



LUND UNIVERSITY

Patch use behaviour in benthic fish depends on their long-term growth prospects

Stenberg, Marika; Persson, Anders

Published in:
Oikos

DOI:
[10.1111/j.0030-1299.2006.13459.x](https://doi.org/10.1111/j.0030-1299.2006.13459.x)

2006

[Link to publication](#)

Citation for published version (APA):

Stenberg, M., & Persson, A. (2006). Patch use behaviour in benthic fish depends on their long-term growth prospects. *Oikos*, 112(2), 332-341. <https://doi.org/10.1111/j.0030-1299.2006.13459.x>

Total number of authors:
2

General rights

Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Patch use behaviour in benthic fish depends on their long-term growth prospects

Marika Stenberg and Anders Persson

Stenberg, M. and Persson, A. 2006. Patch use behaviour in benthic fish depends on their long-term growth prospects. – *Oikos* 112: 332–341.

Animals foraging in a heterogeneous environment may combine prior information on patch qualities and patch sample information to maximize intake rate. Prior information dictates the long-term expectations, whereas prior information in combination with patch sample information determines when to leave an individual food patch. We examined patch use behaviour of benthic feeding fish in their natural environment at different spatial scales to test if they could determine patch quality and if patch use behaviour was correlated with environmental quality. In seven lakes along a gradient of environmental quality (measured as maximum benthivore size), we made repeated measurements of giving-up density (GUD) in artificial food patches of different qualities. At the largest spatial scale, between lakes, we tested if giving-up densities revealed the long-term growth expectation of benthic fish. At the local scale of patches and micro patches we tested for the ability of benthic fish to assess patch quality, and how this ability depended on the patch exploitation levels between the different lakes. We found that GUD was positively related to maximum size of bream, suggesting that short-term behavioural decisions reflected long-term growth expectations. Benthic fish discriminated between nearby rich and poor patches, but not between rich and poor micropatches within a food patch. This suggests that the foraging scale of benthic fish lies between the patch and micro patch scale in our experiments. We conclude that patch use behaviour of benthic fish can provide a powerful measure of habitat quality that reveals how benthic fish perceive their environment.

M. Stenberg and A. Persson, Dept of Ecology, Limnology, Ecology Building, Lund Univ., SE-223 62 Lund, Sweden (marika.stenberg@limmol.lu.se).

Foraging is one of the basic fitness enhancing activities of animals. According to conventional theory, foraging is optimized by maximizing long-term rate of energy gain (MacArthur and Pianka 1966, Pyke 1984, Stephens and Krebs 1986). A basic assumption of many models is that animals are capable of making optimal foraging decisions because they have perfect knowledge about environmental quality. The marginal value theorem (MVT, Charnov 1976), which states that animals should abandon patches at the same quitting harvest rate, assumes that animals know their average long-term intake rate, and that they instantaneously assess the quality of their current patch. This latter assumption is unrealistic,

especially for foragers searching for hidden prey in heterogeneous environments. Instead, animals may use simple strategies, such as devoting a fixed amount of time to each patch regardless of food density in the patch, or estimating patch quality with sample information gained while foraging. The optimal use of sample information (when possible) generally uses an assessment strategy, which combines prior information with sampling information (Green 1980, Iwasa et al. 1981, McNamara 1982, Stephens and Krebs 1986, Alonso et al. 1995, Olsson and Holmgren 1999).

By observing patch exploitation of animals in their natural setting, we may obtain information about how

Accepted 6 September 2005

Copyright © OIKOS 2006
ISSN 0030-1299

they perceive their environment (Brown and Alkon 1990, Kohlmann and Risenhoover 1996, Olsson et al. 1999, van Gils et al. 2003) as well as their ability to assess patch quality. Brown (1988) developed a framework for the use of experimental patches for this purpose, where the giving-up density (GUD) of prey, i.e. prey density upon patch departure, is used as a substitute for the quitting harvest rate. All else being equal (i.e. cost of predation and cost of foraging), foragers in rich environments should leave more food behind in resource patches compared to foragers in poor environments. Studies on both birds (Olsson et al. 1999, 2002) and mammals (Morris and Davidson 2000) have supported the use of GUD as a method to assess environmental quality. These studies linked short-term behavioural decisions made at foraging patches with long-term fitness measures, such as reproductive success. Within a given habitat, foragers that can assess the quality of individual patches should devote more time and effort to rich than poor food patches. Again, both birds and mammals have been shown to make this distinction (Brown 1988, Schmidt and Brown 1996, Morgan et al. 1997, Thompson et al. 2001).

In this paper we report on the patch use behaviour of benthic fish in their natural environment. The novelty of the present study arises from comparing GUDs between different lakes of known environmental quality, and from using fish for the first time as model organisms within this context. We examine patch use behaviours and GUDs at three spatial scales: between lakes, between nearby rich and poor patches, and between micropatches within food patches. The different spatial scales reveal different aspects of the fish's ecology. At the largest scale, between lakes, we ask how benthic fish perceive their environment, hypothesizing that the average GUD should reveal the growth expectation of benthic fish. Fish show indeterminate growth, which means that fish grow towards an asymptotic size (Jobling 2002), reaching a maximum size that may differ substantially between systems, and between generations within the same system (Claessen et al. 2000, Persson et al. 2000). To test how foraging decisions made by benthic fish depend on their growth prospects we selected lakes where benthic fish reach different maximum sizes. In these lakes we measured GUDs in experimental patches that allowed us to provide a standardized foraging environment to the benthivores in each lake. We expected a negative relation between patch exploitation and maximum benthivore size. Food patches should be abandoned at a higher GUDs in lakes where benthivores become large than in lakes where they become small. Because the fish communities of the lakes differed in many other respects, we also tested for relations between GUD and the relative and absolute amount of benthivores and

piscivores (the latter being a measure of predation risk). This would test the alternative hypotheses that GUD is simply a function of the amount of fish, or that it reflects a behavioural response to predation (Brown 1999). In the first case we expect a negative relationship between GUD and the density of benthivores. If patch use is primarily dependent on behavioural responses to predation we expect that GUD relates positively with the density of piscivores, i.e. the fish must trade off food against anti-predator activities such as increased vigilance (Gilliam and Fraser 1987, Brown 1988, Brown et al. 1992).

At the local scale of patches and micro patches we test for the ability of benthic fish to assess patch quality, and how this ability is dependent on patch exploitation level. The quality of an assessment is likely to be dependent on the assessment ability of the animal and the amount of sample information that a forger gains from the patch. The latter, in turn, is likely to be dependent on the size and resource density of the patch, but also on the level of exploitation. Our experiments were performed in lakes where the benthic feeding fish potentially exploited patches to different levels, due to different expectations when entering a food patch. We were interested in how this difference affected assessment ability. GUDs may provide information on a foragers ability to assess patch quality at a local scale (Valone and Brown 1989, Valone 1991). Two main factors may lead to unequal GUDs between rich and poor food patches. Either the heterogeneity in food distribution (i.e. the grain size of the environment) (Wiens 1989, Ritchie 1998, Brown 2000) prevents foragers from distinguishing between rich and poor patches, i.e. the environment is perceived as homogeneous, or the optimal patch departure point is at a food density well above the density of the poorer patch. In both cases GUDs will reflect initial differences in quality among patches, i.e. they will not be equalised. We used two different spatial scales, nearby rich and poor patches and micropatches within a food patch to test the first factor, how benthic fish respond to resource heterogeneity. Performing the experiment in different lakes, in which we expected optimal stopping points to be different, controlled for the second factor, how the optimal departure point correspond to background resource density. Foragers should exploit rich patches more extensively than poor ones, irrespective of growth prospects. For adjacent patches with equal predation and foraging costs, this means that GUDs should be equalised. However, since foragers in poor environments were predicted to harvest the patches more intensively, this was predicted to improve their assessment of patch quality, and hence promote closer equalisation of GUDs in these lakes.

Material and methods

Lake survey

We studied seven lakes (Bosarpsjön, Sövdesjön, Yddingesjön, Snogeholmssjön, Ringsjön, Krankesjön and Krageholmssjön) in June, July and August 2003. All lakes occur in the same southernmost Swedish region (Table 1), but along a gradient of maximum benthivore sizes, i.e. along a gradient of resource availability. In all lakes except Bosarpsjön there was a small-scale fishery directed towards the piscivorous species pike (*Esox lucius*), perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and eel (*Anguilla anguilla*). Bream (*Abramis brama*) are caught regularly in these fisheries, but they are mostly returned to the lakes due to their low commercial value. We sampled each lake's fish community using survey gill nets of the NORDIC type (Appelberg 2000). The nets were composed of twelve different mesh-sizes ranging between 5 to 55 mm knot to knot. Sample intensity differed somewhat between the lakes due to differences in lake size and time restrictions (Table 1). Catch is always analysed as mass per net night (CPUE, catch per unit effort). The catch was expressed as total catch, benthivores (BPUE, benthivores per unit effort), percentage benthivores, piscivores (PPUE, piscivores per unit effort) and percentage piscivores. The fraction of benthivorous fish was calculated using the following assumptions: (i) tench (*Tinca tinca*) and rudd (*Scardinius erythrophthalmus*) are benthivorous their entire life (Kennedy and Fitzmaurice 1970, Johansson 1987, Brönmark 1994). (ii) Some species switch from planktivory to benthivory with increasing size. The fraction being benthivorous is assumed to increase linearly with increasing length, where fish smaller than 120, 150 and 200 mm are completely planktivorous, and fish larger than 180, 200 and 300 mm, completely benthivorous for roach (*Rutilus rutilus*), white bream (*Abramis bjoerkna*) and bream, respectively (Lammens et al. 1986, Persson and Hansson 1999). (iii) Perch switch diet twice: from planktivory to benthivory, and from benthivory to piscivory. Switching thresholds to benthivory is assumed to be 50 and 150 mm, and to piscivory 100 and 200 mm. This is the same principle as used by the national programs for perch to quantify the fraction piscivores (Appelberg 2000), although we have adjusted

the threshold levels somewhat to reflect the fraction benthivores (Lessmark 1983, Persson and Hansson 1999). (iv) pikeperch and pike are piscivorous their entire life.

As our model species of the benthic habitat we used bream (*Abramis brama*), which occur in most south Swedish lakes. They are a larger and more specialised benthivore compared to the more abundant roach (*Rutilus rutilus*) (Persson and Brönmark 2002a). Large bream (> 300 mm) generally feed exclusively on invertebrates that are buried in the sediment, such as chironomids (Lammens et al. 1986, Persson and Hansson 1999). We therefore hypothesize that the maximum size reached by bream would be an indirect and integrated measure of resource availability. Moreover, benthivorous bream are not susceptible to gape-limited piscivorous predators due to their large size (Persson and Brönmark 2002a). Predation costs should therefore not have a significant influence on patch use in benthivorous bream.

From each lake we registered the largest bream caught. Because of the lower sample sizes in Sövdesjön and Snogeholmssjön we also took into account a sample of ten individuals from fish trap catches performed by a local fishery. The population size in Krageholmssjön is very small, and the individuals are extremely large (6000–8000 g, Carlos Piekkari, local fisherman, pers. comm.), which was the major reason why we included this lake in the study. However, because this makes it difficult to catch large bream in this lake (and we did not succeed in this) we used a conservative estimate of maximum size (700 mm and 4330 g) based on previous catches by the local fishery.

Experimental set-up

In each lake, we sought experimental sites of similar appearance. In these sites, the shoreline was mainly vegetated with reeds (*Phragmites australis*). The experimental sites were approximately 30–40 m from the shore, where submerged vegetation was scarce and the sediment consisted primarily of sand and detritus. At each site we placed two stations ~20 m apart at a water depth of approximately 1 m. Each station contained one rich (food density (FD) = 320 food items) and one poor

Table 1. Lake description and sampling efforts for fish.

Lake	Position lat, long	Area ha	Mean/max depth, m	Secchi m	Net nights	Year
Yddingesjön	55°32'N, 13°15'E	202	2/3.5	0.3	16	2000
Bosarpsjön	55°57'N, 13°44'E	69	2.5/5	1.3	24	2003
Sövdesjön	55°34'N, 13°40'E	278	3.4/8	0.6	10	2003
Snogeholmssjön	55°33'N, 13°43'E	258	4/8.5	0.4	7	2003
Ringsjön	55°53'N, 13°33'E	3940	4.6/16	0.8	64	2001
Krankesjön	55°41'N, 13°29'E	339	0.7/3	1.3	24	2003
Krageholmssjön	55°30'N, 13°44'E	211	5/9	0.9	24	2003

(FD = 80 food items) food patch separated by ~2 m. A patch consisted of three plastic trays (30 × 20 × 3.5 cm) representing micropatches that were placed in a steel tray (60 × 30 × 4 cm) and filled with sand (Fig. 1). Micropatches in the poor patch contained 10, 40 and 30 food items respectively, and the rich patch contained 40, 160 and 120 food items (Fig. 1). We used commercial food pellets (crayfish food, Aller Aqua) as food items. These were mixed into the sand before we put the trays in the lake. The patches were available to the fish for two hours, starting from 6.30 – 7.30 AM, because benthivores are generally more active during mornings (and evenings). The top of the patches was covered with a net when handling the patches in the water to prevent food items from falling off the patch.

A small video camera was mounted above the trays in order to assess fish activity in the patches. The video recordings revealed that groups of roach and bream comprised almost all of the foragers at the experimental patches. However, due to high turbidity in some lakes, recordings were not always possible. In turbid lakes we therefore checked for small pits in the sand, which are characteristic traces from foraging benthivorous fish. The presence of such pits confirmed fish activity in the turbid lakes.

Experiments were performed in one or two lakes each day. Due to time restrictions, the number of replicates differed between lakes: six in Bosarpsjön, Sövdesjön and Krankesjön, five in Ringsjön, and four in Yddingesjön, Snogeholmssjön and Krageholmssjön.

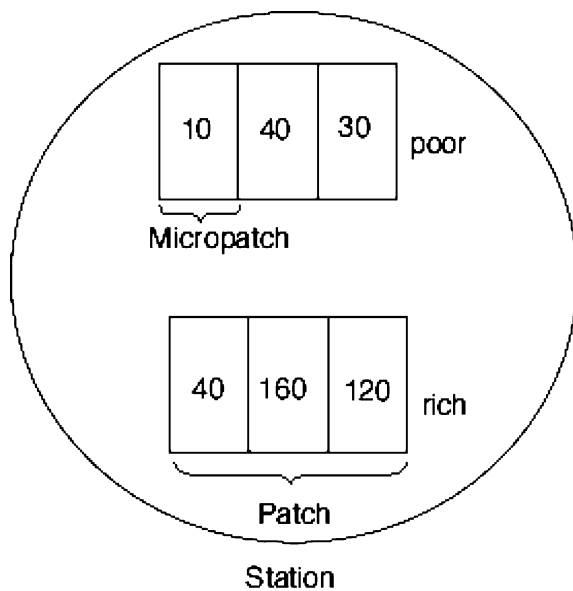


Fig. 1. Experimental set up of food patches. One station consisted of one poor and one rich food patch. Initial food density in the poor patch was totally 80 food items, separated into three micropatches (vertical rectangles), with initially 10, 40 and 30 food items. The rich patch contained totally 320 food items (40, 160 and 120 food items in the micropatches).

Data analyses

GUD provided a measure of habitat quality, from the foragers' perspective, and the percentage of food consumed was used as a measure of patch utilization. The equalisation of GUDs as a measure of equalisation of quitting harvest rates assumes random search within the patch (Olsson et al. 2001). However, the foragers' behavior can affect resource distribution within the patch, and lead to situations where the GUD in the rich patch should be higher than in the poor patch even at equal quitting harvest rates. Deviations from random search may occur as easy food items are collected first, or as stirring by the fish enhances or diminishes the ease of finding additional food items. Harvesting a higher proportion of food from the rich patch provides an alternative and robust way of revealing biased search effort. When a higher proportion of food is harvested from richer food patches relative to poorer, then the forager is revealing the ability to estimate and respond to patch quality.

Between lakes

When we analysed GUDs and % of food items consumed for differences between lakes we used ANOVAs on daily station means. A difference in GUD may potentially emerge from three different processes (Brown 1988). First, (benthic) foragers at higher density may deplete patches to a higher extent than foragers at lower density, simply because patches are visited more frequently in the former case. Second, foragers with lower growth prospects, due to low environmental quality, should deplete patches more thoroughly than foragers with higher growth prospects. Third, foragers experiencing higher predation costs should deplete patches to a lower extent than foragers experiencing lower predation costs should. We tested for such relations using linear regression with GUD as the dependent variable and the amount of fish (CPUE, BPUE and proportion of benthivores), maximum size of bream, and the amount of piscivorous fish (PPUE and proportion piscivores) as independent variables representing the first, second and third processes, respectively. Proportions were arcsine square root transformed prior to analyses.

Within lake-between nearby rich and poor patch

To compare utilization of rich and poor patches, paired t-tests were conducted for each lake separately. Daily mean of GUD and percentage of food consumed in the rich food (FD = 320) and the poor food (FD = 80) patch were compared within one station to assess if fish were able to recognise and distinguish between the rich from the poor patch. If a significantly larger proportion of

food was consumed in the rich patch, we concluded that the foragers were able to assess the difference in patch quality and were able to put more search effort towards rich compared to poor patches. However, if instead there was a significantly higher GUD in the rich patch, we concluded that either patches were not exploited enough to equalise GUDs (due to high expectation of resource density), or, if patches were harvested enough, that the foragers were not able to perfectly assess patch quality. By quantifying patch use in different lakes with different growth prospects, we controlled for the effect of the fish having high expectation of resource density.

To compare the degree of bias towards the rich patch by lake we used an index of food patch quality assessment. If the fish are primarily searching for rather than handling the prey items then patch selectivity can be measured by:

$$\frac{\ln \frac{\text{GUD}_{\text{rich}}}{\text{IPD}_{\text{rich}}}}{\ln \frac{\text{GUD}_{\text{rich}}}{\text{IPD}_{\text{rich}}} + \ln \frac{\text{GUD}_{\text{poor}}}{\text{IPD}_{\text{poor}}}} = \frac{t_{\text{rich}}}{t_{\text{rich}} + t_{\text{poor}}}$$

The index provides an estimate of the proportion of search effort devoted to the rich patch, where IPD is initial prey density and t is a relative measure of search time. A value greater than 0.5 indicates a search bias towards the rich patch, a value less than 0.5 indicates a search bias towards the poorer patch. ANOVA was used to explore differences in patch quality assessment between lakes. One sample t -tests were used to see whether patch quality assessments by lake were significantly greater than 0.5.

Within lake – micropatches within food patch

Assessment ability at the scale of micropatches was tested in a similar fashion as patch assessment using ANOVAs (randomized block design, blocked for day) for rich and poor patches separately. Proportions of food items consumed were arcsine square root transformed before statistical analyses.

Foragers may need to get accustomed to new food items and foraging environments. This may lead to changes in foraging efficiency over time as naive foragers learn where and how to find novel food items. We therefore tested for time effects in patch exploitation in each lake separately with regression analyses, using day as a fixed factor and GUD and percentage of food consumed as dependent variables.

Results

Between lakes

The amount of food consumed per food patch (as measured by the GUDs) differed significantly between lakes (ANOVA, GUD $F_{6,28} = 22.55$, percent consumed $F_{6,28} = 22.15$, $p < 0.001$ for both). There was a gradient of GUD from a station mean of 27 food items in Bosarparasjön to a mean of 376 food items in Krageholmssjön. The percentage of food consumed ranged from 6% in Krageholmssjön to 93% in Bosarparasjön. The amount of fish that we found in the lakes also varied, total CPUE varied from 2216 g in Yddingsesjön to 5713 g in Snogeholmsjön (Fig. 2). Benthivore biomass constituted only 19% of the catch in Yddingsesjön, but was 70% of the catch in Krankesjön. In the other lakes, benthivore biomass varied between 40–53% of total biomass (Fig. 2). There was no significant relationship between GUD and CPUE, CPUE of benthivores, or percentage benthivores (linear regression, $p > 0.2$). No significant relationships were found between GUD and CPUE of piscivores or percentage piscivores (linear regression, $p > 0.2$). There were significantly positive relationships between GUD and maximum size of bream expressed either as length or mass (linear regression, $F_{1,5} = 8.7$, $p = 0.032$, and $F_{1,5} = 17.3$, $p = 0.0088$ respectively, Fig. 3).

Within lake-between nearby rich and poor patch

In the two lakes where fish had the highest consumption of food items (Bosarparasjön and Sövedesjön), GUDs were equalised between the poor and the rich patches (i.e. no significant differences in GUD, but significant difference in % consumed, Table 2). In Snogeholmsjön, Ringsjön, Krankesjön and Krageholmssjön, GUDs were significantly lower in the poor food patches compared to the

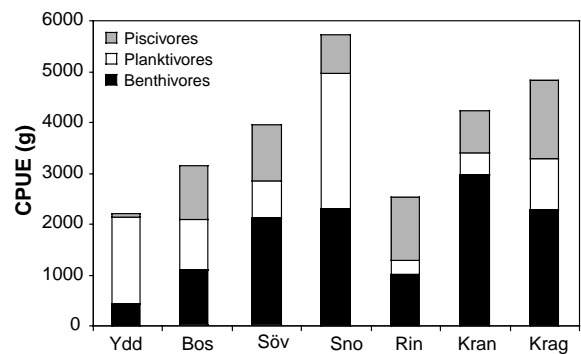


Fig. 2. Catch data from the surveyed lakes. Catch per unit effort (CPUE) refers to catch per net night using multi-mesh gillnets of the NORDIC type (Appelberg 2000). The fractions of functional groups (piscivores, planktivores and benthivores) were calculated from size distributions (Methods). Letters are abbreviations of lake names.

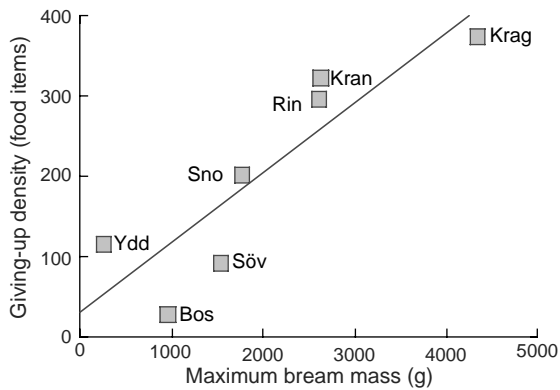


Fig. 3. The relationship between maximum bream size and giving-up density (means of 4–5 sample occasions in each lake) from experimental patches in seven lakes. The equation of the regression line is $y = 0.087x + 30$ ($r^2 = 0.78$, $p = 0.0088$).

rich (paired t-test, Table 2, Fig. 4). In Snogeholmssjön and Ringsjön, two lakes that were harvested to an intermediate extent, GUDs were significantly different between poor and rich patches, although percent food items consumed were higher in the rich patch. In Krageholmssjön, Krankesjön and Yddingesjön there were no significant differences between the utilization of rich patches compared to poor patches when looking at percentage of food consumed (Fig. 4). However, the mean index of food patch quality assessment from all lakes was significantly higher than 0.5 (one sample t-test, $t = 8.958$, $df = 6$, $p < 0.001$), indicating that fish biased their search effort towards the rich food patch. The index varied from 0.596 in Yddingesjön to 0.693 in Snogeholmssjön, but there were no significant differences between lakes (ANOVA, $F_{6,28} = 0.334$, $p = 0.913$).

Table 2. Results from the paired t-test between poor and rich patches in the different lakes. Bold text refers to significant results.

Paired sample t-test	df	t	p
Rich vs poor patch			
GUD			
Yddingesjön	3	-1.58	0.213
Bosarpsjön	5	0.049	0.963
Sövdesjön	5	-1.75	0.140
Snogeholmssjön	3	-3.83	0.031
Ringsjön	4	-13.57	<0.001
Krankesjön	5	-20.54	<0.001
Krageholmssjön	3	-44.66	<0.001
% consumed			
Yddingesjön	3	-1.13	0.341
Bosarpsjön	5	-4.50	0.006
Sövdesjön	5	-2.95	0.032
Snogeholmssjön	3	-5.27	0.013
Ringsjön	4	-2.37	0.077
Krankesjön	5	-1.49	0.196
Krageholmssjön	3	-1.00	0.392

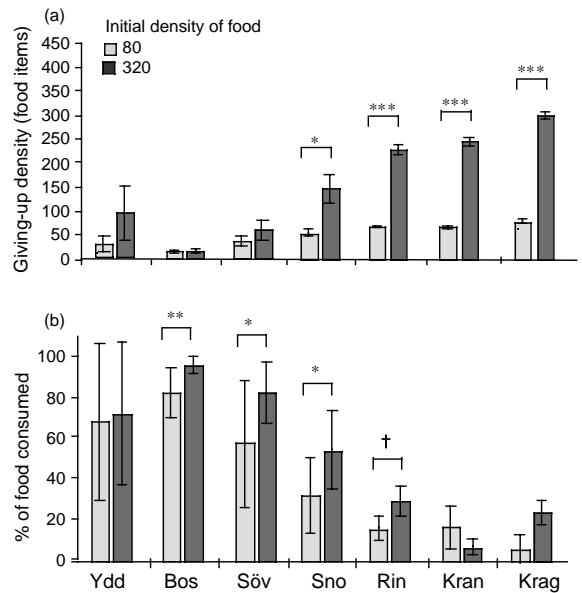


Fig. 4. Giving up densities and percentage of food consumed in the studied lakes, separated into rich and poor food patches. The order of the lakes is along a gradient of maximum bream size. Brackets indicate significant differences (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), or occasionally trends ($\dagger = p < 0.1$). Error bars represent one SE.

Within lake – micropatches within food patches

There was a tendency towards equalisation of GUD in Bosarpsjön, Sövdesjön and Yddingesjön at the micropatch level (Fig. 5a, Table 3). In the other lakes, GUDs differed significantly between micropatches of different value, presumably due to differences in initial food density. The tendency towards equalisation of GUD was not detectable in the percentage of food consumed. There were no significant differences in utilization, in terms of percentage consumed, for micropatches in any of the lakes (Fig. 5b).

Discussion

Foraging theory provides a functional link between short-term and long-term processes by predicting how behavioural decisions are taken to maximise fitness (Stephens and Krebs 1986). Foragers in rich environments should leave a food patch at a higher quitting harvest rate than foragers in poor environments (Charnov 1976). Our main result is the strong positive relationship between giving-up density, a short-term behavioural decision, and asymptotic size of bream, a long-term measure of growth prospects. The observed differences in GUD between lakes clearly demonstrate differences in resource levels (i.e. differences in missed opportunity costs, Brown 1988) in the natural environments of the fish.

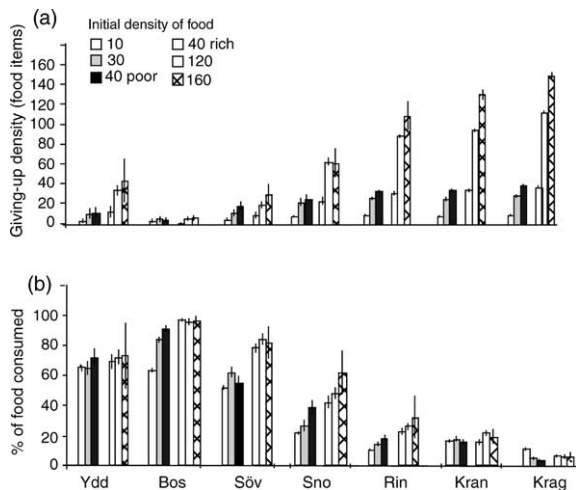


Fig. 5. Giving up densities and percentage of food consumed in the studied lakes, separated into micropatches, rich and poor food patches separately. The order of the lakes is along a gradient of maximum bream size. Error bars represent one SE.

Asymptotic size provided a surrogate for environmental quality. The fish in the different systems undoubtedly valued patches with the same resource level differently. In lakes with small bream (Yddingesjön, Bosarpassjön and Sövdesjön), GUDs were relatively low. In Krankesjön and Krageholmssjön the bream reached the largest maximum size and GUDs were correspondingly highest in these lakes. At a first glance, this might seem contradictory since large fish may have the capacity to harvest resources more extensively than small fish (Lammens et al. 1986, Persson and Brönmark 2002a). But, given that resource availability (and productivity) correlates with growth rate of fish, leaving a foraging patch at a higher resource level should be optimal for fish in a rich environment (i.e. in an environment where the fish become large).

Table 3. Results from ANOVAs (randomized block design, blocked for day) for GUD in the micropatch comparisons. Separate ANOVAs were made for the micropatches in the poor and rich patch. Bold text refers to significant results.

ANOVAs – micropatches		F ₂	p
Randomized block design			
GUD			
Yddingesjön	poor	2.082	0.206
	rich	1.616	0.274
Bosarpassjön	poor	0.704	0.518
	rich	3.968	0.054
Sövdesjön	poor	5.321	0.027
	rich	1.695	0.232
Snogeholmssjön	poor	11.68	0.009
	rich	7.115	0.026
Ringsjön	poor	133.8	< 0.001
	rich	32.34	< 0.001
Krankesjön	poor	133.5	< 0.001
	rich	188.9	< 0.001
Krageholmssjön	poor	2928	< 0.001
	rich	1027	< 0.001

The GUD may be a function of other costs as well (e.g. predation costs), or it may be simply a function of the amount of fish. However, we did not find any relation between GUD and the total amount of fish or the absolute and relative amount of benthivorous fish. Consequently, observed GUDs were not simply a function of the amount of foragers, which has been shown to influence some results in mammals (Mohr et al. 2003). Many studies have shown that GUDs are influenced by the risk of predation with higher GUDs in a risky habitat than in a safe (Brown et al. 1992, Brown and Morgan 1995, Kohlmann and Risenhoover 1996, Olsson et al. 2002) We did not find any such relation between GUD and total predation risk, measured as relative or absolute amount of piscivorous fish. The sites used in the different lakes in our study were similar in appearance, (open water habitat and thus, no vegetation to use as a refuge), and should be considered risky habitats in a within-lake comparison with other habitats. However, due to their large size, bream are generally safe from gape-limited predators once they have become benthivorous (Nilsson and Brönmark 2000, Persson and Brönmark 2002a). Hence, it is quite possible that predation costs are low, at least for bream, and consequently should only be expected to explain a small fraction of the between-lakes variation in the behaviours observed. However, predation costs may still influence GUD within a system, but this was not tested in the present study.

Overall, using GUDs as a measure of habitat quality seems to be applicable to lake communities. Our study shows that measuring GUDs in experimental patches is a powerful tool to gain knowledge about how benthic fish perceive their environment. One argument in favour of our method was that it does not seem to be necessary to train fish how to use the patches, which has been the case in some terrestrial systems (Morris and Davidson 2000). We did not provide a period for the fish communities to acclimate to foraging in our experimental patches, because there were no significant effects of time on the utilization of the patches, although GUDs decreased somewhat (but not significantly) after the first day in Yddingesjön and Sövdesjön. In that respect the fish communities were acting opportunistically. The method as used here, estimates the habitat quality perceived by a guild of benthic fish rather than a single species. Based on the video recordings from two of the lakes, and known size distribution of fish species, we can make some qualitative statements about patch visitors. In Bosarpassjön, in which small sized bream dominate, bream primarily visited patches, whereas in Krankesjön, with large sized bream, roach were the primary visitors. One explanation is that bream size and bream abundance were negatively correlated.

An additional explanation may be that patch quality was too low in large-bream lakes for the bream to even bother harvesting the patches. In either case, the slope of the relationship between GUD and asymptotic fish size would be positive, but the slope would be even steeper if we only consider patches visited by bream. One problem of using roach as a reference species is that roach is more of a generalist with many different alternative foraging opportunities for the same body size than bream have. Hence, the asymptotic size of roach may be a result of feeding on a number of different resources (e.g. detritus, plants, zooplankton and invertebrates, Lessmark 1983, Persson 1983) from different habitats (e.g. pelagic and littoral) and not only a result of feeding on benthic invertebrates. In our study, we did not find any positive relationship between GUD and maximum roach size.

In all lakes, the fish distinguished between the rich and the poor patch by consuming a higher proportion of food in the rich patch, suggesting that GUDs were driven towards equalisation in the lakes. The index of food patch quality assessment showed that fish direct their search effort towards rich patches in all lakes, regardless of background resource levels. Recognizing patchiness at a fine scale can enhance foraging efficiency (Schmidt and Brown 1996). Such ability allows foragers to concentrate foraging effort in rich food patches. Benthic fish in all lakes, in this study, did indeed separate between nearby rich and poor patches. They biased their search effort towards the rich food patches. GUD also seemed to be equalized between micropatches (within food patches) in some lakes, but this was not reflected in the percentage of food consumed. This was despite the presence of clear borders between micropatches, which otherwise may make assessment difficult (Schmidt and Brown 1996). We therefore conclude that the foraging scale of benthic fish lies somewhere between the patch and micro patch level in our study. Several fish foraged in the patch simultaneously; consequently more than one micropatch was normally exploited at the same time. This could result in more information on patch quality being available (resulting in a more accurate patch assessment) when individuals are foraging together in groups compared to when they are alone (Clark and Mangel 1984, Krause and Ruxton 2002). However, local enhancement may also cause over-estimation of adjacent patches, if joining foragers respond to indirect cues, such as the presence of foragers, rather than direct cues such as their foraging success. Space limitation may then force new fish into adjacent patches.

A current emphasis in ecosystems ecology is to integrate processes across different habitats (Polis et al. 1997). In lakes, there has been a focus on benthic habitats and their role in lake ecosystem functioning (Palmer et al. 2000, Schindler and Scheuerell 2002).

Several studies points to the importance of fish as links and integrators of benthic and pelagic habitats (Vander Zanden and Vadeboncoeur 2002). To predict habitat choice it is necessary to assess the relative quality of different habitats. However, measuring resource availability, as perceived by foragers, is tricky, especially in heterogeneous environments where our measurements of prey density may be a poor predictor of availability to the fish. Many fish species use both habitats either daily (Schindler et al. 1993) or over their ontogeny (Werner et al. 1983, Persson and Greenberg 1990, Persson and Brönmark 2002b). Benthic habitats may have strong influences on lake productivity because sediments may be sinks or sources for nutrients. Benthic feeding fish are known to cause dramatic shifts in the trophic state of shallow lakes. By resuspension, large bream affect turbidity and may switch a lake between alternative stable states (Meijer et al. 1990, Breukelaar et al. 1994, Scheffer 1998). Zambrano et al. (2001) predicted that such shifts would be catastrophic, and strongly dependent on the availability of benthic resources. When benthic fish overexploit the benthic resource and availability drops, bream need to intensify their foraging activity and direct it towards deeper layers in order to prevent starvation. This dramatically increases resuspension and may cause shallow lakes to switch from a clear to a turbid state with enormous losses of ecosystem services and biodiversity (Scheffer 1998). The method used in this study may be a tool to predict the probability of switching, which in turn could be used to identify the success of abatement strategies.

Acknowledgements – We thank Erika Nilsson and Marie Svensson for assistance in the field. C. Brönmark, P. A. Nilsson and J. Moll provided valuable comments to a previous draft of the paper. We are especially grateful for the constructive comments, specifically the use of the index, provided by J. S. Brown. Financial support was provided from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning to AP.

References

- Alonso, J. C., Alonso, J. A., Bautista, L. M. et al. 1995. Patch use in cranes: a field test of optimal foraging predictions. – *Anim. Behav.* 49: 1367–1379.
- Appelberg, M. 2000. Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. *Inst. Freshwater Res.*, p. 33.
- Breukelaar, A. W., Lammens, E. H. R. R., Klein Breteler, J. G. P. et al. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll a. – *Freshwater Biol.* 32: 113–121.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – *Behav. Ecol. Sociobiol.* 22: 37–47.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. – *Evol. Ecol. Res.* 11: 49–71.

- Brown, J. S. 2000. Foraging ecology of animals in response to heterogeneous environments. – In: Hutchings, M. J., John, E. A. and Stewart, A. J. A. (eds), *The ecological consequences of environmental heterogeneity*. Blackwell Science Ltd, pp. 181–214.
- Brown, J. S. and Alkon, P. U. 1990. Testing values of crested porcupine habitats by experimental food patches. – *Oecologia* 83: 512–518.
- Brown, J. S. and Morgan, R. A. 1995. Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. – *Oikos* 74: 122–136.
- Brown, J. S., Morgan, R. A. and Dow, B. D. 1992. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. – *Ann. Zool. Fenn.* 29: 311–318.
- Brönmark, C. 1994. Effects of tench and perch on interactions in a freshwater, benthic food chain. – *Ecology* 75: 1818–1828.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – *Theor. Popul. Biol.* 9: 129–136.
- Claessen, D., de Roos, A. M. and Persson, L. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. – *Am. Nat.* 155: 219–237.
- Clark, C. W. and Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. – *Am. Nat.* 123: 621–641.
- Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: a test of a model with foraging minnows. – *Ecology* 68: 1856–1862.
- Green, R. F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. – *Theor. Popul. Biol.* 18: 244–256.
- Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. – *Am. Nat.* 117: 710–723.
- Jobling, M. 2002. Environmental factors and rates of development and growth. – In: Hart, P. J. B. and Reynolds, J. D. (eds), *Fish biology and fisheries*. Blackwell Science Ltd, pp. 97–122.
- Johansson, L. 1987. Experimental evidence for interactive habitat segregation between roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) in shallow eutrophic lake. – *Oecologia* 73: 21–27.
- Kennedy, M. and Fitzmaurice, P. 1970. The biology of the tench *Tinca tinca* (L.) in Irish waters. – *Proc. R. Irish Acad.* 69: 31–84.
- Kohlmann, S. G. and Risenhoover, K. L. 1996. Using artificial food patches to evaluate habitat quality for granivorous birds: an application of foraging theory. – *Condor* 98: 854–857.
- Krause, J. and Ruxton, G. D. 2002. *Living in groups*. – Oxford Univ. Press.
- Lammens, E. H. R. R., Geursen, J. and McGillavry, P. J. 1986. Diet shifts, feeding efficiency and coexistence of bream (*Abramis brama*), roach (*Rutilus rutilus*) and white bream (*Blicca bjoerkna*) in hypertrophic lakes, Univ. Wageningen, Netherlands.
- Lessmark, O. 1983. Competition between perch and roach in south Swedish lakes. – *Ecology*, Lund Univ.
- MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – *Am. Nat.* 100: 603–609.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. – *Theor. Popul. Biol.* 21: 269–288.
- Meijer, M.-L., de Haan, M. W., Breukelaar, A. W. et al. 1990. Is reduction of benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? – *Hydrobiologia* 200/201: 303–315.
- Mohr, K., Vibe-Petersen, S., Lau Jeppesen, L. et al. 2003. Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs. – *Oikos* 100: 459–468.
- Morgan, R. A., Brown, J. S. and Thorson, J. M. 1997. The effect of spatial scale on the functional response of fox squirrels. – *Ecology* 78: 1087–1097.
- Morris, D. W. and Davidson, D. L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. – *Ecology* 81: 2061–2066.
- Nilsson, P. A. and Brönmark, C. 2000. The role of gastric evacuation rate in handling time of equal-mass rations of different prey sizes in northern pike. – *J. Fish Biol.* 57: 516–524.
- Olsson, O. and Holmgren, N. M. A. 1999. Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. – *Oikos* 87: 251–263.
- Olsson, O., Wiktander, U., Holmgren, N. M. A. et al. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. – *Oikos* 87: 264–276.
- Olsson, O., Brown, J. S. and Smith, H. G. 2001. Gain curves in depletable food patches: a test of five models with European starlings. – *Evol. Ecol. Res.* 3: 285–310.
- Olsson, O., Brown, J. S. and Smith, H. G. 2002. Long- and short-term state-dependent foraging under predation risk: an indication of habitat quality. – *Anim. Behav.* 63: 981–989.
- Palmer, M. A., Covich, A. P., Lake, S. et al. 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes. – *Bioscience* 50: 1062–1075.
- Persson, A. and Hansson, L.-A. 1999. Diet shifts in fish following competitive release. – *Can. J. Fish. Aquat. Sci.* 56: 70–78.
- Persson, A. and Brönmark, C. 2002a. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. – *Oikos* 97: 271–281.
- Persson, A. and Brönmark, C. 2002b. Foraging capacity and resource synchronization in an ontogenetic diet switcher, pikeperch (*Stizostedion lucioperca*). – *Ecology* 83: 3014–3022.
- Persson, L. 1983. Food composition and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. – *Oikos* 41: 118–125.
- Persson, L. and Greenberg, L. A. 1990. Optimal foraging and habitat shifts in perch (*Perca fluviatilis*) in a resource gradient. – *Ecology* 71: 1699–1713.
- Persson, L., Byström, P. and Wahlström, E. 2000. Cannibalism and competition in eurasian perch: population dynamics of an ontogenetic omnivore. – *Ecology* 81: 1058–1071.
- Polis, G. A., Anderson, W. B. and Holt, R. D. 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. – *Annu. Rev. Ecol. Syst.* 28: 289–316.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. – *Annu. Rev. Ecol. Syst.* 15: 523–575.
- Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. – *Evol. Ecol.* 12: 309–330.
- Scheffer, M. 1998. *Ecology of shallow lakes*. – Chapman & Hall.
- Schindler, D. E., Kitchell, J. F., He, X. et al. 1993. Food web structure and phosphorus cycling in lakes. – *Trans. Am. Fish. Soc.* 122: 756–772.
- Schindler, D. E. and Scheuerell, M. D. 2002. Habitat coupling in lake ecosystems. – *Oikos* 98: 177–189.
- Schmidt, K. A. and Brown, J. S. 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. – *Am. Nat.* 147: 360–380.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Thompson, A. R., Petty, J. T. and Grossman, G. D. 2001. Multi-scale effects of resource patchiness on foraging behaviour

- and habitat use by longnose dace, *Rhinichthys cataractae*. – *Freshwater Biol.* 46: 145–160.
- Valone, T. J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. – *Anim. Behav.* 41: 569–577.
- Valone, T. J. and Brown, J. S. 1989. Measuring patch assessment abilities of desert granivores. – *Ecology* 70: 1800–1810.
- van Gils, J. A., Schenk, I. W., Bos, O. et al. 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. – *Am. Nat.* 161: 777–793.
- Vander Zanden, M. J. and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. – *Ecology* 83: 2152–2161.
- Werner, E. E., Mittelbach, G. G., Hall, D. J. et al. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. – *Ecology* 64: 1525–1539.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 385–387.
- Zambrano, L., Scheffer, M. and Martinez-Ramos, M. 2001. Catastrophic response of lakes to benthivorous fish introduction. – *Oikos* 94: 344–350.

Subject Editor: Per Lundberg