LABORATORY REFERENCE DOCUMENT NO. 81-23

Examination of Known and Potential Causes of Variation in Fish Feeding Studies[1]

by

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Date *30 Dec 1981*

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July 1981

[1]MARMAP Contribution MED/NEFC 81-18

INTRODUCTION

Studies aimed at describing the diet of fish have recently received considerable attention. The I.C.E.S. ad hoc working group on multispecies assessment model testing recommended an intensive stomach sampling program for cod, whiting, and saithe be conducted in the North Sea in 1981 (Demersal Fish Committee C.M. 1980/G:2). Feeding ecology studies carried out at the Woods Hole Laboratory of the Northeast Fisheries Center (NEFC) located in Woods Hole, Massachusetts, U.S.A., were revised for 1981. The new sampling protocol was designed to provide more precise estimates of the food consumed by species to be used in modeling predator-prey interactions (principally in the Georges Bank-Nantucket Shoals area). Simultaneously, the principal prey of dominant fish species in the survey area (shelf waters from Cape Fear, North Carolina southerly to western Nova Scotia northerly) are to be monitored. Data gathered for large scale studies such as those described immediately above are subject to many forms of variation. Often biological experience and intuition are the only tools available for eliminating bias. Statistical analysis has demonstrated that stomach content data is quite variable (Pennington, et al. 1980). In this paper I address sources of known and potential causes of variation in food data. This work is consistent with the overall objectives of NOAA's MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program in the northeast (U.S.A.).

SOURCES OF INFORMATION

Paragraphs immediately below summarize the sources of information from which this manuscript was formulated.

Examination of feeding study strategies utilized by personnel at the Woods Hole Laboratory of the NEFC since 1963 shows several different approaches have been employed (Langton, et al. 1980). Initially only information on the type of food eaten was gathered; for the 1963-1966 period approximately 18,500 stomachs representing 65 species were examined aboard ship. During the period 1969-1972 a quantitative sampling scheme was undertaken. Data gathered during this period helped to describe the prey biomass utilized by fish populations within the study area. A total of almost 25,000 stomachs from 99 species was excised, preserved, and brought back to the laboratory for analysis. From 1973 to 1980 detailed studies of fish feeding were initiated to determine feeding chronology, digestion rate, consumption, and growth efficiency. The samples collected represent species of relative importance in the Northwest Atlantic ecosystem and are presently being analyzed. More than 40,000 stomachs from 40 species were gathered. Generally, as feeding studies became more detailed, additional sources of variation were observed.

Collection of samples at the NEFC ultimately depends on survey cruise program personnel. The majority of stomachs are collected during bottom trawl surveys. The cruises are primarily designed for describing the distribution and abundance of fish in the study area as part of a larger management scheme. Because of this, the number of stomachs collected and the areas of collection are somewhat predetermined. Survey scientists and technicians often make observations while at sea, and these observations are seldom taken into account when the data are analyzed several years later. Discussions with survey personnel and participation on cruises made me aware of the value of these observations and the problems encountered when collecting samples at sea.

Canvassing of such people as fishermen, fishing gear specialists, oceanographers, fishery biologists, research divers, and aquarium curators was especially informative. Much of their work is either directly or indirectly related to fish behavior, and since fish behavior ultimately determines the catchability of fish and what is found in their stomachs, the information obtained was particularly useful. Additionally, examination of the methods utilized for previous feeding studies provided fundamental information for this document.

Information presented below has been separated into three categories: (1) behavioral, (2) physical, and (3) induced. Some items listed within each category could likely be placed in either of two possible categories. In such instances placement was determined only by personal preference. Sources of variation listed within each category are not necessarily in order of importance. However, I have attempted to list the potentially more serious sources of variation first.

BEHAVIORAL

Size of predator versus size of prey

In Figure 1 type and size of prey are plotted against predator size, in this case for Atlantic cod. Up until cod are about 45 cm in length its diet is composed mostly of crustaceans which, on the average, increase in size as the fish grows. A similar increase in prey size can be seen in the fish category for cod 45 cm and larger. Analogous trends can be seen in the diet of most predatory fish species. The effect of prey size on feeding information is that it can bias the data towards the larger organisms eaten by few fish when the data are presented in terms of percentage weight (in the case of cod toward fish prey), or toward smaller organisms eaten by many fish if it is presented as a percentage occurrence. A second effect results from large organisms not being digested as rapidly as small ones; thus

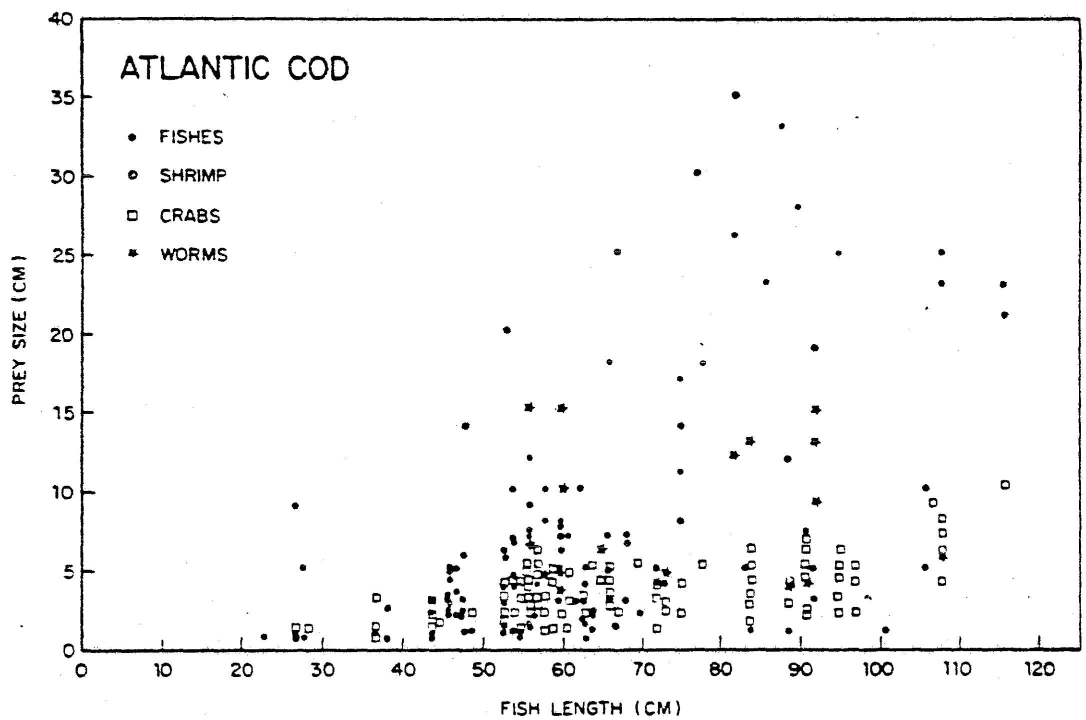

Figure 1. The type and size of prey organisms in the food of cod. The diet reflects both availability of food and the tendency for cod to eat items roughly proportional to its size. Continued feeding on relatively small items may be a necessity. (Data taken from Edwards and Bowman 1979.)

the data tends to overemphasize large prey organisms, especially for large predator species.

Availability of organisms utilized as food

The annual, seasonal, and daily fluctuations in the distribution, abundance, and availability of prey organisms determines what types and quantities of food are consumed. During spawning many invertebrate species become especially vulnerable to predators. For example, the polychaete *Nereis virens* swarms in the water column during spawning as do many amphipod species. The seasonal or yearly changes in the size of organisms (i.e., growth) taken as food by fish often determines which predator species or size of fish may (or will) prey on them. In Figure 1 it can be seen that few crustaceans >8 cm were eaten by cod. The mouth size of larval and juvenile fish (as well as smaller size fish species) determines to a large extent what organisms they eat. Early spawning by prey species can result in their growing too large to be fed upon by juvenile or newly hatched larval fish. Daily activity or seasonal migrations by organisms may cause them to be more susceptible to predation during certain time periods (e.g., predation on squid or juvenile fish). Sampling of fish during certain periods may have a profound influence on the quantities and types of food found in their diet (Steele, et al. 1970; Levings 1974; Levings and Levy 1976).

Variability in feeding

Annual and seasonal fluctuations in the type and quantity of prey consumed have been documented by Tyler (1971) and Bowman (1980B). Population density of the predator species may cause, at least in part, some of the variation detected. Another possibility could be the effect of the physical environment (temperature, salinity, turbidity, or light conditions) on fishes' behavior during different seasons and years.

Diurnal periodicity in feeding occurs in many species (Bowman 1980A; Bowman and Bowman 1980). Figure 2 shows a typical feeding pattern, in this case silver hake which feed at night. The time of day samples are collected should always be taken into account during food studies.

Migrations by predators

Migrating fish pass through areas where the number of prey species and prey density are highly variable (e.g., Nantucket Shoals which is highly productive versus areas in the Gulf of Maine which are not). Stomach content data taken from fish caught while temporarily in (non)productive areas are not representative of fish consumption over long periods of time. A second effect of predator migrations relates to the decimation of prey populations in localized areas (Figure 3). Resident fish species may be left with little food after the migrating species has moved on. Their stomach contents will likely reflect the change in prey density accordingly.

Spawning

During spawning, fish feed less intensively. For example, stomachs of silver hake caught in pre- and post-spawning condition contained ten times more food than fish which were ripe (Bowman 1980B). Data on maturity should be recorded with all samples to insure the quantity of food consumed for a particular species is not over- or underestimated.

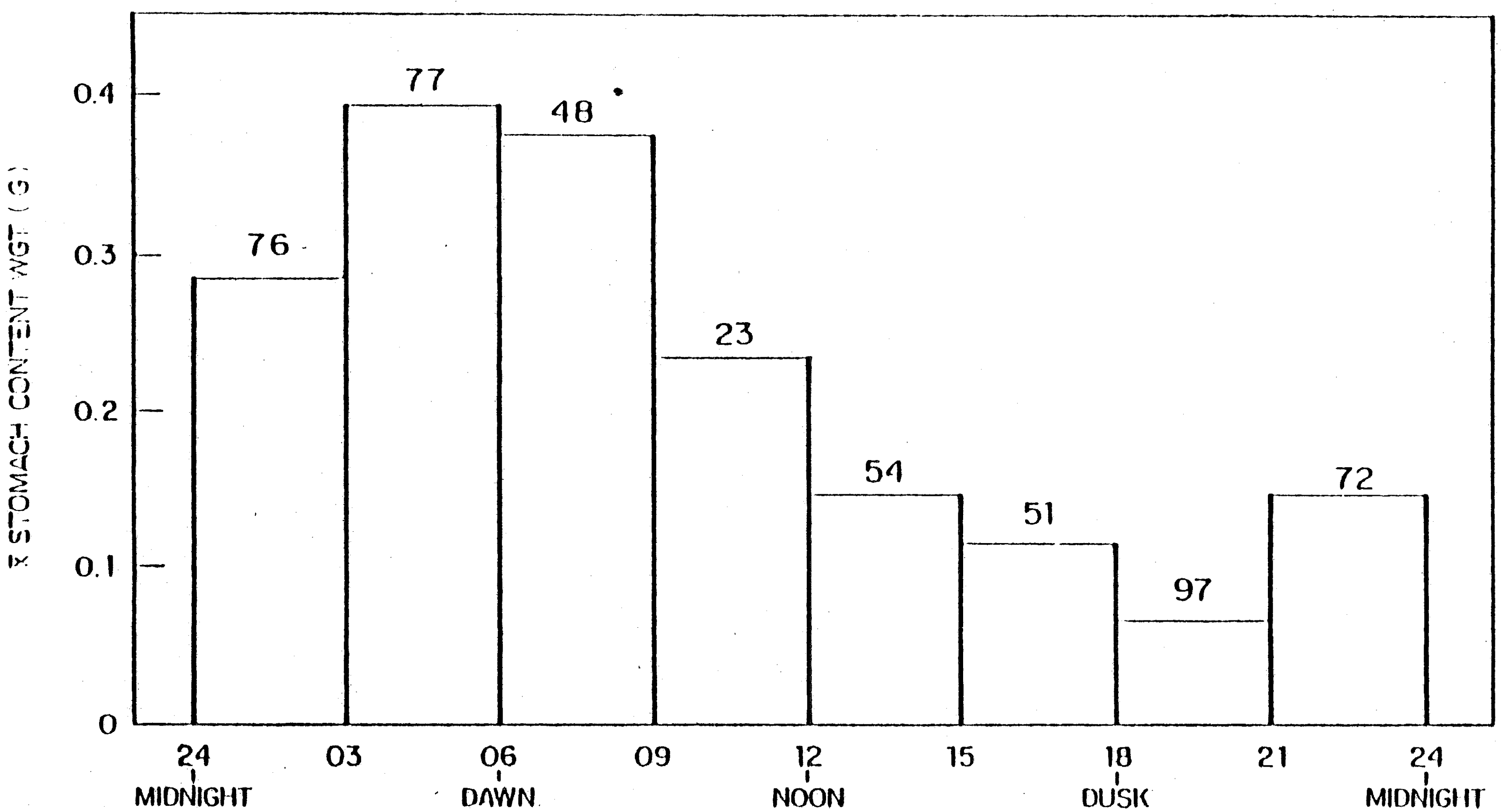

Figure 2. Mean stomach content weight of silver hake versus time of day. Silver hake were collected during a 48-hour study conducted on the southern part of Georges Bank in September of 1978. The number of fish sampled in each time period is given just above the histogram. (Data taken from Bowman and Bowman 1980.)

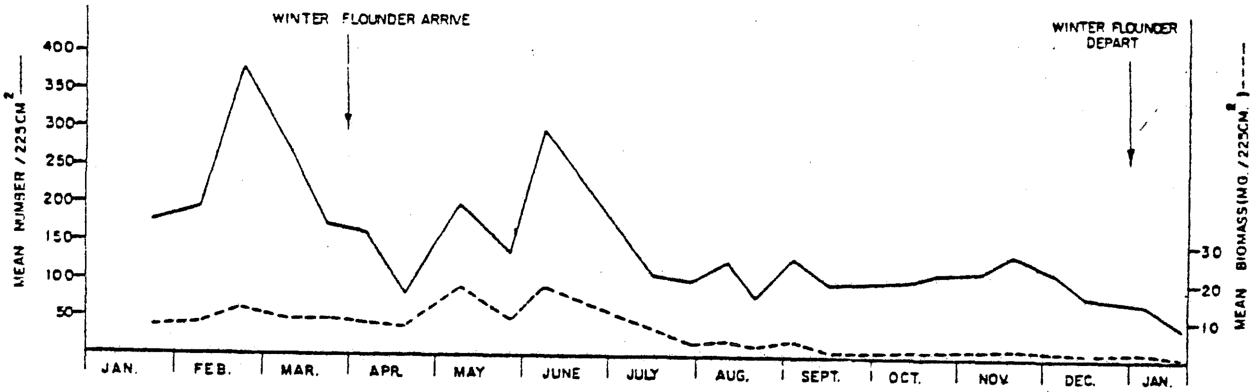

Figure 3a. Temporal changes in abundance (number, biomass) of *Photis reinhardi* at St. Margaret's Bay, Nova Scotia. Winter flounder immigrated to the study area in March, and were absent in winter months. Samples were obtained with an Ekman grab, and mean values per 225 cm^2 (n = 5) are shown. (Data taken from Levings and Levy 1976.)

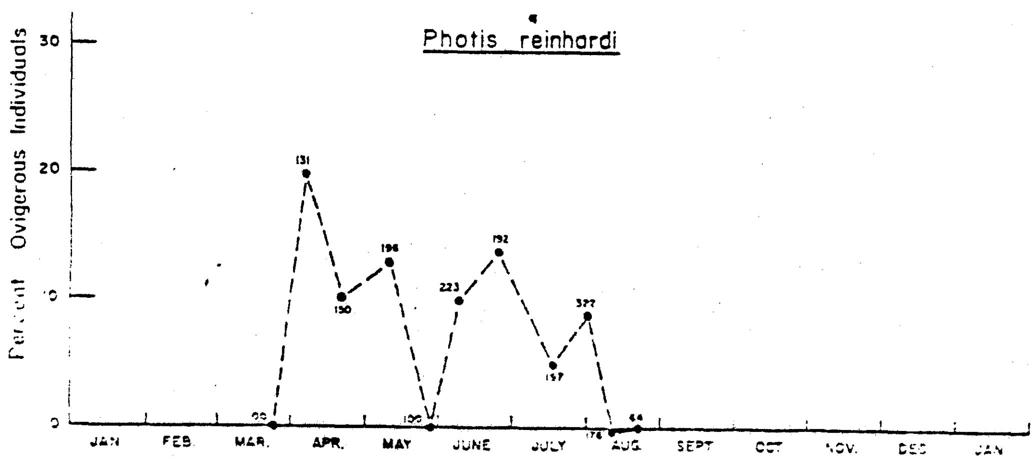

Figure 3b. Temporal changes in frequency of ovigerous females of *P. reinhardi* at St. Margaret's Bay, Nova Scotia. Numerals near data points indicated number of individuals examined (usually <u>ca</u> 100). (Data taken from Levings and Levy 1976.)

Digestibility of prey

Food data tends to be biased toward items which are hard to digest. Organisms such as worms and copepods are digested at a faster rate than whole clams or crabs; therefore the type and quantity of particular prey items may be over- or underestimated. Fish of the same size and species eating foods of different digestibility could lead one to believe that the fish eat different quantities of food, although the actual quantity of food consumed may be the same.

Digestive systems

Digestive systems in fish differ substantially between and within species (Tyler 1973; Edwards and Bowman 1979). The mouths of fish such as bluefish and summer flounder have teeth (in the case of squid, beaks) which are used to reduce the size of their prey by biting it into pieces. Other fish such as goosefish or cod swallow prey whole. Digestion time for prey which has been bitten into pieces is less than that for whole prey because many small pieces present a larger surface area to the digestive juices.

Species such as Atlantic mackerel have a large pylorus while others have organs similar to gizzards (e.g., butterfish and cunner), or spiral valves (e.g., sharks and skates). The weight, which is indicative of size, of stomachs and intestines vary considerably between species (Table 1). Stomachs of some species are large and their intestines small (e.g., four-spot flounder and sea raven) while others have small stomachs and large intestines (e.g., haddock and ocean pout). Digestive systems of different size fish of the same species also differ (Bowman 1980B; 1981[1]). Generally,

[1]Unpublished data.

Table 1. Digestive tract measurements in grams for fish common in the shelf waters of the Northwest Atlantic. (Data taken from Edwards and Bowman 1979.)

Species	No. fish examined	Average digestive-tract/fish wt	Average stomach wt	Average intestine wt	Average pyloric caeca wt	Average stomach wt/ int. and pyl.	Caloric value per gram food
Silver hake	5	3.0	20.97	15.02	-	1.40	1.152
Atlantic herring	26	3.6	0.95	0.35	1.36	0.56	0.971
Spiny dogfish	5	5.5	96.90	62.67	-	1.55	1.180
Haddock	10	3.4	15.73	17.71	21.61	0.40	0.809
Red hake	13	2.1	1.74	1.11	1.45	0.68	1.050
Pollock	12	3.3	19.08	10.52	29.42	0.48	1.084
Thorny skate	8	4.0	16.82	8.43	-	2.00	1.050
Atlantic cod	9	4.6	40.63	22.71	37.03	0.68	1.092
Redfish	7	2.2	1.01	0.96	0.95	0.53	0.963
Little skate	100	2.4	8.30	5.70	-	1.46	1.019
Butterfish	7	2.4	0.76	0.67	0.95	0.47	0.351
Winter skate	10	1.6	45.44	27.25	-	1.67	0.949
Atlantic argentine	9	1.8	4.29	0.93	2.06	1.43	0.955
Winter flounder	11	0.8	1.78	2.89	-	0.62	0.702
Yellowtail flounder	11	1.1	2.23	3.33	-	0.67	0.921
Barndoor skate	1	1.7	5.89	5.05	-	1.17	1.170
Ocean pout	10	2.9	3.86	9.07	4.32	0.29	0.582
Goosefish	6	6.5	204.94	204.65	-	1.00	1.187
American plaice	11	2.3	4.04	13.28	-	0.30	0.600
Atlantic mackerel	14	3.5	3.18	1.31	5.42	0.47	0.849
Alewife	12	2.3	1.17	0.29	1.75	0.57	0.988
White hake	9	2.2	6.47	3.12	5.76	0.73	1.173
Longhorn sculpin	100	3.9	4.40	4.20	-	1.05	1.059
Windowpane	6	2.2	1.50	2.43	-	0.62	1.028
Scup	4	1.3	4.49	26.64	-	0.17	0.636
Witch flounder	10	1.0	0.54	0.50	0.40	0.60	0.831
Fourspot flounder	25	2.1	2.53	1.18	-	2.14	1.114
Sea raven	10	4.9	26.76	8.58	9.04	2.19	1.166

as fish grow in size their stomachs and intestines do not increase in weight at a linear rate to either the fishes' total weight or to each other (Figures 4 and 5). Differences in digestive systems have been related to meal size, type of food eaten, and digestion rate (Edwards and Bowman 1979).

Metabolic requirements

The activity of a particular fish species is especially important when calculating consumption. Bottom dwelling species (e.g., goosefish) expend little energy during daily activities compared to pelagic fish such as skipjack tuna. The amount of food consumed by goosefish and skipjack tuna of the same weight is not likely similar since their metabolic rates differ (Gooding, et al. 1981).

Within the same species smaller fish eat more food than larger fish (i.e., when calculated on a weight of fish versus weight of food consumed basis). The stomachs of small fish are also larger than those of large fish (i.e., on a weight of stomach tissue to whole fish weight basis) and tend to contain more food per gram of fish (Bowman 1980B; 1980C). During years when large numbers of juveniles dominate the population, the consumption of the population may be much more than during years when the population is made up of older mature fish; because of this, consumption estimates should be derived for different sized fish separately. Ultimately the population structure by size should be considered when determining consumption for the population.

Predator behavior

Red hake, white hake, cusk, and tilefish are among the species known to spend part of the day in burrows or depressions on the bottom

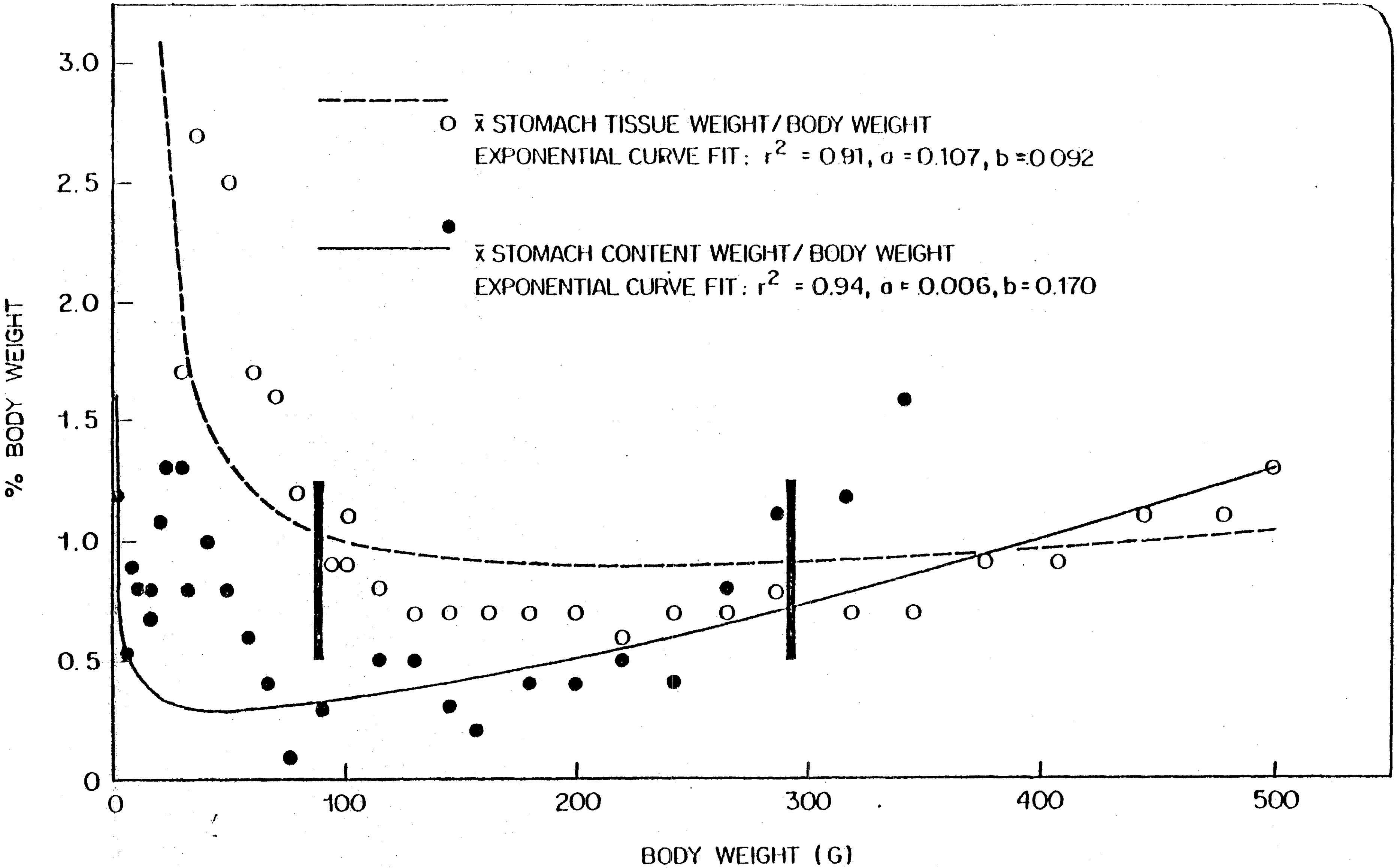

Figure 4. Percentage body weight made up by the stomach tissue weight and the stomach content weight of different size silver hake. Area enclosed by solid lines represents more than 80% (excluding juveniles) of the silver hake population (fish 2-7 years old), based on survey data. Stomach tissue weight/fish length and stomach content weight/fish length data were fit to an exponential curve (form $y=ae^{bx}$). The data are presented in terms of body weight for illustrative purposes.

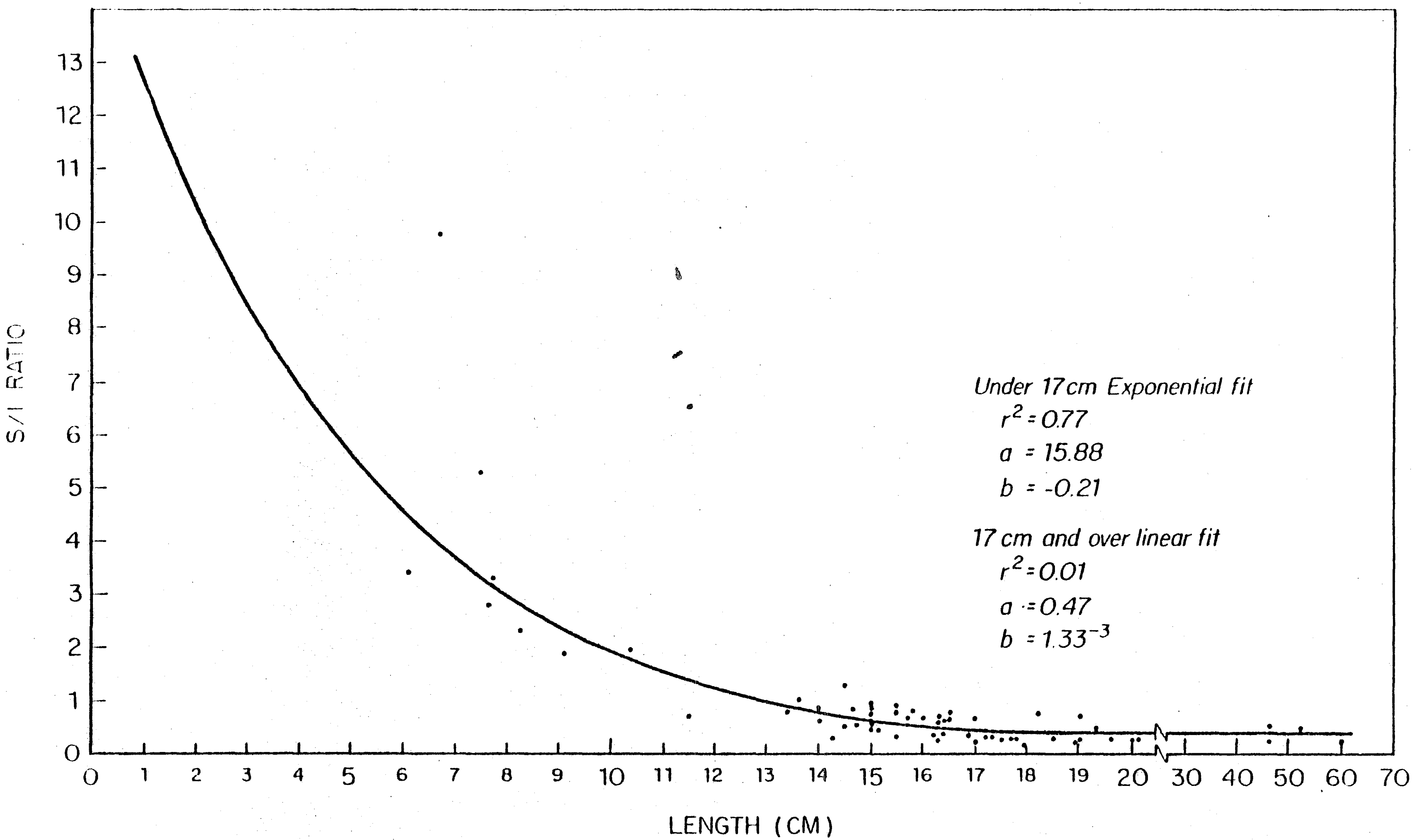

Figure 5. Illustration of the relationship between the weight of stomach(S) and intestine(I) in haddock Note the relative increase in the weight of the intestine compared to the stomach as fish increase in size. (unpublished data, Bowman, R. E., Nat. Mar. Fish. Serv., Woods Hole Laboratory, Woods Hole, MA 02543).

(personal communication, Joseph Uzmann 1981[2]). If fish enter these areas principally when they have full stomachs, and they are less available to bottom trawls when located there, their stomach contents may be underestimated because only fish with mostly empty of partly full stomachs are likely to be caught. The reverse effect may occur for species which are more susceptible to being caught when they have full stomachs. Several flatfish species may belong in the latter category because they are readily caught as they lie on the bottom after feeding (Bowman 1980A).

Parasites and disease

Fish behavior and food consumption may be altered by various kinds of parasites and diseases. Fin rot or ectoparasites around eyes or other sensory organs may affect fishes' behavior (Kelly and Barker 1965). Large numbers of internal parasites such as nematodes, trematodes, cestodes, and acanthocephalans have been observed in many species (personal observations). For example, yellowtail flounder intestines have been observed to be filled with acanthocephalans. The food required to feed parasites is a net loss to the amount of food taken in by fish. There is a possibility that the growth and activity of fish are affected by heavy infestation with parasites.

Intra- and interspecific interactions

Aggregations of several species of predators and one species of prey usually lead to the more adept species of predators obtaining the most food (personal observation). Within populations smaller fish tend to feed after large fish (personal observation). The feeding interactions

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[2] Joseph Uzmann, July 1981, Nat. Mar. Fish. Serv., NEFC, Woods Hole Laboratory, Woods Hole, MA 02543.

between species and within species are probably most evident when prey is limited.

Second order foods

Prey taken by fish which then themselves become prey are released in the stomachs of the larger predators. Since there is no method for indicating which predator ate each particular organism, all prey are usually included in the diet of the larger fish (personal observation). Therefore some organisms listed as prey may not have been directly eaten by its identified predator.

Bioluminescence

During hours of darkness prey species may detect bioluminescent flashes of light caused by attacking predators and escape predation. Some species of fish may avoid (or be attracted to) fishing trawls as they are towed through the water during times when bioluminescence is prevalent; thereby biasing catches.

PHYSICAL

Weather conditions

During storms, periodicity in the feeding of fish is interrupted (personal observations). Immediately after storms fish tend to feed intensively. Predator and prey behavior differences during and after storms can affect the results of feeding studies.

Light intensity

Daylight and darkness, cloud cover, fog, and pollution affect light intensity. Since light intensity governs to a large extent feeding periodicity in many species which depend on sight for obtaining their food, it likely influences the quantity of food found in their stomachs.

Depth

Some bottom living fishes whose distribution extends over wide depth ranges have been shown to feed less intensively in the deeper extension of their range (Bowman 1980B; 1980C). The abundance of many benthic organisms is also known to decline with an increase in depth (Wigley and Theroux 1976). Samples collected in deep water should be treated separately for most species, unless the samples represent a particular species which is principally confined to deep water.

Temperature and salinity

Temperature affects digestion rate and consumption in fish (Olla and Studholme 1975; Elliott and Persson 1978). Water temperature (and salinity) also determines the distribution of many organisms. Short- and long-term fluctuations in water temperature or salinity cause organisms to move, die, or interact differently. Freezing of water masses in winter, or extreme heat in summer, may kill many organisms utilized as food by fish. Warm or cold water mass movements (see Smed 1977) may bring organisms with them or remove organisms from certain areas. Movements of large water masses may also cause the distribution of organisms to shift. Warm core eddies may have similar effects. Predator-prey interactions can potentially be heavily influenced by such water movements.

Turbidity

Storms, waves, tidal action, and warm core eddies tend to cause suspension and movement of bottom sediments. Clams, scallops, and other organisms often seen on beaches immediately after storms is evidence of the substantial bottom movements which occur during storms. Subsequent to disturbances of the bottom the benthos are likely more susceptible to predation. Gardner (1981) observed that turbidity significantly reduces feeding rates in fish.

Oxygen depletion

When dissolved oxygen levels are low, mass mortality may occur among many benthic organisms. Asphyxiated organisms such as clams have been eaten in large quantities by fish in areas off New Jersey during periods of oxygen depletion (personal observation, 1976). The frequency of occurrence of this type feeding phenomenon, or how it affects food data is unknown.

River runoff

River runoff acts as a source of nutrients for marine food webs (Kinne 1970). Variations in runoff between years may affect predator-prey relationships. River runoff may also carry pollutants, increase turbidity, decrease salinity and cause an increase or decrease in the water temperature, all of which can affect the food chain.

Bottom type

Bottom type determines to a large extent which predator and prey populations are found in an area (Wigley and Theroux 1976). Bottom type likely influences the type and quantity of food consumed in different areas for many species.

INDUCED

Sampling

Sampling equally in areas of high and low predator (and prey) density can bias stomach content data. For example, if the northern edge of Georges

Bank is the population center for a species such as haddock, and few haddock are found in Southern New England (or on another part of Georges Bank); and if haddock are sampled equally in both areas; the combined data would probably underestimate the quantity of food they eat and the types of food most important in their diet. Combination of stomach content data collected over such wide geographic ranges must be treated with caution.

Inexperienced personnel aboard ship are not always aware of sampling procedures. Until corrected, people sometimes sample only stomachs with food in them. Empty stomachs don't seem important to people unfamiliar with the feeding ecology of fishes (personal observation). Large fish tend to be sampled more frequently than small fish because they are easier to handle and their stomachs contain large prey items which can be identified immediately (personal observation). Random collections are difficult to attain without close supervision. Sampling design should be attentive to collection methods for insuring samples are collected properly.

Samples are collected from fish caught at different temperatures, depths, and areas, and during various seasons and years. Since the same population, or part of the population of a particular species is not necessarily sampled during each cruise,the food data may not be directly comparable.

Improper identification at sea of species belonging to sympatric pairs such as red and white hake, silver and offshore hake, and little and winter skate may affect the types and quantities of food recorded for these species, especially for the smaller size fish.

Fewer samples are sometimes obtained at stations where many fish are caught (or where stations are close together) than at stations where catches are light (personal observation). The reason for this is because there is much less time available to excise stomachs when catches are large (considerable time is spent sorting, weighing, and measuring the catch).

Thus more stomachs may be collected from areas outside population centers and the more typical predator-prey interactions may be underrepresented.

During storms lack of trawling or poor health among personnel may result in few samples being collected; the effect on food data is unknown.

Artificial predation

Discarded fish (mostly small or "trash" fish), squid, and scallop viscera may be directly eaten by fish as it falls to the bottom, or after it arrives there (Wigley 1965; Bowman 1975). If stomach collections include fish which ate discarded organisms, artificial food webs may be constructed (and abnormal quantities of food may be recorded). A secondary effect of discards is that they attract organisms on the bottom which may then in turn be preyed upon by fish in the vicinity. Piles of discarded squid on the bottom have been reported to attract large numbers of worms, amphipods, and other organisms (personal communication, Joseph Uzmann, 1981[2]).

Over-exploitation of selected species by directed fisheries, or general overfishing, reduces predation pressure on organisms utilized as prey. During such periods prey may rapidly multiply, or could be available in large numbers to remaining fish. Ultimately the entire food web may undergo radical changes. Profound effects on food webs in fresh water systems are known to be caused by overfishing (Stroud and Clepper 1975), and it has been suggested that overfishing also causes large-scale changes in marine systems (Edwards and Bowman 1979).

Damage to bottom living organisms or destruction of their habitat results from operations such as trawling and dredging. Animals damaged as they pass through the netting of trawls and dredges, or crushed as the fishing gear passes over them, become readily available food for fish. Small burrows and other types of shelters are also destroyed by fishing operations, and the organisms which occupy them likely become vulnerable to predation when their habitats are destroyed.

Lobster pots attract an assemblage of fish and other organisms which feed on the lobster bait and use the pots for shelter. Estimates of the quantity of bait used for lobstering each year are substantial, and the bait is an artificial input into the food web. Many predators and prey are influenced by lobster pots, especially in areas which are intensively fished (personal communication, Joseph Uzmann, 1981[2]).

Regurgitation and ingestion in trawls

Regurgitation of stomach contents by fish caught during deepwater tows is common when they are brought to the surface from the bottom (personal observation). Fish, such as silver hake, red hake, white hake, and goosefish often have everted stomachs or severely hemorrhaged esophageal tissue; fish with these characteristics are usually not sampled. However, fish without signs of regurgitation are sampled, and the number of these fish which may have regurgitated their food is unknown.

Swallowing of fish or other materials while predators are in the cod end of the trawl occurs. For example, when goosefish are removed from the trawl their mouths are often full of fish, some of which have been partly swallowed. Squid may bite other squid and fish when they are caught, since many organisms have squid bites when they are taken from trawl catches which include squid. Fish scales and sand are commonly found in the stomachs of many species. Visual observations of bottom trawls being towed show that large quantities of fish scales and sand trail the trawl in the water column. It is likely that fish in the cod end swallow some of this material. The effect of these phenomena on food data is undetermined.

Data analysis

Data presentation such as percentage weight, percentage occurrence, or percentage volume may result in particular prey groups or quantities of prey being over- or underemphasized. Percentage weight data is often biased toward fish or other large prey items, while percentage occurrence information tends to indicate small organisms such as copepods or amphipods are more important in the diet. Volumetric data often includes large quantities of liquid or organisms composed mostly of water which are of little dietary value.

Terms such as an "empty stomach" are not always well defined in food studies. Stomachs examined at the Woods Hole Laboratory are considered empty when no material, or only unidentifiable material weighing less than 0.001 g, is found in them. Parasites found in the stomachs are treated as prey. Terms such as full, one-half full, etc. have been found to be unreliable measurements and should not be used in most circumstances.

Individuals analyzing stomach contents sometimes have difficulty identifying prey organisms. Animals whose specific names are in question should be sent to appropriate specialists for positive identification.

Sensitivity of weighing instruments is important for quantitative stomach content studies. Prey items eaten by smaller size fish are often recorded as "trace" (i.e., <0.001 g at the Woods Hole Laboratory). Since many food items eaten by small fish may be recorded as trace, quantitative information on these fish may be underestimated (small fish being either juveniles or fish species small in size).

Errors when weighing (may occur at the balance or when recording weight information), keypunching, and running computer programs used to summarize the data have been encountered at the NEFC. Further errors may be injected into the data during final summarization and typing.

Station information and benthic codes used for compiling food data at the NEFC sometimes contain errors which are then incorporated into the feeding information. Strata tow numbers, station numbers, and benthic prey codes may be changed without corresponding changes being made to the feeding ecology data base. The effects of these changes have been noted in subsequent summaries of food data at the NEFC. Quality control programs for large long-term data bases are necessary.

Catchability

Various trawl types and configurations catch different species and quantities of fish. For example, bottom trawls with chain sweeps catch more silver hake during daylight hours than similar trawls equipped with roller gear (Bowman and Bowman 1980). One may infer from this that a particular portion of the silver hake population is not available to bottom trawls utilizing roller gear during the daytime; and if fish are not consistently caught in fairly equal numbers both in daylight and during the night the quantity of food eaten by silver hake may be over- or underestimated depending on their feeding periodicity. Another example can be seen in the catchability of semi-pelagic trawls. Many groundfish species tend to lie on the bottom when digesting their food, and are off bottom when feeding. Semi-pelagic trawls may tend to catch feeding fish which have relatively empty stomachs. Since day-night differences in the catchability and feeding of many species are well documented, sampling should always be conducted 24 h/d (Bowman 1980A).

Variability in the fishing power of vessels used for food studies may influence stomach content data. Different vessels towing similar trawls may catch different quantities of fish (Sissenwine and Bowman 1978). One reason for this may be that large ships tend to be more stable in rough seas, and consequently when trawling they fish more effectively. Smaller vessels are most effective at catching fish during fair weather. Even during optimal conditions for fishing, different vessels towing identical trawls may catch different quantities of fish. Ship stability, ship noise, towing methods and speed, haulback procedures, and general fishing experience of the captain and crew can lead to different size catches. Ultimately this indicates that the stomach content data could be influenced since different portions of the fish population(s) may be sampled (see Byrne et al., MS 1981, for a fairly complete treatise on factors affecting variability in trawl catches).

Inshore and offshore movements of sampling vessels are often dependent on weather conditions. During times of the year when offshore winds predominate, ships tend to fish close to shore in daylight and offshore at night. As a consequence of this fishing strategy, samples collected during a particular time of day, and in different areas, may not be representative of the area sampled.

The effect of trawling on the stomach contents of fish caught at the beginning of a tow, compared to those of fish caught at the end of a tow, are unknown. Rapid digestion, evacuation, or regurgitation may occur in fish retained in the trawl throughout the tow.

Preservation

Digestion of food continues after fish are caught. Fish caught at the beginning of a tow and left on deck for periods of up to one hour, before their stomachs are removed, are regularly sampled during bottom trawl surveys. In some instances the total elapsed time before stomachs are preserved may be close to two hours. The effects on the stomach contents during such extended periods are unknown. A comparison of the stomach contents of fish which were frozen whole with others whose stomachs were preserved in formaldehyde showed that the stomach contents of the fish which were frozen (and thawed for examination) contained more liquid and less solids than stomachs placed in preservative (personal observation). Apparently food continues to break down in stomachs during the freezing (and thawing) process. Freezing appears to be an unsatisfactory method of preservation for food studies. The effect of formaldehyde (and other preservatives) on fish length and weight when fish are preserved whole, or on stomach contents is seldom considered.

Pollution

Pollution affects the behavior of predators and prey. Material such as oil can coat organisms and thereby cause erratic movements or nervous system disorders. Studies have demonstrated that fish will eat contaminated organisms (Bowman and Langton 1978). Fish, in some instances, select contaminated prey over uncontaminated organisms (Blackman 1974). Because of potential biomagnification of contaminants through the food web, fish feeding behavior can ultimately be affected.

Pollutants may lead to a vareity of diseases in predator and prey populations. Subsequently, fish feeding data could be influenced in terms of the types and quantities of prey eaten.

CONCLUSIONS

I have shown that many factors can influence the results of any fish feeding study. In most instances individual studies provide information of limited scope. Some investigations only provide information on the types of food eaten; others may describe when or how much food a fish eats. Many of the variables described in this paper can be eliminated depending on the particular study undertaken; others cannot. Information presented here on some of the known and potential causes of variation in food data hopefully will be beneficial to investigators designing new research projects on the feeding of fishes.

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