

Prey selection based on predator/prey weight ratios for some northwest Atlantic fish

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ABSTRACT: As part of the development of a compartmental ecosystem model of Georges Bank, the characteristic ratios of predator-prey weights for 11 northwest Atlantic fish were calculated to aid in the empirical identification of trophic linkages. Distribution functions of preference scores demonstrate differences in prey preference ($SCORE_j = \ln \left(\frac{w_i}{w_j} \right)$; where w_i = predator weight; w_j = prey weight). The mean of each distribution shows the predominant relative size ratio between the predator and its prey. The standard deviation of each distribution measures the degree to which the predator concentrates on prey of this size. A plot of the mean preference scores and their standard deviations places different species into feeding groups or niches which are consistent with the observed diet of the predators.

INTRODUCTION

Size as a controlling factor in prey preference by fish is well documented for a number of marine and freshwater species (Levings, 1974; Moore and Moore, 1976; Ross, 1977; Helfman, 1978; Keast, 1978). Prey size preference is also central to the concept of optimal foraging which is based on the premise of a maximization of energy return to the predator for each prey encounter (Werner and Hall, 1974; Krebs and Davies, 1979). However, factors such as prey abundance and prey species composition must also be considered (Griffiths, 1975).

A predator-prey size ratio has been used to quantify the relation between North Sea cod and dab and their prey (Ursin, 1973). The analytical technique utilized by Ursin was to calculate the ratio of predator and prey weight according to the formula $\ln \left(\frac{w_i}{w_j} \right)$; where w_i = predator weight; w_j = prey weight. In this report, the same analytical methods were employed to evaluate the predator-prey size relations and simplify the diversity of species interactions for 11 species of northwest Atlantic fish. These relations were needed as input for a multispecies predator-prey simulation model of Georges Bank which is under development by the National Marine Fisheries Service, Northeast Fisheries Center (NEFC).

METHODS

The food habits data utilized in this analysis were collected as part of a large-scale study of the food of northwest Atlantic fish. The feeding preference data was collected as part of the NEFC's MARMAP (Marine Resources Monitoring, Assessment and Prediction) program (Sherman, 1980; MARMAP Contribution MED/NEFC 82-45). The scope and general methods of the study were described in Langton et al. (1980). The predators used for the food habits data set were a randomized subsample from the Northeast Fisheries Center's research vessel bottom trawl surveys. The fork length of each predator was measured at sea and converted to weight using unpublished NEFC length-weight equations (pers. comm., R. Bowman, NEFC). Predator stomachs were preserved in formalin at sea and individually analyzed in the laboratory. There, the number of individuals (n_k) per prey type and the total weight of each prey type (Σw_k) were recorded. To estimate the individual weight of the prey, an arithmetic mean was calculated ($\bar{w}_k = \frac{\Sigma w_k}{n_k}$ for the k^{th} prey group). There was bias in these calculations since no attempt was made to correct prey weights for the degree of digestion. In some cases, if the number of prey items could be accurately determined (e.g. fish prey and some crustaceans), individual weights, rather than means, of those particular taxa were recorded and used in this analysis.

Prey size preferences of the various predators were

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described in terms of prey weight relative to predator weight. The relative size of each individual prey organism in each predator's stomach was calculated as the ratio of the predator to prey weight and each ratio was designated as a SCORE. Predator and prey sizes varied over such a wide range, that a logarithmic ratio of sizes was used. Thus, each score was calculated at the $\ln(w_i/w_j)$, where w_i and w_j = individual predator and prey weights, respectively. If a score = $\ln(w_i/w_j)$ = 7.0, this meant that the predator was about 1,000 times heavier than a prey item in its stomach ($e^{7.0} = 1,096.6$). Scores greater than 7.0 indicated that the fish had consumed smaller prey and, conversely, lower scores showed that larger prey were consumed relative to the predator. In most cases, only mean weights of a

given prey organism were available, since each prey type was weighed in aggregate, resulting in identical scores for a given prey type in a given predator stomach. For example, if a predator contained 10 individual prey of a given prey type, than 10 identical SCORES were tallied for this particular prey type. A frequency distribution was then plotted (Fig. 1 A-C) by combining all the scores for each species of fish predator.

The distribution of these feeding preference scores is biased by the actual various prey types in the environment. Ideally, the stomach contents should be corrected for this bias by using empirical estimates of prey abundance. One possible correction would be to divide the observed prey abundance in the predator's stomach by some function of the actual abundance of prey in the field. If predation were a random process, the predator stomach contents should mirror the field prey abundance, and deviations from this would then be an absolute measure of feeding selectivity. Predation probably is not strictly a random process and in any case, the distributions generated by this study were not corrected for prey abundances. The intent of this paper was to demonstrate the relative differences in resource partitioning among a dominant group of northwest Atlantic fish. Had all the prey frequencies in the predator's stomachs been corrected for their actual abundance in the field, the general clustering of feeding types (Fig. 2) would still have been the same, although the scores would be different.

RESULTS

The frequency distribution of a predator species' preference scores can be described by its mean and standard deviation. The mean of this distribution represents the average size relationship between the predator and its prey for all size classes of predator. The standard deviation of this distribution is a relative measure of the predator's prey size selectivity.

Fig. 1 A through 1 C illustrates the frequency distributions of scores for Atlantic cod *Gadus morhua*, silver hake *Merluccius bilinearis* and yellowtail flounder *Limanda ferruginea*. The curve for yellowtail flounder, for example, is shifted to the right of that for Atlantic cod since its prey are relatively smaller than those of the cod. The silver hake curve tends to shift to the left, indicating a selection of prey that is relatively larger than the cod's prey.

The scatter of scores in the distributions in Fig. 1 is a measure of the size selectivity exhibited by a predator relative to the preferred mean size ratio. Feeding selectivity is inversely related to standard deviation of the prey score; a small standard deviation indicates a

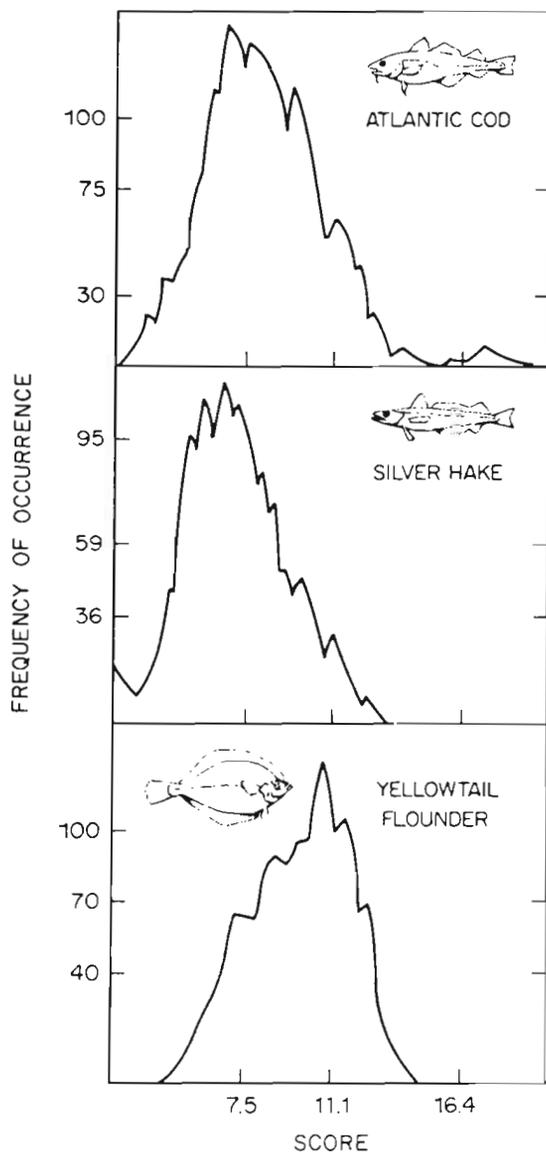


Fig. 1 A-C. Frequency distributions of predator/prey scores for Atlantic cod, silver hake and yellowtail flounder

strong preference for a narrow range of prey sizes and vice versa. In terms of increasing prey selectivity, the 3 fish were ranked: Atlantic cod (S.D. = 2.37), silver hake (S.D. = 2.11), yellowtail flounder (S.D. = 1.98). Sample sizes are different in all 3 distributions (silver hake = 1,791, Atlantic cod = 1,545, yellowtail flounder = 656), and therefore, the heights of the distribution were not of comparative value.

A plot of the mean scores against the standard deviations indicates the predator's mean 'target size' and the selectivity within the prey size spectrum, thus defining a size specific feeding niche for each of the 11 predators (Fig. 2). The values plotted in Fig. 2, considered in relation to the actual composition of the diet of the eleven predators, can be arrayed into 4 general feeding groups or niches. The gadids themselves form 3 groups. Group A includes white hake *Urophycis tenuis* and silver hake, which are both major fish predators (Langton and Bowman, 1980). For each of these species, over 80 % of their diets were found to be fish

(on a percentage weight basis during the years 1973 through 1976).

Group B includes Atlantic cod, red hake *Urophycis chuss* and spotted hake *Urophycis regius*. Red and spotted hake are mixed feeders, relying on both crustaceans and fish (Langton and Bowman, 1980). The cod's feeding habits are size dependent and, as it grows, it quickly changes from a crustacean feeder to a piscivore (Langton, 1982). In this sense, these 3 gadids qualify as mixed feeders.

Group C includes the pollock *Pollachius virens* and haddock *Melanogrammus aeglefinus*. Although the larger specimens of these 2 species include fish as prey, they both feed most heavily on invertebrates for the major part of their life (Langton and Bowman, 1980). Haddock prey on many benthic species, but polychaetes and amphipods are numerically very important. In contrast, pollock consume large numbers of mysids and euphausiids.

The 4 flatfish species cluster in the lower right half of Fig. 2 in a rectangular-shaped grouping. This cluster's position, on the right half of the graph, indicates that the flatfish feed on relatively small prey. The low standard deviations also indicate stronger size selective feeding among the flatfish than among the gadids. The positions flatfish occupy within this rectangular cluster also coincide with their known feeding habits. For example, the witch *Glyptocephalus cynoglossus* and yellowtail flounder both cluster together in the far right of Fig. 2, and both these fish have similar diets of amphipods and polychaete worms (Langton and Bowman, 1981; Langton, 1983). American plaice *Hippoglossoides platessoides* and fourspot flounder *Paralichthys oblongus* are grouped in the mid-portion of the figure but their diets differ significantly. American plaice prey extensively on echinoderms, while fourspot flounder consume a variety of crustaceans, squid and fish (Langton and Bowman, 1981).

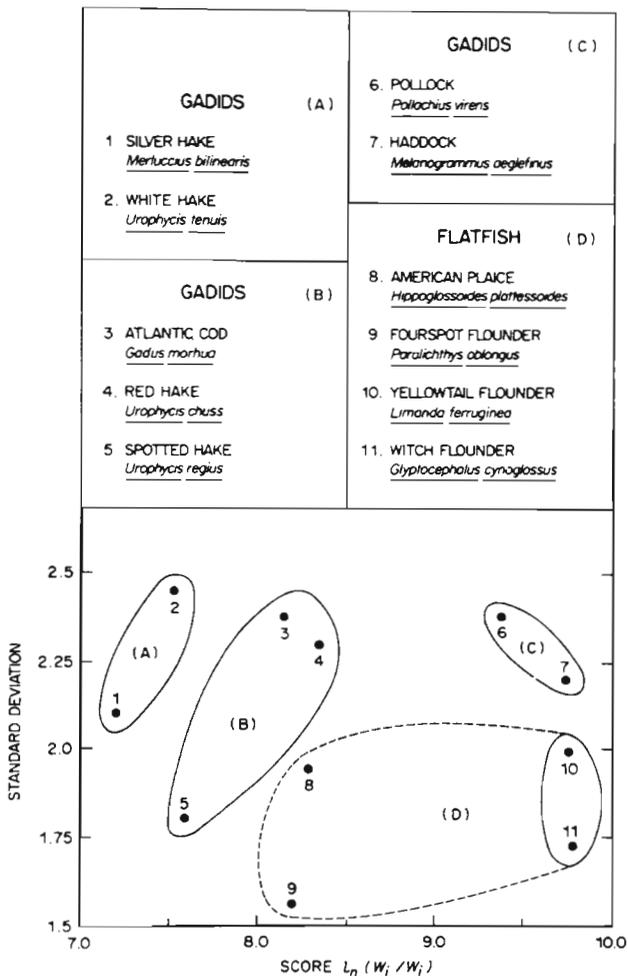


Fig. 2. Plot of mean predator/prey scores versus standard deviation. Groupings suggest feeding niches (see text for details)

DISCUSSION

The use of predator-prey size ratios to quantify feeding types works well for selected northwest Atlantic fish (Fig. 2) when the ratio data are interpreted in accordance with the species composition of the diet. Other techniques, such as gut morphology (DeGroot, 1971; Tyler, 1973) and diet composition (e.g. Langton and Bowman, 1980, 1981; Langton, 1982) have also been utilized to categorize fish feeding types. However, each of these techniques is a simplification of biological observations and they all have their limitations. The limits of the present technique are in part a result of the process of feeding and digestion and the resulting inaccuracy in measuring prey size. In cases

where a predator does not consume the prey as a single item, or when the prey is broken by the labial teeth or pharyngeal teeth as it is being swallowed, individual prey weights are meaningless unless fish and benthic samples are collected at the same station for comparative and/or reconstructive purposes. A good example of this problem occurs with American plaice. These fish are highly predaceous on the sand dollar *Echinarachinus parma* (> 60 % of the diet by weight) and brittle stars (Langton and Bowman, 1981), and fragments of these prey are often found in the stomachs. One less apparent problem, but one that is potentially more difficult to solve, is the differential effect of digestive enzymes on various sizes and types of prey. In this study, if a prey could be identified and counted, it was included in the calculations as a 'whole' prey item, thus these data overestimate the actual predator-prey size ratio. Unless reconstructed prey are used, based on some measure of a digestion resistant body part, there is little that can be done to eliminate such errors. If, on the other hand, exceedingly large sample sizes are collected and only 'fresh' prey saved at sea for weighing in the lab, then predator-prey weight ratios may more accurately reflect the actual prey particle size spectrum. Note that 'fresh' is a subjective measure and in this context would not be the result of feeding in the trawl. This may be the only valid technique for soft-bodied benthic animals such as polychaete worms.

This analysis has assessed the food habits data for each predator independent of predator size. Since fish were randomly collected from the catches for stomach content analyses, the predator-prey weight estimates are representative of the various populations. An evaluation of scores by size class for each predator would, no doubt, present a different picture. This would be true for species such as Atlantic cod, that show a size-related shift in feeding habits. Size class analysis would permit partitioning of predators into more feeding categories.

An interesting aspect of this study is the correlation between predator-prey size scores and the predator's feeding habits. Langton and Bowman (1980) identified the various species of gadids as piscivorous, mixed feeders or invertebrate predators. The same patterns were found in this paper (Fig. 2), although the fish were collected in different years (1969-1972 vs. 1973-1976). There appears to be a high degree of constancy in fish food habits since Grosslein et al. (1980) also found that northwest Atlantic fishes showed the same general feeding habits in 2 different periods (1963-1966 vs. 1973-1976) during which relative species abundance varied significantly.

Another aspect of this study concerns the use of this empirical information when modeling ecosystems with variable trophic linkages (Andersen and Ursin, 1977;

Hahm, 1982). Let $f(i, j)$ be a function that resembles the normal distribution. The function is:

$$g(i, j) = \exp [-(1/n)(w_i/w_j) - N_i]^2/2\sigma^2)$$

where w_i = predator weight; w_j = prey weight. The parameter N_i is the mean value of the predator-prey size ratio distribution for the i^{th} predator (Fig. 1A-C), and σ^2 is the variance of each i^{th} distribution. Each predator will have characteristic mean and variance parameters. Given a predator of weight w_i , it is possible to assess the vulnerability of different prey (w_j). When the predator-prey weight ratio is equal to N_i (the preferred size ratio), $g(i, j)$ equals 1.0. The farther the size ratio is from the preferred size, the smaller $g(i, j)$ is. The function $g(i, j)$ varies between 1 and 0. The Andersen and Ursin (1977) North Sea model and a Georges Bank model (Hahm, 1982), employ this function to determine the strength of linkages between compartments.

An examination of the x-axis of the frequency distribution of mean predator-to-prey scores (Fig. 2) reveals a range of values between 7 and 10. The immediate suggestion is that on an average, the predators are consuming prey that are one to twenty thousandth (1×10^{-3}) their own weight. This erroneous conclusion can be traced to the fact that the prey items found in the predator stomachs do not occur in equal numbers in the natural environment. Platt and Denman's (1978) documentation of field prey abundance suggests that the food habit data are biased heavily to the small prey classes.

The cod in a North Sea study were found to have mean preference scores of roughly 5.0 as opposed to the 8.0 of this study (Ursin, 1973). The difference can be traced to Ursin's assumption that the abundance of the prey categories could be estimated by Platt and Denman's (1978) exponential-fit regression model relating prey abundance to prey size. Using similar assumptions shifts the x-axis values to range between 4 to 7, suggesting that the predators consume prey items one fiftieth to one thousandth ($1/50-1/10^3$) their own size. This correction is necessary when using these parameters in a simulation model. In this paper, the score groupings are presented without making the correction, since the purpose of the article was to illustrate the quantitative feeding groupings without making any assumptions concerning the relative abundance of the various prey types in the northwest Atlantic Ocean.

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