

EFFECT OF REGURGITATION ON STOMACH CONTENT DATA OF MARINE FISHES

by

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Synopsis

Observations on trawl caught fishes from two bottom depth ranges in Southern New England shelf waters provide evidence that some species regurgitate at different rates when sampled at various depths, and further, that fish which regurgitate can't always be detected by external or internal examination. Generally, gadoid fishes are much more prone to regurgitate than flatfish. The consequence of unrecognized regurgitation is discussed in relation to consumption estimates derived by traditional methods.

Introduction

Extreme variability in the types and quantities of food consumed among and within fish species is well documented. Edwards & Bowman (1979) summarized much information on variability in the feeding of Northwest Atlantic fishes. Bowman & Bowman (1980) documented changes in the feeding intensity of silver hake, Merluccius bilinearis, by time of day on Georges Bank, and Bowman (1980, 1984) concluded that annual, seasonal, and areal variability are found in the diet of juvenile haddock, Melanogrammus aeglefinus, and silver hake. Pennington et al. (1982) examined the weight of the stomach contents of Atlantic cod, Gadus morhua, and determined that to estimate the mean stomach content weight during a season within $\pm 10\%$ with 95% certainty, at least 753 fish should be sampled within each 5 cm size class.

Bowman (1981) attempted to list all known and potential causes of variation in fish feeding studies. In that paper it was noted that regurgitation is commonly observed in fishes caught when bottom trawling in deep water (i.e. >100 m). Also mentioned was that some regurgitation may occur and not be detectable when sampling in deep water, thereby biasing stomach content data. The present paper documents observable regurgitation and then addresses the degree of potential bias caused by undetected regurgitation at two depth ranges for several species of marine fish. Silver hake and spiny dogfish, Squalus acanthias, are emphasized because they have been identified as major fish predators in the northwest Atlantic ecosystem (Edwards & Bowman 1979, Grosslein et al. 1980). Data were compiled as part of the Marine Resources Monitoring Assessment, and

Prediction (MARMAP) program of NOAA's National Marine Fisheries Service (NMFS), Northeast Fisheries Center (NEFC).

Methods and materials

Ship operations

The study was conducted aboard the NEFC research vessel DELAWARE II during a 10 day cruise in December 1981 in continental shelf waters south of Martha's Vineyard, Massachusetts. Two sampling areas were chosen according to bottom water depth, and each represented a square area of 259 km² (Fig. 1). Both areas were subdivided into 100 2.6 km² squares from which bottom trawling stations were selected at random without replacement. Each sampling area was occupied for at least three 24 h periods, with 0.5 h trawl hauls commencing every 3 h (i.e. 0300, 0600, 0900, etc.). Totals of 27 and 24 hauls were completed at areas A and B, respectively. Bottom water depth ranged 40-53 m at area A and 70-93 m at area B. Waters were essentially isothermal at the two areas (approximately 8.0°C at both) and cloud cover was almost 100% throughout the study.

Sampling was performed with a standard Yankee No. 36 otter trawl equipped with roller gear and with the cod end and latter section of the upper belly of the trawl lined with 13 mm mesh net to retain small fish. Towing speed was 3.5 knots in the direction of the next random pre-selected station. Catches were processed according to standard NEFC procedures (Grosslein & Azarovitz 1982).

Stomach sampling

Observations first involved an examination of each fish for positive evidence of regurgitation (i.e. everted stomach or partially digested food in the mouth). When no evidence of regurgitation was observed the stomach was removed and the total stomach content volume determined. If the stomach contained only water it was considered empty. Prey were identified and the percentage of the contents made up by each particular type of prey evaluated subjectively. Two species in particular, silver hake and spiny dogfish, were intensively sampled (approximately 50 per tow if available). Sampling of other species was based on their relative abundance and the remaining time available between tows.

For comparison purposes stomach content volume was divided by fish weight to obtain percentage body weight (%BW), assuming 1.0 cc equaled 1.0 g, to adjust for differences in fish length among and within stations. Potential differences in stomach content volumes according to time of day were accounted for by using the unweighted overall means (%BW) of directly comparable time periods for each species between areas.

Results

Catches

A total of 46 species was represented in the combined catches at the two study areas (Table 1). The stomach contents of 5595 individuals, representing 36 species of fish and squid, were examined. Silver hake and

spiny dogfish accounted for 975 and 1678 samples, respectively.

The major species caught (>5% by weight) at area A (40-53 m) were spiny dogfish, little skate, winter flounder, Atlantic cod, Atlantic mackerel, yellowtail flounder, windowpane and goosefish. At area B (70-93 m) the majority of the catch was made up of spiny dogfish, fourspot flounder, silver hake, goosefish, and red hake.

Observed regurgitation

Positive evidence of regurgitation was seen in 8 of the 36 species examined (Table 2). The best comparisons of the incidence of regurgitation between areas were for spiny dogfish, silver hake, and red hake since large numbers were sampled in both areas A and B. Little indication of regurgitation was seen for these species at area A (totals of 0.5, 2.9, and 3.0%, respectively). In area B no clear evidence of regurgitation was seen for spiny dogfish, but for silver and red hake it was substantial (totals of 24.4 and 49.3%, respectively). A more detailed examination of the silver and red hake data revealed that within area B percentage regurgitation was positively correlated with depth for both species (slopes are >0 at the 95% level) (Fig. 2). No such correlation was noted at area A for either species.

The correlation of regurgitation with depth at area B for the hakes is undoubtedly because hakes have closed gas bladders. However, other forms of stress also cause fish to regurgitate. Bowen (1983) noted capture techniques such as rotenone treatment, electroshocking, gillnetting, and trawling at depth may cause regurgitation. Regurgitation in physoclistous

fishes (e.g. silver and red hake) is likely more severe and more easily detected (e.g. everted stomach) than in physostomus fishes or fishes with no gas bladder (e.g. spiny dogfish and yellowtail flounder). Expansion of gas within the bladder, resulting from a decrease in outside pressure as the trawl is rapidly brought to the surface (e.g. haulback times of about 4 and 8 minutes at areas A and B, respectively), enlarges the bladder, or ruptures it and partly fills the body cavity with gas. This is reasonable to assume because the gas within the bladder would expand roughly 6 and 10-fold at A and B, respectively (from bottom to surface according to Boyle's Law). Since the bladder is located in part above and behind the stomach, food in the stomach would probably be expelled, or in extreme cases the stomach would evert, as a result of the increase in pressure within the body cavity. The shape and size of the digestive tract are probably important in this regard since digestive tracts are generally adapted to diet (Lagler et al. 1962). It is recognized that piscivores which eat large prey have large distensible esophaguses and regurgitate more frequently than fishes which feed on small prey and have small esophaguses (Bowen 1983).

Bearing the above in mind, most of the species which had little or no occurrence of observable regurgitation at area B can be grouped into three general categories as follows: (1) cartilaginous fishes—none have gas bladders and diet includes some decapods and fish (e.g. sharks and skates), (2) pelagic fishes—most have gas bladders with various modifications (e.g. in herrings the gas bladder opens to the exterior by a pore near the anus) and mainly feed on small organisms such as copepods, amphipods, and mysids (e.g. herrings, Atlantic mackerel, and butterfish), (3) flatfishes—none have gas bladders when adult, and many species take

small prey such as amphipods and polychaetes (e.g. windowpane and yellowtail flounder). Conversely, the gadiform fishes (e.g. silver, red, and white hake) generally had a high incidence of observable regurgitation. They have closed gas bladders and eat large organisms such as fish and decapods. These observations made it apparent that some combination of the presence or absence of a closed gas bladder and digestive tract morphology (as inferred by prey type which is generally a function of mouth, esophagus and stomach size) influenced observable regurgitation.

Therefore, it might be expected that piscivores and physoclistous fishes with full stomachs (i.e. fish with the least space in the body cavity to accommodate the expanded gas) would regurgitate more often, and perhaps more completely, especially when retrieved from deep water. This would increase the proportion of everted and empty stomachs, as well as truncate the upper portion of the frequency distribution of relative stomach content volumes. Since observed regurgitation was substantially higher in area B, it was suspected that there was also a higher incidence of unrecognized regurgitation.

Unrecognized regurgitation

Examination of stomach content volumes (expressed as %BW) of fishes with no visual signs of regurgitation showed 7 of the 8 species for which there was adequate data for analysis had more food in their stomachs at area A than at area B (Fig. 3). Paired t-tests between data for areas A and B, by individual species, showed significantly more food was present in the stomachs of spiny dogfish, silver hake, red hake, and fourspot flounder at area A ($t=5.75, 7.21, 4.83, 3.23$; D.F.=7, 7, 7, 6, respectively).

A subset of the data for silver hake, red hake, and spiny dogfish (based on strictly comparable length frequencies for each species) was plotted to illustrate the frequency distributions of stomach content volumes in areas A and B (Figs. 4-6). Incidence of visually observed regurgitation is included in the figures for silver and red hake for comparison purposes. In the case of silver hake (Fig. 4) the highest stomach content values ($>2\%BW$) are virtually non-existent from the frequency distribution in area B compared to A, and there was a large increase in the percentage of empty stomachs and detectable regurgitation at B, which is consistent with what was suggested above. The frequency distribution of stomach contents for red hake did not change as much as for silver hake, and there was only a small increase in the percentage empty at area B (Fig. 5). However, the percentage of red hake which regurgitated was much higher in B. This could indicate more complete (i.e. detectable) regurgitation occurred in red hake, possibly because they are more severely affected by a rapid decrease in pressure than silver hake.

For spiny dogfish at B relative to A only a slight decrease was seen in the frequency of stomach contents $>2\%BW$, and only a modest increase was observed in the percentage empty (Fig. 6). The reason spiny dogfish are not often observed with everted stomachs, even though they have large esophaguses, is probably because they have no gas bladder. However, the percentage of fish with stomachs full of water is undoubtedly not a natural phenomenon, and may be an indication of prior regurgitation. Noteworthy in this regard is that spiny dogfish caught in both areas were frequently seen regurgitating as well as gulping down air after the trawl was emptied onto the deck. Apparently spiny dogfish readily regurgitate when caught in trawls. The high percentage of empty stomachs, stomachs full of water,

relatively small quantities of food in the stomachs, and visual observations noted above provide evidence that a large number of dogfish regurgitated in both area A and B.

Without knowing the absolute abundance of preferred prey for each species in each area, it is impossible to sort out the degree to which undetected regurgitation could account for these results. However, as will be shown in the next section, there was no indication of a scarcity of food in B relative to A. This, together with the evidence presented above, suggests that a significant amount of undetected regurgitation probably occurred in area B, especially in silver hake and spiny dogfish, and to a lesser degree in red hake.

Comparison of prey abundance with diet

Relative abundance of prey fish and squid was readily available by calculating the mean catch (No. 30^{-1} min trawl haul) of each species at each area (Table 3). Data for documenting the abundance of benthic and pelagic invertebrates were not available. Eight predators were sampled in sufficient numbers at areas A and B to make dietary comparisons (Table 4).

Fish and squid were important prey (>10% of the diet in terms of percentage total volume) of spiny dogfish, silver hake, red hake, white hake, and fourspot flounder. It is readily seen that both the catch per haul indices (Table 3), and the percentages in the diet of various predators (Table 4), of prey such as American sand lance, herrings, Atlantic mackerel, and silver hake (almost all <15 cm fork length), were highest in area A in almost every instance. Conversely, the values for

squid and butterfish were highest in area B. Other prey groups such as flatfishes and red hake <15 cm didn't appear to be important prey in a particular area, but both were generally more abundant at area A. The "Other fish" prey category (Table 4) was substantial for several predators (e.g. spiny dogfish and silver hake), but since it was almost exclusively unidentified fish flesh, it could not be considered in the comparison with abundance. In the aggregate, it seems somewhat more prey, especially small silver hake, were available for food in area A. However, their certainly wasn't a scarcity of food at area B, as implied by the fact that the major fish predators (spiny dogfish, silver hake and white hake) were all more abundant at area B (Table 1).

Overall, it doesn't appear the slightly higher abundance of prey in area A would be large enough to account for the drastic differences noted in the %BW values between areas. For example, as seen at the bottom of Table 4, species such as silver hake and spiny dogfish had 8.3 and 4.3 times more food in their stomachs at area A, respectively. Also noteworthy is that no large differences were seen between areas for most predators in terms of major taxonomic food categories. For example, spiny dogfish ate mostly fish and squid (>90% in both A and B), alewife stomachs contained almost totally small invertebrates and decapods (both combined equaled >95% in each area), and the three flounders (i.e. fourspot, windowpane, and yellowtail) consumed roughly the same proportions of some combination of fish and squid, polychaetes and small invertebrates, or decapods depending on the particular predator. Generally there were trade-offs among the subgroups which resulted in the diet composition being remarkably similar for the major groupings. The obvious exceptions were silver hake and white hake. In the case of silver hake, chaetognaths taken as food in area B

(18.1%) resulted in corresponding decreases in the percentages of fish, squid, and decapods in their diet. If we assume chaetognaths are not a preferred food of silver hake, then the high percentage found for area B may indicate that other food (e.g. fish, squid, and decapods) was not as available as in area A, but this contradicts what was observed for most other species. For white hake it is likely that the difference seen in the types of food eaten between areas A and B was caused by predator length. The mean total lengths of white hake sampled at areas A and B were 34.2 and 43.2 cm, respectively. It is well established that large white hake eat much larger portions of fish and squid than small white hake (Bowman & Michaels 1984).

Discussion

There is little doubt that variability in stomach contents, caused directly or indirectly by sampling depth, is a complex problem. Depending on the particular predator, we have seen different rates of or no detectable regurgitation, different quantities and types of food in the stomachs, and differences in predator and prey abundance. All of these are somehow apparently related to bottom water depth since variables such as water temperature, time of day, season, year or available prey did not (or, in the latter instance, most likely did not) cause the differences. Of particular interest is that most of the species for which no regurgitation was observed had stomach content volumes which were nearly equal between areas (i.e. alewife, windowpane and yellowtail flounder; with an average

of only 1.1 times more food in the stomachs at area A). These same predators were more abundant at area A, and their average lengths and major prey groups (polychaetes or small invertebrates) were almost identical between areas. Conversely, for species which were observed to regurgitate (e.g. spiny dogfish, silver hake, red hake, and white hake), the quantities of food in their stomachs were much less in area B (average of about 5.7 times less), all were more abundant at area B, and their major prey was mostly large organisms such as fish, squid, and decapods. We must ask why the abundance of spiny dogfish, silver hake, red hake and white hake would be greater in an area where food was scarce? Also, why were significant differences in the stomach content quantities between areas only found in the species which were observed to regurgitate? I believe the above facts and reasoning provide adequate circumstantial evidence to infer that regurgitation occurs and may go undetected in certain species when they are sampled in deep water.

Food consumption by marine fishes has become a central theme of many large scale fishery research programs initiated in the 1980's. Research conducted in the 1970's and early 1980's has provided evidence that piscivorous fish may not only have a major impact on year class success of species taken as prey, but that these predators may consume larger quantities of species of commercial interest than are harvested by the fisheries (for an extensive review see Sissenwine 1984). Accordingly, more quantitative information must be obtained on predator-prey relationships, and major causes of bias or variability in fish stomach content data must be identified to determine their potential impact on estimates of food consumption. In particular, regurgitation which may occur and go undetected when conducting fish food studies may produce severe

underestimation of consumption. Sampling protocols generally address the problem of regurgitation by requesting technicians, at the time samples are collected, to perform the following tasks: (1) inspect the buccal cavity (inside of mouth) for signs of regurgitated food, and the esophageal area (via the body cavity) for eversion. If signs of regurgitation exist discard the fish,¹ (2) expanded stomachs which are empty are to be discarded (Daan 1973). The phenomenon known as regurgitation is well known; e.g. "Many predatory fishes appear to regurgitate large food items from the stomach with great facility. It has been suggested that this is made possible by the pronounced development of striated muscles in the walls of the esophagus extending to the stomach" (Lagler et al. 1962).

The percentage of detectable regurgitation for some species increases considerably with increasing trawl depths. The results presented here document that about 8 times more silver hake and 16 times more red hake regurgitate with an increase of only 40 m bottom water depth (from about 50 to 90 m). Not only is the incidence of detectable regurgitation higher, but even those fish showing no evidence of regurgitation can have measurably lower stomach contents in deep water. In this instance the stomachs of the two species of principal concern, silver hake and spiny dogfish, contained an average of approximately 8 and 4 times more food at the shallow area, respectively. Consumption estimates for these two species could be biased by the same amounts if these differences were caused by undetected regurgitation.

Silver hake and spiny dogfish make up a considerable portion of the total fish biomass and have been identified as the two most significant piscivorous fish in the northwest Atlantic (Edwards & Bowman 1979, Anon. 1983). Because these two species have been shown to, or are suspect of,

¹Taken from NEFC sampling protocol.

regurgitating their food, potential severe bias may be inherent in the data one uses to determine the type and quantity of food they consume. Therefore, stomach content data for these two species must be examined critically before attempting to estimate their predatory impact on other fish populations.

When daily ration is estimated according to the method described by Elliott & Persson (1978) or some similar method (e.g. Pennington 1984), and field gathered data is used for the calculations, the results can be of questionable value, especially when the stomach content samples are obtained from different depths. In a recent paper Daan (1984) documented that about 9% of all Atlantic cod he studied from the North Sea had obvious signs of regurgitation. He estimated cod consumption on the remaining samples, as is done traditionally (e.g. Durbin et al. 1983, Livingston 1983). During the study by Durbin et al. on Atlantic cod and silver hake in the northwest Atlantic, it was noted that a large proportion of the silver hake sampled had empty stomachs. Moreover, the average quantity of food present in the stomachs of both silver hake and Atlantic cod was small based on what is known of their energetic requirements. It is probable that most daily ration estimates based on field data are negatively biased, perhaps to a large degree for species with closed gas bladders.

In conclusion, we have seen that detectable regurgitation varies according to species and increases with sampling depth in species with closed gas bladders. Visually undetectable regurgitation was difficult to document but evidence presented suggests that it also occurs for certain species and results in negative bias in average stomach content estimates. The mechanisms of regurgitation, and the relationship of regurgitation with depth and stomach fullness, might be somewhat clarified through experiments

on fishes within pressure chambers. However the element of stress and the effects of external pressure (analogous to squeezing of fish inside a full cod end) would be difficult to simulate. Therefore the magnitude of possible bias from undetected regurgitation may be best estimated through further experiments such as reported herein, together with analysis of time series data on stomach contents versus depth for selected species.

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Table 1. Mean catch (kg) per 30 min trawl haul, percentage composition of total catch, and number of fish examined for species caught at areas A and B. Listing of species is in phyletic sequence according to Robins (1980).

Species		Area A			Area B		
Scientific name	Common name	(kg)	%	No. exam.	(kg)	%	No. exam.
<u>Petromyzon marinus</u>	Sea lamprey	<0.1	<0.1	0	<0.1	<0.1	0
<u>Squalus acanthias</u>	Spiny dogfish	48.7	30.3	628	86.0	63.4	1050
<u>Torpedo nobiliana</u>	Atlantic torpedo	-	-	-	0.5	0.4	1
<u>Raja erinacea</u>	Little skate	36.2	22.5	149	0.4	0.3	20
<u>Raja laevis</u>	Barndoor skate	0.1	<0.1	1	-	-	-
<u>Raja ocellatus</u>	Winter skate	1.1	0.7	5	-	-	-
<u>Conger oceanicus</u>	Conger eel	-	-	-	<0.1	<0.1	1
<u>Alosa aestivalis</u>	Blueback herring	0.1	<0.1	7	<0.1	<0.1	1
<u>Alosa pseudoharengus</u>	Alewife	4.4	2.7	74	4.0	2.9	95
<u>Alosa sapidissima</u>	American shad	1.0	0.6	39	0.1	0.1	10
<u>Clupea harengus harengus</u> (Engraulidae)	Atlantic herring	0.1	<0.1	2	<0.1	<0.1	1
<u>Synodus poeyi</u>	Anchovy*	<0.1	<0.1	0	-	-	-
<u>Lophius americanus</u>	Offshore lizardfish	<0.1	<0.1	0	<0.1	<0.1	1
<u>Gadus morhua</u>	Goosefish	5.5	3.4	20	6.0	4.4	49
<u>Melanogrammus aeglefinus</u>	Atlantic cod	7.9	4.9	45	0.3	0.2	1
<u>Merluccius bilinearis</u>	Haddock	-	-	-	<0.1	<0.1	12
<u>Pollachius virens</u>	Silver hake	3.9	2.4	404	7.5	5.5	571
<u>Urophycis chuss</u>	Pollock	-	-	-	0.3	0.2	1
<u>Urophycis regia</u>	Red hake	4.5	2.8	161	5.7	4.2	495
<u>Urophycis tenuis</u>	Spotted hake	-	-	-	<0.1	<0.1	1
<u>Lepophidium cervinum</u>	White hake	1.2	0.7	72	1.5	1.1	43
<u>Macrozoarces americanus</u>	Fawn cusk-eel	-	-	-	<0.1	<0.1	18
<u>Gasterosteus aculeatus</u>	Ocean pout	1.4	0.9	44	0.7	0.5	31
<u>Syngnathus fuscus</u>	Threespine stickleback	-	-	-	<0.1	<0.1	0
<u>Centropristis striata</u>	Northern pipefish	<0.1	<0.1	0	<0.1	<0.1	0
<u>Annodytes americanus</u>	Black sea bass	-	-	-	<0.1	<0.1	2
<u>Scomber scombrus</u>	American sand lance	<0.1	<0.1	0	-	-	-
<u>Peprilus triacanthus</u>	Atlantic mackerel	7.3	4.5	24	0.1	0.1	20
<u>Prionotus carolinus</u>	Butterfish	1.7	1.2	25	4.8	3.5	98
<u>Hemirhamphus americanus</u>	Northern searobin	-	-	-	0.1	<0.1	1
<u>Myoxocephalus octodecemspinosus</u>	Sea raven	2.4	1.5	77	<0.1	<0.1	2
<u>Citharichthys arcifrons</u>	Longhorn sculpin	1.6	1.0	106	<0.1	<0.1	2
<u>Paralichthys dentatus</u>	Gulf Stream flounder	-	-	-	<0.1	<0.1	16
<u>Paralichthys oblongus</u>	Summer flounder	<0.1	<0.1	2	3.5	2.6	95
<u>Scophthalmus aquosus</u>	Fourspot flounder	1.7	1.1	65	8.7	6.4	208
<u>Glyptocephalus cynoglossus</u>	Windowpane	6.3	3.9	156	0.5	0.4	47
<u>Limanda ferruginea</u>	Witch flounder	-	-	-	0.2	0.1	5
<u>Pseudopleuronectes americanus</u>	Yellowtail flounder	6.8	4.2	180	0.6	0.4	36
<u>Homarus americanus</u> (Caridea)	Winter flounder	14.6	9.1	189	-	-	-
<u>Cancer irroratus</u>	Northern lobster*	2.0	1.2	0	1.8	1.3	0
<u>Cancer borealis</u>	Caridean shrimp*	0.1	<0.1	0	<0.1	<0.1	0
<u>Rossia sp.*</u>	Rock crab*	<0.1	<0.1	0	-	-	-
<u>Loligo pealei</u>	Jonah crab*	0.1	<0.1	0	0.1	0.1	0
<u>Illex illecebrosus</u>	Long-finned squid*	0.1	<0.1	9	<0.1	<0.1	0
	Short-finned squid*	-	-	-	0.1	<0.1	6
	No. of tows			27			24
	Total No. stomachs examined			2484			3111

* Unidentified species or not listed in Robins (1980).

Table 2. Percentages of various fish species sampled in areas A and B which were positively observed to regurgitate.

Species	Number examined		Everted stomach		Food in mouth		Total regurg.	
	A	B	A	B	A	B	A	B
Spiny dogfish	628	1050	0.2	0.0	0.3	0.0	0.5	0.0
Little skate	149	20	0.0	0.0	0.0	5.0	0.0	5.0
Goosefish	20	49	5.0	4.1	0.0	0.0	5.0	4.1
Silver hake	404	571	2.2	23.5	0.7	0.9	2.9	24.4
Red hake	161	495	1.2	43.0	1.8	6.3	3.0	49.3
White hake	72	43	0.0	9.3	0.0	4.7	0.0	14.0
Fawn cusk-eel	0	18	-	0.0	-	38.9	-	38.9
Northern sea robin	0	1	-	100.0	-	0.0	-	100.0

TABLE 3. Relative abundance of fish and squid taken as prey in areas A and B as determined from trawl catches during study.

Fish and squid	Relative abundance (No. per 30 min tow)	
	Area A (40-53 m)	Area B (70-93 m)
Long-finned squid	1.7	94.9
American sand lance	0.8	0.0
Butterfish	13.1	70.0
Herrings	27.0	15.8
Atlantic mackerel	11.1	0.9
Flatfishes	89.4	56.3
Silver hake >15 cm FL	16.4	39.3
Silver hake <15 cm FL	272.3	3.5
Red hake >15 cm TL	18.7	26.5
Red hake <15 cm TL	0.7	0.2

Table 4. Percentage volume of the total stomach contents of dominant prey for predators sampled in both area A and B. The "Other" categories within major prey groupings (e.g. "Other fish") consisted of mainly well digested organisms which couldn't be identified to species. Mean %BW values at bottom of table are only for fish which had no signs of regurgitation.

PREY	Spiny dogfish		Alewife		Silver hake		Red hake		White hake		Fourspot		Windowpane		Yellowtail	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
FISH AND SQUID	92.6	92.0	-	-	53.5	44.4	8.7	13.9	21.1	83.3	10.2	10.4	0.5	1.0	-	-
Squid	5.0	31.8	-	-	-	11.0	0.2	1.7	-	26.2	-	8.0	-	-	-	-
American sand lance	1.8	-	-	-	11.8	0.2	1.9	-	1.1	-	-	-	-	-	-	-
Butterfish	0.7	3.5	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-
Herrings	3.8	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atlantic mackerel	33.4	6.5	-	-	-	-	-	-	-	5.9	-	-	-	-	-	-
Flatfishes	7.3	2.6	-	-	-	-	-	0.3	1.4	9.8	0.3	0.8	0.5	-	-	-
Silver hake	1.9	-	-	-	19.9	-	3.8	-	6.3	-	-	1.2	-	-	-	-
Red hake	1.9	2.3	-	-	1.5	-	-	-	-	-	1.2	-	-	1.0	-	-
Other fish	36.8	45.3	-	-	20.5	30.7	2.8	11.9	12.3	41.4	8.7	0.4	-	-	-	-
POLY. & SMALL INVERT.	0.1	5.7	85.7	83.4	2.2	20.2	33.9	41.7	17.9	3.0	3.6	2.3	90.7	96.0	96.9	99.2
Polychaeta	0.1	3.1	-	-	0.3	-	8.8	4.1	2.3	1.0	0.1	1.5	0.4	-	36.0	77.9
Amphipoda	<0.1	0.2	38.3	35.8	0.7	1.8	22.6	36.0	14.0	1.0	3.5	0.8	1.6	0.1	60.9	21.3
Mysidacea	-	<0.1	32.2	0.5	1.2	0.2	1.4	0.5	1.5	<0.1	-	-	82.4	4.7	-	-
Other crustaceans	<0.1	0.4	13.7	4.9	<0.1	0.1	0.9	0.5	0.1	-	-	-	0.3	0.1	-	-
Chaetognatha	-	2.0	1.5	42.2	-	18.1	0.2	0.6	-	1.0	-	-	6.0	91.1	-	-
DECAPODS	1.7	0.4	10.2	8.8	41.8	34.0	54.9	37.1	59.8	9.0	85.0	85.1	8.1	3.0	1.3	-
Crangon sp.	<0.1	<0.1	7.4	2.5	24.9	5.3	21.9	2.2	30.2	3.4	28.4	-	7.9	2.1	1.2	-
Pandalidae	<0.1	0.3	2.8	6.3	16.9	28.7	20.5	12.6	19.3	5.6	53.9	48.3	0.2	0.9	-	-
Cancer spp.	0.6	-	-	-	-	-	2.2	6.7	3.6	-	1.3	15.8	-	-	-	-
Other decapod crabs	1.1	0.1	-	<0.1	<0.1	-	10.5	15.6	6.7	-	1.4	21.0	-	-	0.1	-
MISCELLANEOUS	5.6	1.9	4.1	7.8	2.5	1.4	2.5	7.3	1.2	4.7	1.2	2.2	0.7	-	1.8	0.8
No. fish examined	628	1050	74	95	404	571	161	495	72	43	65	208	156	47	180	36
No. empty stomachs	463	785	11	32	83	328	9	34	4	13	8	63	48	8	70	9
Mean fish length (cm)	81.2	63.5	24.4	27.0	27.6	30.6	34.3	35.2	34.2	43.2	35.4	33.8	27.1	26.1	33.2	34.1
Mean %BW stom. cont.	0.52	0.12	0.60	0.50	1.16	0.14	1.07	0.73	1.67	0.19	1.28	0.48	0.77	1.12	0.16	0.11

Fig. 1. Locations (A and B) of regurgitation study conducted aboard the R/V DELAWARE II during Cruise 81-08 on 7-17 December 1981. The center of area A (40-53 m) was located at $40^{\circ}50'N$, $70^{\circ}20'W$ and area B (70-93 m) at $40^{\circ}25'N$, $70^{\circ}20'W$.

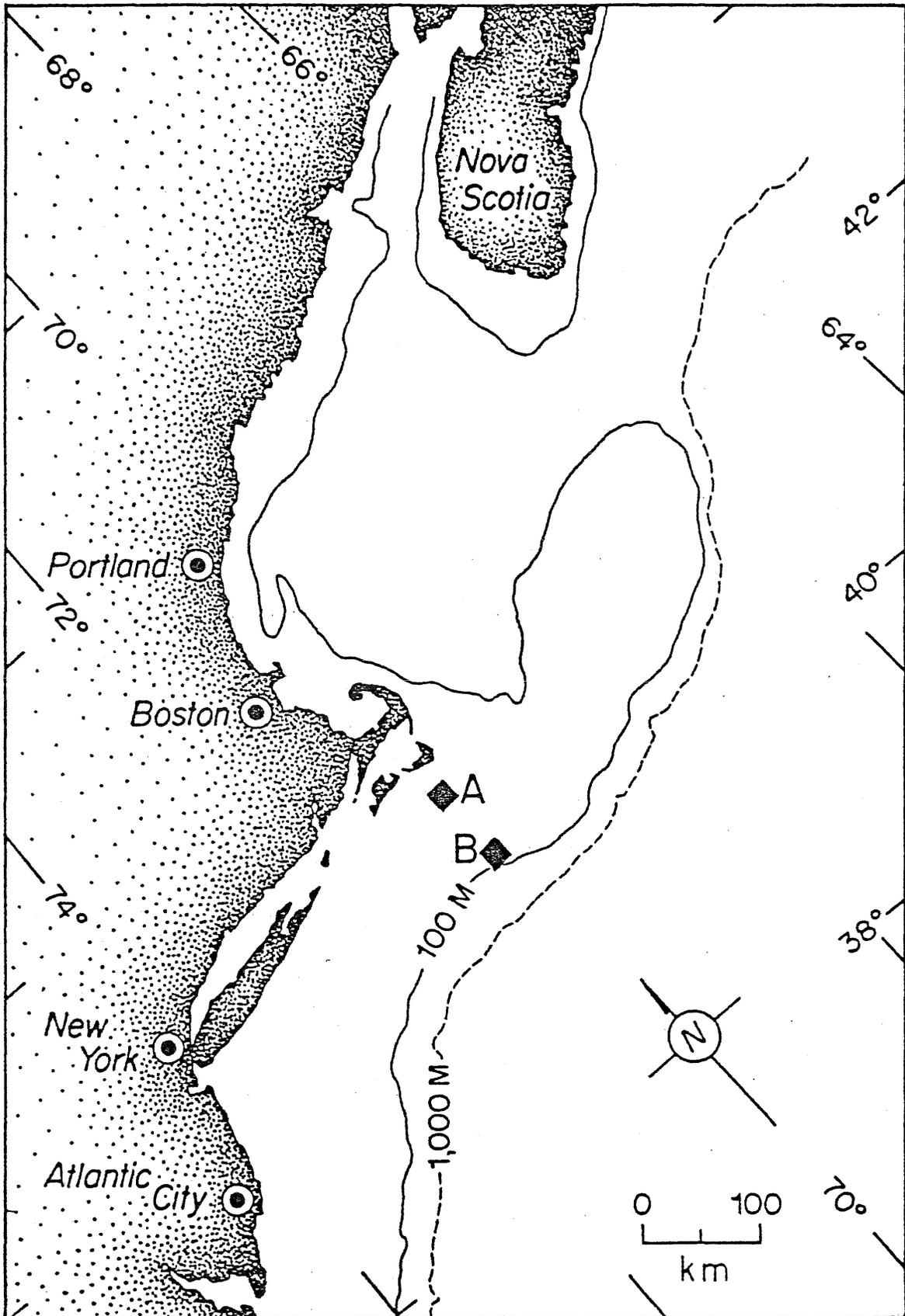


Fig. 2. Percentage detectable regurgitation for silver and red hake sampled at areas A (40-53 m) and B (70-93 m).

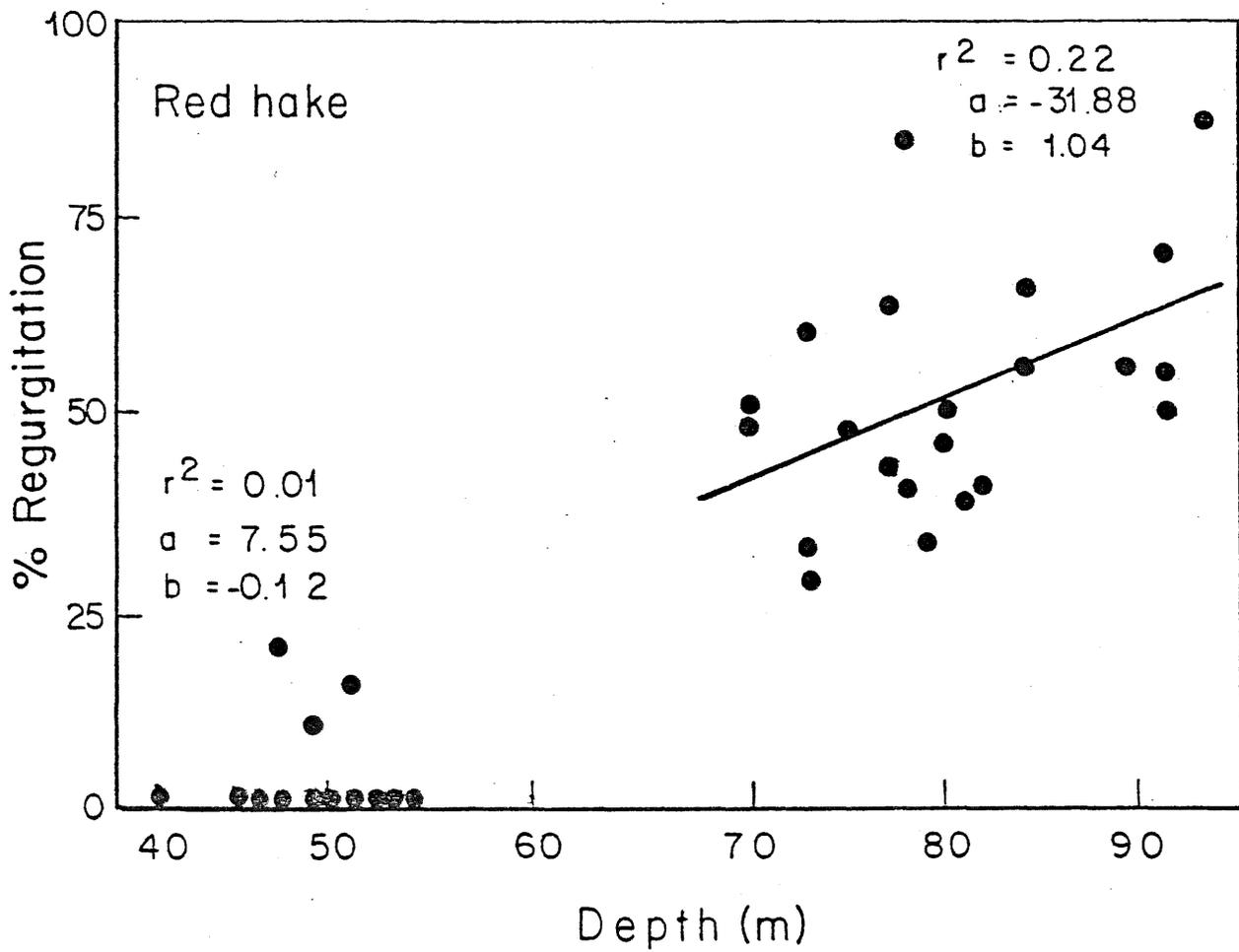
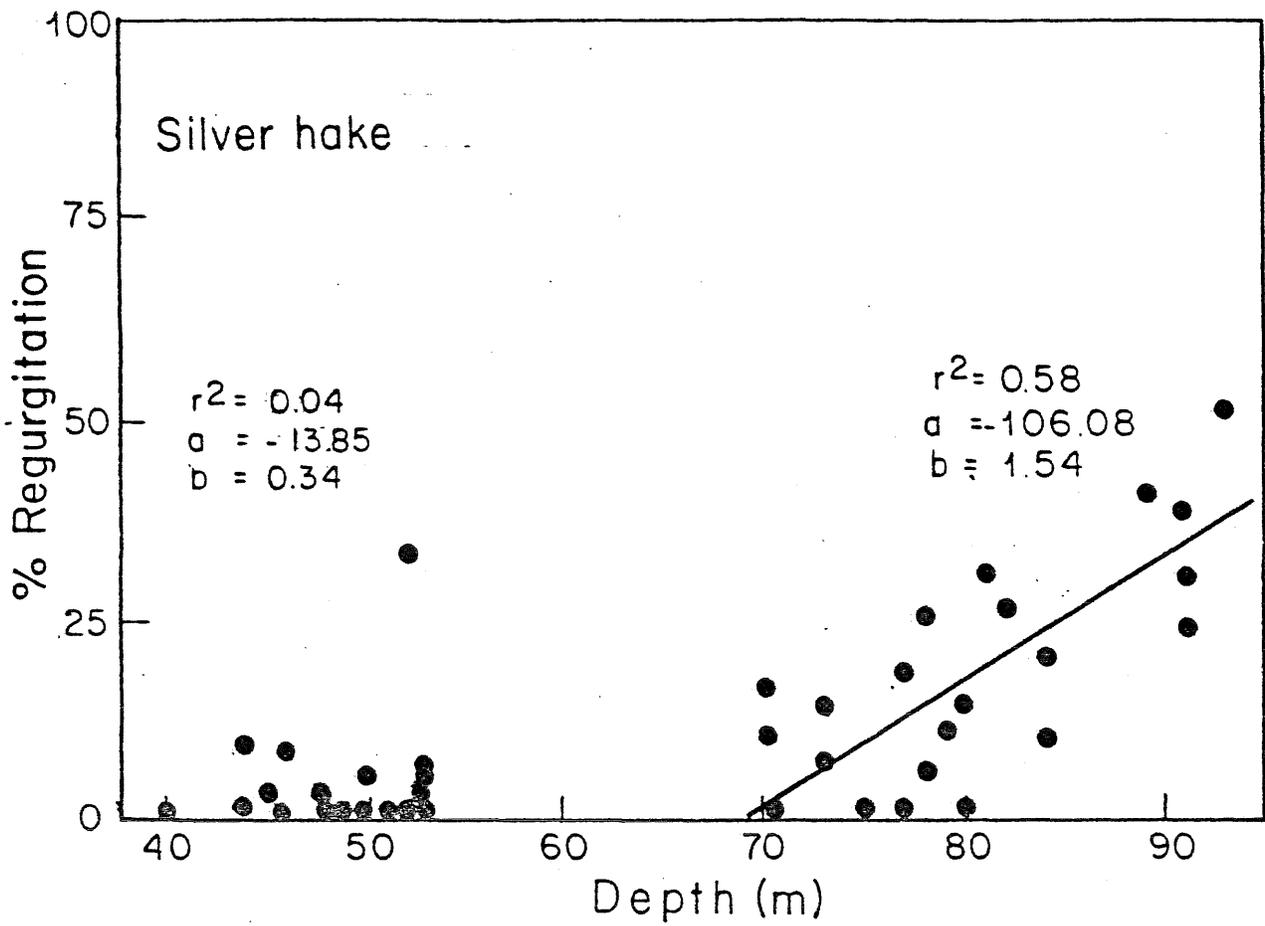
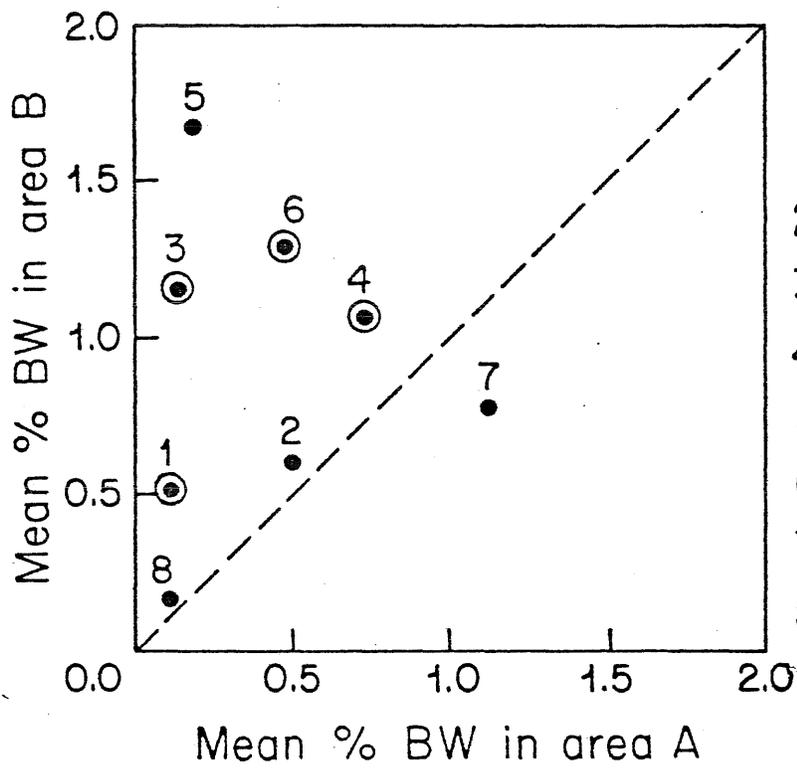


Fig. 3. Scatterplot of the mean %BW values of stomach contents for species sampled at area A versus the same species sampled at area B. Circled data points indicate species for which a significant difference in stomach content volumes was observed between the two areas.



Predator key

- 1 - Spiny dogfish
- 2 - Alewife
- 3 - Silver hake
- 4 - Red hake
- 5 - White hake
- 6 - Fourspot flounder
- 7 - Windowpane
- 8 - Yellowtail flounder

Fig. 4. Percentages of a subset of silver hake sampled at areas A and B which had regurgitated, empty stomachs, and various quantities of food in their stomachs. Number regurgitated was not included in calculation of percentage empty or stomach content values.

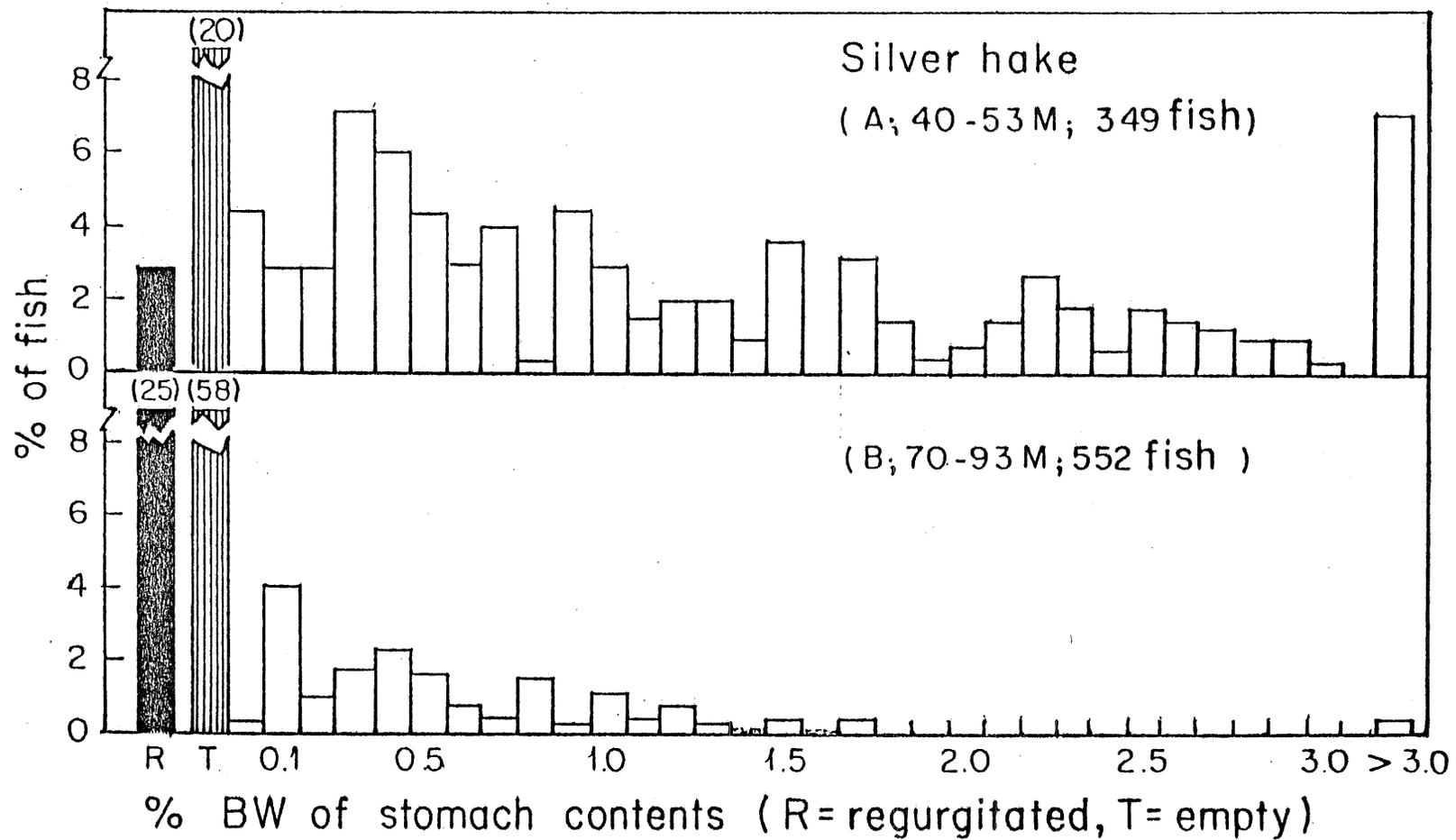


Fig. 5. Percentages of red hake sampled at areas A and B which had regurgitated, empty stomachs, and various quantities of food in their stomachs. Number regurgitated was not included in calculation of percentage empty or stomach content values.

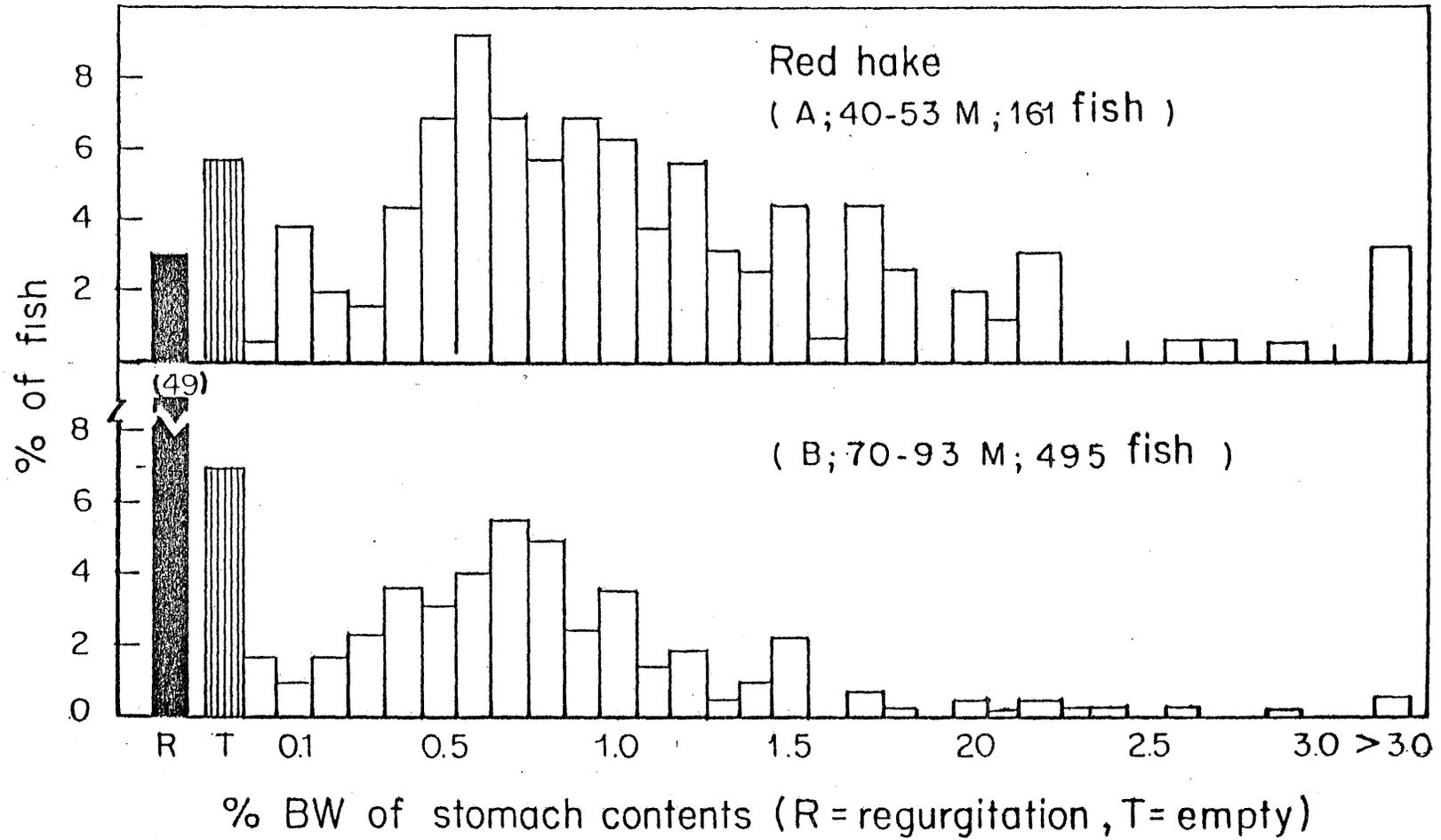


Fig. 6. Percentages of a subset of spiny dogfish sampled at areas A and B which had stomachs full of water, empty stomachs, and various quantities of food in their stomachs. Percentage empty includes stomachs which ^{were} filled with water but contained no food. ^

