

A Linked Foraging and Bioenergetics Model for Southern Flounder

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Abstract.—Few predation models that simulate effects on prey survival and size structure also predict the corresponding effects on predator growth and size structure. To make this link, we parameterized a bioenergetics model for southern flounder *Paralichthys lethostigma* by conducting a series of respiration and feeding experiments as well as obtaining values from the literature. We then linked the bioenergetics model to an existing size-dependent foraging model for southern flounder feeding on spot *Leiostomus xanthurus* and tested it using data from a pond experiment. Integrating these two models allowed us to investigate the effects of size-dependent interactions on predator growth by making predator growth a function of size-dependent foraging success. The linked model predicts spot effects as well as the original foraging model does, but the accuracy of flounder growth predictions were size-dependent. Predictions of prey survival and size structure were robust and were not greatly affected by slight changes in predator foraging rates, but predictions of predator growth rate were very sensitive to slight changes in predicted foraging rates. This asymmetry in the linked model's predictive ability is derived from the nonlinearity of the prey length–mass relationship and the different currencies used by the foraging component (number of prey eaten) and the bioenergetics component (mass of prey eaten) of the linked model. Because bioenergetics model predictions of growth are inherently sensitive to estimates of food consumption, this asymmetry in ability to predict effects on prey numbers and predator growth will likely be a common feature of similarly linked models.

Predator–prey interactions are one of the strongest biological forces structuring aquatic communities (Paine 1980; Kerfoot and Sih 1987; Carpenter 1988). Predation by fishes is often size-dependent (Brooks and Dodson 1965; Werner and Hall 1974; Mittelbach 1981; Stein et al. 1988; Rice et al. 1993a), and in the laboratory the outcome of an individual pairwise interaction can often be predicted fairly well based on predator and prey sizes (Barker 1991). Changes in the relative size of predators and prey often will affect the magnitude of predation (Rice et al. 1993a, 1993b); in the field, however, expected results are not as straightforward to predict. Both predators and prey have variable size distributions that change through time, depending on the magnitude and variability of their growth rates. Furthermore, growth and size structure of predator populations will be affected by changes in relative sizes of individuals in the prey population (Adams and DeAngelis 1987).

In recent years, theoretical and mathematical modeling approaches to predator–prey interactions have made significant progress (Bulmer 1994; Judson 1994). Individual-based models (IBMs) have

become particularly useful when evaluating interactions for which variation among individuals plays a large role (Adams and DeAngelis 1987; Huston et al. 1988; DeAngelis and Gross 1992), as is the case for size-dependent predation (Werner et al. 1983; Wilbur 1988; Rice et al. 1993a). Most simulation studies of predation have focused on survival of the prey population (e.g., Rice et al. 1993b), although some have focused on the growth of individual predators or the predator population (Stockwell and Johnson 1997; Mason et al. 1998; Hayes et al. 2000). Few, however, have used an IBM to simultaneously predict survival of prey and growth of predators (but see Breck 1998).

The interaction between juvenile southern flounder *Paralichthys lethostigma* and age-0 spot *Leiostomus xanthurus* offers a unique opportunity to develop such a joint approach. Both species spawn offshore and their larvae are transported by currents to estuaries along the coast. There, southern flounder quickly become an opportunistic piscivore, and spot are among the most abundant prey fish (Wright 1989; Fitzhugh et al. 1996). If size-dependent interactions were to have a detectable effect in an estuarine environment, where large numbers of both predators and prey coexist, it probably will be evident in flounder–spot interactions. Predation by southern flounder signifi-

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cantly altered age-0 spot survival and size structure in a replicated pond experiment when flounder were the only predators (Wright et al. 1993). These effects were also predicted using a size-dependent foraging model (Rice et al. 1993a).

In addition to prey mortality, it is important to understand the other outcome of the predation process: predator growth. Ecologists have often focused on estimating or describing fish growth and consumption (Elliott and Perrson 1978; Eggers 1979; Kitchell 1983, Rice and Cochran 1984), and techniques for modeling fish growth are well understood (Hanson et al. 1997). By expanding the foraging model (Rice et al. 1993a) to incorporate an energetics component, we can model flounder growth as a function of individual flounder foraging success. The combination of these two models makes it possible to determine how temperature and initial size distributions of predator and prey affect not only prey survival, but also predator growth. In addition, by simulating predator growth in response to their foraging success, the model drops its dependence on field-derived predator growth rate estimates as initial model inputs.

Here, we first describe parameter estimation of a bioenergetics model for southern flounder. Second, we describe how we linked the bioenergetics model with an existing flounder foraging model (Rice et al. 1993a). Finally, we describe the linked model's predictions, as compared with results from a pond experiment, and discuss potential sources of error in the linked model.

The Bioenergetics Model

Models of fish bioenergetics are well developed (Hanson et al. 1997). The model used in this application is a balanced energy equation for which net growth equals ingested energy minus metabolic costs and other losses; that is,

$$G = C(1 - f - u - s) - (R \cdot \text{ACT}), \quad (1)$$

where G represents both somatic and reproductive growth, C is food consumption, f is proportion of consumption lost due to egestion (feces), u is proportion of consumption lost due to excretion (urine), s is proportion of consumption used in specific dynamic action, R equals resting metabolism, and ACT is an activity multiplier. All variables in equation (1), except ACT , are for daily rates.

We assume consumption is equal to maximum consumption, C_{\max} , which takes into account the size of an organism and the temperature to estimate the maximum amount of biomass a fish can ingest:

$$C_{\max} = a \cdot W^b \cdot f(T), \quad (2)$$

where a is the intercept of consumption (grams of food per gram of fish per day), W is the wet mass of the fish (g), b is the weight-dependent exponent of consumption, and $f(T)$ is a temperature-dependent function (equation 2 in Hanson et al. 1997).

The intercept and weight-dependent exponent for the C_{\max} equation were estimated from data collected through a series of feeding trials (Table 1). Eleven flounder (total lengths [TL] = 149–189 mm, mean = 34.4 g, SE = 2.8) collected from the Neuse River, North Carolina, were individually held in 10-L circular tanks at a National Marine Fisheries Service laboratory in Beaufort and allowed to acclimate for 48 h. All tanks were placed in water baths to maintain 28°C ($\pm 0.4^\circ\text{C}$).

Mummichogs *Fundulus heteroclitus* averaging 2.1 g (range = 0.94–4.74 g, SE = 0.04) were used as prey for all feeding trials. Two mummichogs were placed in each tank to determine if the stress from capture and handling would preclude flounder from eating in a closed environment. Only those flounder that immediately ate both prey fish were used in feeding trials. Flounder were then starved for 24 h before any feeding trials began. At the start of a feeding trial, five mummichogs were weighed to the nearest 0.01 g and placed in a tank containing a flounder. After 24 h, any uneaten prey were removed, weighed, and replaced with five recently obtained mummichogs. Only once did a flounder eat all five fish, so we considered five prey enough to ensure ad libitum feeding. This feeding regime was repeated every day for 1 week, at which time the flounder were starved for 24 h to ensure digestion of all prey; they were then weighed (nearest 0.01 g).

To calculate daily specific consumption, we linearly interpolated between starting and ending flounder mass to determine individual flounder mass on any given day. Data from smaller flounder available from previous feeding trials ($N = 8$, mean size = 2.0 g; Davis 1998) were incorporated into the analysis. Least sums of squares was used to estimate average daily maximum consumption from our data and those of Davis (1998; Table 1; $r^2 = 0.72$).

Respiration rates also vary among species and can have a large effect on estimates of growth (Webb 1978; Hanson et al. 1997). Few data, however, are available for metabolic rates of flatfish. Therefore, we measured metabolism, which typically varies with mass, as follows:

TABLE 1.—Parameter estimates used in the bioenergetics model for southern flounder and their sources.

	Description	Value	Source
Consumption			
<i>a</i>	Intercept for maximum consumption (g·g ⁻¹ ·day ⁻¹)	0.1993	This study; Davis 1998
<i>b</i>	Weight-dependent exponent for maximum consumption	-0.31	This study; Davis 1998
<i>q</i> ^a	Slope for temperature dependence of consumption (<i>Q</i> ₁₀)	2.126	Fit to data in Davis 1998
<i>T</i> _{opt} ^a	Optimal temperature for consumption (°C)	30	Peters 1971; Davis 1998
<i>T</i> _{max} ^a	Maximum temperature for consumption (°C)	40	Peters 1971; Reagan and Wingo 1985
Respiration			
<i>c</i>	Intercept for respiration (mg O ₂ ·g ⁻¹ ·h ⁻¹)	0.018	This study; Taylor and Miller (2001); Carlson ^b
<i>d</i>	Weight-dependent exponent for respiration	-0.1397	This study; Taylor and Miller (2001); Carlson ^b
<i>m</i>	Coefficient for temperature dependence of respiration (°C ⁻¹)	0.0811	Trebitz 1991
ACT	Activity multiplier	2.1	This study
Loss			
<i>s</i>	Proportion of consumed energy utilized in apparent SDA	0.161	Jobling and Davies 1980
<i>f</i>	Proportion of consumed energy (C) lost through egestion	0.104	Beamish 1972
<i>u</i>	Proportion of consumed energy (C) lost through excretion	0.079	Beamish 1974
Caloric Densities			
Pred.	Caloric density of predator (kcal·g ⁻¹)	1.025	Thayer et al. 1973
Prey	Caloric density of prey (kcal·g ⁻¹)	1.094	Thayer et al. 1973

^a Parameters used in the $f(T)$ function, equation 2 in Hanson et al. (1997).

^b J. K. Carlson (National Marine Fisheries Service, Panama City Laboratory, personal communication).

$$R = c \cdot W^d \cdot e^{(m)T}, \quad (3)$$

where R is standard or resting metabolism; W is the mass of the organism; T is the water temperature; and c , d , and m are coefficients (Winberg 1956).

Between December 29, 1997, and January 10, 1998, 16 southern flounder were taken from 350-L tanks where they had been held for several months at 25°C and a salinity of 33‰. Flounder lengths ranged from 143 to 300 mm TL (mean = 220.5 mm, SE = 14.8), and masses ranged from 25.9 to 183.6 g (mean = 75.1 g, SE = 16.0). At the beginning of a respiration trial, a flounder was taken from the holding tank and placed in a 16-L plastic tub, which was immersed in a 25°C water bath. A YSI 6000 oxygen probe mounted through the side of the tub allowed continuous monitoring of the oxygen concentration within the system. After a 15-min acclimation period, oxygen concentrations were measured every 30 s for the first 5 min, after which measurements were taken every 5 min until the concentration neared 4.4 mg O₂/L. Measurements were then taken every 30 s for 5 min. Trials were stopped at this point to prevent

any stress due to low oxygen levels. Duration of trials ranged from 45 min to 2 h and 54 min.

Southern flounder respiration data were also available for a 4.7-g fish (Taylor and Miller 2001) and for a 520-g and a 650-g fish (J. Carlson, National Marine Fisheries Service, unpublished data); these researchers used similar testing methods. We used nonlinear least squares to estimate c and d in equation (3) from these combined data (Table 1; $r^2 = 0.24$).

We used information from the feeding trials described earlier to determine an activity multiplier. Because the maximum consumption curve for which these data were collected plays no role in predicting consumption when growth is known, parameter correlation when using this data set was not a concern. For each individual fish, predicted consumption was matched to the observed consumption by adjusting the activity multiplier. The average activity multiplier was 2.1 (SD = 0.15; Table 1), a value close to what Brett and Groves (1979) call "usual" (2.0) and well within the range used for other fish species (Tytler and Calow 1985).

Because of the large number of parameters needed for this bioenergetics model and the relatively limited flatfish energetics research, some of the less sensitive parameter estimates (Bartell et al. 1986) and some for which no data were available were taken from literature on flatfish other than southern flounder and nonflatfish species. A temperature-dependent function, $f(T)$, was included in the calculations of maximum consumption (see Kitchell et al. 1977) to account for the large effect temperature has on the amount of food ingested (Paloheimo and Dickie 1966; Fonds et al. 1992). Consumption increases with temperature (approximating a slope for temperature dependence of consumption or Q_{10}) up to an optimum temperature, T_{opt} , at which point it declines to zero at T_{max} , usually estimated as the upper lethal temperature. For southern flounder, values for T_{opt} , T_{max} , and q were estimated from data on flounder in Peters (1971), Reagan and Wingo (1985), and Davis (1998; Table 1).

Temperature preference of largemouth bass *Micropterus salmoides* is similar to that of southern flounder and its latitudinal range encompasses that of southern flounder. Therefore, we used the temperature-dependent coefficient for respiration, m , that Beamish (1970) estimated for largemouth bass, as modified by Trebitz (1991; Table 1).

We used the estimate of s determined by Jobling and Davies (1980) for American plaice *Hippoglossoides platessoides* (Table 1). Although not much is known about specific dynamic action in flatfishes, this value falls well within the range determined for other fishes (Warren and Davis 1967; Beamish 1974; Hanson et al. 1997). Similar to s , the proportion of ingested energy lost through egestion and excretion is relatively constant across fish species and has low sensitivity in bioenergetics models. Therefore, values determined for largemouth bass were used (Table 1).

As is usually the case in bioenergetics model development, most available data are used in parameter estimation, leaving few independent data for model validation (Rice and Cochran 1984). In this case, one data set was available to roughly evaluate the ability of the bioenergetics model to estimate consumption from growth (Fitzhugh and Rice 1995).

Over the course of the feeding trial described in Fitzhugh and Rice (1995), total food placed in the tank amounted to 2,484 g, and total food removed from the tank was estimated to be 261 g. Because uneaten food was not measured precisely and at least some was not recovered (G. R. Fitzhugh, Na-

tional Marine Fisheries Service, personal communication), the total amount of unaccounted-for food (2,221 g) probably overestimates flounder consumption.

The consumption of individual flounder was not recorded. Therefore, the flounder bioenergetics model was used to estimate consumption of each flounder using its observed growth as input. Model predictions of consumption for all fish were summed for comparison with total estimated consumption in the experiment. Model predictions (1,751.6 g) were moderately lower than the amount of food from the trial that was not accounted for, which included both food eaten by the flounder and uneaten food that was not recovered. No statistics were performed due to the low sample size (one tank). However, the model works adequately well for comparative studies (e.g., to look at the relative effect of changing water temperature or prey size distribution), where any biases would affect absolute predictions but not relative differences, as is the case for this study.

The Linked Model

Rice et al. (1993a) constructed a size-dependent foraging model to predict the effects of predation by flounder on spot survival and size structure. In their model, initial predator and prey size distributions were generated by drawing the appropriate number of animals from a Gaussian distribution with a specified mean and variance. The growth rate of each prey was determined in a similar fashion, whereas predator growth was an input to the model. We assumed that each spot in a simulation had a daily probability of encountering a flounder. If an encounter occurred, the probability that it resulted in an attack and capture was assumed to depend on the predator-prey size ratio according to a dome-shaped profitability function determined through a series of laboratory experiments (Barker 1991). For a more detailed description of the foraging model, see Rice et al. (1993a).

We linked the foraging model of Rice et al. (1993a) with the bioenergetics model so that output of the foraging model served as input to the bioenergetics model. In this linked model, instead of just deleting a consumed spot from the simulation, the weight of spot consumed by each flounder was used as daily consumption in the bioenergetics model to determine daily growth of each flounder.

The C_{max} function estimates average daily consumption of a flounder fed ad libitum. Thus, consumption by an individual may sometimes exceed this estimate. Whenever an eaten spot caused daily

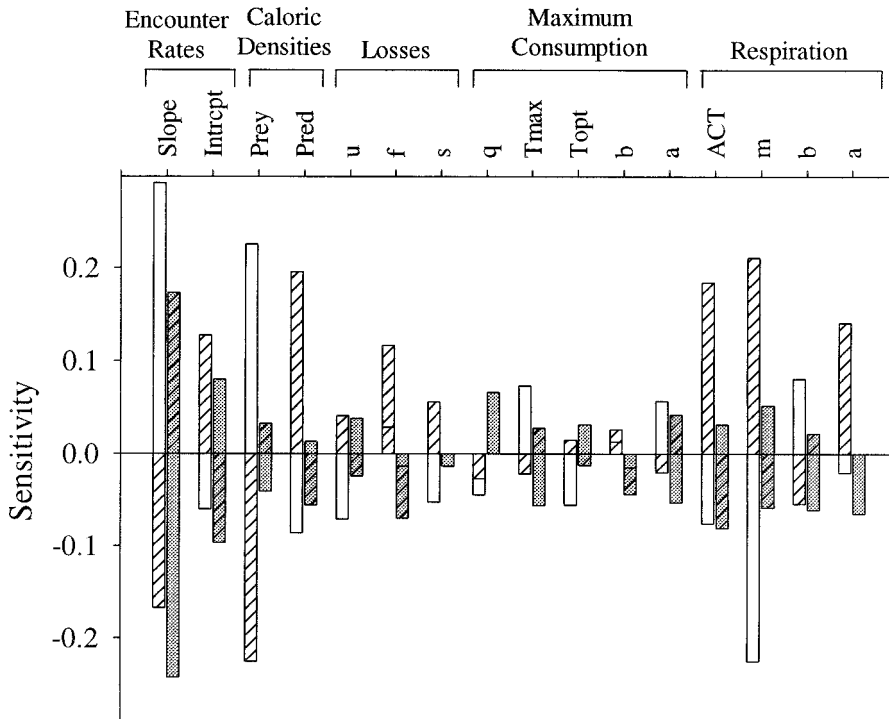


FIGURE 1.—Sensitivity (percent change in model output) of model predictions to parameter estimates. The mean changes in southern flounder growth in grams (white bars) and percent spot survival (gray bars) were derived from 30 simulations. Values were obtained through individual parameter perturbation of +10% (solid bars) and -10% (hashed bars). The model was run for 20 d using the initial conditions in the mixed-flounder treatment (results combine the percent change in growth of both small and large flounder). See Table 1 for parameter symbols.

consumption to exceed C_{\max} , the flounder was restricted from further feeding until the next day.

Variability in predictions of flounder growth and spot survival between simulations was large. However, mean model predictions did not change much after 30 simulations, nor did the confidence limits around the mean (i.e., coefficient of variation did not decrease with additional simulations). Thus, we averaged results from 30 simulations for all applications.

There are several methods to determine parameter sensitivity (Bartell et al. 1986). We decided to employ individual parameter perturbation by varying each parameter estimate by $\pm 10\%$. Sensitivity of the model to a parameter was determined by the average (of 30 model runs) proportional changes in a particular model prediction relative to predictions using the default parameters. We estimated sensitivity of flounder growth (average sensitivity for both small and large flounder) and percent spot survival to model parameters by using initial conditions and duration of the pond experiment (Rice et al. 1993a; Figure 1).

For flounder growth, the model was most sensitive to the slope of the line determining encounter rates as a function of prey size, the caloric density of the prey and predator, and two parameters in the respiration function (Figure 1). Spot survival was most sensitive to the slope and intercept of the size-dependent encounter rate function. Individual parameter perturbation indicates to which parameters model predictions are most sensitive and therefore the parameters we should concentrate on when obtaining additional data.

Application

Rice et al. (1993a) tested the hypothesis that the outcome of the flounder–spot interaction in the field could be dramatically altered by the size structure of the predator population relative to the size distribution of fish in the prey cohort. In this experiment, each pond section was stocked with a bimodal size distribution of age-0 spot and one of four predator treatments: a no-flounder control, a small-flounder treatment (mean = 113 mm TL), a

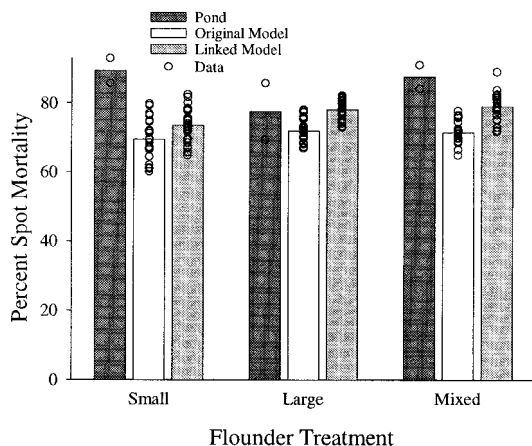


FIGURE 2.—Estimated total percent mortality of spot in each treatment of the pond experiment (predation by southern flounder plus nonpredation mortality; two replicates) and as predicted by the original foraging model and the linked model (30 simulations per model). Bars indicate mean values; circles indicate individual data points. The pond experiment was designed to produce approximately the same spot mortality across treatments (Rice et al. 1993a).

large-flounder treatment (mean = 182 mm TL), and a mixed small and large flounder treatment.

Differences in predator size structure had major effects on spot cohort survival and size structure (Rice et al. 1993a). In addition, the original foraging model successfully predicted the spot survival and size distributions observed at the end of the 20-d experiment.

Because the original foraging model can predict the number and sizes of spot consumed relatively well, we used this same data set to evaluate the ability of the linked model to predict flounder growth and to concurrently test whether the addition of a bioenergetics model significantly altered the ability of the foraging component of the linked model to accurately predict spot survival and size structure. We matched initial predator and prey size distributions and densities, observed mean prey growth rate, and the temperature regime to those in the pond experiment and ran the linked model for 20 d.

Linked-model predictions of spot mortality (Figure 2) and final size structure (Figure 3) matched estimated values in the pond as well as predictions by the original foraging model did. At least for this short-term experiment, allowing flounder growth to vary as a function of foraging success did not compromise the ability of the for-

aging model to predict effects on spot survival and size structure.

However, the linked model was not as successful in predicting flounder growth. Average flounder growth predicted by the linked model was similar to observed growth in the small-flounder treatment, but was more than 50% higher than observed growth in the large-flounder treatment (Figure 4). A similar pattern occurred for small and large flounder in the mixed-flounder treatment.

It was unclear why the linked model did well in predicting spot survival and size structure but produced discrepancies between observed and predicted flounder growth, particularly for the large flounder. Given the limitations of the pond experiment data (e.g., two replicates, variable results within treatments), it would be inappropriate to attribute all the lack of fit between model predictions and experimental results to inadequacies in the model. However, an analysis of model behavior can help elucidate potential sources of error.

To address this issue, we considered whether the discrepancies originate from estimates of consumption by the foraging component of the linked model or from the energy allocation process in the bioenergetics component. Because growth is indirectly determined by consumption, we predicted consumption of spot by flounder using the bioenergetics component of the linked model alone. We also predicted consumption (average of 30 simulations) using the foraging component of the linked model. We then compared these predictions with estimated consumption in the pond experiment to determine from which model component the discrepancies emanated.

Because small and large flounder were simultaneously consuming spot in the mixed-flounder treatment, it would be impossible to estimate the proportion of small and large spot consumed by either size of flounder in this treatment. We therefore focused our analyses on the two treatments that contained only one flounder size, small or large. Because model results within the mixed treatment were similar in pattern to the results from the other two treatments, information from this analysis should be applicable to the mixed treatment.

To predict consumption with the bioenergetics model, we used flounder growth estimated from the change in flounder sizes over the course of the pond experiment and observed temperatures. Because flounder were not individually tagged, we assumed each flounder kept its initial rank in the size distribution throughout the experiment (i.e.,

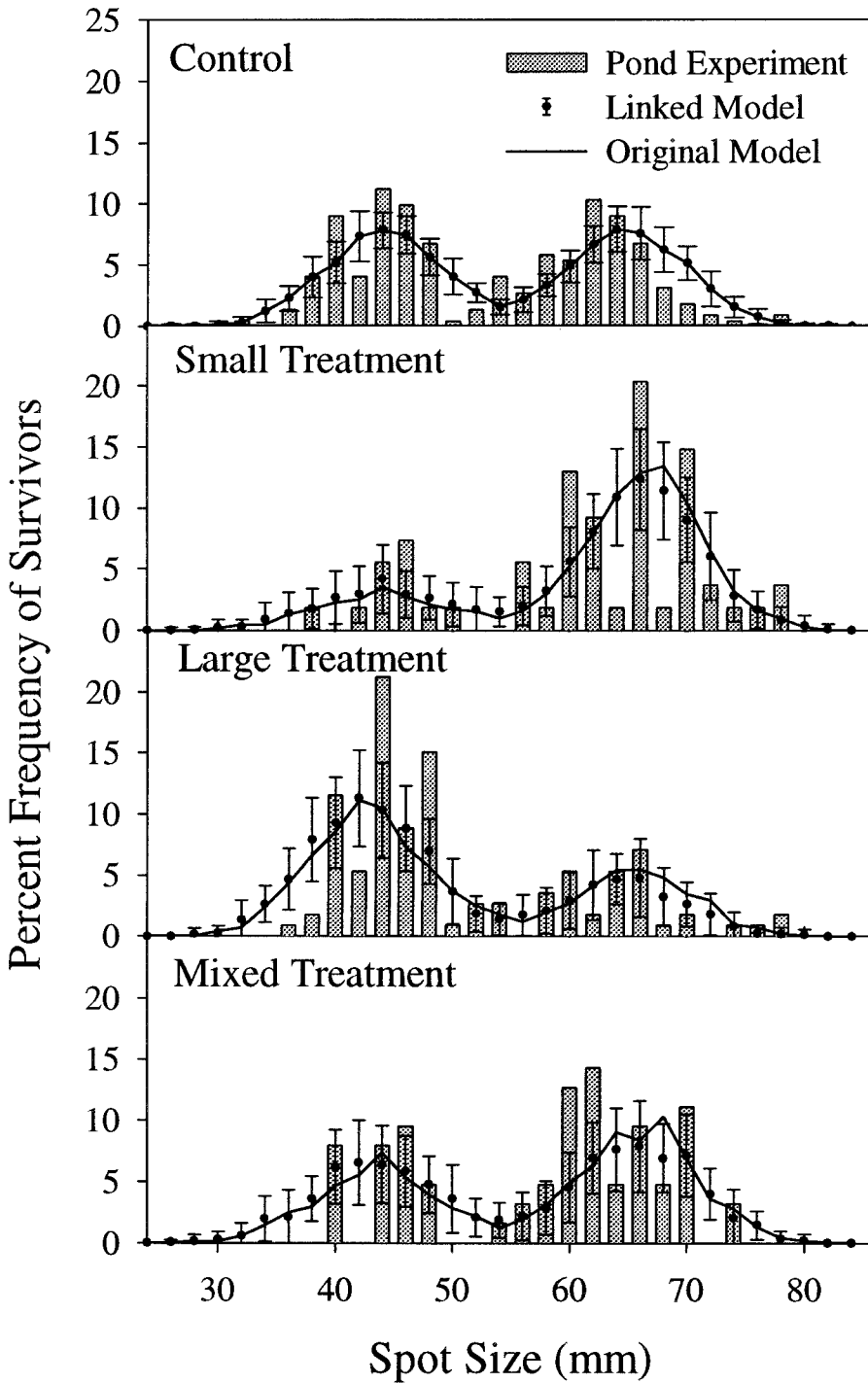


FIGURE 3.—Estimated final size structure of spot in each treatment of the pond experiment (Rice et al. 1993a) and as predicted by the linked model (foraging and energetics model; ± 1 SD) and the original foraging model (Rice et al. 1993a). Predictions from both models represent the mean of 30 model runs.

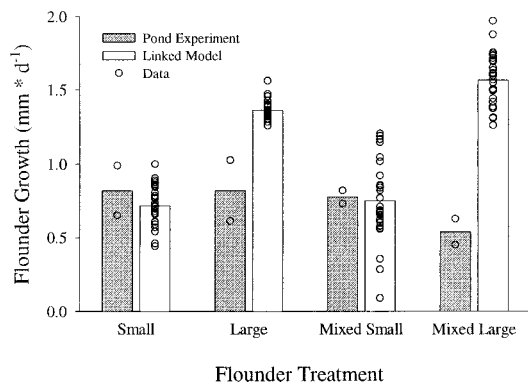


FIGURE 4.—Observed (pond) and predicted (linked model) southern flounder growth. Bars indicate mean values; circles indicate individual data points in the pond experiment (two replicates) and model predictions (30 simulations). Results in the mixed-flounder treatment are shown for both small (mixed small) and large (mixed large) flounder.

the smallest flounder at the beginning of the experiment was the smallest flounder at the end, etc.). Each flounder was simulated individually and consumption was summed across individuals within a replicate.

Predictions of flounder consumption by the bioenergetics model alone, based on observed flounder growth, matched quite well with estimated consumption from the pond in both the small-flounder and large-flounder treatments (Figure 5). However, predictions of consumption by the foraging component of the linked model were less accurate. In the small-flounder treatment, predictions were 21% less than estimated consumption in the pond, and in the large-flounder treatment, predictions of consumption overestimated empirically estimated consumption by 33%. Because the bioenergetics component of the linked model estimated consumption reasonably well but the predictions from the combined foraging and bioenergetics model were less accurate, the discrepancies between observed growth and predictions of growth from the linked model were either derived from dynamics of the foraging component of the linked model or by the interaction of the foraging and bioenergetics components.

We next evaluated whether it is possible for the linked model to successfully predict both the spot cohort and flounder growth or whether these discrepancies are irreconcilable, that is, if the model were forced to predict observed growth, would it no longer correctly predict survival and size structure of the spot cohort? To address this question,

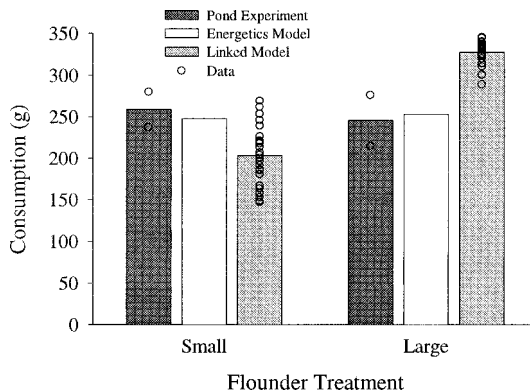


FIGURE 5.—Southern flounder consumption for both the small- and large-flounder treatments estimated for the pond experiment (two replicates) and as predicted by the bioenergetics model alone (deterministic) and the linked model (30 simulations). Bars indicate mean values; circles indicate individual data points.

we ran the simulations again, this time forcing predicted flounder growth rates to match observed growth rates by adjusting encounter rates as necessary. In the small-flounder treatment, where there was a 12% difference between observed and predicted growth, encounter rates needed only minor adjustment (about 7%). In the large-flounder treatment, a larger change in encounter rates (about 31%) was necessary to eliminate the 66% difference between observed and predicted flounder growth (see Figure 4).

After forcing predicted flounder growth to match observed growth, predicted consumption matched estimated consumption quite well, as expected. In the small-flounder treatment, there was only about a 14% difference between observed and predicted consumption, and in the large-flounder treatment there was less than a 6% difference, confirming that the energetics component of the linked model appears to make accurate predictions (i.e., if simulated flounder grow at the observed rate, they consume the observed amount). After matching predicted flounder growth to observed pond values, predictions of spot mortality by the linked model were lower than observed spot mortality (15% in small-flounder and 22% in large-flounder treatments; Figure 6). Spot size structure was not substantially changed in either treatment by forcing flounder growth to match observed values (change in the percent of surviving prey that were originally from the large-prey mode was less than 4% in the small-flounder treatment and less than 6% in the large-flounder treatment).

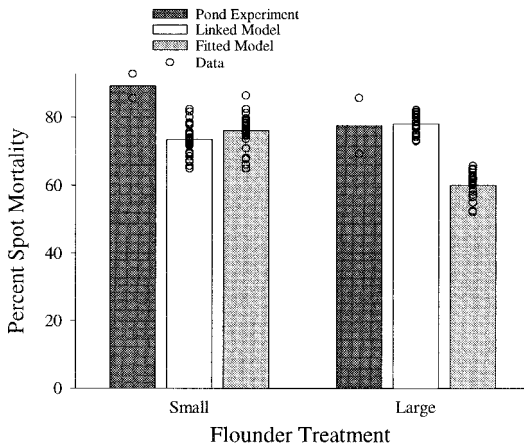


FIGURE 6.—Total percent mortality of spot (southern flounder predation plus nonpredation mortality) estimated in each treatment of the pond experiment (two replicates) and as predicted by the linked model and the fitted model (matching observed growth; 30 simulations per model). Bars indicate mean values; circles indicate individual data points.

Discussion

We were able to successfully combine southern flounder foraging and bioenergetics processes into one model to simultaneously predict effects of size-dependent predation on predator growth and on both prey survival and size structure. The addition of a bioenergetics model to the foraging model, which replaces a fixed predator growth rate with a dynamic growth rate determined by foraging success, does not significantly change predictions of spot survival and size structure. The linked model successfully captures the feedback effects of size-dependent consumption on subsequent size-dependent foraging, thus eliminating the original foraging model's requirement for field-derived predator growth-rate estimates.

In contrast to model predictions of prey size structure, predictions of predator growth rates are sensitive to small changes in foraging rates. Prey survival is intermediate in robustness, resulting in moderate discrepancies between predicted and observed survival with the addition of a bioenergetics model.

Why would the linked model be less successful in predicting flounder growth than spot survival and size structure if both the foraging model and the bioenergetics model work well separately? We believe the answer lies in a difference in currency between the two models. The currency in the foraging model is numbers of spot, and our response variables (spot mortality, size structure) are based

on how many fish fall into certain categories (alive versus dead, small versus large). Therefore, one small spot and one large spot have the same effect on predictions of spot cohort dynamics. However, in the bioenergetics model, the currency changes from numbers of spot to biomass. Because of the nonlinearity in the length–weight relationship for spot, small differences in spot length cause proportionally greater differences in spot mass, and these differences are greater for large spot than for small spot. In the bioenergetics model, the mass of one large spot is equivalent to about three times that of one small spot. Further, small flounder selectively feed on small spot and large flounder selectively feed on large spot, although both small and large flounder consume both small and large spot. The preferences of large flounder for large spot, coupled with the nonlinearity of the length–weight relationship, makes estimates of consumption by large flounder more variable than those for small flounder.

In the large flounder treatment, the difference in consumption between predicted and observed was 24 spot (18% of observed spot mortality). Using the currency of the foraging model, 24 spot equals about 0.3 spot per flounder per day, a small difference in foraging rate, which does not have a large effect on spot survival or size structure. However, when converted to the currency of the bioenergetics model, the difference is nearly 82 g. Because bioenergetics models that are used to predict growth are particularly sensitive to estimates of consumption (Bartell et al. 1986), a difference of 82 g (just over 1 g of spot consumed per flounder per day) can make a big difference in predictions of flounder growth (66% of observed flounder growth rate).

The asymmetry in model prediction accuracy between prey mortality and predator growth—caused by the difference in currency between the foraging (number of prey) and bioenergetics (biomass of prey) portions of the model—will most likely affect predictions of all similarly structured models. Given the inherent sensitivity of bioenergetics models to estimates of biomass consumption (Bartell et al. 1986), small differences in the feeding rate predicted by the foraging model component will result in magnification of errors and higher variability in predator growth rate estimates than in prey-survival estimates.

Combining foraging and energetics models elucidates assumptions in single-species models and increases the potential gain from a modeling exercise. However, combined foraging and energetics

ics models have received little attention (but see Breck 1998; Dong and DeAngelis 1998; Mason et al. 1998). With a linked model, the effects of an action (e.g., a predation event) result in changes in variables (e.g., flounder size) that will directly affect future model behavior (e.g., size-dependent attack and capture rates). In this application, the addition of dynamic flounder growth to the model had the same effect on predictions of spot survival and size structure as did the fixed predator growth rates in the original foraging model. However, had we run the model for an entire growing season, growth rates of flounder almost certainly would influence spot survival and size structure. This feedback from one model to the other captures a complex and potentially important driving force that affects community structure.

This work addresses one of the strongest types of multispecies interactions influencing fish communities: effects of size-dependent predation on survival and size structure of prey populations and growth of predator populations. We recognize that food web dynamics in an estuary are much more complex than the two-species interaction we have modeled here. Flounder feed on a variety of organisms and spot have many predators other than flounder. However, these two organisms are abundant in Atlantic coast estuarine environments and represent a common two-species interaction. By extending this approach to more complex systems, one could explore dynamics in food web structure and qualitatively describe the effects of these interactions on variability in populations.

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