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Effects of intraspecific competition and predation risk in the littoral-benthic community: a case study of juvenile burbot (*Lota lota*)

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The diel activity pattern and substratum preferences of juvenile burbot (*Lota lota*) were investigated in mesocosm experiments. Single specimens as well as groups of six burbot fed *ad libitum*, starved and with a predator present, were continuously monitored over 24 hours. The diel pattern of activity did not change among treatments but absolute activity levels were significantly different. High levels of activity were observed in solitary and starved fish, intermediate when conspecifics were present but significantly lower in the presence of a predator. Solitary specimens preferred stones while fish in a group showed a size dependent use of the substratum. The results classify the crepuscular to nocturnal behaviour of burbot as stenotype behaviour with little modulation due to external stimuli. The absolute levels of activity as well as the substratum selection however seem to be dominated by individual decisions based on a specimen's environment and predation risk.

Introduction

Significant insights into the temporal and spatial patterns of habitat use by fish, as well as the underlying mechanisms, are available for epibenthic and pelagic species from a variety of different studies (Milinski and Heller 1978, Werner *et al*. 1983, Diehl 1988). From these data we know that the risk of predation and the need for optimal foraging are often the main but opposing forces leading to a precisely balanced behaviour with respect to resource utilization. Many studies have also shown that this trade-off is not a simple stereotyped choice between the safe and the profitable habitat. More often, it seems to be an individual decision of a fish, based on a variety of biotic and abiotic environmental parameters but also on an individual's physiological performance, to escape from a potential predator (Werner *et al*. 1983, Lima and Dill 1989, Colgan *et al*. 1991, Gotceitas and Colgan 1991, Bradford and Higgins 2001).

While in most epi-benthic or pelagic species, predator-induced changes in behaviour are observed mainly for the first 24 h after a predator encounter and then cease if there is no new encounter (Gotceitas and Godin Jean-Guy 1992), anti-predator behaviour in benthic species (e.g. hiding in a substratum shelter during daytime) often persists over much longer periods, even when no actual predator threat is present (Fischer 2000b). In a recent study, Fischer (2003) showed that benthic species may even afford such an exaggerated anti-predator behaviour at the expense of significant energetic costs, leading to a reduction in somatic growth in the long term.

Most of our knowledge on species–habitat interactions, however, is based on studies on epi-benthic or pelagic model-species (Werner *et al*. 1977, Persson 1993) and much less information is available on strictly benthic fish. As compared with the epi-benthic or pelagic community, benthic dwellers are often more closely related to certain substratum types providing shelter and camouflage against daytime predators (Ramachandran *et al*. 1996, Palma and Steneck 2001). Because benthic species have often lower swimming performance and therefore escape capacity to fast moving daytime predators (Fischer *et al*. 1992), foraging in benthic species is often restricted to the night. Crepuscular to nocturnal foraging is then assumed to be the safest even though daytime foraging might be energetically advantageous (Fraser *et al*. 1993).

Because of these differences between benthic and epi-benthic or pelagic species, Fischer (2000a) argued that recent theories on species-habitat interaction and prey–predator interaction that are mainly derived from the epi-benthic or pelagic community cannot be simply applied to the benthic community *per se*, but have to be carefully adapted to the benthic environment and the physiological performance of its dwellers.

In this study I present the results of a mesocosm study with juveniles of a benthic fish species, which is common in the northern hemisphere, the burbot *Lota lota*. Juvenile burbot are very abundant in the littoral zone of Lake Constance, Germany (Fischer and Eckmann 1997a). In contrast to adult burbot which are typically solitary, juveniles use substratum interstices between 0 and 50 cm water depth as their preferred habitat (Fischer and Eckmann 1997b) where they aggregate in small groups (< 10 individuals) beneath larger stones and cobbles.

Juvenile burbot are characterised as crepuscular to nocturnal (Ryder and Pesendorfer 1992) and use chironomids as an important food source (Hartmann 1977, Ghan and Sprules 1993). I examined their daytime, twilight and nighttime behaviour in four consecutive case studies, to analyse diel patterns of activity and habitat selection under the influence of intraspecific competition and predation. I first studied the behaviour of a single specimen with *ad libitum* food supply, when completely alone (Exp. 1). I repeated this experiment with a group of six burbot to test for behavioural changes of the individuals within a group of conspecifics (Exp. 2). I then restricted food supply to this group, to increase intraspecific competition (Exp. 3), and finally added predation risk by introducing a large piscivorous predator, an adult burbot (Exp. 4).

Material and methods

Juvenile burbot

All burbot used in the experiments were caught by beach seining in the littoral zone of Lake Constance and stocked in two glass tanks (50 × 40 × 50 cm) for at least one month prior to further handling. During this time, the fish were kept under a light regime similar to the natural light rhythm and were fed daily with defrosted chironomids. The burbot had a mean total length (TL) of 13.1 cm ± 2.6 SD, a mean wet weight of 14.7 g ± 3.1 SD and were all aged 1+. The sample provided a good representation of the sizes and age-class dominating the littoral zone of Lake Constance during summer (Fischer and Eckmann 1997a).

After about one month, all fish were tagged with passive integrated transponders (TROVAN, 18 mm × 2 mm, glass encapsulated), injected into the body cavity as recommended by Prentice *et al*. (1990). In the following two weeks no tag-induced mortality was observed and fish started to feed about two days after tagging.

Experimental design and procedure

Experiments were done in two outdoor mesocosms each with a base dimension of 2 × 2 m and a depth of 50 cm, divided into four 1 × 1-m compartments by dividers (Fig. 1). The four quadrants were connected by tube-like passages (2.5 cm diameter) level with the substratum, in the centre of each divider. In the centre of each of the four compartments of a mesocosm, a substratum area of about 50 × 50 cm was randomly

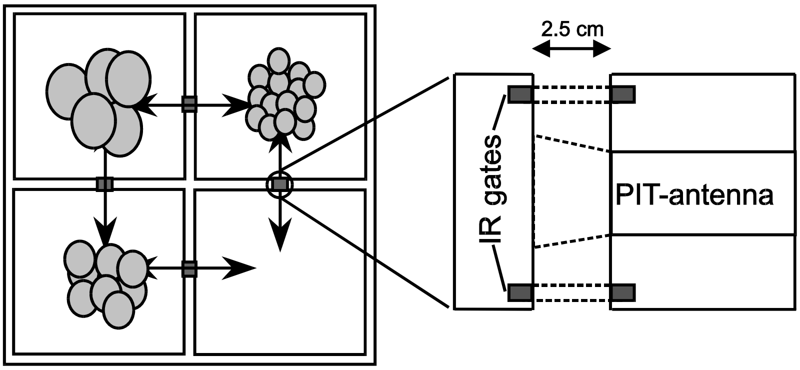

Fig. 1. Schematic picture of the mesocosm with four IR-PIT tube-passages and four different substrates (the pebble substratum is not explicitly drawn). The right IR-PIT tunnel is enlarged to show details of the arrangement of the PIT antenna and the two IR gates. IR-gate and PIT-antenna areas covered by the sensors are shaded grey. Individual parts of the assemblage are plotted to scale.

filled with one of four substratum types: larger stones > 110 mm, cobbles 60–90 mm, gravel 30–50 mm or pebbles < 20 mm. These substratum types were a good representation of the different stone sizes in the littoral zone of Lake Constance, the main habitat of juvenile burbot (Fischer and Eckmann 1997b).

To allow for continuous surveillance of substrate use by each fish over 24 h, as well as its actual level of activity, a passive integrated transponder system combined with infrared gates was installed in the dividers (Fig. 1). This PIT system allowed the detection of any movement among compartments in the mesocosm (subsequently called field change) and, in addition, the IR gates allowed the direction of movement (e.g. cobbles to stones or stones to cobbles) to be determined. In a previous study (Fischer *et al.* 2001), it has already been shown that this system is able to locate the true compartment use as well as the exact time and direction of changes between compartments by any fish in the mesocosm with an efficiency of 92.5%, to any time of the day.

The experiments took place during summer (July to September). The basic experiment (Exp. 1, only one specimen in a mesocosm) was conducted eight times with one fish for seven days each (a total of eight fish) randomly distributed over the total experimental time. Exp. 2 (a group of six conspecifics) and Exp. 3 (same as Exp. 2 but starved) were run for 20–30 days in duplicate, one group (six fish) in each mesocosm. Exp. 4 (a large predator was present in one substratum) was run for 30 days in duplicate or until all juveniles had been preyed upon by the large burbot.

In Exp. 1, 2 and 4, food for all specimens was provided *ad libitum* in each of the four compartments of the mesocosms to ensure that the absolute amount of food per compartment was no stimulus for substratum selection. Preliminary experiments with juvenile burbot had shown a dome shaped function of maximum food uptake versus water temperature which suggested a maximum ration of 0.51 g ww (food) × day^{-1} × g ww (fish)$^{-1}$ at about 18 °C, only slightly lower rations of 0.47 g ww (food) × day^{-1} × g ww (fish)$^{-1}$ at 22 °C and 0.49 g ww (food) × day^{-1} × g ww (fish)$^{-1}$ at 15 °C (P. Fischer unpubl. data). Because water temperatures in the mesocosm never exceeded these temperatures, in a daily or in a seasonal cycle, I assumed 0.51 g ww (food) × day^{-1} × g ww (fish)$^{-1}$ to be a valid approximation to the minimum food required to ensure satiation. At the beginning of each experiment, I calculated the total biomass of fish per mesocosm and then provided double the amount of food per day, in each compartment, which would ensure satiation of all fish in a mesocosm.

We used freshly dead chironomids as food to prevent the behaviour of the food itself from influencing the fish behaviour by actively distributing within the experimental area. Preliminary experiments had shown that juvenile burbot readily accept dead chironomids as food and grow when eating them. To prevent food accumulation during the experiment, remaining food was removed every day prior to feeding. Food was provided every day between 10:00 and 13:00. Daytime feeding was selected because preliminary laboratory experiments showed that food uptake in juvenile burbot mainly takes place during twilight and at night but not during day. Daytime feeding therefore ensured that sufficient food was available for all specimens in all compartments at the beginning of the foraging phase.

Previous experiments in the mesocosms used here (Fischer *et al.* 2001) showed that their light regime and water temperatures were close to *in situ* conditions in the lake littoral, which was about 30 m away from the experimental area. However, besides this advantage of outdoor conditions especially with respect to the light regime, mesocosm experiments in general have the disadvantage of an only semi-controlled experimental environment. This often leads to higher variances in the behavioural data within one experiment as compared with a strictly controlled laboratory approach and therefore leads to a more conservative estimation of differences in behaviour between experiments. This disadvantage in statistical discriminatory power among treatments was accepted for the advantage of quasi-natural light conditions during the experiments. During the experiments themselves, there was no further handling of the mesocosms, in order to avoid any disturbance, except for daily feeding in Exp. 1, 2 and 4.

Predator

In Exp. 4, I used adult burbot as predators of the juvenile burbot. Studies of Chen (1969) as well as own experiments showed that burbot are cannibalistic and prey upon juveniles both under experimental and *in situ* conditions. I collected four large burbot (30–40 cm TL) with trap nets in Lake Constance and held them in a 2 × 2-m outside mesocosm close to the experimental area to ensure identical light and temperature regimes. During pre-experimental housing, the large burbot were maintained on a diet of frozen chironomids and were sporadically fed with juvenile burbot to ensure their potential to prey on juveniles. Two of the four burbot (TL 34 cm and 36 cm) were finally used for the experiments. Because preliminary experiments showed that one large burbot can eat up to four juveniles within two days, we restricted the access of the large burbot to only one compartment within the mesocosm. It was necessary to provide safe refuges for the juveniles in order to run the predator experiments, but also to have a real predator in the immediate vicinity of the juveniles. We selected the cobble substratum as a predator area to provide interstice shelter within the predator area and not to occupy the most preferred substratum (stones) within the mesocosm (Fischer 2000b).

Statistical treatment of the data

For the basic analysis of the activity levels and substratum selections in an experiment, the PIT data were analysed according to Fischer *et al.* (2001) with SAS integrated matrix language (SAS/IML 1985). ANOVA was used for comparing activity levels and substratum selections, mean activity levels, or average time a fish spent per substratum, among experiments and among the diel phases, dawn (astronomical end of the night until sunrise), day (sunrise until sundown), dusk (sundown until astronomical start of the night) and night.

The timing of twilight (dawn and dusk) phases shifted within and between experiments. To simplify the calculations, fixed start and end times were assumed for the two twilight phases within a single experiment, based on the earliest start and the latest end of all twilight phases (either dawn or dusk) during that experiment. As a consequence, the calculated lengths of twilight were several minutes longer than the average length of twilight in an experiment. To overcome the problem of changing lengths (in minutes) of the phases of a day over the total experimental time, the time, which a specimen spent in any substratum during any phase of the day, was expressed as a percentage of the total day length (in minutes). These relative values (% time spent in a certain substratum) were then arc sin transformed to normalise the data and stabilise the variances, as recommended by Sachs (1997).

Due to the continuous monitoring of the activity (compartment changes) and substratum selection of each fish in an experiment by the PIT-System, the data represent a continuum on the time scale. Two adjacent observations cannot therefore be assumed to be independent from each other. However, because the diel cycle of juvenile burbot can easily be classified into distinct phases, with a distinct resting phase during daytime, as well as distinct crepuscular and nocturnal activity phases in which many changes between substrates happen per night (up to 118 substratum changes per night were observed in a preliminary experiment), I classified the *n* observed phases of the days during an experiment as independent observations for one specimen (e.g. 30 dawn phases during a 30 day experiment). This procedure was considered to be valid for calculating average activity values, or substratum selection, during one phase of the day when comparing these data among treatments. Based on these data, I applied ANOVA with subsequent Student-Newman-Keuls (SNK) post-hoc comparison of the mean time fish spent in a certain substratum during the different phases of the day (as recommended by Lozan 1992).

When comparing changes within a certain experiment, e.g. comparing the changes of activity of an individual from dusk to night, we applied ANOVA-Repeated measurement analysis, taking the time dependence of subsequent data for the same specimen (dusk–night–dawn–day) into account.

ANOVA, with subsequent Duncan post-hoc comparison of the mean, was performed in order to test differences in average fish length (TL) and weight (g ww) among the four substrates within a mesocosm in Exp. 2, 3 and 4, when a group of six conspecifics was present. Because these data revealed a specimen-specific substrate selection in the presence of conspecifics, a subsequent logistic regression analysis was applied to calculate each individual's probability of using a certain substrate within the mesocosm, depending on body length and weight. All statistical evaluation was carried out using SAS/STAT (1988).

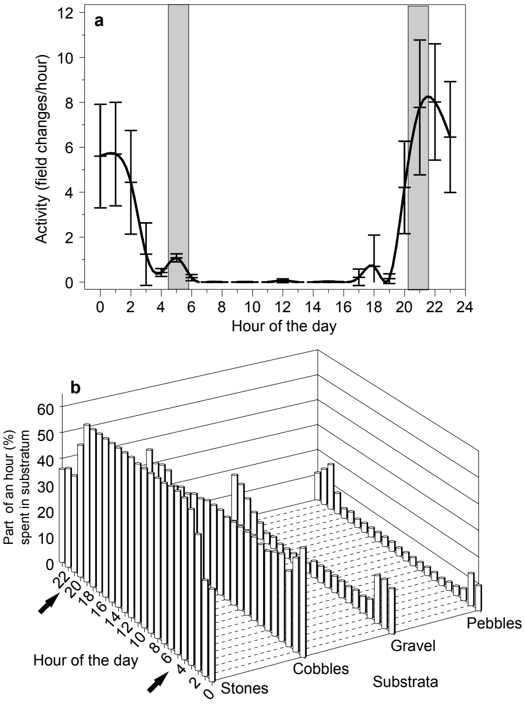

Fig. 2. (**a**) Activity (average numbers of field changes per hour) of eight specimens, each monitored separately for seven consecutive days, and (**b**) substratum selection of solitary juvenile burbot, fed *ad libitum*. Shadings mark the twilight phases in the upper graph. In the lower graph, an arrow marks the hour of the day in which the majority of a twilight phase is located.

Results

Exp. 1: Single juvenile burbot, fed *ad libitum*

In Exp. 1, the burbot showed highly significant diel activity patterns (ANOVA: $F = 62.3$, df = 3, $p < 0.0001$) with a lowest value of 0.3 ± 0.08 SE field changes per hour during daytime (Fig. 2a). Immediately after sundown, activity significantly increased (ANOVA repeated-measurement: $F = 69.9$, df = 1, $p < 0.0001$) to a peak value of 8.9 ± 2.0 SE field changes per hour during dusk. Activity remained at a fairly high level of about 6.0 ± 0.9 SE field changes per hour during the night but ceased to almost no field changes about two to three hours before sunrise (ANOVA repeated-measurement; burbot: $F = 69.9$, df = 1,

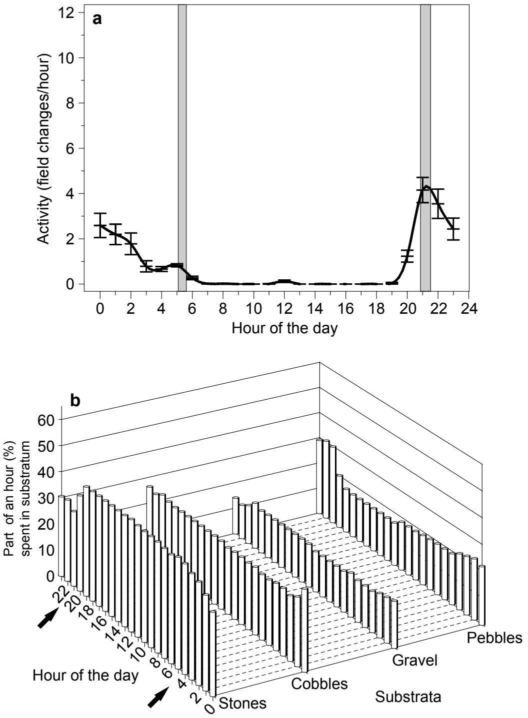

Fig. 3. (**a**) Activity (average numbers of field changes per hour) of six conspecifics, each monitored separately for 30 consecutive days, and (**b**) substratum selection of a group of six juvenile burbot each, fed *ad libitum*. Shadings mark the twilight phases in the upper graph. In the lower graph, an arrow marks the hour of the day in which the majority of a twilight phase is located.

$p < 0.0001$). This nocturnal resting phase lasted exactly until dawn when the activity increased again during sunrise. Activity during the dawn phase, however, never reached the high levels recorded during dusk and at night, and activity again ceased immediately after daybreak.

Analysis of substratum preferences during the different phases of the diel cycle showed a significant preference for the stony substratum during the day (Fig. 2b). Then, solitary burbot spent an average of 59.9% ± 7.7% SE of their time in the stony substratum and significantly less in the cobbles (29.3% ± 7.1% SE), gravel (7.5% ± 3.8% SE) and pebbles (4.2% ± 2.5% SE), ($n = 152$, $F = 19.3$, df = 3, $p < 0.001$). This preference for the stony substratum decreased to 49.2% ± 8.3% SE during dusk and even further, to 43.6% ± 5.7% SE, during the night when preference for either the stony or the cobble substratum was no longer evident ($n = 128$, $F = 14.6$, df = 3, $p > 0.05$) but the gravel and pebble substrates were still significantly less used ($n = 128$, $F = 14.6$, df = 3, $p < 0.001$).

Exp. 2: Six conspecifics, fed *ad libitum*

In Exp. 2 a group of six conspecifics was present in each mesocosm. Their patterns of diel activity were almost identical to those of the individuals in Exp. 1, with highest activity levels immediately after sunset, slightly lower values during the night and lowest activity levels during daytime (Fig. 3a). As in Exp. 1, a pre-dawn resting phase was observed about two to three hours before sunrise. Significant differences were, however, found in the absolute levels of activity. When conspecifics were present, the fish significantly reduced their nocturnal activity by 48.4%, from 8.9 ± 2.0 SE to 4.6 ± 0.3 SE field changes per hour during dusk (ANOVA: $n = 201$, $F = 18.71$, df = 1, $p < 0.001$) and an even more marked decrease in activity (53.4%) was observed during the night from 6.0 ± 0.9 SE to only 2.8 ± 0.2 SE field changes per hour (ANOVA: $n = 220$, $F = 18.71$, df = 6, $p < 0.0001$).

The presence of conspecifics also significantly affected the substratum use of the juvenile burbot. During daytime, the fish in conspecific company spent significantly less time (ANOVA: $n = 229$, $F = 28.84$, df = 1, $p < 0.001$) in the stony substratum (42.1% ± 3.4% SE), as compared with solitary individuals (58.6% ± 3.4% SE) and used the stones and cobbles almost equally often (Fig. 3b; ANOVA: $n = 406$, $F = 0.02$, df = 1, $p = 0.889$). The gravel and pebble substrates, less used by the solitary fish, were now used significantly more often (ANOVA: $n = 597$, $F = 17.63$, df = 1, $p < 0.001$) and fish spent 15.3% ± 1.4% SE of their time in the gravel substratum and 18.1% ± 2.6% SE in the pebbles. However, as compared with the stones and the cobbles, these two substrates were still used significantly less (Fig. 3b, ANOVA$_{\text{(Duncan's Multiple Range Test)}}$: $n = 812$, $F = 9.14$, df = 3, $p < 0.001$).

During dusk and at night, substratum use by the burbot in conspecific company changed significantly and became more balanced. Especially in the night phase, the fish spent almost equal, rather than significantly different, amounts of time in the three substrates, stones (30.8% ± 2.4% SE), cobbles (29.1% ± 2.4% SE) and pebbles (24.1% ± 1.9% SE), (ANOVA: $n = 565$, $F = 2.35$, df = 2, $p = 0.096$). Only the gravel was used significantly less often as compared with all other substrates: 15.8% ± 1.8% SE (ANOVA: $n = 752$, $F = 9.57$, df = 3, $p < 0.01$).

Analysis of substratum preferences of the individual fish in the group of conspecifics revealed that the shift in substratum use from the stones and cobbles to the previously avoided gravel or pebble substrates was not due to an averaged movement of all fish in the group towards these alternative substrates. ANOVA with a fish-id variable (a name for each fish) nested in the variable substratum, revealed a significant specimen-specific substratum shift within the group, both during the day (ANOVA: $n = 796$, $F = 8.41$, df = 48, $p < 0.0001$) and at night (ANOVA: $n = 752$, $F = 11.84$, df = 48, $p < 0.0001$). In this model, the variable fish-id explained 48% of the observed variability in substratum use at night and 40% during the day (Table 1). This shows that the increase in use of the alternative substrates was mainly explained by some fish of the group, which spent a disproportionate part of their time there, while others remained in the stones.

ANOVA furthermore revealed that these differences in substratum use during the day were mainly explained by wet weight of the fish. Specimens which mainly stayed in the stones were significantly heavier ($n = 315$, $F = 11.26$, df = 3, $p < 0.001$) as compared with the displaced fish. During the night, this segregation between the stony and other substrates was even more distinct (ANOVA: wet-weight: $n = 633$, $F = 17.65$, df = 3, $p = 0.0001$) and significant differences were then found also in body length (ANOVA: $n = 633$, $F = 7.01$, df = 3, $p = 0.0001$). When calculating the probability that a specimen of a certain length or weight will be found in either of the four substrata, by logistic regression analysis (SAS/STAT 1988), a significant correlation (Nominal Logistic fit: df = 9, $\text{Chi}^2 = 6674$, $p < 0.0001$), with high predictive power, was found (Table 1). When using the variable 'body length × wet-weight' nested in the variable 'substratum', the model explained 51% of the observed variability in substratum use at night and 41% during the day (Table 1). This indicates that body length and wet weight are major factors significantly determining a specimen's capability of competing with conspecifics for its preferred substrate, with body weight being a slightly stronger factor as compared with body length (Wald Chi^2: wet weight = 2478; body length = 2128).

Exp. 3: Six conspecifics, starved

Competitive interactions among conspecifics should increase when fish starve. Exp. 3 was a replication of Exp. 2 under starvation conditions. Activity significantly increased by about 32% during dusk (Fig. 4a, ANOVA: $n = 316$, $F = 10.06$, df = 1, $p = 0.0017$) and by 58% during the night (2.9 to 4.6 field changes per hour, ANOVA: $n = 324$, $F = 32.2$, df = 1, $p < 0.0001$) as compared with that under the treatment with food.

In contrast to activity, substratum preference patterns did not change significantly as compared

Table 1. Predictive power (R^2) of the ANOVA analysis (first row) and the Nominal logistic fit (NLF: second to fourth row) for substratum use by juvenile burbot in a mesocosm experiment with four different substrates (stones, cobbles, gravel and pebbles) under the two treatments 'group of six conspecifics fed *ad libitum*' and 'group of six conspecifics starved' during day and night. Significances (*** = $p < 0.001$) of the appendant ANOVA/NLF models are presented (for details of the experiment *see* text).

Statistic applied	Explanatory variables	Group of six conspecifics fed *ad libitum*		Group of six conspecifics starved	
		Day	Night	Day	Night
ANOVA	Fish-id	0.40 ***	0.48 ***	0.48 ***	0.59 ***
NLF	Length (TL; cm)	0.30 ***	0.36 ***	ns	ns
NLF	Wet weight (g)	0.38 ***	0.46 ***	ns	ns
NLF	Length × weight	0.41 ***	0.51 ***	ns	ns

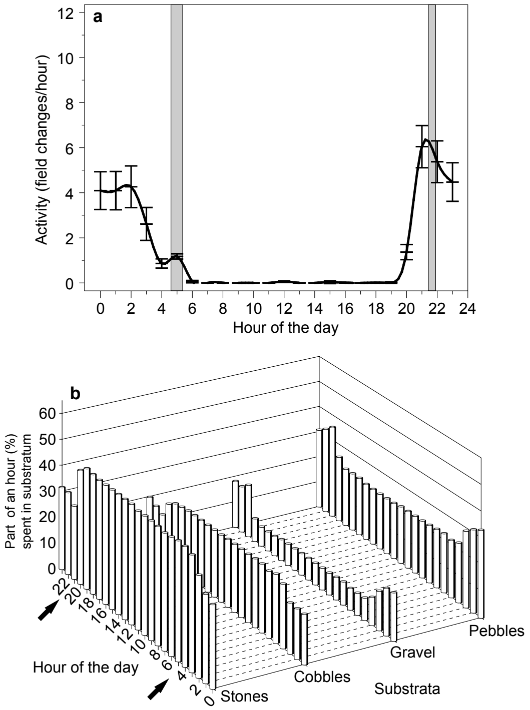

Fig. 4. (**a**) Activity (average numbers of field changes per hour) of six conspecifics, each monitored separately for 30 consecutive days, and (**b**) substratum selection of a group of six juvenile burbot, starved. Shadings mark the twilight phases in the upper graph. In the lower graph, an arrow marks the hour of the day in which the majority of a twilight phase is located.

with those in the 'fed *ad libitum*' treatment (Fig. 4b). Significant changes were observed in the gravel substratum, which was now used a significantly shorter time (7.9%) as compared with the 'fed *ad libitum*' treatment (15.3% — ANOVA: $n = 346$, $F = 4.79$, df = 1, $p = 0.029$).

As in the 'fed *ad libitum*' treatment, ANOVA with the variable fish-id nested in the substratum type, revealed that individual fish stayed for a significantly greater proportion of the day ($\text{ANOVA}_{\text{(fish-id nested in substrata during day)}}$: $n = 588$, $F = 7.14$, df = 67, $p < 0.0001$) or night ($\text{ANOVA}_{\text{(fish-id nested in substrata during night)}}$: $n = 544$, $F = 10.39$, df = 67, $p < 0.0001$) in a specific substratum when starved. With R^2 values of 0.59 during the night and 0.48 during daytime (proportion of variability in substratum use which is explained by the preferences of individual fish), substratum–specimen associations were even stronger under starvation conditions as compared with those in the 'fed *ad libitum*' treatment (Table 1).

However, contrary to Exp. 2, this segregation was not explained by the body length or weight of the individual fish. When analysing the substratum preferences of the starving fish with logistic regression analysis, no significant relationship was found between body length or wet-weight of a fish and its substratum use (Table 1; Nominal Logistic fit: df = 3, Chi^2 = -323, $p > 0.05$).

Exp. 4: Predator present, fed *ad libitum*

In Exp. 4, we exposed the juvenile burbot to a severe predation risk, by introducing a large predator (burbot, TL 35–40 cm). Food was provided *ad libitum* in all substrata. The activity of the juvenile burbot declined to very low values during the night with only 0.7 ± 0.4 SE field changes per hour on average (Fig. 5a). This meant a 75% reduction in activity as compared with an average activity of 2.8 field changes per hour in the 'without predator, fed *ad libitum*' treatment (two-sample *t*-test: $n = 11$, $t = -7.56$, df = 10, $p < 0.0001$) and 86% reduction in activity as compared with the 'without predator — starved' treatment where an average of 5.0 field changes per hour were observed. Activity however remained high during dusk and dawn with similar activity levels to those in the 'no predator' treatment.

Contrary to the changes in activity, substratum preferences did not change (Fig. 5b). Integrated over the entire diel cycle, juvenile burbot spent about 41.4% ± 1.6% SE of their time in the stony substratum and even a certain time (16.5% ± 1.2% SE) in the cobbles, where the predator was located, even though this time was significantly less compared to Exp. 2, when no predator was present (ANOVA: $n = 431$, $F = 23.41$, df = 1, $p = 0.0001$). Fish now used the pebble substratum significantly more often (ANOVA: $n = 431$, $F = 13.93$, df = 1, $p = 0.0002$), with 34.7% ± 1.5% SE of their time, but almost completely avoided the gravels (7.2% ± 0.8% SE).

During the three-week experiment, only one burbot died in the system, after ten days: it was found in the stony substratum with fatal bite injuries obviously caused by the large burbot. With a wet weight of 22.6 g prior to the experiment, this fish was the largest juvenile burbot in the system.

Discussion

Diel activity pattern

Our results show a significant and complex diel activity pattern in juvenile burbot. In all experiments, peak values were observed immediately after sundown. Movement activity remained at a fairly high level during the night and declined to low values in the early morning hours prior to dawn. A second smaller, but persistent, activity peak occurred during dawn followed by low overall activity during the daytime. This diel pattern of activity was persistent in terms of timing except in the predation experiment, where a significantly lower activity was observed during the night. Metcalfe *et al.* (1999) proposed that the time of day when a fish forages is a decision of each individual based on a trade-off between foraging efficiency and the risk of predation. He derived this hypothesis from data of Fraser and Metcalfe (1997) on salmon, which switch to nocturnal activity when the acute daytime predation risk increases above a certain level. Crepuscular to nocturnal activity is then assumed to be the safest time to forage.

The acute predation risk in my experiments was zero except in experiment 4 and also avian predation was not present. Therefore, an acute predation risk is most unlikely to be the main reason for the nocturnal behaviour of juvenile burbot in this experiment.

Pääkkönen *et al.* (2000) assumed that nocturnal activity in burbot enhances its foraging success when preying on fast moving prey. However, in my experiments, food was provided *ad libitum* in the form of dead chironomids each day at about 10:00 to 13:00. Therefore, an increase in foraging efficiency is also most unlikely to be the main reason for nocturnal crepuscular-behaviour in burbot.

Different to the findings on epi-benthic fast moving salmon (Metcalfe *et al.* 1999), I therefore assume a basic difference in the effect of predation in the benthic burbot as compared with that in salmon. Because of the comparatively low swimming and escape capacity of the benthic burbot, daytime foraging may be simply too risky even under objectively safe conditions. Under this assumption, a theoretical (daytime) and not the acute predation risk is taken into account when a fish decides if to forage or not at a certain time of the day. However, foraging efficiency and the risk of predation are then no longer two equally conflicting demands as clearly showed by Cerri and Fraser (1983) and Werner *et al.* (1983) for the epi-benthic and pelagic community.

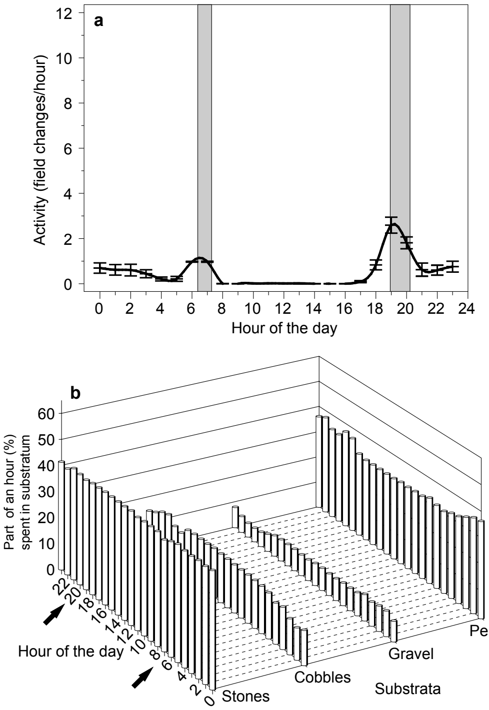

Fig. 5. (**a**) Activity (average numbers of field changes per hour) of six conspecifics, each monitored separately for 30 consecutive days, and (**b**) substratum selection of a group of six juvenile burbot, fed *ad libitum* in the presence of a predator in the substratum 'cobbles'. Shadings mark the twilight phases in the upper graph. In the lower graph, an arrow marks the hour of the day in which the majority of a twilight phase is located.

Predator avoidance then outstrips foraging optimization in its relevance for a fish's behaviour and therefore can act as a superior controlling factor. Such a behaviour might be especially important in benthic species which have a low swimming performance and escape capacity (Fischer *et al*. 1992) and are, therefore, more vulnerable to fast moving visually oriented daytime predators.

Group size

Conspecifics are most efficient competitors for food. Therefore, an increasing, or at least constant, foraging activity is expected for the individual specimen when conspecifics are present during foraging in order to get as much food as possible before the resource becomes depleted. However, juvenile burbot significantly reduced their nocturnal foraging activity in conspecific company by about 50% as compared with that of both solitary fish and the starved group. Because the general procedure of daily feeding, as well as the amount of food available per fish, remained constant among the experiments, foraging as a group member must have significant advantages for the individual fish, allowing this decrease in energy expenditure when foraging.

There is a massive literature on the effects of being a member of a group of conspecifics. In terrestrial communities the presence of conspecifics can decrease the time an individual must be vigilant and therefore increases its time for energy intake (Caracao 1979, Ekman 1987, Pöysä 1987). The studies of Magguran *et al*. (1985) provide limited evidence for similar effects in epi-benthic fish shoals, but these data are only suggestive. Milinski (1987) provided a general idea of mechanisms improving a specimen's performance as a group member in the 'tit for tat' hypothesis. However, most of these studies are closely related to advantages with respect to predation risk. Because predation risk did not change in our experiments, it is most unlikely to be a major factor reducing the individual fish's activity during the night in our experiments.

Kils (in Pitcher 1996) suggested that foraging is enhanced by the presence of conspecifics in pelagic fish, such as the herring *Clupea harengus,* by structured shoaling and food density dependent swimming speed, summarized as synchrokinesis. Swaney *et al*. (2001) also provided evidence for a mechanism of foraging enhancement due to membership of a group. He showed that guppies can learn the route to a food source by shoaling with knowledgeable conspecifics, and that they prefer to shoal with experienced foragers and familiar fish. The observed significant decrease in average activity of the juvenile burbot in our experiments when foraging in a group of conspecifics suggest a similar increase in foraging efficiency in juvenile burbot, even when the underlying mechanisms in juvenile burbot are not yet clear.

Foraging under the risk of predation

Nocturnal activity declined to very low values when a predator (large burbot) was present in the mesocosm. Most interestingly, both twilight activity peaks were still distinct. Adult burbot are well known as nocturnal foragers (Müller 1973) and the predation threat in our experiments was acute, indicated by the death of one juvenile, severely injured by the predator. According to Rader (1997), however, invertebrate emergence from the bottom substrate is often highest during twilight. This suggests that juvenile burbot in our experiment reduced exposure time to the predator during the night but remained foraging during twilight in order to obtain a maximal ration with minimal risk of predation.

A twilight foraging window due to predation has also been suggested by Clark and Levy (1988) for pelagic planktivorous fish and Helfman (1986) provided experimental evidence that juvenile grunts (Haemulidae) adapt their off-reef foraging times to the local abundance of predatory lizzardfishes. Lima and Dill (1989) and Bradford and Higgins (2001) showed that adaptations to the timing of activity are a common strategy to minimize predation risk. By reducing exposure time during the main activity phase of a predator but remaining foraging during twilight, individuals under the acute risk of predation may balance their risk of predation against the need to forage on a fine-grained time scale. Our results support this hypothesis for juvenile burbot and also indicate that in addition to a fish's temporal foraging efficiency at different times of day, the timing of hazard from the potential predator is also taken into account in the decision process of each individual fish.

Substratum preferences

In addition to their activity, juvenile burbot showed significant diel patterns in their substratum preferences. Solitary individuals preferred the stony substratum during the entire diel cycle. This is in good agreement with previous experiments of Fischer (2000b), which showed a clear preference of juvenile burbot for coarse substrates, with distinct interstitial shelter, during the day. With the onset of twilight, the fish started to forage and now also used the cobble substratum but never completely abandoned their preference for the stones and retreated towards the stony substratum prior to dusk. Fischer (2000a) showed that foraging success, in terms of net energy intake, in juvenile burbot does not significantly differ when foraging on either stones or cobbles. Nevertheless, solitary burbot significantly preferred stones to cobbles during daytime and twilight and, even more, when a predator was present in the system. This indicates that habitat selection was dominated by the effort to minimize potential predation risk, even during the main foraging phase at night.

Similarly, but less distinctly than solitary fish, burbot in conspecific company also significantly preferred the stony substratum during the day. During dusk and at night, however, substratum preferences faded and the fish foraged for about equal times in all four substrates. A detailed analysis of the substratum preferences of each individual fish in the group, however, revealed a distinct size (weight) segregation among substrata. The largest fish remained in the preferred stony substratum during foraging while the smaller ones were gradually displaced towards less safe and less profitable substrata according to their size. This indicates competition among conspecifics with a distinct size-structured hierarchy in the group. Because this size-segregation was found during the day, but to be even stronger at night, intraspecific competition seems to be primarily triggered by limited space but reinforced by competition for food during the night.

Substratum selection when under the risk of predation reflects the most complex pattern in my experiments. I expected a distinct avoidance of the cobble substratum where the predator was caged, at least during its main foraging phase, the night. Our results showed, however, that the gravel substratum was used least and fish even spent a certain time in the predator's habitat. This may lead to the assumption that juvenile burbot in my experiments simply did not count large burbot as a real predatory threat, but probably more as an intraspecific, even though dangerous, competitor. This is supported by the observation that one juvenile was mortally wounded but not eaten by the adult burbot and therefore, by definition (Wootton 1998), competition but not predation was present between the adult and the juvenile. On the other hand, my preliminary investigations clearly showed that the adult burbot used in those experiments preyed upon juveniles of the sizes used in these experiments and furthermore, juveniles significantly reduced their activity when a large burbot was in the system. It is well known that animals under an acute risk of predation significantly reduce their spontaneous activity levels (*see* review in Dill 1987). This behaviour also significantly affects foraging patterns (Fraser and Gillam 1987) and shelter use (Rahel and Stein 1988) and may therefore lead to the observed more complex distributions than basically assumed.

The results classify the crepuscular to nocturnal behaviour of burbot as stenotype behaviour with little modulation due to external stimuli. The absolute levels of activity as well as the substratum selection, however, seem to be dominated by individual decisions based on a specimen's environment and predation risk.

As compared with those for the epi-benthic or pelagic community, the results of our study classifies the diel activity pattern of burbot as a stenotype behaviour with only little modulation due to external stimuli. In contrast, absolute level of activity during the main foraging phases as well as the diel substratum selection pattern seem to be dominated by short-term individual decisions based on a specimen's actual physiological state and predation risk. Because benthic species are often dependent on daytime shelter (Fischer 2000a) and, additionally, have a comparatively low swimming and escape capacity, these factors seem to play a dominant role in determining a specimen's behaviour more than any state-dependent behaviour related to a relationship between body size and fitness at some time in the future (Lima and Dill 1989). Furthermore, our study revealed another most interesting phenomenon. The effects of sociality in our experiments were both positive and negative depending on the time of day and the environment provided in the experiments. Our results showed that activity during the night significantly decreased when conspecifics were present. Without knowing the long-term consequences in detail, a positive effect for the individual specimen is most likely, e.g. in terms of increasing somatic growth due to energy saving while foraging. On the other hand, our experiments also show a distinct competition between conspecifics during daytime when no predator is present, resulting in a displacement of smaller specimens to less profitable or even more dangerous habitats. Social structures and their implications for the individual members of a community have been studied in detail in a variety of terrestrial taxa and also in fish (Gotceitas and Godin 1991, Gotceitas and Godin Jean-Guy 1992, Sloman *et al*. 2000, Alanara *et al*. 2001). Joining forces versus conspecific separation within the same community, separated only by diel temporal windows and based on the skills and needs of each single fish in the group indicates a complex group structure and social organization within the benthic community. It should be the aim of future studies to understand these patterns and the underlying mechanisms in the benthic community in more detail in order to finally come to a better understanding of the processes and mechanisms which profoundly affect not only the benthic group but fish communities in general.

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