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LINKING PATCH-USE BEHAVIOR, RESOURCE DENSITY, AND GROWTH EXPECTATIONS IN FISH

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Abstract. Optimality theory rests on the assumptions that short-term foraging decisions are driven by variation in environmental quality, and that these decisions have important implications for long-term fitness. These assumptions, however, are rarely tested in a field setting. We linked behavioral foraging decisions in food patches with measures of environmental quality covering larger spatial (resource density) or temporal (growth parameters) scales. In 10 lakes, we measured the food density at which benthic fish give up foraging in experimental food patches (giving-up density, GUD), quantified the biomass of benthic invertebrates, and calculated the maximum individual size (L_{∞}) of bream (*Abramis brama* L.), a typical benthivore in these lakes. We found positive relationships between resource density and both GUD and L_{∞} , and a positive relationship between L_{∞} and GUD. Prey characterized as vulnerable to predation contributed most to the relationships between resource density and either GUD or L_{∞} . A path analysis showed that resource density and L_{∞} directly explained 54% and 28%, respectively, of the variation in GUD, whereas 86% of the variation in L_{∞} was explained by resource density, with mostly indirect contribution from GUD. We conclude that the short-term foraging behavior of benthivores matched our expectations based on optimality theory by being positively linked to variables on environmental quality operating at both a larger spatial scale and a longer temporal scale.

Key words: benthic invertebrates; bream, *Abramis brama*; fish growth; giving-up density; lakes, southern Sweden; optimality theory; patch-use behavior; resource density.

INTRODUCTION

Optimality theories assume that natural selection shapes behavioral decisions to maximize lifetime reproductive success. However, the applicability of such rate-maximizing models is dependent on the relationship between the immediate payoff (e.g., intake rate) of a certain behavioral decision and measures of fitness operating over larger scales, such as lifetime reproductive success. There has therefore been an increased awareness of the need to choose the proper temporal and spatial scale of foraging decisions when correlating with fitness measures. For example, maximizing immediate intake rate does not necessarily maximize fitness if several constraints, such as handling and digestive capacity, are considered simultaneously (Fortin et al. 2002). It is therefore important to evaluate how the payoff of a certain behavior at small temporal and spatial scales relates to what is expected for foragers maximizing fitness (Ritchie 1990, Morris and Davidson 2000, Olsson et al. 2002).

The scale of foraging decisions also has implications for the appropriate resolution at which to observe resource heterogeneities (Morgan et al. 1997, Klaassen et al. 2006, Stenberg and Persson 2006). Resource

density may not necessarily positively relate to resource availability from a forager's perspective, because availability is the function of density and vulnerability to capture, the latter being a context-dependent function of prey and predator behavior, morphology, and energy content. Hence, to deduce what distinguishes a rich environment from a poor one may be a difficult task. One option is to use behavioral measures, such as empirical studies of patch use, as indicators of a forager's assessment of environmental quality (Kohlmann and Risenhoover 1996, Olsson 1998) and correlate this measure to different properties of the environment.

In this paper we test if short-term behavioral decisions in food patches correspond to what would be expected to match environmental quality measured as either resource density or average-fitness expectation. Patch-use models predict that rate-maximizing foragers should leave a resource patch when foraging costs exceed foraging gain. All else being equal, a forager should abandon a patch when the harvest rate in the patch drops below the average harvest rate of the environment (Charnov 1976). Further assuming that harvest rate is positively related to food density in the patch (Brown 1988), animals in richer environments should give up a patch at a higher food density (giving-up density, GUD) compared to animals in poorer environments.

We use the GUD of benthivorous fishes feeding in experimental patches in different lakes as a measure of immediate payoff and hypothesize a positive relation-

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ship between GUDs and resource density in these lakes. In this test we also evaluate the relationship between resource density and availability because previous studies of benthic predator–prey interactions have shown that interaction strength is dependent on both the spatial position and the identity of prey (Persson and Svensson 2006). We separate benthic resources spatially in two classes; (1) those vulnerable to predation by being present at the sediment surface, and (2) those partially protected by being present in deeper layers of the sediment. In addition, we divided benthic resources into four groups of organisms that differed in vulnerability to predation due to their size, mobility, and habitat preferences.

We continued our analyses by testing for a positive relationship between resource density and fitness expectation, two measures of environmental quality representing different temporal scales. We used the maximum size of bream, *Abramis brama*, a typical benthivore in European lakes, as a measure of average long-term fitness expectation of benthivores. In fish, individual size is often strongly positively correlated with fitness because a larger size allows for higher fecundity (Wootton 1988), survival (Nilsson and Brönmark 2000), mating success (Jones and Hutchings 2002), or larger egg size (Kamler 1992). In species showing indeterminate growth, such as fish, individuals in richer environments should become larger because a higher resource density allows for higher intake rate, faster growth, and ultimately a larger size than in poor environments. In a previous paper we suggest that maximum size could be used as a measure of growth expectation (Stenberg and Persson 2006). Here we expanded the analysis and estimate the asymptotic length (L_{∞}) of bream in different lakes from growth data fitted to the von Bertalanffy growth equation. We then test for a positive relationship between resource density and asymptotic size of bream in these lakes, hypothesizing that fish grow larger in richer environments. Finally, we test for a positive relationship between the patch-use behavior of benthic fish (GUDs) and their long-term growth expectations.

MATERIALS AND METHODS

The study was performed during 2003–2004 in 10 shallow eutrophic lakes (Bosarpasjön, Sövdesjön, Ydingesjön, Snogeholmssjön, Sätöftasjön, Krakesjön, Kragholmssjön, Ellestadssjön, Dagstorpssjön, and Kvesarumssjön) situated in the southern part of Sweden (mean depth, 1–5 m; area, 0.48–4.2 km²). In each lake we chose an experimental site along a ~150-m shoreline with 1.5–3 m water depth and with sediment consisting primarily of sand and detritus.

Resource density

To assess resource density at the experimental sites, we sampled benthic invertebrates with a tube sampler (diameter: 70 mm) by taking 16 cores, each 8 cm long, at

random locations with 1.5–3 m water depth. The foraging ability of benthivores is greatly reduced with sediment depth, and animals deep in the sediment may not be available to benthivores (Lammens 1986, Persson and Svensson 2006). Therefore, to test the influence of availability on behavior and growth, the sediment cores were immediately separated in the field in two different layers (0–3 cm and 3–8 cm depth) and preserved in 70% alcohol for later analysis (Persson and Svensson 2006). In the laboratory, samples were sieved through a 0.3-mm mesh net and stained with Rose Bengal. Invertebrates were identified, counted, and measured to the nearest 0.1 mm. Lengths were transformed to dry mass using regressions (Persson and Hansson 1999, Persson and Svensson 2006). Benthic invertebrates were divided into groups that mirror their vulnerability to benthivores based on their size and behavior. These are, in descending order of vulnerability, (1) mollusks (snails and small mussels), representing larger slow-moving prey on or below the sediment surface; (2) other macroinvertebrates, representing larger (>1 mm) mobile prey of various taxa on the sediment surface (mainly *Cloeon* sp., *Asellus aquaticus*, *Gammarus* sp., and various species of Trichoptera); (3) diptera (mainly chironomids), representing small stationary or slow-moving burrowing insects; and finally (4) meiofauna (cladocerans and copepods), representing particularly small infauna <1 mm in length.

Behavioral studies

We estimated the GUD (giving-up density of food by fish) in experimental food patches placed at the experimental sites in the 10 lakes during the period between 7 and 18 June 2004. We visited each lake once, during which we used 10 patches with an initial density of 320 food items, placed at least 10 m apart, in each lake. Patches were available for foraging for two hours, starting at ~1000 hours. At the end of the experiment we collected the patches and counted the remaining food items to determine the GUD. A patch consisted of a tray (60 × 30 × 4 cm) filled with sand and commercial food pellets (dry diameter: ~2 mm; Aller Aqua, Christiansfeld, Denmark) used as food items. Previous studies have shown that benthic fish (primarily cyprinids) readily visit such patches with pellets and that they are capable of discriminating between patches of the size used in the present study (Stenberg and Persson 2006). Moreover, these previous experiments, which were performed over several days, showed no time effects, suggesting no need for acclimation period (Stenberg and Persson 2006). Patches were placed in the lakes by wading or from a boat. The top of each of the patches was covered with a net when handling the patches in the water to prevent food items from falling out of the patch.

Bream growth

We collected bream (*Abramis brama*) during the summers of 2003 and 2004 with multi-mesh gillnets (12

different mesh sizes ranging between 5 and 55 mm, knot to knot, following a geometric series) of the NORDIC type according to standard methods (Appelberg 2000), with two additional gillnets with larger mesh sizes (50–75 mm knot to knot) in each lake, and with commercial fish traps (see Stenberg and Persson [2006] for more details). We determined the individual wet mass and total length to the nearest millimeter of each bream. We also collected scales from each individual from an area between the dorsal and the anal fins for age and growth analysis on a Canon 100 microfilm reader in the laboratory.

We chose bream as a representative species for the benthic fish community because it is common and because it is a specialized freshwater benthivore in northern Europe (Lammens 1986, Persson and Brönmark 2002). To test if maximum size reached by bream is a good indicator of benthic-resource availability we calculated the asymptotic size in each lake separately from growth trajectories (length-at-age data) derived from back calculations. For eight lakes, at least 25 individuals were examined. Because we were interested in covering a wide range of maximum bream sizes, we included Krageholmssjön and Ellestadssjön, where bream are rare, but grow to extreme sizes. Due to the low population sizes, we caught only two large individuals from each of these lakes, and these were analyzed for growth trajectories. Using least-square regression, growth trajectories for each lake were fitted to the standard von Bertalanffy growth model:

$$L_t = L_\infty [1 - e^{-k(t-t_0)}]$$

where L_t is the length at t , L_∞ is asymptotic (maximum) length, k is the growth coefficient, and t_0 is the time at which length is zero. Lester et al. (2004) showed that the von Bertalanffy equation is a good descriptor of somatic growth after maturity, and L_∞ based on data from adult individuals should therefore be a measure of potential lifetime reproductive effort. Bream mature at a total length ≥ 200 mm, a size also corresponding to switching from planktivorous to benthivorous feeding (Lammens 1986, Persson and Brönmark 2002). Because we were interested in the growth relationships during benthic feeding, we based our estimates of L_∞ on data from bream >200 mm, i.e., both adult and benthivorous individuals (Persson and Brönmark 2002). The only exception was in Yddingesjön, where maximum bream length was only 300 mm and where growth rate showed a consistent pattern between early and late stages.

We tested for the relationships between resource density, GUD, and L_∞ among lakes by using linear regression (Norusis 2002) on the average GUDs and resource densities for each lake, and on the lake-specific L_∞ 's derived from Eq. 1 using nonlinear regression. Since there is a theoretical upper limit of GUD and a practical upper limit of L_∞ , these relationships are only valid within the data ranges of this study. We also performed multiple regressions to assess which benthos

groups were driving the general patterns. Data were tested for normality using the Lilliefors' test. To meet the assumptions of the tests, regressions were performed on log-transformed benthos data.

To assess the drivers of GUD and L_∞ , we performed a path analysis to separate the correlations between the predictor variables and the response variable into direct and indirect effects. We constructed two different multiple-regression models with either GUD or L_∞ as response variable, using benthos biomass as a fixed factor. In the first model, GUD is the result of the immediate resource density of the environment and the fitness expectation upon entering a patch. In the second model, L_∞ is the consequence of resource density and behavioral decisions. The path models were then constructed using the three correlation coefficients and the standardized partial regression coefficients from the multiple regressions.

RESULTS

The average biomass of benthos in the top 8 cm of the sediment ranged from 3.1 ± 0.43 g/m³ (mean ± 1 SE) in Bosarpasjön to 182 ± 52 g/m³ in Ellestadssjön. The top layer (0–3 cm) had >5 times higher density than the bottom layer (3–8 cm) in all lakes except for Dagstorpssjön, which had equal biomass in the two layers. In lakes with low invertebrate biomass, the community was dominated by meiofauna and chironomids, whereas mollusks dominated in lakes with high biomass of benthos.

There was a positive relationship between the average biomass of benthos and the food density in the patch at which fish gave up (giving-up density, GUD) (linear regression $F_{1,8} = 15.1$, $P = 0.005$, $R^2 = 0.65$; Fig. 1). Separating benthos into two different strata revealed that benthos of the surface layer (0–3 cm) explained a higher proportion of the variation in GUD compared to benthos of the deeper layer (3–8 cm) (linear regression 0–3 cm, $MS = 4380$, $F_{1,8} = 11.5$, $P = 0.01$, $R^2 = 0.59$; 3–8 cm, $MS = 4024$, $F_{1,8} = 9.4$, $P = 0.015$, $R^2 = 0.54$), although both relationships were weaker than the relationship with total benthos density. A multiple regression with all benthos groups as dependent variables showed that the best model included only GUD and mollusk density ($MS = 4641$, $F_{1,8} = 13.3$, $P = 0.007$, $R^2 = 0.62$), although linear regressions revealed a positive relationship between GUD and the density of other macroinvertebrates ($MS = 4025$, $F_{1,8} = 9.4$, $P = 0.015$, $R^2 = 0.54$; Fig. 2).

Estimates of L_∞ , the asymptotic length of bream, varied between 300 and 906 mm, being lowest in Yddingesjön and highest in Ellestadssjön. There was a strong positive relationship between resource density measured as the total benthos biomass and L_∞ (linear regression $MS = 2.5 \times 10^5$, $F_{1,8} = 58.8$, $P < 0.001$; Fig. 1). There were also positive relationships between benthos biomass in both the top and the bottom sediment layers and L_∞ ($MS = 2.2 \times 10^5$ and 1.2×10^5 , $F_{1,8} = 28$ and 6.1 , and $P < 0.001$ and 0.04 , respectively). Benthos biomass

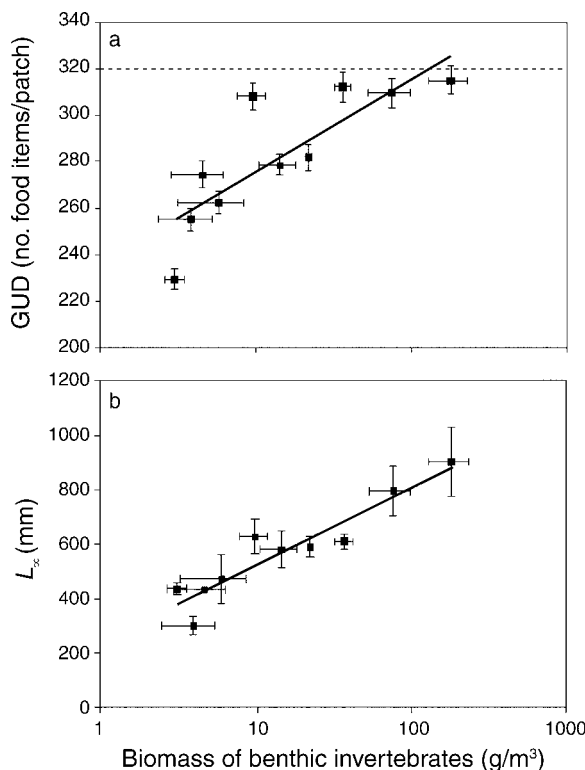


FIG. 1. The relationship between (a) benthos biomass and giving-up density (GUD), and (b) benthos biomass and calculated asymptotic size in bream (L_{∞}). Note the logarithmic scaling of the x-axis. Error bars denote \pm SE (benthos biomass and GUD) or 95% confidence interval (L_{∞}). Solid lines are the linear regressions: (a) $GUD = 39 \log_{10}(\text{benthos biomass}) + 238$, (b) $L_{\infty} = 283 \log_{10}(\text{benthos biomass}) + 243$. The dashed line in (a) is initial food density at the start of the patch experiments (320 food items per $60 \times 30 \times 4$ cm food patch).

of the top sediment layer explained a higher proportion of the variability in L_{∞} than the biomass of benthos of the bottom layer ($R^2 = 0.78$ and 0.43 , respectively; Fig. 1). However, as in the relationships between GUD and benthos, the strongest relationship was obtained when using L_{∞} and total benthos biomass ($R^2 = 0.88$).

The relationship between the biomass of benthos and L_{∞} was present in most invertebrate groups as well. L_{∞} was positively related to the densities of mollusks, other macroinvertebrates, and diptera ($F_{1,8} = 36.2$, 20.4 , and 15.2 , respectively; $P < 0.005$), whereas there were no significant relationships between L_{∞} and meiofauna density (Fig. 2). However, the best model included only the densities of mollusks and other macroinvertebrates as dependent variables (stepwise multiple regression, $MS = 1.3 \cdot 10^5$, $F_{1,8} = 39.1$, $P < 0.001$). As hypothesized, there was a positive relationship between long-term growth expectation of bream (L_{∞}) and foraging decisions in benthivores (GUD) (linear regression, $MS = 4484$, $F_{1,8} = 12.1$, $P = 0.008$, $R^2 = 0.62$; Fig. 3).

The path analyses (Table 1) suggest that the effect of benthos biomass on either GUD or L_{∞} is primarily

direct, whereas the effects of L_{∞} on GUD, and to an even higher extent the effects of GUD on L_{∞} , is primarily indirect through benthos biomass. The path model using L_{∞} as a response variable explained a higher proportion of the variation than the path model using GUD as a response variable ($R^2 = 0.88$ and 0.66 , respectively).

DISCUSSION

Based on theory (Brown 1988), we predicted that benthivores would leave experimental patches at a higher giving-up density (GUD) in richer environments. Our data support this prediction by demonstrating positive relationships between resource density in the environment and GUD of fish foraging in patches within that environment (Fig. 1). We also found a positive relationship between giving-up density and long-term growth rates (Fig. 3). Hence, the present study links three measures of environmental quality relevant at completely different temporal and spatial scales. At one end, asymptotic size integrates processes at long temporal and large spatial scales. At the other end, the patch-use behavior provides a snapshot picture of the short-term and small-scale conditions present to a forager. In between these two, the resource density shows the environmental conditions at an intermediate spatial and temporal scale. The fish visiting our patches followed the optimality paradigm and harvested the patches in a way that followed their long-term growth expectations, which in turn should correlate with potential lifetime reproductive effort. The path analyses suggest that benthos biomass directly drives both GUD and L_{∞} , whereas the effects of GUD and L_{∞} on each other were primarily indirect via benthos biomass.

Animals have multiple needs, and it may therefore be difficult to make an appropriate description of the environment even if several habitat variables are quantified. Studies applying the GUD approach on birds and mammals have shown that it is possible to quantify ecologically relevant variables such as habitat quality (Morris and Davidson 2000, Olsson et al. 2002), predation cost (Brown and Kotler 2004), and competitive ability (Brown et al. 1997, Shochat et al. 2004) by observing the patch-leaving decisions of animals foraging in artificial patches. Here, we show that this technique could also be used on fish to compare environmental characteristics of different systems. GUD correlated positively with those benthos that are characterized as being vulnerable to predation due to their large size (mollusks and other macroinvertebrates), limited mobility (mollusks), or position on the sediment surface (other macroinvertebrates), whereas benthos with smaller size (meiofauna) or associated with a burrowing behavior (most species within the diptera group) were not correlated with GUD. Hence, there was also a stronger relationship when using data from the sediment surface compared to when using data from the deeper layer of the sediment. This agrees with previous

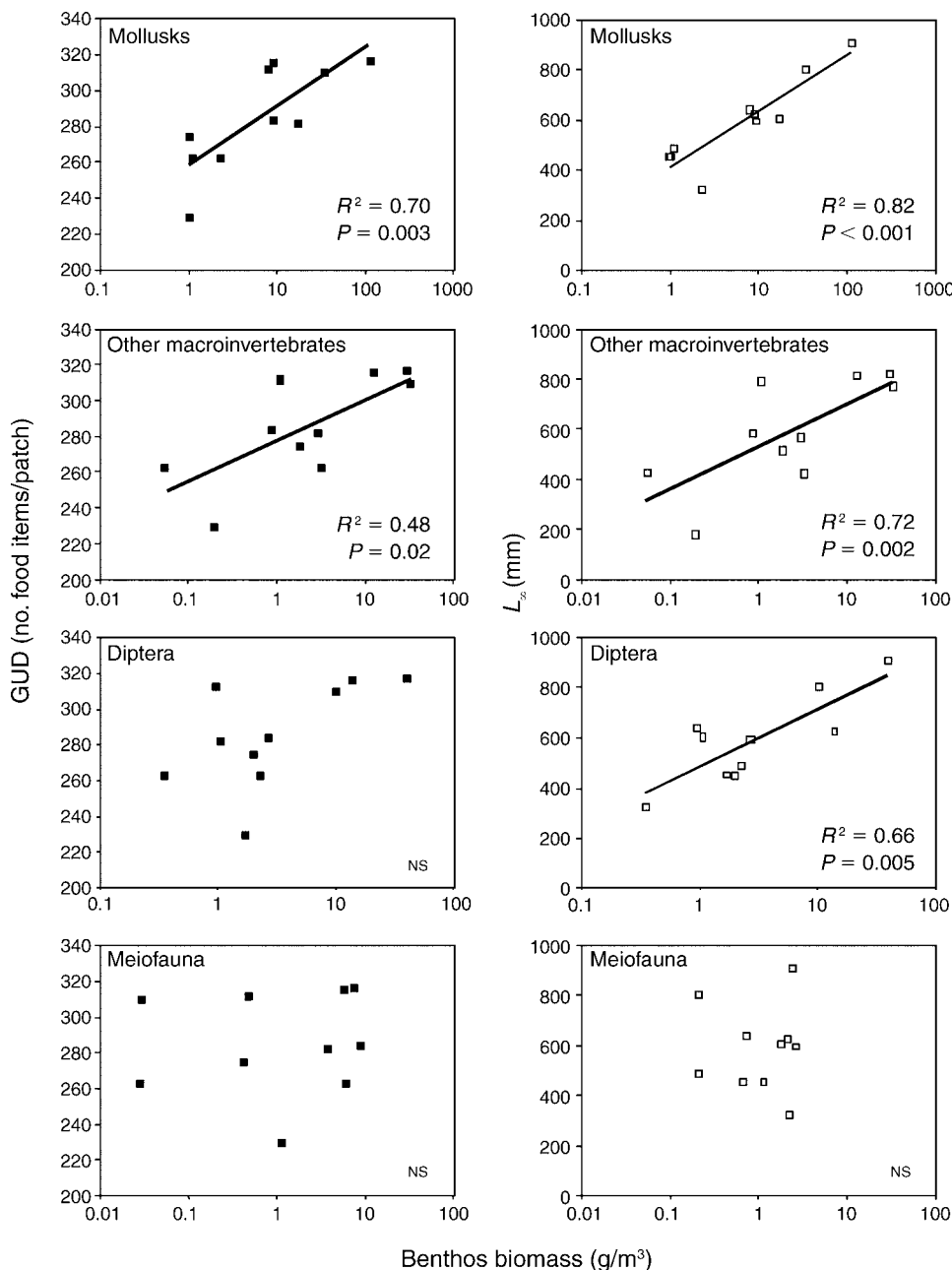


FIG. 2. Relationships between biomass of different benthos groups and GUD (left panels and solid squares) or asymptotic length (L_{∞}) of bream (right panels and open squares). Benthos groups are ordered with the most vulnerable benthos group at the top and least vulnerable at the bottom. Solid lines are linear regressions. Benthos biomass was $\log(x)$ -transformed (other macroinvertebrates, diptera and meiofauna) or $\log(x + 1)$ -transformed (mollusks) to meet the assumption of the regressions. Multiple regressions with all benthos groups as dependent variables were used to determine which group combination best explained variations in GUD and L_{∞} . The best model explaining GUD included only mollusks, whereas the best model explaining L_{∞} included both mollusks and other macroinvertebrates (standardized coefficients 0.61 and 0.43, respectively; see *Results*). Results in panels labeled "ns" are not significant ($P > 0.05$).

findings in experiments by Persson and Svensson (2006) showing that the effects of benthivores on benthos attenuated with sediment depth. Even though the spatial and taxonomic resolutions of the data provide some insights as to which sediment depth and which interaction was responsible for shaping the general

pattern, the strongest relationship was between total benthos biomass and GUD.

The parameter L_{∞} is a measure of potential lifetime growth of survivors, which in turn should be positively correlated to reproductive output. The relationship between resource density and L_{∞} therefore describes

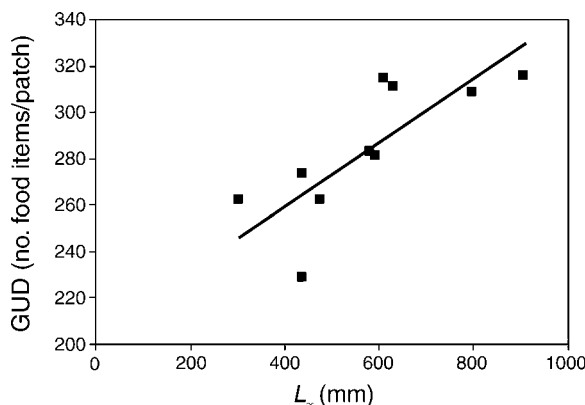


FIG. 3. Relationship between the asymptotic sizes of bream (L_{∞}) in 10 different lakes in southern Sweden, calculated from the von Bertalanffy growth equation, and the giving-up density (GUD) in experimental patches in the benthic habitat of these lakes. The solid line is the linear regression: $GUD = 0.12 L_{\infty} + 212$.

something in between a functional response (per capita intake rate) and a numerical response (per capita reproductive rate as a result of a specific intake rate), where L_{∞} is the long-term consequence of the short-term intake rate. The long-term growth expectation of fish described a decelerating function of resource density. From the relationship we may infer survivor's fitness (Brown 1988, 1992) in a specific habitat as the slope of the curve at the resource density of that habitat. For example, doubling resource density from 4 to 8 g/m³ increases L_{∞} by 21%, whereas doubling resource density from 64 to 128 g/m³ increases L_{∞} by only 11%. Hence, there is a large difference between poor and rich environments, assuming that body size correlates with reproductive output. Moreover, probability of survival increases with body size, and a large proportion of benthivores in a lake may be in a size refuge from piscivores (Nilsson and Brönmark 2000).

Our approach assumes that the GUD of the last individual leaving a patch correlates with bream growth and with environmental quality in a way that makes it possible to compare different systems. This assumption is not necessarily valid because different systems may have different community structures of benthivorous fish that utilize the habitat in different ways. For example, some species may be "cream skimmers" dependent on a high spatial or temporal variability in resource abundance rather than high average resource density, such as the example with Crested Larks coexisting with gerbils at the Negev Desert (Brown et al. 1997). The use of bream growth as a measure of long-term environmental quality has the advantage that large individuals are usually dependent on benthic resources, whereas other species such as roach may rely on alternative resources such as plants, detritus, or zooplankton (Persson 1983). Bream is also the most efficient benthivore in these lakes, and it will therefore be the last

TABLE 1. Effect coefficients with direct and indirect effects on the giving-up density (GUD) or the asymptotic length of bream (L_{∞}), derived from path analyses performed with benthos biomass (log-transformed) as a fixed factor.

Predictor	Effect coefficients		
	Direct	Indirect	Pooled†
GUD			
Benthos	0.54	0.27	0.80
L_{∞}	0.28	0.50	0.79
L_{∞}			
Benthos	0.86	0.08	0.94
GUD	0.10	0.69	0.79

† Direct and indirect together.

species to abandon the benthic habitat. The availability of benthic resources to other species will therefore be dependent on the abundance of bream. Moreover, Stenberg and Persson (2006) concluded that neither fish density nor predation risk explain the positive relationship between GUD and maximum size of bream, suggesting that the difference in GUD between lakes is mainly driven by differences in environmental quality.

We have shown previously that benthivorous cyprinids possess the ability to assess patch quality in a way that drives patches of different qualities towards equalization (Stenberg and Persson 2006). In the present study, we continue and show that benthivores harvest and leave experimental patches at harvest rates (i.e., GUD) that correspond to both the quality of the surrounding environment and to their prior expectations of potential lifetime growth. Hence, the very strong relationships between our measured variables show that patch-use behavior may be used successfully to gain insights about the ecology of benthivorous fish (e.g., competitive ability of different species) and ultimately to gain insights into properties of different lake ecosystems (e.g. to reveal which mechanisms structures communities).

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