

## Effects of water depth and hydrodynamics on the growth and distribution of juvenile cyprinids in the littoral zone of a large pre-alpine lake

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In enclosure experiments in the littoral zone of Lake Constance, Germany, juvenile cyprinids showed significantly reduced somatic growth in the shallow eulittoral zone (0.5 m depth) compared to the sublittoral zone (1.6 m depth). Growth was especially reduced in larger and more deep-bodied fish groups, providing evidence that this is due to increased hydrodynamic stress, induced by ship and wind waves, in the shallow habitats compared to the deep habitat. Other factors such as water temperature and food availability seemed to be of minor importance for the observed growth differences. Gillnet catches at the experimental site and an adjacent site showed that most juvenile cyprinids, including the species from the enclosure study, bream *Abramis brama* and dace *Leuciscus leuciscus*, nonetheless prefer shallow habitats compared to deeper sublittoral habitats. Juvenile cyprinids in Lake Constance may prefer these shallow habitats as refuges against larger piscivorous predators, mainly perch *Perca fluviatilis*, despite the cost in terms of reduced somatic growth indicating that juvenile cyprinids first of all optimize survival rate instead of somatic growth rate.

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**Key words:** body shape; enclosure experiment; habitat choice; hydrodynamic stress; otolith daily increment; somatic growth.

### INTRODUCTION

The littoral zone is often described as the most important habitat for fishes in lakes. The greater structural complexity generally associated with the littoral zone compared to other lake habitats can provide more diverse food resources and a greater potential for ecological niche separation (Tonn & Magnuson, 1982; Benson & Magnuson, 1992; Lewin *et al.*, 2004), leading to greater fish abundances and increased species diversity (Keast, 1985). Most lake fish species

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use the littoral zone, at least periodically, primarily in the juvenile phase (Fischer & Eckmann, 1997*a, b*; Eckmann & Rösch, 1998).

Recruitment of juvenile fishes is often dependent on growth during their first summer (Hjort, 1926; Koonce *et al.*, 1977) and body size at the end of the first autumn may affect survival over the first winter (May, 1974; Mills & Mann, 1985). Maximum growth, especially during the first year of life, is therefore important for juvenile fishes.

Since the growth of juvenile fishes depends on abiotic and biotic habitat factors, habitat choice can thus be viewed from the point of fitness maximization, where there is a trade-off between costs (habitat-specific energy requirements, predation risk and competition) and benefits (food intake, growth, shelter from predation and competition avoidance) (Power, 1984; Hill & Grossmann, 1993; Garner *et al.*, 1998).

Although habitat preferences of certain fish species, or age classes, are often well known, knowledge on the ultimate factors behind these preferences is often limited (Benson & Magnuson, 1992; Baras, 1995; Fischer & Eckmann, 1997*a*; Lewin *et al.*, 2004; Reyjol *et al.*, 2005).

Without a detailed assessment of the habitat costs and benefits, however, the ultimate factors responsible for the selection of a certain habitat at a certain time are difficult to unravel.

Many studies have shown that the availability of refuge habitats including complex natural or artificial structures or shallow areas serving as refuge against predators decreases predation pressure (Crowder & Cooper, 1982; Savino & Stein, 1989). Alternatively, the availability of adequate food has also been shown to be most important for the growth of a fish directly but also indirectly since fast growth allows it to escape from the predation window of gape size-limited predators and thus decreases predation pressure (Mittelbach, 1981; Holland & Huston, 1985).

The often warmer and highly productive shallow water zones may allow higher food ingestion rates, greater agility and higher acceleration rates compared to cooler and deeper littoral habitats. Juvenile fishes have a comparatively limited scope for activity, so shallow habitats, that may provide both higher somatic growth rates and decreased risk of predation (Allen, 1982; Baras, 1995) should be beneficial for juvenile fishes. In contrast, especially in large lakes with long wind fetches, the shallow water zone is most exposed to hydrodynamic stress due to surface waves, which may form one of the most important abiotic habitat factors for juvenile fishes. Most studies on habitat choice of fishes, however, were performed in small lakes with negligible exposure to surface waves (Bryan & Scarnecchia, 1992; Brosse *et al.*, 2001; Lewin *et al.*, 2004). Furthermore, in large lakes, like Lake Constance, in addition to wind-induced waves, the frequent passage of recreational and commercial ship traffic can cause pronounced gradients in hydrodynamic stress across the littoral zone (Hofmann *et al.*, 2008). If and how this gradient affects the juvenile fish community has not been well studied.

Most information on the effects of hydrodynamic disturbances, forces and stress on juvenile fish distribution is from river systems (Baras, 1995; Baras & Nindaba, 1999). In rivers, which are not subject to shipping, the shallowest littoral zones generally represent the habitats with the lowest current velocities

and hence low hydrodynamic stress. In contrast, the shallow littoral zones of large lakes are the habitats most affected in terms of hydrodynamic stress, where most of the kinetic energy induced by surface waves is dissipated (Hutter, 1984; Kundu & Cohen, 2002). Thus, the habitat characteristics of the shallowest zones in large lakes and rivers may not be comparable.

This study, a 4 week enclosure experiment in the littoral zone of a large lake, performed during August 2004, aimed to relate growth rates of the two bream species bream *Abramis brama* (L.) and white bream *Blicca bjoerkna* (L.) and dace *Leuciscus leuciscus* (L.) of two age classes (0 and 1 years) to water temperature, oxygen saturation, food availability, food uptake and hydrodynamic stress. Growth rates of the fishes were assessed by measuring specific somatic growth rates in terms of wet mass ( $M_W$ ) and fork length ( $L_F$ ) over the experimental period and by daily increment analysis of the otoliths (Panella, 1971). Additionally, the *in situ* distribution of the littoral fish species in the two habitats was monitored to test whether juvenile fishes are distributed between the shallow and deep littoral habitats as predicted by their habitat-specific growth rates.

## MATERIAL AND METHODS

### STUDY SITE

Lake Constance is the second largest, oligotrophic, pre-alpine lake in Central Europe (47° N; 09° E). The surface area covers 534 km<sup>2</sup>, the maximum depth is 254 m and the mean depth is 101 m. In Upper Lake Constance, the littoral zone, which Wetzel (1983) defines as the shallow-water area of a lake down to the lower edge of aquatic macrophyte vegetation distribution, varies between 20 and 2000 m in width, and reaches down to a water depth of *c.* 5 m in summer (Nümann, 1973). It comprises *c.* 12% of the lake surface.

A typical littoral habitat on the southern shore of Upper Lake Constance, with a narrow (*c.* 50 m) shelf-like littoral zone, was selected for the experiments (Fig. 1). There, the shallowest habitat (0.5 m water depth; shallow) is characterized by gravel and cobble, in-filled with finer sediments and interspersed with some larger boulders. The deeper sublittoral areas (1.6 m water depth; deep) are dominated by a sandy substratum with sparse aquatic macrophyte vegetation (*Chara* spp., *Potamogeton pectinatus* L. and *Potamogeton perfoliatus* L.). The proportion of fine, resuspendable substratum of a grain size of <0.063 mm was approximately the same in both habitats, with mean  $\pm$  s.d.  $11.7 \pm 4.5\%$  in the deep habitat and  $8.3 \pm 7.1\%$  in the shallow habitat. There are no coarse woody habitats present at the experimental site, which is typical for the littoral zone of Lake Constance.

### EXPERIMENTAL DESIGN AND PROCEDURES

To compare *in situ* growth rates of fishes exposed to the shallow and deep habitats, three replicate net enclosures (2 m<sup>2</sup> area each) separated by 1.2 m gaps between them were installed in the shallow area and in the deep habitat. Each enclosure consisted of a square metal frame (side length 1.4  $\times$  1.4 m) laid out on the substratum and an attached net wall of the same side length reaching at least 0.5 m above the water surface and supported by poles on the outside. To prevent fishes from escaping through the bottom substratum, the metal frames were tightly held down with sand bags on the outside. The mesh-size of the netting was 4 mm, allowing all planktonic and benthic invertebrates available to move freely in and out. The enclosures were set up 1 week prior to the start of the experiment with the net walls rolled up on the bottom to allow

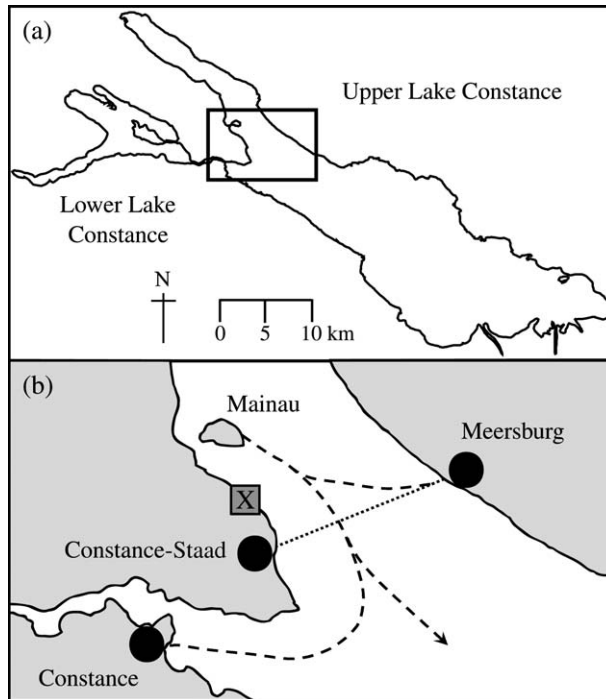


FIG. 1. (a) Map of Lake Constance. (b) Magnification of the rectangle shown in (a). **X**, the site where the mesocosm experiment took place. **.....**, the ferry route between, **●**, Constance-Staad and Meersburg; **----**, the passenger ship routes to the Island of Mainau.

recovery of the benthic invertebrate community after the disturbance caused by assembling the enclosure. Preliminary experiments showed that the benthic invertebrate community recovery occurs within a few days. Directly before the start of the experiment, the net walls were pulled up to the surface and the tops of the enclosures were covered with a 20 mm fine-threaded mesh to prevent bird predation. The net walls could move with the waves, such that waves could pass through the enclosure without visible alteration of wave characteristics.

Bream and dace were chosen as model species for the experiment because they differ most in their body morphology among the cyprinids that commonly occur in the littoral zone of Lake Constance. While dace have a fusiform body shape throughout their lives, bream become increasingly deep-bodied from their first summer on, giving similar body length to body depth ratios in age 0 year bream and dace but different ratios in age 1 year (Fig. 2). Dace were caught in Lake Constance by electric fishing 1 month prior to the experiment and bream were reared at the Limnological Institute from eggs collected in Lake Constance. All fishes were kept in 300 l tanks under a natural photoperiod ( $47^{\circ}41'$ ) and were fed *ad libitum* with a diverse diet of living water flea *Daphnia magna* L., frozen chironomids and commercial fish flakes. Due to an accident in the aquarium not enough age 1 year bream were left for the experiment, some white bream age 1 year were included in this group. These fish were caught with trap nets in small lakes adjacent to Lake Constance. Since the body morphology of age 1 year bream and white bream (ANOVA,  $F_{1,100}$ ,  $P > 0.05$ ), as well as their growth rates in the enclosure experiment [Lord-test,  $M_W$ :  $n = 34$ ,  $P > 0.05$ ;  $L_F$ :  $n = 34$ ,  $P > 0.05$ ], did not differ significantly, and their ecological niche is similar in juvenile stage (Simonian *et al.*, 1995; Specziár *et al.*, 1997), data for the two species were pooled (breams). Bream could not be replaced completely, as no age 0 year white bream could be obtained.

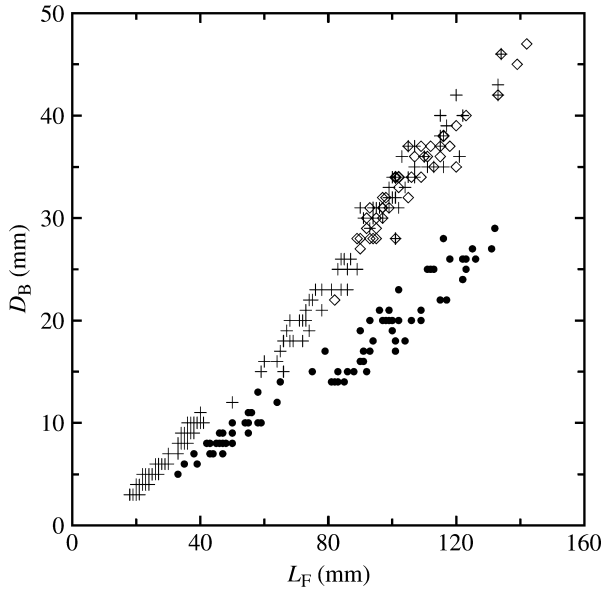


FIG. 2. Development of body shape [the relationship between body depth ( $D_B$ ) and fork length ( $L_F$ )] in juvenile bream (+), age 1 year white bream ( $\diamond$ ) and dace ( $\bullet$ ).

At day 0 of the experiment, eight age 1 year dace, eight age 1 year breams, 12 age 0 year dace and 30 age 0 year bream (Table I) were put into each of the six enclosures. The numbers of individuals used per enclosure were a trade-off between previously assessed re-catch rates from the enclosures, to make sure that a sufficient number of fishes was available for statistical analysis (*e.g.* re-catch rate of age 0 year bream from a test enclosure was about three times lower than age 1 year breams, which could be recaptured completely) and certainty that fish densities used could not create food shortage in the enclosures. During the 30 day experiment, all enclosures were monitored daily to observe fish behaviour and to check for dead fishes. At 10 day intervals, two individuals of each fish species and age class were sampled from each enclosure with a dip-net ( $n = 6$  for each species, age-class and habitat). These fishes were immediately killed with trichlormethyl-propanol ( $2 \text{ g l}^{-1}$ ). The heads of the fishes were preserved in 70% ethanol for otolith extraction, while the rest of the body was preserved in 4% formaldehyde for gut content analysis. After each sampling, the sampled fishes and any fishes that had died were replaced in order to keep the number of fish in each enclosure constant.

TABLE I. Mean  $\pm$  s.d. initial fork length ( $L_F$ ) and mass ( $M_W$ ) of the four groups of juvenile cyprinids, age 1 year dace (D1), age 0 year dace (D0), age 1 year bream (B1) and age 0 bream (B0) in the enclosure experiment in Lake Constance

Group	Initial size	
	$L_F$ (mm)	$M$ (g)
D1	$97.2 \pm 8.9$	$9.0 \pm 2.7$
D0	$46.1 \pm 10.9$	$1.0 \pm 0.6$
B1*	$104.1 \pm 11.8$	$17.1 \pm 6.4$
B0	$22.5 \pm 2.2$	$0.13 \pm 0.05$

\*Consisted of bream and white bream.

At the final sampling date, all the fishes were caught by electric fishing. Fish sampling was always done in the morning between 0900 and 1200 hours to keep gut contents comparable.

All age 1 year fishes were tagged with coded wire tags<sup>®</sup> (Northwest Marine Technology Inc., Shaw Island, WA, U.S.A.) and  $L_F$  ( $\pm 0.05$  mm) and  $M_W$  ( $\pm 0.02$  g) of all age 1 year fishes were measured immediately before release ( $L_{F\ start}$  and  $M_{W\ start}$ ) and after the recatch ( $L_{F\ end}$  and  $M_{W\ end}$ ). These variables were used to establish individual specific daily growth rates ( $G_L$  and  $G_M$ ), calculated as:  $G_L = 100(\ln L_{F\ end} - \ln L_{F\ start}) (t_{end} - t_{start})^{-1}$  and  $G_M = 100(\ln M_{W\ end} - \ln M_{W\ start}) (t_{end} - t_{start})^{-1}$ , where  $t_{end} - t_{start}$  is the time (days) each individual fish was present in the experiment (Busacker *et al.*, 1990).

The age 0 year dace were too small to be tagged without the risk of severe damage. To estimate individual growth rates of age 0 year dace,  $L_F$  data for each enclosure at both the start and end of the experiment were later sorted by size and paired, assuming that all fish grew in a similar way and the smallest fish before the experiment was the smallest fish after the experiment. This method was validated with all 12 enclosure groups of age 1 year breams and dace used in the experiment, where fishes could be recognized individually by the tags. In no case did average specific growth rates vary from the exact result by  $>2\%$ .

The more sensitive age 0 year bream were only weighed before the experiment and their  $L_{F\ start}$  was calculated from a  $M_W$  (g) and  $L_F$  (mm) regression obtained from 30 freshly dead bream age 0 year from the same experiment stock (best fit:  $L_F = 6.32 \ln M_W + 35.64$ ;  $r^2 = 0.92$ ). Specific growth rates were calculated in the same way as for age 0 year dace.

The period of time each individual fish was present in an enclosure, which was necessary to calculate individual specific growth rates, was obtained from the otolith readings.

## OTOLITH DAILY INCREMENTS

To analyse the growth patterns of the different fish species and age classes on a daily basis, the widths of the daily growth increments on the otoliths were measured during the experimental period. For this, the lapilli of all fishes used in the experiment were extracted, rinsed and dried. The right lapillus was embedded in epoxy resin on a microscope slide and ground down to the nucleus and polished. The increment widths during the experiment were measured under a microscope at  $\times 400$ – $1250$  magnification with image analysing software (G. Heine, pers. comm.). To assign daily increments on the otoliths to the individual days of the experiment, the clearly visible handling stress mark on the lapilli, formed on the day when the fishes were tagged and placed in the enclosures, was used to indicate the day on which each individual fish was introduced in the experiment (Fig. 3). Further, the clear change of ring width at the sudden

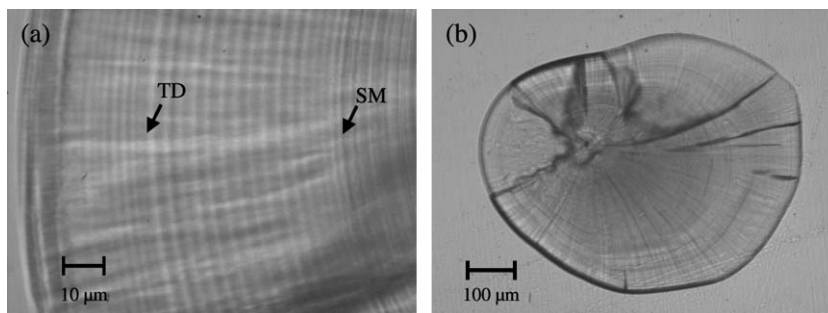


FIG. 3. (a) Lapillus of bream age 0 years from the deep habitat. SM, the stress mark from handling and introducing the fish into the enclosures; TD, the temperature drop on 14 to 16 August which is reflected in ring widths. (b) Complete lapillus of age 0 year bream from the deep habitat.

temperature drop on 14 to 16 August (Fig. 4) provided orientation on the otoliths of the age 0 year fishes. Starting from the stress mark, increments could be assigned to days towards the edge of the otolith. By the number of increments between the stress mark and the otolith edge and the location of the temperature drop mark, it was possible to estimate how long each fish had been present in the experiment. Increment widths were always measured in the same sector of the otolith and readings were verified by two independent observers. To allow for recovery from stress after release of the fishes into the enclosures, the first 2 days after the release were considered as acclimatization time and their otolith readings were discarded.

## FOOD AVAILABILITY AND GUT FULLNESS

To assess the possible effects of food restriction on growth of the fishes, zooplankton and benthic invertebrate densities were estimated inside and outside the enclosures. Zooplankton was sampled with a hand-held dip-net (mesh-size 100  $\mu\text{m}$ , diameter 25 cm) pulled vertically from the bottom to the surface with three replicates taken in each enclosure at the end of the experiment. Individuals  $>150 \mu\text{m}$  were counted at species or genus level. Smaller individuals were not counted since no prey items of this size were found in the fish guts. Benthos was sampled quantitatively inside a 250  $\times$  250 mm frame by scuba divers using a 'suction' sampler as described in Baumgärtner (2004). One sample was taken from each enclosure before and after the experiment. All hard substrata or macrophytes from the sample area were transferred into a hand-net (200  $\mu\text{m}$ ); the upper finer sediment layer was then carefully raised and 'suctioned' with continuous pumping. The adjusted permanent 'suction' current during sampling minimizes the number of escaping mobile individuals. Suspensions and escaping organisms were retained within a filter inlet (200  $\mu\text{m}$  gauze), then added to the hard substratum fraction, and processed in the laboratory. Samples were taken immediately before fishes were placed into the enclosures and directly after fishes were removed from the enclosures at the end of the experiment. Additionally, natural controls were sampled outside the enclosures within the same habitats to detect cage effects at the end of the experiment.

All benthic samples were brought to the laboratory and processed immediately after sampling. The coarse substratum within each basket was carefully brushed and rinsed to remove all attached invertebrates. Fine sediments were repeatedly floated to suspend all invertebrates in the water column. Invertebrates were accumulated on a 200  $\mu\text{m}$

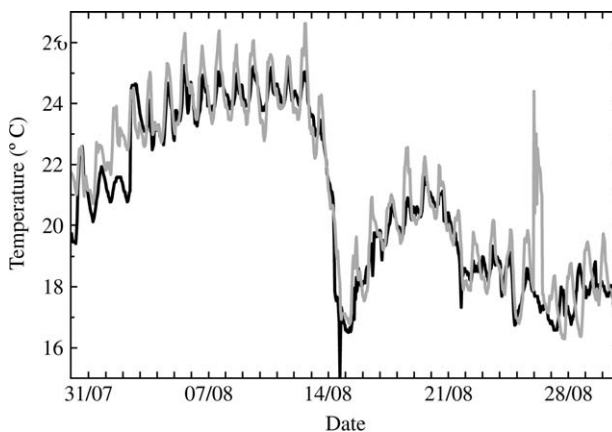


FIG. 4. Water temperatures in the shallow (—) and the deep (—) habitat in Lake Constance throughout the enclosure experiment. A summer storm event on 14 to 16 August caused upwelling of colder water into the littoral zone.

sieve and preserved in 70% ethanol. Under a dissection binocular microscope at  $\times 10$  magnification, invertebrates were identified to the species or nearest taxonomic level and counted.

The gut contents of a sub-sample of 20 individuals per fish group from the shallow and deep habitat enclosures as well as wild fishes caught at the same site and time by electrofishing and briefly set gillnets, if available, were analysed to species or nearest taxonomic level, as far as possible given 'crushing' and the degree of digestion, under a dissection binocular microscope at  $\times 10$  magnification. Further, the percentage of the gut length filled with food compared to total gut length was estimated.

## ABIOTIC ENVIRONMENT

Water temperatures during the experiment were measured every 10 min in both habitats (shallow and deep) by two loggers (Onset Computer Corp., Bourne, MA, U.S.A.) moored at half the water depth in each of the two habitats.

It was not possible to make measurements of hydrodynamic stress in terms of three-dimensional current velocity induced by ship and wind waves during the experiment itself, because no adequate equipment was available at that time. Instead, three-dimensional current velocities for all components of the wave field at the experimental site were measured during an independent field study at the same site in 2005 (Hofmann *et al.*, 2008). The timetable of ships passing the experimental site was the same in summer 2004 and 2005 and typical summer weather conditions with calm days or slight westerly winds, interspersed with rare summer storm events prevailed during summer 2005 as during the enclosure experiment in August 2004.

A Nortek vector-acoustic doppler velocity meter (ADV; Nortek, Rudd, Norway) with a sampling rate of 8 Hz was moored 0.05 m above the sediment at 1.0 m water depth. For further analysis, the absolute value of the two horizontal current velocity components was calculated.

Maximum near-bottom horizontal orbital velocities associated with surface waves  $u_{\max}$  were estimated using:  $u_{\max} = \pi H [T \sinh(2\pi d \lambda^{-1})]^{-1}$ , (Brown *et al.*, 2005), where  $H$  denotes wave height,  $d$  water depth and  $\lambda$  and  $T$ , wave length and period, respectively. The input wave parameters for calculation of the current velocity at 0.5 m (shallow habitat) and 1.6 m (deep habitat) were calculated from the averaged measured data at 1 m depth for slight wind, storm, ferry and passenger ship waves by using linear wave theory (Kundu & Cohen, 2002).

Turbidity was measured as an indicator of hydrodynamic stress over a diurnal cycle at both habitats during the experiment on days with typical and comparable weather conditions (c. 22° C air temperature, 10–20% cloud coverage, no rain, no or slight winds from the west). Turbidity measurements were conducted with a Seapoint turbidity sensor and (Seapoint Sensors Inc., Exeter, NH, U.S.A.) Micromec® Multisens (Technetics Messwerterfassungssysteme, Freiburg, Germany) data logger moored at the half water depth of each habitat.

Oxygen saturation was measured at a frequency of six per h with a WTW Cellox 325 sensor (Advance Instruments Inc., Canonsburg, PA, U.S.A.) equipped with a propeller type BR 325 moored at half the water depth at each habitat. Data were stored on a logger type WTW Oxi 340.

## FISH DISTRIBUTION

The *in situ* fish distribution between the shallow and the deep littoral zone was assessed by gillnetting with a standardized set of gillnets (mesh-sizes 6, 9, 12 and 15 mm bar mesh, each net 2 m long). All nets reached from the bottom to the water surface, independent of site depth. Nets were deployed fortnightly from June to September 2004 during day and night, and were emptied during dusk and dawn. Unfortunately, the juvenile cyprinid catches were exceptionally low in 2004 with only 16 dace age 0 years in the shallow littoral zone and only one dace age 0 years in the deep littoral zone while



perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.) dominated the catches. It is a common pattern in Lake Constance that the juvenile fish community is either dominated by percids or cyprinids in different years (unpubl. data). Therefore, catches from an earlier sampling session at a nearby littoral habitat with the same attributes from July to November 1993, with repeated short deployments of gillnets (every full hour for 15 min, mesh-sizes 7, 10, 14, 28 and 32 mm bar mesh, each net 5 m long) during day and twilight (Fischer, 1994) were re-analysed with respect to the distribution of juvenile cyprinids between the shallow and the deep littoral. It was assumed that habitat preferences of the most common fish species in Lake Constance have not changed since then.

## STATISTICS

Data were statistically evaluated to a significance level of  $P = 0.05$ , using appropriate tests proposed by Lozán (1992), according to data structure in terms of normality, tested with Shapiro & Wilk test, and homoscedasticity, tested with Bartlett's test.  $t$ -test and ANOVA were used when possible, but for small sample sizes, Lord's tests were applied. This test is analogous to the  $t$ -test and is used to compare the mean values of two small ( $n < 20$ ) random samples using ranges instead of s.d. as a measure of variation. The test power is similar to the  $t$ -test (Lord, 1950).

## RESULTS

### SOMATIC GROWTH

ANOVA showed that somatic growth rates of the fishes did not differ significantly between replicate enclosures in the same habitat, either for  $G_L$  or  $G_M$  [Table II(a); Tukey-HSD test,  $G_L$ :  $q = 2.88$ ,  $P > 0.05$ ;  $G_M$ :  $q = 2.88$ ,  $P > 0.05$ ], only 3% of the total variance in  $G_L$ , and 0% in  $G_M$  was explained by enclosure replicates.

Overall, fishes in the shallow eulittoral habitat showed significantly lower or even negative growth rates compared to fishes in the deep sublittoral habitat [Fig. 5 and Table II(a)]. But, a significant interaction between fish group and habitat indicated that growth differences between the two habitats were not the same for all four fish groups. Breams age 1 year (B1) suffered the greatest relative growth depression in the shallow habitat with a growth in  $L_F$  of  $-83\%$  ( $-0.018\%$  day $^{-1}$  in the shallow habitat compared to  $0.015\%$  day $^{-1}$  in the deep habitat) and a growth in  $M_W$  of  $-84\%$  ( $-0.200\%$  day $^{-1}$  compared to  $0.238\%$  day $^{-1}$ , respectively) of the specific growth rate achieved in the deep habitat. Bream age 0 years (B0) had the lowest growth losses with 41% of the specific growth rate achieved in the shallow habitat compared to the deep habitat in  $L_F$  growth ( $0.741\%$  day $^{-1}$  compared to  $1.605\%$  day $^{-1}$ , respectively) and 46%  $M_W$  growth ( $5.283\%$  day $^{-1}$  compared to  $2.180\%$  day $^{-1}$ , respectively; Fig. 5).

Growth depression of the four fish groups in the shallow habitat in comparison to the deep habitat were further analysed with contrast analysis, testing the hypothesis that affiliation to fish species, age (or  $L_F$  or  $M_W$ ) class, or body shape of the fishes can explain the percentage growth losses of the four fish groups in the shallow habitat. The effect of age could not be separated from the effects of  $L_F$  and  $M_W$ , as they co-varied in the four fish groups investigated.

TABLE II. (a) Results of ANOVA analysing specific growth rates (in fork length,  $G_L$ , and mass,  $G_M$ ) of individual fish used in the enclosure experiment in Lake Constance and (b) following contrast analysis on the interaction term habitat  $\times$  fish group, testing the hypothesis if fish species, fish age (which co-varies with  $L_F$  and  $M_W$ ) or fish body shape can explain the growth decrease in the shallow habitat compared to the deep habitat

	$G_L$				$G_M$					
	SS	MS	d.f.	$F$	$P$	SS	MS	d.f.	$F$	$P$
(a)										
Habitat	7.00	7.0	1,4.6	49.00	0.001	159.60	159.6	1,5.50	221.6	<0.001
Fish group	53.00	17.7	3,181	235.50	<0.001	567.00	189.0	3,1830	241.6	<0.001
Habitat $\times$ fish group	5.20	1.7	3,181	23.10	<0.001	50.20	16.7	3,1830	24.4	<0.001
Enclosure (habitat) $\times$ random	0.60	0.2	4,181	2.00	>0.05	2.80	0.7	4,1830	0.9	>0.05
(b)										
Species (breams and dace)	0.01		1,181	0.20	>0.05	2.66		1,183	3.40	>0.05
Age, $L_F$ , $M_W$ (age 0 years, age 1 years)	3.44		1,181	45.90	<0.001	25.90		1,183	33.10	<0.001
Body shape (breams age 1 years, other groups)	6.17		1,181	82.20	<0.001	123.21		1,183	157.48	<0.001

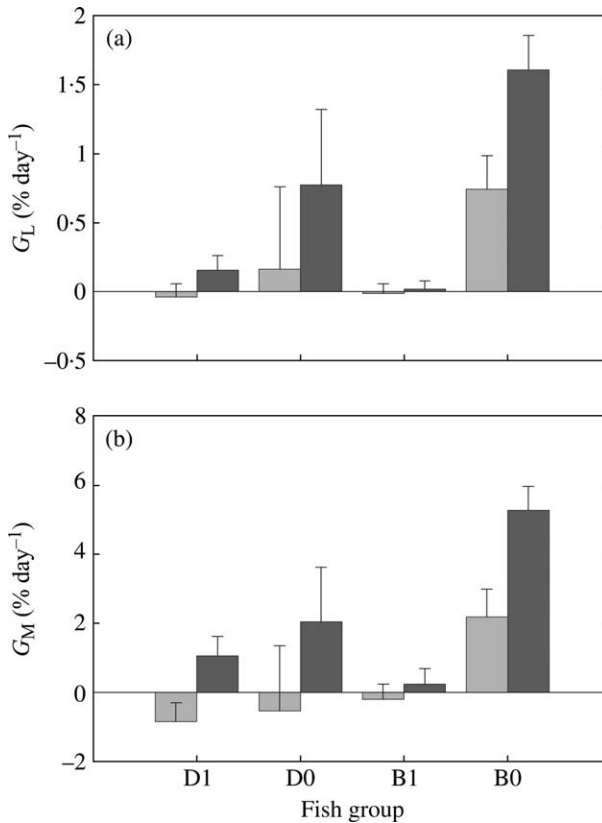


FIG. 5. (a) Mean  $\pm$  s.d. specific fork length ( $G_L$ ) and (b) mass ( $G_M$ ) growth rates in the shallow (—) and deep (—) habitat for the four groups of fishes used in the enclosure experiment: dace age 1 years (D1), dace age 0 years (D0), breams age 1 years (B1) and bream age 0 years (B0).

No species effect were found [Table II(b)], but age 1 year fishes suffered significantly higher growth losses in the shallow habitat than age 0 year fishes. Especially high growth losses in the shallow habitat were recorded in deep-bodied breams age 1 years compared to all three other groups of fusiform fishes.

#### OTOLITH DAILY INCREMENTS

Independent of species, the widths of the daily increments in the otoliths of the age 0 year fishes matched well with their somatic growth pattern, showing significantly wider average ring widths in the deep habitat compared to those in the shallow habitat [Fig. 6(a), (b); pair-wise  $t$ -tests using days as replicates; dace age 0 years:  $n = 27$ ,  $P < 0.001$ ; bream age 0 years:  $n = 27$ ,  $P < 0.001$ ]. This was not the case, however, in age 1 fishes. Even though age 1 year breams and dace grew significantly less in the shallow water compared to the deeper habitat, their average otolith ring widths were significantly wider in the shallow habitat [Fig. 6(c), (d); dace age 1 years:  $n = 27$ ,  $P < 0.001$ ; breams age 1 years:  $n = 27$ ,  $P < 0.05$ ].

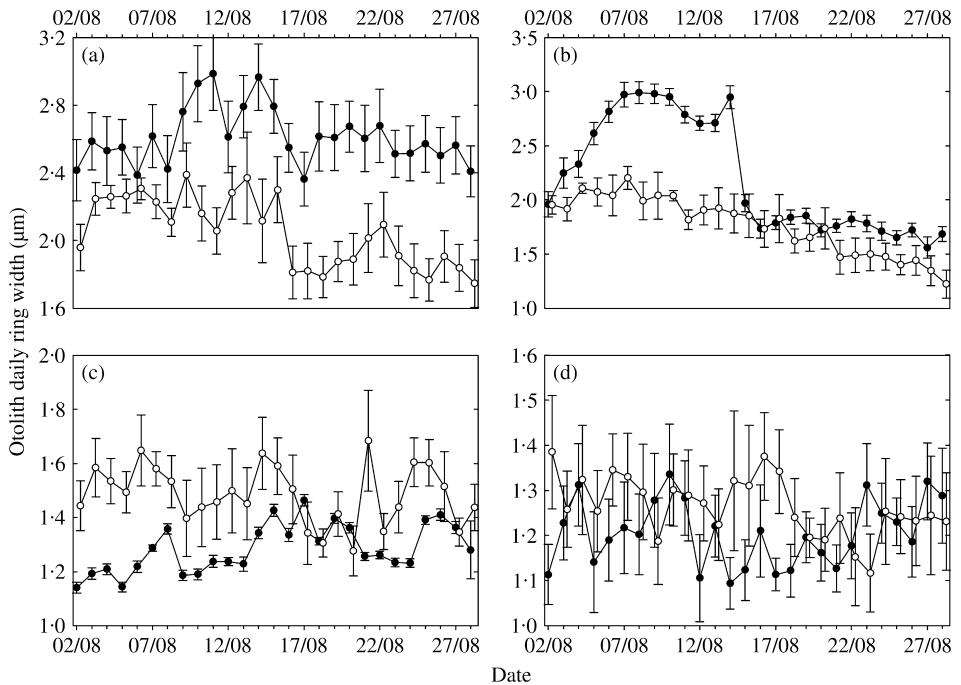


FIG. 6. Mean  $\pm$  s.e. daily ring widths of (a) dace age 0 years, (b) bream age 0 years, (c) dace age 1 years and (d) breams age 1 years during the enclosure experiment in Lake Constance in the deep (●) and in the shallow (○) habitat.

## FOOD AVAILABILITY AND GUT FULLNESS

Zooplankton densities were not significantly different between the shallow and deep enclosures (Lord's test,  $n = 18$ ,  $P > 0.05$ ), and there were even significantly higher zooplankton densities inside the enclosures compared to outside (Lord's test,  $n = 24$ ,  $P < 0.05$ ). The density of benthic invertebrates was similar between the inside and the outside of the enclosures.

During the experiment, 18 species or higher order groups were consumed, including a variety of insects such as chironomids (all three subfamilies, pupae) and caseless and case-bearing caddisflies, other groups such as benthic cladocerans, amphipods, oligochaetes and molluscs as well as non-animal foods such as the macrophyte *Chara* spp. and filamentous algae. Other than benthic cladocerans, none of the zooplankton taxa dominant in the field samples (nauplii, rotifers, *Bosmina* sp., cyclopoid and calanoid copepods) were found within the fish guts. Benthic cladocerans were mainly consumed by breams and comprised 83% of the total biomass consumed in age 0 year breams and 57% in age 1 year breams. Dace consumed plankton only occasionally (age 0 year: 2%; age 1 year: <1%).

Dace of both age classes and age 1 year breams fed considerably on molluscs [mainly *Dreissena polymorpha* (Pallas); dace age 0 years: 59%; dace age 1 years: 38%; breams age 1 years: 32%]. The largest proportion of food items in guts of age 1 year dace were macrophytes, mainly *Chara* spp. (42%). In all fish groups, the diet composition was similar in the shallow and deep habitat.

The gut fullness of the different groups did not change during the enclosure experiment (ANOVA,  $F_{2,137}$ ,  $P > 0.05$ ). The mean  $\pm$  s.d. gut fullness of the different groups was between  $87 \pm 4\%$  in dace age 1 years and  $68 \pm 5\%$  in bream age 0 years. Comparisons of the gut fullness of the four fish groups between the two habitats and fishes caught outside the enclosures showed no general trend. On three occasions, significant differences between the gut fullness were found among the two enclosure habitats. In two cases, the guts of fishes in the deep habitat were filled to higher proportions than those in the shallow habitat (age 1 year dace: ANOVA,  $F_{1,10}$ ,  $P < 0.01$ ; age 1 year bream: ANOVA,  $F_{1,10}$ ,  $P < 0.05$  on 19 August), and *vice versa* in one case (age 0 year bream: ANOVA,  $F_{1,8}$ ,  $P = 0.01$  on 9 August). In all cases, the guts of fishes in the lake were filled to a similar degree to the guts of fishes in the enclosures.

## WATER TEMPERATURE

Daily mean and minimum temperatures in the shallow and the deep habitat were not significantly different (Fig. 4; pair-wise Wilcoxon tests, mean temperature:  $n = 30$ ,  $P > 0.05$ ; minimal temperature:  $n = 30$ ,  $P > 0.05$ ). Daily maximum temperature and daily temperature amplitude in the shallow habitat were significantly higher compared to those in the deep habitat (average difference of maximal temperature shallow *v.* deep =  $1.1^\circ\text{C}$ ,  $n = 30$ ,  $P < 0.01$ ; average difference of temperature amplitude =  $1.0^\circ\text{C}$ ,  $n = 30$ ,  $P < 0.01$ ). On the 14–16 August, a summer storm event caused upwelling of colder water, resulting in a distinct temperature drop (Fig. 4).

## TURBIDITY

In the deep habitat, turbidity values were small, with maximal FTU (formazine turbidity unit) values of 5 in the course of the day (Fig. 7). Turbidity in the shallow habitat showed a diurnal cycle, with maximum values of 190 FTU reached during daytime and 5 FTU, the same value as in the deep habitat, during the night (Fig. 7).

## HYDRODYNAMICS

During summer, the study site is mainly exposed to ship waves caused by regular car ferries shuttling between the cities of Constance-Staad and Meersburg every 20 min during daytime and once an hour during night-time, and passenger ships to the Island of Mainau, passing the experimental site at a distance of 1–3 km with a frequency of two to four times per hour during daytime. Wind waves, in contrast, occur more frequently during winter and are rare during summer (Hofmann *et al.*, 2008). In August 2005, the wave field at the study site was dominated by ship waves, and wind waves were of minor importance. This corresponded to the conditions during the enclosure experiment in August 2004, except for the storm event on the 14 to 16 August 2004. For all kind of wave pattern possible at the experimental site (ship waves are always present and wind waves may occur additionally), ratios of current velocities between the deep and the shallow habitat (Table III) were calculated

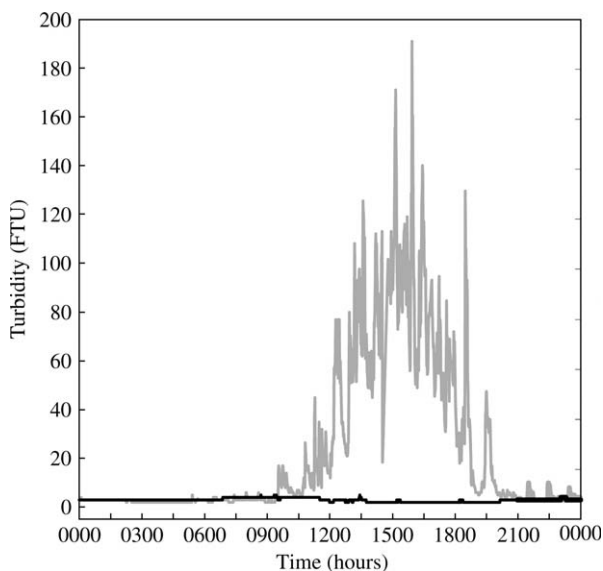


FIG. 7. Mean turbidity in the shallow (—, 27 August 2004) and the deep (—, 24 August 2004) habitat in Lake Constance at 1 min intervals during 24 h sampling.

using the parameters of the different wave types from Hofmann *et al.* (2008), who measured the wave field at the same site over a whole year in 2005.

The dominating wave type in August were ship waves reaching maximum near-bottom, horizontal orbital current velocities of *c.*  $0.24 \text{ m s}^{-1}$  at a depth of 1 m, resulting in calculated current velocity of  $0.37$  and  $0.17 \text{ m s}^{-1}$  at 0.5 m (shallow habitat) and 1.6 m (deep habitat), respectively (Fig. 8). Thus, under all wave patterns possible at the experimental site (ship waves alone or combined with wind waves), the shallow habitat is exposed to much greater hydrodynamic stress, indicated by approximately two- to three-fold higher maximum

TABLE III. Maximum current velocities ( $u_{\max}$ ) induced by slight wind, storm, ferry and passenger ships calculated from wave parameters wave period ( $T$ ) and wave height ( $H$ ) measured in Hofmann *et al.* (2008) at the site in Lake Constance where the enclosure experiment was conducted. Measurements were taken at 1 m water depth, from which maximum current velocities in 0.5 m (shallow habitat) and 1.6 m (deep habitat) water depth were calculated using linear wave theory

Water depth (m)	$u_{\max}$ ( $\text{m s}^{-1}$ )			
	Slight wind ( $T = 2 \text{ s}$ ) ( $H = 0.1 \text{ m}$ )	Storm ( $T = 2 \text{ s}$ ) ( $H = 0.4 \text{ m}$ )	Ferry ( $T = 3.7 \text{ s}$ ) ( $H = 0.1 \text{ m}$ )	Passenger ship ( $T = 2.9 \text{ s}$ ) ( $H = 0.2 \text{ m}$ )
0.5	0.18	0.74	0.21	0.37
1.0	0.10	0.41	0.14	0.24
1.6	0.06	0.23	0.10	0.17
Ratio 0.5–1.6 m	3.00	3.22	2.10	2.18

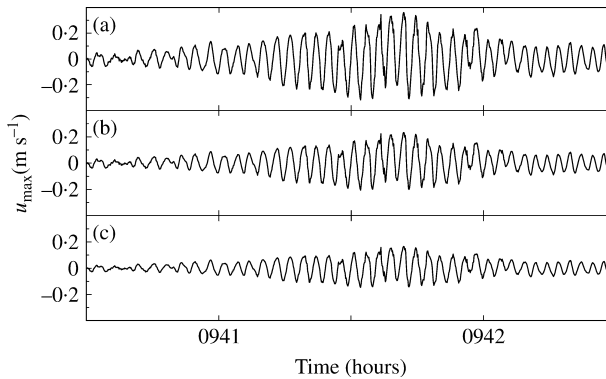


FIG. 8. Near-bottom horizontal current velocity ( $u_{\max}$ ) at (a) 0.5 m (calculated), (b) 1.0 m (measured) and (c) 1.6 m (calculated) water depth during a characteristic single passenger ship-induced group of waves on 3 August 2005.

current velocities, compared to the deep-water site. The remobilization of particles in the shallow habitat is therefore enhanced and could be measured as high turbidity values (Fig. 7).

#### OXYGEN SATURATION

In the deep habitat, fluctuations in oxygen saturation were less pronounced than in the shallow habitat. Oxygen saturation increased after sunrise and peaked in the afternoon with 110% saturation in the deep and 120% saturation in the shallow habitat. In none of the habitats did oxygen saturation drop below 93%.

#### FISH DISTRIBUTION

Gillnet catches during the enclosure experiment were exceptionally low with only 16 age 0 year dace caught in the shallow littoral zone and no age 0 year dace caught in the deep habitat. Catch data from an earlier fishing campaign at a similar littoral site (Fischer, 1994) was re-analysed instead. Both age 0 year dace and bream showed a significant preference for the shallow as compared to the deep habitat (Table IV). In contrast, the large, potentially piscivorous, perch of age  $\geq 1$  years showed a significant preference for the deep habitat (Table IV).

#### DISCUSSION

The growth of age 0 year bream in the enclosures agreed well with growth rates of bream age 0 years in comparable habitat conditions described by Hartmann (1983) who reported average relative (not specific)  $G_L$  of 2.97% day<sup>-1</sup> for bream age 0 years in Lake Constance, while  $2.10 \pm 0.52\%$  day<sup>-1</sup> was found in this study in the deep habitat. For breams age 1 years and dace, no growth rates suitable for comparison could be found in the literature.

TABLE IV. The five most frequent species in gillnet catches at the littoral site 'Wallhausen' in Lake Constance during daytime and twilight, from July to November 1993.  $\chi^2$ -tests were applied to test for habitat preferences of the different groups

Species	Number				Age 0 years prefer shallow habitat		Age 1+ years prefer deep habitat	
	Shallow		Deep		$\chi^2$ (d.f.)	<i>P</i>	$\chi^2$ (d.f.)	<i>P</i>
Age (years)	0	1+	0	1+				
<i>Abramis brama</i> (L.)	21	0	4	0	6.54 (1,24)	<0.05	—	—
<i>Leuciscus leuciscus</i> (L.)	129	191	43	164	22.93 (1,171)	<0.001	1.03 (1,354)	>0.05
<i>Rutilus rutilus</i> (L.)	104	0	100	0	0.04 (1,203)	>0.05	—	—
<i>Alburnus alburnus</i> (L.)	38	57	16	51	4.68 (1,53)	<0.05	0.17 (1,107)	>0.05
<i>Perca fluviatilis</i> L.	98	26	106	294	0.16 (1,203)	>0.05	136.09 (1,319)	<0.001

Growth might have been slightly reduced in all enclosures compared to wild fishes due to the confinement to limited space and the inability of the fishes to choose their optimal microhabitat depending on varying needs throughout a day. Thus, confinement to limited space is hard to avoid in enclosure experiments assessing habitat-specific costs.

None of the fish groups used in this study, however, is reported to perform periodical migrations, e.g. diel horizontal migrations (Gauthier & Boisclair, 1997; Gliwicz *et al.*, 2006). They are rather stationary in their preferred littoral habitats throughout the day, as clusters with a strong representation of the modality time of day are weakly represented in the self-organizing mapping analysis of their distribution pattern in different littoral habitats at Lake Constance (Reyjol *et al.*, 2005).

All the groups of fishes showed significantly higher somatic growth rates in the deep habitat compared to the shallow habitat. Although differences in gut fullness were found in single groups at single times, there was no clear pattern in food uptake favouring either the shallow or the deep habitat. Furthermore, in the enclosures no top-down effects of the fishes on the benthic invertebrate and plankton communities were found and also no clear differences in gut fullness between the fishes in the enclosures and fish of the same species and age-class caught outside. Food shortage in the shallow habitat is therefore unlikely to be responsible for the depression of growth rates in the shallow habitat.

Besides food, temperature is a major factor affecting growth in fishes. In this study, the shallow and the deep habitats did not differ significantly in terms of average daily temperature. Moreover, as the daily maximum temperatures were even higher in the shallow water, fishes in this habitat may have benefited from higher temperatures during some time of the day (Beamish, 1978; Kaufmann & Wieser, 1992; Baras, 1995). On the other hand, greater diurnal temperature fluctuations occurred in the shallow habitat, which may pose a strain on fish metabolism forcing it to adapt to changing temperatures (Wildhaber & Crowder, 1990). Even though significant, the absolute differences in the temperature amplitudes between the shallow and the deep habitat were only *c.*  $1.0 \pm 0.9^\circ \text{C}$  (mean  $\pm$  s.d.), an amplitude difference, which can hardly explain negative growth in all fish groups except for age 0 year bream in the shallow habitat.



Thus, temperature is unlikely to be a key factor for the observed growth depression in the shallow habitat, especially as the temperature range of 18–24° C during the experiment is well inside the preferred range of bream and dace (Staaks, 1996; Kucharczyk *et al.*, 1998) and therefore definitely not suboptimal.

Another environmental factor known to affect fish metabolism is extreme oxygen saturation. Oxygen saturation levels in both habitats were measured over the diurnal cycle on two occasions with representative environmental conditions. With maximal values of 120% saturation during the afternoon and minimal values not <93%, oxygen saturation was well inside the tolerance levels of juvenile dace and bream (Kuhlmann *et al.*, 1988; Kaufmann & Wieser, 1992), indicating that oxygen saturation also cannot explain the observed depression of growth in the shallow habitat.

Wave-induced, near-bottom current velocities cause remobilization and resuspension of particles from the sediment surface. The amount of resuspension depends on the current velocity itself and the grain size of the particles. The turbidity values measured were much higher in the shallow compared to the deep habitat. The rhythm and the distinct turbidity peaks in the shallow habitat can be explained by the occurrence of ship waves from car ferries and passenger ships passing close by the experimental site.

Similar fish sizes to age 1 years in this study were used by Gregory & Northcote (1993) in their study of Chinook salmon *Oncorhynchus tshawytscha* (Walbaum). These fish showed increased consumption rates at 18–150 FTU for benthic and planktonic prey compared to zero turbidity, and expanded their search for food to areas closer to the water surface, which they avoided in clear water conditions, possibly due to reduced predation pressure in the turbid habitats (Gregory, 1993). At these medium turbidity values, which also prevailed during 48% of the daytime (0600–2100 hours) during the enclosure experiment in the shallow habitat, but never in the deep habitat, feeding success is often maximized, as the contrast of planktonic prey organisms to the background is increased over short distances in good light conditions (Hinshaw, 1985; Miner & Stein, 1993). The increased turbidity values found in the shallow habitat in this study thus should rather increase growth rates but not lead to a serious growth depression.

Additionally, turbidity can be seen as a proxy for current velocity, which could not be measured during the experiment, but as ship waves dominate the hydrodynamic regime, could be measured 1 year later. Itineraries of passenger ships and car ferries, the only large ships on Lake Constance, were the same, and weather conditions were typical for the enclosure experiment during direct wave measurements.

Wave-induced, near-bottom current velocities are approximately two to three times higher in the shallow habitat, indicating much greater hydrodynamic stress compared to the deep habitat. There are no direct measurements of energy expenditure of fishes in waves, as typical wind- or ship-induced waves would be difficult to generate in small respiration chambers. Enders *et al.* (2004) showed that turbulence, generated by modulating the flow velocity in a flow-through respirometer, significantly increased the metabolic rate of juvenile Atlantic salmon *Salmo salar* L. An increase in the s.d. of a mean current velocity of 0.23 m s<sup>-1</sup> from 0.05 to 0.08 m s<sup>-1</sup> caused an increase in total

swimming costs by a factor of 1.4. This shows that fluctuating current velocities are energy demanding for fishes. The reduction in somatic growth in the shallow habitat could be caused by elevated energy expenditures for position control and swimming in the shallow habitat.

Large fishes, represented by age class 1 years, and especially fishes with a deep-bodied morphology, represented by age 1 year breams suffered the highest growth losses in the shallow habitat. This provides more evidence for hydrodynamic stress being a crucial factor for fish growth in the shallow littoral zone. The greater ability of small fishes to cope with hydrodynamic stress may be due to small fishes being able to seek shelter in or close to the coarse bottom substratum during wave events, where current velocities are reduced by friction. Such a bottom-dwelling, sheltering behaviour among larger stones could be observed repeatedly throughout the enclosure experiment in age 0 year dace, but also on several other occasions when electrofishing in shallow littoral areas of Lake Constance. This sheltering behaviour could be a response, especially of small juvenile fishes, to reduce hydrodynamic stress in the shallow habitat with increased near-bottom velocities.

Bottom-dwelling or sheltering behaviour was never observed in older (larger) fishes, either in the enclosure experiments or in other fishing sessions. Body size prevents larger fishes from using interstitial substratum shelters and forces them to stay in the water column above the ground, where they are exposed to higher current velocities and acceleration rates. Deep-bodied fishes, in these experiments represented by age 1 year breams, have a larger body area exposed to the current than torpedo-shaped fishes of the same size (*e.g.* age 1 year dace) and thus might have to spend more energy when manoeuvring in waves. Enders *et al.* (2004) obtained similar findings for juvenile Atlantic salmon, where a slender body, plus large head and fins lead to lower metabolic rates under turbulent conditions compared to more deep-bodied individuals with smaller heads and fins. This might explain the especially large growth depressions observed in deep-bodied age 1 year breams in the present study.

The daily otolith increment patterns of the fishes in the two habitats support the assumption of significantly higher energetic costs for larger (age 1 years) fishes when staying in the shallow habitat. Otolith ring width in age 0 year fishes reflected the somatic growth patterns among the shallow and the deep habitat well, with wider daily increments in the deep habitat, where higher somatic growth rates were observed. In contrast, in age 1 year fishes the opposite relationship was observed with significantly wider otolith daily increments in the shallow habitat but a significantly higher somatic growth in the deep habitat. This indicates a decoupling of otolith and somatic growth in the larger age 1 year fishes in the shallow habitat. While in the long term, otolith daily increment widths generally correlate well with somatic growth rates (Volk *et al.*, 1984; Campana & Neilson, 1985); this is not always the case in short-term studies on fish growth under suboptimal conditions. Otolith growth and somatic growth can be decoupled at low food availability (Reznick *et al.*, 1989; Wright *et al.*, 1990), at higher than optimal temperature (Mosegaard *et al.*, 1988) or with a combination of both factors (Barber & Jenkins, 2001). Some studies show that otolith growth does not correlate with somatic growth but with metabolic rate and thus is only indirectly correlated to somatic growth

(Mosegaard *et al.*, 1988; Wright, 1991; Yamamoto *et al.*, 1998). Positive somatic growth in fishes is possible when the energy expenditure for routine metabolism and specific dynamic action is lower than the total energy uptake. Only then, a positive net energy balance allows energy investment into somatic growth, such that somatic growth and otolith growth are positively related. Negative somatic growth but wide otolith increments, as observed in this experiment in the age 1 year fishes in the shallow habitat may indicate a high metabolic rate and thus high otolith growth rate. In this case, the total energy balance may turn negative when energy expenditure for navigation and position control in shallow wave exposed habitat becomes too high to be compensated for by food intake. Then, little or even negative somatic growth may occur in combination with a high otolith growth rate.

Results from this study suggest that in large lakes with widely exposed shores, hydrodynamic stress due to ship and wind waves can play an important role for the energy budget of fishes in the littoral zone. This has not been reported yet for lacustrine environments, as most of the available studies on habitat selection of littoral dwelling fishes species in inland waters have been done in small lakes (Werner *et al.*, 1977; Mittelbach, 1981; Pierce, 1994; Magnhagen & Heibo, 2004).

This study indicates that habitat choice of fishes in large lakes should be compared to estuarine and sea shore habitats (Lubbers *et al.*, 1990; Ruiz *et al.*, 1993), as environmental factors, including hydrodynamic stress, occur in more similar combinations than in small lakes or rivers.

Even though all fish groups in this study grew significantly better in the deep habitat, the gillnet catches revealed a clear preference for the shallow habitat in many age 0 year fishes, among them, bream and dace. Because habitat choice is normally considered as subject to fitness maximization, there must be another relevant factor besides maximizing growth rate, even overruling this need. Werner *et al.* (1977) has shown that fishes avoid habitats with high predation pressure. Gillnetting revealed that potentially piscivorous age  $\geq 1$  year perch preferred the deep habitat and were abundant there. Stomach content analysis of age  $\geq 1$  year perch in the same area showed that  $>50\%$  of these perch included age 0 year fishes in their diet during the summer months (Schleuter & Eckmann, in press). Predation pressure in the deep habitat may be the main factor leading to an increased use of the shallow habitat by juvenile dace and bream, even though they suffer growth depression there. Turbidity levels of permanently 30–120 FTU in the daytime further reduce the risk of predation in the shallow areas (Miner & Stein, 1996).

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## References

- Allen, L. G. (1982). Seasonal abundance, composition, and productivity of the littoral fish assemblage in Upper Newport Bay, California. *Fishery Bulletin* **80**, 769–790.
- Baras, E. (1995). An improved electrofishing methodology for the assessment of habitat use by young-of-the-year fishes. *Archiv für Hydrobiologie* **134**, 403–415.
- Baras, E. & Nindaba, J. (1999). Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. *Environmental Biology of Fishes* **56**, 183–197.
- Barber, M. C. & Jenkins, G. P. (2001). Differential effects of food and temperature lead to decoupling of short-term otolith and somatic growth rates in juvenile King George whiting. *Journal of Fish Biology* **58**, 1320–1330.
- Baumgärtner, D. (2004). Principles of macroinvertebrate community structure in the littoral zone of Lake Constance. PhD Thesis, Heidelberg, Ubstadt-Weiher, Basel, Switzerland.
- Beamish, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, Vol. 7 (Hoar, W. S. & Randall, D. J., eds), pp. 101–187. London: Academic Press.
- Benson, B. J. & Magnuson, J. J. (1992). Spatial heterogeneity of littoral fish assemblages in lakes: relation to species diversity and habitat structure. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1493–1500.
- Brosse, S., Giraudel, J. L. & Lek, S. (2001). Utilisation of non-supervised neural networks and principal component analysis to study fish assemblages. *Ecological Modelling* **146**, 159–166.
- Brown, E., Colling, A., Park, D., Phillips, J. D. R. & Wright, J. (2005). *Waves, Tides and Shallow-water Processes*. Boston, MA: Butterworth-Heinemann.
- Bryan, M. D. & Scarnecchia, D. L. (1992). Species richness, composition, and abundance of fish larvae and juveniles inhabiting natural and developed shorelines of a glacial Iowa lake. *Environmental Biology of Fishes* **35**, 329–341.
- Busacker, G. P., Adelman, I. R. & Goolish, E. M. (1990). Growth. In *Methods for Fish Biology* (Schreck, C. B. & Moyle, P. B., eds), pp. 363–382. Bethesda, MD: American Fisheries Society.
- Campana, S. E. & Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1014–1032.
- Crowder, L. B. & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**, 1802–1813.
- Eckmann, R. & Rösch, R. (1998). Lake Constance fisheries and fish ecology. *Archiv für Hydrobiologie* (Special Issues: Advances in Limnology) **53**, 285–301.
- Enders, E. C., Boisclair, D. & Roy, A. G. (2004). The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2302–2313.
- Fischer, P. (1994). Litorale Fischbiozöosen in einem großen See – der Bodensee. PhD Thesis, University of Constance, Germany.
- Fischer, P. & Eckmann, R. (1997a). Spatial distribution of littoral fish species in a large-European lake, Lake Constance, Germany. *Archiv für Hydrobiologie* **140**, 91–116.
- Fischer, P. & Eckmann, R. (1997b). Seasonal changes in fish abundance, biomass and species richness in the littoral zone of a large European lake, Lake Constance, Germany. *Archiv für Hydrobiologie* **139**, 433–448.
- Garner, P., Clough, S., Griffiths, S. W., Deans, D. & Ibbotson, A. (1998). Use of shallow marginal habitat by *Phoxinus phoxinus*: a trade-off between temperature and food? *Journal of Fish Biology* **52**, 600–609.
- Gauthier, S. & Boisclair, D. (1997). The energetic implications of diel onshore–offshore migration by dace (*Phoxinus eos* x *P. neogaeus*) in a small oligotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1996–2006.
- Gliwicz, Z. M., Slon, J. & Szykarczyk, I. (2006). Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. *Freshwater Biology* **51**, 823–839.
- Gregory, R. S. (1993). Effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 241–246.

- Gregory, R. S. & Northcote, T. G. (1993). Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 233–240.
- Hartmann, J. (1983). Two feeding strategies of young fishes. *Archiv für Hydrobiologie* **96**, 496–509.
- Hill, J. & Grossmann, G. D. (1993). An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* **74**, 685–698.
- Hinshaw, J. M. (1985). Effects of illumination and prey contrast on survival and growth of larval yellow perch *Perca flavescens*. *Transactions of the American Fisheries Society* **114**, 540–545.
- Hjort, J. (1926). Fluctuations in the year classes of important food fishes. *Journal du Conseil international pour l'Exploration de la Mer* **1**, 5–38.
- Hofmann, H., Lorke, A. & Peeters, F. (2008). The relative importance of wind and ship waves in the littoral zone of a large lake. *Limnology and Oceanography* **53**, 368–380.
- Holland, L. E. & Huston, M. L. (1985). Distribution and food habits of young-of-the-year fishes in a backwater lake of the Upper Mississippi River. *Journal of Freshwater Ecology* **3**, 81–91.
- Hutter, K. (1984). *Hydrodynamics of Lakes*. Berlin: Springer-Verlag.
- Kaufmann, R. & Wieser, W. (1992). Influence of temperature and ambient oxygen on the swimming energetic of cyprinid larvae and juveniles. *Environmental Biology of Fishes* **33**, 87–95.
- Keast, A. (1985). Development of dietary specializations in summer community of juvenile fishes. *Environmental Biology of Fishes* **13**, 211–224.
- Koonce, J. F., Bagenal, T. B., Carline, R. F., Hokanson, K. E. F. & Nagiéc, M. (1977). Factors influencing year-class strength of percids: a summary and a model of temperature effects. *Journal of the Fisheries Research Board of Canada* **34**, 1900–1909.
- Kucharczyk, D., Luczynski, M., Kujawa, R., Kaminski, R., Ulikowski, D. & Brzuzan, P. (1998). Influences of temperature and food on early development of bream (*Abramis brama* L.). *Archiv für Hydrobiologie* **141**, 243–256.
- Kuhlmann, H., Koops, H. & Wienbeck, H. (1988). *Gutachten im Auftrag des Ministeriums für Forschung und Technologie: Bedeutung gelöster Gase für die Fischhaltung, Förderungs-kennzeichen MFE 0531 O*. Hamburg: Bundesforschungsanstalt für Fischerei.
- Kundu, P. K. & Cohen, I. M. (2002). *Fluid Mechanics*. London: Academic Press.
- Lewin, W.-C., Okun, N. & Mehner, T. (2004). Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. *Freshwater Biology* **49**, 410–424.
- Lord, E. (1950). Power of a modified *t*-test (*u*-test) based on range. *Biometrika* **37**, 64–77.
- Lozán, J. L. (1992). *Angewandte Statistik für Naturwissenschaftler*. Berlin, Hamburg: Paul Parey Verlag.
- Lubbers, L., Boynton, W. R. & Kemp, W. M. (1990). Variations in structure of estuarine fish communities in relation to abundance of submerged vascular plants. *Marine Ecology Progress Series* **65**, 1–14.
- Magnhagen, C. & Heibo, E. (2004). Growth in length and in body depth in young-of-the-year perch with different predation risk. *Journal of Fish Biology* **64**, 612–624.
- May, R. C. (1974). Larval mortality in marine fishes and the critical period concept. In *The Early Life History of Fish* (Blaxter, J. H. S., ed.), pp. 3–13. New York, NY: Springer-Verlag.
- Mills, C. A. & Mann, R. H. K. (1985). Environmentally-induced fluctuations in year-class strength and their implications for management. *Journal of Fish Biology* **27** (Suppl. A), 209–226.
- Miner, J. G. & Stein, R. A. (1993). Interactive influence of turbidity and light on larval Bluegill (*Lepomis macrochirus*) foraging. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 781–788.
- Miner, J. G. & Stein, R. A. (1996). Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. *Transactions of the American Fisheries Society* **125**, 97–103.
- Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**, 1370–1386.

- Mosegaard, H., Svedäng, H. & Taberman, K. (1988). Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1514–1524.
- Nümann, W. (1973). Versuch einer Begründung für den Wandel in der qualitativen und quantitativen Zusammensetzung des Fischbestandes im Bodensee während der letzten 60 Jahre und eine Bewertung der Besatzmaßnahmen. *Hydrologie* **35**, 206–238.
- Panella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science* **173**, 1124–1127.
- Pierce, C. L. (1994). Littoral fish communities in Southern Quebec lakes: relationship with limnological and prey resource variables. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1128–1138.
- Power, M. E. (1984). Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *Journal of Animal Ecology* **53**, 357–374.
- Reyjol, Y., Fischer, P., Lek, S., Rösch, R. & Eckmann, R. (2005). Studying the spatio-temporal variation of littoral fish community in a large prealpine lake, using self-organizing mapping. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2294–2302.
- Reznick, D., Lindbeck, E. & Bryga, H. (1989). Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 108–112.
- Ruiz, G. M., Hines, A. H. & Posey, M. H. (1993). Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99**, 1–16.
- Savino, J. F. & Stein, R. A. (1989). Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* **37**, 311–321.
- Schleuter, D. & Eckmann, R. (in press). Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. *Ecology of Freshwater Fish* doi: 10.1111/j.1600-0633.2007.00262.x
- Simonian, A., Tátrai, I., Biró, P., Paulovits, G., G-Tóth, L. & Lakatos, G. (1995). Biomass of planktonic crustaceans and the food of young cyprinids in the littoral zone of Lake Balaton. *Hydrobiologia* **303**, 39–48.
- Specziár, A., Tölg, L. & Biró, P. (1997). Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *Journal of Fish Biology* **51**, 1109–1124.
- Staaks, G. (1996). Experimental studies on temperature preference behaviour of juvenile cyprinids. *Limnologica* **26**, 165–177.
- Tonn, W. M. & Magnuson, J. J. (1982). Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* **63**, 1149–1166.
- Volk, E. C., Wissmar, R. C., Simenstad, C. A. & Eggers, D. M. (1984). Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 126–133.
- Werner, E. E., Hall, D. J., Laughlin, D. R., Wagner, D. J., Wilsman, L. A. & Funk, F. C. (1977). Habitat partitioning in a freshwater community. *Journal of the Fisheries Research Board Canada* **34**, 360–370.
- Wetzel, R. G. (1983). *Limnology*. Philadelphia, PA: Saunders College Publications.
- Wildhaber, M. L. & Crowder, L. B. (1990). Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) response to food availability and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1664–1671.
- Wright, P. J. (1991). The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **38**, 929–933.
- Wright, P. J., Metcalfe, N. B. & Thorpe, J. E. (1990). Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. *Journal of Fish Biology* **36**, 241–249.
- Yamamoto, T., Ueda, H. & Higashi, S. (1998). Correlation among dominance status, metabolic rate and otolith size in masu salmon. *Journal of Fish Biology* **52**, 281–290.