Effect of wave exposure dynamics on gut content mass and growth of young-of-the-year fishes in the littoral zone of lakes

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Total length, body mass and gut content mass of young-of-the-year (YOY) perch *Perca fluviatilis*, dace *Leuciscus leuciscus* and bleak *Alburnus alburnus* were recorded over the summer of 2006 at three littoral sites at Upper Lake Constance. In *P. fluviatilis* and *L. leuciscus*, gut content mass correlated positively with wave-induced energy flux (E_F) of the respective site and sampling day, while no correlation of gut content mass with E_F was found in *A. alburnus*. It was assumed that benthivorous *P. fluviatilis* and *L. leuciscus* profited from suspended or uncovered benthic food items generated by wave action at sites and periods with high E_F. *Alburnus alburnus*, in contrast, feeding mainly on zooplankton in upper parts of the water column, could not profit from increased E_F. In *P. fluviatilis*, increased gut content mass during periods of high E_F resulted in higher growth rates. For *L. leuciscus*, no real growth rates in local fish populations could be determined, as individuals were less sedentary, and when increased growth occurred at sites during the periods of high E_F, migration of fish levelled out the resulting size differences within few days. The results of this study show that dynamic habitat variables affect site profitability in the littoral zone of lakes, especially in benthivorous fishes. Therefore, dynamic habitat variables should be considered in addition to fixed habitat properties in analyses of habitat choice of fishes in the littoral zone of lakes. © 2010 The Authors

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Key words: *Alburnus alburnus*; dynamic habitat factor; foraging success; *Leuciscus leuciscus*; *Perca fluviatilis*; wave-energy flux.

INTRODUCTION

One of the key questions in ecology since the emergence of this field of research is how environmental conditions affect the individual organisms and populations that live in a habitat (Chapman, 1931). In lake fish ecology, many studies are available that investigated the effects of fixed physical properties of a habitat such as substratum type, submerged plant coverage, water depth or complexity of habitat structure on diversity and density of fish populations (Tonn & Magnuson, 1982; Lyons, 1987; Benson & Magnuson, 1992; Bryan & Scarnecchia, 1992; Chick & McIvor, 1994;

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Pierce, 1994; Fischer & Eckmann, 1997; Lewin *et al.*, 2004) as well as on species interactions as competition and predation (Savino & Stein, 1989*a*, *b*; Pierce, 1994; Dietrich *et al.*, 2004).

A typical problem that arises when collecting fish samples for such studies is that the variability between replicate samples is high and large parts of this variability typically remain unexplained by fixed physical habitat properties (Jackson *et al.*, 2001). Some of this remaining variability may be explained by dynamic habitat variables. Dynamic habitat variables may change in an irregular way throughout the sampling period, thereby affecting the profitability of habitats over time. Wildhaber & Crowder (1990) showed that fishes can respond rapidly to changes in site profitability.

In stream ecology, dynamic habitat variables are well studied. Discharge, and thereby current velocity, is often regarded as the most important dynamic habitat variable affecting costs of activity, food accessibility and predation pressure (Schlosser, 1985). Habitat use varies with discharge for a number of species, including juvenile grayling *Thymallus thymallus* (L.) (Valentin *et al.*, 1994), brown trout *Salmo trutta* L. (Heggenes, 1988) and Atlantic salmon *Salmo salar* L. (Debowski & Beall, 1995). Growth and survival of young-of-the-year (YOY) fishes may also be affected (Schiemer *et al.*, 2001).

In lake ecosystems, in contrast, the role of dynamic habitat variables is poorly investigated. Studies comparing the energy budget of littoral fishes in different habitats, however, suggest that in littoral habitats, activity costs of fishes may be significant and much more variable than previously assumed (Boisclair & Leggett, 1989; Boisclair & Tang, 1993).

Hydrodynamic stress is not restricted to rivers and streams. Fishes living in the littoral zone of lakes are also exposed to significant water movements created by wind-generated waves and, increasingly, to anthropogenic waves generated by ships. The hydrodynamic stress from such waves may impose significant energetic costs on littoral fishes (Stoll *et al.*, 2008), but these may be balanced by gains derived from wave action. Lienesch & Matthews (2000) showed that daily abundances of some littoral fish species correlate positively with wave variables, possibly because of improved feeding opportunities resulting from suspension of benthic food items (Gabel *et al.*, 2008).

Temperature is another important dynamic habitat variable affecting physiological processes in fishes (Jobling, 1994). Temperature trajectories vary within sites from day to day and also between sites due to the degree of shading by shoreline vegetation and local water currents. Thus the profitability of different sites is influenced by temperature in potentially irregular and unpredictable ways.

This study examines the effect of dynamic habitat variables, wave energy flux (E_F) and temperature on the juvenile fish populations at three different sites in Lake Constance over a three-month period in summer 2006. Three focal species, perch *Perca fluviatilis* L., dace *Leuciscus leuciscus* (L.) and bleak *Alburnus alburnus* (L.), were sampled at three different sites at intervals of 7–14 days. In the first step, a test was made of whether gut content mass, and thus feeding success, depends on ambient wave energy flux and temperature. The three focal species were chosen because they differ in feeding strategy. During the summer months, the diet of *P. fluviatilis* <95 mm total length (L_T) comprises mostly benthic invertebrates in the littoral zone (Schleuter & Eckmann, 2008). Juvenile *L. leuciscus* also feed on benthic invertebrates. In addition, *L. leuciscus* consume epilithon (Weatherley, 1987),

which they scrape from hard substrata with their horny lower lip. Gut content mass of these species should correlate with E_F, as they can profit from resuspension of benthic food items. *Alburnus alburnus*, in contrast, typically swim further up in the water column feeding on planktonic prey and wind-borne items from the water surface (Białokoz, 1990; Vašek & Kubečka, 2004). The availability of these prey types is not influenced by resuspension and thus should not be correlated with E_F. A second step tested whether differences in feeding success related to E_F resulted in growth differences in the local fish populations. It was assumed that the effect of E_F on local fish growth rates could be found in *P. fluviatilis* and *L. leuciscus*, but not in *A. alburnus*.

MATERIALS AND METHODS

STUDY AREA

Lake Constance is a large, warm-monomictic pre-alpine lake situated at the boundary of Germany, Switzerland and Austria (47°N; 09°E) at an altitude of 395 m a.s.l. The lake comprises two basins, the deep oligotrophic Upper Lake Constance and the relatively shallow, mesotrophic Lower Lake Constance [Fig. 1(a)]. The wave field of Lake Constance is characterized by wind waves and periodically occurring ship waves (Hofmann *et al.*, 2008). With the exception of private boating, most ship traffic is scheduled and hence more or less consistent between days throughout the whole summer. The contribution of wind waves varies with wind intensity and direction. Over the period of a year, the prevailing winds over Lake Constance are westerlies, with the second most frequent winds coming from the south-east during summer and north-east during winter.

The three sampling sites used in this study were littoral areas located in the north-western area of Upper Lake Constance. They were selected with respect to maximal uniformity on the basis of abiotic and biotic habitat variables such as substratum quality, angle of inclination
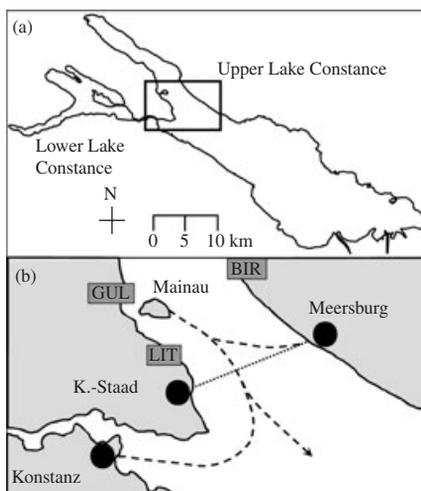

FIG. 1. (a) Map of Lake Constance, situated at the border between Germany, Switzerland and Austria. (b) Magnification of (□) in (a). Three sampling sites: Birnau (BIR), Lower Güll (GUL) and Littoral Garden (LIT). ....., the ferry line between Konstanz-Staad and Meersburg. ---, the passenger ship lines to the Island of Mainau.

and plant coverage, while exposure to surface waves at each site was different [Fig. 1(b)]. At the seaward edge, they all reach a water depth of 4–5 m. There the bottom drops to water depths >50 m with an angle of c. 45°.

Site Birnau (BIR) is located on the northern shoreline. At BIR, the littoral shelf extends c. 150 m into the lake. BIR is exposed to winds from the south-west, but few ship waves occur at this site. The substratum is characterized by gravel and pebbles, infilled with sandy sediments. Soft sediments predominate in deeper areas (>3 m water depth) with a sparse coverage of submerged macrophytes, mainly *Potamogeton pectinatus*. A small quantity of *Chara* spp. is present in all water depths.

Site Lower Güll (GUL) is situated on the south-western shoreline. The littoral width is c. 300 m. GUL lies to the northern side of the bay behind the Island of Mainau and is sheltered from both ship and wind waves, with the exception of those driven by a rare straight easterly wind. The substratum is dominated by pebbles in the shallow (<0·5 m), and at greater depth by sandy or soft sediments, the latter covered with *Chara* spp.

The site Littoral Garden (LIT) is also situated on the south-western shoreline, c. 3 km south-east of GUL. The littoral width is c. 80 m. LIT is fully exposed to frequent ship waves generated by the car ferries shuttling between the cities of Konstanz-Staad and Meersburg, and by passenger ships heading to and from the Island of Mainau. On average, ship waves contribute 40–50% of the total E_F to this part of the shoreline during the main navigation period in summer and 41% over the whole year (Hofmann *et al.*, 2008). The substratum at LIT is dominated by sand and pebbles, interspersed with few stones. Submerged macrophyte coverage is sparse during summer, comprising mainly *Chara* spp. and some *P. pectinatus* and *Potamogeton perfoliatus* L., the last two only present at water depths between 3 and 5 m.

FISH SAMPLING

Sampling was conducted at the three sampling sites on a weekly to bi-weekly basis between July and October 2006 (Table I). Fishes were caught in a beach seine 16 m long and 1·5 m high with a 4 mm bar mesh, hauled in to the shore from 1·2 to 1·3 m water depth (the maximum depth that could be reached with waders). On each sampling day, the three sites were sampled in a random order between 1000 and 1600 hours. YOY *P. fluviatilis*, *L. leuciscus* and *A. alburnus* were chosen as focal species, as they represent different feeding behaviour (*P. fluviatilis*: benthos; *L. leuciscus*: benthos and epilithon; *A. alburnus*: plankton) and were most abundant in the seine catches at all three sites, comprising >95% of the YOY fishes caught. On each occasion, fishing was continued until 20 individuals of each focal species were caught, or for a maximum of four hauls per site to limit the impact on the site and its fish community. Fishes for analysis were killed immediately with 2-phenoxyethanol solution and stored on ice until they reached the laboratory (maximum 4 h) where they were immediately frozen until further processing. Surplus catch not required for the analysis was immediately released.

In the laboratory, fishes were thawed carefully in ice water. L_T was measured to the nearest 0·5 mm and wet mass (M_W) was taken (±0·01 g). Then guts were dissected out, from the oesophagus to the anus. Reliable identification of gut contents was impossible due to the degree of crushing and digestion; thus, only wet mass of the gut contents (M_{GC}) was recorded (±0·001 g).

ABIOTIC HABITAT VARIABLES

Water temperatures were recorded continuously with a sampling resolution of 12 h^{-1} throughout the whole summer season. A temperature logger (Onset Computer Corp.; www. onsetcomp.com) was moored at c. 1·25 m (range ± 0·10 m) water depth at each of the three sites, and the position of the loggers was adjusted twice according to the water level. Because temperature data were distributed normally, daily means were calculated for each sampling site for analysis in relation to M_{GC} and sampling period means for the analysis of population structure development.

TABLE I. Data coverage during the total sampling period (11 July to 4 October 2006) for abiotic habitat factors temperature and energy flux (E_F) at the sampling sites Birnau (BIR), Lower Güll (GUL) and Littoral Garden (LIT) (see Fig. 1). Data gaps resulted from battery replacement and theft of one sensor. If data coverage of a sampling period was <50%, data were not included in the analyses and values in this table are shown in parentheses

| | | | Data coverage (%) | | | |
| | | | | E_F | | |
Sampling periods	Period number	Days between samplings (n)	Temperature, all sites	BIR	GUL	LIT
11 to 18 July	1	7	100	85	100	(0)
18 to 31 July	2	13	100	50	100	(45)
31 July to 9 August	3	9	100	(0)	100	80
9 to 18 August	4	9	100	(20)	85	100
18 to 31 August	5	13	100	100	100	100
31 August to 12 September	6	12	100	100	100	90
12 to 19 September	7	7	100	85	83	100
19 September to 4 October	8	15	100	100	100	100

Surface wave fields at each of the three sites were monitored using custom-made pressure sensors (PS; based on sensor PDCR 1730, GE Druck; www.gesensing.com; refitted for long-term energy supply and data storage at the Technical workshop of the University of Konstanz), deployed at a water depth of 2 m. The stands of the PSs were 1 m high, and thus measurements were recorded in the middle of the water column. Each PS had a full-scale range of 7 m, an accuracy of 0·1 mbar and a maximum stand-alone deployment time of 45 days. Pressure measurements were made at a sampling frequency of 16 Hz during the entire deployment period. Data gaps resulted from battery replacement, which had to be done in the workshop, and the theft of one sensor. The subsurface pressure measurements were converted to a time series of surface elevation following the procedure described by Hofmann *et al*. (2008). Wave variables (*i.e.* wave height and period) were estimated for sets of 1024 (64 s) samples using the zero-upcrossing method (IAHR, 1989; Hofmann *et al*., 2008). Wave energy flux (E_F) is an ecologically relevant property of wave action (Hofmann *et al*., 2008). E_F associated with motion per unit length of wave crest (W m^{-1}) can be estimated as the product of group velocity and wave energy using the formulas given in Hofmann *et al*. (2008). E_F data were skewed, especially at the site LIT, where low background values throughout most of the day were punctuated by short periods of high E_F values, when a ship was passing the site. Therefore, for E_F, daily medians and sampling interval medians were used for the analyses.

DATA PROCESSING AND STATISTICS

For each of the focal species, M_{GC} of individual fishes were analysed with respect to site, M_W without stomach content ($M_W - M_{GC}$), median E_F of the sampling date and mean temperature of the sampling date using general linear models (GLM). For continuously scaled variables (M_W, E_F and temperature), slope estimates are given to indicate the direction of the correlation. *t post hoc* tests were applied when effects of the nominally scaled variable site were found.

The mean absolute growth rate G of the local fish populations at the three sampling sites was calculated for each species: $G = (M_i - M_{i-1})\Delta t^{-1}$, where M_i is the average body mass in a fish population at sampling i, and Δt is the number of days between the samplings i and i-1. Since open YOY fish populations were sampled in this study, the composition of the fish populations sampled at any one site may have varied throughout the sampling season. Therefore, the calculated growth rates may reflect not only growth, but also emigration from or immigration into a local fish population.

The growth rates were based on M_W, so no systematic change in magnitude occurred during the summer season (ANOVA testing the effect of week of year on growth rate: $F_{1,52} = 0.34$, $P > 0.05$). Development of L_T, in contrast, followed a logarithmic function, and thus growth rates based on L_T were highest during early summer and declined towards the end of the summer. Where a sampling session at a site yielded fewer than four individuals of a focal species, data were not included in the analysis.

To elucidate whether local fish growth rates were dependent on dynamic abiotic habitat variables, the growth rates of each of the three focal species were related to site, E_F and temperature of the respective periods using general linear models (GLM). *t post hoc* tests were applied when effects of the nominally scaled variable site were found.

All tests were performed with a significance level of $P = 0.05$. Only periods with E_F data coverage >50% were included in the analysis (Table I). Before each test, normal distribution and homogeneity of variances were tested using Shapiro–Wilk's and Bartlett tests and appropriate tests for further data analysis were chosen accordingly (Lozàn & Kausch, 1998).

RESULTS

Fish were sampled nine times in the summer of 2006 at each of the three sampling sites BIR, GUL and LIT. A total of 1213 YOY fishes were caught for analysis, among them were 330 *P. fluviatilis*, 430 *L. leuciscus* and 453 *A. alburnus* (Table II). *Perca fluviatilis* were present throughout the whole summer season at GUL and from 31 July at the site LIT. At BIR, *P. fluviatilis* occurred only incidentally. *Leuciscus leuciscus* were present at all three sampling sites from the beginning of the sampling. The sampling at 31 July and 9 August at GUL yielded insufficient numbers of *L. leuciscus* for analysis. *Alburnus alburnus* were present at BIR from the beginning of the study and appeared at GUL on 17 July and at LIT on 31 July and remained present at all sites throughout the rest of the summer (Table II).

The L_T and M_W of *P. fluviatilis*, *L. leuciscus* and *A. alburnus* generally increased throughout the summer, though there were some periods, over which mean L_T and M_W of local fish populations decreased between consecutive sampling dates (Fig. 2). In *P. fluviatilis*, in particular, mean L_T and M_W did not increase synchronously at the sites GUL and LIT, and after 12 September 2006 (end of sampling period six), L_T and M_W of *P. fluviatilis* at LIT were significantly higher than at GUL (*t*-test, 12 September 2006: d.f. = 32, $t = 5.01$, $P < 0.001$; 19 September 2006: d.f. = 38, $t = 7.93$, $P < 0.001$; 04 October 2006: d.f. = 36, $t = 7.13$, $P < 0.001$).

Daily median E_F in the range between 0.02 and 18.5 W m^{-1} was measured at the three sampling sites [Fig. 3(a)]. Daily median E_F intensities differed significantly between the three sampling sites (median test: $\chi^2 = 140$, d.f. = 2, $P < 0.001$). The lowest E_F values were recorded at the most protected site GUL, with an exception on 17 July [Fig. 3(a)]. Intermediate wave energy fluxes were recorded at BIR, and highest values were measured at LIT. A strong wave event occurred at BIR on 29 August, and at LIT on 8 September, resulting in peak median E_F in sampling period five in BIR and six in LIT [Fig. 3(a)–(c)].

Daily mean water temperatures recorded during the entire sampling period ranged between 14.5 and 27.2° C [Fig. 3(d)]. Daily mean water temperatures did not differ significantly between sampling sites (ANOVA for paired data: $F_{2,257} = 1.99$, $P > 0.05$); however, using sampling period means, significant differences could be found (Friedman test: $Xr^2 = 12.3$, $P < 0.05$), as during all sampling periods, the average temperature was 0.5–1.5° C higher at site GUL than at sites BIR and LIT

TABLE II. Number of (a) *Perca fluviatilis* (b), *Leuciscus leuciscus* and (c) *Alburnus alburnus* caught at the sampling sites Birnau (BIR), Lower Güll (GUL) and Littoral Garden (LIT) (see Fig. 1) on the nine sampling dates in summer 2006. If number of fish (*N*) was ≤3, data were not included in the analyses and values in this table are shown in parentheses

Sampling site	Fish (*N*) caught at sampling								
	11 July	18 July	31 July	9 August	18 August	31 August	12 September	19 September	4 October
(a) *Perca fluviatilis*									
BIR[a]		4	11		(3)			16	
GUL	20	20	20	20	20	20	19	20	20
LIT			4	20	20	20	15	20	18
(b) *Leuciscus leuciscus*									
BIR	16	16	20	15	20	20	14	20	20
GUL	10	11	(2)	(2)	19	19	13	18	6
LIT	20	16	20	19	17	20	17	20	20
(c) *Alburnus alburnus*									
BIR	8	20	20	20	20	20	19	20	20
GUL		20	8	20	20	20	20	20	20
LIT				20	20	20	20	20	18

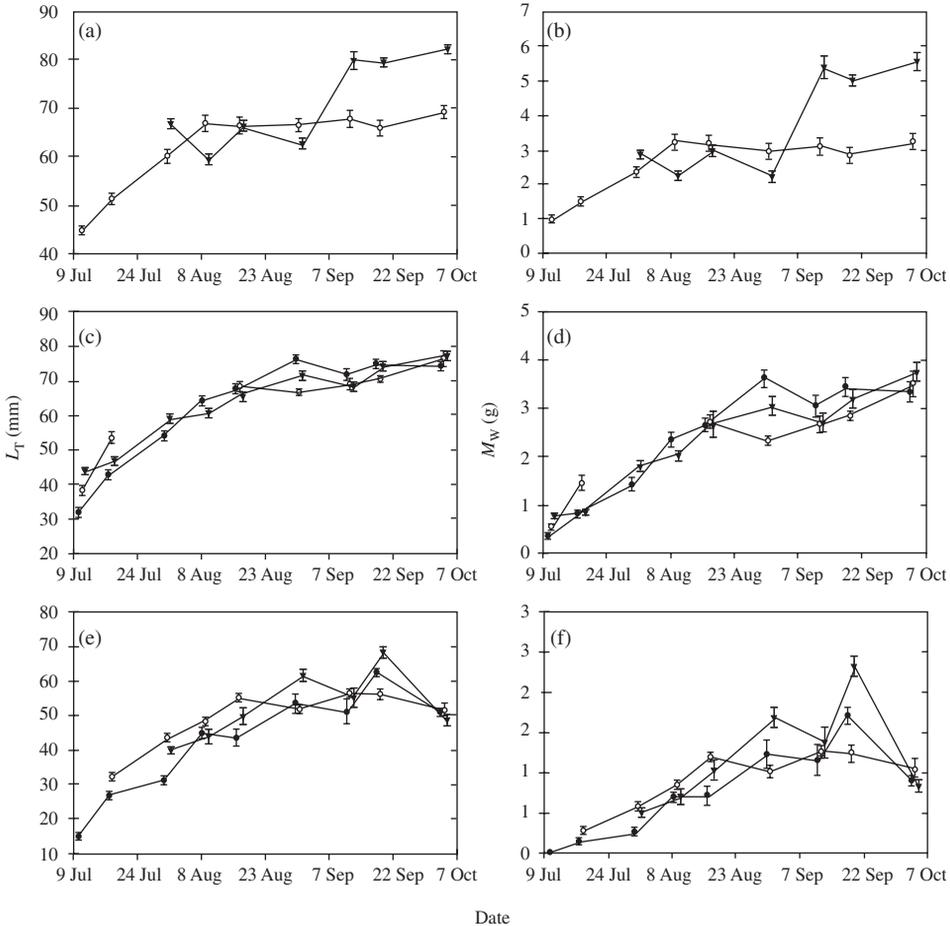[a]Could not be considered in the analysis due to scarcity of data.

FIG. 2. Mean ± S.E. (a), (c), (e) total length (L_T) and (b), (d), (f) wet body mass (M_W) of the three fish species (a), (b) *Perca fluviatilis* (c), (d), *Leuciscus leuciscus* and (e), (f) *Alburnus alburnus* throughout the sampling season in summer 2006 at the three sampling sites Birnau (●), Lower Güll (○) and Littoral Garden (▼) (see Fig. 1).

[Fig. 3(e), (f)]. A drop in water temperature occurred during the first days of August, when strong winds caused upwelling of colder water at all three sites.

No completely empty guts were found. In all three fish species, M_{GC} was highly correlated with M_W (Table III). The M_{GC} differed significantly between sites in all species. *Post hoc* tests revealed that *P. fluviatilis* and *L. leuciscus* consumed significantly more food at LIT than at the other sites, and *A. alburnus* consumed more food at GUL than at BIR, with intermediate consumption at LIT. In *P. fluviatilis* and *L. leuciscus*, M_{GC} correlated positively with E_F and with temperature, but not in *A. alburnus* (Fig. 4).

In *P. fluviatilis*, growth rates differed significantly between sites, with lower values at GUL than at LIT (Table IV). Furthermore, increase in M_W was positively correlated with E_F but not with temperature. In *L. leuciscus* and *A. alburnus*, no
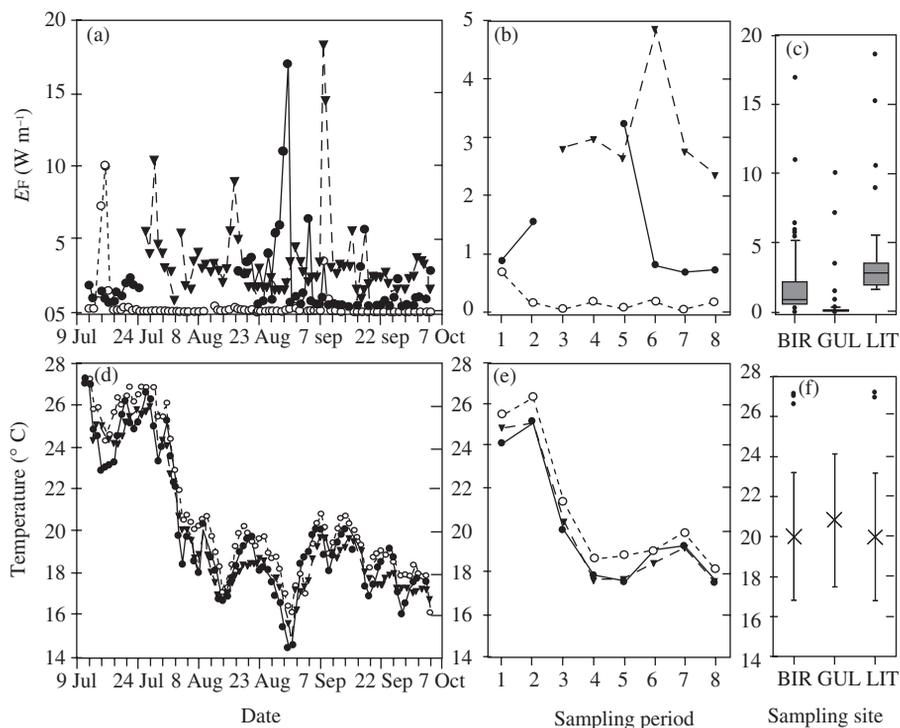
FIG. 3. (a), (b), (c) Wave energy flux (E_F) at 1·25 m water depth and (d), (e), (f) water temperature at the sampling sites Birnau (BIR, ●), Lower Güll (GUL, ○) and Littoral Garden (LIT, ▼) (see Fig. 1). Daily (a), (d) (b), (e), sampling period and (c), (f) whole summer medians of E_F and means of water temperature are given, respectively. For whole summer medians of E_F, 10th, 25th, 75th and 90th percentiles and outliers are plotted, while S.D. and outliers of double S.D. are given for whole summer means of temperature. Significant differences in E_F (Nemenyi *post hoc* test) and water temperature (Wilcoxon–Wilcox *post hoc* test) between sites are indicated with different uppercase letters.

significant correlations between increase in M_W and site, E_F and temperature could be found (*L. leuciscus*: total $R^2 = 0.05$, all $P > 0.05$; *A. alburnus*: total $R^2 = 0.03$, all $P > 0.05$).

DISCUSSION

This study shows that local YOY fish populations in littoral habitats of a lake respond to dynamic changes in abiotic environmental variables. According to the predictions, M_{GC} mass of benthivorous *P. fluviatilis* and *L. leuciscus* correlated positively with E_F. It is assumed that in periods when wave action and thus E_F were high, benthic food items were suspended, or at least uncovered at the substratum surface, and that *P. fluviatilis* and *L. leuciscus* profited from the resultant increase in food accessibility (Lienesch & Matthews, 2000). This mechanism was previously demonstrated by Gabel *et al.* (2008) in laboratory studies, showing that benthic invertebrates may be lifted into suspension in the water column by waves, especially where

TABLE III. General linear model (GLM) results analysing the gut content mass (M_{GC}) of (a) *Perca fluviatilis*, (b) *Leuciscus leuciscus* and (c) *Alburnus alburnus*. In order to give the direction of the correlation, slope estimates (mean ± S.E.) are given if the variable is scaled continuously. The results of *t post hoc* tests are given for the nominally scaled variable site. Different uppercase letters indicate significant differences, the highest value is assigned to the letter A, the order of the three sites is alphabetical, Birnau (BIR), Lower Güll and Littoral Garden

Variable	d.f.	SS	F	P	Slope estimate *post hoc* test results
(a) *Perca fluviatilis*, $R^2 = 0.65$					
M_W	1	307 034	342	<0.001	33.79 ± 1.83
Site[a]	1	4125	4.60	<0.05	(a) B, A
E_F	1	8410	9.37	<0.01	7.38 ± 2.41
Temperature	1	27 378	30.50	<0.001	3.94 ± 0.71
Error	192	203 788			
(b) *Leuciscus leuciscus*, $R^2 = 0.62$					
M_W	1	419 666	294	<0.001	42.35 ± 2.47
Site	2	19 706	6.91	<0.01	B, B, A
E_F	1	55 943	39.23	<0.001	10.43 ± 1.67
Temperature	1	20 684	14.50	<0.001	2.86 ± 0.75
Error	425	540 520			
(c) *Alburnus alburnus*, $R^2 = 0.61$					
M_W	1	107 418	413	<0.001	28.48 ± 1.40
Site	2	1752	3.37	<0.05	B, A, AB
E_F	1	100	0.39	>0.05	−0.57 ± 0.91
Temperature	1	170	0.65	>0.05	−0.23 ± 0.29
Error	448	103 802			

[a]Due to scarcity of data, site BIR was omitted from the analysis.
M_W, wet body mass; E_F, wave energy flux.

TABLE IV. General linear model (GLM) results analysing the effect of sampling site (Birnau, BIR; Lower Güll, GUL; Littoral Garden, LIT), wave energy flux (E_F) and temperature on the growth of *Perca fluviatilis*. In order to give the direction of the correlation, slope estimates (mean ± S.E.) are given in case the variable is scaled continuously. The results of LSM *t post hoc* tests are given for the nominally scaled variable site

Variable	d.f.	SS	F	P	*Post hoc* test result/slope estimate
Perca fluviatilis, $R^2 = 0.64$					
Site[a]	1	0.05	12.50	<0.01	LIT > GUL
E_F	1	0.07	17.28	<0.01	0.13 ± 0.03
Temperature	1	<0.01	0.03	>0.05	0.001 ± 0.007
Error	10	0.04			

[a]Due to scarcity of data, site BIR was omitted from the analysis.
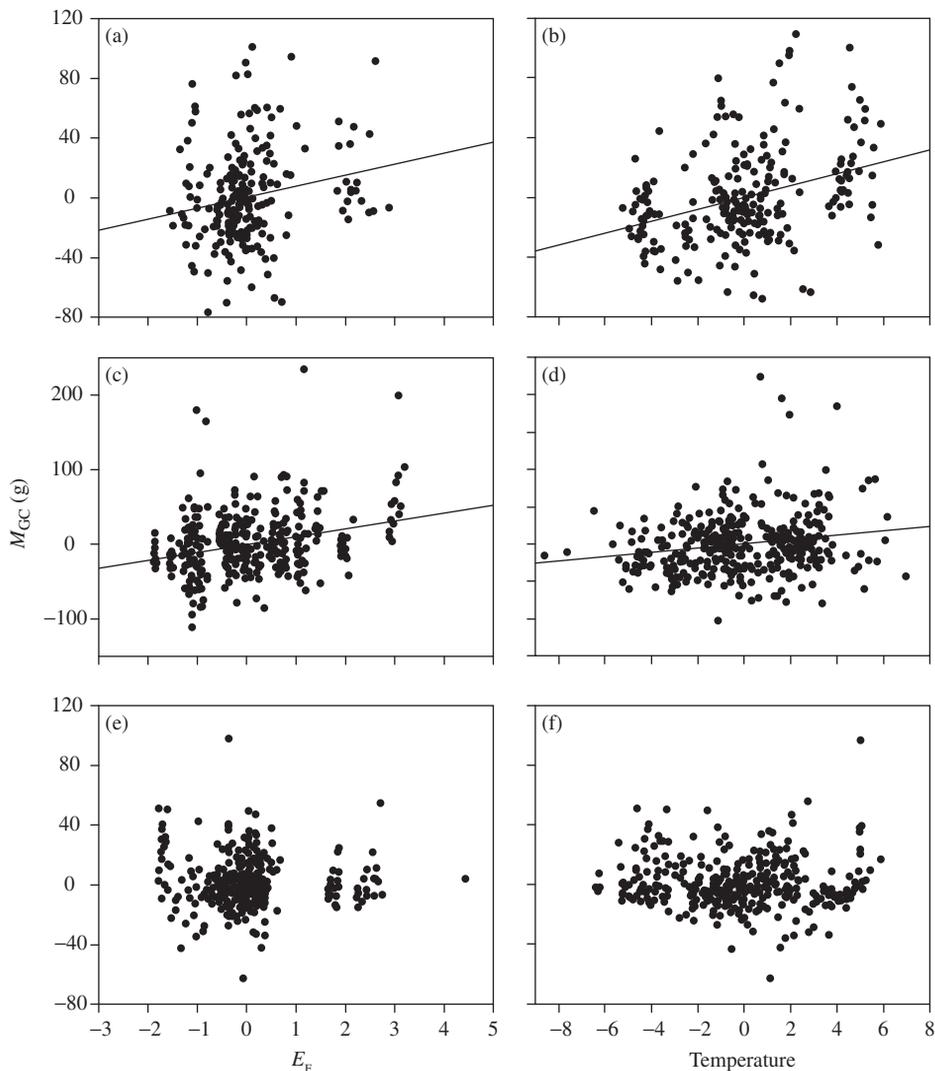
FIG. 4. Partial regression plots showing the relation of gut content mass (M_{GC}) of (a), (b) *Perca fluviatilis* (c), (d) *Leuciscus leuciscus* and (e), (f) *Alburnus alburnus* to (a), (c), (e) wave energy flux (E_F) and (b), (d), (f) temperature when all other variables in the model are held constant. On both axes, residuals of the indicated variables are plotted. (a) $P < 0.01$; (b) $P < 0.001$; (c) $P < 0.001$; (d) $P < 0.001$; (e) $P > 0.05$; (f) $P > 0.05$.

the structural complexity of the substratum is low. Also in streams, resuspension of invertebrates resulted in an increased foraging success in some benthivorous fishes (Blanchet *et al*., 2008).

In planktivorous *A. alburnus*, M_{GC} did not correlate with E_F. Other authors found that planktivores may profit from limited turbulence, but this effect has only been demonstrated for small fish larvae with a restricted mobility, but not for larger fishes

(MacKenzie *et al.*, 1994; Utne-Palm & Stiansen, 2002; Utne-Palm, 2004). Furthermore, the levels of turbulence these authors used were much lower than the level of turbulence recorded here.

Rising temperature increased the M_{GC} of *P. fluviatilis* and *L. leuciscus*. This may result from an increase in activity of the predator, the prey or both, at higher temperatures. Temperature optima of *c*. 23°C for *P. fluviatilis* (Mélard *et al.*, 1996) and 24–30°C for *L. leuciscus* (Staaks, 1996), which are in the upper area of the temperature range measured in this study, suggest that *P. fluviatilis* and *L. leuciscus* were foraging more actively at higher temperatures. But, many taxa of their benthic invertebrate prey are also more active at higher temperatures in the temperature range of this study (Wijnhoven *et al.*, 2003), and thus may become more accessible for predators at higher temperatures.

In *A. alburnus*, no experimentally assessed optimum temperature could be found in the literature; however, the species is characterized as a eurytherm (Schiemer & Waidbacher, 1992). Thus, food consumption in *A. alburnus* may be less affected by temperature within the temperature range experienced in this study, and also the accessibility of free-swimming planktonic food is probably less dependent on temperature than accessibility of hiding or camouflaging benthic invertebrates.

The factor site comprised all fixed differences between the three sampling locations. Even though sampling sites were chosen that were as similar as possible in their physical habitat conditions, the three sampling sites were not identical. For instance, substratum grain sizes in the shallow water were largest at LIT, and E_F and site co-varied to some extend, with LIT being the most wave-exposed habitat and GUL being the least wave-exposed habitat most of the time. These principal habitat differences were important to explain M_{GC} in all species. The M_{GC} of *P. fluviatilis* and *L. leuciscus* was highest at the most exposed site LIT. Furthermore, grain size of the substratum was coarsest at LIT which may have promoted feeding success of *L. leuciscus* on periphytic biofilms (Weatherley, 1987; Cowx, 1988). The M_{GC} of *A. alburnus* was highest at GUL, where E_F was generally low. Calm waters may have promoted feeding success in planktivorous *A. alburnus*. The results show that some proportion of the variability in the M_{GC} data can be explained by static differences between different habitats, which are covered by the factor site. The dynamic habitat factors E_F and temperature, however, explain a higher proportion of the variability, and thus are useful predictors of M_{GC}.

Do the dynamic habitat variables that lead to increased gut fullness also lead to higher growth rates in the local fish populations? Differential growth rates due to dynamic habitat variables could only be found in *P. fluviatilis*. *Perca fluviatilis* grew faster in periods with high E_F as it was expected from M_{GC} analysis. The most pronounced increase in size occurred during sampling period six (31 August to 12 September) at LIT, where exceptionally high E_F was recorded. The resulting size difference between the local populations persisted until the end of the summer season, showing that *P. fluviatilis* are rather stationary and exchange between the local populations is low, even though LIT and GUL were on the same side of the lake and only 3 km apart.

No consistent correlation between E_F and growth rates could be found in *L. leuciscus*. High growth rates occurred for instance during sampling period one (11 to 18 July) at GUL and sampling period five (18 to 31 August) at BIR where

maximum E_F were measured at the respective sites. This pattern was not consistent over all sampling periods and sites. Furthermore, differences in size between sampling sites did not persist over time. These findings suggest that *L. leuciscus* migrate greater distances than *P. fluviatilis*, such that emerging differences in body size between local populations are levelled out again within few days. In these open, changing local populations of *L. leuciscus*, no real growth rates could be determined, as the observed changes in size over time were caused not only by fish growth but also by emigration and immigration between local fish populations. Migrations of fish are also able to explain the decreases of average size of fish that could be observed in the local populations during some periods.

In *A. alburnus*, M_{GC} was independent of E_F and temperature, and accordingly, no effect of these variables on growth rates could be found. Although M_{GC} correlated with temperature in *P. fluviatilis* and *L. leuciscus*, no effect of temperature on growth rates was found in these species.

However, not only feeding success but also metabolic rates, however, increase with temperature (Jobling, 1994). Therefore, increased energy uptake may have been balanced by higher metabolic rates, resulting in no higher growth rates when temperatures were high. The results of this study suggest that in addition to fixed habitat attributes, dynamic variables, such as temperature and wave exposure, should be considered in studies on habitat choice of fishes in the littoral zone of lakes. This may improve the previously often limited predictive value of habitat choice models in littoral fishes.

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