Dogfish, Goosefish, and Summer Flounder used in evacuation rate experiments with temperatures, number of trials, numbers of fish used, mean weights, mean lengths, mean weight of food eaten in experiments, and mean percent body weight of prey eaten relative to predator weight (% bw).

Species	Temperature (°C)	Number of trials	N	Weight (g)	Weight range (g)	Length range (cm)	Food eaten (g)	% bw eaten
Spiny Dogfish	12	40	15	3,009	2,228–3,950	83–93	61.6	2.03
Spiny Dogfish	15	30	8	2,663	2,912–3,447	81–89	63.4	2.40
Goosefish	10	45	17	4,591	2,803–6,306	56–72	211.3	5.15
Goosefish	15	33	12	4,193	2,627–5,319	56–72	260.6	6.16
Summer Flounder	15	48	17	762	415–1,259	33–48	14.6	1.83
Summer Flounder	20	57	22	733	390–1,240	32–48	12.7	1.96

TABLE 2. Parameter estimates for the exponential models (equation 2) of evacuation rate in the laboratory for Spiny Dogfish, Goosefish, and Summer Flounder, omitting fish with empty stomachs. Temperature ($^{\circ}\text{C}$), equation used, average weight of food consumed per predator weight per day (avg. % bw/d), y -intercept (W_0), evacuation rate (R), standard errors (SE) of W_0 and R , and hours until complete (95%) evacuation estimated using an exponential model are reported.

Species	Temperature	Avg. % bw/d	W_0		R		Hours until evacuation
			Estimate	SE	Estimate	SE	
Spiny Dogfish	12	2.10	1.203	0.075	0.047	0.002	68
Spiny Dogfish	15	2.40	1.129	0.075	0.063	0.006	49
Goosefish	10	5.15	0.958	0.094	0.011	0.002	268
Goosefish	15	6.16	0.091	0.096	0.018	0.002	166
Summer Flounder	15	1.96	1.159	0.106	0.094	0.009	33
Summer Flounder	20	1.84	1.038	0.056	0.141	0.011	22

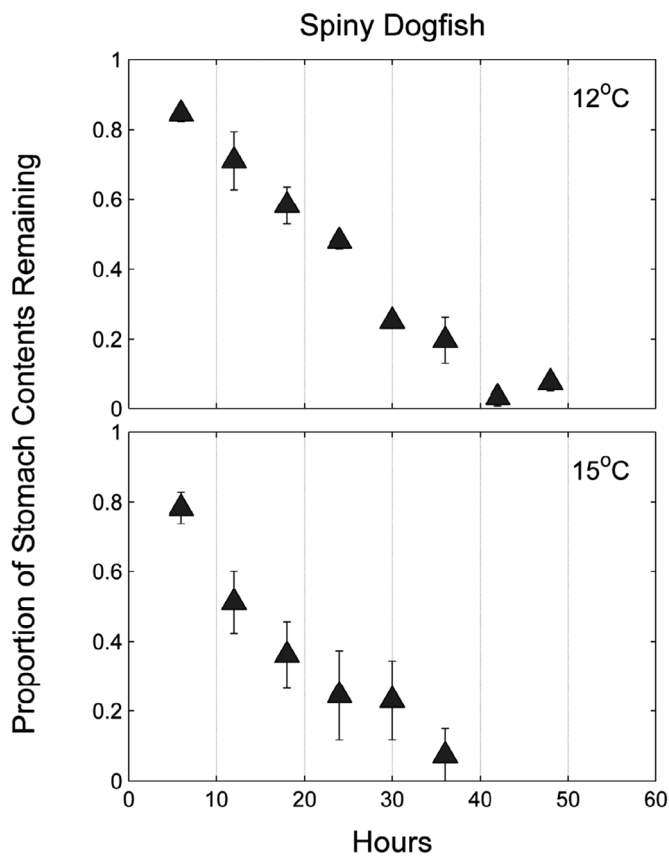


FIGURE 1. Percent of food remaining in stomachs of Spiny Dogfish in the laboratory at two temperatures. Each data point is the mean of all fish tested and one standard error.

for 1 month at the test temperatures (15°C or 12°C) before experimentation. They were fed a maintenance ration ad libitum of Atlantic Silverside *Menidia menidia*, Sand Lance *Ammodytes* sp., or chopped Atlantic Herring *Clupea harengus*. Only fish that ate consistently and showed no external abrasions or injuries were used in experiments.

For experiments, a total of 15 fish were tested at 12°C , and 8 fish were tested at 15°C . Randomly selected Spiny Dogfish were measured, weighed, tagged with t-bar tags, and transferred to aquaria (1.8 m diameter) for experiments. They were allowed to acclimate to the experimental tank for 1–2 d after being transferred and before use in experiments.

Adult Goosefish ($N=17$; males and females; length range = 56–72 cm; Table 1) were held individually in tanks and acclimated for at least 1 month at each of the experimental temperatures (15°C or 10°C) before being used for evacuation trials. Tetracycline was administered by injection once a month to combat possible bacterial infections. Goosefish were fed thawed whole Atlantic Herring by hand using forceps. Only fish that ate consistently and showed no external abrasions or injuries were used in experiments. Meal size was determined by examining diet data collected by the Northeast Fisheries Science Center Food Web Dynamics Program (Smith and Link 2010; B. Smith, Northeast Fisheries Science Center, unpublished data) which indicated an average 26 g of food per stomach in the 60–69-cm length-class of Goosefish.

Adult Summer Flounder ($N=17$ –22; males and females; length range = 32–48 cm; Table 1) were held in aquaria in groups and acclimated for at least 2 weeks at each of the experimental temperatures (20°C or 15°C). They were fed a maintenance ration of Atlantic Silverside or Sand Lance ad libitum. Only fish that ate consistently and showed no external abrasions or injuries were used in experiments. For experiments, 8–12 Summer Flounder were measured, weighed, tagged with t-bar tags, and transferred to round aquaria (1.8 m diameter) alone, in pairs, or in groups of three.

Evacuation experiments.—Evacuation rates were determined in the laboratory by feeding one premeasured meal per day to experimental fish and then weighing the food remaining in individual fish over a selected postprandial time series. Spiny Dogfish and Summer Flounder were not

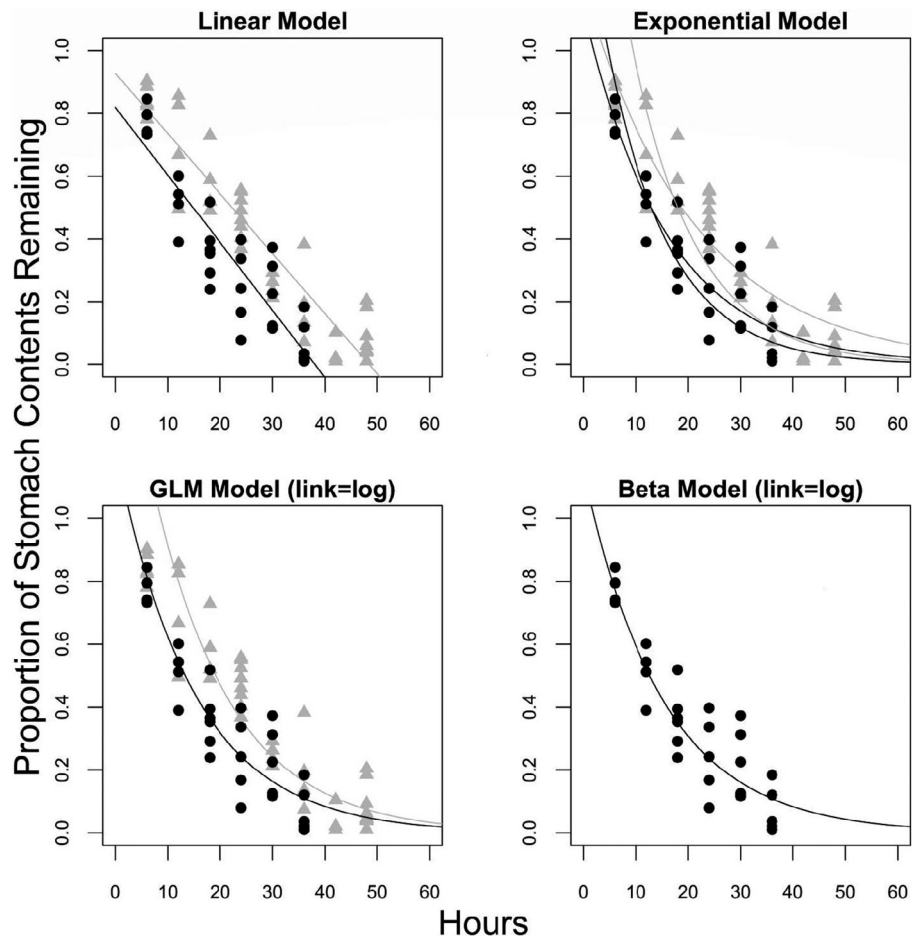


FIGURE 2. Comparison of models for Spiny Dogfish evacuation rates. Black circles are for 15°C; gray triangles are for 12°C.

fed for ≥ 2 d before each trial. The experimental Goosefish population was limited in size which meant individuals were reused. Naïve Goosefish were not fed for 1 week before a trial. Goosefish used in previous trials were allowed to rest for at least 1–2 d before being used in another trial. After two or three lavages, fish were returned to holding aquaria and not used again in another trial.

For evacuation trials, Spiny Dogfish were fed thawed Sand Lance (130–150 mm SL; mean mass = 14 g each), and those that consumed three or more Sand Lance were used for lavage experiments. After feeding, fish were left undisturbed until removal for lavage. Dogfish held at 12°C were lavaged at the following number of hours postfeeding: 6, 12, 18, 24, 30, 36, 42, and 48. Dogfish held at 16°C were lavaged at the following number of hours postfeeding: 6, 12, 18, 24, 30, and 36.

For evacuation trials, Goosefish were fed two thawed whole Atlantic Herring (approximately 20 cm TL; mass = 50–150 g each), then left undisturbed until removal for lavage. Goosefish held at 10°C were lavaged at the

following number of hours postfeeding: 24, 48, 72, 96, 120, 144, 168, 192, and 240. Goosefish held at 15°C were lavaged at the following number of hours postfeeding: 24, 48, 72, 96, 120, 144, and 168.

We found that Summer Flounder held in groups of two or three ate more readily than those held alone, so they were grouped, and the consumption of individuals was monitored by their tags. Summer Flounder that consumed two or more Sand Lance (80–100 mm SL; mean mass = 4.2 g each) were included in experiments. Summer Flounder held at 15°C were lavaged at the following number of hours postfeeding: 4, 6, 8, 12, 13, 14, 16, 20, and 24. Summer Flounder held at 20°C were lavaged at the following number of hours postfeeding: 2, 3, 4, 6, 8, 10, 12, 14, 16, 18, 19, and 21.

Pulsed gastric lavage (Kamler and Pope 2001) was used to retrieve the stomach contents of each species. At the predetermined time, a fish was removed from its aquarium and sedated in a solution of seawater and MS-222 (tricaine methanesulfonate) mixed in an insulated cooler.

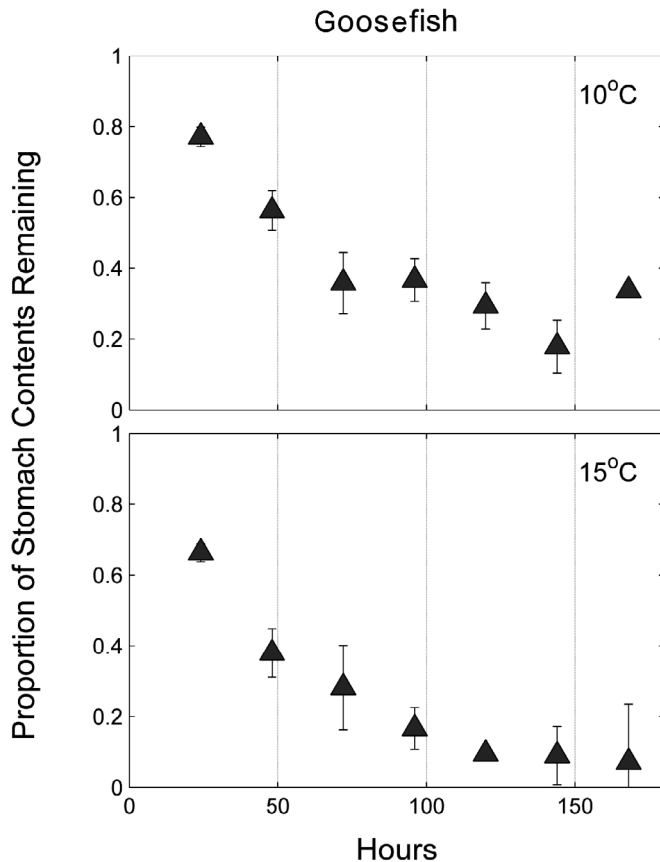


FIGURE 3. Percent of food remaining in stomachs of Goosefish in the laboratory at two temperatures. Each data point is the mean of all fish tested and one standard error.

The concentration of MS-222 was 133 mg/L for Spiny Dogfish, 125 mg/L for Goosefish, and 75 mg/L for Summer Flounder. Each fish remained in the cooler for 6–10 min until it could not right itself when turned over yet continued to respire. Once sedated, the fish could be handled, and the jaws and esophagus relaxed. The lavage apparatus was a clear plastic tube with 5 cm diameter for Spiny Dogfish and Goosefish or with 1.0 or 1.5 cm diameter for Summer Flounder attached to a hose (1 cm diameter for Spiny Dogfish and Goosefish, 0.4 cm diameter for Summer Flounder) from an aquarium pump delivering gently flowing seawater. A person held the animal on its side or with the ventral side up above a tray while another person inserted the tubes through the esophagus and into the stomach. Water and stomach contents flowed out and were collected on a 1.0-mm mesh sieve. The fish's stomach was rinsed several times until the water ran clear, then the fish was returned to its aquarium. Recovery from sedation occurred within 15 min with no observable negative effects from sedation or lavage.

The evacuated material was drained on the sieve, removed, blotted on a paper towel to remove moisture,

and weighed (± 1.0 g wet weight). If the weight of food washed out of the stomach was 5% or less of the consumed weight, digestion was considered complete (Andersen 2012; Smith, personal communication).

Analysis.—Evacuation rate was estimated by statistically modeling percent weight of prey remaining in the stomach over time. Percent digested (W_p) was calculated by dividing the stomach content weight at the time of sampling (W_t) by the total weight of prey presented to each individual. Evacuation is expressed as a linear, exponential, logarithmic, or other function. Most authors conclude that the exponential model of evacuation rate is appropriate for carnivorous fish that eat large prey items (Elliott and Persson 1978; Bromley 1994). We fit both a linear (equation 1) and an exponential (equation 2) model:

$$W_p = W_0 - Rt \quad (1)$$

$$W_p = W_0 e^{-Rt}, \quad (2)$$

where W_p is the proportion remaining, t is the time of sampling, W_0 is an estimated parameter of the proportion of the meal that enters the stomach, and R is an estimated parameter of the evacuation rate per hour. The value of W_0 is often less than 100% owing to the initial expression of liquid from the prey (Olson and Boggs 1986).

We fit equation (1) using linear least squares (lm function in R) and equation (2) using several statistical fitting procedures: nonlinear least squares (nls function in R), ln transformed linear least squares (lm function in R), a general linear model (GLM) with gamma distribution and a log link (using the glm function in R), and a beta regression with a log link (using the betareg function in R; Stehlik et al. 2015). Models were compared using Akaike's information criterion (AIC), but direct comparison of all the models was not possible because of the different transformations and estimation procedures. To avoid errors with log-transforming observations of empty stomachs at specific times, it was assumed that 0.01 of the original contents remained.

Evacuation rate decreases with decreasing temperature (Durbin et al. 1983) following an exponential model:

$$R = ae^{bT}, \quad (3)$$

where a and b are gastric evacuation constants, T is temperature, and R is evacuation rate. This model was fit using the two estimates of evacuation rate at the two temperatures. Although only two data points were used to fit these models, our purpose was simply to obtain estimates for the parameters a and b to be able to compare to a review study (Durbin et al. 1983). The parameter a defines species-specific differences in evacuation rate, and parameter b defines the temperature dependence of evacuation rate.

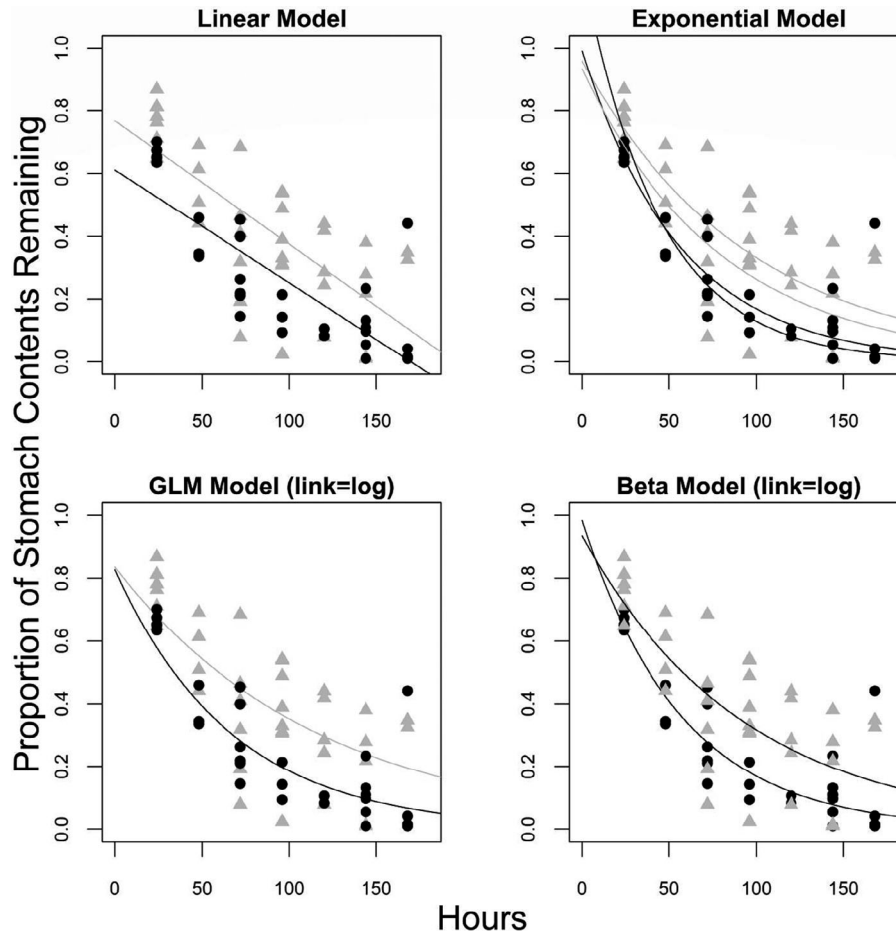


FIGURE 4. Comparison of models for Goosefish evacuation rates. Black circles are for 15°C, gray triangles are for 10°C.

Durbin et al. (1983) concluded that parameter b should be the same across species and proposed a value of 0.11.

RESULTS

Feeding Behavior in the Laboratory

Spiny Dogfish were active in the aquaria during some hours and remained on the bottom at others. We kept them in pairs or trios during holding to stimulate movement. Several pups were released during captivity. When given food, they swam above but near the bottom (moving around the tank) and returned to the bottom after eating. The average percent body weight consumed by the fish chosen for lavage was 2% (Table 1).

Goosefish were mostly inactive in the aquaria at either temperature and only occasionally swam. They did not lunge for food or attack small live fish that were placed in the aquaria. To conduct the feeding trial, Goosefish were offered thawed, whole Atlantic Herring placed head-first near the mouth using forceps. When an Atlantic Herring

was aligned straight toward the esophagus, it would be slowly drawn in with the pharyngeal teeth. The fish chosen for lavages consumed an average of 5–6% of body weight per meal (Table 1).

Frequently, Goosefish spontaneously regurgitated a meal in the laboratory, casting back partially digested fish or vertebral columns. The incidence of regurgitation by Goosefish in the laboratory suggests that they are sensitive to captivity, or alternatively, regurgitation is a normal behavior to rid the stomachs of indigestible materials. We suggest this because the diameter of the intestine is very small, and we did not find any bones in the feces—only paste or small pellets of flesh.

Summer Flounder swam rapidly in the aquaria at times during the day, and they consumed food readily. The fish chosen for lavage consumed an average of 2% of body weight (Table 1).

Evacuation Rates

In Spiny Dogfish, the cardiac stomach shape is an oval with a constriction at the distal end closing off the

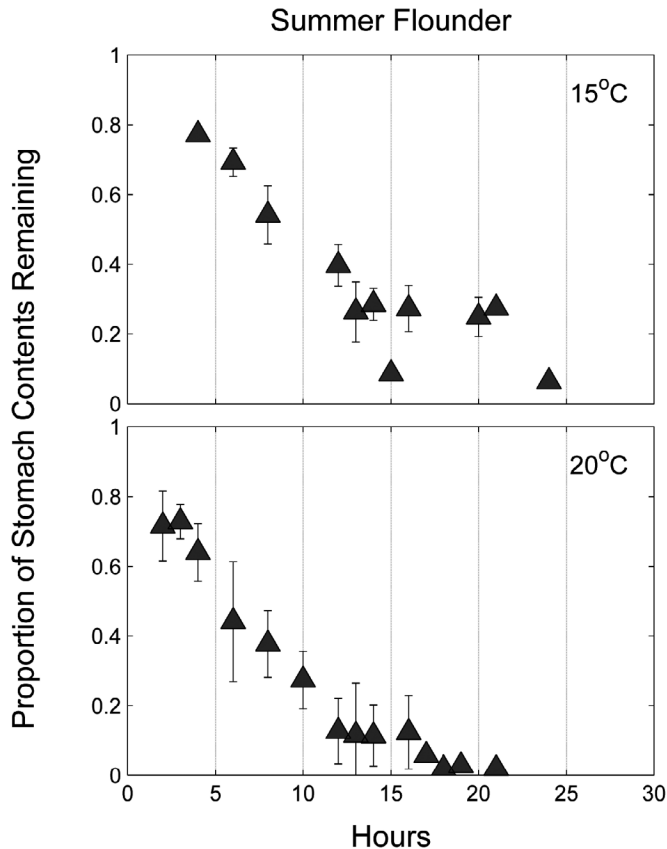


FIGURE 5. Percent of food remaining in stomachs of Summer Flounder in the laboratory at two temperatures. Each data point is the mean of all fish tested and one standard error.

pyloric section and spiral valve. Prey items within the cardiac stomach were easily lavaged out. After a few rinses, the water became clear. Evacuation rate at 12°C averaged 0.047, and at 15°C it averaged 0.063 (Table 2; Figures 1, 2). The average number of prey items eaten was 4.5 individuals. The exponential model (equation 2) fit the data better than the linear model or the other models (equation 1; Table 2; Figures 1, 2). The time to near total evacuation (5% remaining) was 68 h at 12°C and 49 h at 15°C. The model of temperature dependence in Spiny Dogfish (equation 3) estimated $a=0.0144$ and $b=0.0989$.

The gastric lavage procedure worked very well in Goosefish. The stomach shape is a simple bag with no constrictions, so food washed out easily. While sedated, the fish remained fairly inactive during lavage. Prey items could be felt through the wall of the belly and were eased toward the opening of the evacuation tube. After a few rinses, the water became clear. The entrails of the prey were digested first, followed by the skin, scales, fin rays, head, ribs, neural and hemal spines, swimming muscles, and lastly the vertebral column. Atlantic Herring have

delicate head bones which rapidly disarticulated and were completely digested. Evacuation rate at 10°C was slower than that at 15°C and best fit an exponential model (equation 2) or a GLM model (link = log) at both temperatures (Table 2; Figures 3, 4). The calculated time to near total evacuation (5% remaining) was 268 h at 10°C and 166 h at 15°C. The model of temperature dependence in Goosefish (equation 3) estimated $a=0.0038$ and $b=0.1022$. Two Goosefish produced egg veils in the laboratory, and during the weeks leading up to their spawning, the evacuation rates of these spawning Goosefish were more rapid than the average of the other Goosefish in the laboratory.

The stomach shape of Summer Flounder is a flattened balloon with a constriction before the intestine. Prey items within the stomach were easily lavaged out. The exponential model (equation 2) fit the data better than the other models (Table 2; Figures 5, 6). The evacuation rate was higher at the higher temperature (Figure 5). The calculated time to near total evacuation (5% remaining) was 33 h at 15°C and 22 h at 20°C. The model of temperature dependence in Summer Flounder (equation 3) estimated $a=0.0279$ and $b=0.0811$.

DISCUSSION

Evacuation rates of Summer Flounder were approximately ten times those of Goosefish, another teleost, and five times those of Spiny Dogfish (Table 2) and Clearnose Skates (Stehlik et al. 2015). These comparisons lead to the conclusion that evacuation rates within teleosts are not always higher than evacuation rates in elasmobranchs. Further, in elasmobranchs, evacuation rates determined for Spiny Dogfish (this study) and Clearnose Skate (Stehlik et al. 2015) were higher than estimates in generally used models (Figure 7) and would be unsuitable for highly active elasmobranchs such as Shortfin Mako *Isurus oxyrinchus*.

Evacuation Rates among Elasmobranchs

The evacuation of Spiny Dogfish in our study showed some similarities and several differences compared to other studies on the genus *Squalus*. The gastric evacuation rates of Spiny Dogfish in our study were intermediate in range among published studies on elasmobranch evacuation rates (Table 3). Bangle and Rulifson (2014) determined an evacuation rate of 114 h compared to the Spiny Dogfish in our study that evacuated in 35 or 48 h to completion (at 12°C or 15°C, respectively). However, they used Atlantic Menhaden *Brevoortia tyrannus* as prey compared to the softer-bodied Sand Lance used in our study which likely were digested and evacuated faster.

The Pacific Spiny Dogfish *S. suckleyi*, described as a separate species (Ebert et al. 2010), attained complete

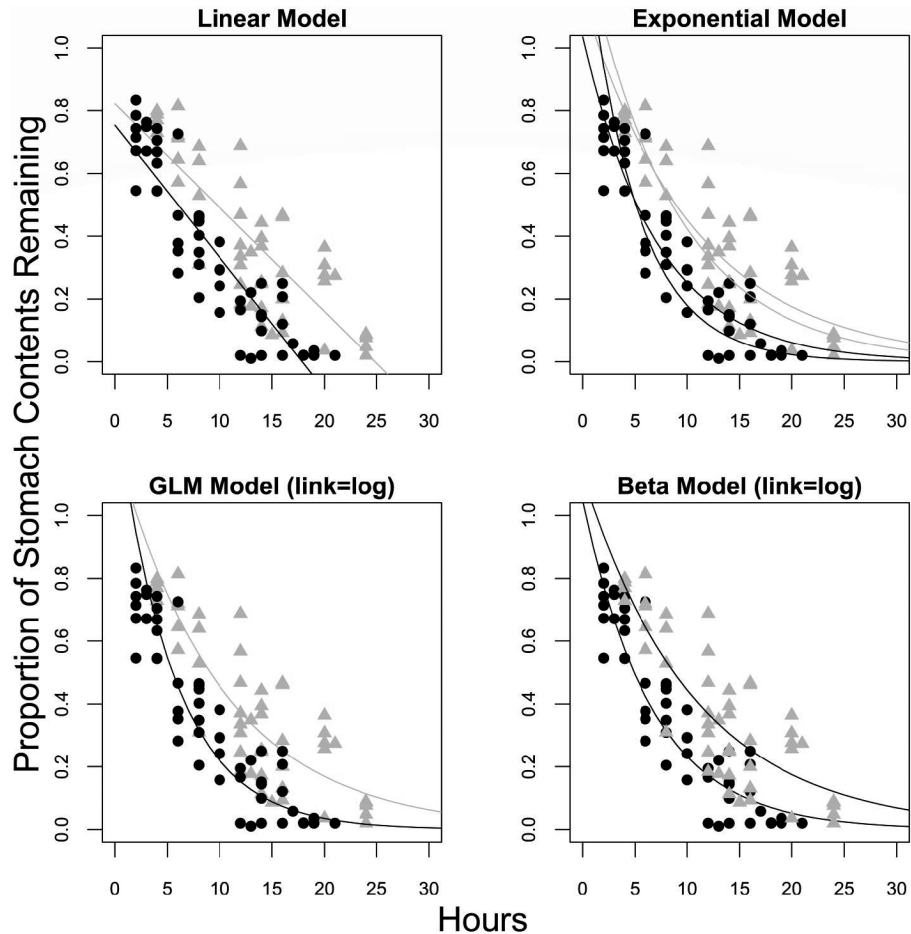


FIGURE 6. Comparison of models for Summer Flounder evacuation rates. Black circles are for 20°C, gray triangles are for 15°C.

evacuation at 10°C at 124 h and 103 h in two studies (Jones and Geen [1977] and Hannan [2009], respectively). However, the Pacific Spiny Dogfish has a slower growth rate, later maturation, longer life span, and larger asymptote of size (Ketchen 1972; Saunders and McFarlane 1993; Tribuzio et al. 2010) than Spiny Dogfish from the Atlantic coast (Nammack et al. 1985; Sosebee 2005) which likely affects digestion and evacuation.

Highly active elasmobranchs such as Shortfin Mako (Wood et al. 2009) and Scalloped Hammerhead *Sphyrna lewini* (Bush and Holland 2002) evacuated very rapidly, within 23 h (Table 3). In contrast, Sandbar Shark *Carcharhinus plumbeus* completed their digestion more slowly, in 70 to 92 h (Medved 1985). Evacuation rate and time to complete (95%) evacuation in Lesser Spotted Dogfish *Scyliorhinus canicula* was extremely slow, regardless of meal size (Sims et al. 1996). Clearnose Skates had evacuation rates ranging from 0.046 to 0.102 (Stehlik et al. 2015), which was faster than most of the sharks in Table 3.

Evacuation Rates among Teleosts

There were large differences between the evacuation rates of the two teleosts, Goosefish and Summer Flounder. Evacuation rates and times to complete digestion in Goosefish were very slow compared with those of other piscivorous teleosts (Table 4). Relatively inactive marine fish that have a sit-and-wait feeding style have slower metabolisms, while those involved in active swimming and migration have increased energy demands and higher metabolisms (Seibel and Drazen 2007). Goosefish are mainly ambush predators. Video from a remotely operated underwater vehicle was described and illustrated in still photographs by Laurenson et al. (2004) and shows partially buried Anglers *Lophius piscatorius* lunging out of the sediment to attack and swallow prey. The Florida Gar *Lepisosteus platyrhincus*, another sit-and-wait predator, completely evacuated its stomach in a laboratory study (Hunt 1960) after a relatively long time (42 h; Table 3). A field study on the evacuation rate of wild-caught Devil Anglerfish *Lophius upsicephalus* near Namibia estimated

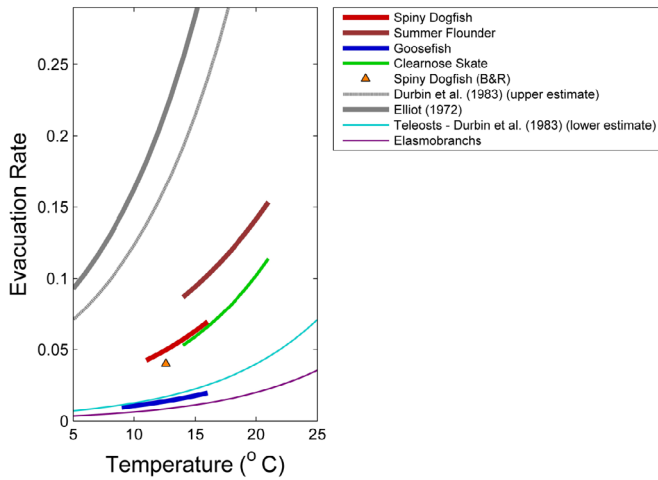


FIGURE 7. Evacuation rates by temperature from this study and from other studies. Data from Spiny Dogfish (red line; this study), Summer Flounder (brown line; this study), Goosefish (dark blue line; this study), Clearnose Skate (green line; Stehlik et al. 2015), and Spiny Dogfish (triangle; Bangley and Rulifson 2014). Rates used by the Northeast Fisheries Science Center for teleosts and elasmobranchs are included for comparison (purple and light blue lines).

evacuation rate as 0.054 at 9.5°C in 72 h (Macpherson 1985). The number of days between feedings averaged 9 (214 h) in most months and 19 in winter (456 h).

Infrequent feeding and very slow evacuation rates in Devil Anglerfish are congruent with the estimates obtained for Goosefish in our study (268 h at 10°C). Wilson (1937) and Laurensen et al. (2004) observed respiration in Anglers to be very slow. So, although metabolic rates of Goosefish are yet to be studied, they are also known to undergo depth changes, along-shelf movements, and off-bottom migrations during different seasons which indicates a possible change in energy demand (Rountree et al. 2008; Sherwood et al. 2009; S. Cadrin, University of Massachusetts Dartmouth, personal communication) due to temperature (season) or life history conditions.

Our results place Summer Flounder among teleosts with moderate evacuation rates (Table 4). Summer Flounder have a relatively small stomach capacity relative to body size which necessitates more frequent refilling. Summer Flounder had a high evacuation rate (0.094 at 15°C and 0.141 at 20°C) which is higher than the evacuation rate of Winter Flounder *Pseudopleuronectes americanus* (Huebner and Langton 1982) and similar to more active species such as Atlantic Cod (Table 4). Summer Flounder was the most active species we tested, but they are less active and have lower metabolic rates compared to pelagic teleosts such as tunas (Olson and Boggs 1986; Fonds et al. 1992; Capossela et al. 2012). Skipjack Tuna *Katsuwonus pelamis*, highly active teleosts, evacuated their stomachs in 12 h at 23.3–25.7°C in a lab study (Magnuson 1969).

TABLE 3. Elasmobranch evacuation rates reported in the literature in order with most rapid first. Type of study (either field data obtained from sampling at various times of the day or laboratory or enclosure study), food, temperature (°C), average weight of food consumed per predator weight per day (avg. % bw/d), evacuation rate, and hours until complete (95%) evacuation (evac) estimated using an exponential model are reported.

Species	Type of study and food	Temperature	Avg. % bw/d eaten	Evacuation rate	Hours until evac	Source
Shortfin Mako	Field, mixed prey	Varying	4.4	0.115–0.218	18–20	Wood et al. 2009
Clearnose Skate	Lab, sand lance	20	1.7	0.102	24	Stehlik et al. 2015
Scalloped Hammerhead	Pens, fish	27	4.1	0.093 ^a	23	Bush and Holland 2002
Clearnose Skate	Lab, Sand Lance	15	1.4	0.102	48	Stehlik et al. 2015
Sandbar Shark	Pens, crab	23–30		0.043 ^a	70.7	Medved 1985
Sandbar Shark	Pens, Atlantic Menhaden	23–26		0.032 ^a	92.3	Medved 1985
Pacific Spiny Dogfish	Lab, Pacific Herring <i>Clupea pallasii</i>	10	2.0	0.029 ^a	103	Hannan 2009
Spiny Dogfish	Lab, Atlantic Menhaden	12.6	0.26	0.027 ^a	114	Bangley and Rulifson 2014
Pacific Spiny Dogfish	Pens, Atlantic Herring	10		0.024	124	Jones and Geen 1977
Lesser Spotted Dogfish	Lab, squid	15	7.4	0.009	200	Sims et al. 1996

^aValues are calculated using equation (3; $R = ae^{bT}$) and information provided in the cited references.

TABLE 4. Teleost evacuation rates reported in the literature in order with most rapid first. Predator activity level, type of study (either field data obtained from sampling at various times of the day or laboratory or enclosure study), food, temperature (°C), average weight of food consumed per predator weight per day (avg. % bw/d), evacuation rate (evac), and hours until complete (95%) evacuation estimated using an exponential model are reported. Where temperatures were not specified in the study, the season is given.

Species	Activity mode	Type of study and food	Temperature	Avg. % bw/d eaten	Evacuation rate	Hours until evac	Source
Silver Hake >20 cm	Active	Field, fish prey	Fall	0.8–2.2	0.15–1.46		Durbin et al. 1983
Atlantic Cod >30 cm	Active	Field, fish prey	Fall	0.9–1.5	0.09–0.90		Durbin et al. 1983
Skipjack Tuna	Highly active	Lab, Surf Smelt <i>Hypomesus pretiosus</i>	23–26	8.6	0.10	12	Magnuson 1969
Yellowfin Tuna	Highly active	Outdoor tanks, mixed prey	24–26	3.9	0.09	5–12	Olson and Boggs 1986
Bluefin Tuna	Highly active	Field, fish prey	Winter	2.0	0.12	20	Butler et al. 2010
Winter Flounder	Benthic grazer	Lab, squid	5–7	1.8–2.4	0.08	24	Huebner and Langton 1982
Florida Gar	Stalker	Lab, Mummichog <i>Fundulus heteroclitus</i>	23–26		0.06	42	Hunt 1960
Devil Anglerfish	Ambush predator	Field, mixed prey	10	0.55–1.6	0.05	72	MacPherson 1985

Yellowfin Tuna *Thunnus albacares* completed evacuation in 5–12 h at 23.5–25.5°C in outdoor tanks (Olson and Boggs 1986), and Bluefin Tuna *Thunnus thynnus* completed evacuation in 20 h based on field collections (Butler et al. 2010).

Variability in Evacuation Rates

Temperature influences digestion and gastric evacuation rates (Paloheimo and Dickie 1966; Bromley 1994; Benkwitt et al. 2009; Griffiths et al. 2009; Gillum et al. 2012). We found a decrease in evacuation rates at lower temperatures in all three species tested (see Figure 8), which was also true in previous studies (Elliott 1972; Durbin et al. 1983; Stehlik et al. 2015). Beyond temperature, other studies have suggested that a variety of variables influence digestion. He and Wurtsbaugh (1983) indicated that food particle size was important while Elliott (1972) found that prey type was important. Swallowing prey whole can also affect evacuation rate (Andersen 2012). Swallowing prey whole, as Goosefish do, leads to slower digestion, because only the surface of the prey is penetrated by the pharyngeal teeth. We found that prey fish lavaged from the stomachs of Spiny Dogfish and Summer Flounder were partially bitten or chewed, which allows quicker penetration of digestive enzymes. Durbin et al. (1983) listed temperature and food type as the strongest influence but

because of the uncertainty concerning the value of a for fish prey, Durbin et al. (1983) provided two estimates for food type representing a maximum ($a = 0.0406$) and minimum ($a = 0.00406$) limit to the true value of R (Table 5). Curti (2012) set evacuation for teleosts to 0.004 and for elasmobranch species to 0.002 following Overholtz et al. (2000) who used $a = 0.004$ as a conservative value for teleost fishes.

We suggest that the very conservative broad class-level grouping of teleosts and elasmobranchs in models is too coarse, especially when consumption rate estimates depend on evacuation rates. Species-specific evacuation rates should be used where possible, and further experiments should be conducted. Durbin et al. (1983) stated that it was necessary to determine the feeding habits and daily ration of the major species in order to understand the role of fish predators within the northeast Atlantic ecosystem. At the time, those species were Silver Hake *Merluccius bilinearis* and Atlantic Cod, but today the ecosystem has changed, and pelagic species and elasmobranchs dominate the ecosystem (Curti 2012). Further, with ocean temperatures rising and species distributions changing, further differences in food habits, digestion, and evacuation are possible. Increased accuracy in the feeding rates of natural fish populations that help quantify predation can only improve multispecies models.

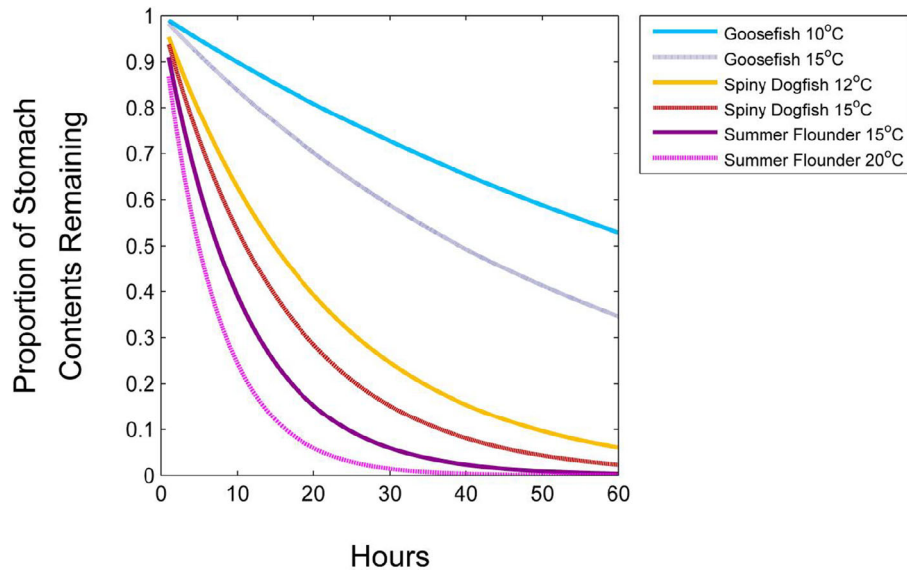


FIGURE 8. Evacuation rates of Spiny Dogfish, Goosefish, and Summer Flounder, based on exponential models, at several temperatures.

TABLE 5. Summary of evacuation rate parameter estimates for fish species from Durbin et al. (1983) compared with other studies. Parameter *a* defines species-specific differences in evacuation rate and parameter *b* defines the temperature dependence of evacuation rate.

Study	Species	<i>a</i>	<i>b</i>
Elliott (1972)	Brown Trout <i>Salmo</i>	0.530	0.112
Durbin et al. (1983)	<i>trutta</i>	0.004	0.110
	Silver Hake and Atlantic Cod	(lower) 0.041 (upper)	
This study	Spiny Dogfish	0.014	0.099
This study	Summer Flounder	0.028	0.081
This study	Goosefish	0.004	0.102
Stehlik et al. (2015)	Clearnose Skate	0.011	0.109
	Teleosts	0.004	0.115
Curti (2012)	Elasmobranchs	0.002	0.110

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