

Body Size and the Ontogeny of the Functional Response in Fishes

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The development of foraging abilities is crucial to the survival and subsequent recruitment of young fishes. We examined experimentally the notion that the foraging abilities of species are so different that useful generalizations across taxa are impossible. We investigated the ontogeny of feeding, reflected in their functional responses, in three Great Lakes' fishes, alewife (*Alosa pseudoharengus*), yellow perch (*Perca flavescens*), and bloater (*Coregonus hoyi*). No strong evidence of species-specific differences in the ontogeny of feeding ability was found. A single size-based relationship explained 52–88% of the variation in the parameters of the functional response equation. We conclude that interspecific differences in feeding abilities of larval fishes may have been over-emphasized, and we suggest that interspecific differences should only be addressed within a size-based framework. This approach appears to provide an acceptable basis for first-order predictions of foraging abilities across taxa, for the identification of exceptional abilities which may lead to advances in the understanding of foraging ability, and for estimating foraging rates for important species for which data are now lacking.

Le développement de l'aptitude au broutage est extrêmement important pour la survie et le recrutement subséquent des jeunes poissons. Nous avons testé la notion selon laquelle les aptitudes au broutage des espèces sont si différentes qu'il est impossible de faire des généralisations utiles d'un taxon à l'autre. Nous avons étudié l'ontogénie de l'alimentation, reflétée par les réponses fonctionnelles de trois poissons des Grands Lacs, la gaspareau (*Alosa pseudoharengus*), la perchaude (*Perca flavescens*) et le cisco de fumage (*Coregonus hoyi*). Très peu d'observations permettent de croire qu'il existe des différences propres aux espèces dans l'ontogénie de l'aptitude à s'alimenter. Un seul rapport basé sur les tailles expliquait 52–88 % des variations des paramètres de l'équation de la réponse fonctionnelle. Nous concluons qu'on a pu accorder trop d'attention aux différences interspécifiques dans les aptitudes à s'alimenter des larves de poissons, et nous suggérons qu'on ne devrait étudier les différences interspécifiques qu'en fonction des tailles. Cette approche semble fournir une base acceptable pour des prévisions du premier ordre des aptitudes au broutage chez les taxons, pour l'identification d'aptitudes exceptionnelles rendant possibles des progrès dans la compréhension de l'aptitude au broutage et pour évaluer les taux de broutage des espèces importantes, pour lesquelles nous ne disposons pas d'un volume suffisant de données.

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A common view in the literature is that the mechanisms controlling recruitment will be specific to individual species because larval survival and subsequent recruitment depends upon a species' unique biological response to its biotic and abiotic environment (Lasker 1987, p. 9). There are important implications for fisheries ecology if we must consider species in isolation. If, for example, the feeding abilities of species are unique, then the detailed information gathered to date about the foraging abilities of many species contributes little to making predictions regarding foraging in an unstudied species. Clearly, species differ in many aspects of their biology. Yet, it is not clear whether species-specific information must always be included or whether general relationships will suffice to explain patterns in the ontogeny of larval and juvenile fishes. Must we begin anew every time we study a different species? Or can we develop expectations for the foraging abilities of an unstudied species from the data available on other species?

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Recently, larval size has been suggested as a scale around which to organize information on the early life history of fishes. Miller et al. (1988) investigated the association between fish length throughout the larval period and several key early life history features. Their results indicate that, across species, fish that are larger at hatching are also capable of feeding earlier, have a longer period before reaching irreversible starvation or point of no return, and take longer to absorb their yolk sacs than those hatching at smaller sizes. Furthermore, after hatching, larger fish can generally swim faster (Hunter 1981; Blaxter 1986; Miller et al. 1988), see further (Breck and Gitter 1983; Blaxter 1986), and may be less vulnerable to predation than smaller fish (Brownell 1985; Folkvord and Hunter 1986; Pepin et al. 1987; Miller et al. 1988; Fuiman 1989). Importantly, similarly sized fish appear to have similar abilities, regardless of species or the size at which they hatched (Miller et al. 1988).

The importance of foraging ability in regulating the growth rate and survival rate of young fish is widely recognized (Houde 1987; Persson 1989). The foraging abilities of fish change dramatically between hatching and metamorphosis (Werner and Gilliam 1984). In fact, many species do not have fully devel-

oped sensory or digestive systems until sometime after hatching (Blaxter 1986; Govoni et al. 1986; Mark et al. 1989). After first feeding, individual fish improve their foraging efficiency rapidly as they develop (Braum 1967; Rosenthal and Hempel 1970; Houde and Schekter 1980; Drost and van den Boogaart 1986; Wanzenböck and Schiemer 1989). These changes in foraging ability are expressed as increased larval growth rates, which, in turn, are significant determinants of larval survival (Houde 1987; Luecke et al. 1990; Rice et al., unpubl. data).

The goals of this paper are to examine to what extent considerations of body size can explain the foraging abilities of three species of fish that hatch at different sizes. We used Holling's type II functional response as an index of feeding ability, which describes the relationship between the number of prey ingested and the prey concentration for each species. This equation is appropriate in situations where a predator is exploiting a single class of particulate prey (Abrams 1990). To assess the importance of species-specific differences in functional responses, parameter estimates for the three species will be compared. This will involve estimating experimentally the parameters of the functional responses for a range of size and species combinations and testing for species effects against the statistical null hypothesis of no species difference.

Materials and Methods

We investigated feeding ability as a function of body size during ontogeny in three common Great Lakes fishes, alewife (*Alosa pseudoharengus*), yellow perch (*Perca flavescens*), and bloater (*Coregonus hoyi*). These species are from different families and hatch at substantially different sizes: alewife hatch at the smallest size, approximately 3.8 mm (Heinrich 1981); yellow perch are intermediate in size, hatching at about 5.5 mm (Scott and Crossman 1973; Cucin and Faber 1985); and bloater hatch at the largest size of the three species, approximately 9.8 mm (Rice et al. 1987). These three species span >80% of the size range of pelagic marine and freshwater fish at hatching. Although they differ substantially in morphology, they do not fully reflect the variety of morphologies found in fishes in general (Moser 1981). In Lake Michigan, larvae of the three species show considerable spatial and temporal overlap (Wells 1980; Auer 1982; Rice et al. 1987).

Experiments were conducted from May to September 1989 at the Center for Great Lakes Studies, Milwaukee, Wisconsin. All fish used in experiments were raised in the laboratory from eggs obtained from natural populations. Peak hatching of bloater occurred on May 5–6 with a mean total length (TL) of 9.67 ± 0.22 mm (mean \pm SD). Peak hatching for the Green Bay strain of yellow perch occurred on May 12 and for the Lake Michigan strain on June 25. The average TL's at hatch were 5.32 ± 0.32 and 5.93 ± 0.44 mm (mean \pm SD), respectively. Peak hatching of alewife occurred on August 3, with mean TL at hatch of 3.87 ± 0.54 mm (mean \pm SD). After hatching, larvae of all three species were transferred to fiberglass tanks, fed on a mixture of *Artemia* supplemented with frozen commercial feed, and maintained on a 12-h light : 12-h dark cycle at 12–15°C until required for an experiment.

To describe the functional response of each size and species of fish, we exposed fish to a range of five different *Artemia* densities (nominal concentrations of 10–1000 nauplii/L). Although *Artemia* is not a natural prey, its use does allow feeding abilities to be investigated independent of differential prey effects. All functional response trials were conducted in 20-L aquaria maintained under gentle aeration at 15°C, a temperature typically experienced by all three species in the wild.

We used a volumetric technique to generate the prey densities required in the experiments. Prior to all experiments, we determined the relationship between the weight of *Artemia* added to an aquarium and the prey concentration produced. For each set of trials, the wet weight of *Artemia* required to generate the desired prey concentration, calculated as wet weight (grams) = 3.022×10^{-4} prey concentration (number per litre) + 0.0141, $r^2 = 0.997$, $n = 49$, was divided by the weight of a standard volume of naupliar suspension (grams per litre) to estimate the volume of suspension (litres) to be added to the aquaria.

We conducted two replicates of each fish size and species combination. The sizes and ages of fish used in the experiments are given in Table 1. To initiate an experiment, 10 similarly sized fish were added to each aquarium and starved for 24 h to standardize experimental conditions and to empty their guts. All fish used in trials were within 2 mm of the target length. Immediately prior to each set of trials, we siphoned the bottom of the aquaria to remove extraneous material and placed four rubber stoppers randomly on each tank bottom. The experimental rations were then added to the aquaria. Gentle aeration kept the *Artemia* suspended and well distributed in the tank.

Fish <20 mm were exposed to the nauplii for 30 min and those ≥ 20 mm for 15 min. These times were based on preliminary trials, as they balanced the need to allow fish to fill their guts at the higher prey concentrations, but did not allow them to deplete the resource significantly (maximum change in prey concentration $\approx 20\%$) or to defecate material. To assess prey densities at the end of the prescribed feeding period, we lowered four PVC tubes over the stoppers, thus sampling a volume of water and the *Artemia* it contained. The fish were then netted out of the aquaria and killed with MS222. In the laboratory, the nauplii in each fish stomach were removed and counted. The tube samples were poured into measuring cylinders, their volumes recorded, and sieved through 64- μ m Nitex. The nauplii retained on the sieve were preserved in 5% formalin for later enumeration and subsequently counted and converted to prey concentrations.

Functional response data were analyzed for goodness of fit to Holling's type II equation, defined by

$$(1) N_{\text{eaten}} = \frac{a \cdot T_f \cdot P}{1 + a \cdot T_h \cdot P}$$

where a is the instantaneous rate of discovery or attack constant (attacks per second). This parameter is the product of the animal's rate of searching and the probability of finding a prey and combines both the encounter and attack components of predation (Holling 1959). The other parameters of the equation are T_f , the total time available for foraging (seconds), T_h , the handling time per prey (seconds), and P , the prey concentration (number per litre) (Holling 1959, 1966). Parameter estimates (\pm SE) were obtained using Marquardt's method of nonlinear regression (Procedure NLIN; SAS Institute 1985). Data from the two trials were combined to produce more accurate estimates of a and T_h (Houck and Strauss 1985). Prey saturation values, N_{max} , were estimated from T_h as

$$(2) N_{\text{max}} = \frac{T_f}{T_h}$$

Parameter estimates were log transformed to stabilize variance. Analysis of covariance (ANCOVA) was used to detect species differences between the size-dependent relationships for the individual parameters (Snedecor and Cochran 1980). We

TABLE 1. Parameter estimates for Holling's type II functional response equation (\pm asymptotic SE) as obtained from nonlinear regression. Regressions are based on the mean gut content data from two trials ($n = 10$). Estimated parameters are instantaneous rate of discovery, a , and handling time, T_h . Prey saturation levels, N_{max} , are calculated using Eq. 2.

Species	TL (mm)	Age (d)	Holling equation			
			a (s^{-1})	T_h (s)	R^2	N_{max} (no./900 s)
Alewife	10	10	2.85×10^{-5} (6.2×10^{-6})	58.12 (16.58)	0.98	15.5
	15	12	5.2×10^{-7} (7×10^{-10})	0 0	—	—
	20	36	0.0028 (0.003)	3.47 (1.34)	0.71	259.4
	30	37	0.0021 (9.7×10^{-4})	0.88 (0.36)	0.95	1023.9
	40	45	0.054 (0.023)	0.94 (0.084)	0.98	954.1
Bloater	10	8	2.4×10^{-4} (9×10^{-5})	118.41 (8.56)	0.98	7.6
	15	37	0.0039 (0.006)	39.15 (9.42)	0.91	23.0
	20	37	0.015 (0.0063)	3.19 (0.315)	0.96	281.9
	30	67	0.024 (0.0026)	1.39 (0.038)	0.99	646.6
	40	96	0.063 (0.017)	0.531 (0.038)	0.96	1694.9
Yellow perch	10	6	3.6×10^{-5} (2×10^{-5})	53.62 (24.94)	0.94	16.8
	15	31	0.0014 (0.001)	8.80 (1.56)	0.97	102.4
	20	34	0.0011 (2×10^{-4})	2.13 (0.30)	0.99	423.1
	30	65	0.0019 (7×10^{-4})	1.49 (0.43)	0.97	606.1
	40	94	0.014 (0.005)	0.61 (0.089)	0.98	1478.5

tested for differences in the slopes of the lines using an F test for the species \times size interaction effect in a full model. We set $\alpha = 0.1$ in these tests to protect the power of the test (Cohen 1988). When we could not reject the assumption of equality of slope, the adjusted means for species were tested using an F test for species in the reduced model at $\alpha = 0.05$. In all cases the assumption of linearity of the parameter estimates with the covariate was checked and could not be rejected. When between-species differences could not be detected a general size-dependent relationship was reported.

We estimated the statistical power (Peterman 1990) of the tests to assess the strength of our inferences using relationships given by Cohen (1988). The power, $(1 - \beta)$, of the test of a null hypothesis is the probability that it will lead to rejection of a false null hypothesis.

Results

The functional responses of all combinations of species and sizes were described well by Holling's type II functional response equation (Fig. 1), except in the case of 15-mm alewife (Table 1). With this exception, the R^2 values were consistently high (mean = 0.95, range = 0.71–0.99). Fifteen millimetre alewife failed to feed at prey concentrations less than 200 prey/L. Consequently, nonlinear regression for this size and species

failed to converge on a set of positive values. These data were therefore excluded from the analysis. ANCOVA revealed no significant differences between the slopes of the regression relationships for the three species or between the adjusted means for the three species for either parameter of Holling's equation (Table 2). Although the power of the tests for the instantaneous rates of discovery is good, the power of the tests for the handling times is low. Generally, $(1 - \beta) \geq 0.8$ is considered acceptable. The calculated power of these tests suggests that we would fail to reject the null hypothesis of no difference between the slopes, if it were false, about 3 times out of 10.

Body size significantly influenced both the instantaneous rate of discovery or attack constant, a ($p < 0.008$), and the handling time, T_h ($p < 0.006$) (Table 2; Fig. 2). As ANCOVA did not detect differences among the three species, we developed a general size-dependent relationship for each parameter. Predicted instantaneous rates of discovery or attack constant increased with fish size in all three species (Fig. 2A). In contrast, predicted handling times decreased with fish size (Fig. 2B). The size-dependent relationships we developed for individual species explained between 82 and 95% of the variation in the log-transformed data. The general size-dependent relationships explained 71 and 91% of the variation in the data, respectively.

We converted T_h values to their N_{max} equivalents to evaluate how the patterns in prey saturation values varied among the

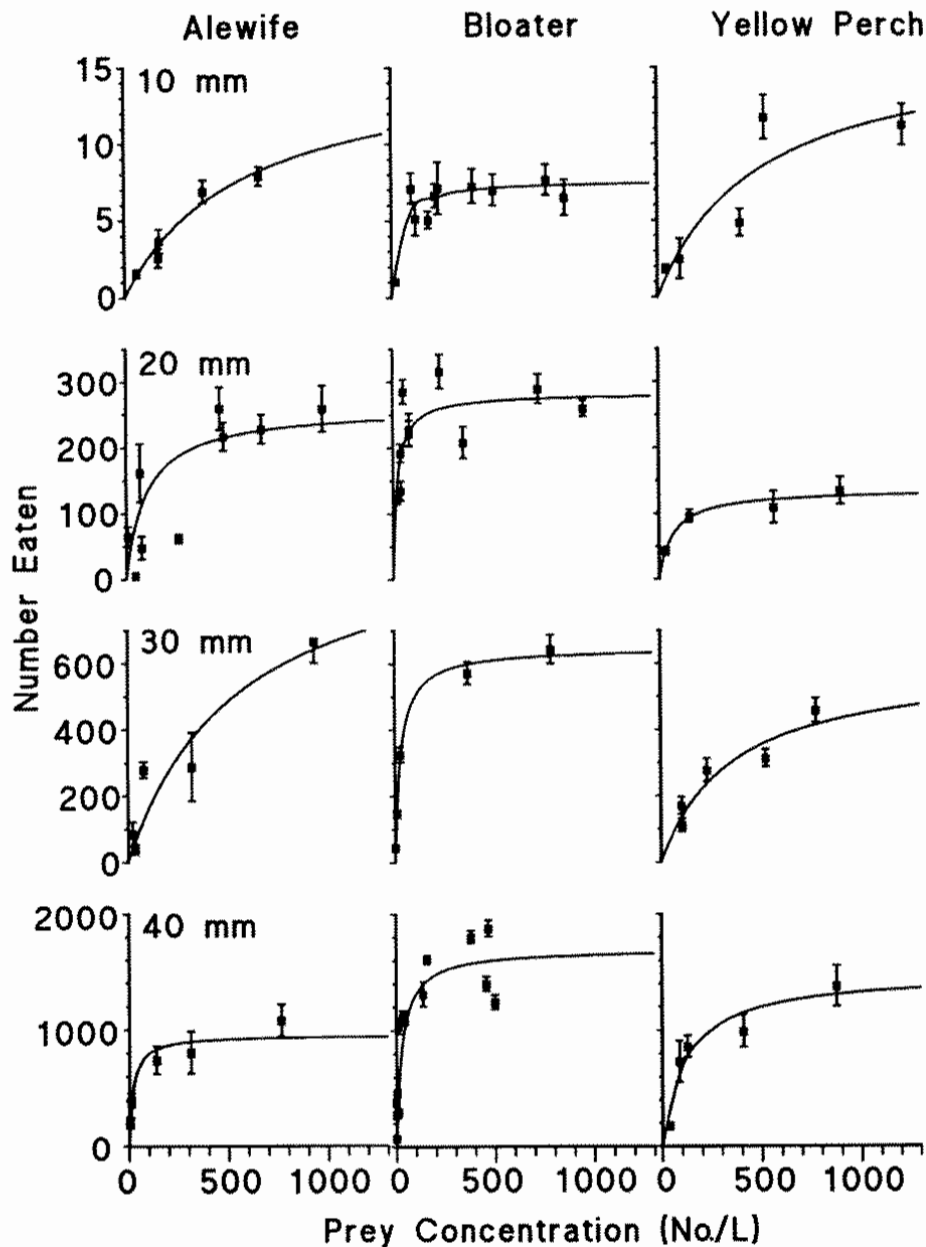


FIG. 1. Nonlinear regression estimates of functional response relationships based on Holling's type II equation (Eq. 1). Individual data are mean gut contents (\pm SE) of 10 like-sized fish from a single tank trial standardized to a 15-min exposure to a single concentration of *Artemia* prey.

species. N_{max} is a simple transformation of T_h . Therefore, ANCOVA results for the two variables are identical. We developed a general size-based relationship for prey saturation values. Species-specific prey saturation values regressed against body size explained 91–95% of the variation present (Fig. 3). The combined data explained 91% of the variation in the data (Fig. 3).

Discussion

If one begins to examine the foraging abilities of larvae of an unstudied species, what insights can be gained from a review of the literature of the ontogeny of feeding in other species? One view, common in the literature, is that species are so dif-

ferent that meaningful generalizations are improbable (Lasker 1987). This view, if fully accepted, leads to the requirement that each species for which no information is available be studied in detail. More recently, Miller et al. (1988) have suggested that larval size may be a character on which to base interspecific comparisons. If this view can be supported, then general relationships derived from a review of well-studied species could be used to develop expectations for relatively unstudied species.

In this study, we attempted to verify the validity of the latter view by assessing the foraging ability of three species of fishes. Despite species differences in the measures of foraging we considered, our data support the notion that body size accounts for a sizeable portion of the overall variation and that species-specific differences are most effectively resolved after first

TABLE 2. Summary of ANCOVA results and tests of power, $(1 - \beta)$, for the parameters of Holling's type II functional response equation. All analyses were conducted on log-transformed values of both the independent and dependent variables.

Instantaneous rate of discovery					
Source	df	SS	F	p	$(1 - \beta)$
<i>Equality of slopes</i>					
Species	2	2.73	1.3	0.33	0.76
Size	1	12.06	11.07	0.008	0.94
Sp. \times size	2	1.79	0.8	0.47	0.76
Error	9	9.81			
<i>Equality of adjusted means</i>					
Species	2	5.87	2.78	0.11	0.76
Size	1	12.06	11.4	0.006	0.94
Error	11	11.61			
Handling time					
Source	df	SS	F	p	$(1 - \beta)$
<i>Equality of slopes</i>					
Species	2	0.1737	1.5	0.27	0.64
Size	1	7.8289	139.3	0.0001	0.99
Sp. \times size	2	0.1347	1.2	0.35	0.67
Error	8	0.452			
<i>Equality of adjusted means</i>					
Species	2	0.1272	1.09	0.37	0.64
Size	1	7.8941	135.10	0.0001	0.99
Error	10	0.581			

accounting for differences associated with larval size. It is important to emphasize that we do not conclude from our inability to detect species-specific differences among these three species that they do not exist or that they may not be important in other cases. Considering body size alone clearly does not explain all of the variation in feeding abilities among all species. Yet, it does represent a good first approximation.

Our inability to detect species-specific differences may result from two factors: statistical power and the species chosen for our experiments. Some of the tests we employed had lower power than the 0.8 considered acceptable (Cohen 1988), particularly the tests for handling times. Thus, we cannot deny the possibility of having failed to reject a false null hypothesis.

We may also have detected a species effect if we had chosen species that differed more in morphology or differed less in size. The three species were chosen because of their differences in hatching size, yet they do not fully represent the range of morphologies exhibited by larvae of different species (Moser 1981). A different set of species may have indeed yielded significant species effects. We acknowledge that species effects do exist, but suggest that in many cases they may not be so large as to deny the possibility of useful generalizations.

Further, the experiments were conducted using *Artemia* nauplii. This prey is known to be particularly vulnerable to fish predation, and thus its use may have obscured differences in ability or behavior that would have been apparent if a natural prey had been used. However, the use of a natural prey assemblage would have greatly complicated the interpretation of the results. It would have been extremely difficult to separate

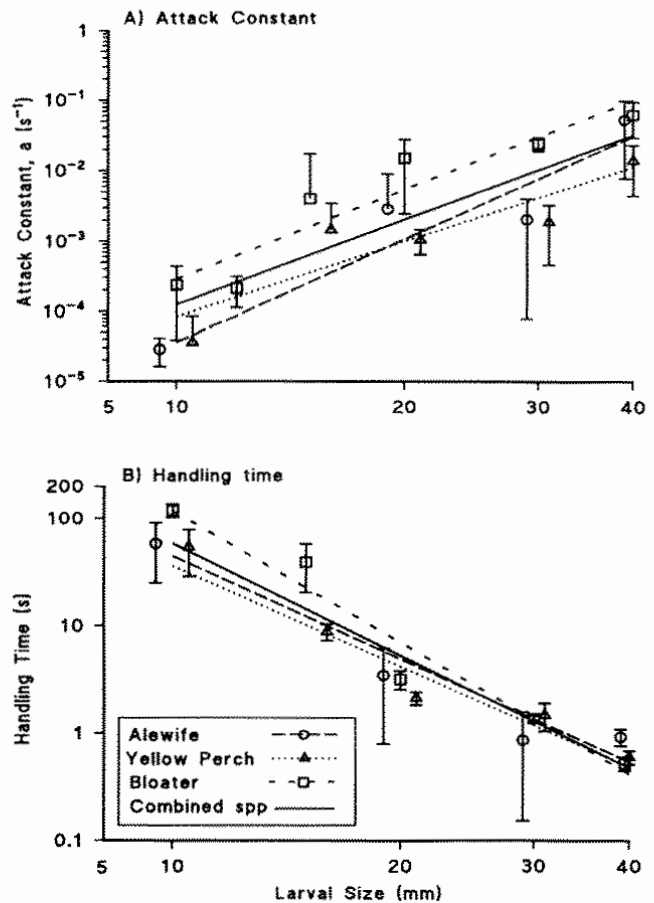


FIG. 2. Relationship between parameter estimates for Holling's type II equation and fish size. Data for alewife and yellow perch have been plotted at slightly smaller and slightly larger sizes, respectively, to improve the visual presentation. (A) Attack constants or instantaneous rate of discovery, a (± 2 SE). Individual species regressions: alewife, $\log(a) = 6.14 \cdot \log(\ell) - 10.77$, $r^2 = 0.83$, $n = 5$, $p < 0.05$; bloater, $\log(a) = 4.24 \cdot \log(\ell) - 7.78$, $r^2 = 0.88$, $n = 6$, $p < 0.05$; yellow perch, $\log(a) = 3.54 \cdot \log(\ell) - 7.62$, $r^2 = 0.82$, $n = 5$, $p < 0.05$. Combined taxa: $\log(a) = 4.43 \cdot \log(\ell) - 8.39$, $r^2 = 0.73$, $n = 16$, $p < 0.05$. (B) Handling time, T_h (± 2 SE). Individual species regressions: alewife, $\log(T_h) = 4.82 - 3.16 \cdot \log(\ell)$, $r^2 = 0.94$, $n = 4$, $p < 0.05$; bloater, $\log(T_h) = 6.22 - 4.06 \cdot \log(\ell)$, $r^2 = 0.95$, $n = 5$, $p < 0.05$; yellow perch, $\log(T_h) = 4.65 - 3.10 \cdot \log(\ell)$, $r^2 = 0.94$, $n = 5$, $p < 0.05$. Combined taxa: $\log(T_h) = 5.22 - 3.46 \cdot \log(\ell)$, $r^2 = 0.91$, $n = 14$, $p < 0.05$.

effects on feeding ability that resulted from differences in prey behavior, or prey distributions among trials, from those relating specifically to differences in the ability of the fishes themselves. As *Artemia* are not the natural prey of any of the species tested, our results may not be readily transferable to the field (MacKenzie et al. 1990).

Our finding that size-dependent patterns are important in the ontogeny of foraging ability in fishes is consistent with the results of other recent studies in this area. MacKenzie et al. (1990) recently reviewed the influence of body size, temperature, food density, and experimental protocol on the ingestion rates of larvae of 11 fish species. Their results, which are based on a multiple regression analysis of previously published data, suggest that body size is the single best predictor of ingestion rate, explaining nearly 60% of the variation in the data. When combined with data on the temperature at which experiments

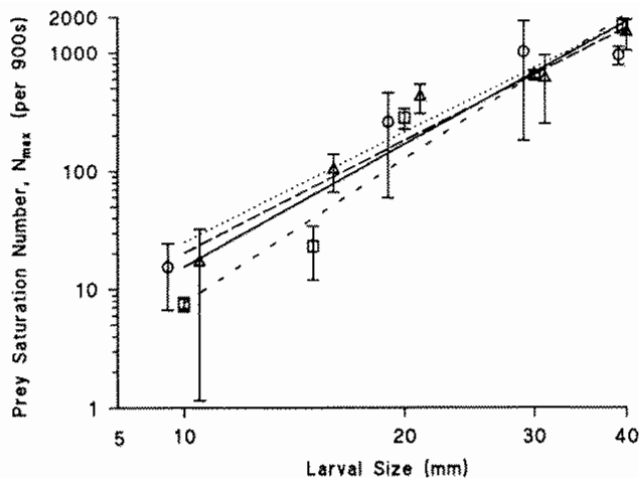


FIG. 3. Prey saturation values as a function of larval size (± 2 SE). Species data are as indicated in Fig. 2. Data for alewife and yellow perch have been plotted at slightly smaller and slightly larger sizes, respectively, to improve the visual presentation. The solid line indicates the general size-based function. Individual species values: alewife, $\log N_{\max} = 3.17 \cdot \log(\ell) - 1.86$, $r^2 = 0.94$, $n = 4$, $p < 0.05$; bloater, $\log N_{\max} = 4.05 \cdot \log(\ell) - 3.17$, $r^2 = 0.95$, $n = 5$, $p < 0.05$; yellow perch, $\log N_{\max} = 3.09 \cdot \log(\ell) - 1.69$, $r^2 = 0.94$, $n = 5$, $p < 0.05$. Combined taxa: $\log N_{\max} = 3.45 \cdot \log(\ell) - 2.26$, $r^2 = 0.91$, $n = 14$, $p < 0.05$.

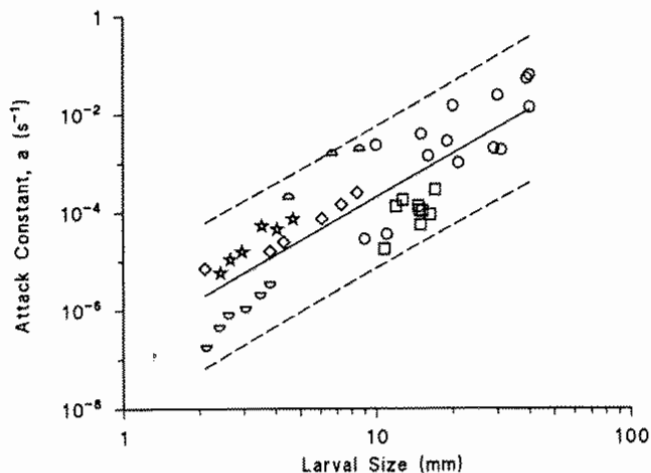


FIG. 4. Relationship between published attack constants or instantaneous rates of discovery and fish size for several species. The data were derived from the sources indicated below and were standardized to litres per second. Regression relationship for the combined data: $\log(a) = 2.94 \log(\ell) - 6.65$, $n = 48$, $r^2 = 0.73$, $p < 0.001$. Broken lines are 95% confidence intervals for single observations. Symbols: \circ , this study (sizes for alewife and yellow perch have been altered to improve clarity); \square , Atlantic-herring (Werner and Blaxter 1981); \diamond , lined sole (Houde and Schekter 1980); \triangle , bay anchovy (Houde and Schekter 1980); \star , sea bream (Houde and Schekter 1980); \circ , winter flounder (Laurence 1975, 1977).

were conducted, these two variables explained over 80% of the variation in ingestion rates.

The results of functional response studies on other species also lend some support to our findings. We found a strong relationship between the attack constants or instantaneous rate of discovery, a , and size during ontogeny. Houde and Schekter (1980) observed that the instantaneous rate of discovery

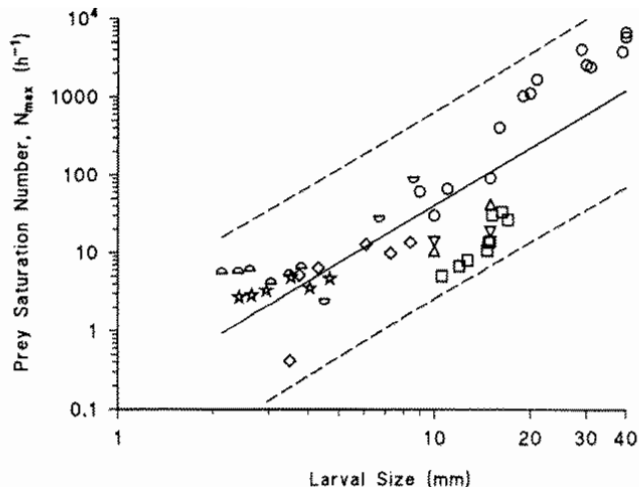


FIG. 5. Relationship between published saturation prey numbers and fish size for several species. Data have been standardized to numbers per hour. Regression relationship for the combined data: $\log N_{\max} = 2.45 \cdot \log(\ell) - 0.84$, $n = 48$, $r^2 = 0.71$, $p < 0.001$. Broken lines are 95% confidence intervals for single observations. Data sources are as detailed in Fig. 4, with the addition of the following: \triangle , Atlantic herring (Blaxter 1962); ∇ , Atlantic herring (Rosenthal and Hempel 1980).

increased markedly during early development in bay anchovy (*Anchoa mitchelli*), sea bream (*Archosargus rhomboidalis*), and lined sole (*Achirus lineatus*). But both Laurence (1975, 1977) and Werner and Blaxter (1981) found no evidence of similar trends in instantaneous rates of discovery in winter flounder (*Pseudopleuronectes americanus*) and Atlantic herring (*Clupea harengus*), respectively. However, in these studies the size ranges investigated were very small, 4.5–8.6 and 10–17 mm, respectively. Consequently, it may be difficult to detect a size-dependent relationship in these data. The exact nature of the size-dependent relationship for attack constants or instantaneous rates of discovery remains equivocal and deserves further study. However, there does appear to be a common pattern in the available data (Fig. 4). The degree to which the substantial variation in the data now available reflects real species-specific differences as opposed to consequences of methodological differences in estimating instantaneous rates of discovery remains to be assessed.

We found that saturation prey levels increased with body size in all species studied. Blaxter (1962), in a study of the functional response of Atlantic herring larvae, found that the saturation prey value increased from 10 to 40 *Artemia* nauplii as larvae grew from 10 to 15 mm standard length. Rosenthal and Hempel (1970) reported saturation prey values for 10- and 15-mm Atlantic herring feeding on *Artemia* to be 15–20 nauplii. Houde and Schekter (1980), who investigated the functional response of bay anchovy, sea bream, and lined sole, observed a 16–229% increase in the saturation prey value over a range of fish dry weights from 10 to 200 μg . Laurence (1975, 1977) and Werner and Blaxter (1981) found similar patterns in the prey saturation values of larval winter flounder and Atlantic herring. The generality of these findings is illustrated in Fig. 5, where we have combined the results of all studies, noted above, including our own. However, although size indeed seems to dominate the relationship overall, it should be noted that the size-dependent relationships within species may be different. But the potential deviation of individual taxa can only be rec-

ognized when the expected relationship is known. Similar patterns are found in many other allometric relationships (Peters 1983).

There have been relatively few studies of the size dependence of N_{\max} in fishes. To permit comparisons among the studies, we expressed N_{\max} as an exponential function of size. Stepien (1976) investigated the age dependence of N_{\max} in sea bream feeding on prey at 1000/L at 23, 26, and 29°C. He reported the age dependence as a general exponential form. We converted his data to the general form using the length-age relationships he provided to yield exponent values of 2.96, 3.46, and 2.01, respectively, for the three different temperatures. The corresponding intercept values are 0.47, 0.53, and 3.17. Houde and Schekter (1980) reported N_{\max} values as a function of age and weight. We expressed these data in the general form using length-age relationships in Houde and Schekter (1981). The equations for the three species are as follows: bay anchovy, $N_{\max} = 0.073 \cdot \ell^{2.72}$; sea bream, $N_{\max} = 0.079 \cdot \ell^{3.20}$; and lined sole, $N_{\max} = 0.37 \cdot \ell^{2.57}$. The relationships for the species we studied are as follows: alewife, $N_{\max} = 0.014 \cdot \ell^{3.16}$; bloater, $N_{\max} = 0.006 \cdot \ell^{4.05}$; yellow perch, $N_{\max} = 0.020 \cdot \ell^{3.10}$. Although the exponent values reported compare favorably, this is not true of the intercept values. The reasons for this wide discrepancy are unclear. The intercept values dominate the N_{\max} function when fish are small, and thus these differences may have large potential effects on growth rates of larval and juvenile fishes. Their resolution will require a fuller investigation of the nature of size dependency and prey saturation values in fishes.

To conclude, we have documented clear size dependencies in the functional responses of larval and juvenile fish during development. Alewife, yellow perch, and bloater dramatically improved their foraging abilities as they developed, in accordance with several other species studied recently. Species-specific differences, while present, were not statistically different, possibly as the range of larval types was too restrictive and the range of sizes too broad. This constraint notwithstanding, we feel that the evidence presented here and elsewhere is sufficient to support the hypothesis that the importance previously accorded to species-specific differences has been overemphasized. This results, we believe, from a failure to quantitatively standardize components of foraging ability for larval size or temperature prior to making interspecific comparisons. We do not suggest that species are unimportant and that fish size is the sole determinant of foraging ability during the fish early life history. We do conclude, however, that body size can provide first-order predictions of the probable foraging abilities of young fishes across a broad range of taxa. Such an approach would allow investigators to identify, and study, species that deviate from the general expectation. This approach should enhance our ability to understand more fully the dynamics of foraging in larval fishes and its relevance to growth and survival.

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