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Estimates of Gastric Evacuation and Consumption Rates in Little Skate (*Raja erinacea*)

G. A. Nelson and M. R. Ross

Department of Forestry and Wildlife Management
204 Holdsworth Hall
University of Massachusetts
Amherst, Massachusetts 01003
USA

Abstract

Estimates of prey consumption by fishes are important for understanding predator-prey interactions in multispecies fish communities. Laboratory studies of gastric evacuation and twenty-four hour diel samples of stomachs were used to estimate daily consumption of benthic prey by little skate (*Raja erinacea*) on Georges Bank. Gastric evacuation was determined at 10°C using polychaetes (*Glycera* spp.), krill (*Meganictiphanes norvegica*), clams (*Spisula solidissima and Placopecten magellanicus*) and sand lance (*Ammodytes dubius*), and at 16°C using polychaetes (*Nereis* spp.) and shrimp (*Palaemonetes* spp. and *Crangon septimspinosus*) as prey. Evacuation data for polychaetes, krill, clams and sand lance at 10°C are modelled best by linear and square root equations. At 16°C, exponential and logistic models described the evacuation data for polychaetes and shrimp best. Consumption was estimated using models by Eggers (1979), Elliot and Persson (1978), and Pennington (1985). Estimates of seasonal daily ration (expressed as a percentage of body weight (BW)) ranged from 0.47% to 1.74% BW for little skates 10-19 cm in length to 0.08% to 0.77% BW for skates 50-59 cm in length. Annual consumption ranged from 0.085 kg $fish^{-1}$ yr^{-1} for 10-19 cm little skates to 0.860 kg $fish^{-1}$ yr^{-1} for 50-59 cm little skates.

Introduction

In the northwest Atlantic, both species abundances and composition have changed dramatically over the last twenty years. Many economically-important demersal species like Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and yellowtail flounder (*Limanda ferruginea*) have declined to historically-low abundance levels due to heavy exploitation by distant water fleets prior to 1975-1976, and domestic vessels thereafter. Skate populations were similarly depleted by distant water fleets (Murawski and Almeida, MS). Domestic harvesting of skates has, until recently, been insignificant (<3000 mt/year). Recent development of a bait and food market has triggered an increase in landings; in 1991, total nominal catch reached about 11,300 mt. Despite this increase in domestic harvesting, elasmobranch abundances, particularly winter skates (*Raja ocellata*) and little skates (*Raja erinacea*), have increased to historically high levels, and these species now represent a higher proportion of the exploitable biomass on Georges Bank (NEFC/NMFS, 1989; Murawski and Idoine, MS).

Little is understood about the interspecific interactions between elasmobranchs and demersal fishes. There appears to be a substantial overlap in food resource utilization within and between the groups, (Grosslein et al., 1980), and fisheries biologists and managers are concerned that food resources once available to demersal fishes for production are possibly being consumed by the more abundant elasombranchs (Murawski and Idoine, MS; Murawski and Almeida, MS). A reduced availability of food to the groundfishes may negatively impact production dynamics, such as growth and fecundity, and potentially impede the recovery of the groundfish stocks (Murawski and Idoine, MS).

The impact of predation on food resources can be examined by estimating the proportion of prey production that is consumed by a predator population, and inferring from this proportion whether the abundance of a prey species is regulated by this predator (Collie, 1987). This method requires prey production values, diet composition, and estimates of consumption for predator populations. Production rates of benthic prey and diet composition of little skate are available from the literature, but consumption estimates have not been derived for this skate species.

To study the impact of the increasing skate population on Georges Bank food resources, quantitative estimates of daily ration by little skates are needed. In this study, we derived consumption estimates using daily ration models that require measurements of stomach content weights and rates of gastric evacuation. Additionally, we conducted experiments to derive gastric evacuation rates for little skates using five prey types at two temperatures.

Methods and Materials

Gastric Evacuation

Little skates were captured from Georges Bank, Massachusetts Bay, and Nantucket Shoals during National Marine Fisheries Service and Massachusetts Division of Marine Fisheries survey cruises in March, June, and September of 1991 and March of 1992 using otter trawls. All skates were kept in live wells until they were transported to the NOAA Aquarium in Woods Hole, MA.

In the laboratory, skates were held in two 2.4 m X 0.91 m X 0.39 m fiberglass troughs with a 1.5 cm layer of coarse gravel covering the bottom of each trough.

Trough water was filtered with a commercial pool sand filter at a rate of 277 l/h. Temperature was maintained by two 1/2 h.p. chilling units, and a small inflow of Woods Hole Harbor seawater. Photoperiod was produced with commercial flourescent lights controlled by an electric timer. Timer adjustments were made every two week to simulate natural photoperiod.

Skates that survived the handling process began to feed within 2-3 weeks after capture. Skates were fed Atlantic herring (*Clupea harengus*) *ad libitum* three to four times a week. Uneaten food was usually removed the next morning. Meals were supplemented ocassionally with squid (*Loligo pealai* and *Illex illecebrosus*), polychaetes (*Nereis* spp. and *Glycera* spp.), shrimp (*Paleomonetes* spp. and *Crangon septemspinosa*), and clam tissue (*Spisula solidissima* and *Placopecten magellanicus*).

Experiments were conducted at 10$\pm$1°C and 16$\pm$1°C. Water temperature was adjusted to the desired level, and skates were acclimated for 2-3 weeks. A day prior to the start of each treatment run, troughs were divided in half with plastic mesh partitions which allowed easier identification of individual skates. Each half contained about 6-9 skates.

An experiment began after skates were starved for three days at 10°C and two days at 16°C. Each skate was fed a preweighed meal by placing it in front of or under its rostrum. At 10°C, meals consisted of one polychaete worm (*Glycera* spp.) cut to 1.24-1.75 g ($\bar{X}$=1.53 g), thawed whole krill (*Meganistaphanes norvegica*) 0.88-1.5 g ($\bar{X}$=1.14 g), sand lance (*Ammodytes dubius*) 4.40-9.07 g ($\bar{X}$=4.82 g), or clam foot/muscle (*Spisula solidissima* and *Placopecten magellanicus*) 1.51-4.70 g ($\bar{X}$=2.74 g). At 16°C, meals consisted of one polychaete worm (*Nereis* spp.) 1.42-1.88 g ($\bar{X}$=1.70), or 6-11 whole, thawed shrimp (*Paleomonetes* spp. and *Crangon septimspinosus*) collectively weighing 1.64-1.86 g ($\bar{X}$=1.74 g). Meal weights used at both temperatures, except for those of sand lance, approximated the average weight of stomach contents found in wild skates during late spring and late summer months. Skates usually consumed a meal voluntarily within 15 sec to 2 min. All fish were fed within 30-45 min from the start of the feeding routine. Time at ingestion and identity of each skate, using natural markings or dorsal fin clips, was recorded.

Stomach contents were removed at selected time intervals by gastric lavage. At times after feeding, a skate was selected and anaesthetized in a bath of metomidate (dose:0.5 g/l) for 45 sec to 2 min or until it was relaxed enough to handle. The individual was then carefully placed on a 61 cm X 30.5 cm plexiglass board, and its mouth centered over a 6 cm X 3 cm square cut at one end that allowed access to the mouth for lavaging. The skate was secured to the board, measured to nearest cm, and weighed with the board to the nearest 1 g. Total wet weight was determined by subtracting the weight of the board (wet) alone from fish and board weight.

Stomach contents were lavaged by inserting a 3-mm diameter medical feeding tube into the stomach of each skate. A metal bar supported the chondrocranium from inside the mouth as it tended to compress the esophagus and block water flow out of the stomach. 30 cc of seawater were then forced into the stomach using a 60 cc syringe. Contents were then aggitated by repeatedly extending and compressing the plunger until the remaining 30 cc was dispensed. This procedure was repeated until food remains were no longer found in the water stream. All particles were collect in a pan below, removed from the bolus, blotted dry, and wet weight determined to the nearest 0.01 g. Each skate was returned to its appropriate trough and allowed to recover for two weeks before it was reused in other experiments. Treatments were repeated 2-3 times to obtain sufficient data for analyses, except for the experiment using sand lance as prey; in this case, all skates were sacrificed and stomach contents removed by dissection.

Linear, square root, and exponential models were fitted to weight of food remaining in the stomachs, expressed as a percentage of the initial weight consumed, and hours after feeding to obtain evacuation relationships for each temperature and prey type. The following model forms were used:

Linear

$$(1) \quad Y = A + B * X$$

Square Root

$$(2) \quad \sqrt{Y} = \sqrt{A} + B * X$$

Exponential

$$(3) \quad Y = A * \exp^{(-B*X)}$$

where Y is the percentage of the initial food weight remaining, X is hours after feeding, A is the estimated Y intercept, and B is the regression coefficient.

The linear and square root models were fitted to the data by least squares method using SAS linear regression (PROC REG), and the exponential model was fitted using SAS nonlinear regression (Proc NLIN) with the optional derivative free method (DUD). Residual mean squares (RMS) and plots of the residuals were used to evaluate the fit of each model. The RMS of the square root model could not be compared to the other models and subsequently, r^2 values were calculated for the linear and nonlinear models as follows:

Linear

$$(4) \quad r^2 = 1 - \frac{RSS}{TSS}$$

Nonlinear

$$(5) \quad r^2 = 1 - \frac{RSS}{(n-1) * Var_w}$$

where RSS is the residual sum of squares, TSS is total sum of squares, Var_w is the variance of the dependent variable, and n is sample size. r^2 values were adjusted for the number of parameters in each model (Sokal and Rohlf, 1981) by

$$(6) \quad adj.\ r^2 = 1 - (1 - r^2) * \left(\frac{n-1}{n-k-1}\right)$$

where k is the number of regression parameters.

Consumption Estimates

Estimates of total daily consumption (in g) and ration (consumption expressed as a percentage of body weight; BW) were made using modified models of Eggers (1979) and Elliot and Persson (1978) for exponential evacuation, and Pennington (1985) for square root evacuation. Daily consumption and ration were calculated for five prey groups (Arthropoda, Annelida, Cnidaria, Mollusca, and Pisces) consumed by little skates using the prey-specific rates obtained in the gastric evacuation experiments (Cnidaria was assumed to be digested at the same rate as clams). Daily consumption was estimated in a single step using Eggers' model, which takes the form

$$(7) \quad \sum_{j=1}^{np} C_j = R_j * (\overline{S} * P_j) * 24$$

where C_j is daily consumption of prey type j by a skate, R_j is the instantaneous rate of gastric evacuation for prey type j, S is the mean stomach content weight over a 24 hr period, and P_j is the proportion of prey type j found in the stomachs of little skates. Total daily consumption was calculated by summing C_j over j. Daily ration was calculated by substituting the mean stomach weight/mean body weight ratio, multiplied by 100, for $\overline{S}$ in equation 7.

The Elliot and Persson (1978) and Pennington (1985) models require that a series of fish stomachs is collected at selected intervals of time over a 24 hr period. The mean stomach content weight at each sample period is then used to estimate consumption during the time between samplings. These models take the forms

Elliot & Persson

$$(8) \quad \sum_{i=1}^{T} \sum_{j=1}^{np} C_{i,j} = \frac{((P_{t+1,j} * \overline{S_{t+1}}) - (P_{t,j} * \overline{S_t}) * \exp^{(-R_j*((t+1)-t)}) * R_j * ((t+1)-t)}{1 + \exp^{(-R_j*((t+1)-t))}}$$

Pennington

$$(9) \quad \sum_{i=1}^{T} \sum_{j=1}^{np} C_{i,j} = R_j^{0.5} * \frac{P_{t+1,j} * \sum_{k=1}^{n} \sqrt{S_k}}{n} + \frac{(P_{t+1,j} * \overline{S_{t+1}} - P_{t,j} * \overline{S_t})}{(t+1)-t}$$

where $C_{i,j}$ is the consumption of prey type j during interval i, $P_{t+1,j}$ and $P_{t,j}$ are the proportions of prey type j found in the stomachs of little skates at sampling times t+1 and t of interval i, $\overline{S}_{t+1}$ and $\overline{S}_t$ are the mean stomach content weight at sampling time t+1 and t, S_k is the stomach content weight of the kth stomach, R_j is the instantaneous evacuation rate of prey type j, T is the number of sample intervals, np is the number of prey types, and n is the number of stomachs collected at sampling time t+1. Total daily consumption was calculated by summing over j and i. Similarly, daily ration was estimated by calculating the mean stomach weight/body weight ratio, multiplied by 100, for each time interval, and substituting these values for $\overline{S}_{t+1}$ and $\overline{S}_t$ in equations 8 and 9.

Stomach Sampling

Stomach content weights used in the consumption models were collected on Georges Bank (Figure 1) during National Marine Fisheries Service bottom trawl surveys, Bureau of Land Management cruises in 1982 and 1983, and a National Marine Fisheries Service gear comparison cruise during January of 1991.

The National Marine Fisheries Service collected stomachs of little skates during their spring and autumn groundfish surveys from 1973 to 1980 (See Grosslein, 1969 and Azarovitz, 1981 for more detail on survey design). Sampling during spring and autumn occurred generally in March to May and September to November, respectively, using a #36 or # 41 Yankee otter trawl with a 1.25 cm stretched mesh codend liner was towed approximately 3.5 kn for 30 min over a 24 hr period. No more than 10 stomachs of little skates were sampled from each trawl and not from consecutive stations unless numbers were low (see Langton et al. 1980). Due to the low numbers collected annually, stomach samples from 1973 to 1980 were combined for this study.

The purpose of the Bureau of Land Management study was to investigate the impact oil exploration and oil rig discharge might have on the benthic community of Georges Bank. Little skate stomachs were collected quarterly from tows made every 3 hr during 1982 and 1983 from sites 5 and 10 (Figure 1) established on Georges Bank. Five hundred and seventy-eight of 1100 little skate stomachs were subsampled randomly in 1990 and transferred to 50% isoproprYl alcohol to facilitate sorting.

The NMFS gear comparison cruise was designed to estimate catchability differences between Polyvalent and BWV otter trawl doors. A 9.2 x 9.2 km^2 grid was mapped on the northeast peak of Georges Bank (Figure 1) and tow stations randomly selected within 0.5 x 0.5 km^2 blocks. A 30 min tow was made every 1.5 hr at 3.5 kn using a #36 Yankee otter trawl. Otter trawl doors were switched after 24 hr.

Length and sex of each skate was determined at sea, the stomach removed, individually labeled, and preserved in 10% formalin during all cruises. Stomach contents collected by NMFS from 1973 to 1980 were sorted in the laboratory to the lowest taxonomic level possible, and weighed (wet) to the nearest 0.01 g. All stomach contents of little skates collected during the BLM study were first weighed to the nearest 0.001 g, and then sorted to the lowest taxonomic level. Individuals of each identifiable species were counted, blotted dry, and weighed. Stomachs collected during the NMFS gear comparison cruise were transferred to 50% isoproprYl after 48 hrs of preservation, and contents only weighed to the nearest 0.001 g; no further sorting was done.

The mean weight of stomach contents, including empty stomachs, was calculated by season for little skates grouped into 10 cm length-intervals. Further, mean stomach weight was also calculated from tows within each successive 3-hr period for use in the Elliot and Persson and Pennington models.

The proportion of the stomach contents that each prey group comprised was calculated by dividing the weight of a prey group summed over all stomachs by the total weight of all prey groups. Since samples collected during the NMFS gear comparison were not sorted, the proportions from the NMFS winter cruise were applied to the stomach weights in the consumption models.

Total weight of each skate was calculated from length using the length-weight relationship

$$\text{Log } W = -2.5875 + 3.2066 \text{ Log } L$$

where W is weight in grams and L is total length in cm (Waring, 1980). These estimated values were used to calculate the mean weight of little skates.

Quarterly and annual estimates of consumption were calculated for each length interval by averaging the daily ration estimates from the Eggers and Elliot and Persson models over all databases, and interpolating between seasons (i.e. calculating the area under the curve). The same estimates were calculated for the Pennington model. If an estimate of daily consumption for a given length interval was missing in either winter or summer, the estimate for the following season was used in the computation.

Results

Little skates ranged in size from 33 cm to 51 cm ($\bar{X}$= 44 cm) and weight from 218 g to 737 g ($\bar{X}$= 573 g). Individuals used in the experiments were mostly female (82%).

At 10°C, the gastric evacuation of polychaetes (Figure 2A) is adequately described by the square root model, as indicated by the high adjusted r^2 value (Table 1). The residuals for this model show a random pattern that also support the appropriateness of the fit. Although adjusted r^2 values were high, residual plots of the other models show varying patterns of non-randomness, suggesting lack of fit and possible violations of the least square fitting procedures. The estimated Y-intercept of the square root model (97.2%; Table 1) is close to the initial meal percentage (100%) offering further support for the adequacy of this model.

Low RMS and high r^2 value indicate the linear model (Table 1) fit the krill data best (Fig. 2B). Residual plots show a near-random pattern for this model, but systematic patterns for the other models. The linear model also estimates the initial meal percentage better than the square root or exponential models (Table 1).

Gastric evacuation relationship for sand lance (Figure 2C) is best described by the linear model (Table 1). However, the plot of the residuals for this model shows a non-random pattern. Points clustered between 5 and 20 hours (Fig. 2C) suggest the pattern may be due to a lack of data at the beginning and end of the digestion process. The Y-intercept estimated by the linear model is lower than the initial meal percentage (Table 1), indicating this model greatly underestimates the weight of food remaining in stomach during initial stages of digestion. The best prediction of the Y-intercept is given by the square root model (87.0%). Residuals of the square root model are more randomly distributed than the linear model, which implies a better fit regardless of the higher RMS and lower adjusted r^2 values.

Low numbers of data collected on clams (Fig. 2D) did not allow adequate diagnosis of the model fits. However, the exponential model has the highest r^2 (Table 1), but also the higher RMS. Due to low sample size, residual plots are of little use to judge the adequacy of each model. The Y-intercept of the exponential model predicts the initial percentage closer than the other models.

At 16°C, the exponential model fits the polychaete data best (Figure 3A). The RMS value is low compared to the linear model, and the adjusted r^2 value is highest for all models (Table 1). Plots of the residuals of all models show some degree of non-randomness, but those of the exponential model are closer to being random. Although this model over-estimates the initial meal percentage by 31.9% (Table 1), suggesting substantial over-estimation of food weight during early hours of digestion, this deviation is intermediate to the other models.

Of the three evacuation forms, the linear model best fits the shrimp data (Figure 3B; Table 1). However, residual plots of this and the other models show systematic patterns, suggesting that these models are inappropriate to describe the gastric evacuation data for shrimp in spite of good fits. Subsequently, a logistic model

$$(10) \quad Y = 100 - A / (1 + \exp^{(B * (X + C))})$$

was fit to the shrimp data using SAS nonlinear regression. A higher r^2 value, lower RMS (Table 1), and random residual pattern show that the fit of the logistic model is better than the linear, square root, or exponential models.

At 10°C, krill and clams digested faster than polychaetes and sand lance. Evacuation rates (B parameter of each model; Table 1) are highest for these prey items regardless of model type. At 16°C, polychaetes digested faster than shrimp (Table 1).

The differences in evacuation rates between prey types and temperatures are also apparent when predicted times required to fully evacuate the meal were examined (Y = 0%). At 10°C, time at 0% for krill and clams (Table 2) was reached 10-40 hours faster than that for polychaetes and sand lance. Similarly, polychaetes digested 9-39 hours faster than shrimp at 16°C, depending on model type (Table 2).

The type of model selected to describe the evacuation of polychaetes differed between 10°C and 16°C. The square root model is more appropriate at 10°C, whereas the exponential model is more appropriate at 16°C. Regardless of model type, polychaetes at 10°C digested almost ten times slower rate than those at 16°C (Table 1).

Evacuation rate (R) and temperature (T in °C) relationships for the exponential and square root models were derived using the prey-specific rates at 10°C and rates of the exponential and square root model fitted to the shrimp data at 16°C, excluding data before six hours after feeding. This assumed that the remaining data approximated the evacuation trajectory for a thin-shelled invertebrate (see Discussion). The relationships were

Exponential

$R = 0.012 * \exp^{(0.171*T)}$, $r^2=0.757$, n=5

Square Root

$R = 0.045 * \exp^{(0.175*T)}$, $r^2=0.778$, n=5.

Consumption Estimates

Seasonal mean bottom temperature at capture sites of little skates are listed in Table 3.

Mean weights of stomach contents of little skates varied between databases, depending upon season and length interval. Mean stomach content weight of the BLM dataset for all length intervals was generally higher than the mean of those skates collected during NMFS cruises in spring and autumn (Table 4). In winter, mean weight of stomach contents of skates $\geq$ 40 cm was heavier than the mean weights for skates during the BLM cruises. Stomach content weight increased in little skates as length increased in all databases (Table 4).

Gastric evacuation rates used in the consumption models were adjusted for temperature using evacuation-temperature relationships (see Results) and seasonal mean temperature of bottom water at capture sites of little skates. Each rate predicted by the evacuation-temperature relationships was further adjusted to account for differences between evacuation rates of prey types. The original prey-specific rates at 10°C were subtracted from the rate predicted at 10°C by the equations, and these deviations were then added to rates predicted at other temperatures. These adjusted rates were used in the consumption models.

Estimates of daily consumption and ration derived from the Eggers model are given in Table 4. In general, consumption estimates were lowest in winter and spring and increased in summer and autumn. For winter and spring, daily ration ranged from 0.07 to 0.14 g/d for 10-19 cm little skates to 0.64 to 3.64 g/d for skates 50-59 cm in length. Summer and autumn estimates were lowest for 10-19 cm little skates, ranging from 0.11 to 0.37 g/d, and highest at 4.58 g/d for 50-59 cm skates. Daily ration varied seasonally and declined in all seasons as length increased. Little skates 10-19 cm generally consumed the highest %BW in any season (winter and spring - 0.47% to 1.06% BW/d; autumn - 1.74% BW/d) whereas estimates for 50-59 cm skates were lowest (winter and spring - 0.08% to 0.47% BW/d; summer and autumn - 0.22% to 0.77% BW/d)(Table 4).

Estimates of daily consumption and ration using the Elliot and Persson (1978) and Pennington (1985) models were made for the 30-39 cm, 40-49 cm, and 50-59 cm length intervals from the NMFS food habits and BLM databases, and 40-59 cm length range from the NMFS gear comparison in spring because sufficient sample sizes were only available for these categories. Estimates from the Elliot and Persson model were closest to those calculated from the Eggers model (Table 5). The Pennington square root model produced higher estimates of both daily consumption and ration (Table 5).

Most food consumed by little skates were arthropods in all seasons, but diversity of prey items increased as the skates grew in length (Table 6). Molluscs and fish became increasingly important in the diets of little skate $\geq$40 cm. Similar to the estimates for total daily ration, the Pennington model produced higher estimates than the Eggers and the Elliot and Persson methods.

Consumption estimates for the Egger and the Elliot and Persson models are lowest in the winter-spring quarter, and highest during the summer-autumn quarter for all lengths. Annual consumption ranged from 0.085 kg $fish^{-1}$ yr^{-1} for skates 10-19 cm to 0.860 kg $fish^{-1}$ yr^{-1} for skates 50-59 cm in length. The quarterly estimates made from the Pennington model are similar. Annual consumption could not be calculated for the Pennington model because of lack of data.

Discussion

Based on comparisons of the residual mean squares, r^2 values, and plots of residuals, models that describe the decline in stomach contents for little skates varied among prey types and temperatures. At 10°C, the linear or square root model best fit the data and predicted the Y-intercept for polychaetes, krill, and sand lance (low sample size for clams precluded accurate assessment of model fits). At 16°C, the exponential and logistic models explain a high proportion of the variation in the polychaete and shrimp data, respectively. In our study, sample sizes were somewhat low (n<24), making model difficult in some cases. Lack of data near the end of the digestion process, especially at 10°C, also may have influenced the model fits.

Gastric evacuation has been shown to vary with different prey types in teleost and elasmobranch fishes. Polychaetes are digested exponentially in winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoides*), and oceanpout (*Macrozoarces americanus*) (MacDonald et al., 1982), as are thin-shelled or chopped invertebrates in chain dogfish (*Scyliorhinus canicula*), Atlantic cod (*Gadus morhus*) and brown trout (*Salmo trutta*) (Tyler, 1970; Elliot, 1972; MacDonald et al., 1982, MacPherson et al., 1989). Linear, exponential, and square root models describe evacuation data of fish as prey in whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), black rockfish (*Sebastes melanops*), Atlantic cod, spiny dogfish (*Squalus acanthias*), chain dogfish, and walleye (*Stizostedion vitreum*) (Swenson and Smith, 1973; Jones, 1974; Jones and Green, 1977; Brodeur, 1986; Bromley, 1988; MacPherson et al., 1989; Bromley, 1991). With the exception of shrimp as prey, our results are similar.

A logistic model best fits the shrimp data, indicating that an initial lag occurrs in the digestion process. This lag may be explained by the body makeup of the shrimp; *Palaemonetes* spp. and *Crangon septemspinosus* are benthic crustacea that possess thick, chitinous exoskeletons that probably resists attack by digestive enzymes, and a lag in the digestion results. It took approximately five hours before the gastric enzymes dissolved through the flexible membranes between the exoskeletal plate and the energy-rich protein could be catabolized. In contrast, krill are pelagic crustaceans with very thin exoskeletons; digestion was linear. No initial lag was evident because the digestive enzymes rapidly dissolved the thin integument.

Initial lags in digestion have been argued as artifacts of different methodological approaches. Prolonged starvation prior to feeding and force-feeding of fishes has been shown to delay the initiation of digestion (Fange and Grove, 1979). Wet weight determinations of stomach contents can also affect the choice of models (Daan, 1973; Brodeur, 1986). Medved (1985) found an initial lag phase during digestion of soft blue crabs (*Callinectes sapidus*) and Atlantic menhaden (*Brevoortia tyrannus*) for fed to the sand bar shark, but contrary to his conclusions, flushing the stomachs before feeding and excess handling (each shark spent <10 min out of water) could have produced the initial lag in digestions due simply to stress. In our study, starvation was not extensive, and force-feeding or handling was not performed because skates voluntarily consumed food when presented meals. Although method effects due to wet weight determination of digested food cannot be ruled out completely, lack of initial lags in the evacuation relationships of the other prey items suggests that it is not an artifact for the shrimp data.

Differences in digestion rates among prey items where found. At 10°C, krill and clams digested faster than polychaetes and sand lance, and polychaetes digested faster than shrimp at 16°C. Several studies have demonstrated that prey type may influence digestion and evacuation rates (Elliot, 1972; Jones, 1974; Fange and Grove, 1979; MacDonald et al., 1982; Brodeur, 1986; MacPherson et al., 1989; Bromley, 1991) due to prey-specific differences in body composition. Composition of surface integument, fat content of tissue, and internal skeletal structure may delay initial or complete digestion (Windell, 1967; MacDonald et al., 1982; MacPherson et al, 1989; Bromley, 1988). Results from this and other studies suggest the order of digestibility of prey types is: small or thin-shelled invertebrates < fish and polychaetes < thick-shelled or squid-like invertebrates.

Different model forms were selected for polychaetes at the two treatment temperatures. The square root models fit the polychaete data best at 10°C; whereas the exponential model describes the relationship adequately for polychaetes at 16°C. This difference may not be solely related to temperature, but may be explained by the preprandial condition of the polychaetes. *Glycera* spp. survived the cutting process by contracting their circular muscles tightly which stopped bleeding, and were alive when fed to the skates. In contrast, *Nereis* spp. did not possess this ability and were dead when presented to the skates. The coelom of this species was probably exposed to digestive enzymes freely, and digested proteinous matter rapidly. The marked differences in evacuation rates between the two temperatures (rate at 10°C was ten times slower than 16°C) could be explained by these disparate conditions. The evacuation curve at 16°C is probably not a true representation of what might occur in the wild.

Many researchers have argued extensively that the appropriate evacuation form is the exponential model (Tyler, 1970; Elliot, 1972; Jobling, 1981). Low sample sizes, high variation in data, varying experimental designs, and limited species coverage have contributed to the confusion over the biologically-correct model. One aspect of experimental design that largely contributes to this confusion is the condition of prey items fed to fishes. Preparation of food in evacuation experiments has been extremely varied in the literature. Prey are either pelletized (Elliot, 1972; MacDonald et al., 1982), cut into pieces (Tyler, 1970; polychaetes in this study), or served whole (MacPherson et al. 1989; this study). This conclusion reinforces the need to standardize experiments so that results are directly comparable. Until that time, the search for a biologically-realistic model of gastric evacuation will continue, and generalizations about the digestion process will probably continue to be conflicting.

Consumption Estimates

Seasonal estimates of daily consumption and ration for little skate differed among datasets. These differences are attributed to spatial and temporal variations as well as sampling design. Little skates were collected from sites throughout Georges Bank during the NMFS food habit cruises, and daily consumption and ration estimates represent an average for little skates throughout the Bank for the 1973 to 1980 period. In contrast, the BLM samples and NMFS gear comparison samples were collected at specific locations, and estimates reflect the true temporal and spatial nature of the data. By chance, the prey availability may have been higher at these sites, and is simply reflected in the mean weights of stomach contents.

Seasonal estimates of daily ration derived from the Eggers (1979), Elliot and Persson (1978), and Pennington (1985) models ranged from 0.47% to 1.74% BW/d for 10-19 cm little skates to 0.08% to 0.77% BW/d for 50-59 cm little skates. For elasmobranchs in general, estimates of daily ration have ranged from 0.5% BW/d to 1.4% BW/d for spiny dogfish, 0.93 % to 1.32% BW/d for sandbar sharks, and 3.0% BW for the shortfin mako shark (*Isurus oxyrinchus*) (Holden, 1966; Jones and Green, 1977; Stillwell and Kohler, 1982; Medved et al. 1988). In teleosts, Durbin et al.(1983) estimated daily ration for Altantic cod and silver hake (*Merluccius bilinearis*) to range from 1.42% to 1.66% BW/d and 1.82% to 4.65% BW/d, respectively. Other studies have produced estimates in teleosts as low as 0.1 % BW/d (Doble and Eggers, 1978) to as high as 28% BW/d (Spanovskaya and Gryygorash, 1977). Although not directly comparable because daily ration varies with temperature and fish weight, estimates made for little skate appear to be within the range for elasmobranchs, but at the lower end of those for teleost, indicating little skates do not consume as much as this diverse group.

Annual estimates of consumption for little skate on Georges Bank increased as the fish grew larger. Consumption ranged from 0.085 kg $fish^{-1}$ yr^{-1} for 10-19 cm little skates to 0.860 kg $fish^{-1}$ yr^{-1} for little skates 50-59 cm in length. Values for little skates $\geq$40 cm are similar to 0.48 to 0.82 kg fish-1 yr-1 estimated for 31-35 cm yellowtail flounder on Georges Bank by Collie (1987).

Daily consumption and ration estimates produced by the Eggers (1979) and Elliot and Persson (1978) models may be biased. The gastric evacuation experiments indicate that prey in the stomachs of little skates do not decline exponentially, but in a linear or square-root fashion. Also, the exponential model predicts a much slower rate of evacuation than the linear and square root models. This would translate to lower estimates of consumption by little skates. Thus, daily consumption and ration estimates derived from models assuming an exponential decay of prey items may represent minimum estimates for little skate. However, the daily consumption values derived from the Pennington square-root model were close to those estimated by the Eggers and the Elliot and Persson, suggesting these estimates are not grossly biased.

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Table 1. Estimated parameters and associated statistics of linear, square root, and exponential models fitted to the gastric evacuation data of little skate (Raja erinacea). RMS = residual mean square.

Model	Parameters A	Parameters B	Parameters C	Adjusted r^2	RMS
		10°C			
		Polychaete (n=24)			
Linear	93.61	-2.777		0.933	37.94
Square Root	97.21	-0.191		0.941	0.157
Exponential	100.16	-0.049		0.924	41.38
		Krill (n=21)			
Linear	103.00	-5.123		0.907	41.53
Square Root	111.30	-0.354		0.894	0.23
Exponential	112.41	-0.079		0.844	65.52
		Sand Lance (n=17)			
Linear	77.43	-2.468		0.890	47.97
Square Root	87.05	-0.217		0.876	0.43
Exponential	86.95	-0.056		0.830	69.19
		Clam (n=7)			
Linear	92.18	-4.912		0.801	83.70
Square Root	93.89	-0.309		0.838	0.26
Exponential	103.76	-0.094		0.884	146.90
		16°C			
		Polychaete (n=18)			
Linear	66.99	-7.556		0.727	211.26
Square Root	78.32	-0.838		0.885	0.91
Exponential	131.76	-0.414		0.937	45.77
		Shrimp (n=17)			
Linear	114.37	-6.612		0.900	112.97
Square Root	134.10	-0.525		0.852	1.12
Exponential	121.46	-0.095		0.753	261.28
Logistic	111.51	-0.356	-10.74	0.945	57.52

Table 2. Estimates of the time required to entirely evacuate the stomach contents predicted by the models fitted to gastric evacuation data for little skate.

	Time (hrs) required to reach 0%		
	Linear	Square Root	Exponential
		10°C	
Polychaete	33.7	51.6	94.0
Krill	20.1	29.8	59.8
Sand Lance	31.4	43.0	79.7
Clam	18.8	31.4	49.4
		16°C	
Polychaete	8.9	10.6	11.8
Shrimp	17.3	22.1	50.5

Table 3. Mean temperature of bottom water at capture for little skate (*Raja erinacea*) from National Marine Fisheries Service (NMFS) and Bureau of Land Management (BLM) cruises.

Cruise	Period	Season	Temperature (°C)
NMFS	1973-1980	Spring	5.3
		Autumn	13.1
	1991	Winter	6.5
BLM	1982-1983	Winter	6.3
		Spring	7.0
		Summer	10.4
		Autumn	10.1

Table 4. Numbers (n), mean weight of stomach contents (S), mean body weight (BW), Egger (1977) model estimates of daily consumption (DC; in grams) and daily ration (DR; expressed as a percentage of body weight) of little skate (*Raja erinacea*) by length interval collected during National Marine Fisheries Service (NMFS) and Bureau of Land Management (BLM) cruises.

Period	Season	Length	n	S (g)	BW (g)	DC (g)	DR (%BW)
			NMFS				
73-80	Spring	10-19	62	0.05	10	0.05	0.54
		20-29	22	0.47	84	0.42	0.49
		30-39	22	0.80	248	0.61	0.25
		40-49	187	1.24	558	1.20	0.22
		50-59	18	0.83	806	0.64	0.08
	Autumn	10-19	31	0.12	21	0.37	1.74
		20-29	29	0.35	69	1.45	2.11
		30-39	32	0.59	211	1.65	0.78
		40-49	149	1.21	557	3.45	0.62
		50-59	42	1.60	778	4.58	0.59
1991	Winter	30-39	2	0.25	224	0.28	0.12
		40-49	107	1.61	568	1.79	0.31
		50-59	80	2.12	790	1.85	0.23
			BLM				
82-83	Winter	10-19	17	0.06	15	0.07	0.47
		20-29	9	0.33	79	0.32	0.41
		30-39	18	0.49	198	0.51	0.26
		40-49	31	1.82	597	1.43	0.24
		50-59	2	0.75	725	0.77	0.11
	Spring	10-19	61	0.11	13	0.14	1.06
		20-29	27	0.25	89	0.31	0.35
		30-39	59	0.56	215	0.66	0.31
		40-49	139	1.39	577	1.60	0.28
		50-59	18	3.95	768	3.64	0.47
	Summer	10-19	5	0.13	20	0.27	1.33
		40-49	21	2.06	651	3.34	0.51
		50-59	8	3.49	798	6.11	0.77
	Autumn	10-19	5	0.06	18	0.11	0.62
		20-29	49	0.51	84	0.96	1.14
		30-39	27	0.70	237	1.31	0.55
		40-49	50	1.40	595	2.62	0.44
		50-59	2	1.13	749	1.63	0.22

Table 5. Sample size (n) and seasonal estimates of daily consumption (DC) and daily ration (DR) by length interval for little skate (*Raja erinacea*) from the National Marine Fisheries Service (NMFS) and Bureau of Land Management (BLM) databases using Elliot and Persson (1978) and Pennington (1985) models.

Period	Season	Length	n	E & P DR (g)	E & P DR (%BW)	Pennington DR (g)	Pennington DR (%BW)
			NMFS				
73-80	Spring	40-49	187	1.04	0.19	1.32	0.24
		50-59	18	0.61	0.08	0.92	0.11
1991	Winter	40-59	187	1.23	0.16	1.47	0.23
			BLM				
82-83	Spring	30-39	59	1.05	0.28	1.15	0.49
		40-49	139	1.66	0.28	1.68	0.30

Table 6. Estimates of daily ration (in %BW) of prey groups by little skate (*Raja erinacea*) from the Eggers (EG), Elliot and Persson (E&P), and Pennington (PN) models.

	Annelida			Arthropoda			Cnidaria			Mollusca			Pisces		
Length	EG	E&P	PN	EG	E&P	PN	EG	E&P	PN	EG	E&P	PN	EG	E&P	PN
NMFS Spring 73-80															
10-19	0.00			0.53											
20-29	0.04			0.45											
30-39	0.04			0.21						0.00					
40-49	0.01	0.01	0.01	0.20	0.17	0.23	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
50-59	0.01	0.01	0.01	0.06	0.06	0.10				0.00	0.00	0.00	0.00	0.00	0.00
Autumn 73-80															
10-19	0.07			1.67											
20-29	0.53			1.47									0.10		
30-39	0.14			0.57									0.06		
40-49	0.11			0.48			0.00			0.00			0.02		
50-59	0.08			0.44			0.01			0.01			0.04		
Winter 1991															
30-39	0.01			0.12									0.00		
40-49	0.01	0.00	0.03	0.29	0.16	0.19	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
50-59	0.04			0.15						0.01			0.02		

Table 6 contd.

			BLM Winter		
10-19	0.00	0.49			
20-29	0.05	0.36			
30-39	0.02	0.17	0.00	0.05	0.02
40-49	0.02	0.13	0.00	0.00	0.08
50-59	0.01	0.09			0.01
			Spring		
10-19	0.00	1.06			
20-29	0.01	0.33		0.00	
30-39	0.02 0.02 0.03	0.24 0.22 0.42	0.00 0.00 0.00	0.04 0.03 0.03	
40-49	0.03 0.04 0.03	0.18 0.18 0.21	0.03 0.03 0.02	0.03 0.03 0.03	0.00 0.00 0.00
50-59	0.03	0.17	0.05	0.02	0.20
			Summer		
10-19	0.02	1.33			
40-49	0.60	0.20		0.01	0.24
50-59	0.08	0.46		0.03	0.20
			Autumn		
10-19		0.62			
20-29	0.02	1.11		0.00	0.01
30-39	0.02	0.52	0.01	0.01	
40-49	0.04	0.16	0.18	0.01	0.04
50-59	0.12	0.10		0.00	

Table 7. Quarterly and annual estimates of consumption (in kilograms) by little skate (*Raja erinacea*) on Georges Bank using the Eggers (1979) and Elliot and Persson (1978) models, and Pennington (1985) model.

Length	Quarterly Estimates				Annual
	Win-Spr	Spr-Sum	Sum-Aut	Aut-Win	Consumption
	Egger and Elliot and Persson				
10-19	0.006	0.021	0.034	0.023	0.085
20-29	0.027	0.080	0.128	0.094	0.329
30-39	0.046	0.100	0.136	0.106	0.388
40-49	0.106	0.213	0.293	0.241	0.853
50-59	0.115	0.211	0.286	0.248	0.860
	Pennington				
40-49	0.111				
50-59	0.090				

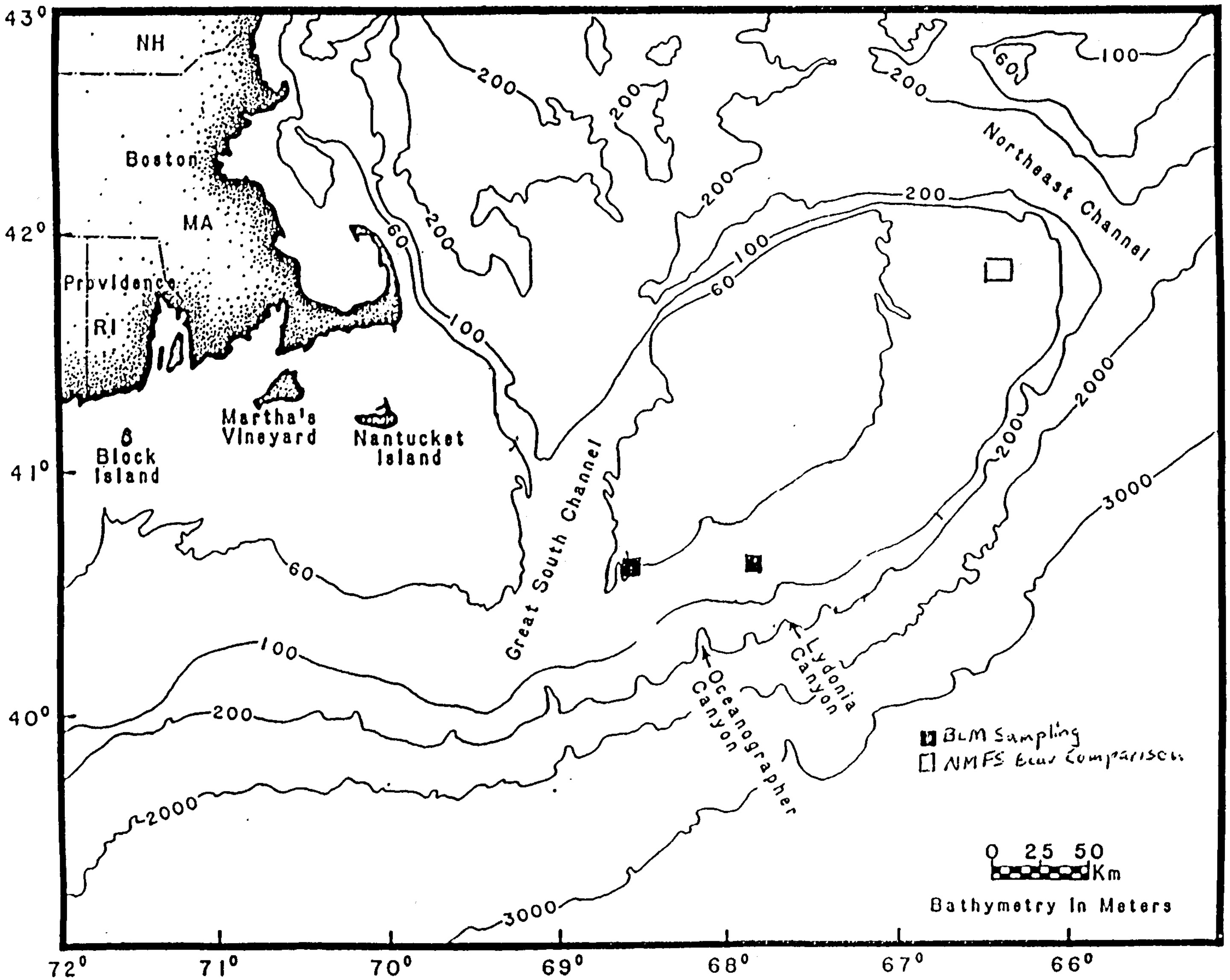

Figure 1. Map of sites where little skate stomachs were collected during the National Marine Fisheries Service gear comparison and the Bureau of Land Management cruises on Georges Bank.

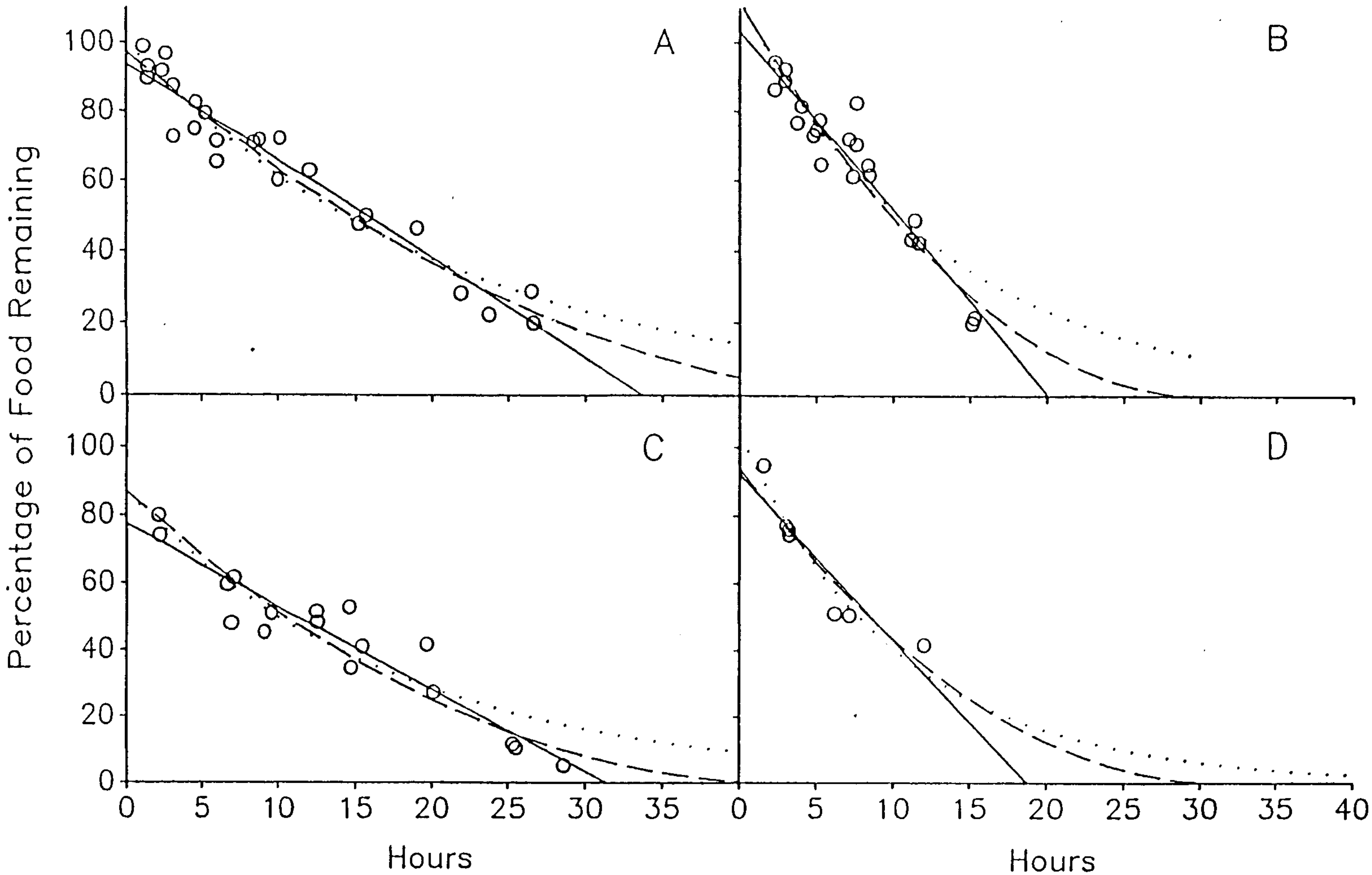

Figure 2. Percentage of food remaining in the stomachs of little skates versus hours after feeding for polychaetes (A), krill (B), sand lance (C), and clams (D), and relationships predicted by the linear (—), square-root (- -), and exponential (···) models at 10°C.

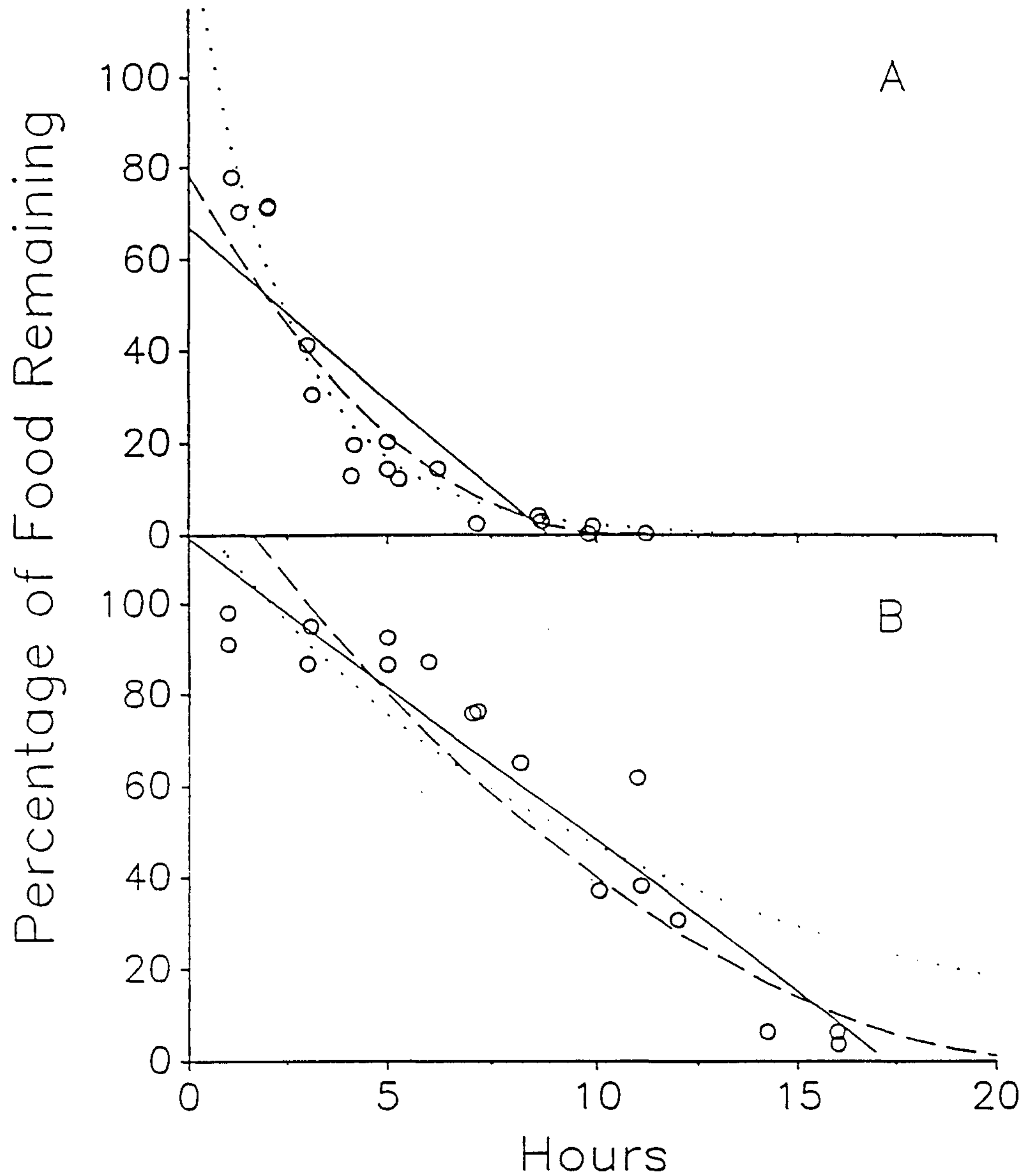

Figure 3. Percentage of food remaining in the stomachs of little skates versus hours after feeding for polychaetes (A) and shrimp (B) , and relationships predicted by the linear (—), square-root (- -), and exponential (•••) models at 16°C