

Virtual reality of planktivores: a fish's perspective of prey size selection

Jiangang Luo^{1,*}, Stephen B. Brandt¹, Michael J. Klebasko^{2,**}

¹Great Lakes Center, SUNY College at Buffalo, 1300 Elmwood Ave., Buffalo, New York 14222, USA

²Chesapeake Biological Laboratory, University of Maryland, Solomons, Maryland 20688, USA

ABSTRACT: Traditionally, field studies of size selective predation by visual-feeding planktivorous fish compare the size distribution of prey in stomachs to that of zooplankton measured in the field. However, the size frequency of prey perceived by a fish may differ from that measured by researchers using integrative plankton nets. In this study, a mechanistic spatial foraging model was developed to test the hypothesis that size-selective predation by visual-feeding planktivorous fish can arise simply by random encounters with prey. Our model was based on movement of a single predator and a size structured prey population distributed in 3-dimensional space. The model assumed that a predator's encounters with prey was a function of prey size and predator swimming speed. Upon encounter, the predator either selected prey by random choice or the largest apparent size. The size frequency and distance distribution of prey encountered, selected, and captured were estimated using Monte Carlo techniques. The model performance was initially evaluated with hypothetical prey size frequencies, and different light attenuation coefficients, capture efficiencies, visual distances and predator swimming speeds. Simulation results showed that the size frequency of prey encountered randomly by a predator is very different from the size frequency of the ambient prey in the environment. The size frequency of prey selected by random choice only differed from that selected by apparent size choice when visual distance was greater than reactive distance. Prey distance distribution, which was defined as frequency of prey encountered at different distances, showed that as prey density increased predators selected prey at closer distances by the largest apparent size choice than by random choice. We also tested the model specifically for the bay anchovy *Anchoa mitchilli*. Ambient zooplankton size frequencies found in mid-Chesapeake Bay were used to predict the size frequencies of zooplankton consumed by fish. Predicted prey size frequency in the diet matched the size frequency of zooplankton found in bay anchovy stomachs. We conclude that prey size selection by fish can be described mechanistically by differential random encounter from a fish's perspective, and that behavioral choice plays a minor role in prey size selection.

KEY WORDS: Spatial foraging model · Prey size selection · Visual-feeding planktivore

INTRODUCTION

Planktivorous fishes can be very effective at altering the size distribution and abundances of zooplankton in aquatic systems (Ivlev 1961, Brooks & Dodson 1965,

Hutchinson 1971, Sprules 1972, Lynch 1979, O'Brien 1979, Vanni 1986, Luecke et al. 1990, MacDonald et al. 1990). Effects of changes in size structure of the zooplankton community can permeate throughout the food web and change production dynamics and rates of nutrient cycling (e.g. Stein et al. 1988). Predicting prey size selectivity by a planktivore is critical to evaluating effects of predation on the zooplankton community as well as the relationship of zooplankton production to planktivore production. Traditionally, size selectivity has been evaluated by comparing the size distribution of prey found in fish stomachs to that

Present addresses:

*University of Miami, Rosenstiel School of Marine & Atmospheric Science, Division of Marine Biology and Fisheries, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA.
E-mail: luo@marlin.rsmas.miami.edu

**McCarthy Associates, Inc., 14458 Old Mill Rd, Suite 201, Upper Marlboro, Maryland 20772, USA

of zooplankton measured in the field. We contend that interpretations of those types of analyses may represent a biased view of prey size selectivity because we are using our perception of prey size availability instead of the fish's.

Many studies have suggested that apparent zooplankton size and encounter frequency determine prey size selection (Werner & Hall 1974, O'Brien et al. 1976, 1985, Eggers 1977, 1982, Gardner 1981, Mittelbach 1981, Pastorok 1981, Butler & Bence 1984, Wetterer & Bishop 1985, Wetterer 1989). Other studies have attempted to measure prey size selection by comparing the size composition of zooplankton in a predator's diet to the size composition of prey in the surrounding water (Baird & Hopkins 1981, Scott & Murdoch 1983, Mikheev 1984, Magnhagen 1985, Main 1985, Grover & Olla 1986, Khadka & Ramakrishna 1986, Schmitt 1986, Collie 1987, Confer et al. 1990, Forrester et al. 1994). Size distribution of prey, as perceived by the predator, may differ from that measured with field sampling approaches that integrate across relatively large volumes of water. A typical index used to quantify prey size selection is often calculated as an 'odds ratio' or a 'forage ratio' (Fleiss 1973, Jacobs 1974, Chesson 1978, Gabriel 1979, Confer et al. 1990, Johnson et al. 1990). An example of such indices is defined as $E_i = S_i/P_i - 1$ (Confer et al. 1990), where E_i is the electivity index of the i th size class prey, S_i is the percent of the i th size class prey in the diet, and P_i is the percent of the i th size class prey in the plankton. An index value equal to zero indicates no selection (or neutral selection) for that size class of prey. Values greater than zero indicate positive selection for a prey size class, and those less than zero suggest negative selection for a prey size class. An index calculated in this form is not really an electivity index from the fish's perspective. This index is more appropriately called a 'size difference index' since it uses our perspective of ambient zooplankton size rather than the fish's.

In this paper, we develop a spatial foraging model to examine prey size selectivity from a fish's perspective, and to compare prey size selectivity by random choice (RC) to that by apparent size choice (AC; O'Brien et al. 1976, 1985). Prey size selectivities are influenced by many physiological (visual ability, swimming speed), biological (predator and prey size), and environmental (light intensity, turbidity) factors. Also, many of those factors combine to determine what a predator can see in the water column (Gerritsen & Strickler 1977, MacKenzie & Leggett 1991, Aksnes & Giske 1993). To evaluate the effects from combined factors, we conducted simulation experiments with different hypothetical prey size frequencies at different prey densities, light attenuation coefficients, capture efficiencies, visual distances and predator swimming speeds. Then,

we used zooplankton size frequency data collected from integrated net tows in Chesapeake Bay to predict the size of prey in the diet of an abundant planktivorous visual feeder, the bay anchovy *Anchoa mitchilli* (Johnson et al. 1990, Klebasko 1991, Luo 1991, Luo & Brandt 1993). Model predictions of the size frequency of prey eaten were compared to the size frequency of prey found in the diet.

METHODS

Model description. The 3-dimensional spatial foraging model (SFM) counts the number of prey encountered in a series of size classes as a predator swims through the water. An encounter between the predator and prey depends on the predator's visual ability (biologically determined), light intensity (e.g. day or night), water turbidity (clear or murky), prey size, and the predator and prey swimming speeds. For convenience, all abbreviations and symbols are summarized in Appendix 1.

We simulated the movement of a predator and its prey in a 3-dimensional space. We estimated the encounter rate of predator with prey using Monte Carlo techniques. This approach differs substantially from probabilistic models such as the optimal foraging model 'OFM' (Werner & Hall 1974), the encounter frequency model 'EFM' (Confer & Blades 1975, Gerritsen & Strickler 1977), the apparent size model 'ASM' (O'Brien et al. 1976, 1985), and the reactive field volume model 'RFVM' (Eggers 1977, 1982). In those models, the encounter rate is estimated as a function of probabilities, whereas, in the SFM, the encounter rate is measured directly from individual selection events.

We modeled the predator and prey as objects, where each object has a spatial location, size, and swimming speed. In the model, we have 1 predator and a number (N) of prey of size l_i belonging to m different size classes (L_j) where i ranges from 1 to N and j ranges from 1 to m . The predator is located at (x_p, y_p, z_p) , and the i th prey is located at (x_i, y_i, z_i) . At the beginning of the simulation, N prey are distributed randomly in a defined 3-dimensional volume ($1000 \times 1000 \times 1000$ mm), and the predator is located at the center of the volume. The predator has the swimming speed of v (mm s^{-1}), and each prey has a swimming speed of u_i (mm s^{-1}) which is a function of prey size l_i (mm). Over each time interval t , the predator and prey swim in random directions. Movements of prey are defined as:

$$x(i)_t = x(i)_{t-1} + u(i) \cos(\phi) \sin(\theta) \quad (1)$$

$$y(i)_t = y(i)_{t-1} + u(i) \cos(\theta) \quad (2)$$

$$z(i)_t = z(i)_{t-1} + u(i) \sin(\phi) \sin(\theta) \quad (3)$$

where $\phi = 2\pi \cdot \text{random}(\text{seed1})$, the swimming angle in the x - z plane, and $\theta = \pi \cdot \text{random}(\text{seed2})$, the swimming angle in the y - z plane. Two different seeds (*seed1*, *seed2*) were used because there are 2 degrees of freedom in a 3-dimensional space. $\text{Random}(\text{seed})$ returns a pseudo-random real number uniformly distributed between 0.0 and 1.0 (Park & Miller 1988). We used a reflective boundary condition to keep the prey inside the modeling domain. The movement of the predator was similarly defined using speed v , *seed3*, and *seed4*. For each time interval, we calculated the distance (d_i) between the predator and the i th prey:

$$d_i = \sqrt{(x_i - x_p)^2 + (y_i - y_p)^2 + (z_i - z_p)^2} \quad (4)$$

The visual distance (Vd_i) of prey was calculated as a function of predator size, prey size, and light attenuation. The visual distance is the maximum distance at which the predator can see a prey of a given size within a set of environmental conditions (Munk & Kiørboe 1985). Light intensity was assumed constant within the volume. Vd_i (mm) was defined as:

$$Vd_i = cL_p l_i e^{-0.001/kd_i} \quad (5)$$

where c is a proportionality constant, L_p is the predator length (mm), l_i is the size (mm) of prey i , and k is the light attenuation coefficient (m^{-1}). The apparent size (A_i) of a prey was defined as:

$$A_i = 2 \arctan \left(\frac{l_i}{2d_i} e^{-0.001/kd_i} \right) \quad (6)$$

The reactive distance (Rd) was defined as the maximum distance at which the predator would attack a prey at that time step (Munk & Kiørboe 1985). $Rd_i = vt$ if $Vd_i \geq vt$, and $Rd_i = Vd_i$ if $Vd_i < vt$. An encounter was determined if $d_i \leq Rd_i$. When there was only 1 prey in the predator's reactive field (a sphere with radius Rd to the largest prey size class), an attack was assumed. If several prey were in the reactive field within a time step, 1 of 2 criteria was used to select a prey for attack: a prey with the largest apparent size will be selected (AC), or a prey will be selected randomly (RC). Capture success was determined stochastically using a probability density function of capture efficiency. We assumed that capture efficiency was constant or decreased linearly with increase in prey size. In the latter case, we defined capture efficiency (CE) as a negative linear function (Miller et al. 1988) of prey size (l_i):

$$CE = a - bl_i \quad (7)$$

where a and b are constants determining the intercept and slope of the line.

Prey density and size distribution remained constant during each simulation run. The program generated a same-sized prey at a random location in the modeling space when a prey was eaten by the predator. Once a

prey was captured, we assumed that an attack could not be initiated during the next time step. The numbers of prey encountered ($En(L)$), selected ($Se(L)$), and captured ($Ca(L)$) for each length class L_j were computed as:

$$En(l_i) = En(l_i) + 1 \quad \text{if prey } i \text{ in reactive field} \quad (8)$$

$$Se(l_i) = Se(l_i) + 1 \quad \text{if prey } i \text{ is the largest apparent size in the reactive field (AC) or if prey } i \text{ is in the reactive field (RC)} \quad (9)$$

$$Ca(l_i) = Ca(l_i) + 1 \quad \text{if prey } i \text{ is captured} \quad (10)$$

where $l_i \in [L_1, L_m]$. Frequency distributions of prey encountered ($Enf(L)$), selected ($Sef(L)$), and captured ($Caf(L)$) for each length class L_j are estimated as:

$$Enf(L_j) = \frac{En(L_j)}{\sum_1^m En(L_j)} \quad (11)$$

$$Sef(L_j) = \frac{Se(L_j)}{\sum_1^m Se(L_j)} \quad (12)$$

$$Caf(L_j) = \frac{Ca(L_j)}{\sum_1^m Ca(L_j)} \quad (13)$$

Prey distance distribution was defined as the proportion of prey at each distance interval D_j (such as, 0 to 10, 10 to 20, ... 90 to 100 mm) from the predator. By replacing l_i with d_i and L_j with D_j in Eqs. (8) to (13), we calculated the prey distance distribution. Distance distribution from a predator's perspective is the distance distribution of prey encountered by the predator.

Simulation experiments. Six types of simulation experiments were conducted to compare size frequencies of prey captured to size frequencies of prey in the environment, and to examine prey size selectivity for 2 types of prey choices (RC and AC) with different parameters and prey size distributions. The predator used in simulations was a 50 mm total length adult bay anchovy. Ten size classes of copepods (ranging from 0.1 to 1.0 mm) were used as prey. We used the model to test the effects of: (1) random seeds, simulation time steps, and types of prey distributions (even, negative linear, negative exponential), (2) prey density, (3) light attenuation coefficient, (4) capture efficiency, and (5) predator swimming speed and visual distance on prey size selectivity. We also used the model (Expt 6) to predict the size frequencies of zooplankton consumed by the bay anchovy based on the size frequencies of zooplankton measured in mid-Chesapeake Bay. Parameters used in the experiments are presented in Table 1.

We used size frequency plots to compare the ambient size distributions of prey to the predicted size frequency distributions of prey encountered, selected, and captured under different assumptions. No statistical tests were performed for the hypothetical prey size experiments (Expts 1 to 5) because the simulations were run with a 'large' number of time steps and the

Table 1 Parameters used in simulation experiments

Expt	Vd (mm)	v (mm s ⁻¹)	k (m ⁻¹)	CE	N (no. m ⁻³)	t
1	100	100	0	1.0	2500	500–5000
2	100	100	0	1.0	200–100000	5000
3	150	150	0, 3	1.0	2500	5000
4	100	100	0	0.1–1.0	200–2500	5000
5	50–150	100–200	0	1.0	2500	5000
6	50–150	100–200	2	0.5–1.0	2500	5000

results were considered as 'steady-state' size frequency distributions. For the field data, we used the Kolmogorov-Smirnov goodness-of-fit test (Zar 1984) to compare differences between prey size distributions in bay anchovy stomachs and in water column samples. We set $\alpha = 0.05$ for a Type I error.

RESULTS

Model performance

We tested the sensitivity of the model by running simulations with hypothetical prey size distributions at different time steps and random seeds (Fig. 1). Predator swimming speed was set to 2 body lengths s⁻¹ (100 mm s⁻¹, Table 1). Simulation results indicated large variations with seeds in predicted size frequency

of prey encountered when simulations were run with a small number of time steps (Fig. 1A). Variations decreased dramatically as the number of time steps increased (Fig. 1B, C). At simulation time steps above 2000, the predicted size frequencies showed no apparent differences from the steady-state size frequencies of prey encountered by the predator (Fig. 1D). This indicates that in predicting the size frequency of prey encountered, the model is insensitive to initial seeds when simulation time steps are larger than 2000. Therefore, all later simulations were run with time steps larger than 2000.

The size frequency of prey encountered for all 3 types of prey size distributions (Fig. 2A, even; 2B, negative linear; 2C, negative exponential) differed dramatically from the input size frequency of prey. The size frequency of prey encountered represents the prey size distribution from a predator's perspective.

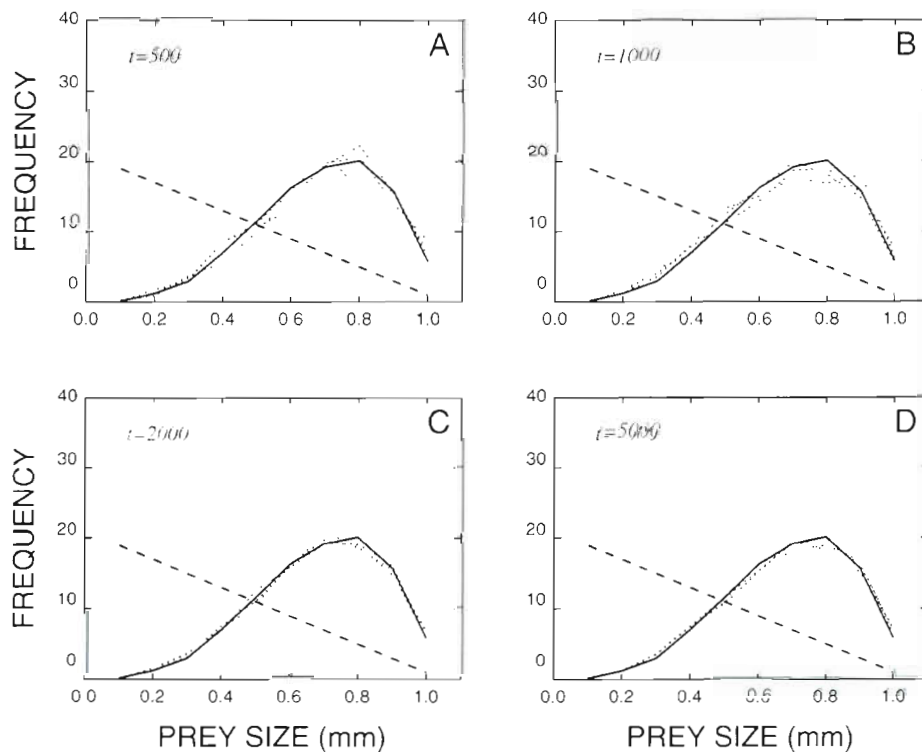


Fig. 1. Predicted size frequencies of prey encountered by a predator from a negative linear distribution of ambient prey (dashed line) at different simulation time steps (A), (B), (C), and (D) and different random seeds (dotted lines). The solid line is the steady-state simulation curve at $t = 10000$. Parameter values: $v = 100$ mm s⁻¹, $Vd = 100$ mm, $N = 2500$ m⁻³, $k = 0$, and $CE = 1$.

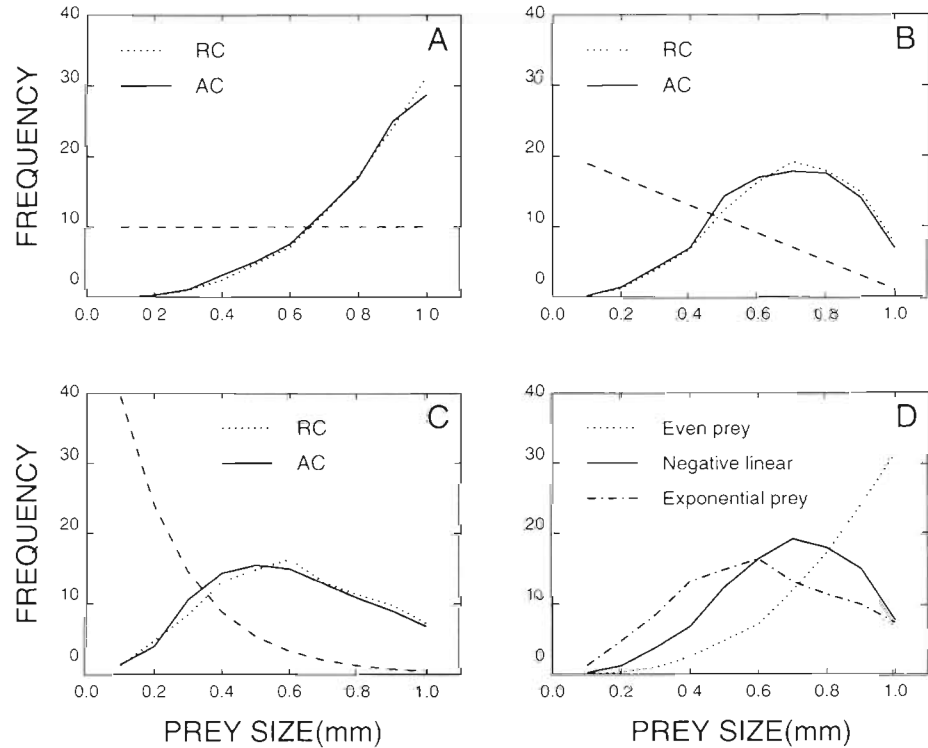


Fig. 2. Predicted size frequencies of prey selected by RC (dotted line) and selected by AC (solid line) given different ambient prey size frequencies (dashed line): (A) even distribution; (B) negative linear; (C) negative exponential; (D) comparison of the 3. Parameter values are the same as in Fig. 1

The predator 'sees' proportionally more larger prey than small prey compared to what is present in the environment because larger prey can be seen at further distance. The size frequency of prey selected by RC did not differ from that selected by AC for 3 types of ambient prey size frequency (Fig. 2).

Prey density

To test the effect of prey density on prey size selection, we ran simulations for different prey densities for 5000 time steps. Results (Fig. 3A) indicated that the predator encountered relatively fewer large prey at a lower prey density of $N = 200 \text{ m}^{-3}$ than at $N = 2500 \text{ m}^{-3}$. At $N > 2500 \text{ m}^{-3}$, there were no apparent differences in the size frequencies of prey encountered (Fig. 3A). There were no differences in the predicted prey size frequencies between RC and AC at all prey densities (Fig. 3B, C, D). In contrast, there were differences in the predicted prey distance distributions between RC and AC simulations at higher prey densities (Fig. 4). We know that there are more prey at further distances from the predator (density \times volume). But from a predator's perspective, most prey are somewhere in the middle distance of its visual field (Fig. 4A) depending on the types of prey size distribution (Fig. 4D). At higher prey densities, the predator selected prey at closer distances than at lower prey density (Fig. 4A, B, C).

Light attenuation

We tested the effect of light attenuation on prey size selection by running simulations with 2 different light attenuation coefficients ($k = 0, 3 \text{ m}^{-1}$) for 5000 time steps. k has only a slight effect on the size frequency of prey encountered (Fig. 5). With a larger k , the predator selected relatively fewer large prey than it did at a smaller k (Fig. 5A). There were still no differences in the predicted size frequencies of prey between RC and AC simulations (Fig. 5C). However, the distance distribution of prey encountered and selected showed large differences between the 2 levels of light attenuation (Fig. 5B, D).

Capture efficiency

We ran 2 simulations with differing capture efficiencies to evaluate their effects on prey size selection. In the first case, we set $CE = 1$ for all prey size classes ($a = 1, b = 0$ in Eq. 7). In the second case, we defined CE as a declining linear function of prey size classes ($a = 1.1, b = 1$ in Eq. 7). Results indicated that prey capture efficiency not only determines the capture success (Fig. 6B, D) but also affects the encounter frequency (Fig. 6A). Decrease of capture efficiency of large prey size classes increased the encounter frequency of large prey size classes at the

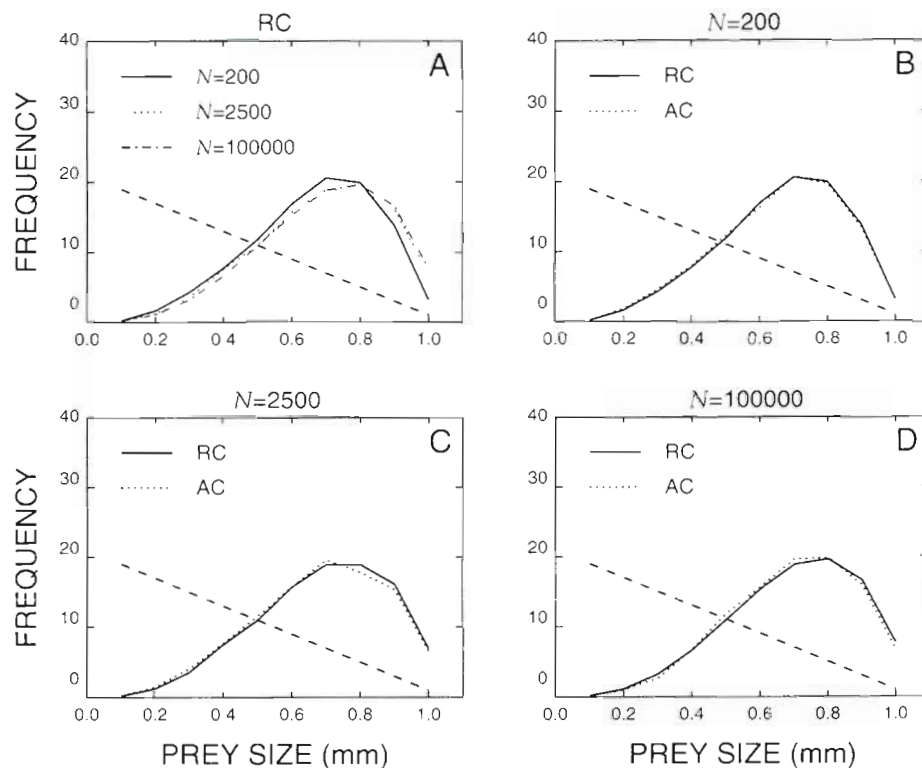


Fig. 3. Effects of prey density on prey size selection. Parameter values used are the same as in Fig. 1 except for prey densities. (A) Effect of prey density on the size frequency of prey encountered by RC; (B, C, D) comparison of the size frequency of prey selected by RC (solid line) and AC (dotted line) at different prey densities

lower prey density ($N = 200 \text{ m}^{-3}$) because larger prey escaped from the predator were most likely still in the vicinity of the predator with the chance for re-

encounter still high. As prey density increases, the effect of capture efficiency on encounter frequency decreases (Fig. 6C).

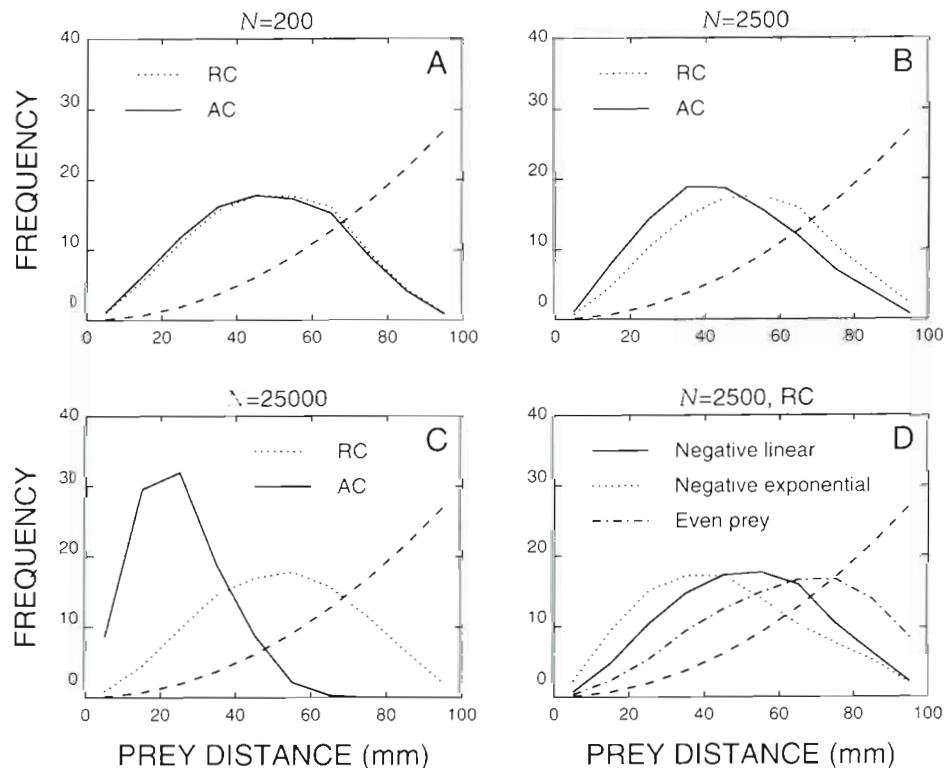


Fig. 4. Distance distribution of prey selected by either RC or AC by a bay anchovy from a negative linear prey size distribution at different prey densities (A, B, C), and RC among different input prey size distributions at $N = 2500$ (D). All other parameter values are the same as in Fig. 1. The dashed line represents the ambient prey distance distribution

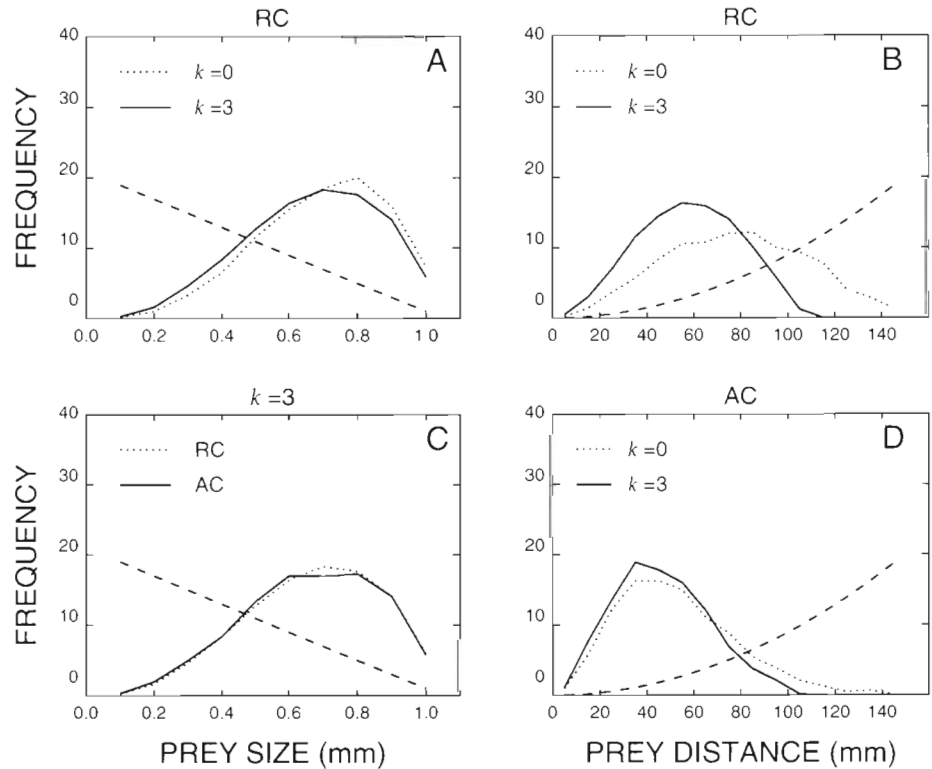


Fig. 5. (A) Size frequencies of prey encountered at different light attenuation coefficients, (B) distance distributions of prey encountered at different light attenuation coefficients, (C) size frequency of prey selected by RC and AC at $k = 3 \text{ m}^{-1}$, (D) effects of k on distance distributions of prey selected by AC. Parameter values used in simulations are $v = 150 \text{ mm s}^{-1}$, $Vd = 150 \text{ mm}$, $N = 2500 \text{ m}^{-3}$, $k = 0, 3 \text{ m}^{-1}$, and $CE = 1$

Visual distance and swimming speed

We tested the effects of visual distance and predator swimming speed on prey size selectivity by running

simulations with combinations of 3 visual distances ($Vd = 100, 150$, and 200 mm) and 3 predator swimming speeds ($v = 50, 100$, and 150 mm s^{-1}). Both visual distance and predator swimming speed have large effects

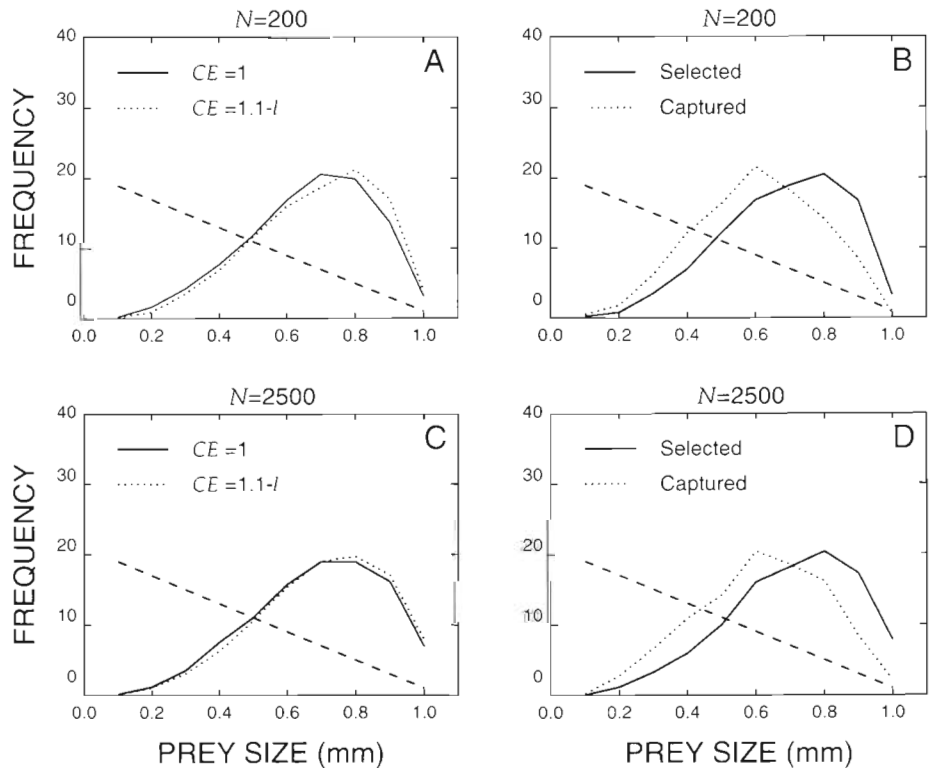


Fig. 6. Effects of capture efficiency on size frequencies of prey encountered by a bay anchovy at different prey densities: (A) $N = 200 \text{ m}^{-3}$, (C) $N = 2500 \text{ m}^{-3}$. Size frequencies of prey selected with AC and captured at different prey densities: (B) $N = 200 \text{ m}^{-3}$, (D) $N = 2500 \text{ m}^{-3}$. Parameter values used in simulations are $v = 100 \text{ mm s}^{-1}$, $Vd = 100 \text{ mm}$, $N = 200, 2500 \text{ m}^{-3}$, and $k = 0$

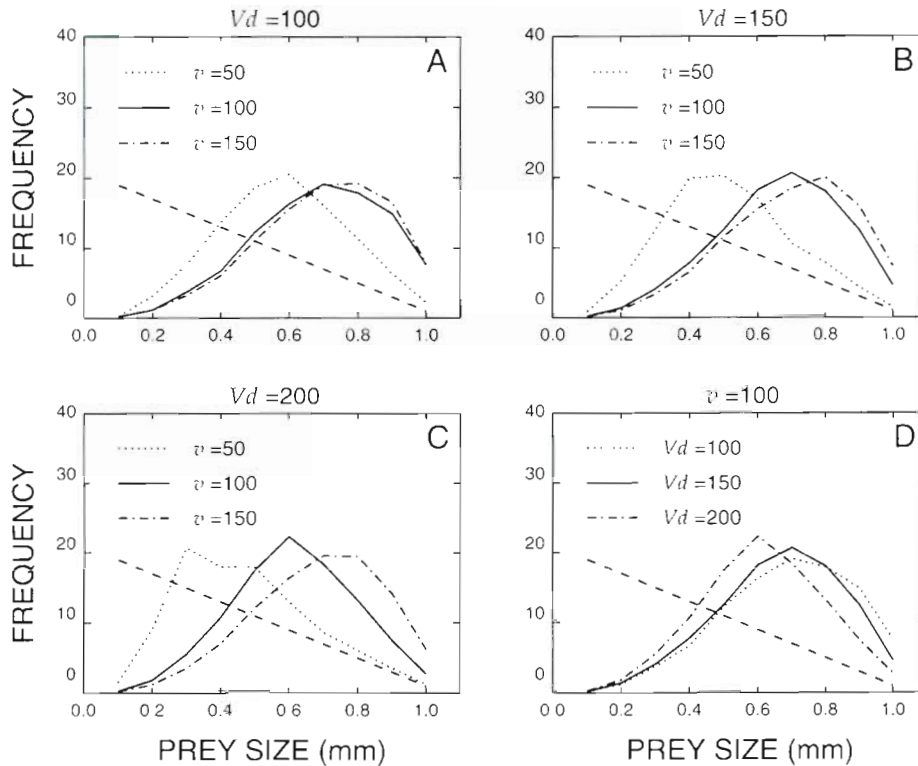


Fig. 7. Effects of visual distance and predator swimming speed on size frequencies of prey encountered. Three values of v are used at (A) $Vd = 100$ mm, (B) $Vd = 150$ mm, (C) $Vd = 200$ mm. (D) Three values of Vd are used at $v = 100$ mm s^{-1} . All other parameter values are the same as in Fig. 1

on the size frequency of prey encountered (Fig. 7). When we held the visual distance constant, increasing predator swimming speed increased the proportion of larger prey encountered (Fig. 7A, B, C). When we held predator swimming speed constant, increasing the visual distance decreased the proportion of larger prey encountered (Fig. 7D).

We compared the simulated size frequencies of prey selected by the bay anchovy as determined by the prey choice (RC and AC) and for different visual distances and predator swimming speeds (Fig. 8). There were differences in sizes of prey selected between the 2 assumptions when the reactive distance was below the visual distance (Fig. 8). Earlier results (Fig. 4A, B) showed that there was no differ-

ence between the 2 assumptions at different prey densities if the visual distance and reactive distance were equal.

Bay anchovy diet and model predictions

Prey size selection of the bay anchovy was evaluated by running the model using actual zooplankton data collected at the same location and time as the fish during daylight hours in mid-Chesapeake Bay in April, May, August, and October 1990 (Klebasko 1991). Different combinations of predator swimming speed, visual distance, and capture efficiency were used (Table 2). Predicted size frequencies of diets were

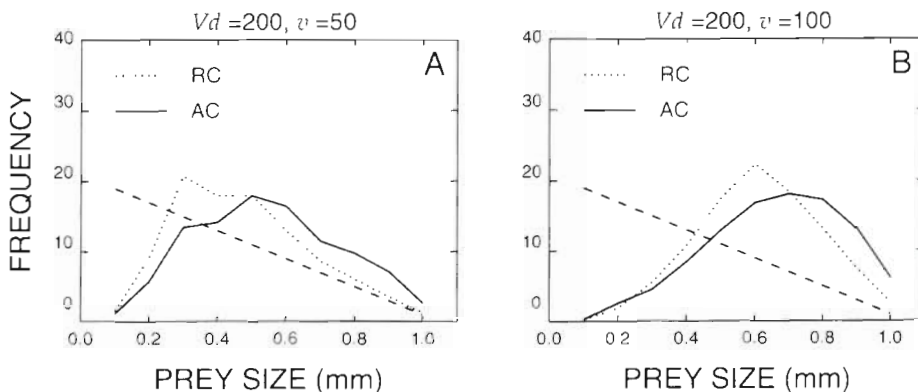


Fig. 8. Effects of visual distance and predator swimming speed on size frequencies of prey selected by RC and AC: (a) comparison at $Vd = 200$ mm and $v = 50$ mm s^{-1} ; (B) comparison at $Vd = 200$ mm and $v = 100$ mm s^{-1} . All other parameter values are the same as in Fig. 1

Table 2. Kolmogorov-Smirnov goodness-of-fit test for comparing model predicted prey size frequencies with prey size frequencies found in bay anchovy stomachs in April, May, August, and October 1990 in mid-Chesapeake Bay. d_{max} is the test statistic (Zar 1984) and values in parenthesis are p values

Vd	v	CE	d_{max}			
			April	May	August	October
100	100	1	8.6 (0.21) ^a	12.0 (0.051) ^b	20.1 (0.001) ^b	11.0 (0.075)
100	100	1 - 0.5I	13.5 (0.015)	7.1 (0.40)	15.7 (0.004)	7.2 (0.40)
100	50	1	18.5 (0.001)	4.2 (0.70)	10.0 (0.10)	7.0 (0.40)
100	50	1 - 0.5I	24.2 (0.001) ^b	8.7 (0.25)	7.7 (0.35) ^a	14.2 (0.01) ^b
200	100	1	9.9 (0.11)	8.7 (0.25)	16.1 (0.003)	11.1 (0.075)
200	100	1 - 0.5I	14.7 (0.004)	4.0 (0.75) ^a	11.5 (0.065)	7.0 (0.40) ^a
200	150	1	11.7 (0.06)	8.5 (0.26)	16.3 (0.003)	9.3 (0.16)
200	150	1 - 0.5I	18.0 (0.001)	4.5 (0.70)	10.3 (0.08)	7.9 (0.30)

^aBest fit, ^bworst fit, to the size frequency of prey found in the bay anchovy

compared to actual diets obtained from bay anchovies ranging from 40 to 60 mm total length. We set $k = 2 \text{ m}^{-1}$ (Harding 1994) for all simulations to reduce the number of simulation runs. We selected fish swimming speeds (v) of 50, 100, and 150 mm s^{-1} (Beamish 1978). Visual distance to a 1 mm prey was set at 100 or 200 mm (Aksnes & Giske 1993).

The model-predicted size frequencies of anchovy diet accounted for most of the observed patterns of prey size selection by the bay anchovy (Fig. 9). We

compared the predicted dietary prey size frequency to the observed size frequency of prey found in the bay anchovy stomachs using Kolmogorov-Smirnov goodness-of-fit test (Table 2). In April, 3 out of 8 tests showed no statistical difference between predicted and actual size distributions of prey consumed (Table 2), and the best fit to the observed was $Vd = 100 \text{ mm}$, $v = 100 \text{ mm s}^{-1}$, and $CE = 1$ ($p = 0.21$). In May, all 8 tests showed no statistical difference between the prediction and actual size distribution, and the best fit was for $Vd = 200 \text{ mm}$, $v = 100 \text{ mm s}^{-1}$, and $CE = 1 - 0.5I$ ($p = 0.75$). In August, 4 out of 8 tests showed no statistical difference

between prediction and actual size distribution, and the best fit was for $Vd = 100 \text{ mm}$, $v = 50 \text{ mm s}^{-1}$, and $CE = 1 - 0.5I$ ($p = 0.35$). In October, 7 out of 8 showed no statistical difference, and the best fit was for $Vd = 100 \text{ mm}$, $v = 50 \text{ mm s}^{-1}$, $CE = 1$ ($p = 0.40$). The best and worst fit curves of predicted dietary prey size frequencies for each month are shown in Fig. 9. It is apparent that even the worst fit curve characterized the general pattern of the dietary prey size frequency given expected variabilities in fish diets.

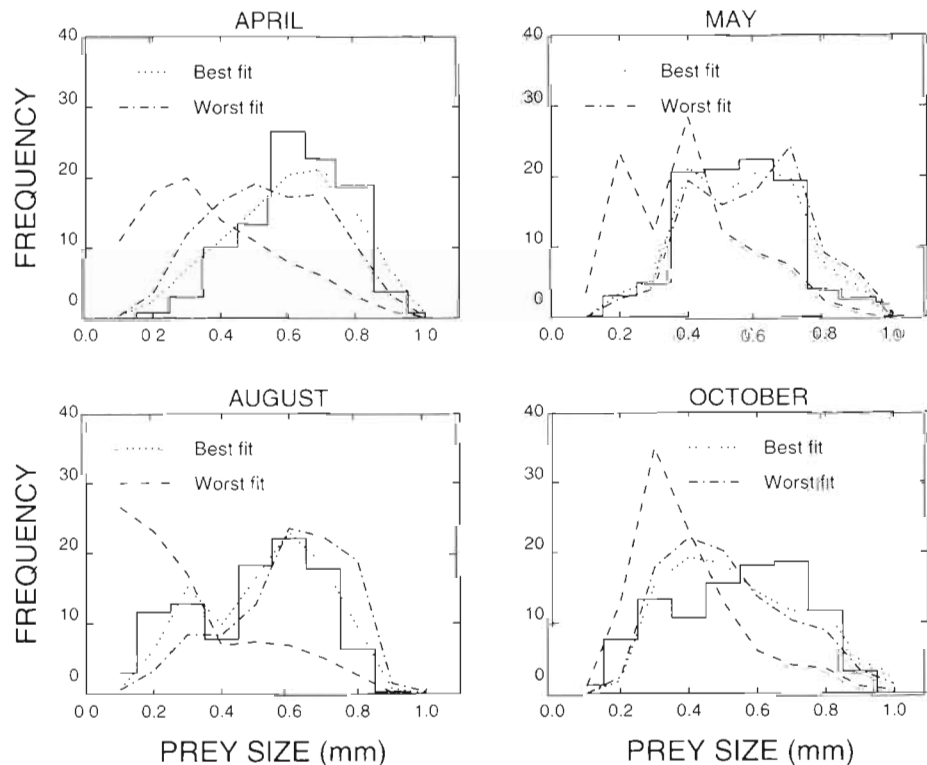


Fig. 9. Zooplankton size frequencies in Chesapeake Bay (dashed line), in bay anchovy diet (stepped line), and in predicted diet (dotted and dash-dotted line) for April, May, August, and October 1990. $t = 5000$; $N = 2500$; $k = 2 \text{ m}^{-1}$; other parameter values are presented in Table 1

DISCUSSION

The SFM is a flexible model requiring few assumptions. In probabilistic models (such as OFM, EFM, ASM, and RFVM), there are 3 fundamental assumptions: (1) prey are distributed randomly, (2) size classes of prey are independently distributed so that the probability of mutual occurrence is the product of the separate probabilities of occurrence for each prey size, (3) fish are exposed to the average conditions in the entire environment without consideration of local deviations in density of certain prey sizes. In this study, although we used random distribution, movement and uniform environment, the above assumptions are not required for the SFM. In the SFM, random distribution and movement of organisms is just one out of thousands of possible distributions and movement patterns. Also, any environmental variations (e.g. temperature, light level, dissolved oxygen) can be included in the model if their effects on predator and prey interactions are known.

As predicted, the size frequency of prey encountered by a visual feeding planktivore was dramatically different from the ambient size frequency of prey (Fig. 2). This difference was merely a result of differential random encounter from a predator's perspective, and not a result of any assumptions concerning active behavioral selection. To determine if a predator behaviorally selects prey by size, we need to compare the diet of the predator with the size frequency of prey encountered, not with the ambient size frequency of potential prey in the environment. We can obtain ambient prey size frequencies by field sampling and laboratory measurement, but we cannot measure the size frequency of prey encountered by a predator. Therefore, we must use a model to predict the size frequency of prey encountered. As our results show, many biological, physiological, and environmental parameters may influence the sizes of prey encountered. The accuracy of predicting size frequency of prey encountered will depend on the accuracies of those factors. We need to understand the sensitivity of the model to each factor so that we can set the accuracy we need for measuring these factors.

Prey density had little effect on the size frequency of prey encountered but larger effects on the distances at which prey were encountered. Prey density only affects the size frequency of prey encountered at very low prey densities. There were no differences in the size frequency of prey selected using RC or AC foraging strategies at all prey densities when reactive distance and visual distance were equal. Wetterer & Bishop (1985) reported similar results while comparing prey selection between the RFVM and the ASM. However, for prey distance distribution, as the prey density increased, the difference between RC and AC increased. At low prey densities, a predator rarely sees 2

prey within the same time interval, so no 'decision' is required. At higher prey densities, the predator may see 2 or more prey and therefore a choice must be made. At high prey densities (Fig. 4B, C), using the AC foraging strategy, more prey were selected at a closer distance than if selected at random. From an energetics point of view, a predator should use the AC model to select prey. Selecting prey at closer distances saves energy in reaching the prey and potentially increases capture efficiency (i.e. increasing energy return per unit energy expended). This may help explain why larval fish require higher prey densities than average to survive (Lasker 1975, 1978, Houde 1978), even though the expected encounter rates from models are high enough for survival at lower prey densities.

Light attenuation had only a slight effect on the size frequency of prey encountered, but a substantial effect on the distance distribution of prey encountered. Light level attenuates exponentially with distance. Visibility of an object further away is affected more than a closer object. Larger prey, that can be seen at a long distance in clear water, may not be seen in murky water. Therefore, light attenuation affects encounter rates of larger prey more than it affects encounter rates of smaller prey (Fig. 5A). A predator would encounter (Fig. 5B) and select (Fig. 5D) more prey at closer distances at a higher light attenuation coefficient. However, we found no difference in prey size frequency between RC and AC (Fig. 5C). Light attenuation coefficients in Chesapeake Bay generally range from 0.75 to 3.0 m^{-1} (Harding 1994). Light attenuation also affects light intensity at deeper water. We must differentiate light attenuation from light intensity. Light intensity depends on both the light source and the optical properties of the water, whereas light attenuation is determined only by the optical properties of the water. The effect of light intensity is discussed later.

Prey capture efficiency affected the size frequency of prey encountered at low prey densities. In our model, larger prey have a greater chance to escape an attack by a predator due to a smaller capture efficiency. Escaped prey, however, are most likely still in the vicinity of the predator, and therefore have a greater chance of being encountered by the predator than other prey. Thus, when capture efficiency is low for larger prey, it will increase the encounter rate of larger prey relative to small prey. This may compensate somewhat for the escape of larger prey. To our knowledge, this behavioral effect has not been previously reported. This is not included in the OFM (Werner & Hall 1974), the EFM (Confer & Blades 1975; Gerritsen & Strickler 1977), the ASM (O'Brien et al. 1976), or the RFVM (Eggers 1977). Visual distance and predator swimming speed affected the size frequency of prey encountered when the visual distance was greater

than the distance the predator could swim in one time step (i.e. $Vd > Rd$). Luecke & O'Brien (1981) have shown that fish could visually locate prey at considerably greater distances than the reactive distances. An increase in visual distance and v will increase the encounter rate of predator with prey (Gerritsen & Strickler 1977). It has not been demonstrated how changes in visual distance and predator speed will affect the size frequency of prey encountered by predator. In our model, an encounter is determined by the apparent size (function of visual distance) and predator swimming speed. For example, a predator may see a 1 mm prey at a distance of 200 mm, but if the predator can not swim 200 mm in a time interval, then the predator will not encounter the prey within this time interval. Alternatively, a predator may capture a 0.5 mm prey at a distance of 100 mm which will have the same apparent size as a larger prey at the further distance. Therefore, an increase in predator swimming speed increases the reactive distance, which enables the predator to encounter an increased number of prey over longer distances. An increase in visual distance gives the predator more opportunities to encounter smaller prey within the reactive field determined by the predator swimming speed. If we increase both predator swimming speed and visual distance, it increases the overall encounter rate but does not change size frequencies of prey encountered. Our results also indicated that when the reactive distance was below the visual distance, there were differences in sizes of prey selected between random and largest AC. Wetterer & Bishop (1985) reported a similar result for brook stickleback *Culaea inconstans* when reactive distances were not directly proportional to prey length.

The model prediction of prey size frequency matched reasonably well with the size frequency of prey found in bay anchovy stomachs despite many possible errors involved. First, the patchiness of zooplankton in the water column could give a different prey distribution from what bay anchovies were really feeding on. Second, errors could have been caused by integrative water column sampling (from bottom to surface). Third, errors could have been caused by the size selectivity of the sampling gear (missing small sizes by the net, missing large sizes by the pump). Errors could also have occurred in processing the samples, such as, error in measuring preserved zooplankton, error in measuring partially digested prey from fish stomachs. Finally, light intensity at different depths could also contribute to variability in diet size. As shown in Table 2, the best fit for each month came from a different combination of visual distance, swimming speed, and capture efficiency. Is it reasonable to assume that these are variable across seasons or days? Visual distances and the capture efficiencies are functions of light intensity,

predator size, prey size, prey motility, and prey transparency (Wright & O'Brien 1984, Aksnes & Giske 1993, Miller et al. 1993). Since our bay anchovy samples were collected with midwater trawls at different depths (7 to 30 m, Klebasko 1991) in the months sampled, light intensities at those depths could affect visual distance, swimming speed, and capture efficiency. For example, if the light intensity at the surface is 1000 lux and the light attenuation coefficient is 1 m^{-1} , the light intensity at 5 m and 10 m will be 6.7 and 0.05 lux, respectively. Aksnes & Giske's (1993) theoretical visual feeding model predicts that for a 10 cm predator and 1 mm prey, the visual range is approximately 80 cm at 1000 lux light intensity, 20 cm at 10 lux light intensity, and less than 5 cm at 0.1 lux light intensity. Therefore, depth is likely to affect the visual distances of the bay anchovy. Also, swimming speeds among schooling fish is quite variable (Beamish 1978). Swimming speed depends on species, fish size, location, water temperature (Bergman 1987), and light intensity (Blaxter & Batty 1985). In our model, we used swimming speeds ranged from 50 to 150 mm s^{-1} (1 to 3 body lengths s^{-1}), which are within the range found in clupeoids (Beamish 1978). Since our results indicated that even the worst fit curves matched the general pattern of size frequencies of prey consumed by the bay anchovy, we believe the parameters used were reasonable and the technique is robust.

In summary, model simulations demonstrate that the size frequency of prey randomly encountered by a visual feeding planktivore is different from the size frequency of prey in the surrounding water. Model simulations indicate that there is no difference in the size frequency of prey selected by RC or by AC when the reactive distance is equal to the visual distance. There are differences between the 2 choices when the reactive distance is less than the visual distance. In prey distance distribution, the AC assumption always results in more prey being selected at closer distances. In a comparison with field data, the model predictions successfully characterize the size frequency of prey found in the stomachs of the bay anchovy in mid-Chesapeake Bay. We conclude: (1) the apparent prey size selection by the bay anchovy can be described mostly by differential random encounter from a fish's perspective, and that the behavioral choice only plays a minor role in prey size selection; (2) the 'traditional' approach used for assessing prey selectivity by comparing prey size distribution in the environment to that in the diet is incorrect because the prey size distribution actually perceived by the fish differs appreciably from that in the environment; (3) the ability of larger prey to escape from the predator is compensated for by the higher encounter rate.

The SFM has good potential for the study of planktivore and plankton interactions in aquatic systems. The

model is only applicable to a pelagic predator (i.e. piscivore or planktivore) that visually feeds on individual prey organisms. If the model works for other visual feeding planktivorous species, it could provide an excellent tool for mechanistically predicting prey size selectivity of these fishes in the field based on knowing the size distributions of predators and prey. Conversely, if we have preserved fish collected long ago we may be able to reconstruct the ambient prey size distribution in the water column. Model results also can be used to estimate the relative size dependent mortality due to planktivore predation. Future model developments include changing the randomness assumption in prey and predator movements, allowing predation to alter prey density and size distribution through time, incorporating additional environmental parameters and running the model in a spatially heterogeneous environment (Brandt & Kirsch 1993, Mason & Patrick 1993).

Appendix 1. Abbreviations and symbols used in the model

A_i	Apparent size of the i th prey
AC	Apparent size choice
ASM	Apparent size model
$Ca(L)$	Number of prey captured
$Caf(L)$	Frequency distribution of prey captured
CE	Capture efficiency
D_i	Prey distance distribution, proportion of prey at each distance interval
d_i	Distance between the predator and the i th prey
EFM	Encounter frequency model
$En(L)$	Number of prey encountered
$Enf(L)$	Frequency distribution of prey encountered
i	Index of L_i
j	Index of L_j
k	Light attenuation coefficient (m^{-1})
L_j	Prey size class variable, $j = 1, \dots, m$
L_i	Size of the i th prey (mm)
L_p	Predator length (mm)
m	Number of prey size classes
N	Number of prey
OFM	Optimal foraging model
RC	Random size choice
Rd	Reactive distance, maximum distance at which the predator would attack a prey
RFVM	Reactive field volume model
$Se(L)$	Number of prey selected (attacked)
$Sef(L)$	Frequency distribution of prey selected
SFM	Spatial foraging model
t	Time step
$u(i), u$	Swimming speed of the i th prey ($mm\ s^{-1}$)
v	Predator swimming speed ($mm\ s^{-1}$)
Vd_i	Visual distance, maximum distance at which the predator can see the i th prey
$x(i), x$	x coordinate of prey i
$y(i), y$	y coordinate of prey i
$z(i), z$	z coordinate of prey i
x_p	x coordinate of predator
y_p	y coordinate of predator
z_p	z coordinate of predator

Acknowledgements. We thank Kyle Hartman, John Horne, Doran Mason, Gary Mittelbach, Jeffrey Tyler, and anonymous reviewers for their helpful comments on the manuscript. This research was supported in part by grants from the National Science Foundation, Biological Oceanography Program (OCE-9116071 and OCE-9415740) and the Environmental Protection Agency Chesapeake Bay Program.

LITERATURE CITED

- Aksnes DL, Giske J (1993) A theoretical model of aquatic visual feeding. *Ecol Model* 67:233–250
- Baird RC, Hopkins TL (1981) Trophodynamics of the fish *Valenciennellus tripunctulatus*. 2. Selectivity, grazing rates and resource utilization. *Mar Ecol Prog Ser* 5:11–19
- Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) *Fish physiology*, Vol VII. Locomotion. Academic Press, New York, p 101–189
- Bergman E (1987) Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. *Environ Biol Fish* 19:45–53
- Blaxter JHS, Batty RS (1985) Herring behaviour in the dark: responses to stationary and continuously vibrating obstacles. *J Mar Biol Assoc UK* 66:1031–1049
- Brandt SB, Kirsch J (1993) Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans Am Fish Soc* 122:845–869
- Brooks JL, Dodson SI (1965) Predation, body size, and composition plankton. *Science* 150:28–35
- Butler SM, Bence JR (1984) A diet model for planktivores that follow density-independent rules for prey selection. *Ecology* 65:1885–1894
- Chesson J (1978) Measuring preference in selective predation. *Ecology* 59:211–215
- Collic JS (1987) Food selection by yellowtail flounder (*Limanda ferruginea*) on Georges Bank. *Can J Fish Aquat Sci* 44:357–367
- Confer JL, Blades PI (1975) Omnivorous zooplankton and planktivorous fish. *Limnol Oceanogr* 20:571–579
- Confer JL, Mills EL, O'Bryan L (1990) Influence of prey abundance on species and size selection by young yellow perch (*Perca flavescens*). *Can J Fish Aquat Sci* 47:882–887
- Eggers DM (1977) The nature of prey selection by planktivorous fish. *Ecology* 58:46–59
- Eggers DM (1982) Planktivore preference by prey size. *Ecology* 63:381–390
- Fleiss JL (1973) *Statistical methods for rates and proportions*. John Wiley and Sons, New York
- Forrester GE, Chace JG, McCarthy W (1994) Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environ Biol Fish* 39:301–311
- Gabriel WL (1979) Statistics of selection. In: Lipovsky SJ, Simenstad CA (eds) *Outshop 1978: fish food habits studies*. Proceeding of the 2nd Pacific Northwest Technical Workshop. Washington Sea Grant, Seattle, p 62–66
- Gardner MB (1981) Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* 62:571–578
- Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J Fish Res Bd Can* 34:73–82
- Grover JJ, Olla B L (1986) Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*. *Fish Bull US* 84:484–489
- Harding LW Jr (1994) Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. *Mar Ecol Prog Ser* 104:267–291

- Houde ED (1978) Critical food concentrations for larvae of three species of subtropical marine fishes. *Bull Mar Sci* 28: 395–411
- Hutchinson BP (1971) The effect of fish predation on the zooplankton of ten Adirondack lakes, with particular reference to the alewife, *Alosa pseudoharengus*. *Trans Am Fish Soc* 100:325–335
- Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven
- Jacobs J (1974) Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* 14:413–417
- Johnson WS, Allen DM, Ogburn MV, Stanczyk SE (1990) Short-term predation responses of adult bay anchovies *Anchoa mitchilli* to estuarine zooplankton availability. *Mar Ecol Prog Ser* 64:55–68
- Khadka RB, Ramakrishna RT (1986) Prey size selection by common carp (*Cyprinus carpio*) larvae in relation to age and prey density. *Aquaculture* 54:89–96
- Klebasko MJ (1991) Feeding ecology and daily ration of bay anchovy (*Anchoa mitchilli*) in the mid-Chesapeake Bay. MS thesis, Univ of Maryland, College Park
- Lasker R (1975) Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish Bull US* 73:453–462
- Lasker R (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp PV Reun Cons Int Explor Mer* 173:212–230
- Luecke C, O'Brien WJ (1981) Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Can J Fish Aquat Sci* 38:1264–1270
- Luecke C, Nanni MJ, Magnuson JJ, Kitchell JF, Jacobson PT (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: implications for the spring-water phase. *Limnol Oceanogr* 35:1718–1733
- Luo J (1991) The life history of the bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay. PhD dissertation, College of William and Mary, Williamsburg, VA
- Luo J, Brandt SB (1993) Bay anchovy, *Anchoa mitchilli*, production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. *Mar Ecol Prog Ser* 98:223–236
- Lynch M (1979) Predation, competition, and zooplankton community structure: an experimental study. *Limnol Oceanogr* 24:253–274
- MacKenzie BR, Leggett WC (1991) Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. *Mar Ecol Prog Ser* 73:149–160
- Magnhagen C (1985) Random prey capture or active choice? An experimental study on prey size selection in three marine fish species. *Oikos* 45:206–216
- Main KL (1985) The influence of prey identity and size on selection of prey by two marine fishes. *J Exp Mar Biol Ecol* 88:145–152
- Mason DM, Patrick EV (1993) A model for the space-time dependence of feeding for pelagic fish populations. *Trans Am Fish Soc* 122:884–901
- McDonald ME, Crowder LB, Brandt SB (1990) Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in fish community. *Limnol Oceanogr* 35:220–227
- Mikheev VN (1984) Prey size and food selectivity in young fishes. *J Ichthyol* 24:66–76
- Miller TJ, Crowder LB, Rice JA, Marschall EA (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can J Fish Aquat Sci* 45:1657–1670.
- Miller TJ, Crowder LB, Rice JA (1993) Ontogenetic changes in behavioural and histological measures of visual acuity in three species of fish. *Environ Biol Fish* 37:1–8
- Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386
- Munk P, Kjørboe T (1985) Feeding behaviour and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. *Mar Ecol Prog Ser* 24:15–21
- O'Brien WJ (1979) The predator-prey interaction of planktivorous fish and zooplankton. *Am Sci* 67:572–581
- O'Brien WJ, Evans B, Luecke C (1985) Apparent size choice of zooplankton by planktivorous sunfish: exceptions to the rule. *Environ Biol Fish* 13:225–233
- O'Brien WJ, Slade NA, Vinyard GL (1976) Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57:1304–1310
- Park SK, Miller KW (1988) Random number generators: good ones are hard to find. *Commun ACM* 31:1192–1201
- Pastorok RA (1981) Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62:1311–1424
- Schmitt PD (1986) Prey size selectivity and feeding rate of larvae of the northern anchovy, *Engraulis mordax* Girard. *Calif Coop Oceanic Fish Invest Rep* 27:153–161
- Scott MA, Murdoch WW (1983) Selective predation by the backswimmer, *Notonecta*. *Limnol Oceanogr* 28:352–366
- Sprules WG (1972) Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology* 53:375–386
- Stein RA, Threllkeld ST, Sandgren CD, Sprules WG, Persson L, Werner EE, Neill WE, Dodson SI (1988) Size-structured interactions in lake communities. In: Carpenter SR (ed) *Complex interactions in lake communities*. Springer-Verlag, New York, p 161–179
- Vanni MJ (1986) Fish predation and zooplankton demography: indirect effects. *Ecology* 67:337–354
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Wetters JK (1989) Mechanisms of prey choice by planktivorous fish: perceptual constraints and rules of thumb. *Anim Behav* 37:955–967
- Wetters JK, Bishop CJ (1985) Planktivore prey selection: the reactive field volume model vs. the apparent size model. *Ecology* 66:456–464
- Wright DI, O'Brien WJ (1984) The development and field test of a tactical model of the planktivorous feeding white crappie (*Pomoxis annularis*). *Ecol Monogr* 54:65–98
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall, Inc, Englewood Cliffs, NJ