

A General Model of Selectivity for Fish Feeding: A Rank Proportion Algorithm

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Abstract.—Given that various prey are available to fish in a particular ecosystem, by default fish feed selectively. Studies of fish feeding ecology have provided key insights into the dynamics of aquatic ecosystems, yet prey selectivity is the least addressed component of these studies. This may be due to the higher level of effort associated with examining both the stomach contents and ambient prey abundance, the assumption that a determined diet composition is static, or the lack of a predictive protocol for a priori estimates of prey selectivity and diet composition. Here I present a rank proportion algorithm (RPA) model that predicts prey preference from first principles of predation that, when coupled with ambient prey concentrations, can predict prey utilization (i.e., diet composition). I applied the model to benthivore, planktivore, and piscivore examples from lentic, lotic, estuarine, and marine ecosystems. Compared with observed stomach contents, the RPA model's predictions of diet composition exhibited more than 83% accuracy, and in most of the cases the model predicted the predominant prey item accurately; the entire prey rank order was predicted correctly on the order of 70–80% of the time. Additionally, more than 85% of the prey items were predicted to be within 10% of observed values, and over 70% were within 5%. The results of the RPA model were notably different from those of the null model of no selectivity. The results suggest that the RPA model is a useful tool when prey preference or stomach composition data are limited but required for other applications and that a general knowledge of the predation process is useful in obtaining quantitative information about fish diet.

Understanding how aquatic organisms interact and the derivatives of these interactions (i.e., ecosystem structure, function, production, and dynamics) is inherently valuable and socially beneficial. Predator–prey interactions can ultimately determine the fate and flux of every population in an ecosystem, particularly upper-level consumers of economic importance (Sissenwine 1984; Carpenter et al. 1985; McQueen et al. 1986; Bax 1991, 1998; Christensen 1996; Mittelbach and Persson 1998). The vast majority of secondary, tertiary, and other apex consumers in aquatic ecosystems are fish; thus, the impacts and dynamics of fish feeding have implications for nearly every aquatic ecosystem.

Given that various prey are available to fish in a particular ecosystem, by default fish feed selectively. Fish consume whatever they feasibly can given their anatomical, physiological, and prey abundance constraints. Yet fish can learn to focus on a particular group of prey that are relatively abundant or easy to capture (Ware 1971, 1973; Vinyard 1980; Dill 1983; Keiffer and Colgan 1992; Reiriz et al. 1998). Therefore, all fish feed

opportunistically but exhibit noticeable prey preferences (Gerking 1994).

Studies of fish feeding ecology have provided key insights into the dynamics of aquatic ecosystems. Theories and approaches such as particle size dynamics (Sheldon et al. 1972; Thiebaut and Dickie 1993), size-selective predation (Hrbacek 1962; Brooks and Dodson 1965; Hall et al. 1976), optimal foraging (Werner and Hall 1974; Charnov 1976; Mittelbach 1981), mass balance (e.g., bioenergetic modeling: Ney 1990; Hewett and Johnson 1992; Jobling 1994; ECOPATH/ECOSIM: Christensen and Pauly 1992; Walters et al. 1997), and multispecies virtual population analysis (Andersen and Ursin 1977; Helgason and Gislason 1979) implicitly assume prey selectivity. When prey selectivity is coupled with estimates of consumption rates, functional and numerical responses, predator biomass, or prey biomass, then critical fisheries and ecological issues can be addressed. Yet of these, prey preference and utilization are the factors that are least addressed in the majority of studies and monitoring efforts due to the higher level of effort and cost associated with examining both the stomach contents and ambient prey abundance, the assumption that a determined diet composition is static, or the lack of a predictive protocol for a priori estimates of selectivity and diet

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composition. Often parameterization of preference and diet composition is ad hoc, derived from the literature, based on the assumption that prey preference is equal to prey abundance, or simply not done.

Predation has been decomposed into a sequence of components (Holling 1959; O'Brien 1979). Generally, these components are detection (or encounter, which implies search), pursuit, attack (often combined with pursuit in the term "reaction"), capture (or handling), and retention, ultimately ending in ingestion. The process of detection involves a fish's encountering, locating, and identifying a prey item. In pursuit, a fish alters swimming velocity and course to intercept the prey. An attack involves coordinating acceleration through the location of a prey item and either inhalation of a volume of water to bring the prey item toward the buccal cavity or mandibular contraction on the prey item. Capture occurs when a prey item (or significant portion thereof) enters the buccal cavity and mandibular manipulation keeps the prey item inside that cavity. Retention involves the movement of a prey item across the gill rakers toward the esophageal tract. At each step in the predation process, selectivity occurs.

There is a suite of terms associated with selectivity (Manly et al. 1993). Here I define *selectivity* (in the context of predators eating certain prey items from a suite of potential items) as the entire process associated with "choosing" (either actively or instinctively) among all possible prey, such that preferential utilization is exhibited by a predator. Electivity is a synonym for the entire process of selectivity. I define *preference* as the favored choice of a predator due to the morphological, physiological, ontogenetic, and environmental factors associated with both predator and prey. Prey suitability or prey choice are synonyms for prey preference. I define *utilization* as the realized preference when preferences are coupled with an actual set of available prey (i.e., the ambient prey field), usually presented as diet composition. Diet composition is a synonym for prey utilization.

If one observes the "foraging" on donuts at a conference or seminar, a pattern typically emerges. Generally, the donuts with icing and those that are sprinkled with little candies tend to be consumed first, followed by those with plain icing, those that are sugared, and finally the plain ones. The pattern only differs if the abundance of a particular type of donut is altered (e.g., there are lots of plain donuts and only a few sprinkled ones). I propose

an "icing-on-the-donut," general selectivity theory for fish feeding. This differs from other selectivity and foraging models in making no assumptions as to energetics, profitability (i.e., optimal cost-benefit ratios), or risk trade-offs; rather, it is based on the physiological or anatomical constraints of predator preference coupled with the available prey items in a given environment. The hypothesis is that there is a set of general criteria—based on the past 40 or so years of empirical evidence—whereby one can determine a priori the prey preference of fish species given their characteristics and environmental conditions. Additionally, with this information and estimates of ambient prey concentrations, one can predict the prey utilization (diet composition) of fish. I develop and apply this generalized model to planktivorous, benthivorous, and piscivorous fish examples to predict prey preference and utilization.

Methods

An algorithm for a priori estimation of prey preference and utilization.—I submit that there is a generalized model whereby one can predict the prey preference and utilization of fish. Based on our understanding of each step in the predation process, one can assign priority to a suite of prey types for a particular predator under a given set of conditions. The model examines each component of predation as an individual event and ranks each prey item with respect to that factor for a particular predator. This set of ranks can then be combined into a simple formula, collectively termed the rank proportion algorithm (RPA), to simultaneously assess the preference of a particular predator for all potential prey items under a given set of conditions.

A preliminary step is to assess the general characteristics of a given predator j . In this regard, one should ask whether there are any conspicuous morphometric features that provide a clue as to the trophic ecology of the fish. For example, if the general body plan is dorsoventrally flattened (as in the Pleuronectiformes), one would suspect a benthic prey orientation for that fish. Is the caudal fin-aspect ratio particularly distinct? This ratio is indicative of the speed at which the predator swims (Palomares and Pauly 1989) and might provide some insight into whether the fish is more pelagic in orientation and a continual swimmer, thus being a tracker-chaser rather than a more dormant, ambush type of predator. Does the predator have a unique detection system that might be advantageous in some habitats but not in others? If so,

this may enhance or limit the types of prey that can be consumed. And so on, the point of this exercise being to determine whether there are any defining characteristics of the predator that would strongly influence the predation process.

The first step in the RPA is to determine all of the possible prey available (N) to predator j . This would not consist of all conceivable prey in the ecosystem but only those prey that are in the range that can actually be eaten by the predator (Scharf et al. 1998, 2000). Then the relative abundance (A ; also termed the null ambient) of each prey i can be estimated, ranging from 0 to 1 as percentages of the available prey field. The RPA model can accept abundance units as either numbers or biomass; the units simply need to be consistent with those of the stomach contents. Relative abundance negates the need to determine absolute abundance, which is often more difficult, and relative abundance is also unitless. If it is not possible to estimate relative abundance, these values can be set to unity for all prey and the RPA still executed. In that case the results will only provide predictions of prey preference and not prey utilization. This is an important distinction, as prey abundance can overshadow the importance of other components involved in prey selectivity (Gerritsen and Strickler 1977; Gerking 1994; Link and Keen 1999).

The next step in the RPA is to estimate the spatiotemporal overlap (O_{ij}) between the fish predator j and each prey species i . Fish cannot eat a particular prey if the two are not in the same place at the same time, even if they have a strong preference for that item. Schoener's (1970), Williamson's (1993; Williamson et al. 1989), and related overlap indices are germane for this purpose. Again, if these values are difficult or infeasible to estimate, they can be set to unity and the RPA executed assuming complete overlap of predator and prey. The overlap values are not required to run the RPA, but the model can accommodate them when available to provide a more refined estimate of feasible prey.

The next step in the RPA is to rank (R) each prey item i with respect to each factor m of the predation process, 1 being the highest rank and N (i.e., the total number of prey) the lowest, using an average value for the ranks of ties. Here it is important to determine whether there are any special prey attributes that would alter the ranking of any prey item for any component of the predation process. Prey attributes such as size (especially relative to other prey), color, spines, camouflage,

swimming speed and motion, and so forth, are vital in determining the importance of each step in predation. Habitat considerations are also important; for example, a visual predator will be more likely to express a prey preference under nonturbid, adequately lit water conditions. Given these considerations, ranks for detection, reaction, capture, and ingestion should be estimated for every feasible prey i . The model also has an "icing factor" whereby one can rank a particular prey item higher based on some special or localized knowledge (e.g., the fish have learned to feed on a particular type of prey, have a historical preference for a certain type of prey in a particular ecosystem, etc.). Like relative abundance or overlap, the icing factor is optional and can be set to unity for all prey if not used. Each factor m is weighted the same in the RPA across all the possible factors (M ; here equal to 5). This step of ranking each prey i for each factor m is arguably the most important part of the RPA and relies heavily on prior empirical observations.

After ranking, an adjusted (or inverse) rank R' for each factor should be calculated as follows

$$R'_{ijm} = |(N + 1) - R_{ijm}| \quad (1)$$

to account for the fact that 1 is the highest possible rank. Next, one should sum all the adjusted ranks for each factor m across all N prey items and then divide the adjusted rank by that sum to obtain a rank proportion (P) for each prey i :

$$P_{ijm} = \frac{R'_{ijm}}{\sum_{i=1}^N R'_{ijm}}, \quad (2)$$

where the denominator should be calculated as

$$\sum_{i=1}^N R'_{ijm} = \frac{N \cdot (N + 1)}{2}. \quad (3)$$

These rank proportions indicate the relative importance of each prey i for each factor m . Then the rank proportions should be multiplied across all factors (M) for each prey i to estimate the ultimate rank proportion (S_{ij}):

$$S_{ij} = \prod_{m=1}^M P_{ijm}. \quad (4)$$

This product can be considered an estimate of a preference proxy of predator j for each prey i .

The value of S_{ij} can be multiplied by the spatial overlap and the relative abundance (A_i) (when the latter two are available) of each prey i to provide

a proxy for prey utilization (i.e., diet composition, D_{ij}):

$$D_{ij} = S_{ij} \cdot O_{ij} \cdot A_i, \quad (5)$$

which, when evaluated relative to the summed value across all N prey provides a prediction of the diet composition of prey i in predator j (D'_{ij}):

$$D'_{ij} = \frac{D_{ij}}{\sum_{i=1}^N D_{ij}}. \quad (6)$$

If O_{ij} is not available, it can be set to unity and the diet composition estimated with the caveat that this consideration was not assessed. If A_i is not available, the preferences of predator j for each prey i (S'_{ij}) can be calculated in a similar fashion by substituting the preference proxies, S_{ij} s (equation 4), for the D_{ij} s (equation 6).

The null model of no selectivity and no dietary preference assumes no preference for any prey i across all M factors, each rank proportion for each factor m being set equally to

$$R_{ijm, \text{null}} = \frac{1}{\sum_{i=1}^N R_{ijm}}. \quad (7)$$

Substituting the values from equation (7) into the rest of the RPA provides the null prediction of no selectivity (termed null selectivity), effectively, equal preferences across all prey i with a preference value (S'_{ij}) of unity divided by N :

$$S'_{ij, \text{null}} = \frac{1}{N}. \quad (8)$$

If the abundance of each prey (A_i) is available, the null prediction of prey utilization can similarly be estimated. In such a case, the results of the null model (termed the null ambient) are determined entirely by relative prey abundance, prey utilization ($D'_{ij, \text{null}}$) being equal to the relative prey abundance (A_i).

Examples of the rank proportion algorithm.—Examples of the application of the RPA model are given in the Appendix. In the first example, a simple, two-prey situation is evaluated with respect to a large-gaped piscivore. In this hypothetical example, both prey items are equally abundant in the water column but one is preferred because it is less able to evade attacks, is captured easily, and is ingested with minimal difficulty. Thus we assign a rank of 1 to the first prey fish with respect to

reaction, capture, and ingestion and give the next highest rank (in this case, 2) to the other prey fish. The second fish can be more readily detected but can swim faster than the first fish. Thus we assign a rank of 1 to this second fish with respect to detection and the next highest rank to the first fish. We also assign a rank of 1 to the first prey item for the icing factor because we suspect that it is the preferred prey item. Assuming an overlap of 1, the rank matrix would be filled for all the predation factors.

Once the ranks are assigned, the RPA model can be executed on the proportional ranks, the product calculated, and model output, null selectivity, and null ambient values presented. Because in this case there were relative abundances for both prey, the RPA model can predict prey utilization. The result demonstrates a higher selectivity for the first prey item, as one would expect given the hypothetical conditions.

The second example of the application of the RPA model involves yellow perch *Perca flavescens* from an enclosure experiment (Confer et al. 1990). The first step in the RPA process is to note that in freshwater ecosystems yellow perch can be both benthivores and planktivores (e.g., Keast 1977; Mills and Forney 1981; Tyson and Knight 2001); however, this particular case was a field experiment and thus had a predetermined prey field of zooplankton. Because this was an experimental situation in 50 L of water, I set the spatiotemporal overlap values to unity for all prey items in the RPA. Only three species of prey were included in the experiments, two copepods and one cladoceran; in this particular example, the calanoid copepod was more abundant than the *Daphnia* or the cyclopoid copepod.

It is generally well known that visually feeding planktivores such as juvenile perch encounter large prey at a higher rate than small prey (Confer et al. 1978; Mills et al. 1984; Miller et al. 1993). Similarly, these fish react to and attack large prey more readily than small prey (Mills et al. 1984; Miller et al. 1993; see also Luecke and O'Brien 1981; Dunbrack and Dill 1984; Wright and O'Brien 1984; O'Brien 1987; Link 1998); notably, they pursue cladocerans more readily than copepods of the same size due to the former's slower swimming ability (Mills et al. 1984; O'Brien 1987). Thus, I ranked *Daphnia* first for detection and reaction, calanoid copepods second, and cyclopoid copepods third. However, large prey generally have a higher probability of escaping than small prey, as do copepods relative to cladocerans

of a similar size (Mills et al. 1984; see also Confer et al. 1978; Wright and O'Brien 1984; O'Brien 1987; Link 1996). Thus I ranked *Daphnia* first for capture, cyclopoid copepods second, and calanoid copepods third. Cladocerans are retained on the gill rakers much more than copepods of a similar size (Galbraith 1967; O'Brien 1987) due to their body shape. In general, cyclopoid copepods are rounder than calanoid copepods, and that was true in this case. I ranked *Daphnia* first for the ingestion factor, followed by cyclopoid copepods and calanoid copepods. Finally, most fish develop a learned response to prefer cladocerans over copepods (in the sense of Ware 1971, 1973 and Vinyard 1980). I used the icing factor to incorporate this suspected response by ranking *Daphnia* first, followed by calanoid copepods and cyclopoid copepods.

Once the ranks were assigned, the RPA model was executed on the proportional ranks, the product calculated, and model output, null selectivity, and null ambient values presented. The relative abundances (i.e., null ambient) of these prey were determined a priori as part of a series of experiments. Thus, the RPA model could predict prey utilization, which was then compared with observed stomach contents (see below). The example effectively reveals the preference for *Daphnia* that one would expect. This particular example and the associated model diagnostics are discussed further below.

The third example of the application of the RPA model involves lake herring *Coregonus artedii* from Lake Superior. The first step in the RPA process was to note that lake herring are principally planktivores and not likely to be large piscivores or benthivores (although it is possible for herring to consume both other fish and benthos). I did not have an index of spatiotemporal overlap, so I set those values to unity for all of the prey items in the RPA. At the same time as the stomach collections were made, plankton tows were taken to evaluate the prey field; from that set of information seven probable prey items were identified and their relative abundances estimated (Link et al. 1995).

From my own experience and the literature (Link et al. 1995; Link 1996; Link 1998; Link and Keen 1999), adult *Limnocalanus macrurus* is the largest calanoid copepod found in Lake Superior, followed by *Diaptomus sicilis*, juvenile *L. macrurus*, *Cyclops* spp., juvenile cyclopoid copepods, and nauplii. These organisms reasonably represent the prey field of Lake Superior pelagia in the winter, only nauplii exhibiting a different (i.e., steady-

er) swimming behavior. Based primarily on the size of these copepods, I ranked *L. macrurus* first in terms of detection and reaction by lake herring and so on down through the nauplii, a choice that was affirmed by reactive volume experiments on lake herring (Link 1998). In other words, species with the largest reactive volumes were ranked first for detection and reaction. I effectively reversed the order for capture, ranking the smallest and most weakly swimming nauplii first and so on up through *L. macrurus*, again a choice augmented by capture probability experiments on lake herring (Link 1996). Those species with the highest capture probabilities were ranked highest for capture. Ingestion was ranked equally for the first three species based on the lengths, widths, and breadths of *L. macrurus*, *D. sicilis*, and *Limnocalanus* copepodites and prior work on lake herring gill raker retention probabilities (Link and Hoff 1998). Species with the highest retention probabilities were ranked first for ingestion; this was continued through to the smallest prey. Finally, knowing that fish can learn to focus on common or preferred prey (Ware 1971, 1973; Vinyard 1980; Dill 1983; Keiffer and Colgan 1992; Reiriz et al. 1998), I ranked *D. sicilis* first in terms of the icing factor since it was the most abundant zooplankton species in Lake Superior during the early 1990s and we suspected that most fish had "learned" a search pattern for this particular prey item, as seen in prior diet studies. I then ranked the remaining species for this factor generally based on size and associated swimming strength and body dimensions. Unlike the previous example, which estimated different prey preferences based on a broader range of other factors, this example of the RPA effectively represents size-selective planktivory (Hrbacek 1962; Brooks and Dodson 1965; Hall et al. 1976).

Once the ranks were assigned, the RPA model was executed on the proportional ranks, the product calculated, and model output, null selectivity, and null ambient values presented. Because there were estimates of relative prey abundance, the RPA model could predict prey utilization, which was then compared to observed stomach contents. The example reveals the preference for *D. sicilis*, as one would expect.

Applying the algorithm to actual cases.—I calculated prey utilization (D'_{ij}) estimates with the RPA model for two planktivorous, four benthivorous, and two piscivorous fish species from various types of ecosystems (Table 1). These predictions were then compared with the stomach con-

TABLE 1.—Information about the fish used to test the rank proportion algorithm model. Each example included estimates of both stomach contents and ambient prey abundances.

Fish species	Life stage	Size (mm) ^a	Expected trophic type	Source	Location	Type of ecosystem	Date	Station and situation
Yellow perch	Young	45–54	Planktivore	Confer et al. 1990	Oneida Lake, New York (experiments)	Lacustrine	20 Jul 1983	50 L; enclosures
Lake herring	Adult	280–550	Planktivore	Link et al. 1995; Link and Keen 1999	Lake Superior	Lacustrine	9 Mar 1994	Chaquemagon Bay, Apostle Islands; all fish sizes
Dover sole <i>Microstomus pacificus</i>	Juvenile to adult	11–42	Benthivore	Gabriel and Pearcy 1981	Northeastern Pacific off Oregon	Marine	20–24 Jun 1976	SG29 (119 m) using numerical abundance; all fish sizes
Catfish ^b <i>Synodontis zambezensis</i>	Mainly adult	12–39.2	Benthivore	Sanyanga 1998	Lake Kariba, Zimbabwe	Lacustrine	Nov 1995–Feb 1996	Fothergill using numerical abundance; all fish sizes
Brown trout <i>Salmo trutta</i>	Juvenile	~40	Benthivore	Kreivi et al. 1999	River Kuusinkijoki, Finland	Riverine	15 Jul 1991	Day; Raatekoski rapids
Shortfinned eel <i>Anguilla australis</i>	Adult	200–300	Benthivore	Sagar and Glova 1998	Cust River, New Zealand	Riverine	3–4 Feb 1997	Large fish
Bluefish <i>Pomatomus saltatrix</i>	Age 0	61–142	Piscivore	Juanes et al. 2001	Great South Bay, Long Island, New York (experiments)	Estuarine/marine	30 Jun 1999	Only shrimp and fish prey categories
Bluefish	Juvenile	~100–150	Piscivore	Buckel et al. 1999; Buckel, personal communication	Hudson River, New York	Estuarine	1–17 Jul 1990	Numerical abundance; (minor) invertebrates excluded

^a Centimeters for Dover sole and catfish (plain squeaker).

^b Also known as plain squeaker.

tents of these fish as well as with the null selectivity and null ambient values. To determine how well the RPA model performed, a two-sided Wilcoxon signed ranks test was applied to the RPA model output and observed diet composition (Kohler and Ney 1982). A test was not executed if there were less than three prey types for a predator. The statistical tests evaluated model accuracy for each case.

To further evaluate RPA model accuracy, I determined whether the dominant prey item was predicted correctly and how well the predicted rank order of all prey items compared with the observed ranks. This evaluation of correct rank order provided another indication of model accuracy. Additionally, I tallied the absolute difference (in per-

cent) between the diet composition predicted by the RPA model and that observed in the stomachs to further evaluate model accuracy. Differences of less than 10% were deemed reasonably precise, and differences of more than 10% were particularly notable. All indices of accuracy were evaluated across all examples to ascertain overall RPA model performance.

Results

In a rather simple scenario, the RPA model accurately predicted the diet composition of an example planktivore, the juvenile yellow perch, which exhibited a notable preference for *Daphnia* (Figure 1A; Table 2). There was no significant difference between the predicted and observed diet

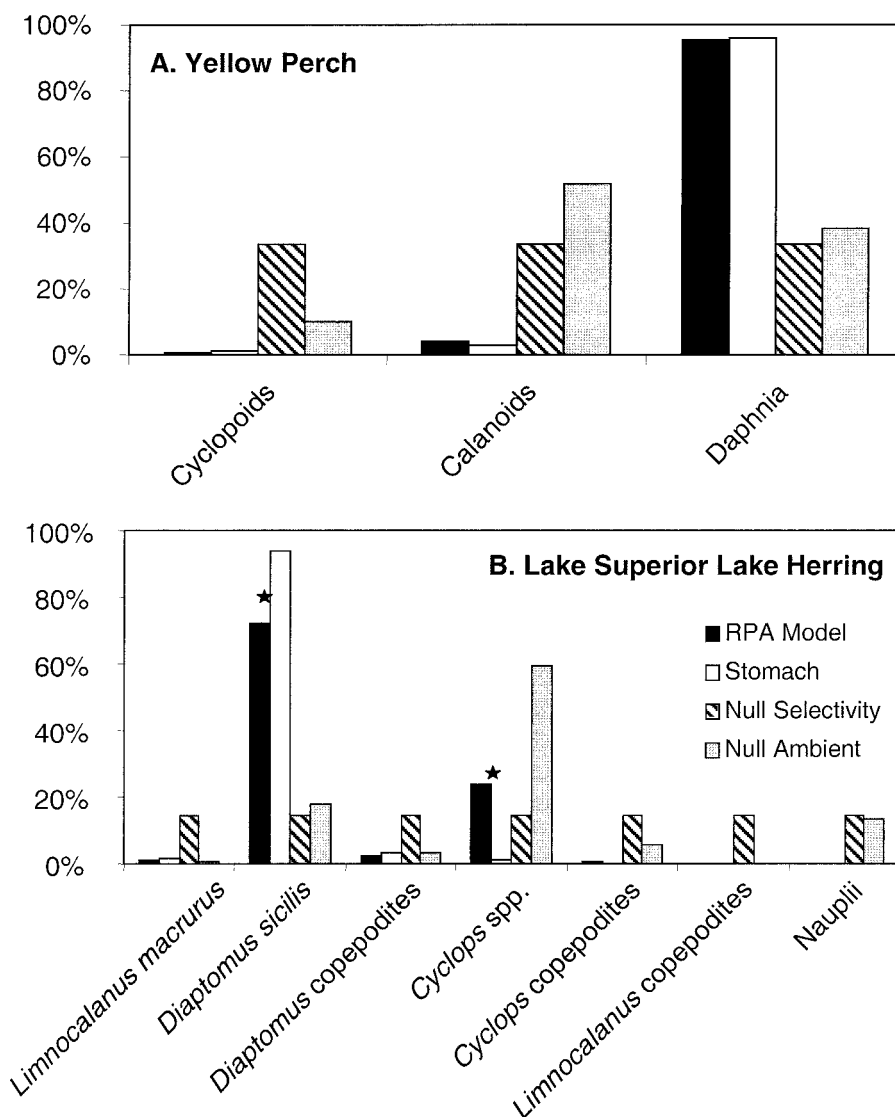


FIGURE 1.—Percent diet composition predicted by the rank proportion algorithm (RPA) model and that observed in the stomachs of (A) yellow perch and (B) Lake Superior lake herring contrasted with the null selectivity (random) and null ambient (relative-abundance) estimates of diet composition. Stars indicate prey items that exhibited notable differences (>10%) between the RPA model predictions and stomach contents. The differences between the model predictions and null selectivity were notable, indicating that fish were engaged in nonrandom feeding.

compositions across all three prey items for this fish (Tables 2, 3). The model was accurate, correctly predicting the rank order of all three prey, and all predictions were within 2% of the observed stomach content values. The differences between the RPA model and null selectivity were notable, indicating nonrandom feeding. Additionally, the observed fish stomachs and RPA model output both exhibited prey selectivity very different from the ambient prey field.

The predictions of the RPA model were not significantly different from the observed stomach contents in the other planktivore example (lake herring; Figure 1B; Table 2). The first prey item was predicted correctly, and the model was 85% accurate in terms of prey rank order. However, diet composition was incorrectly predicted for *D. sicilis* and *Cyclops* spp. (Table 3), the observed diet compositions differing from the predicted values by 15–25%. The remaining 71% of the RPA model

TABLE 2.—Evaluation of the accuracy of the rank proportion algorithm (RPA) model’s output relative to observed stomach contents. Whether a scenario was significantly different or not was based on the Wilcoxon signed ranks test. Two examples had no significant differences but were not tested due to the small number of categories. Whether the RPA model correctly predicted the most important prey (first rank correct; yes [Y] or no [N]) is also noted, as is the order (correct rank order) of RPA model predictions compared with observed stomach contents, defined here as a difference of no more than rank. Numbers in parentheses denote the percentage of all prey items within each category; NS = not significant ($P > 0.10$).

Fish species	Number of prey	Significant difference	First rank correct	Correct rank order (+/- 1 rank)
Yellow perch	3	NS	Y	3 (100%)
Lake herring	7	NS	Y	6 (85.7%)
Dover sole	10	NS	Y	8 (80%)
Catfish ^a	9	$P < 0.02$	N	4 (44.4%)
Brown trout	8	NS	N	6 (75%)
Shortfinned eel	19	NS	Y	14 (73.7%)
Bluefish (age 0)	2	NA	Y	2 (100%)
Bluefish	5	NS	Y	3 (60%)
Overall	63	5/6 (83.3%)	6/8 (75%)	46 (73%)

^a Also known as plain squeaker.

prey composition predictions were within 2% of the observed values. The differences between the RPA model and null selectivity were notable, indicating nonrandom feeding. Also, the observed fish stomachs and RPA model output both exhibited prey selectivity very different from the ambient prey field.

The RPA model output for the marine benthivore example (Dover sole) did not significantly differ from the observed stomach contents (Figure 2A; Table 2). Dover sole primarily ate polychaetes and amphipods, which the RPA model accurately predicted. The model was 80% accurate in terms of prey rank order, and 100% of prey composition predictions were within 10% of observed stomach contents, 80% of those predictions being within 2% (Table 3). The differences between the RPA

model and null selectivity were notable, indicating nonrandom feeding. The RPA model and observed fish stomachs did reflect some of the ambient prey field, but feeding on polychaetes and amphipods still appears to be greater than what would be predicted solely by the ambient prey field.

The RPA model output was significantly different from the observations for the lentic benthivore example (an African catfish also known as the plain squeaker; Figure 2B; Table 2); this was the worst fit of all the examples. The first prey item was predicted incorrectly, and the model was only 44% accurate in terms of prey rank order. The diet compositions for two of the prey were incorrectly predicted for this fish, with a difference greater than 25% between the observed and predicted values (Table 3). A major shift in the trend of the

TABLE 3.—Evaluation of the precision of the rank proportion algorithm (RPA) model’s output relative to observed stomach contents. The term “difference” refers to the absolute value of the difference in the percentages of predicted and observed diet composition. Numbers in parentheses denote the percentage of all prey items within each category. There were seven prey items that were notably different (>10%) between the RPA model output and observed stomach contents.

Fish species	Number of prey	Difference						
		>25%	15–25%	10–15%	5–10%	2–5%	1–2%	<1%
Yellow perch	3						1 (33.3%)	2 (66.7%)
Lake herring	7		2 (28.5%)				1 (14.3%)	4 (57.1%)
Dover sole	10				2 (20%)		2 (20%)	6 (60%)
Catfish ^a	9	2 (22.2%)			1 (11.1%)	2 (22.2%)	1 (11.1%)	3 (33.3%)
Brown trout	8		1 (12.5%)		2 (25%)	2 (25%)	1 (12.5%)	2 (25%)
Shortfinned eel	19			2 (25%)	2 (10.5%)	2 (10.5%)	1 (5.3%)	12 (63.1%)
Bluefish (age 0)	2							2 (100%)
Bluefish	5			2 (40%)	2 (40%)			1 (20%)
Overall	63	2 (3.2%)	3 (4.8%)	4 (6.3%)	9 (14.3%)	6 (9.5%)	7 (11.1%)	32 (50.8%)

^a Also known as plain squeaker.

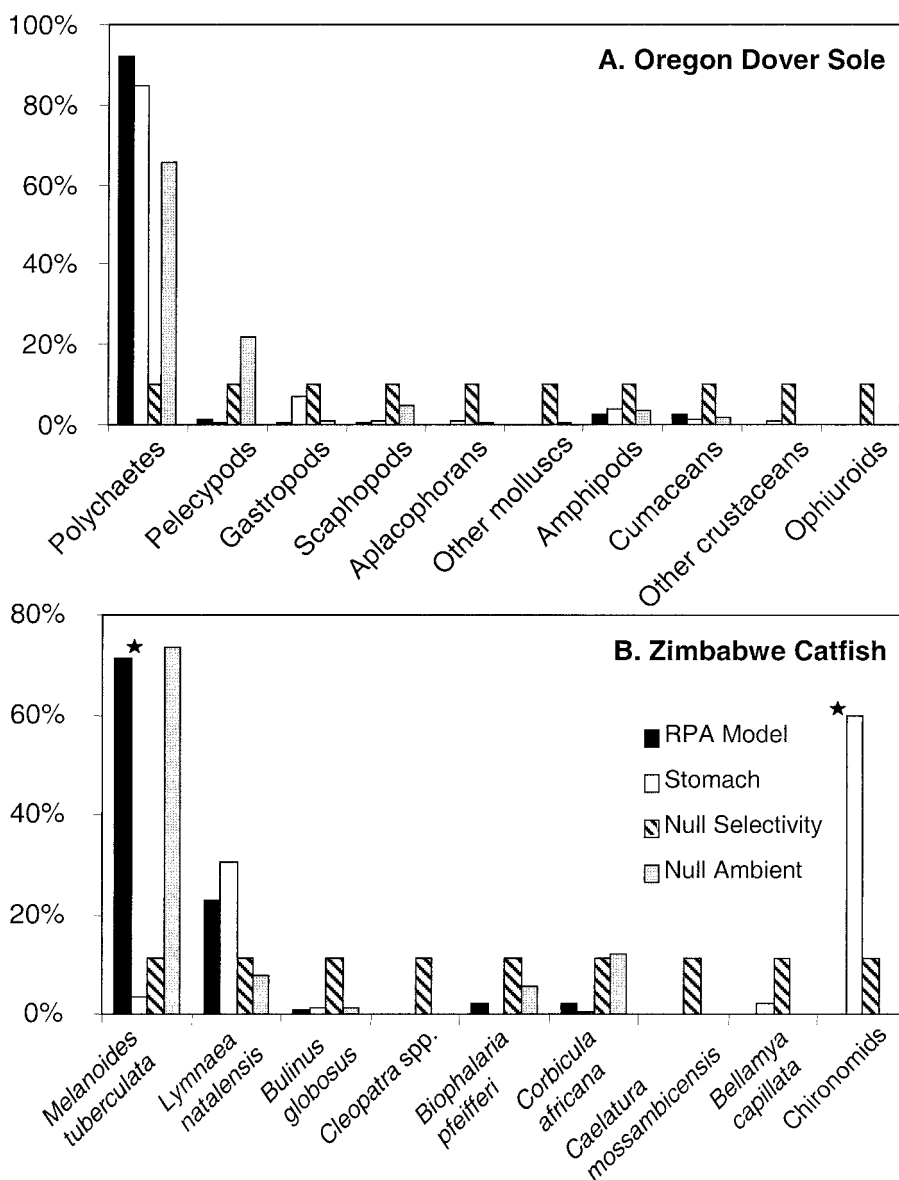


FIGURE 2.—Percent diet composition predicted by the rank proportion algorithm (RPA) model and that observed in the stomachs of (A) Oregon Dover sole and (B) Zimbabwe catfish contrasted with the null selectivity (random) and null ambient (relative-abundance) estimates of diet composition. Stars indicate prey items that exhibited notable differences (>10%) between the RPA model predictions and stomach contents. The differences between the model predictions and null selectivity were notable, indicating nonrandom feeding.

dominant prey item from chironomids in the observed diet to *M. tuberculata* (Mollusca: Gastropoda) in the predicted stomach contents is the primary reason the model did perform well in this example. Interestingly, 66.6% of the prey for this fish were predicted within 5%, most prey being predicted and observed to comprise a relatively small portion of the diet.

The RPA model results for a lotic benthivore (brown trout from Finland) were not significantly different from the observed stomach contents (Figure 3A; Table 2). The first prey item was predicted incorrectly, and the model was 75% accurate in terms of prey rank order. One prey item, chironomids, accounted for more than 15% of observed and predicted diet compositions (Figure 3A; Table

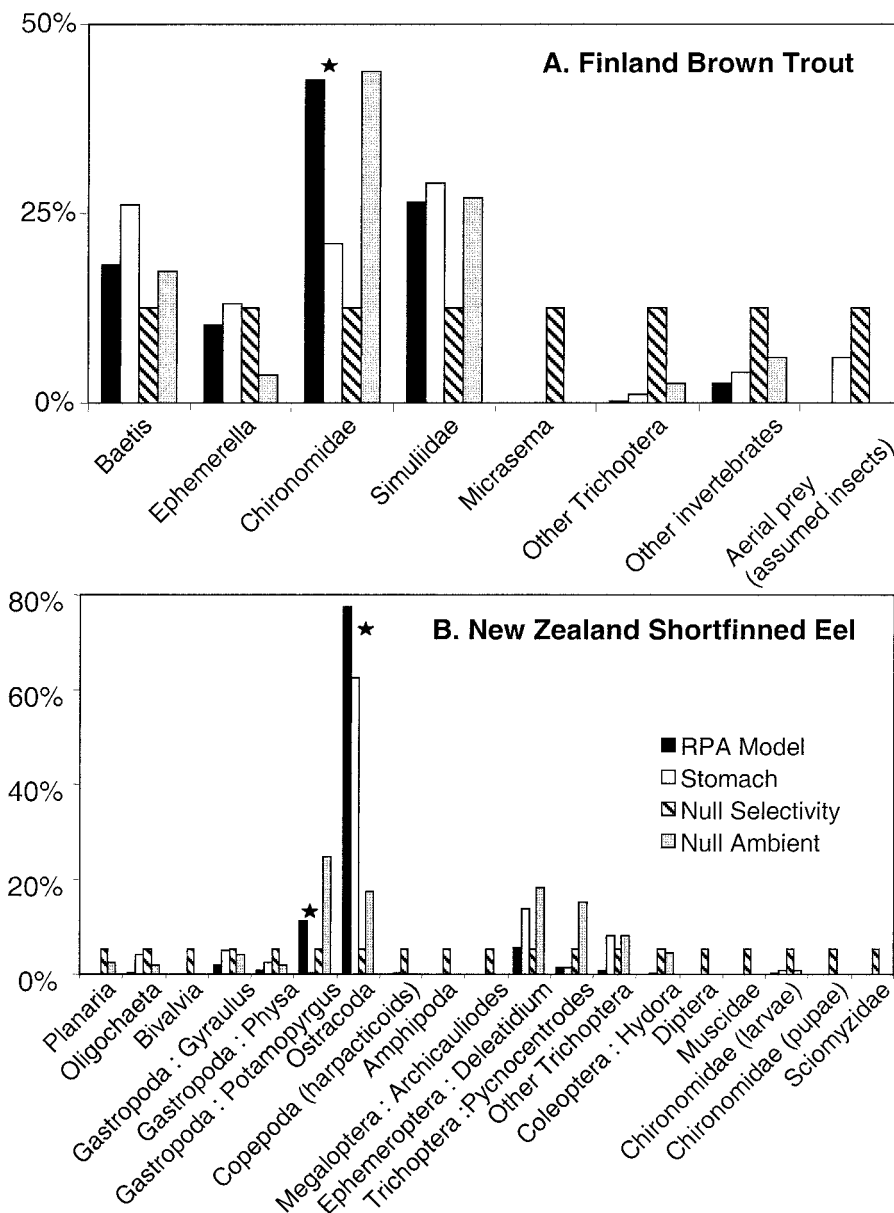


FIGURE 3.—Percent diet composition predicted by the rank proportion algorithm (RPA) model and that observed in the stomachs of (A) Finland brown trout and (B) New Zealand shortfinned eel contrasted with the null selectivity (random) and null ambient (relative-abundance) estimates of diet composition. Stars indicate prey items that exhibited notable differences (>10%) between the RPA model predictions and stomach contents. The differences between the model predictions and null selectivity were notable, indicating nonrandom feeding.

3). The remaining 87.5% of predicted prey values were within 10% of observed values. The differences between the RPA model and null selectivity were notable, indicating nonrandom feeding. The RPA model did reflect some of the ambient prey field, but the observed fish stomachs did not.

The RPA model results for the other lotic benthivore example (shortfinned eel from New Zealand) were not significantly different from the observed stomach contents (Figure 3B; Table 2). The first prey item was predicted correctly and the model was 74% accurate in terms of prey rank

order for this example. For 2 of the 17 prey items there was more than a 10% difference between the predictions and the observed stomach contents (Table 3). Yet nearly 80% of the predictions were within 5% of the observed values.

In the simplest example, the RPA model accurately predicted age-0 bluefish stomach contents (Figure 4A; Table 2). These fish exhibited a preference for fish over the more abundant shrimp, and the RPA model correctly predicted this preference. The model predicted diet compositions within 1% of observed stomach content (Table 3).

The RPA model output for the other piscivore example was not significantly different from the observed stomach contents (Figure 4B; Table 2). Although the model predicted the first prey accurately, only 60% of the rank order was predicted accurately. This probably reflects the fact that these somewhat larger bluefish exhibited a slight preference for age-0 striped bass, which the RPA model did not predict. The model was less precise than in the other examples, only 60% of its predictions being within 10% of the observed stomach content values (Table 3). The differences between the RPA model and null selectivity were notable, indicating nonrandom feeding. Additionally, the observed fish stomachs and RPA model output both exhibited prey selectivity very different from the ambient prey field.

Across all eight examples, the RPA model was 83% accurate in terms of not significantly differing from observed stomach contents. Two cases exhibited 100% accuracy with respect to the rank order of the prey; the worst case was on the order of 45%, the remainder being in the 70–80% range. In most cases the model predicted the dominant prey item accurately. Although the absolute diet composition was notably different in some cases, with the exception of the African catfish (Figure 2B), the trends in overall diet composition were adequately represented (Tables 2, 3). More than 85% of the prey items were predicted to be within 10% of observed values, over 70% were within 5%, and over 60% were within 2% (Table 3). Certainly, there were a few instances in which the model was generally accurate but exhibited major differences in diet composition for one or two prey items; however, most of the model results exhibited reasonable differences (i.e., <5%).

In all examples, the model's results were notably different from null selectivity (i.e., random feeding). Additionally, in most cases the observed fish stomachs and RPA model output both exhibited prey selectivity very different from the ambient

prey field. These results imply that fish generally feed selectively and that the model tracks this selectivity reasonably well.

Discussion

The RPA model predicts fish prey preference and utilization reasonably well for a wide range of ecosystems and a wide range of fish, with an overall accuracy of 80–85%. The fish examined in this study also exhibit a wide range of feeding strategies, the results of which are accurately represented by the model. Certainly the model could use a broader range of testing and validation from other ecosystems and types of fish (e.g., reef fish, detritivores, etc.), yet it was designed to be and should be robust for the vast majority of situations. Overall, the RPA model adequately represents the predation process for a wide range of fish.

The RPA results confirm and accurately convey general paradigms of fish feeding theory. The results for the two planktivores are consistent with size-selective planktivory (Hrbacek 1962; Brooks and Dodson 1965; Hall et al. 1976). The results for the benthivorous Dover sole are consistent with other observations of small-gaped flatfish (e.g., Pearcy and Hancock 1978; Livingston 1987; Zhang 1988). The piscivore examples are generally consistent with what one would expect these fish to eat, particularly in light of ontogenetic changes in the younger fish (Juanes et al. 1994; 2002). The very good fits for stream-dwelling benthivores are also consistent with what one would expect from similar series of evidence (e.g., Newman and Waters 1984; Newman 1987; Dunbrack 1992).

The chief limitation of the RPA approach is its reliance on expertise, including expert knowledge of the local system, the particular fish species under examination, the appropriate taxonomy to ascertain the relevant prey field, and fish feeding ecology in general. This limitation is not entirely negative, but it may preclude the use of the RPA model by all but those individuals familiar with a particular ecosystem or set of fish and their prey. However, most trained aquatic science professionals have an adequate working knowledge of the particular system under examination (or the resources [or colleagues] to obtain such knowledge) and should be able to reasonably replicate RPA results. Further refinements of the model should derive from model performance based on a wider set of test cases. These refinements could provide some perspective on the variance of the currently deterministic RPA model outputs.

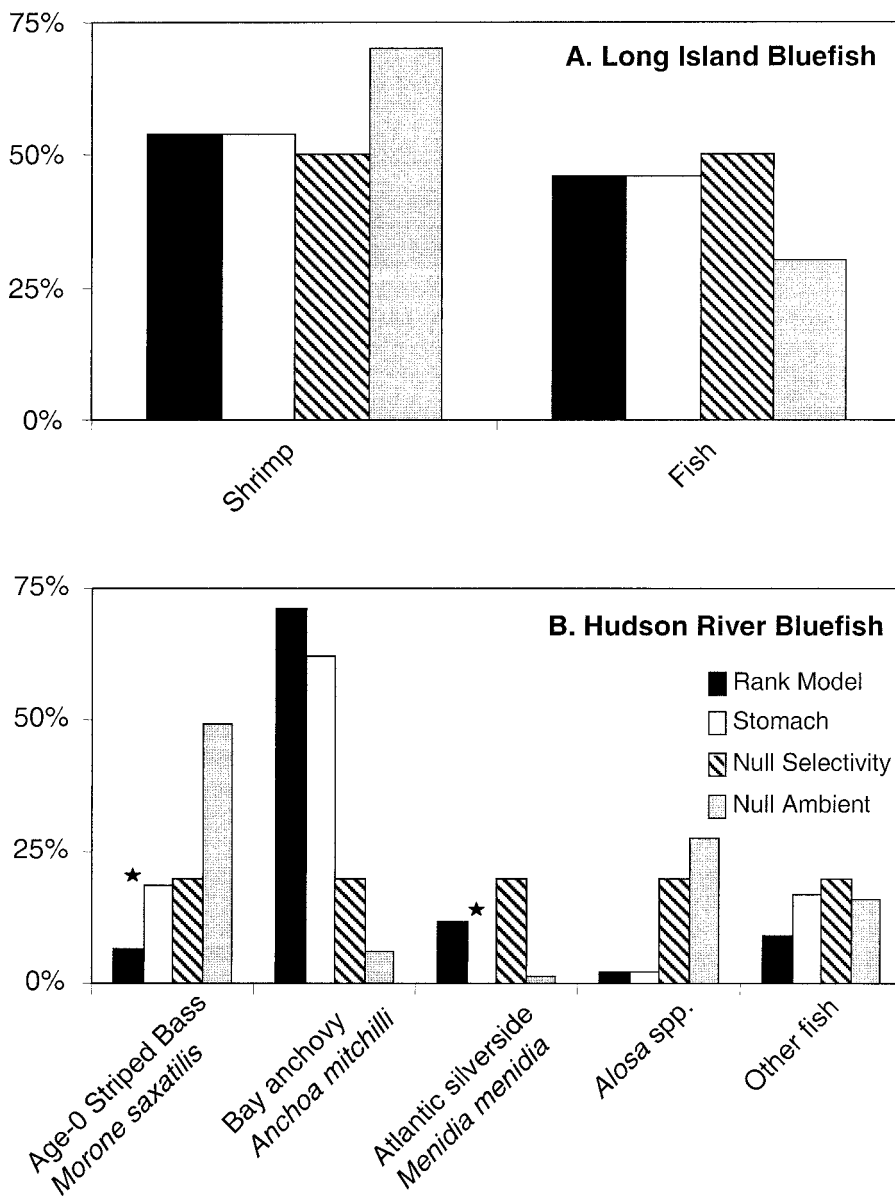


FIGURE 4.—Percent diet composition predicted by the rank proportion algorithm (RPA) model and that observed in the stomachs of (A) age-0 Long Island bluefish and (B) juvenile Hudson River bluefish contrasted with the null selectivity (random) and null ambient (relative-abundance) estimates of diet composition. Stars indicate prey items that exhibited notable differences (>10%) between the RPA model predictions and stomach contents. The differences between the model predictions and null selectivity were notable, indicating nonrandom feeding.

The other major weakness of the RPA approach is not knowing the prey field adequately, as in the African catfish example. Although the preference predicted for this fish is arguably reasonable, chironomids were only detected as trace amounts in the prey sampling due to methodological considerations and hence were predicted to comprise a

small part of the diet (Sanyanga 1998). Had a broader suite of ambient prey been included in the prey field, it is likely that chironomids would have been more important in the predictions of diet composition. Collapsing the prey field into broad categories may be a caveat of the model that could minimize inaccuracies of model predictions, albeit

at the expense of taxonomic resolution. This is seen in the two examples with a limited (<3) number of prey categories (i.e., yellow perch and age-0 bluefish). Collapsing the prey field may not always result in improved accuracy, however, as some of the more accurate model predictions occurred in cases with a large number of prey (e.g., Dover sole and shortfinned eel). Additionally, the RPA results predict an average prey preference and utilization for a given predator. This metric may miss some of the underlying variability among a population of fish that feeds on a broad range of prey, different individuals exhibiting drastically different diets. If species such as the African catfish can switch feeding modes to consume both benthic and pelagic prey, the ambient prey field should reflect this possibility. I am not espousing a combined benthic-plankton-fish survey every time one needs to estimate what fish eat but rather the importance of having a reasonable working knowledge of the relevant prey field for the fish under examination. Yet not knowing that a major prey item of a fish is abundant or even available in the ambient ecosystem is a potential shortcoming not only of the RPA but also of most other models of fish feeding.

The RPA model is distinct from other models of fish feeding. Models that rely on optimal foraging or optimality approaches (e.g., Werner and Hall 1974; Charnov 1976; Mittelbach 1981) assume a cost-and-benefit structure for fish prey selection. Bioenergetic models (e.g., Ney 1990; Hewett and Johnson 1992; Jobling 1994) also make an assumption about prey energetics or preference and are typically parameter intensive. Predator-to-prey ratio models (e.g., Hahm and Langton 1984) of prey preference and diet composition are usually overly simplistic and miss much of the behavior associated with the predation process. The apparent-size model and reactive-field-volume models (Werner and Hall 1974; O'Brien et al. 1976) for visually feeding fish focus on just one or two aspects of the predation process. Even those approaches that capture the entire predation process as a Markovian series of probabilities (Holling 1959; O'Brien 1979; Wright and O'Brien 1984; Link and Keen 1999) require that each probability be experimentally determined. Using previously published electivity indices (Manly et al. 1993) coupled with ambient prey fields to predict prey utilization is limited by the conditions of the original electivity calculations and does not adequately capture inherent prey preference. The RPA model makes no assumptions of cost-benefit trade-

offs, predator avoidance, prey energetics, optimization, maximization, or minimization constraints, or the importance of just one element of the predation process. The RPA model is not without assumptions, the chief of which is that the assigned ranks adequately represent each step of the predation process. Yet the RPA model has limited assumptions as to underlying processes and resultant model structure, maintaining a rather simple format and limited need for parameter precision.

The RPA is not the first attempt to codify predation in aquatic ecosystems. Obviously, several models have been developed to simulate fish feeding (e.g., Werner and Hall 1974; Charnov 1976; O'Brien et al. 1976; O'Brien 1979; Mittelbach 1981; Hahm and Langton 1984; Wright and O'Brien 1984; Ney 1990; Hewett and Johnson 1992; Jobling 1994; Link and Keen 1999). Most of the models of selective fish predation attempt to alter perceived flaws of previous models (Ware 1973; Werner and Hall 1974; Confer and Blades 1975; Gerritsen and Strickler 1977; Schmidt and O'Brien 1982; Dunbrack and Dill 1983; Wright and O'Brien 1984; Newman 1987; Dunbrack 1992; Giske et al. 1994; Rincon and Lobon-Cervia 1995; Manatunge and Asaeda 1999; Caparroy et al. 2000), argue for a different philosophical approach (Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Eggers 1977; Confer et al. 1978; Dunbrack and Dill 1983; Wright and O'Brien 1984; Marschall et al. 1989; Aksnes and Giske 1993; Giske et al. 1994; Luo et al. 1996; Wanzenboeck 1996), predict fish feeding for differing conditions or types of fish (most of the above plus MacKenzie and Kiorboe 1995; Beauchamp et al. 1999; Link and Keen 1999; Flore et al. 2000), or contrast the various models with simulations of those simulations (Gardner 1981; Eggers 1982; Butler and Bence 1984; Li et al. 1985; Wetterer and Bishop 1985). With few exceptions, these models focus on one aspect of predation, provide evidence for a proposed change in that aspect, and then assume that all other factors affecting fish feeding are negligible. Additionally, only a few have actually been validated with field-caught fish. Most reviews have shown that simulations of most of these models produce empirically similar results under the same constraints and conditions (Gardner 1981; Eggers 1982; Li et al. 1985; Wetterer and Bishop 1985). Yet it is unclear how well these other models will work beyond the specific scenarios for which they were designed (e.g., in going from planktivores to benthivores).

The RPA is the first attempt to generalize the size and type selectivity of fish feeding relative to a broad suite of empirically based theories of the predation process while minimizing assumptions as to underlying processes. The value of the RPA approach is fivefold: it provides representation of all components of the predation process without imposing additional constraints; it allows one to make predictions in situations in which there are limited field data; it is adaptable to a wide range of fish and ecosystems; it has been validated with both field-caught and experimentally manipulated fish; and it simplifies the evaluation of predation into an intuitive, empirically backed algorithm that is easily used.

Since fish feeding ultimately influences population and community dynamics in every aquatic ecosystem, the RPA approach has several applications and uses. Bioenergetic modeling (Ney 1990; Hewett and Johnson 1992; Jobling 1994), ECOPATH/ECOSIM (Christensen and Pauly 1992; Walters et al. 1997), multispecies virtual population analysis and similar multispecies models (Andersen and Ursin 1977; Helgason and Gislason 1979; Daan and Sissenwine 1991), other mass balance, energy budget, consumption, and food web models (e.g., Polis and Winemiller 1996), among others (Hollowed et al. 2000; Whipple et al. 2000), all have an implicit underpinning of prey selectivity. Prey preference (or suitability) and utilization are usually the factors that are least addressed in the majority of these approaches due to the high level of effort and expense associated with sampling and examining both the stomach contents and ambient prey abundance or the assumption that a determined diet composition is static. Often diet composition and prey preference are taken from the literature, assumed to equal prey relative abundance, or estimated on a very ad hoc basis. In addition to the fact that those solutions are arbitrary, the RPA results and stomach observations generally suggest that, although important, the relative abundance of prey is not a good predictor of diet composition. The utility of the RPA approach is that a knowledge of the ambient prey field should minimize the need to explicitly and exhaustively sample fish stomachs every time a knowledge of fish diets is needed. The predictive protocol for a priori prediction of prey preference and utilization provided by the RPA is useful for other applications, particularly when process rates need to be allocated, as in the models and approaches described above. The RPA model pro-

vides an intuitive, process-based approach to estimating such factors.

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Appendix—Examples of Rank Proportion Model Application

1. A Hypothetical Example

Assume there is a large-gaped, visually oriented piscivore that has two equally abundant fish prey in its prey field, one of which is much better at predator avoidance than the other. Assigning ranks (R_{ijm} ; see text for exact symbol definitions) for each step in the predation process would give us the following rank matrix:

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	“Icing”
Prey fish 1	1	2	1	1	1	1
Prey fish 2	1	1	2	2	2	2
Summation		3	3	3	3	3

This would produce the following proportion matrix (P_{ijm}):

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	“Icing”
Prey fish 1	1	0.33333	0.66667	0.66667	0.66667	0.66667
Prey fish 2	1	0.66667	0.33333	0.33333	0.33333	0.33333

Finally, given an unknown spatial overlap and equal relative abundance in the water column (i.e., the null ambients are equal), we would get the following RPA model output for predicted diet composition (without relative abundance, the RPA model output would represent prey preference and not prey utilization):

	Product (D_{ij})	RPA Model	Null selectivity	Null ambient (A_i)
Prey fish 1	0.03292	88.9%	50%	50%
Prey fish 2	0.00411	11.1%	50%	50%
Summation	0.03703			

2. Yellow Perch (Confer et al. 1990)

We would assign the following ranks for the steps in the predation process (R_{ijm}):

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	“Icing”
Cyclopoids	1	3	3	2	2	3
Calanoids	1	2	2	3	3	2
<i>Daphnia</i>	1	1	1	1	1	1
Summation		6	6	6	6	6

This would produce the following proportion matrix (P_{ijm}):

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	“Icing”
Cyclopoids	1	0.16667	0.16667	0.33333	0.33333	0.16667
Calanoids	1	0.33333	0.33333	0.16667	0.16667	0.33333
<i>Daphnia</i>	1	0.50000	0.50000	0.50000	0.50000	0.50000

Finally, given the fixed spatial overlap and known relative abundance in the experiments (the null ambient), we would get the following RPA model output for predicted diet composition:

	Product (D_{ij})	RPA Model	Null selectivity	Null ambient (A_i)
Cyclopoids	0.00005	0.4%	33.3%	10.1%
Calanoids	0.00053	4.2%	33.3%	51.5%
<i>Daphnia</i>	0.01199	95.4%	33.3%	38.4%
Summation	0.01257			

3. Lake Superior Lake Herring

We would assign the following ranks for the steps in the predation process (R_{ijm} ; see Link and Keen 1999):

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	“Icing”
<i>Limnocalanus macrurus</i>	1	1	1	7	2	2
<i>Diaptomus sicilis</i>	1	2	2	5	2	1
<i>Diaptomus</i> copepodites	1	5	4	3	4.5	4.5
<i>Cyclops</i> spp.	1	4	5	5	4.5	4.5
<i>Cyclops</i> copepodites	1	6	6	2	6	6
<i>Limnocalanus</i> copepodites	1	3	3	5	2	3
Nauplii	1	7	7	1	7	7
Summation		28	28	28	28	28

Appendix—Examples of Rank Proportion Model Application

This would produce the following proportion matrix(P_{ijm}):

	Overlap (O_{ij})	Detection	Reaction	Capture	Ingestion	"Icing"
<i>Limnocalanus macrurus</i>	1	0.25000	0.25000	0.03571	0.21429	0.21429
<i>Diaptomus sicilis</i>	1	0.21429	0.21429	0.10714	0.21429	0.25000
<i>Diaptomus</i> copepodites	1	0.10714	0.14286	0.17857	0.12500	0.12500
<i>Cyclops</i> spp.	1	0.14286	0.10714	0.10714	0.12500	0.12500
<i>Cyclops</i> copepodites	1	0.07143	0.07143	0.21429	0.07143	0.07143
<i>Limnocalanus</i> copepodites	1	0.17857	0.17857	0.10714	0.21429	0.17857
Nauplii	1	0.03571	0.03571	0.25000	0.03571	0.03571

Finally, given an unknown spatial overlap and known relative abundance in the water column (the null ambient), we would get the following RPA model output for predicted diet composition:

	Product (D_{ij})	RPA Model	Null selectivity	Null ambient
<i>Limnocalanus macrurus</i>	0.000007	1.1%	14%	0.7%
<i>Diaptomus sicilis</i>	0.00463	72.4%	14%	17.6%
<i>Diaptomus</i> copepodites	0.00013	2.1%	14%	3.1%
<i>Cyclops</i> spp.	0.00153	23.9%	14%	59.6%
<i>Cyclops</i> copepodites	0.00003	0.5%	14%	5.5%
<i>Limnocalanus</i> copepodites	0	0.0%	14%	0.0%
Nauplii	0.000006	0.1%	14%	13.6%
Summation	0.00639			