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GRADIENT OF FISH PREDATION ALTERS BODY SIZE DISTRIBUTIONS OF LAKE BENTHOS

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Abstract. We used normalized size spectra analysis (originally developed in the study of pelagic communities) and a fish bioenergetics model to examine whether predation by fishes affects the size structure of macrobenthos. We conducted the study over five years in three north temperate lakes in which fish were experimentally manipulated while allowing for natural recruitment and mortality in lakes with fish. The resulting variation in predator populations allowed us to address how prey community size structure responds to a gradient of predation pressure. The slopes of normalized size spectra were used to characterize whether community biomass is relatively distributed as smaller or larger individuals with regard to mass. We ask whether predator effects on prey are manifested through fish presence/absence or if a gradient of predation pressure is important. In addition, we examined whether consumption rate of prey by fish is a better measure of predation effects on prey size structure than fish biomass alone.

Our results suggest that benthos size structure responds to a gradient of fish consumption, rather than a qualitative distinction of fish presence or absence. Consumption rates by fish on benthos explained more of the variation in slopes of normalized size spectra of benthos than fish biomass alone. Slope values were more variable at lower consumption rates, which included no predation by fish. Conversely, high consumption rates by fish produced consistent, predictable body size distributions of benthos in which large individuals were relatively underrepresented. However, these results may not be apparent through more traditional analyses based on predator or prey presence/absence, abundance, or taxonomic-based measures. Generalizations addressing patterns of body size distributions within and among ecosystems may be advanced by examining predation and other underlying size-structuring mechanisms.

Key words: *benthic-pelagic links; benthos; body size distribution; fish bioenergetics; Micropterus; normalized size spectra; predation, size selective; predator-prey.*

INTRODUCTION

Body size is one of the most-studied aspects of animal ecology (LaBarbera 1989, Blackburn and Gaston 1994). Body size scales with metabolic and nutrient turnover rates of organisms, production rates of populations, density of individuals, and number of species (Banse and Mosher 1980, Peters 1983, Damuth 1987, Brown and Maurer 1989, Elser et al. 1996). Because body size scales with important ecosystem, population, and community parameters, researchers have sought mechanisms or environmental variables associated with variation in body size distributions in a variety of habitats (Brown and Maurer 1986, Sprules and Munawar 1986, Cyr et al. 1997a). However, body size distribution may be affected by abiotic and biotic factors, which interact in complex ways and differ among habitats. For example, the contrasts in habitat structure of terrestrial and pelagic ecosystems may foil gener-

alizations regarding influences on body size distributions (Maurer and Brown 1988, Steele 1991).

Body size distributions have been linked to physical habitat structure in terrestrial ecosystems (Holling 1992). Aquatic ecologists have emphasized the role of biotic interactions on body size distributions (Stein et al. 1988). Holling (1992) suggested that species' body size distributions in many terrestrial systems reflect the "texture" of the landscape. Structures in landscapes are partitioned into niche space, and community structure is influenced by the body shapes and sizes of species best able to exploit these spaces (Brown and Maurer 1989). Since pelagic habitats lack the physical substrates of terrestrial landscapes, it is thought that body size distributions in pelagic and terrestrial habitats are dictated by fundamentally different processes (Holling 1992). For example, predation is often the primary factor determining organismal size distributions and consequent effects on ecosystem properties in pelagic systems (Platt and Denman 1978, Borgmann 1987, Dickie et al. 1987, Carpenter et al. 1996).

Pelagic communities have been a logical focus of research into trophic interactions (Strong 1992), and

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specifically the role of body size (Stein et al. 1988). However, predator and prey sizes may have several feedbacks in nature that may be experimentally intractable. First, because many fishes in lakes maximize energetic efficiency on the basis of predator:prey body size ratios (Werner 1977), impacts on prey size distribution should vary with predator size (Rice et al. 1993). If predators are food limited and their densities increase, energetically optimal (often large) prey sizes become rare, and the body size range of selected prey should increase (Pyke 1984). The effect of fish predation on prey size distribution is thus a function of both predator size and abundance. Second, the food energy required for standard metabolism per unit fish mass varies greatly with fish size and water temperature, suggesting that total predator biomass alone is not an accurate predictor of consumption rates on prey or valid for intersystem or interseason comparisons (Bartell et al. 1986, Hewett and Kraft 1993). Finally, the availability of preferred prey sizes for generalist predators may vary among habitats within lakes (Werner et al. 1983, Persson and Greenberg 1990). Predator biomass is thus a template for potential predation, but other factors impact realized predation rates. We therefore expect that measurements of habitat-specific consumption rates by predators, rather than total predator biomass alone, may be the most effective way to integrate predator-prey size feedbacks and estimate the effects of predation on the size structure of prey communities.

Although studies of size-structured trophic interactions in lakes have focused on pelagic food webs, many fishes rely on benthic prey for much of their growth and production (Hanson and Leggett 1982, Hodgson and Kitchell 1987, Boisclair and Leggett 1989, He et al. 1994). However, the presence of physical structure suggests that influences on body size structure of benthic communities may be more similar to terrestrial than pelagic habitats (Schoener 1989, Hairston and Hairston 1993). For example, the size distribution of benthos may reflect the availability and organization of habitat structures (Mittelbach 1981a, Lodge et al. 1988, Hanson 1990, Rasmussen 1993). Many benthic macroinvertebrates also have complex and body-size-invariant behavioral adaptations to predation risk (review in Ringler 1978, McPeck 1990, Johnson 1991), including the use of refuges provided by structure (Hershey 1985, Diehl 1988, Garvey et al. 1994). Relative to pelagic prey, the diversity of taxa, body shapes, and modes of habitat use of benthic organisms may function to defuse the effects of predation on benthic community size structure (Mittelbach 1981b, Boisclair and Leggett 1989). Responses of body size distributions to fish predation may therefore be less sensitive in benthic relative to pelagic communities (Strayer 1991).

Studies examining the effects of fish predation on benthic communities have typically used artificial or small partitioned habitats over short time scales, with

a focus on either the manipulation of fish presence/absence or fish abundance at specific and fixed levels (review in Diehl 1993, Diehl and Kornijów 1997, Lodge et al. 1998). This approach reflects some logistical and statistical constraints of experimental design which hinder comparisons with natural settings. For example, most lakes differ by the composition or abundance of fish assemblages rather than presence or absence. Reduced experimental scales may also artificially bias direct effects of predators on prey mortality (de Fontaine and Leggett 1987, Englund 1997, Sarnelle 1997), and are of uncertain value in extrapolating to the natural, long-term, large-scale environment (Hengeveld 1987, Thrush et al. 1997). Recruitment of predator and prey populations in natural settings is important to understanding community patterns, but is often eliminated as a factor at abbreviated scales (Frost et al. 1988, Yodzis 1988). Comparing a gradient of predator consumption rates with prey body size distributions at appropriate scales of observation should provide a more direct determination of effects of fish on prey communities than through static and discrete measures of predator assemblages.

In this study, we examine how the size structure of benthos in lakes and predation by fishes were related over five years under seminatural gradients of fish biomass and predation pressure in three north-temperate experimental lakes. Fishes were removed from one of the lakes for the first four of the five study years, but were continually present in the others. In lakes with fish, fish populations varied in biomass and mean size between lakes and years. If predation by fish is an important factor in the size structure of benthos (as it is for pelagic prey), we would expect high predation pressure to result in prey communities in which large prey are relatively underrepresented. We compare fish biomass and consumption rates on benthic prey as determinants of variation in benthos body size distribution, and demonstrate that benthos body size distribution responds to a gradient of predation.

METHODS

Study site

We examined benthic communities and predation by fishes in experimental lakes at the University of Notre Dame Environmental Research Center (Gogebic County, Michigan; 46° N, 89° W) during the summer seasons of 1991–1995 (Table 1). As part of a larger experiment established to examine interactions of nutrient loading and food web structure on lake community and ecosystem processes (Carpenter et al. 1995, 1996, Schindler et al. 1997a), Long Lake was separated into three distinct basins (East Long, Central Long, and West Long) with plastic curtains in the spring of 1991. Fish densities in the central basin prior to curtaining were ~200 fish/ha (average of 1989 and 1990 estimates; D. E. Schindler, *personal communication*). Immediately

TABLE 1. Lake morphometric and water-column physical parameters for 1991–1995.

| Parameter | Lake | | |
|------------------------------------|-----------|--------------|-----------|
| | Paul | Central Long | West Long |
| Surface area (ha) | 1.7 | 2.1 | 3.4 |
| Mean depth (m) | 3.7 | 1.9 | 4.7 |
| Maximum depth (m) | 12 | 5 | 18 |
| Mean thermocline depth (m) | 3.6 | 3.0 | 3.5 |
| Epilimnetic temperature range (°C) | 17.3–21.2 | 17.6–20.7 | 16.7–21.6 |

Notes: Mean thermocline depth and epilimnetic temperature are average summer means from the five years of the study. Within-year thermocline temperature averages are calculated from geometric means of weekly measurements.

after curtaining, all fishes were removed from Central Long. Largemouth (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*) were transferred to West Long, while yellow perch (*Perca flavescens*) were transferred to a nonexperimental lake. Over the duration of the study, most of the fish biomass in West Long was largemouth bass. Immediately after the fish manipulations, rotenone was then applied (0.025 mg/L active ingredient of toxaphene) to ensure the fishless status of Central Long. An experimental manipulation of rotenone concentrations (control, 1 × lake dose, 2 × lake dose) added to in situ 2000 L mesocosms (described in Blumenshine et al. 1997) resulted in no among-treatment differences in the mortality of benthic macroinvertebrates enclosed in flow-through sediment chambers after 48 h of exposure within mesocosms (S. C. Blumenshine, unpublished data). Subsequent electroshocking and observations by divers over the years of this study confirmed that few fish recolonized Central Long. During May–August of 1995, fish populations in West Long were augmented with adults from a nearby lake (88 smallmouth bass, 59 largemouth bass, and 118 yellow perch). Adult fish were reintroduced to Central Long in late May 1995 (9 smallmouth bass, 9 largemouth bass, and 155 yellow perch). Paul Lake served as a reference system for the overall experiment, with an unmanipulated fish assemblage, which was dominated by largemouth bass. Limnological profiles and lake morphometrics are provided in Table 1 and detailed elsewhere (Carpenter and Kitchell 1993, Carpenter et al. 1996, Christensen et al. 1996, Schindler et al. 1997a).

The littoral sediments of the experimental lakes are primarily flocculent organic material including abundant epipelton. Macrophyte growth is sparse in all lakes with the exception of small patches of *Isoetes*, *Nuphar*, and *Sparganium*.

As part of the overall larger experiment, the epilimnia of Central and West Long were enriched daily with liquid fertilizer (NO₃, NH₄, and PO₄; N:P ratio 25:1 by atoms) from May through September of 1993–1995 (see Carpenter et al. 1995, 1996 for additional details). Phosphorus (P) addition rates to the epilimnion of these lakes were adjusted for seasonal variation in flushing rate, resulting in average P loading rates during 1993,

1994, and 1995 respectively, of 1.59, 0.90, and 0.90 mg·m⁻³·d⁻¹ in Central Long, and 1.43, 0.86, and 0.40 mg·m⁻³·d⁻¹ in West Long. Baseline P loading rates are around 0.1–0.2 mg·m⁻³·d⁻¹ (Carpenter et al. 1996). These water-column nutrient enrichments should not affect our analysis here for several reasons. First, these loading rates are lower than other whole-system nutrient addition experiments in which benthic responses were detected (Hall et al. 1970, Davies 1980, Hershey 1992), and did not drive pelagic chlorophyll or dissolved oxygen concentrations to levels considered eutrophic (Carpenter et al. 1996). Second, a prior nutrient addition experiment using similar nutrient loading rates in experimental 2000 L, 2 m deep mesocosms situated in Central Long (i.e., the same community) showed that epipelton, a primary food resource of herbivorous benthos (S. C. Blumenshine and Y. Vadeboncoeur, unpublished data), did not increase with nutrient enrichment (Blumenshine et al. 1997).

Cyr et al. (1997a) found that variation in primary production among lakes is most likely to affect abundances of the smallest organisms in lake food webs, with little effect on larger organisms such as fish and their macroinvertebrate prey. In fact, we found no relationship between epilimnetic phytoplankton chlorophyll *a* concentration and littoral macroinvertebrate biomass on whole-lake and multiyear scales (S. C. Blumenshine and D. M. Lodge, unpublished manuscript). We thus expect that nutrient enrichment would not alter the relationship of fish predation and size structure of their benthic prey. However, in our data plots, we have distinguished nutrient-enriched lake-years from nonenriched lake-years so that any impact of enrichment on our conclusions may be assessed.

Fish populations, diets, and consumption rates

Fish were sampled with boom electroshockers and angling during mid-May and mid-August during 1991–1995. All captured adult fish were marked with numbered floy tags for later identification, and juveniles were fin clipped. Population estimates for each May and August period were generated using Peterson mark-recapture methods described in Hodgson et al. (1993). In addition, up to 26 juvenile (60 mm < total length < 150 mm) or adult (>150 mm total length)

TABLE 2. Parameters of fish assemblages (juveniles and adults) and their consumption of benthos.

| Year | Total fish biomass (kg/ha) | | | Mean individual fish mass (g) | | | Percentage benthos of total consumption | | | Mean daily consumption rate on benthos (mg · m ⁻² · d ⁻¹) | | |
|------|----------------------------|-----------|--------------|-------------------------------|-----------|--------------|---|-----------|--------------|--|-----------|--------------|
| | Paul | West Long | Central Long | Paul | West Long | Central Long | Paul | West Long | Central Long | Paul | West Long | Central Long |
| 1991 | 20.4 | 21.4 | ... | 50 | 220 | ... | 59.3 | 63.8 | ... | 9.23 | 7.15 | ... |
| 1992 | 17.7 | 23.6 | ... | 140 | 305 | ... | 24.7 | 32.7 | ... | 1.65 | 2.62 | ... |
| 1993 | 24.4 | 4.6 | ... | 154 | 406 | ... | 16.8 | 48.3 | ... | 1.48 | 0.97 | ... |
| 1994 | 31.1 | 4.8 | ... | 147 | 489 | ... | 44.9 | 61.7 | ... | 4.38 | 1.16 | ... |
| 1995 | 27.3 | 15.0 | 2.4 | 37 | 249 | 91 | 46.1 | 21.1 | 59.6 | 7.72 | 1.27 | 1.11 |
| Mean | 24.2 | 13.9 | 2.4 | 106 | 334 | 91 | 38.4 | 45.5 | 59.6 | 4.89 | 2.63 | 1.11 |

Notes: Annual estimates of fish density and mean mass were generated from May and August censuses. Parameters of consumption on benthos were calculated from a fish bioenergetics model used to estimate daily consumption rates during mid-May through August. Ellipses (...) indicate fish not present.

individuals of each fish species in Paul and West Long were sampled by hook-and-line or electroshocking approximately biweekly between mid-May to mid-August for diet analysis and length (nearest 1 mm) and mass (nearest g) measurements. Young-of-year fish were excluded from this analysis because they primarily consume zooplankton (Post et al. 1997) and contribute little to total fish biomass (Schindler et al. 1997b). Most diet samples included at least 20 adult or juvenile fish; those with <4 fish were not used to avoid bias by individual fish. Stomachs were evacuated using gastric lavage methods within 1 h of capture (Hodgson and Kitchell 1987). Prey were counted and identified to order in most cases (Hodgson et al. 1993). Prey numbers and mass in diet samples were averaged within age class, sampling dates, fish species, and lake (Hodgson et al. 1993).

A fish bioenergetics model (Kitchell et al. 1977) developed as software by Hewett and Johnson (1992) was used to estimate daily consumption rates of juvenile and adult fishes from 20 May to 10 August of each year (Table 2). Consumption rate estimates were generated from measurements of fish size, growth, diet composition, thermal history of the habitat, prey and predator caloric densities, and predator species-specific metabolic rates included in the model, but derived from other primary sources (Kitchell et al. 1977, Rice et al. 1983, Shuter and Post 1990). Model predictions, sensitivity, and effects of parameter perturbation on model output have been thoroughly examined elsewhere (Kitchell et al. 1977, Rice et al. 1983, Rice and Cochran 1984, Bartell et al. 1986, Whitley and Hayward 1997). Estimates of consumption rates based on known growth rates of fish match well with field data in other studies, and are robust to parameter perturbation (Rice and Cochran 1984, Bartell et al. 1986). In this study, mean epilimnetic water temperatures measured weekly from each lake and year were used as model inputs. Predator and prey caloric densities were taken from Rice et al. (1983) and Cummins and Wuycheck (1971). In summary, calculation of total consumption rates by predators is the estimate of total predator biomass com-

bined with individual-based variation in consumption rate, which includes several nonlinear allometric functions.

The most influential factors in estimating consumption by individuals are their mass and thermal history, while variation in the determination of total consumption by fishes is in estimating the biomass of fish in a population or cohort (Bartell et al. 1986, Hewett and Johnson 1992). Procedures to minimize these sources of error during this study included weekly, depth-integrated lake temperature profiles, repeatedly electroshocking the entire shorelines of lakes during population census, tagging all captured adult fish with numbered Floy tags, and fin clipping smaller fishes. Adults and juveniles were grouped into several size categories if warranted by inspection of size-frequency distributions of May and August population censuses. Constant mortality rates of fish were assumed within age or size class, species, and lake-year. Consumption rates were converted to areal (m²) rates to compare predation pressure among lakes and to achieve common units with benthic community parameters. Total consumption rates on benthos were divided by the littoral area based on hypsometric and limnological data. We expect consumption rate to be a better index of predator effects on prey than total fish biomass alone because the actual rate of prey consumption varies with individual-based parameters of fish metabolism, which are accounted for by the bioenergetics model.

Benthic sampling

Benthic prey assemblages were estimated based on 10 Ekman grab (232 cm²) samples collected from epilimnetic sediments at a depth of 1.5 m from each lake during the first 2 wk in June, July, and August of each year. This sampling frequency should be adequate to represent the summer growing season. For example, Hanson et al. (1989) found that biweekly samples of benthos had similar size-distributions as those taken at 4–6 wk intervals from a lake at a similar latitude (54° N). The average interval from the first day of estimated

consumption by fish (20 May) to the first benthic sampling (June) was 14 d.

Choice of specific sample sites for each month and lake was based on a stratified random design in which one sample was taken from a randomized position in each of 10 equidistant shoreline sectors in each lake. The sampling depth of 1.5 m was near the midpoint of the epilimnion depth in each lake (Table 1). Samples were kept in a cooler and sieved through 250- μ m mesh within 24 h of collection. Retained organisms were preserved in 70% ethyl alcohol and later sorted using sugar floatation. During this process, sample sorting trays were thoroughly checked for uncommon, high-density animals such as bivalves unaffected by sugar floatation.

Organisms were typically identified to genus, or sub-family level for more common taxa. Some larger, less common taxa such as leeches were directly weighed. Masses of taxa with relatively large individuals such as odonates, caddisflies, and megalopterans were estimated by determining allometric relationships (from ≥ 20 individuals) of linear body dimensions such as head capsule widths or body length to dry mass specific for these lakes. Allometric relationships used the equation $W = aX^b$, where W is the organism mass in milligrams dry mass, X is a linear body dimension, and a and b are coefficients. These relationships were genus specific for odonates and megalopterans (typically *Sialis*), and at the family level for caddisflies. Masses for individuals of other taxa were estimated through equations in the literature (Smock 1980, Nolte 1990).

Body size structure of benthos

We analyzed benthos size structure for all organisms >2.0 mg dry mass ($>\log_2 = 1$) to avoid potential inefficiencies in sampling very small organisms (Schlacher and Wooldridge 1996). Fish bioenergetics model output demonstrates that this criterion accounted for $>96\%$ of annual mean fish consumption of benthos during this study. The biomass of benthos for each lake-year was assembled into a normalized size spectrum (Sprules and Munawar 1986), which characterizes the distribution of community biomass over an axis of body size. Biomasses of benthos were summed within \log_2 size classes (milligrams dry mass) regardless of taxa. Normalized size distribution was generated by plotting the value $\log_2(\text{sum of biomass in each size class/range of the size class})$ against the maximum body size in each body size class on a \log_2 scale. The slopes of the normalized size spectra may therefore be used to systematically compare body size distributions among systems or over time. The normalized size spectrum differs from a regression with biomass alone as the abscissa, which would produce a slope = 0 if the summed individual biomasses in each size class were equal (sensu Sheldon et al. 1972). In a normalized size spectrum, equal biomass in each \log_2 size class would produce a slope = 1. A community that contained a relatively low

TABLE 3. Regression parameters for normalized size spectra of benthos for each lake-year.

| Year | Lake | Fish status | Slope | SE _{slope} | r ² |
|------|--------------|-------------|--------|---------------------|----------------|
| 1991 | Central Long | Absent | -0.487 | 0.156 | 0.764 |
| 1992 | Central Long | Absent | 0.155 | 0.155 | 0.178 |
| 1993 | Central Long | Absent | 0.105 | 0.550 | 0.012 |
| 1994 | Central Long | Absent | -0.788 | 0.219 | 0.812 |
| 1995 | Central Long | Present | -0.891 | 0.106 | 0.959 |
| 1991 | Paul | Present | -0.915 | 0.273 | 0.790 |
| 1992 | Paul | Present | -1.161 | 0.304 | 0.829 |
| 1993 | Paul | Present | -0.888 | 0.266 | 0.789 |
| 1994 | Paul | Present | -1.022 | 0.427 | 0.657 |
| 1995 | Paul | Present | -1.110 | 0.086 | 0.982 |
| 1991 | West Long | Present | -1.123 | 0.308 | 0.816 |
| 1992 | West Long | Present | -0.517 | 0.147 | 0.805 |
| 1993 | West Long | Present | -0.201 | 0.452 | 0.062 |
| 1994 | West Long | Present | -0.696 | 0.403 | 0.598 |
| 1995 | West Long | Present | -0.058 | 0.235 | 0.020 |

Notes: Reciprocals of slope standard errors (SE_{slope}) were used as weighting variables for slope vs. consumption rate and fish biomass regressions in Fig. 3.

proportional biomass of large organisms and high proportion of small-bodied forms would have a more negative slope than the opposite case.

Regression parameters of normalized size spectra have been used to compare biomass distributions in lake pelagic (Peters 1983, Sprules and Munawar 1986, Gaedke and Straile 1993, Gaedke et al. 1996) and benthic communities (Hanson et al. 1989, Hanson 1990, Rasmussen 1993, Rodríguez and Magnan 1993), primarily for the purpose of comparisons among lakes, or temporal or spatial variation within lakes. We know of no study using normalized size spectra against a measure of predation. We focus on slopes of size spectra to characterize the distribution of community biomass instead of intercepts that may be used to compare community biomass (Sprules and Munawar 1986). In this paper we analyze the variation in slopes of normalized size spectra against a gradient of fish biomass and predation pressure (expressed as consumption rates on benthic prey). A relationship between slopes of normalized size spectra and either fish biomass or consumption rates by fish on benthos would suggest that size-selective predation by fish affects body size distributions of benthos. We expect a negative relationship of slopes with fish biomass and consumption rates on benthos. Furthermore, the shape of these relationships should reveal whether the presence/absence of fish or a gradient of fish predation pressure is sufficient to account for variation in the size distributions of benthos.

In order to account for variation in the errors of slope estimates, we used slope values weighted by the inverse of their standard error (Table 3) for each lake-year to test the relationships of slopes against fish biomass and consumption rates. Slopes from normalized size spectra with relatively little error thus had a greater influence on the overall regressions of slopes vs. consumption

rates by fish or total fish biomass. The standard errors of slope estimates were not significantly correlated with either consumption rates by fish ($r^2 = 0.008$, $F_{1,13} = 0.103$, $P = 0.753$), or total fish biomass ($r^2 = 0.001$, $F_{1,13} = 0.010$, $P = 0.922$), suggesting that the influence of slopes with low errors was not unequally distributed over the gradients of consumption rates or total fish biomass.

Although benthic community size structure may vary within lake-years, the time scale of lake-year comparisons is appropriate for the recruitment frequency of fish and most benthos in these lakes. A finer temporal resolution, such as months, would be more likely to impart serial dependence and is less biologically relevant than years (Frost et al. 1988). Annual means have been used to compare broad patterns in body size distributions elsewhere (Cyr et al. 1997a, b). Reproduction of fish and invertebrates in the spring and overwinter mortality may reduce the influence of past predator and prey assemblages on an annual basis (Post et al. 1997). In addition, density-independent factors such as annual variation in weather can influence recruitment success for fish and for insects with synchronized terrestrial adult stages (Corbet 1962, Post et al. 1997).

We tested for serial dependence of slopes from normalized size spectra within lakes by comparing the absolute value of the means of observed consecutive-year differences in slopes (e.g., $\text{year}_n - \text{year}_{n-1}$, over the five years of the study) with the absolute values of 1000 means of randomized slope pair differences within lakes (e.g., 1000 means of four differences each). The randomized year-pairs were constrained so that a given year was not paired with itself. If slopes between consecutive years were not independent and exhibited serial correlation, we would expect a significant proportion (for $\alpha = 0.05$, 950/1000) of differences from randomized slope pair means to exceed the observed means of slope differences between consecutive years (Manly 1991). We found a lack of evidence for serial correlation by this analysis. Observed mean differences in slopes from consecutive years were greater than 220, 414, and 596 of the 1000 random differences for Central Long, Paul, and West Long, respectively.

Our overall prediction is that the weighted slopes of normalized size spectra would be negatively related to fish biomass and consumption rates on benthos on the basis of experiments demonstrating size selection for large prey by many fish predators (Mittelbach 1981b, Crowder and Cooper 1982, Persson et al. 1996). We expected consumption rates by fish on benthos would account for more variability (higher coefficient of determination) in slopes of size spectra than fish biomass, and that slopes would differ along a gradient of consumption rates rather than simply between the presence or absence of fish.

RESULTS

Fish populations and consumption rates

Differences in fish biomass ranged from 0 to 31 kg/ha, and consumption rates on benthos from 0 to 9.72

mg·m⁻²·d⁻¹ among lakes and years of this study (Table 2), allowing us to test whether benthic size structure responds to gradients of fish biomass and predation. Fish in Paul Lake were unmanipulated during the study and characterized by relatively constant biomass and smaller individuals compared to the fish assemblage in West Long. The mean fish sizes are aggregates of all juveniles and adults intended primarily to illustrate the lack of a relationship with total fish abundance (Table 2). Fish were segregated into finer size classes to estimate consumption rates with the bioenergetics model as described earlier. The ranges of mean fish size among lake-years correspond to an approximately twofold difference in mass-specific maximum consumption rates of bass during simulations at constant temperatures (Rice et al. 1983). The range of water temperatures observed among lake-years (Table 1) has a less dramatic effect, yet ~50% more food energy is required by similar-sized fish at the maximum (21.6°C) vs. minimum (16.7°C) observed lake-year average water temperatures.

Total consumption rates by fish, and the proportion of prey consumed from benthic sources, varied both within and among lake-years (Fig. 1). Consumption of benthos as a percentage of total prey consumption was neither related to mean fish size ($r^2 = 0.007$, $F_{1,9} = 0.068$, $P = 0.800$), nor the total biomass of juvenile and adult fish ($r^2 = 0.113$, $F_{1,9} = 1.15$, $P = 0.313$, Table 2). Fish biomass was a poor predictor of consumption rate on benthos when fish biomass was >10 kg/ha (8 of the 11 lake-years with fish) ($r^2 = 0.178$, $F_{1,6} = 1.30$, $P = 0.298$). We enhanced fish abundance in West Long during 1995 (as might be done with managed systems for public use), which coincided with relatively high recruitment of young-of-year fish (J. R. Hodgson, unpublished data). Despite this increase in fish biomass from 1994 to 1995 in West Long, consumption rates on benthos were similar between these years as fish included less benthic prey in their diets in 1995. Prey consumed by fish added to Central Long in 1995 were mostly from benthic sources (59.6%), but total consumption rate on benthos was low (1.11 mg·m⁻²·d⁻¹), likely due to low fish biomass. Variation in fish biomass, and proportions of prey from benthic sources were important factors generating the observed gradient of consumption rates on benthos.

Fish diets and benthos body size distributions

Most of the biomass of benthic prey consumed consisted of leeches (Hirudinea 23.7%) and immature dragonflies (Odonata 41.9%) based on lake-year means. These two taxa are the largest common benthic prey available to fish based on the mean size of captured individuals. Other benthos common in diets (2% < lake-year mean < 7% of total benthos biomass consumed) included molluscs, beetles (Coleoptera), and immature caddisflies (Trichoptera), and chironomids (Diptera). Fishes also consume other less common

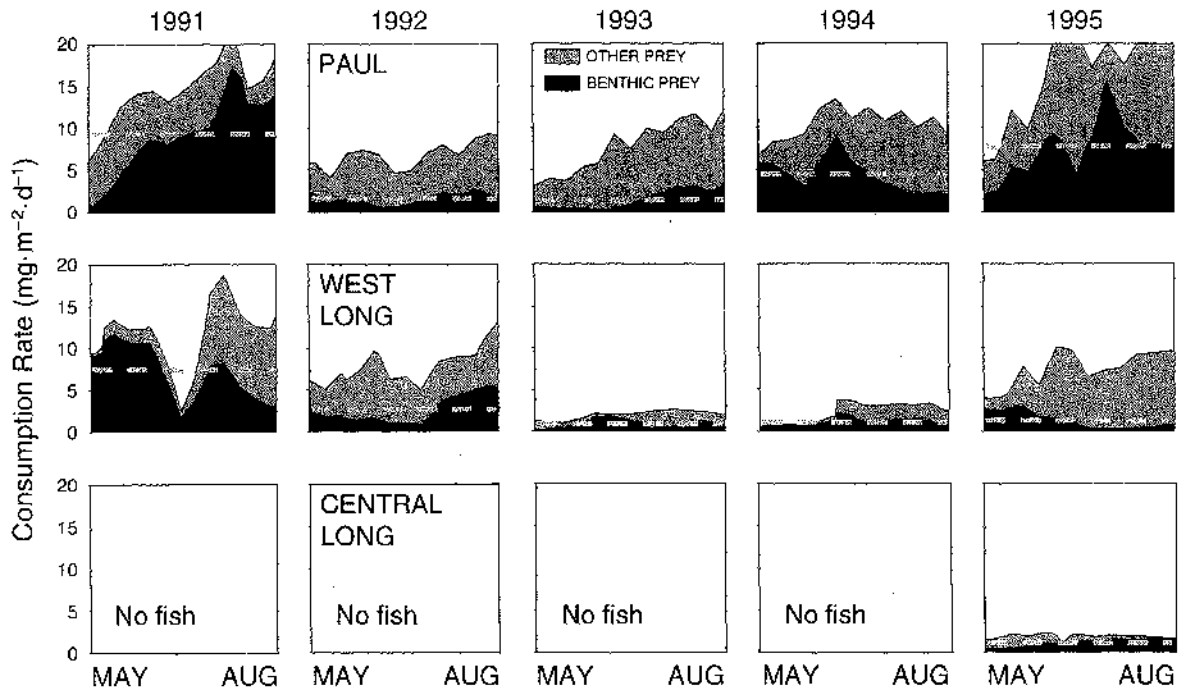


FIG. 1. Daily consumption rate estimates generated by a bioenergetics model for fish in Paul, West Long, and Central Long lakes for 1991–1995. Rates are the milligrams dry mass of prey consumed per square meter of littoral area (<3 m depth) per day during mid-May through August. Horizontal dashed lines in each panel represent means of daily consumption rates on benthos for each lake-year. Benthic prey were primarily dragonfly (Odonata) nymphs and leeches and also included Amphipoda, Chironomidae (Diptera), Coleoptera, Ephemeroptera, Mollusca, Trichoptera, and other unidentified benthic prey. Other prey comprised primarily fish and also included cladoceran and chaoborid zooplankton, amphibians, and small mammals. Additional methodological details on diet categories and processing of fish diet samples are outlined in Hodgson et al. (1993). Bioenergetics model software and fish species' metabolic parameters are from Hewett and Johnson (1992).

prey, and other life stages of the prey listed above including Chironomidae pupae as they migrate through the water column and subsequently eclose at the water surface, or odonate adults alighting upon surface waters (Hodgson and Kitchell 1987, Hodgson et al. 1993). Although these life stages represent benthic production, they are excluded from our analyses because these life stages are not truly benthic dwelling and thus do not directly contribute to benthos size structure. An analysis of benthic prey taxa selection by fish demonstrates that size accounts for a very large proportion of the variation in prey selection, but that other characteristics of prey taxa may be important. For example, selectivity for odonates, but not leeches, is higher than would be predicted by size alone (S. C. Blumenshine, D. M. Lodge, and J. R. Hodgson, *unpublished manuscript*).

Slopes of normalized size spectra from Central Long were particularly variable among the five years of the study ($SD = 0.490$; Fig. 2 and Table 3), and function as an indicator of variation in benthos body sizes in the absence of high consumption rates by fish. In contrast, slopes were much less variable among the five lake-years with the highest consumption rates ($SD = 0.249$; Fig. 2 and Table 3).

Relationship of benthos size structure to fish biomass and consumption rates

As expected, slopes of normalized size spectra were negatively related to fish biomass and consumption rates on benthos, but consumption rate was a better predictor of slope values (Fig. 3). While fish biomass alone explained 30.9% of the variation in weighted slopes of normalized size spectra among lake-years ($F_{1,13} = 5.965$, $P = 0.031$, Fig. 3a), consumption rates explained 44.4% of the variation ($F_{1,13} = 10.37$, $P = 0.007$, Fig. 3b). The overall relationship of slopes from normalized size spectra and fish consumption rates was not affected by the nutrient loading status of lakes. The relationship of slopes and fish consumption rates did not change when the data were analyzed with (slope = $-0.330 - 0.793 \times \log_{10}[\text{consumption rate} + 1]$; $SE_{\text{slope}} = 0.246$), or without (slope = $-0.245 - 0.899 \times \log_{10}[\text{consumption rate} + 1]$; $SE_{\text{slope}} = 0.256$) lake-years with nutrient enrichments (test for homogeneity of slopes; $t = -0.211$, $P \gg 0.05$). The absolute value of residuals from the slope-consumption rate regression (Fig. 4), but not the slope-fish biomass regression ($r^2 = 0.104$, $F_{1,13} = 1.50$, $P = 0.242$), were negatively related to consumption rate on benthos ($r^2 = 0.363$, $F_{1,13} = 7.39$, $P = 0.018$).

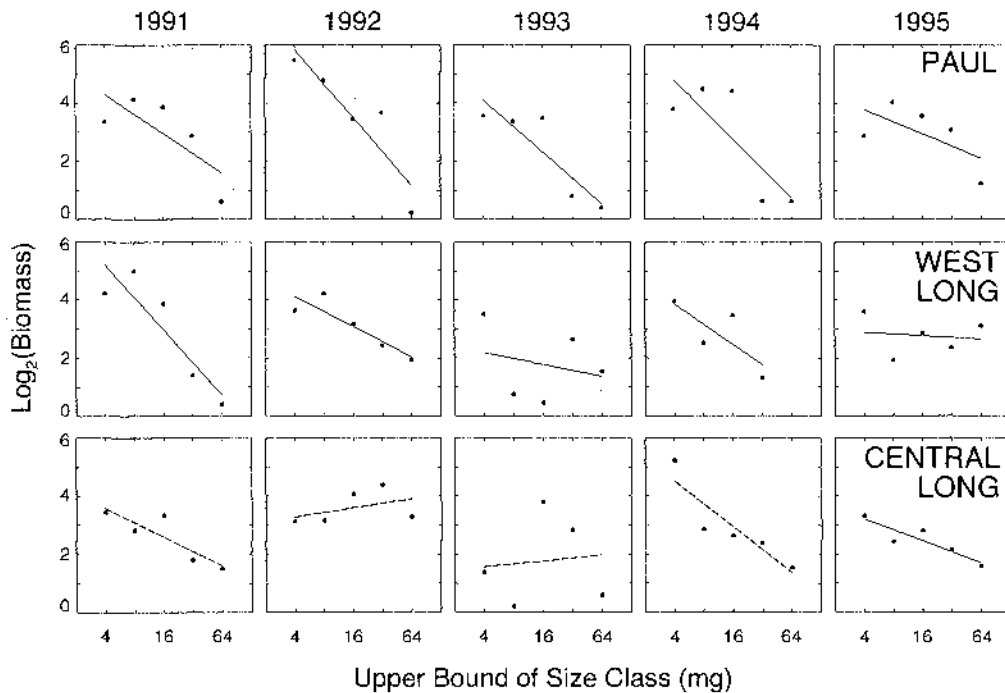


FIG. 2. Plots of normalized size spectra of benthos for each lake-year (June–August). Points are based on the total biomass (original data in milligrams) of individual organisms within specific ranges of biomass or size classes based on \log_2 intervals. Lines in each plot are linear least-squares regressions. For reference, equivalent biomasses in each size class result in a slope = -1 . Dashed lines represent lake-years without fish. Line slopes, standard errors, and coefficients of determination given in Table 3.

DISCUSSION

A primary objective of this study was to examine the intensity of size-selective predation as a mechanism accounting for variation in prey body size distributions in natural settings. We found that consumption rates by fish on benthos, more than fish biomass alone, are negatively related to the slopes of normalized size spectra for benthic prey based on data from three lakes over five years. Associating fish predation with reduced proportions or abundances of larger organisms in prey communities is not new, but our approach differed from previous investigations primarily in scale, and the measurement of mechanisms and responses.

Results taken primarily from smaller scale experiments suggest that contrasts in benthic density or biomass are greatest between no fish and low fish density treatments (review in Diehl and Kornijów 1997). However, if the presence or absence of fish was the primary regulating factor of benthos body size distributions, then the slope values of normalized size spectra in this study would be near parallel with the axes of slopes vs. fish biomass or consumption rates. Rather, our results suggest that benthos size structure responds to a gradient of fish consumption, in contrast to a qualitative distinction of fish presence or absence. Because most lakes vary in the abundance or composition of fish assemblages rather than by fish presence/absence, ex-

periments focusing on variation in predation intensity would be most profitable in addressing applied fisheries and lake food web issues.

Factors producing variation in predation pressure

Variation in fish size, temperature regimes, and fish diets among lake-years may decouple consumption rates and total predator biomass (Hewett and Kraft 1993), and thus the interpretation of how fish predation affects prey communities. Information from prior explicit tests of the fish bioenergetics model (Kitchell et al. 1977, Rice et al. 1983, Rice and Cochran 1984, Bartell et al. 1986) suggests that estimates of specific consumption rates are especially sensitive to fish size and thermal history. For example, using the endpoints of the range of mean fish size in this study (Table 2) and fish bioenergetics model simulations by Rice et al. (1983), we would expect approximately a twofold difference in specific consumption rates (grams per gram per day) by largemouth bass feeding at their thermal optimum temperature for consumption (27.5°). Because our study site is near the northern limit for largemouth bass (Carpenter and Kitchell 1993), mean epilimnion temperatures were below the thermal optimum for consumption, but in the range of maximum rate of change in the temperature–maximum consumption rate relationship (Rice et al. 1983). Our point is not to explicitly

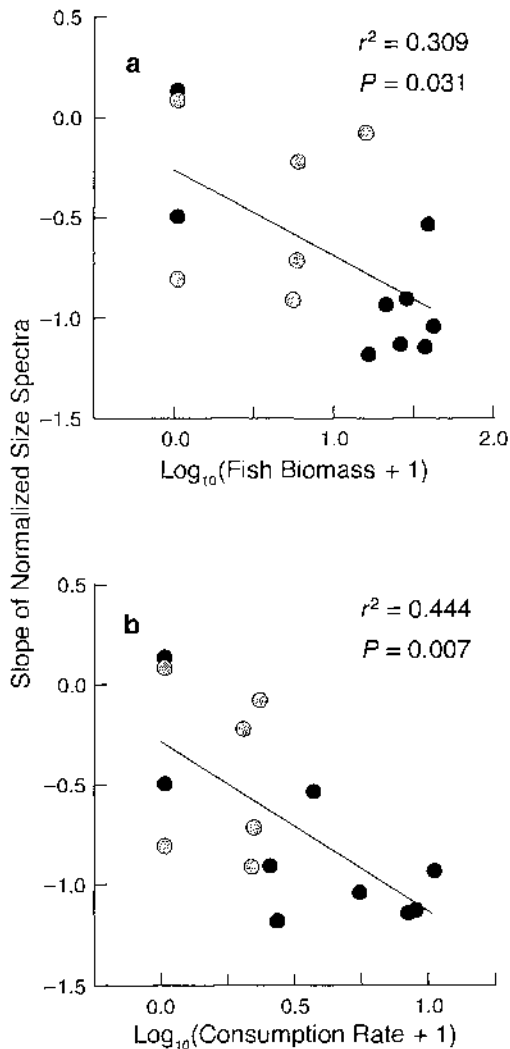


FIG. 3. Slopes of normalized size spectra plotted against mid-May through August means of (a) fish biomass (original data in kilograms per hectare) and (b) fish consumption rates on benthic prey (original consumption-rate data in milligrams per square meter per day). Regressions are based on slope values weighted by the inverse of their standard error ($1/\text{SE}_{\text{slope}}$; Table 3). Consumption rates and biomass are $\log_{10} + 1$ transformed to improve the fit to a least-squares linear regression model. Shaded symbols represent lake-years of epilimnetic nutrient enrichment (1993–1995). The P values and coefficients of determination (r^2) are from all points. The regressions of slopes vs. consumption rates or fish biomass are not affected by the inclusion or exclusion of shaded points (see *Results*).

test these effects or their interactions, but to note that even within the setting of this study, fish size and thermal history may vary greatly, independent of total fish biomass with consequences for trophic dynamics. The differences in the relationships of fish consumption rate and biomass with benthos size distributions are thus conservative in this study if applied over even broader scales. Greater contrasts in fish assemblages, mean fish

size, and lake temperatures would likely further highlight disparities between fish biomass and consumption rates on particular prey communities.

Another source of variation in predation pressure on benthos is the flexible use of prey resources by juvenile and adult fish (e.g., Hodgson and Kinsella 1996). The percentage of total prey biomass consumed by fish from benthic sources varied nearly threefold (range 16.8%–63.8%) among all lake-years. These percentages were not correlated with mean fish size or total biomass of juvenile and adult fish, but are a factor in consumption rates on benthic prey (see *Results*). Whether generalist fish predators focus on benthic or pelagic prey has been linked to relative energetic profitability, which is influenced by predator size and competition for prey that ultimately affect prey body size and abundance (Mittelbach 1981b, Werner et al. 1983, Persson and Greenberg 1990). However, the link between energetically optimal foraging and fish diets is not always as clear in nature as predicted by theory and laboratory experiments (Anderson 1984, Hodgson and Kitchell 1987, Schindler et al. 1997b).

Juvenile and adult fish in these lakes rely on spring recruitment pulses and subsequent consumption of young-of-year fish to maximize growth rates, but are otherwise sustained on benthic prey (Schindler et al. 1997b). Based on known predator and prey sizes (Hodgson et al. 1993), this agrees with a model by Werner (1977) relating net energy gain by largemouth bass to predator-prey size ratios. Nonetheless, predation pressure on benthos is apparently not a direct compensatory response to a lack of prey fish. The 1993 and 1994 cohort, or young-of-year fish density in Paul Lake was respectively 3.5 and 6 times higher than any other

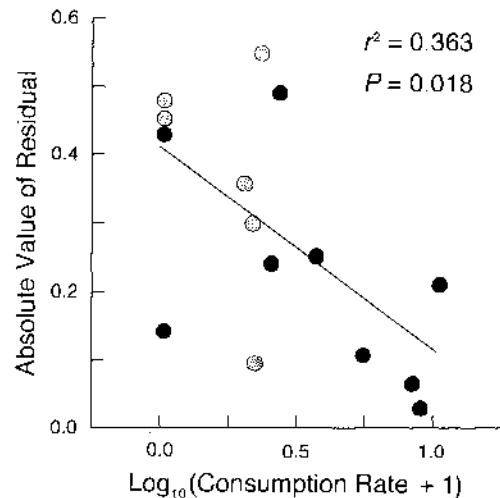


FIG. 4. Absolute values of residuals from regression of slopes plotted against consumption rates by fish on benthos (original data in milligrams per square meter per day) as in Fig. 3b. Shaded symbols represent lake-years of epilimnetic nutrient enrichment (1993–1995). The P value and coefficient of determination (r^2) are from all points.

year since 1984 (Post et al. 1997). The percentage of prey consumed by juvenile and adult fish from benthic sources in Paul Lake during 1993 was relatively low (16.8%) as would be expected due to the abundance of fish prey. In contrast, both young-of-year fish densities and the percentage of prey consumption from benthic sources was high (44.9%) during 1994 (Table 2). Thus, this example suggests that knowledge of fish biomass and the availability of alternative, energetically preferred prey may be an imprecise and inconsistent predictor of predation pressure on benthos. Evidence from these sources and this study further emphasize the need to elucidate the most direct mechanisms possible (consumption rates) to relate the effects of predators on prey communities.

Prey community dynamics

The relative importance of predation rates on prey community structure depends not only on how it varies over space and time, but also on prey recruitment and production rates (Robles 1997). A separate analysis (S. C. Blumenshine, *unpublished data*) of consumption rates by fish on larval odonates with the production rates of this main benthic prey of fish (see *Results*) during 1994 demonstrates that consumption rates in Paul ($1.16 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were near the estimated production rates of odonates ($1.66 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). In contrast, consumption rates on odonates in West Long during 1994 were nearly an order of magnitude less than production (1.09 vs. $0.13 \text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). The relationship of slopes of normalized size spectra and consumption rates (Fig. 3b), and the residuals from this relationship (Fig. 4) show that variation among slope values is highest in the lower range of the consumption rate gradient. Although we do not have production data for other taxa, this information suggests that fish limited the biomass accumulation of some larger benthos when consumption rates were high. At lower consumption rates, other factors limited benthos production rates and resulted in slopes of normalized size spectra generally higher but more variable at the lower end of the consumption rate gradient (Fig. 3).

Experiments or observations over periods less than predator and prey generation times, that reduce variation in predation intensity or predator access to prey communities, will be limited in the ability to account for these sources of variation in natural settings (Frost et al. 1988, Fisher 1994). Variation in predation pressure, lake epilimnion temperatures, availability of alternative prey, and observations longer than the generation times of predators are likely important to trophic dynamics and the consequent effects on prey community structure. However, they are often omitted in experiments at abbreviated scales. Thus, experiments as large scale as ours are valuable because they include natural sources of variation in predation rates and prey production rates.

Potential influence of habitat structure

The habitat we examined in this study is relatively homogeneous soft organic material, with sparse macrophyte coverage. However, habitat physical heterogeneity is likely greater and may be important in cross-system comparisons. In benthic habitats, the abundance and arrangement of physical structures may interact with predation in affecting benthos body size distributions. Mittelbach (1981a) found different spatial and temporal patterns in macroinvertebrate distributions among open water, bare marl, and vegetated habitats in Lawrence Lake, Michigan. Benthos body size distributions also differ between the presence or type of submerged aquatic vegetation (Hanson 1990, Rasmussen 1993). The density and complexity of the structure provided by submerged aquatic vegetation may alter the influence of prey size on predator diets in fish and birds (Crowder and Cooper 1982, Diehl 1992, Brodmann et al. 1997). Potential effects and interactions of structure and predation in benthic habitats can thus incorporate influences associated with both terrestrial and pelagic communities in Holling's (1992) model of community body size distributions. Other studies that examine the interaction of predation and structural complexity on prey body size distributions would greatly enhance the identification and understanding of mechanisms driving body size patterns in communities.

Do general properties link predation and prey body size distributions across ecosystem types?

Producing general rules for body size distributions across ecosystem types may be confounded by several methodological and natural contrasts between terrestrial and aquatic systems. Community ecologists focus primarily on body size distributions of species and the role of competition (Brown and Maurer 1989), while an ecosystem approach would examine the distribution of biomass and the flow of energy (e.g., Sheldon et al. 1977, Platt and Denman 1978, Borgmann 1987). Unfortunately, this division corresponds respectively with terrestrial and aquatic studies of body size distributions (Maurer and Brown 1988, Cyr and Pace 1993, Cyr et al. 1997a).

Cyr et al. (1997a) address this dichotomy by comparing the biomass distributions in terrestrial and aquatic communities with a species density-based approach and a single size measure for individuals of each species. This method was quantitatively similar to a biomass-based size spectrum. However, reliance on a single size to characterize individuals of a species is less relevant in lakes than in most terrestrial communities because of indeterminate growth in many temperate fish species (Kozlowski 1996a, b), and the continuous growth of the aquatic stages of many benthic organisms such as insects and amphibians.

The potential effects of predation on the prey size structure may differ based on morphological properties of predators in aquatic and terrestrial habitats. Liem

(1990) suggests that the aquatic medium has led to a clear separation in the feeding modes of aquatic and terrestrial vertebrates. Specifically, the precise functional design in the feeding modes of terrestrial relative to aquatic vertebrates reduces opportunism in prey capture, leading to competition for specific prey sizes and character displacement (cf. Robinson and Wilson 1998). Interspecific competition for food resources in terrestrial communities may thus be a mechanism to prevent the overlap of species' body sizes (Brown and Maurer 1989). Indeed, in an analysis of food web linkages, Cohen et al. (1993) found higher correlation coefficients of predator-prey body sizes in terrestrial food webs than in either freshwater, coastal, or marine habitats. Food web connectance and linkage density are also relatively high in aquatic communities, indicative of generalist feeding habits (Warren 1990, Bengtsson 1994). This evidence suggests that the influence of apical predators in aquatic food webs are more likely to overlap and be more apparent over a broader range of prey sizes relative to terrestrial habitats. Basic differences in feeding mode must therefore be considered with the existing methodological difficulties in comparisons of body size distributions across ecosystem types.

Conclusion

Models attempting to predict regularities and variation in body size structure in ecosystems will benefit from examining underlying size-structuring mechanisms. A number of studies have examined patterns of body size distribution in benthos across or within systems, with little consensus toward general principles (review in Strayer 1991). Our results suggest a mechanism to account for observed variations in body size distributions across similar systems and over time. Specifically, we found that fish predation shifts benthos size structure toward smaller organisms, but suggest that the result may not be apparent through more traditional analyses of abundance or taxonomic-based measures alone. Recent considerations (Holling 1992, Hairston and Hairston 1993) of the feedbacks between environmental structure, energy availability and use, and body size distributions should provide the most productive path toward identification of mechanisms that create and are affected by body size distributions in communities.

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