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Life at turbulent sites

Benthic communities in lake littorals interacting with abiotic and biotic constraints

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Chapter 1

General introduction

Historical background and methodological constraints

Benthic communities in the littoral zone of large oligotrophic lakes have been investigated since studies in limnology began (e.g. Wesenberg-Lund 1908; Moon 1934; Muckle 1942). In the first half of the 20th century, the emphasis was usually placed on qualitative descriptive studies (Wesenberg-Lund 1908, 1912; Muckle 1942), yet some complex processes were also addressed, e.g. effect of water-level fluctuations on benthic communities accompanied by rapid colonisation (Moon 1935, 1940). The wave-exposed shore of the upper eulittoral zone was also recognised early on as a habitat with marked similarities to lotic habitats (Moon 1934).

Recent studies include a large-scale comparison of the benthic communities in stony habitats of streams and wind-swept shores of lakes in Sweden (Johnson *et al.* 2004). The stream communities were found to be generally more diverse and species rich, with higher proportions of grazers, shredders, and passive filter feeders, than lake communities. The lake communities, on the other hand, had higher proportions of predators and collector-gatherers (Johnson *et al.* 2004). Besides these marked differences, a variety of taxa were found in both habitats, but often in different abundances (Quinn *et al.* 1996, 1998b; Johnson *et al.* 2004).

Most of the limnological research of lakes, however, was and still is clearly dominated by pelagic studies. During the past decades, investigations have also focused on benthic communities in lotic or marine habitats. The land–water interface of lakes, in contrast, has been often ignored. This is somewhat surprising as this area is usually highly impacted by various anthropogenic and commercial uses, activities, and interests, and, therefore, also is of ecological and recreational importance to the public (e.g. Scheurell & Schindler 2004). The lack of interest can presumably be ascribed to methodological difficulties in the quantitative sampling of lake littoral zones, especially in large oligotrophic lakes, where littoral zones are often steep and narrow. Sampling is therefore restricted to arm length at the eulittoral zone, unless scuba divers are available. Sampling in lake littoral zones is further complicated by the roughly bi-directional currents in contrast to the underlying uni-directional currents in lotic habitats. Various attempts to standardise sampling methods in lentic systems have failed because of the various substrate grain sizes present, ranging from fine sediment to cobblestones or gravel. However, the recently established suction pump method developed by Baumgärtner (2004) and Mörtl (2003) is most promising. We used this method, with a slightly modified eulittoral device in our study (see Chapters 2 and 6 for details).

Benthic communities and their abiotic and biotic constraints

Today, the littoral zone is known to play an important role in the energy transfer of lake ecosystems (James *et al.* 2000a; Tolonen *et al.* 2001; Vadeboncoeur *et al.* 2003), affecting various trophic levels within benthic-coupled food webs. Littoral zones of shallow oligotrophic lakes in particular are likely to mediate whole lake productivity up to 80–98% (Vadeboncoeur *et al.* 2003), whereas pelagic primary production is less important (Hecky & Hesslein 1995; Schindler & Scheurell 2002). Even in large, deep, oligotrophic lakes, where littoral zones represent often a very small portion of the entire lake area, this habitat is presumably a very important but also limited resource for benthic invertebrate settlement and as a fish-spawning and foraging area.

Macroinvertebrates in benthic communities are an inherent part of the energy transfer to upper levels (Gilinsky 1984; Gilliam *et al.* 1989; James *et al.* 2000a). The composition and dynamics of benthic communities depend on (1) the taxa present, their historical or recent arrival, and large-scale factors, e.g. climate and geographical distribution; (2) their physiological constraints in relation to their abiotic environment, e.g. temperature, oxygen, nutrients, hydrodynamics, and substrate; (3) inherent life history patterns; (4) the biotic interaction of taxa, e.g. competitive abilities, predation pressure, and resource utilisation; and (5) other indirect factors, e.g. non-lethal effects of predation. However, their community structure, population dynamics, habitat association, and trophic interactions are still poorly understood. Especially the relative importance of biotic and abiotic factors in structuring benthic communities needs to be studied further.

Abiotic parameters range from large scale (landscape) to regional or local scale (habitat). These parameters, e.g. climate and geology, are often interrelated with other factors, e.g. soil type, vegetation type, geographical relief (water retention), and the input of organic matter in water systems (Johnson & Goedkoop 2002; Johnson *et al.* 2004). Lake productivity, water chemistry, temperature, morphometry, and other factors are good predictors of lake communities (Brodersen *et al.* 1998; Tolonen *et al.* 2001; Vadeboncoeur *et al.* 2003). The linkage between terrestrial and aquatic systems has been discussed in earlier classical works (Likens & Bormann 1974; Vannote *et al.* 1980). More recent results indicate that this interaction also accounts for the community response following large disturbance events in streams. Collier & Quinn (2003) showed that the severeness and recovery speed depends on the land use of the catchment area. Scheurell & Schindler (2004) found that spatial aggregation of littoral fish is related to a residential development gradient, e.g. the number of refugia, and resource heterogeneity decreases when the development level increases.

However, the habitat structure explained the greatest portion of benthic variability more than any other spatial scale considered (e.g. catchment, ecosystem) and accounted for nearly 25% of the variance in taxonomic composition in the study of Johnson & Goedkopp (2002). Hydrodynamic processes and water-level fluctuations are also recognised as major causes of habitat alteration and heterogeneity in large lakes (Keddy 1982; Palomäki 1994; James *et al.* 1998). Hydrodynamic processes can alter sediment structure, i.e. size-class composition (Hakanson & Jansson 1983; Schmieder *et al.* 2004). Thus, the amount of interstitial refuges available for macroinvertebrates (Gjerlov *et al.* 2003) and benthic fish (Fischer 2000) change. Wave action at littoral sites strongly depends on shore exposure to wind- or boat-generated waves, frequency and duration of such events, and on lake morphology, such as slope and lake size, which affect wind fetch across the lake surface (e.g. Hakanson 1977; Hakanson & Jansson 1983; Cattaneo 1990;

Petticrew & Kalff 1991; Rowan *et al.* 1992; Rasmussen 1993; Hamilton & Mitchell 1996; Rasmussen & Rowan 1997). On a vertical and horizontal scale, the intercorrelation with other parameters has been documented, e.g. temperature, light penetration, sediment characteristics, macrophytes, and periphyton growth and productivity (e.g. Rasmussen & Rowan 1997; Cyr 1998a; Finlay *et al.* 2001; Madsen *et al.* 2001; Donahue *et al.* 2003a).

Biotic interaction can also greatly contribute to spatial and temporal variability at all trophic levels. Such patterns have been documented in the relationships between the periphyton and benthic herbivores (e.g. Cattaneo & Kalff 1986; Liess & Hillebrand 2004), in predator–prey interactions between invertebrates only (e.g. Peckarsky *et al.* 1990; Lancaster 1996), and in consumption rates of invertebrates by fish (e.g. Gilinsky 1984; Gilliam *et al.* 1989; Diehl 1995), crayfish (e.g. Macisaac 1994; Nystrom *et al.* 1999; Lewis 2001), and waterfowl (Werner *et al.* 2005). Direct predation effects can lead to removal of specific prey, and indirect predation effects can lead to increased periphyton growth when invertebrate grazers are removed (McIntosh & Townsend 1996). Alterations in prey behaviour, morphology, and even life history traits of various invertebrates as a response to chemical cues released by potential predators have also been documented (Crowl & Covich 1990; Culp *et al.* 1991; Arnqvist & Johannsson 1998; Baumgärtner *et al.* 2002; Peckarsky *et al.* 2002). Such non-lethal effects can comprise suppressed growth rates, reduced reproduction success, and habitat shifts, as documented for gastropods (McCollum *et al.* 1998; Lewis 2001; Turner & Montgomery 2003; Turner 2004).

Various taxa show a seasonality in their feeding activities, and this further complicates such biotic interactions. For example, leech (Wrona *et al.* 1978), crayfish (Lewis 2001), and perch (Eckmann 2004) consume less in winter and the early spring months than during the growing season. In contrast, diving waterbirds feed on zebra mussels more heavily in the winter months owing to the vast increase in the number of waterbirds at a wintering site (Werner *et al.* 2005). A variety of taxa at all trophic levels also exhibit day/night changes in spatial distribution, habitat preference, and feeding activity (Eckmann & Imbrock 1996; McIntosh & Townsend 1996; Marklund *et al.* 2001; Elliot 2005). Other factors likely to contribute to the outcome of biotic interactions include alterations in food quantity and quality (Ahlgren *et al.* 1997; Fink 2005; Liess & Hillebrand 2005). Prey accessibility *vs.* potential availability

(Boisclair & Leggett 1985) could be another factor influencing the success of the predators and is likely to be altered by habitat complexity, e.g. vegetation stands (Crowder & Cooper 1982; Gilinsky 1984; Diehl 1993). These patterns account for the lower perceptibility of prey organisms (Gilinsky 1984), the restricted manoeuvrability of predators (Winfield 1986), or the altered behavioural patterns of specific prey taxa (McCollum *et al.* 1998).

The introduction or arrival of new species often leads to a vast alteration of the macroinvertebrate community and leads to changes in benthos abundances, biomass, and species composition. Invasive taxa can cause considerably ecological and economic damage (Adams 1994; Mack *et al.* 2000; Ricciardi & MacIsaac 2000). Such occurrences are predicted to be the major factor of changes in freshwater biodiversity in the future (Sala *et al.* 2000). These new taxa are often characterised by a spectacular increase in their populations, followed by elimination of native or previously invasive taxa within short time spans (Dick & Platvoet 2000). Newcomers can also have positive effects on established communities. For example, zebra mussels enhanced the abundances and biomass of various invertebrates by providing new hard-substrate habitats with their shells and by providing additional food resources by increasing organic matter or enhancing habitat stability (Wisenden & Bailey 1995; Stewart *et al.* 1998b; Mörtl & Rothhaupt 2003).

The effects of invasive taxa in littoral lake habitats in the northern hemisphere have been intensively studied, including the zebra mussel *Dreissena polymorpha* (Macisaac 1996), the ruffe *Gymnocephalus cernuus* (Pratt *et al.* 1992; Winfield *et al.* 1998), the crayfish *Orconectus* spp. (Nystrom *et al.* 1999), and the amphipod *Dikerogammarus villosus* (Dick & Platvoet 2000; Dick *et al.* 2002; reviewed in Lodge 1993; Ricciardi & Rasmussen 1998; Ricciardi & MacIsaac 2000). *D. polymorpha* (Werner *et al.* 2005 and citations therein) and *G. cernuus* (Roesch & Schmid 1996) became well established in Lake Constance, the site of the present studies, in the mid-1960s and mid-1980s, respectively. The most recent arrivals in Lake Constance are *D. villosus* (Mürle *et al.* 2004) and the mussel *Corbicula fluminea* (Werner & Mörtl 2004). Both have attained considerable abundances and *D. villosus* presumably caused alteration of previous abundant native amphipod *Gammarus roeseli* (Mörtl *et al.* 2005). The studies presented here represent the trophic state prior to the introduction and massive expansion of *C. fluminea,* although *D. villosus* was present during parts of the studies (Chapters 2, 3, 6; 2002–2003), namely during the enclosure experiments (Chapters 4, 5; 2004). The outcome of a specific invasion is difficult to predict (Lodge 1993), and the consequences for benthic communities or higher trophic levels, e.g. prey consumption by fish, will be investigated in future studies.

Study aims

The present thesis investigates benthic communities in lake littoral zones and the effect of abiotic and biotic constraints. I expected wave exposure to be the most influential abiotic source of alterations in upper littoral zones, thus influencing benthic communities directly or indirectly. The indirect cause of variability includes other abiotic habitat variables such as substrate composition. Biotic factors include interactions with other trophic levels. I expected these interactions to be influenced in their severeness by the background abiotic environment.

Wave turbulence induced by wind- or ferry-generated waves can produce small-scale habitat alterations (e.g. overturned stones, abrasion of stone surfaces). Large-scale habitat alterations can be caused by pronounced water-level fluctuations, which provide large, freshly submerged new habitats at high water levels and lead to a vast loss of settlement area at low water levels. Benthic invertebrates need to be able to resist or avoid such strong impacts either by finding refuges to maintain during unfavourable conditions or by finding new habitats for the short term. Chapter 2 therefore focuses on the recolonisation abilities of macrobenthic fauna within a 73-day period at three different sites in Lake Constance. I expected that the different levels of wave exposure of the sites would influence the colonisation process, either in speed or occurrence of taxa, and that both might depend on the disturbance history of the sites.

Chapter 3 focuses on a single species, the common herbivorous grazer *Radix ovata*. This snail is widespread in the littoral zone of Lake Constance on a horizontal scale. On a vertical scale, it is found over a wide depth range, from the splash zone to the acclivity ridge. I posed the question whether its distribution patterns differed along a gradient of wave exposure on both scales. If wave exposure affects *R. ovata* distribution, I assumed that the behavioural or life history patterns of this taxon would also be affected. I therefore studied the activity and growth of *R. ovata* within outdoor mesocosms exposed and not exposed to waves experimentally generated with a pneumatic wave machine, developed earlier in cooperation with P. Klahold (Fish Ecology).

The predation pressure of benthivorous fish might mask or obscure other abiotic or biotic interactions within benthic communities. Therefore, I examined in two enclosure/exclosure studies the effects of predation by the most abundant fish taxa on benthos in Lake Constance: Chapter 4, perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*); and Chapter 5, bream [*Abramis brama* (L.)], white bream (*Blicca bjoerkna*), and dace [*Leuciscus leuciscus* (L.)]. Both studies were carried out in cooperation with members of the Fish Ecology group: Chapter 4, D. Schleuter; and Chapter 5, P. Klahold and S. Stoll. Biotic interactions were often studied without the consideration of abiotic interferences. Wave exposure in particular is likely to modify the outcome of predation pressure on benthic prey. I therefore examined the effects of fish predation under different hydrodynamic regimes and field conditions. Chapter 4 focuses on short-term predation effects of perch and ruffe and restricted benthos migration. The predation of cyprinids on benthic prey was studied *in situ* during a longer period in which benthic recolonisation was allowed (Chapter 5).

To obtain better insights into benthic communities in littoral lake habitats and their patterns and processes, I investigated different littoral communities during a complete seasonal cycle (2002–2003) in Lake Constance. Chapter 6 describes the monthly results of the field study carried out at three characteristic lake sites at 0.4-m depth. This is the first quantitative study to assess spatial and temporal variations of benthic communities on such a fine time scale. I expected the environmental factors wave exposure and water-level fluctuation to be the most influential and to alter habitat conditions directly and indirectly as well as species distribution itself. I therefore compared benthic community dynamics at those sites and investigated the effect of changes in wave exposure and water-level fluctuation on the community patterns and differentiated between short-, medium-, and long-term influences.

Study sites

All comparative and experimental studies were carried out at sites in Upper Lake Constance (Fig. 1). Six study sites were chosen, and each study, presented in the various chapters, was carried out at only some of these sites (see Table 1). The site Litoralgarten at the south-western shore was examined in all studies, and the site Meersburg on the opposite shore was examined in four out of five studies (not in the study presented in Chapter 5). These two sites have in particular contrasting wind- and ferry-generated wave exposure owing to their exposure to prevailing winds and ferry lines and to different slopes of the banks.

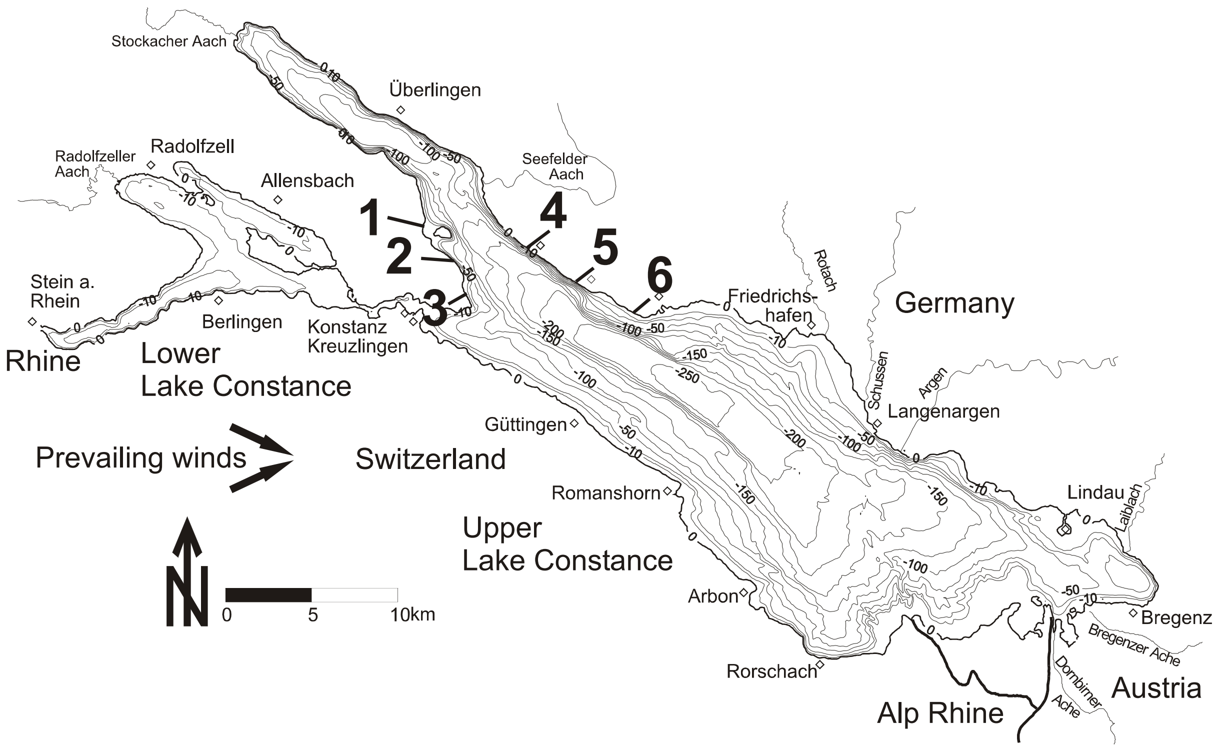

Figure 1: Map of Lake Constance, modified after Wessels (1998). The sites 1-6 of the field experiments and field samplings are indicated. See Table 1 for detailed information on the specific sites used in each study.

Table 1: Overview of the experimental and sampling sites studied, the chapters in which the studies are presented, and the abbreviations used. LS: lake shore; for the exact GPS coordinates, see the respective chapters. For comparison the expected overall exposure of sites was roughly estimated by grouping the exposure and slope variables into three sub-classifications (exposure: sheltered, intermediate, exposed; slope: shallow, intermediate, steep). For exact measurements and comparisons, see the respective chapters.

No. in Fig. 1	Position		Chapter					Exposure		Slope
	Site	LS	2	3	4	5	6	Wind	Ferry	
1	Güll	SW				$S2_{shallow}$		sheltered	sheltered	shallow
2	Litoralgarten	SW	Lit S2	Lit S1	Lit S1	$S1_{shallow}$ $S1_{deep}$	Lit	intermediate	intermediate	intermediate
3	Staad	SW	Sta S3	Sta S4				sheltered	intermediate	shallow
4	Meersburg	NE	Mee S1	Mee S5	Mee S2		Mee	exposed	exposed	steep
5	Hagnau	NE		Hag S3				exposed	intermediate	intermediate
6	Immenstaad	NE		Imm S2			Imm	exposed	intermediate	shallow

Chapter 2

Colonisation patterns of macroinvertebrates at three differently exposed lake sites

Summary

Colonisation of littoral macroinvertebrates on hard substrates was studied at exposed, intermediate, and sheltered sites at Upper Lake Constance, Germany. Unconditioned concrete stones were sampled after 3, 7, 11, 31, and 73 days and compared with natural substrates sampled after 3, 31, and 73 days as a control for seasonally induced community shifts. Colonisation was fast at all sites, but differed between sites (Dunnett test). Differences in abundance at the exposed, sheltered, and intermediate sites were restricted to the first 3, 7, and 11 days, respectively. When comparing sites and sampling dates with a MANOVA, only the sampling date, but not site or interaction, had a significant effect on abundance. In controls, a seasonal shift occurred only within the first month. Colonisation on concrete stones at the sheltered site differed from the other sites; control stones at all sites were comparable. In contrast to multivariate methods, non-metric multidimensional scaling revealed a slower total community colonisation at all sites. Colonisation attained natural levels after 73 days at the exposed and sheltered sites, but not at the intermediate site. Mayflies and chironomids were the fastest colonisers, followed by high abundances of caddisflies and molluscs, and less-abundant annelids and ostracods. Snails, amphipods, or hirundinea occurred continuously, but in low numbers. Taxa richness was highest after 31 days of colonisation.

Keywords: benthos community structure, lake littoral zone, wave exposure, recolonisation

Introduction

Disturbance processes are widely recognised as major forces in structuring communities (Sousa 1984; Pickett & White 1985). In aquatic systems, severe physical disturbance regularly occurs as floods or spates, and milder disturbances occur because of variation of discharges in river systems. The reduction in the abundance of species is dependent on the intensity of the impact (Townsend 1989; Lake 2000). Recolonisation has been predominantly studied in surveys or experimental settings in lotic systems (Moser & Minshall 1996; Robson 1996; Williams & Smith 1996; Melo & Froehlich 2004) or in marine habitats (Clarke *et al.* 1993; Austen *et al.* 1998; Underwood 1999; Burton *et al.* 2002). Recovery to the original abundance and number of taxa is generally fast (Matthaei *et al.* 1996, 1997), and depends on factors such as distance from unaffected refuges (Lancaster & Hildrew 1993; Gore 1996), mobility of colonisers (Brooks & Boulton 1991; Matthaei *et al.* 1997), colonisation abilities (Downes & Lake 1991), season (Moser & Minshall 1996; Matonickin *et al.* 2001), and biotic interaction (Lancaster 1990, 1996) and for a review, see Mackay (1992). However, disturbance history can have long-term effects on the distribution of lotic invertebrates and therefore can be an important cause of invertebrate patchiness in streams (Matthaei & Townsend 2000b).

Recolonisation patterns in lake littoral zones, on the other hand, have been studied less (Moon 1940; Wisenden & Bailey 1995; Quinn *et al.* 1996, 1998a, b; Mörtl & Rothhaupt 2003). It is widely accepted that in lake littoral zones, wind-generated wave action is a main factor in determining the substrate structure and macrophyte and benthic composition (e.g. Barton & Hynes 1978a, b; Dall *et al.* 1984; Brodersen 1995; Cyr 1998a; James *et al.* 1998; Tolonen *et al.* 2001; Weatherhead & James 2001; Morris *et al.* 2002). The settlement area, especially hard substrates, is very limited and is usually restricted to the upper eulittoral zone, and hence is highly susceptible to wave disturbance. Wave activity directly impacts with turbulence and currents that result in individual dislodgement from hard substrates (Underwood 1999), and in addition probably creates new habitat patches, as in lotic systems. Dislocation of single stones can temporarily and spatially create new habitats on a smaller scale (N. Scheifhacken, unpublished data). The complex mosaic of different successional stages of benthic communities depends on the disturbance frequency and intensity. Severe wind events can produce larger disturbed patches to be left to recolonisation succession with an even more complex bed scour or fill pattern (Scheifhacken & Rothhaupt 2003; N. Scheifhacken, unpublished data). Rapidly fluctuating water levels are another possible disturbance factor, which can provide new habitats for benthic colonisers. Settlement areas and biomass of well-established communities can be reduced if the water level increases or rapidly decreases (Palomäki 1994).

Without unidirectional flow as in lotic systems, colonisation by single taxa of newly created littoral habitat patches might be more difficult to detect. Moon (1940) observed rapid colonisation, whereas Wisenden & Bailey (1995) reported a slower succession with a distinct species order. Artificial substrates were denser colonised by macroinvertebrates at higher structural complexity here living zebra mussel *Dreissena polymorpha* compared to empty shells both glued to ceramic tiles or bare tiles (Mörtl & Rothhaupt 2003). Wisenden & Bailey (1995) came to similar results in their field study, but they found also evidence, that zebra mussel stones at the turbulent site facilitate amphipod colonisation by increasing habitat stability, whereas other taxa i.e. snails, various insect larvae were outcompeted for space. Both studies however, were conducted at the littoral zone just below the high-energy wave zone at 2 m depth. Quinn *et al.* (1998b) found different colonisation strategies between a lake outflow (stream) and two littoral sites, but not between the two littoral sites, where rapid colonisation of common taxa occurred within one day. Stream insects were slower and showed a higher variety in colonisation strategies. However, taxa that occurred in both systems showed similar patterns, but were more abundant in the lake, whereas seasonal differences were greater in the stream.

In this study, I investigated whether colonisation patterns differed between three different, but closely related lake sites. I studied colonisation within a 73-day period and analysed community patterns of concrete stones (treatment) with natural hard substrates (control). If inherent colonisation strategies apply for each taxon, similar colonisation patterns would be expected in general for all three closely related sites. Dissimilarities would indicate a regulating outside factor. I expected that wave exposure would be the main abiotic factor influencing colonisation. Hence, I predicted different patterns and recovery speed depending on the natural disturbance history at the sites. I also expected fast colonisers, e.g. mayflies (*Ecdyonurus* spp.), to occur foremost, thus to be wider spread and more regularly distributed in high disturbance environments, followed by later succession taxa (Trichoptera, e.g. *Tinodes* spp.) with more complex habitat demands and lower mobility rates.

Methods

Study sites

The study was carried out in Lake Constance in central Europe (9°18’ E, 47°39’ N). Upper Lake Constance is a deep (maximum depth 254 m, mean depth 101 m), large (472 km^2 surface, 47.6 km^3 volume), oligotrophic, pre-alpine freshwater lake (Hase *et al.* 1998; Stabel 1998; Wessels 1998). The littoral zone comprises less than 10% of the total lake area. The River Rhine is the main tributary (62% mean runoff) of its total catchment area (Wessels 1998). It drains parts of the European Alps, resulting in an annual water level fluctuation of up to 2 m (Luft & Vieser 1990), with low levels in winter and high inflow rates after snowmelt in summer. Westerly winds prevail throughout the year, with a second less-dominant peak of easterly winds, especially in winter (Bäuerle *et al.* 1998).

The experiment was conducted at three sites. Site S1 (9°16’11.66’’ E; 47°41’37.249’’ N) on the northeastern shore is highly exposed to westerly wind. Sites S2 (9°12’18.778’’ O; 47°41’29.946’’ N) and S3 (9°12’53.463’’ E, 47°40’25.686’’ N) on the southwestern shore are more sheltered, but differ in slope and wave exposure derived from wind or ferries and leisure boats. The substrate composition of the sites is similar and contains cobblestones of 5–14 cm (mean ± SE: 6.9 cm ± 2.7, n = 161); site S3 has a higher percentage of finer sediments. Simpson substrate diversity showed no significant differences between sites ($p = 0.085$, $F_{2.517}$, $df_{2;158}$).

Experimental procedure

Samples were taken from 2 August to 15 October, 2002 at a water depth of 0.4–0.5 m. At each site, 30 unconditioned concrete stones (A_o = 300 cm^2) were randomly placed among the natural cobblestones. After 3, 7, 11, 31, and 73 days of exposure, 5 concrete stones per site were recollected randomly and taken to the laboratory. All stones were sampled using a gauze hand net (200-µm mesh size). The net was slowly lowered through the water column to minimise turbulence and positioned behind and facing the stone; the stone was then rapidly lifted into the net. Adjacent stones were not disturbed to avoid drifting of attached benthos. The sampled stones were transferred from the hand net into small plastic buckets for transport and were kept submerged in filtered (<30 µm) lake water until being processed in the laboratory. Five natural stones (controls) at each site were randomly sampled at the same water depth.

Transport to the laboratory took no longer than 2 h. Unhandled samples were stored in a 4°C climate chamber for no longer than 2 h. Invertebrates were carefully removed from the stones by hand or by scrubbing under flowing tap water, accumulated within a 200 µm sieve and preserved in 70% ethanol. Species were counted and identified to the lowest possible taxonomic level using a stereomicroscope (10×magnification). Dimensions of individual control stones (length, width, height) were determined using a slide gauge (0.01 mm). Stone surface area was calculated using equation $A_o = (LW+LH+WH)*\pi/3$ of (DALL 1979), where L is the length, W is the width, and H is the height. Species abundances from control stones were adjusted to the surface area of the concrete stones (300 cm^2) to allow data comparison.

Data analysis

Colonisation was examined using total abundance, dominant taxa abundances, species richness, and taxa density per stone as parameters. Abundance and taxa data were log(x+1) transformed to gain homogeneity of variances. First, all relevant parameters within each site were separately tested, and data from concrete stones from each sampling date were compared with pooled data from control stones using a one-way analysis of variance (ANOVA). If differences were detected, control samples were compared with treatment samples using the Dunnett post-hoc test (Day & Quinn 1989). Data from all three control samplings per site were pooled, thereby ignoring seasonal changes in this analysis. Further, a two-factorial multivariate analysis of variance (MANOVA) was calculated to compare sites independently for control (data not pooled) and treatment substrates, with sites and days of colonisation as factors (SPSS Software version 11.0). Differences among sites and days of colonisation were calculated for dominant and characteristic taxa, e.g. Trichoptera (mainly *Tinodes waeneri)*, Ephemeroptera (*Caenis* spp. and *Ecdyonurus dispar*), Mollusca (mainly *Dreissena polymorpha*), and chironomids (all subfamilies).

Non-metric multidimensional scaling (nMDS) and the PRIMER 6b software package (Clarke & Gorley 2001; Clarke & Warwick 2001) was used to evaluate the recovery of species composition and the relative abundance between sites and days of colonisation. In order to recognise the contribution of less-abundant species to community composition, square-root transformed data were used. McCabe & Gotelli (2000) showed that decreasing species richness in small-scale disturbances is strongly influenced by reduced treatment abundance. Therefore, the same data set was standardised to unique total abundance to analyse the relative composition pattern and to avoid effects based on early low abundance, allowing calculations that rely only on species composition and relative abundance (Quinn *et al.* 1998b; McCabe & Gotelli 2000).

The Bray-Curtis index was used to calculate the similarity matrix in order to measure distances between samples (treatment only, control only, treatment and control). Taxa assemblages were compared between days of colonisation, sites, and substrate per site and date. All nMDS plots were based on 100 iterations. A stress value below 0.2 can be regarded as a reliable mapping of the community in a two-dimensional plot. However, differences were tested on a background similarity matrix using ANOSIM statistics (Clarke 1993). Species turnover was calculated with ANOSIM applied to standardised data (total sample unit). The BVStep analysis (Clarke & Warwick 1998) in the PRIMER 6b software package was applied to the similarity matrix to search for a subset of species that explain most ($\rho > 0.95$) of the pattern of the full data set. The PRIMER 6b software package was used for calculating diversity metrics (d, MARGALEF species richness), diversity (H'loge, SHANNON) and evenness (J', PIELOU).

Wave exposure

Gypsum dissolution rate was used as a time-integrating method for measuring near-bottom water motion to compare and quantify exposure to waves and currents at all three sites during the experiment. This method proved to be an accurate measurement of average water motion if prepared under standardised conditions (N. Scheifhacken, unpublished data). It has been used successfully in various marine and freshwater environments (Petticrew & Kalff 1991; Jokiel & Morrissey 1993; Thompson & Glenn 1994; Angradi & Hood 1998; Johnston 2000), but Porter *et al.* (2000) have raised critical comments. The spheres (∅ 7.6 cm, ratio 1.5 kg gypsum to 900 ml water, Knauf® EN ISO 9001) were casted in one piece within plastic molds, enclosing a central plastic reel for exposure in the field. Mold halves where spread sparsely with Vaseline® to allow easy removal of spheres after casting. The molds were then tightly closed with screws on each edge. Gypsum was thoroughly stirred in a plastic container and then poured into the molds through a vent; the molds were vigorously tapped and rocked to remove all air bubbles. The gypsum solidified within 1 h at room temperature. The molds were then opened, and the spheres were transferred to a climate chamber (55 °C) for further hardening until a constant weight was achieved (48 h). All spheres were individually marked and weighed to the nearest 0.01 g on a Sartorius scale. In the field, the spheres were attached to rods at 0.4-m water depth (n = 5 per site), left for one week, retrieved, and reweighed after drying in a climatic chamber (55 °C). The weight loss (g/h) was calculated per site and week of exposure. A two-factorial analysis of variance with site and sampling date as factors was used to test for overall differences in exposure (including Tukey post-hoc test). The specific weeks were analysed with separate ANOVAs to differentiate interaction between site and week of exposure.

Results

Wave exposure

The gypsum dissolution rate differed significantly between sites ($F_{158.6}$, $df_{2,50}$ $p < 0.001$), week of exposure ($F_{101.1}$, $df_{4,50}$ $p < 0.001$), and interaction of both factors ($F_{10.47}$, $df_{8,50}$ $p < 0.001$) (Table 1). The results of Tukey post-hoc test revealed the lowest exposure to waves at site S3, an intermediate exposure at site S2, and highest exposure at site S1. The rank order of dissolution rate per week affirmed differences in wave exposure throughout the experiment with higher wave action at the beginning (week: 5 = 4 < 4 = 2 < 3 < 1). Separate ANOVAs for each week of exposure were calculated to differentiate the interaction term (Table 1). Site S1 remained the most-exposed site in four of the five weeks; in week 4, there were no significant differences between the sites. In weeks 2 and 5, sites S2 and S3 had the same wave exposure, but site S3 had the lowest exposure in weeks 1 and 3.

Table 1: Dissolution rate (g/h) of gypsum spheres (mean ± SE) after one week of exposure at sites S1, S2, and S3. ANOVA results for each week are given separately. Rank order was calculated with the Tukey post-hoc test.

	Site S1		**Site S2**		**Site S3**					**Weekly exposure**
Week	mean	SE	mean	SE	mean	SE	df	F	p-value	(rank order)
1	1.741	0.036	1.114	0.008	0.921	0.023	2,11	318.9	<0.001	S3<S2<S1
2	1.222	0.013	0.501	0.018	0.316	0.083	2,6	93.3	<0.001	S3=S2<S1
3	1.208	0.019	0.733	0.013	0.616	0.022	2,9	287.5	<0.001	S3<S2<S1
4	0.768	0.079	0.549	0.062	0.521	0.115	2,12	2.4	0.138	S3=S2=S1
5	0.685	0.011	0.476	0.008	0.492	0.013	2,12	110.4	<0.001	S2=S3<S1

Benthos colonisation

Colonisation of the bare concrete stones was fast at all three sites, and the overall abundance of the colonisation processes were very similar (Fig. 1, Table 2). Colonisation reached the control level almost within 11 days, and always within 1 month, with a peak after 1 month and a slight decline thereafter. Abundance continually increased from day 3 to day 31, and the level at day 3 was already high.

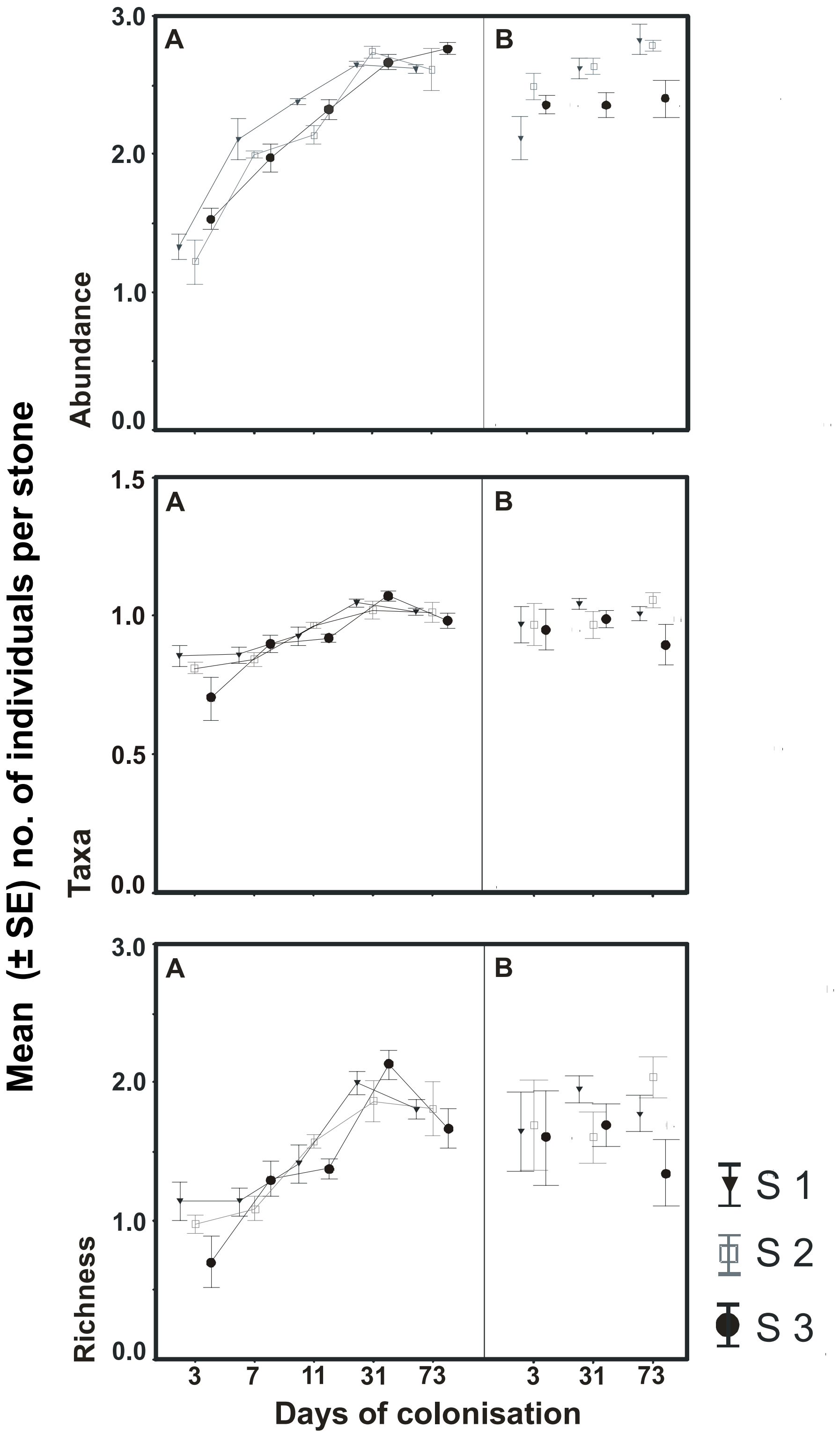

Figure 1: Total invertebrate abundance (N), taxa density (S), and Margalef species richness (d_s) (mean ± SE) during the colonisation process. All parameters are log(x+1)transformed, and richness is standardised to unit abundance. **A**: Treatment samples left **B**: Control samples right. Symbols per sampling date are slightly shifted to avoid overlapping. The wave exposure of the sites decreased in the order S1 (exposed)>S2 (intermediate)>S3 (sheltered).

Table 2: Mean metric ± SE per stone (A_o = 300 cm^2), abundance, number of taxa, Margalef species richness (d_o based on original N, d_s standardised to unit N), Shannon diversity (H'), and Pielous evenness (J') per site and days of colonisation for treatment and control stones.

		Abundance (N)		**No. of taxa (s)**		**Margalef richness (d_o)**		**Margalef standard (d_s)**		**Shannon diversity (H')**		**Pielous evenness (J')**	
site	day	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
						Treatment stones							
	3	22	5	6.3	0.6	1.82	0.37	1.14	0.14	1.60	0.15	0.87	0.04
	7	147	34	6.3	0.5	1.10	0.11	1.14	0.10	0.85	0.23	0.46	0.12
	11	241	12	7.5	0.6	1.19	0.12	1.41	0.14	1.00	0.10	0.51	0.07
	31	449	19	10.2	0.4	1.51	0.07	2.00	0.08	1.16	0.05	0.50	0.02
S1	73	417	26	9.3	0.3	1.38	0.05	1.81	0.07	1.07	0.11	0.48	0.04
	3	19	6	5.5	0.3	1.75	0.26	0.98	0.06	1.44	0.09	0.85	0.06
	7	99	5	6.0	0.4	1.09	0.09	1.09	0.09	0.65	0.13	0.36	0.06
	11	142	20	8.3	0.3	1.48	0.07	1.57	0.05	0.69	0.17	0.33	0.08
	31	560	55	9.6	0.7	1.36	0.10	1.87	0.15	1.08	0.11	0.48	0.04
S2	73	457	141	9.3	0.9	1.38	0.07	1.81	0.19	1.15	0.14	0.51	0.05
	3	35	7	4.3	0.9	0.94	0.27	0.71	0.19	1.00	0.26	0.69	0.08
	7	102	28	7.0	0.6	1.32	0.10	1.30	0.13	1.36	0.15	0.70	0.06
	11	215	33	7.3	0.3	1.19	0.05	1.38	0.07	1.15	0.00	0.58	0.01
	31	476	60	10.8	0.5	1.60	0.10	2.13	0.11	1.61	0.05	0.68	0.03
S3	73	584	52	8.7	0.7	1.20	0.10	1.66	0.14	1.23	0.04	0.57	0.01
						Control stones							
	3	160	39	8.6	1.3	1.52	0.19	1.65	0.29	1.21	0.12	0.57	0.02
	31	442	63	10.0	0.4	1.50	0.10	1.95	0.10	1.42	0.04	0.62	0.02
S1	73	750	131	9.2	0.6	1.26	0.08	1.78	0.13	1.08	0.11	0.48	0.04
	3	336	64	8.8	1.5	1.34	0.23	1.69	0.32	1.26	0.08	0.61	0.04
	31	449	63	8.4	0.9	1.21	0.13	1.61	0.19	1.06	0.10	0.51	0.06
S2	73	618	52	10.4	0.7	1.47	0.11	2.04	0.15	1.40	0.07	0.60	0.03
	3	237	34	8.4	1.6	1.34	0.26	1.61	0.34	1.47	0.16	0.71	0.05
	31	244	42	8.8	0.7	1.44	0.13	1.69	0.16	1.55	0.08	0.72	0.05
S3	73	304	87	7.2	1.1	1.10	0.18	1.35	0.24	1.3	0.1	0.71	0.06

Differences between sites were detected with the Dunnett post-hoc test for abundance, number of taxa, and diversity metrics (Table 3). At site S1, the total abundance on the concrete stones was significantly lower only on day 3 ($p < 0.001$). At sites S2 and S3, equal abundances of concrete and control stones were achieved first after 1 month and 11 days, respectively. Surprisingly, the abundance on concrete stones at site S3 remained significantly higher than on the control stones. Equal numbers of taxa were found after 7 days at site S3 and after 11 days at sites S1 and S2. No significant differences were detected for the original richness data, but were found after standardisation (Table 3). Then richness was significantly lower after 3 days at site S3, and after 7 days at the other two sites. Evenness was significantly different at site S1 on day 3 and at site S2 until day 11, but not at site S3. The Shannon diversity of the treatment stones was only significantly different from the control stones at the beginning of colonisation process, at site S2 on days 7 and 11, and at site S3 only on day 3 (Table 3).

Table 3: Effects of colonisation time on abundance and number of taxa [both log(x+1) transformed] and diversity metrics (all untransformed), as shown by Margalef species richness (d_o) based on original N, Margalef richness (d_s) standardised to unit N, Pielous evenness (J'), and Shannon diversity (H'). One-way analysis of variance per site was used to compare days of colonisation (treatment; day 3, 7, 11, 31, and 73) with natural stone samples (control, pooled) using the Dunnett post-hoc test. Significant values are in bold, n.s.: not significant. Wave exposure at the sites decreased in the order S1>S2>S3.

Site	**Metric**	**Analysis of variance**		**p-values with Dunnett post-hoc test (treatment *vs.* control)**				
		F	**p**	**3**	**7**	**11**	**31**	**73**
S1	Abundance N	12.561	**<0.001**	**<0.001**	n.s.	n.s.	n.s.	n.s.
S2	Abundance N	43.533	**<0.001**	**<0.001**	**<0.001**	**<0.001**	n.s.	n.s.
S3	Abundance N	25.410	**<0.001**	**<0.001**	**0.003**	n.s.	**0.020**	**0.010**
S1	No. of taxa s	5.890	**0.001**	**0.007**	**0.008**	n.s.	n.s.	n.s.
S2	No. of taxa s	4.520	**0.004**	**0.006**	**0.029**	n.s.	n.s.	n.s.
S3	No. of taxa s	4.917	**0.002**	**0.004**	n.s.	n.s.	n.s.	n.s.
S1	Richness d_o	2.313	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S2	Richness d_o	1.816	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S3	Richness d_o	1.507	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S1	Richness d_s	6.055	**0.001**	**0.007**	**0.007**	n.s.	n.s.	n.s.
S2	Richness d_s	4.506	**0.004**	**0.006**	**0.021**	n.s.	n.s.	n.s.
S3	Richness d_s	5.078	**0.002**	**0.009**	n.s.	n.s.	n.s.	n.s.
S1	Evenness J'	7.989	**<0.001**	**<0.001**	n.s.	n.s.	n.s.	n.s.
S2	Evenness J'	11.958	**<0.001**	**0.001**	**0.008**	**0.002**	n.s.	n.s.
S3	Evenness J'	1.581	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S1	Diversity H'	3.884	**0.008**	*0.092*	*0.066*	n.s.	n.s.	n.s.
S2	Diversity H'	7.425	**<0.001**	n.s.	**0.001**	**0.002**	n.s.	n.s.
S3	Diversity H'	2.710	**0.040**	**0.048**	n.s.	n.s.	n.s.	n.s.

A two-factorial MANOVA of concrete stones with site and sampling dates as factors revealed that only the day of colonisation is highly significant ($p < 0.001$), but not site ($p = 0.131$) or interaction of both factors ($p = 0.182$; Table 4). Differences between 3, 7, and 11 days of colonisation and all others are highly significant ($p < 0.001$ or 0.006), but not between the last two sampling dates ($p = 0.998$). The Tukey post-hoc test confirmed homogenous groups with the increasing values

3 > 7 > 11 > 73 = 31; however, the inverted position of the last two sampling days should be noted (Table 4).

Table 4: Differences in total abundance, taxa density, and dominant taxa abundance on treatment and control stones. Results of MANOVA with Bonferroni adjustment of p-values are given. Rank order between the sites (S1, S2, S3) and days of colonisation was determined with the Tukey post-hoc test. Significant results are in bold.

		Treatment			Control		
		$df_{eff,err}$	F	p value	$df_{eff,err}$	F	p value
Abundance	Site	2,44	2.134	0.131	2,36	5.356	**0.009**
	Days	4,44	131.064	**<0.001**	2,36	9.605	**<0.001**
	Interaction	8,44	1.510	0.182	4,36	3.162	**0.025**
	Rank order			S1=S2=S3			S3=S1<S1=S2
				T1<T2<T3<T4=T5			T1<T4=T5
Taxa	Site	2,44	0.726	0.489	2,36	1.143	0.330
	Days	4,44	31.453	**<0.001**	2,36	0.369	0.694
	Interaction	8,44	1.927	0.080	4,36	0.903	0.472
	Rank order			S1=S2=S3			S1=S2=S3
				T1<T2=T3<T4=T5			T1=T4=T5
Chironomidae	Site	2,44	0.842	0.438	2,36	10.298	**<0.001**
	Days	4,44	91.479	**<0.001**	2,36	0.777	0.467
	Interaction	8,44	2.367	**0.033**	4,36	3.435	**0.018**
	Rank order			S1=S2=S3			S3<S1=S2
				T1<T2<T3=T5<T4=T5			T1=T2=T3
Trichoptera	Site	2,44	3.695	**0.033**	2,36	4.097	**0.025**
	Days	4,44	96.067	**<0.001**	2,36	13.434	**<0.001**
	Interaction	8,44	1.903	0.084	4,36	3.646	**0.014**
	Rank order			S1=S2<S2=S3			S1=S2<S2=S3
				T1=T2=T3<T4<T5			T1=T4<T5
Ephemeroptera	Site	2,44	11.732	**<0.001**	2,36	5.318	**0.009**
	Days	4,44	6.590	**<0.001**	2,36	4.727	**0.015**
	Interaction	8,44	1.776	0.108	4,36	5.318	**0.009**
	Rank order			S2<S1=S3			S2=S3<S1
				T5=T1<T1=T4<T4=T2=T3			T4=T5>T4=T1
Mollusca	Site	2,44	2.445	0.098	2,36	2,932	**0.066**
	Days	4,44	58.803	**<0.001**	2,36	1,606	0.215
	Interaction	8,44	3.195	**0.006**	4,36	2,904	**0.035**
	Rank order			S1=S2=S3			S1=S2=S3
				T1=T2<T3<T4<T5			T1=T2=T3
Gastropoda	Site	2,44	10.450	**<0.001**	2,36	12.963	**<0.001**
	Days	4,44	2.346	0.110	2,36	2.286	0.199
	Interaction	8,44	0.938	0.453	4,36	0.821	0.588
	Rank order			S3=S1<S2			S3=S1<S2
				T1=T2=T3=T4=T5			T1=T4=T5
Gammaridae	Site	2,44	7.033	**0.003**	2,36	36.160	**<0.001**
	Days	4,44	2.346	0.110	2,36	2.286	0.075
	Interaction	8,44	1.315	0.283	4,36	3.309	**0.005**
	Rank order			S2=S1<S3			S1=S2<S2=S3
				T1=T2=T3=T4=T5			T1=T4=T5
Oligochaeta	Site	2,44	0.654	0.526	2,36	0.654	0.526
	Days	4,44	12.338	**<0.001**	2,36	12.338	**<0.001**
	Interaction	8,44	1.619	0.191	4,36	0.938	0.453
	Rank order			S2=S1<S1=S3			S1=S2=S3
				T3=T2=T1<T4=T5			T1<T4=T5

A seasonal shift in control samples was detected, which showed significant differences in log(x+1) abundance in all categories: site (p = 0009), date (p = <0.001), and the interaction site×date (p = 0.025). However, significance is based on differences between sites S2 and S3 (Tukey post-hoc test, p = 0.007) and differences between the first sampling dates and the two later dates at sites S1 and S2. Taxa density [log(x+1)-transformed] was only significant for days of colonisation (p = <0.001) on concrete stones, relying on differences between the first three sampling days (3, 7, 11) and all others, but not between days 31 and 73 (Table 4).

Dominant Taxa

A clear succession of the main taxa (Table 5) was found. Chironomids (all subfamilies) and mayflies (*Ecdyonurus dispar*, *Caenis* spp.) were the fastest colonisers at all sites, followed by high abundances of caddisflies (mainly *Tinodes waeneri*) and molluscs (mainly *Dreissena polymorpha,* early-settlement larvae) and lower abundances of annelids and ostracods. Snails (*Radix ovata, Bithynia tentaculata*), amphipods (*Gammarus roeseli*), and leeches (*Glossosoma complanata*, *Erpobdella octoculata*, *Helobdella stagnalis*) were found continuously throughout the sampling period, but only in low numbers.

Mayfly abundance differed between treatment and control stones on days 3 and 11 but not on day 7 at site S1, and differed on day 7 at site S3; no differences were found at site S2 (Table 5). Chironomid abundance differed between treatment and control stones on days 3 and 7 at site S2 and on day 3 at site S1, but not at site S3 (Dunnett test). Caddisfly abundance differed between treatment and control stones on days 3, 7, and 11 at all sites, but only increased to a significantly higher level at day 73 at site S3. Annelid abundance also differed between treatment and control stones on days 3, 7, and 11, but not thereafter. Mollusc abundance reached control levels the fastest, at sites S1 and S3 by day 7, and at site S2 by day 11.

Multivariate analysis confirmed differences between treatment and control stones for some taxa (Ephemeroptera, Chironomids) in the site and days of colonisation (Table 4). Mayfly abundance was significantly lower on treatment stones at site S2 than at the other sites, whereas highest abundance on control stones was found at site S1. Chironomids were significantly lower in abundance on control stones at site S3.

Table 5: Effects of colonisation time on dominant taxa (Trichoptera, Chironomidae, Mollusca, Ephemeroptera, Oligochaeta) pooled to the order level. All data were log(x+1) transformed. One-way analysis of variance per site was used to compare days of colonisation (treatment; day 3, 7, 11, 31, and 73) with natural stone samples (control, pooled) using the Dunnett post-hoc test. Significant values are in bold, trend values are italicised. n.s.: not significant. Wave exposure at the sites decreased in the order S1>S2>S3.

Site	Metric	Analysis of variance		p-values with Dunnett post-hoc test treatment *vs.* control				
		F	p	3	7	11	31	73
S1	Trichoptera	13.087	**<0.001**	**<0.001**	**<0.001**	**0.001**	n.s.	n.s.
S2	Trichoptera	26.855	**<0.001**	**<0.001**	**<0.001**	**<0.001**	n.s.	n.s.
S3	Trichoptera	28.984	**<0.001**	**<0.001**	**<0.001**	**0.001**	n.s.	**0.026**
S1	Chironomidae	17.247	**<0.001**	**<0.001**	n.s.	n.s.	n.s.	n.s.
S2	Chironomidae	40.408	**<0.001**	**<0.001**	**0.004**	*0.072*	n.s.	n.s.
S3	Chironomidae	2.771	**0.037**	n.s.	n.s.	n.s.	n.s.	n.s.
S1	Mollusca	7.763	**<0.001**	**0.003**	**<0.001**	n.s.	n.s.	n.s.
S2	Mollusca	20.081	**<0.001**	**<0.001**	**<0.001**	**<0.001**	n.s.	*0.068*
S3	Mollusca	7.179	**<0.001**	**<0.001**	***0.051***	n.s.	n.s.	n.s.
S1	Ephemeroptera	5.852	**0.001**	**0.029**	n.s.	**0.022**	n.s.	n.s.
S2	Ephemeroptera	0.389	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S3	Ephemeroptera	3.726	**0.010**	n.s.	**0.043**	n.s.	n.s.	n.s.
S1	Oligochaeta	12.356	**<0.001**	**0.001**	**<0.001**	**<0.001**	n.s.	n.s.
S2	Oligochaeta	9.540	**<0.001**	**0.001**	**0.001**	**0.001**	n.s.	n.s.
S3	Oligochaeta	16.509	**<0.001**	**<0.001**	**0.001**	**0.001**	*0.070*	n.s.

Community Structure

Community structures showed a clear temporal development from day 3 to the end of the experiment on day 73, and the samples decreased in variability as the colonisation proceeded. All nMDS plots used non-standarised, square-root-transformed abundance data, and for better visibility they are plotted separately; treatment, control, and treatment×control data with either days of colonisation or site highlighted as the factor (Fig. 2). Treatment samples from days 3, 7, and 11 are highly separated from treatment and control samples from days 31 and 73. The highest differences in community structure occurred between days 7 and 11 and the last two sampling dates ($R = 0.823$–0.947, $p < 0.001$). Least differences were detected between days 7 and 11, but were still significant ($R = 0.247$, $p < 0.001$). Interestingly, a slight decrease in community distance also occurred between days 31 and 73. Sites clearly differed throughout the colonisation process averaged across all sites (Table 6), especially between sites S1 and S3 ($R = 0.639$, $p < 0.001$) and between sites S2 and S3 ($R = 0.708$, $p < 0.001$); the R value of a comparison between sites S1 and S2 was borderline, however, still significantly different ($R = 0.298$, $p < 0.001$) compared with the random distribution of all samples with the maximum possible number of permutations. When site per sampling day of treatment samples with all logical combinations are cross analysed (2-way crossed ANOSIM), highly significant differences were found in most cases throughout the colonisation process, except sites S1 and S2, and sites S1 and S3 on day 3; sites S1 and S3 on day 7; sites S1 and S2 on day 73, and in sites S2 and S3 on day 73; in the latter case, only borderline differences (R value) were found (Table 6). BVStep analysis revealed that 8 of 17 taxa explain most of the total dataset during the recolonisation process ($\rho = 0.956$, $p = 0.001$): Hirundinea, Oligochaeta, Mollusca, Ephemeroptera, Gammaridae, Chironomidae, Acari, and Hydra.

The n-MDS plots were standardised to total unit N and compared with square-root transformed data to test for effects of data transformation of community assemblages (Fig. 3). Only the factor treatment×control is highlighted. The general pattern is apparent in the two treatment×control plots. The first three sampling dates in the treatment samples are clearly separated from the last two sampling dates in the clustered control and treatment samples (see Table 6 for details).

A significant seriation pattern (sensu Clarke *et al.* 1993) within the colonisation process was found ($R = 0.748$, $p = 0.001$, Spearman rank correlation, number of permutations: 999, Relate procedure, PRIMER 6b), thus indicating that samples from all sites follow a linear trend, with adjacent samples being closer in species composition than samples further apart.

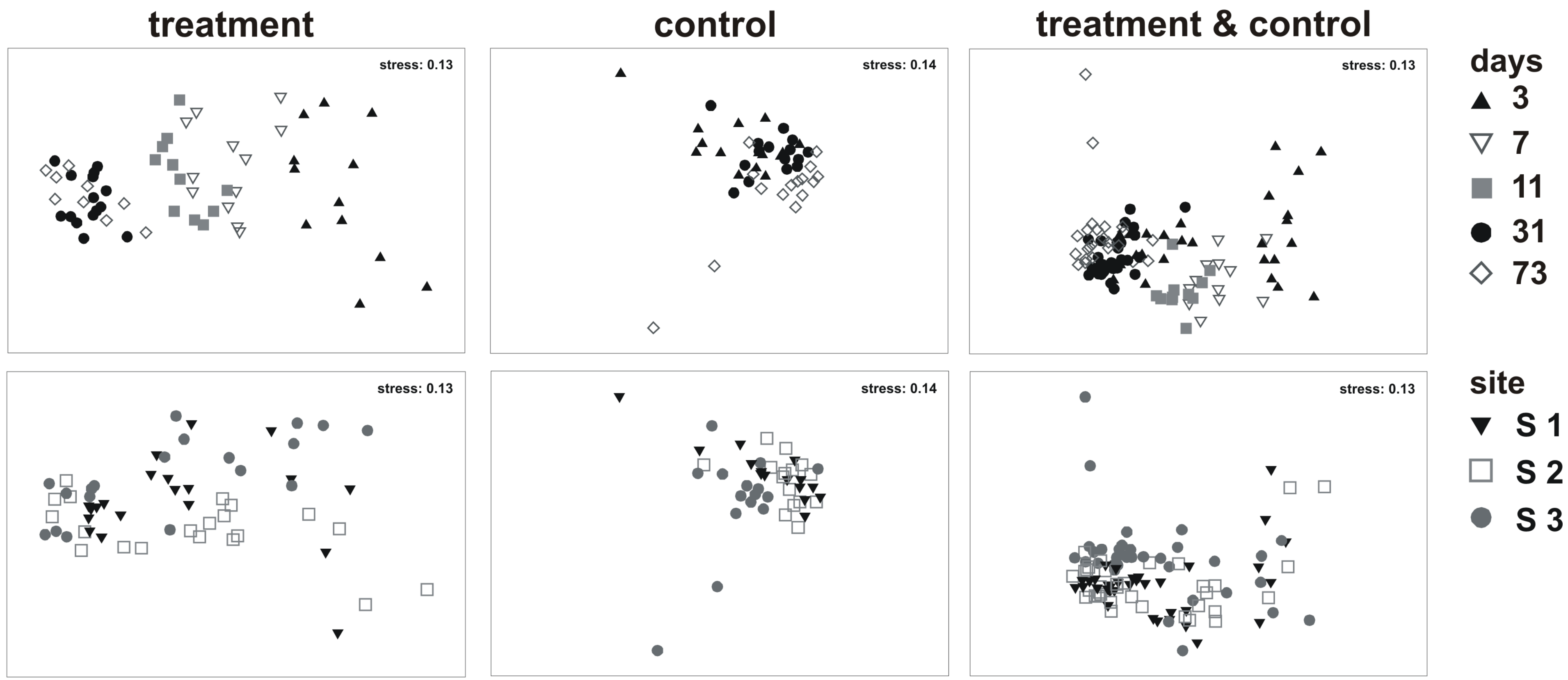

Figure 2: NMDS plots of invertebrate community composition during the colonisation process. For reasons of illustration, the treatment, control, and combined data are plotted separately. Either days of colonisation or site are highlighted. Data are square-root transformed, and the Bray-Curtis similarity index was applied. Days of exposition 3, 7, 11, 31, and 73. The wave exposure of the sites decreased in the order S1 (exposed)>S2 (intermediate)>S3 (sheltered).

Table 6: ANOSIM comparison of invertebrate composition on treatment (t), control (c), and treatment×control at sites S1, S2, and S3, after 3, 7, 11, 31, and 73 days of colonisation (S1_3, S1_7 etc.).

Treatment

Factor: (exposition) 3, 7, 11, 31, 73 days averaged across all site groups			**Sites: S1, S2, S3 averaged across all date groups**		
Global R: 0.642 p<0.001			Global R: 0.558 p<0.001		
Pair-wise test date	**R Statistic**	**p-level**	**Pair-wise test site**	**R Statistic**	**p-level**
3, 7	**0.406**	0.002	S1 & S2	**0.298**	p<0.001
3, 11	**0.436**	0.002	S1 & S3	**0.639**	p<0.001
3, 31	**0.733**	0.001	S2 & S3	**0.708**	p<0.001
3, 73	**0.654**	0.001	⇑ Random distribution R 0.18–0.26		
7, 11	**0.247**	0.029			
7, 31	**0.823**	0.001			
7, 73	**0.951**	0.001			
11, 31	**0.900**	0.001	⇐ Random distribution R 0.16–0.24		
11, 73	**0.947**	0.001			
31, 73	**0.812**	0.001			

Factor: site per date S_d

S1_3	S1_7	S1_11	S1_31	S1_73
S2_3	S2_7	S2_11	S2_31	S2_73
S3_3	S3_7	S3_11	S3_31	S3_73

Pairwise test (site-date)	**R Statistic**	**p-level**	**Pairwise test (site-date)**	**R Statistic**	**p-level**
S1_3, S2_3	0.229	n.s.	S2_11, S3_11	**0.611**	p<0.001
S1_3, S3_3	0.188	n.s.	S2_31, S3_31	**0.776**	p<0.001
S2_3, S3_3	**0.406**	p<0.001	S2_31, S1_31	**0.444**	p<0.001
S1_7, S2_7	**0.500**	p<0.001	S3_31, S1_31	**0.952**	p<0.001
S1_7, S3_7	0.281	n.s.	S2_73, S3_73	**0.333**	borderline
S2_7, S3_7	**0.563**	p<0.001	S2_73, S1_73	-0.037	n.s.
S1_11, S2_11	**0.854**	p<0.001	S3_73, S1_73	**1.000**	p<0.001
S1_11, S3_11	**0.500**	p<0.001	Random distribution R_{max} = 0.16		

Control

Factor: exposition 3, 7, 11, 31, 73 days averaged across all site groups			Sites: S1, S2, S3 averaged across all date groups		
Global R: 0.356 p<0.001			Global R: 0.450 P<0.001		
Pair-wise test (site-date)	**R Statistic**	**p-level**	**Pair-wise test (site-date)**	**R Statistic**	**p-level**
31, 73	**0.560**	0.002	S2 & S3	0.473	0.001
31, 3	**0.232**	0.002	S2 & S1	0.473	0.001
73, 31	**0.308**	0.001	S3 & S1	0.492	0.001
Random distribution R_{max}=0.16			Random distribution R_{max} = 0.20		

Treatment and Control - 31 and 73 days of colonisation per site

Factor: site (control/treatment) per date

S1_3_T	S1_7_T	S1_11_T	S2_31_T	S2_73_T	S2_73_C	S2_31_C	S2_3_C
S2_3_T	S2_7_T	S2_11_T	S3_31_T	S3_73_T	S3_73_C	S3_31_C	S3_3_C
S3_3_T	S3_7_T	S3_11_T	S1_31_T	S1_73_T	S1_73_C	S1_31_C	S1_3_C

Global R: 0.598 p<0.001

Pair-wise test (site-date)	**R Statistic**	**p-level**	
S2_31_T, S2_31_C	**0.324**	0.048	
S3_31_T, S3_31_C	**0.244**	0.008	
S1_31_T, S1_31_C	**0.432**	0.026	
S2_73_T, S2_73_C	**0.508**	0.036	
S3_73_T, S3_73_C	-0.097	0.643	
S1_73_T, S1_73_C	0.272	0.143	Random distribution R = 0.160

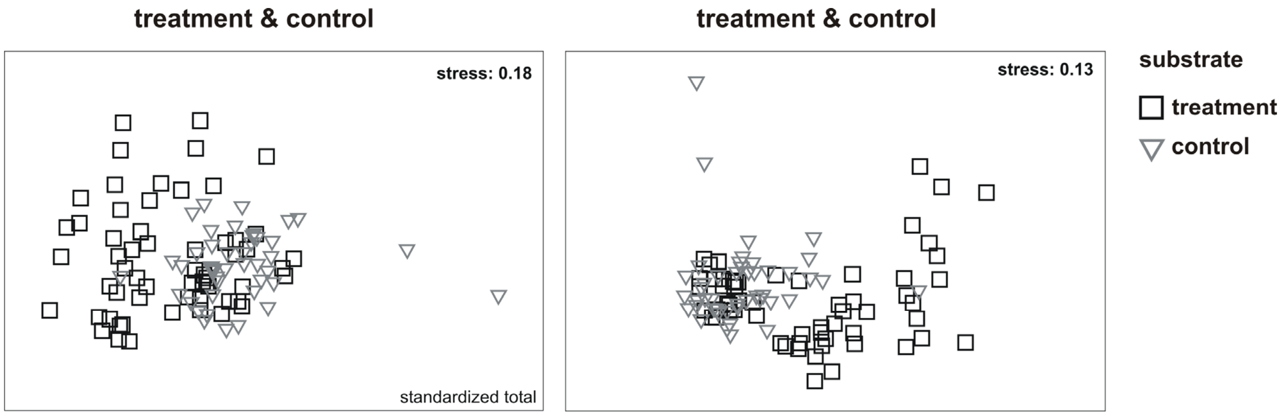

Figure 3: NMDS plot comparison of abundance data, standardised to unit N (left) and original data set (right). All data are square-root transformed, and the Bray-Curtis similarity index was applied.

Discussion

The colonisation (total abundance and taxa density) of bare, hard substrate was relatively fast and was completed within a month after exposure. Differences in recovery speed of total abundance, taxa density, and specific taxa occurrence at the sites were found when concrete stones were compared with the natural substrate (Dunnett test). Total abundance recovery was fastest at the highly exposed site S1, being completed by day 7, and was slowest at the intermediately exposed site S2, being completed by day 31. Abundance at the most-sheltered site S3 recovered by day 11 to the control level, and attained a significantly higher level thereafter (on days 31 and 73; Dunnett test). When sites and sampling date are compared with a MANOVA, differences were restricted to days of colonisation; no significant differences between sites and no interaction were detected. On control stones, a seasonal shift occurred within the first month, but there were no significant differences thereafter. However, the general colonisation patterns at all three sites were similar in terms of colonisation curves, Dunnett and MANOVA results, and also the observed increase of similarities between replicates through colonisation process in nMDS plots. Results from nMDS and analysis of similarity confirm differences between days of colonisation found with MANOVA and more important site differences determined with the Dunnett test. Only the treatment stones at sheltered site S3 differed the most from the other two sites; control stones at all sites shared a comparable dissimilarity. Furthermore, nMDS results point to a considerably slower colonisation of total community composition at all three sites than detected with univariate and multivariate methods. A direct comparison of treatment and control samples showed that colonisation exceeded the natural level on day 73 at sites S1 (exposed) and S3 (sheltered), but was still significantly lower at site S2 (intermediate exposure). This indicates the importance of the choice of statistical tools and the advantage of non-metric analyses to detect effects within community data.

The taxa found in the littoral wave zone in the present study agree with those of Barton (2004), who describes insects, especially Chironomids, Ephemeroptera, and Trichoptera, as the dominant taxa, and less-abundant Oligochaeta and Amphipoda. The present results contrast those of Quinn *et al.* (1996; 1998b), who found that the littoral benthos of Lake Purrumbete, Australia, was dominated by crustaceans, gastropods, and planarians. In the latter studies, the authors found no significant differences between the differently exposed lake sites, but rather a higher seasonal component at the exposed shore. However, the taxa composition between the lake sites and the connecting outlet stream differed markedly, and only the stream was dominated by insects. Also, a seasonal shift in total abundance on the control stones only was documented at the exposed (S1) and intermediate sites (S2), but not at the sheltered site (S3).

The recovery results in the present study are similar to those found by others in streams (Melo & Froehlich 2004) and lake littoral zones (Quinn *et al.* 1998b), but also faster colonisation rates have been described (see Mackay 1992 for a review). The present results confirm that fast colonisation occurs even on a less-favorable habitat with a low food supply of periphyton or organic matter. Osborne (1983) found maximum primary production in an ungrazed community after 21 days. Some taxa might prefer an early stage in periphyton succession, especially in less-frequently disturbed habitats, as demonstrated by Lake & Doeg (1985) for a dominant scraping caddisfly *Agapetus* spp., and thus higher densities were found on colonisation stones than on controls. The authors suggested that an early stage of periphyton succession and a lower percentage of silt coverage were favored by this taxon. Also, higher total abundances of Trichoptera (*Tinodes waeneri*) on concrete stones were found on days 31 and 73 at the sheltered site S3, as well as higher, but insignificant numbers of Ephemeroptera and Oligochaeta. Therefore, less-frequently disturbed habitats seem to benefit from occasional disturbance, resulting in higher productivity rates when unsilted hard substrates are a limited resource.

The occurrence of completely bare stones surrounded by untainted substrate is an unlikely event in natural habitats. More likely, singles stones would be overturned by waves or a storm event, resulting in a partly abraded epilithic layer depending on the severeness of the impact. Overturning of stones significantly reduced invertebrate abundance and number of taxa in a fifth-order stream (Boulton *et al.* 1988). Mobile organisms recovered within 24 h, less mobile taxa within 4 days. Boulton *et al.* (1988) also examined the effect of intensive brushing the epilithion of a stone; a thin layer of periphyton remained after the brushing, which thus facilitated a faster periphyton recovery compared to recovery of acid-scoured stones completely freed of epilithion. The structure, complexity, and composition of periphyton alter the attraction to macroinvertebrates (for a review, see Mackay 1992), but Boulton *et al.* (1988) found a similar rate of recovery of invertebrates in both treatments.

Recolonisation regularly occurs on a larger scale in Lake Constance because of the pronounced water-level fluctuations, which can be up to 2 m per year. During spring and early summer, the water level can increase up to 10 to 40 cm per day, but is usually restricted to a steady increase of a few centimeters per day. This provides benthic communities with a wide range of new habitats. Palomäki (1994) stated that benthos biomass in oligotrophic lakes decreases at all depths in the littoral zone with increasing water level fluctuation. He further predicted that the abundance development of the benthos community within 0–3 m water depth can be related to the water-level fluctuation of the previous year. Benthic fish communities also benefit from a increased habitat source (Fischer & Eckmann 1997a).

Sources of colonisation from drift or active swimming are likely (Mackay 1992). It is unclear whether bare, isolated substrates are found by chance or by active movement caused by a specific attraction to chemical cues of the periphyton layer, as has been shown in marine (Zimmer-Faust & Tamburri 1994) and freshwater habitats (Brendelberger 1995; Watson 2003). Tamburri *et al.* (1996) presented evidence that such chemical cues can be further triggered by hydrodynamic compounds. Gregarious settlement of several taxa, e.g. cnidarians, molluscs, annelids, and arthropods, has been discussed (Burke 1986). In a comparison of macroinvertebrate colonisation rates on hard substrates from the water column and the lake bottom, Quinn *et al.* (1998a) found a significantly slower colonisation on suspended stones than on bottom stones, but similar taxa colonised the two substrates, which indicated that the invertebrates were highly mobile, including benthic taxa usually considered as having lesser swimming abilities, such as gastropods and oligochaets. The authors assumed a constant movement of the lake benthos as a response to resource shortage.

Positive and negative interactions of macroinvertebrate development associated with *Dreissena polymorpha* settlements have been described (Mörtl & Rothhaupt 2003; Wisenden & Bailey 1995). *D. polymorpha* can out-compete others in space, e.g. snails, but facilitates scavenger-omnivores, e.g. amphipods and flatworms (Wisenden & Bailey 1995). Mörtl & Rothhaupt (2003) found significantly higher total and single taxa abundance of chironomids, *Gammarus roeseli*, *Caenis* spp., and *Bithynia tentaculata* on shell-only blocks and living-mussel blocks than on blank blocks, but in some cases they found even higher abundances on shell-only blocks than on living-mussel blocks, which thus indicates a predation interaction on the living-mussel blocks. The authors argue that increased substrate complexity enhances invertebrate abundance of chironomids, amphipods, and snails benefiting from the altered physical structure. However, these results are based on adult mollusc settlements, and thus unlikely conflict with the present results with newly settled *D. polymorpha* larvae.

The stones were colonised with high abundances of early-instar individuals of Trichoptera (*Tinodes waeneri*) and Ephemeroptera (*Caenis* spp., *Ecdyonurus dispar*) and first-settled juveniles of zebra mussel (*D. polymorpha*). Ephemeroptera and Chironomidae were early colonising taxa, with clear site differences. Trichoptera and Oligochaeta were later succession taxa, without significant site differences in recovery speed; both attained control levels by day 31. The first settlement of *D. polymorpha* differed between the sites, with an intermediate overall settlement speed. As predicted, the present results provide evidence that the colonisation pattern within similar benthos communities differed between sites with varying wave exposure. The most positive effects were found for the most sheltered site, with higher abundances than in control samples. Fastest colonisation rates were obtained at the sheltered and exposed sites, lowest at the intermediate site. The exposed site

S1 should contain the highest habitat heterogeneity with respect to the amount of interstitial refuges, distributional variation of finer substrates, and periphyton covering hard substrates. Site S1 could thus support a benthos community with higher resilience (the ability to return rapidly to pre-disturbance densities) and resistance (ability to withstand disturbance) pattern (Townsend & Hildrew 1994). Gjerlov *et al.* (2003) investigated macroinvertebrate recolonisation rates in relation to habitat heterogeneity in seven streams and assumed that high-refugium sites have a high proportion of low shear stress areas, whereas low-refugium sites lack such areas. They found increased colonisation rates with increased disturbance levels at low-refugium sites, but high-refugium sites always colonised faster than low-refugium sites, independently of its disturbance regime. Increased habitat heterogeneity seems to support higher benthos abundances partly due to a lower mobility risks in the study of Gjerlov *et al.* (2003). I would assume similar mechanism for the exposed site in the present study. However, in the most sheltered site, deploying bare stone seems to increase habitat heterogeneity temporary by supporting higher benthos abundances than in control samples.

In summary, the results indicate, that community pattern here observed as colonisation rates can markedly differ between related sites with similar substrate, geology and connected by the same water body. The chosen statistical tools further strongly influence the outcome of a study as non-metric multidimensional scaling revealed a slower recolonisation rate to control conditions than multivariate methods indicated.

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Chapter 3

Physical disturbance strongly influences distribution, activity and growth of a littoral zone gastropod

Summary

In a field experiment, the distribution of the pulmonate freshwater snail *Radix ovata* was quantitatively recorded under ambient hydrodynamic conditions at five littoral sampling sites and the depth dependency was exemplarily examined at one site. In an outdoor mesocosm, the influence of wave exposure on *R. ovata* behaviour and growth rates was examined experimentally. Two wave conditions common to large lakes were tested: permanent waves, i.e. representing long-lasting wind conditions; and periodic waves, i.e. representing regular short-term exposure to ferry boats, followed by calm conditions. The effects of the waves on snails were compared to control conditions. The depth dependency of snail activity, place of residence (0.2- and 0.4-m depth), and growth rates (0.2-, 0.4-, 0.8-m depth) were recorded.

The grazing and moving activities were significantly lower when *R. ovata* was exposed to permanent waves than under control conditions, but individuals were able to remain attached and forage under turbulent conditions. Growth rates were also significantly reduced under permanent wave conditions at all depths. Permanent wave exposure led to high mortality rates (up to 90%) after two weeks at 0.2- and 0.4-m depth. Periodic wave exposure led to reduced growth rates at 0.2-m depth. All snails survived throughout the experiment.

Highest abundances of the snails in the field were found at sites with intermediate wave disturbance, but no clear depth dependency was observed. Nevertheless, the mesocosm and field results support the hypothesis that the field distribution of the gastropod is strongly influenced by hydrodynamic turbulences within the uppermost exposed water depths, either directly owing to the effect on growth and reproduction success or indirectly by altering habitat conditions and food supply by wind abrasion or sediment accumulation. As an ecological consequence, a reduced grazing pressure, i.e. a top-down control of this herbivore on its periphyton food source under unfavourable turbulent conditions is assumed, which might thereby also affect other trophic levels or biotic interactions.

Keywords: lake littoral, benthic herbivore, wave exposure, wave mesocosm, pneumatic wave machine

Introduction

Abundance, biomass, and diversity are often used for analysing and characterising macroinvertebrate communities with respect to their biotic and abiotic environment. We found distinct differences in abundance, biomass of various invertebrate taxa, and overall community composition in a comparison of five sites within the same sampling depth in the littoral zone of Upper Lake Constance in a monthly sampling programme (Chapter 6, Scheifhacken *et al.* 2007). Most of the community variability in the upper eulittoral zone of one site in Lake Constance was explained not only by seasonal variability, species turnover, and biotic interactions, but also by water level fluctuations (Chapter 6, Baumgärtner 2004).

Also Palomäki (1994) argued from results obtained from a Finnish oligotrophic lake survey that benthic biomass production strongly depends on water-level fluctuations in the previous year and decreases with increasing fluctuations. However, the gauge fluctuation should affect all sites in a lake alike. Hence, other background abiotic conditions, such as littoral slope, exposure to waves, or a combination of both are expected to structure habitat conditions constantly and thereby also structure the occurrence of taxa as well as the biomass accumulation. This subject has recently been under debate for littoral lake habitats (e.g. Rasmussen 1993; Strand & Weisner 1996; Hamilton & Mitchell 1997; James *et al.* 1998; Barton 2004), after years of almost exclusively focusing on marine habitats (e.g. Atkinson & Newbury 1984; Brown & Quinn 1988; Hobday 1995; Tanaka *et al.* 2002; and many others; see Denny 1995 for a general overview). The impact of wave action on morphology, behavioural traits, and distribution patterns in marine habitats of sessile (McQuaid *et al.* 2000; Marchinko & Palmer 2003; Fitzhenry *et al.* 2004) and mobile organisms (e.g. Brown & Quinn 1988; Jenkins & Hartnoll 2001; Tanaka *et al.* 2002) has been studied.

The experimental studies in the literature are mainly restricted to flow-tank experiments and have focused on marine organisms (Trussell 2002; Gagnon *et al.* 2003). One exception is the documented suppressed growth of the subtidal plant *Vallisneria americana*, which was studied in a wave mesocosm and compared to a control mesocosm (Doyle 2001). An initial study on freshwater gastropods in a flow tank have been reported (Dussart 1987). However, to date, little is known about the impact of physical factors, such as wave exposure, on freshwater snails in lake littoral zones even though gastropods are important herbivore grazers in many lotic or littoral freshwater habitats (Cattaneo & Kalff 1986; Feminella & Hawkins 1995). They often occur in high abundances and can control their peripython food source (James *et al.* 2000b). Even in low numbers, they presumably contribute to structuring littoral food webs because of their comparatively high biomass (Cattaneo & Kalff 1986; Feminella & Hawkins 1995) compared to other insect grazers. Gastropods are also known to link primary production to higher trophic levels, such as waterfowl (Werner *et al.* 2005), fish (Brönmark 1994; McCollum *et al.* 1998), or crayfish (Nystrom *et al.* 1999) feeding on them. However, periphyton–grazer interactions are rather complex, and factors often interact (reviewed by Liess & Hillebrand 2004).

In this study, the common snail *Radix ovata* was chosen as the key species. This taxon is widespread in the littoral zone of Upper Lake Constance and is easy to collect from the field and handle in the laboratory. *R. ovata* occurs from the splash zone to the acclivity ridge down to 10-m depth during spring and late summer. It feeds predominantly on epilithic algae (Calow 1970; Lodge 1986).

Here, it was hypothesised that (**i**) distribution patterns of *R. ovata* would differ among five sites along a gradient of wave exposure and that avoidance of exposed sites or low survival rates would be responsible for the horizontal distribution of *R. ovata* within the lake. In a vertical gradient, a retreat to greater water depths as well as burrowing in sediments or hiding in macrophyte stands might be survival strategies in a turbulent environment. Turbulences could directly affect parameters such as shell damage, suppressed growth rates, or reduced reproduction success. In addition, increased hydrodynamic conditions could possibly indirectly affect substrate composition, periphyton quantity and quality, and the proportion of fine sediment layer.

Wave exposure in large lakes is generated by wind-induced surface waves and also often by ferry or leisure boats. I therefore examined the effect of water depth and wave exposure on the activity and growth of *R. ovata* using a self-constructed pneumatically operated, wave machine within concrete outdoor basins. I hypothesised that (**ii**) the activity and (**iii**) growth rate of *R. ovata* would be lower under turbulent conditions, with (**iv**) lesser effects in increasing water depths.

Methods

Study site

The field study was conducted in the oligotrophic Upper Lake Constance (9°18'E, 47°39'N), which is the second-largest, pre-alpine lake in central Europe (surface area: 472 km^2, total volume: 47.6 km^3, maximum depth: 254 m, mean depth: 101 m). Throughout the year, the lake is highly susceptible to wind-induced surface waves. Predominantly westerly winds prevail throughout the year; a second less-dominant peak of easterly winds occur mainly in winter (Bäuerle *et al.* 1998). Various ferries and leisure boats also generate waves. The Rhine River comprises 62% of the mean runoff (Wessels 1998) and drains parts of the European Alps, resulting in annual water-level fluctuations up to 2 m (Luft & Vieser 1990), with low water levels during winter and high inflow rates after snowmelt in early summer. The substrate in the upper littoral zone mainly consists of cobblestones covered with a thin silt layer and loosely embedded within finer sediment (Schmieder *et al.* 2004).

Radix ovata

I identified snails as *Radix ovata* (Draparnaud, 1801, Gastropoda: Pulmonata, Lymnaeidae) following taxonomic traits described in Glöer & Meier-Brook (1998). Lymnaeid systematics and species distinction is controversial and still under revision. Some authors accept only one genus (*Lymnaea*), while others prefer up to seven different genera (e.g. *Galba*, *Stagnicola*, *Radix*, *Lymnaea*). Various species names can be found in the literature, including *Lymnaea ovata*, *Lymnaea auricularia ovata,* and *Radix balthica*. Furthermore, *Radix ovata* and *Radix peregra* are regularly treated as different species by some authors (Glöer & Meier-Brook 1998; Wullschleger & Jokela 2002), while others consider them as morphs of one species with a wide phenotypic plasticity (Hubendick 1951; Okland 1990). I decided to recognise the literature concerning both the genus *Radix* and the genus *Lymnaea* with the species specification *R. (L.) ovata* and *R. (L.) peregra* because shell shape is known to be variable. The morphometric dependency is discussed as either relying on environmental habitat conditions or based on genetic distinction (Hubendick 1951; Calow 1981; Dussart 1987; Lam & Calow 1988; Wullschleger & Ward 1998; Wullschleger & Jokela 2002; Garbar & Korniushin 2003; Stift *et al.* 2004).

Field study

Quantitative samples of benthic invertebrates on littoral hardsubstrates were taken in October 2002 and April 2003 to determine the horizontal distribution at five sampling sites in 0.4-m water depth, with four replicates per site in October and three in April. The sites chosen represent an exposure gradient to the prevailing westerly winds (Fig. 1). All sites at the north-eastern shore are highly exposed (S5⇒S3⇒S2 with increasing fetch length) throughout the year. However, littoral slope counteracts wind exposure (e.g. Hakanson 1977; Duarte & Kalff 1986; Rasmussen & Rowan 1997). Site S5 has a steep slope, sites S2 and S4 have extremely shallow slopes, and sites S1 and S3 have intermediate slopes (Fig. 1). Regular wave action is also commonly generated by leisure boats or ferry traffic at all chosen sites, but predominantly at sites S1 (moderate) and S5 (exposed). In summary, I assumed from earlier observations that the highest wave action will occur at site S5, the lowest at site S4, and intermediate exposure at sites S1, S2, and S3.

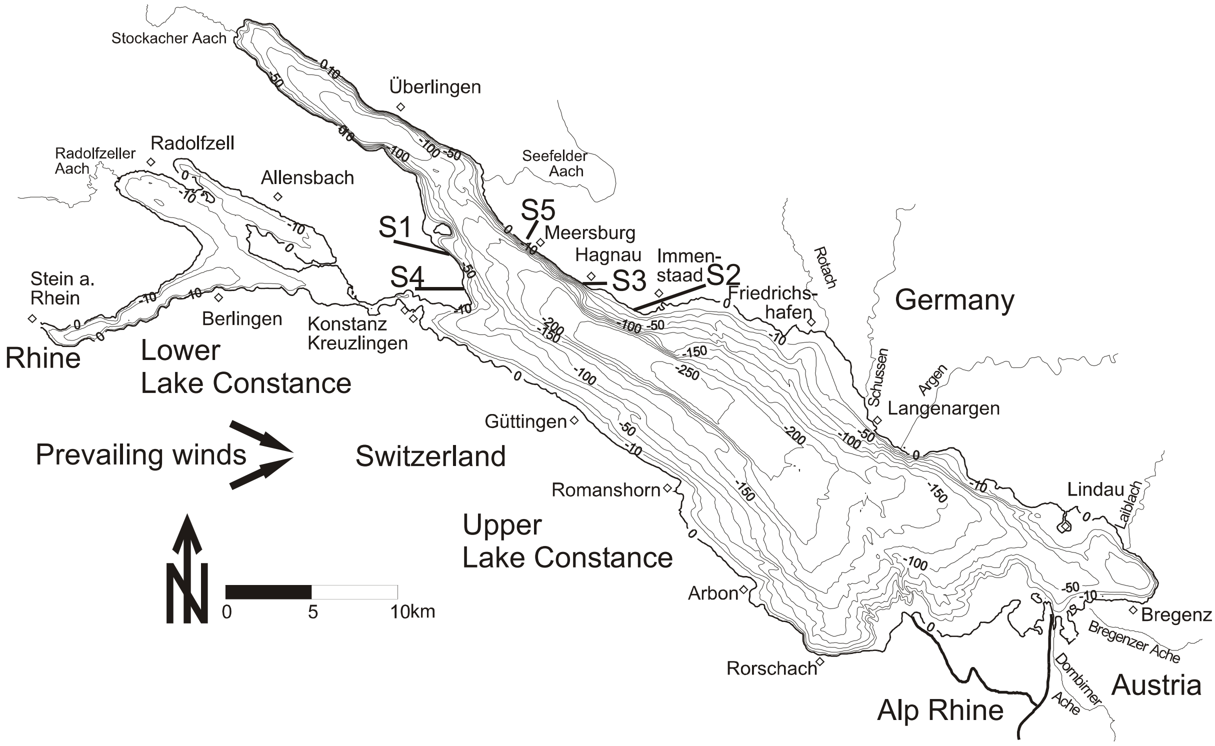

Figure 1: Map of Lake Constance, sites **S1** Litoralgarten, **S2** Immenstaad, **S3** Hagnau, **S4** Staad, **S5** Meersburg. Wave exposure of sites: **S1** (intermediate), **S4** (sheltered) at the southwestern shore, **S2, S3, S5** (exposed) at the northeastern shore. map coordinates: S1: Litoralgarten 47°41'26,668''N; 9°12'18,355''E, S2 Immenstaad 47°39'46,808''N; 9°20'50,093''E, S3 Hagnau 47°40'44,005''N; 9°18'11,806''E, S4 Staad 47°40'25,686''N; 9°12'53,463''E, S5 Meersburg 47°41'37,249''N; 9°16'11,660''E.

For vertical distribution studies, samples were taken monthly at site S1 at six water depths: three depths referring to the actual water depth (splash zone, 0.4 m, 1 m) and three depths dependent on the long-term average low water line (LWL), (LWL-1m, LWL-3m, LWL-7m).

I used a suction sampler as described in Baumgärtner (2004), but with modifications. The height of the side walls was increased to minimise the escape of mobile taxa (Fig. 2). The sampled area was reduced to 25×25 cm (A_o = 625 cm^2) to adjust to the same size as the infralittoral samples and to scale down labour expenditure. Samples in water depths ≥1 m were taken by scuba divers; all others were taken from the water surface. All hardsubstrates from the sample area were transferred into a hand net while the pump ran continuously; this minimises the number of individuals escaping. Suspended organisms were retained within a filter inlet (200 µm gauze), added to the hardsubstrate fraction, transferred to the laboratory immediately, and processed. Coarse substrates were washed, carefully brushed, and rinsed within a basket (200 µm) to remove all attached invertebrates. Fine sediments were repeatedly floated to suspend all invertebrates in the water column. All fractions were filtered through a 200-µm sieve, and the organisms remaining on the sieve were preserved in 70% alcohol. *Radix* individuals were counted, and the remaining invertebrates were kept for further investigations (Chapter 6, plus N. Scheifhacken unpublished data).

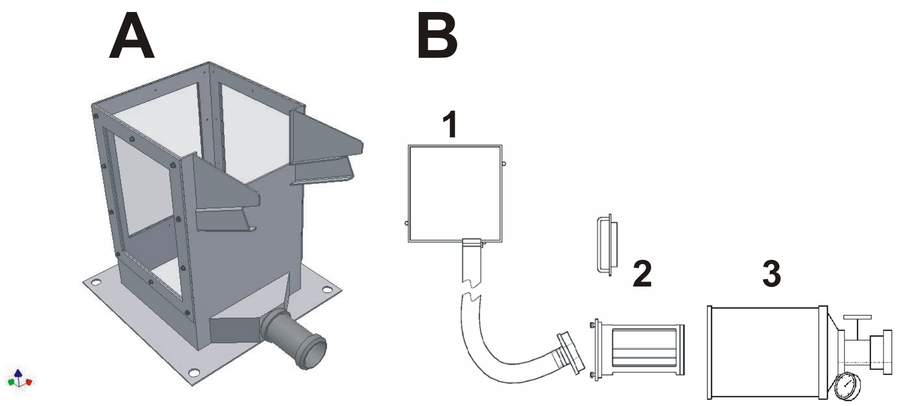

Figure 2: Benthos suction sampler with modifications at the eulittoral device **A**: eulittoral **B**: infralittoral device, sample area 25 x 25 cm^2; Suction sampling device **1** - : frame; **2** - filter inlet 200 µm; **3** - suction pump.

Wave mesocosm and wave machine

Two concrete basins (10 m length, 1 m width, 1 m height) were equipped with an artificial littoral zone at one end of each basin (wave and control) (Fig. 3 B). The profile (slope 10% top, 16% bottom) was similar to that of the natural shoreline at some sites in Lake Constance. The slope was made with a metal grid covered with aquarium foil and a thin layer of substrate (10 cm). The grid was mounted stably on hooks and on the concrete side walls; water exchange throughout the basin was allowed. The substrate consisted of washed cobblestones from a nearby gravel pit in size classes (range 9.1–18.0 cm, mean length 12.45 cm ± 0.24 SE, n = 55) similar to those commonly found in Lake Constance. The substrate roughness, and hence the shear stress to the applied waves, was also similar to those in the lake. The water level was maintained at 0.8-m depth; water was added at 2–2.5 l min^{-1} to compensate for evaporation loss and to ensure sufficient oxygen saturation. The water came from Lake Constance pumped from a depth of 12–16 m, depending the on actual gauge level, and was filtered through a 300-µm mesh.

Wave action was generated by a self constructed pneumatic wave machine. The device (Fig. 3 A) generates wave action at different intensities and frequencies by adjusting either pressure (intensity), deflection (stroke length), and/or velocity rates (choke valve) through specific pneumatic elements. Deflection and velocity rates were kept at maximum. Wave duration was regulated through the time switch modus: either permanent wave exposure over a specific period or periodic at regular intervals. A pneumatic cylinder, i.e. a double-acting piston activated by a compressor, ran the working motion. The piston rod (400 mm total stroke length and 40 mm in diameter) powered a flapping metal board (0.9 m x 0.5 m). The board has hinged lids that are closed during forward movement to maximise applied power but opened while retracting to reduce water impedance. Furthermore, the board moves forward rapidly and retracts slowly to minimise counter current.

Collection and handling of snails

One to two days before the start of the experiment, medium-sized snails were collected in 500-ml polyethylene bottles by scuba divers at 1–2-m water depth. Sampling was restricted to site S1—Litoralgarten, and occurred in September 2003 for the activity experiment and in July/August 2004 for the growth experiment. All snails were kept in the laboratory in small water tanks (25×15×15 cm) in a climatic chamber (15 °C, day/night cycle 12/12 h) with oxygen aeration and *ad libitum* food supply (TetraPlecoMin®) for maximally 2 days prior to experiments. Snail growth was measured as shell length. Shells were measured 1–2 h before the start of the experiments and after 1 and 2 weeks of mesocosm exposure. Maximum shell length of individuals retreated in their shell was measured to the nearest 0.01 mm from the apex to the basal lip from fixed images made with a dissection microscope connected to a digital image analysis system. Shell length was restricted to 8–12 mm because growth declines with the onset of reproduction (Fink 2005) and because this size range is easily handled in outdoor mesocosm experiments.

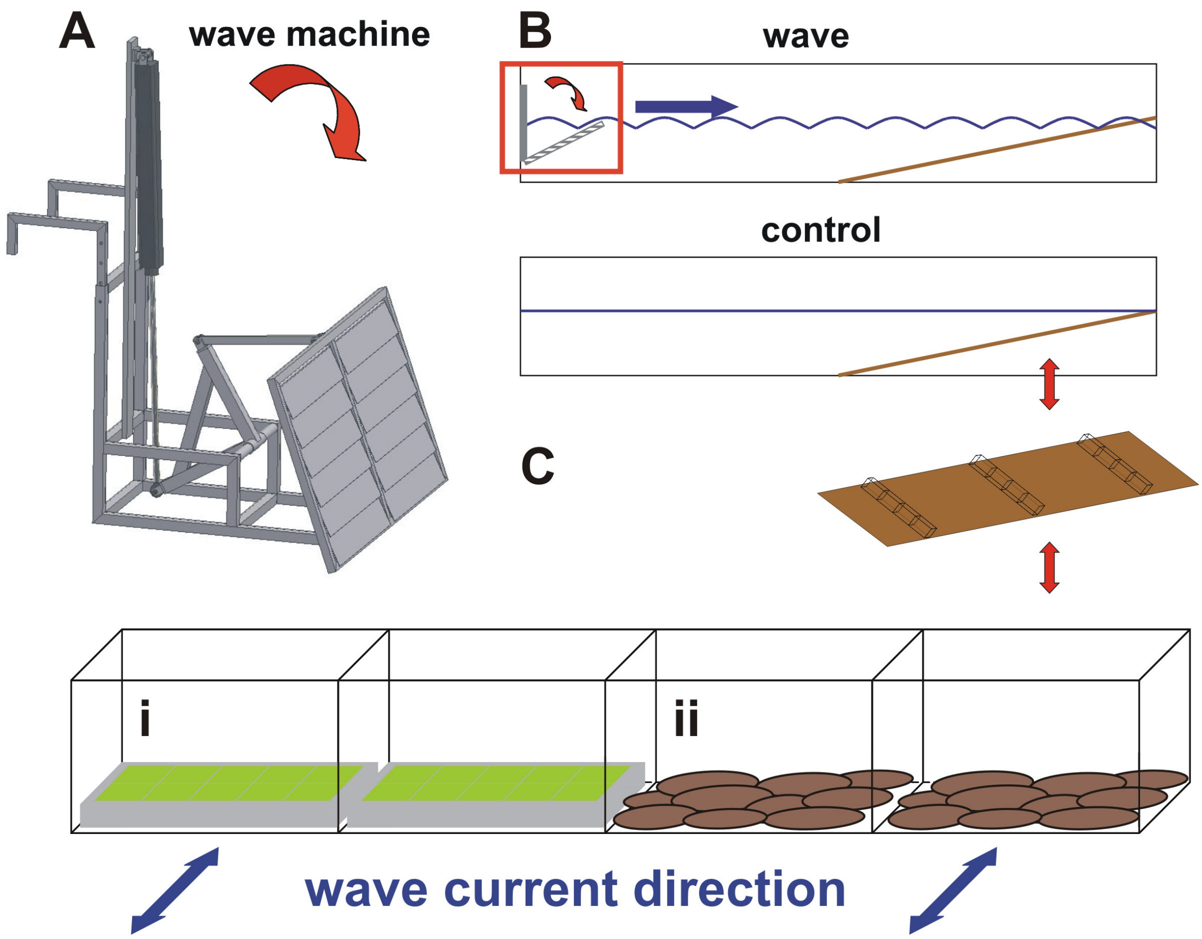

Figure 3: Experimental design for measuring *Radix ovata* mesocosm activity and growth. (A) Pneumatic wave machine with flapping board, (B) wave and control raceways with artificial bank slope, and (C) experimental units filled with pre-colonised (i) concrete stones covered with tightly glued ceramic tiles in the activity experiment and (ii) natural cobblestones in the growth experiments under different wave regimes.

Experimental units for exposing snails to waves were fixed at 0.2-, 0.4-, and 0.8-m depth. The aluminium units consisted of four identical compartments (Fig. 3 C, 25×15×15 cm). The front and back sides of the units contained a wide mesh (4 mm mesh size, polyester, 0.8 mm fibre) to allow maximum wave flow through, yet to hinder snails from leaving the compartments. Sides were closed with sheet plates (2 mm). I observed earlier that *R. ovata* remained attached to the substrate during a wave pressure of 3–5 bar (0.1–0.25 m s^{-1}), but the number of floating individuals increased at higher pressures. To ensure grazing at all three water depths, I restricted the maximum wave pressure to 3 bar.

Wave measurement

Wave action was measured using an acoustic Doppler velocity meter (ADV) at the three experimental depths, 5 cm above the substrate surface (Scheifhacken, Klahold & Hofmann submitted). To compensate for the methodological constraints of ADV, especially at the uppermost depth of 0.2 m, also the dissolution rate of gypsum spheres (n=5) was used to characterise turbulence at all depths and in all treatments (see Chapter 2 and also Petticrew & Kalff 1991, Porter *et al.* 2000). These two methods were used before the units were stocked with *R. ovata*. Waves were continuously recorded online with a wave pendular (N. Scheifhacken, unpublished data) connected to a computer to control a constant system run. For comparison of turbidity at lake sites, gypsum spheres were deployed 4 times for one week between August 02—October 02 at 0.4-m depth at three sites only: S1-Litoralgarten, S4-Staad, S5-Meersburg and once at all five sampling sites S1-S5.

Snail activity

In the activity experiment (Fig. 3 C i), units were filled with eight ceramic tiles (4.7×4.7 cm; A_o = 22.09 cm^2, A_{sum} = 176.72 cm^2) tightly glued to a concrete block (20×10×5 cm) with aquarium silicone. The tiles were previously exposed for 6 weeks at 0.5-m depth in Lake Constance to allow adequate growth of periphyton. Unglazed tiles have been used successfully in studies of periphyton growth (James *et al.* 2000b; Cardinale *et al.* 2002). In the activity experiment I preferred artificial substrates to standardise offered surface area exposed to waves. *R. ovata* activity was recorded eight times over 3 days with permanent waves (3 bar); the control basins had no waves. The activity of snails (5 snails per chamber, 20 snails per depth and treatment, i.e. 80 snails total) was recorded using a bathyscope; the chamber lid was opened for a short period while the wave machine kept running. This restricted handling to arm length, and therefore to 0.2- and 0.4-m water depth. The categories of activity were defined as active, inactive, and unclear by evaluating the amount of visible body parts (head, feet, tentacles) and movements. Active snails showed either movement and/or full body structures, such as tentacles. Retreated and unmoving snails were classified as inactive. All ambiguous individuals were counted as unclear. The place of residence of each individual was reported in four categories: food (periphyton tiles, wave-exposed), current (front and side areas around concrete stones exposed to waves, except tile surfaces); shelter (back of concrete stones, all metal edges), and unclear (all other cases). The last category was omitted from analyses because it occurred rarely.

Snail growth

In the growth experiments, natural substrate from the nearby littoral zone and at 0.3–0.5-m depth was sampled to ensure natural feeding conditions on periphyton community. We know from a previous study (pooled brush samples) that the chlorophyll *a* and organic matter contents of the periphyton community are satisfactorily homogeneous at a given depth at the same site (Peters *et al.* 2005). Cobblestones were randomly chosen and redistributed within the experimental units and replaced with fresh substrate after one week. Any spatial differences in periphyton quantity and quality should have been sufficiently compensated by the variety of cobblestones offered per unit. However, the periphyton content (dry mass/ash-free dry mass) was determined parallel in the field at the start of the experiment for five replicates; in controls and in the wave mesocosm experiments, the content was determined after one week of exposure at all depths and within each compartment, using standard methods as described in Peters *et al.* (2005).

In the growth experiment units (4 snails per chamber, 16 snails per depth and treatment, i.e. 96 snails total) were exposed at 0.2-, 0.4-, and 0.8-m depth to permanent waves (3 bar) or periodic waves (5 min waves, 25 min pause; 3 bar). The permanent waves reflected constant light-to-moderate wind events, which can last for one or two weeks under natural conditions. Periodic waves reflected ferry-induced waves and were simulated with a time switch gear by adjusting the intervals to the current ferry timetables. Snail growth, i.e. shell length, was measured at the start and after 1 and 2 weeks.

Statistical analysis

The distribution patterns of *R. ovata* abundance were tested with univariate statistics after square-root (x+0.5) transformation to achieve homogeneity of variances

(Levene test) with site and season as factors, followed by a post-hoc comparison with Tukey's HSD. Snail activity, place of residence, and growth rates were tested with repeated measurement MANOVA with treatment (wave, control) and depth (activity experiment: two depths; growth experiment: three depths) as factors. Turbidity was tested with a two-factorial analysis of variance with treatment and depth as factors in the mesocosm and with site and sampling date as factors in the field. Specific weeks of field exposure were analysed with separate ANOVAs to differentiate the interaction term. All analyses were Bonferroni corrected (Rice 1989). Growth rates were log (x+1) transformed to homogenise variances. Again, a post-hoc comparison with Tukey's HSD was applied when significant effects were detected. For all statistical analyses, the software package SPSS 13.0 was used.

Results

Field distribution of R. ovata

The total abundance of *R. ovata* (mean $\pm$ SE individuals per m^2) was 189.3 (± 49.7) pooled over all sampling dates and sites (median: 48, n = 35 samples). However, the distribution patterns differed significantly between sites and season ($F_{4,25} = 16.275$ and $F_{1,25} = 21.543$, both $p < 0.001$), but the interaction of site and season was not significant ($F_{4,25} = 2.327$, $p = 0.084$) (Fig 4 A). Significantly higher abundances of *R. ovata* were found at site S1 (mean 599 ± 146 SE) than at all other sites at 0.4-m depth (post-hoc comparison with Tukey's HSD). Intermediate abundances were found at sites S2 (197 ± 83) and S3 (85 ± 59); the lowest abundance was found at sites S4 (41 ± 13) and S5 (25 ± 15), and these did not differ significantly. Autumn samples contained generally more snails at all sites, but abundances were always highest at site S1. In contrast, no depth preferences could be detected in the vertical distribution from the splash zone to LWL-7 m at site S1 ($F_{5,66} = 0.893$, $p = 0.491$, Fig. 4 B).

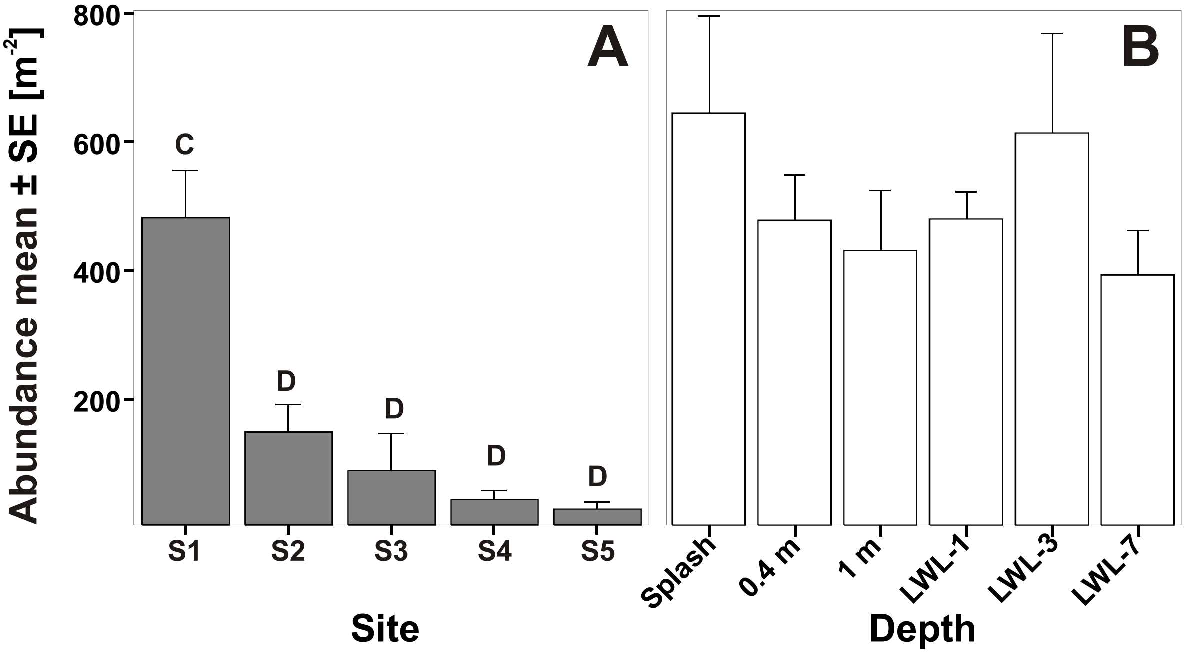

Figure 4: Mean abundance of *Radix ovata* per square meter. **A:** Mean abundance at the five sampling sites at Upper Lake Constance within 0.4-m depth, order sorted at decreasing abundances from left to right. The data from October 2002 and April 2003 were pooled, n=35. Wave exposure at sites: S1 Litoralgarten, intermediate; S4 Staad, sheltered at the south-western shore; S2 Immenstaad, S3 Hagnau, S5 Meersburg, exposed at the north-eastern shore. Different capital letters indicate significant differences between sites; post-hoc comparision with Tukey's HSD after 2-way ANOVA. **B:** Depth distribution at site S1: LWL, low water line (long-term average); LWL-1m, LWL-3m, LWL -7m, n=84.

Activity and place of residence of R. ovata

Snail individuals remained on the substrate throughout all treatment conditions (permanent and periodic waves) in all experiments (measurement of activity and growth), except for a few accidental losses. In these cases, the individuals reattached quickly and easily. In general, more individuals were active in the control mesocosm (14.6 ± 1.0, mean ± SE, out of 20 individuals) than in the wave mesocosm (3.6 ± 1.0) (data pooled over all depths and measuring periods) (Fig. 5). In the wave mesocosm, 14.2 (± 1.0) inactive individuals were found; in the control mesocosm, only 1.0 (± 0.3) individual was found. An unclear activity status was recorded for 1.0 (± 0.3) individual in the control mesocosm and for 2.1 (± 0.4) individuals in the wave mesocosm. Treatment effects were highly significant ($p < 0.001$) for active and inactive individuals and significant for unclear activity status ($p < 0.011$) (see Table 1). The

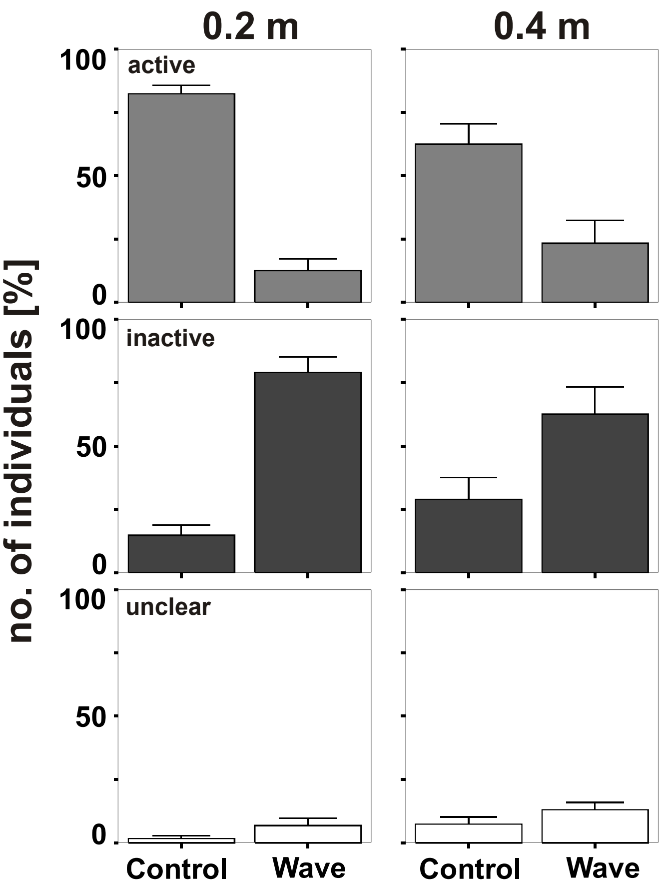

Figure 5: Activity of *Radix ovata* in % within wave and control mesocosms at two depths (0.2 and 0.4 m) under permanent wave conditions (3 bar) for three days.

factor depth was not significant except in the unclear activity category (p = 0.022), whereas the interaction between treatment and depth was significant in both the active and the inactive categories (p = 0.003, Fig. 5, Table 1). Furthermore, a significant time effect was detected for all categories, with more individuals active in the first and the last three recordings in the control and wave mesocosms at both water depths; the effect was more pronounced at greater depths.

Significant differences between treatments within all three main categories of place of residence were detected (Table 2). Significantly fewer individuals exposed to waves were found on top of the peripython tiles (food, but wave exposed) and in sheltered sites compared to the control; significantly more snails were found within the current (no food source). Depth effects were significant, with fewer individuals at 0.2-m depth than at 0.4-m depth in the current on peripython tiles (p = 0.031). Conversely, more individuals were found at 0.4-m depth in the current (no food) than at 0.2-m depth, but the difference was hardly not significant (p = 0.051). Also significant date effects and interactions of date and treatment were found, but after sequential Bonferroni adjustment, only one effect remained significant, namely current (date D1 < date D2, see Table 2).

Table 1: Results of repeated measurement ANOVA for three activity classifications with recording times D1–D7. The main effects were compared in a post-hoc comparison with Tukey's HSD. The p-values in boldface are significant after sequential Bonferroni adjustment.

Status	Source	$Df_{eff,err}$	F	p	Post-hoc
Active	Date	6, 7	29.953	**<0.001**	D1 > D2, D3, D4
	Date×Treatment	6, 7	0.267	0.936	p=0.008; p<0.001; p=0.009
	Date×Depth	6, 7	7.418	**0.009**	
	Date×Treatment×Depth	6, 7	0.946	0.519	
	Treatment	1, 12	169.222	**<0.001**	Wave < Control
	Depth	1, 12	1.222	0.291	
	Treatment×Depth	1, 12	13.366	**0.003**	
Inactive	Date	6, 7	15.192	**0.001**	D1 < D2, D3, D4
	Date×Treatment	6, 7	1.403	0.332	p=0.002; p<0.001; p<0.001
	Date×Depth	6, 7	3.786	0.052	
	Date×Treatment×Depth	6, 7	1.621	0.270	
	Treatment	1, 12	149.968	**<0.001**	Control < Wave
	Depth	1, 12	0.320	0.860	
	Treatment×Depth	1, 12	14.303	**0.003**	
Unclear	Date	6, 7	4.668	**0.032**	D1 > D3 p=0.022
	Date×Treatment	6, 7	4.566	**0.033**	
	Date×Depth	6, 7	1.511	0.299	
	Date×Treatment×Depth	6, 7	2.270	0.154	
	Treatment	1, 12	8.938	**0.011**	Control < Wave
	Depth	1, 12	6.959	**0.022**	
	Treatment×Depth	1, 12	0.310	0.863	

Mesocosm growth rates of R. ovata

I initially intended to record snail growth for a longer period up to four weeks. The period then had to be restricted to two weeks because of high mortality rates in the upper two depths (up to 90%) during permanent wave conditions. The mean shell length (± SE) at the start was 11.81 mm (± 0.09) in the permanent wave units and 11.83 mm (± 0.11) in the periodic wave units. In the permanent wave units, the mean growth (± SE) per day was 0.051 mm (± 0.11) within the first week and 0.034 mm (± 0.08) in the second week [total mean: 0.042 mm (± 0.08), data pooled over all treatments and depths]. However, growth (mean ± SE) differed considerably

($p < 0.001$) between treatments, with negative values in the wave mesocosm (–0.018 ± 0.009) and high positive values in the control mesocosm (0.103 ± 0.007) (Fig. 6, Table 3). I found also significant depth effects, with lower growth rates at 0.2-m and 0.4-m depth than at 0.8-m depth in both treatments ($p < 0.001$). No significant differences occurred between sampling dates or interaction of factors.

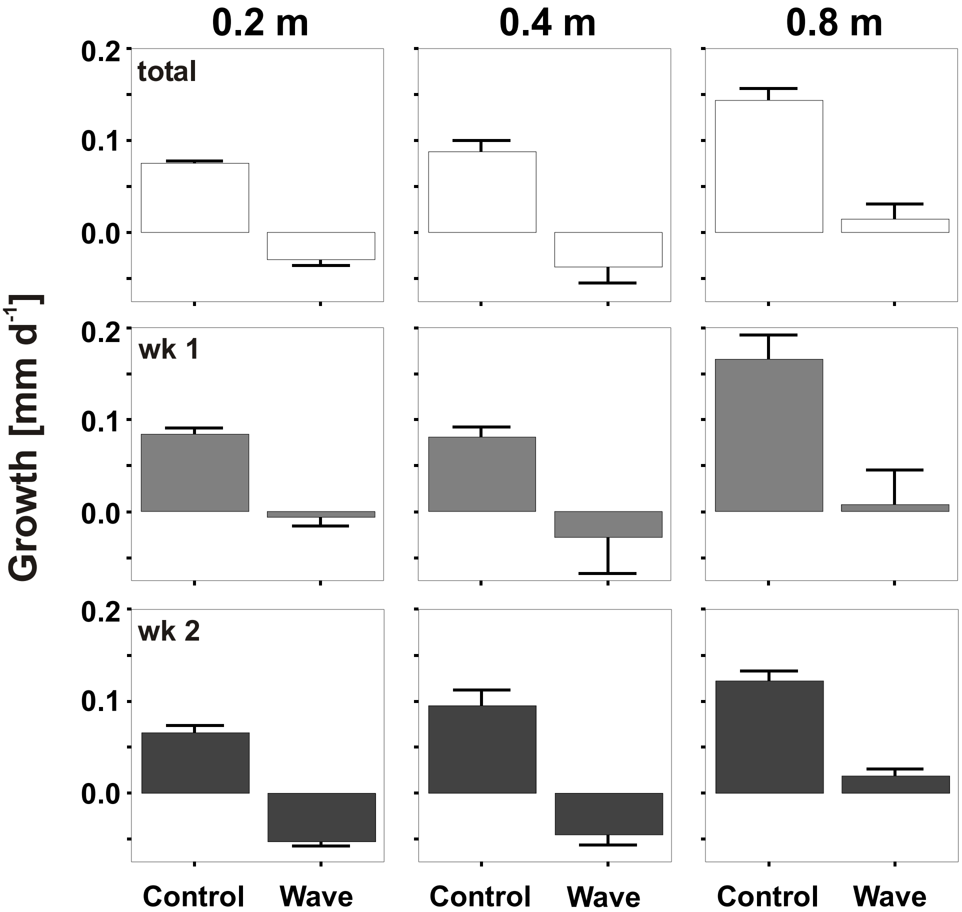

Figure 6: Shell length growth [mm d^{-1}] of *Radix ovata* within wave and control mesocosms at three depths (0.2, 0.4, and 0.8 m) under permanent wave conditions (3 bar) for two weeks (total, wk 1, wk 2).

In the periodic wave experiment, the mean growth per day was 0.077 mm (± 0.058) (all data pooled) and was lower in the wave mesocosm [0.065 mm (± 0.056) per day] than in the control mesocosm [0.089 mm (± 0.059) per day]. However, the variability of growth rates was higher than in the permanent wave experiment. Growth rates were still significantly lower in the wave mesocosm than in the control mesocosm ($p = 0.033$). Furthermore, the interaction of treatment and depth was significant (p = 0.049) (see Table 3). I therefore examined growth rates in separate analyses of treatment by depth and depth by treatment. These analyses revealed that differences were based on lower growth rates at 0.2-m depth (p = 0.005). At 0.8-m depth, growth increased in the control from the first to the second week, but decreased in the wave mesocosm, whereas at 0.4-m depth, growth generally decreased in the wave mesocosm and in the control mesocosm, but was more pronounced in the control mesocosm.

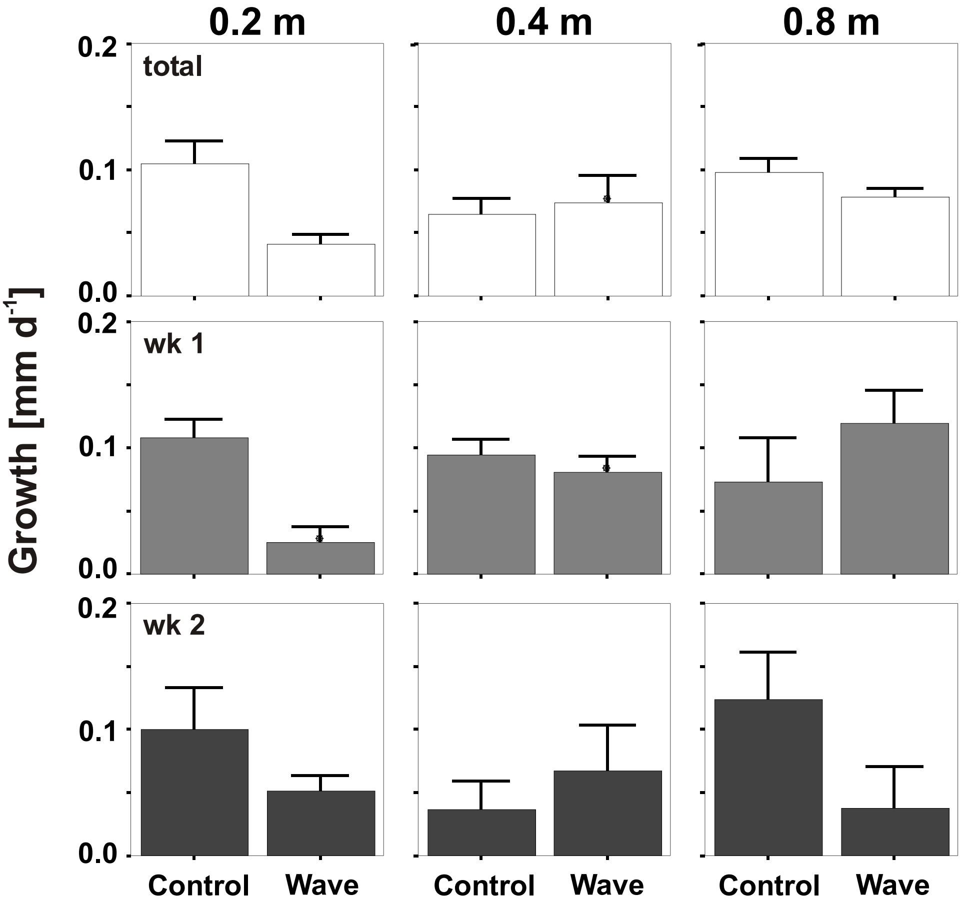

Figure 7: Shell length growth [mm d^{-1}] of *Radix ovata* within wave and control mesocosms at three depths (0.2, 0.4, and 0.8 m) under periodic wave conditions (3 bar, 5 min waves, 25 min pause) for two weeks (total, wk 1, wk 2).

Table 2: Results of repeated measurement ANOVA of actual place of residence (food: within current, current: no food, sheltered: no food) at recording times D1–D7. The main effects were compared in a post-hoc comparison with Tukey's HSD. The p-values in boldface are significant after sequential Bonferroni adjustment.

Status	Source	$Df_{eff,err}$	F	p	Post-hoc
Food	Date	6, 7	1.361	0.345	
	Date×Treatment	6, 7	6.656	0.012	
	Date×Depth	6, 7	0.587	0.733	
	Date×Treatment×Depth	6, 7	1.248	0.385	
	Treatment	1, 12	5.348	**0.039**	Wave < Control
	Depth	1, 12	5.926	**0.031**	0.2 < 0.4
	Treatment×Depth	1, 12	0.370	0.554	
Current	Date	6, 7	11.296	**0.003**	D1 < D2
	Date×Treatment	6, 7	2.752	0.106	
	Date×Depth	6, 7	0.497	0.794	
	Date×Treatment×Depth	6, 7	0.811	0.593	
	Treatment	1, 12	11.059	**0.006**	Control < Wave
	Depth	1, 12	4.704	0.051	
	Treatment×Depth	1, 12	<0.001	1.000	
Sheltered	Date	6, 7	11.484	0.003	
	Date×Treatment	6, 7	11.798	0.002	
	Date×Depth	6, 7	2.484	0.130	
	Date×Treatment×Depth	6, 7	0.513	0.783	
	Treatment	1, 12	11.027	**0.008**	Wave < Control
	Depth	1, 12	3.610	0.082	
	Treatment×Depth	1, 12	1.299	0.277	

Table 3: Results of repeated measurement ANOVA of growth rates per day (mm) under permanent wave conditions and periodic wave conditions. The main effects were compared in a post-hoc comparison with Tukey's HSD. The p-values in boldface are significant after sequential Bonferroni adjustment.

Source	$Df_{eff,err}$	F	p	Post-hoc
	Permanent			
Date	1, 90	1.215	0.273	
Date×Treatment	2, 90	0.834	0.438	
Date×Depth	1, 90	0.006	0.939	
Date×Treatment×Depth	2, 90	1.266	0.297	
Treatment	1, 90	129.715	**<0.001**	wave < control
Depth	2, 90	10.301	**<0.001**	0.2m = 0.4m < 0.8m
Treatment×Depth	2, 90	0.509	0.603	
	Periodic			
Date	1, 89	0.908	0.343	
Date×Treatment	2, 89	0.280	0.598	
Date×Depth	1, 89	0.630	0.535	
Date×Treatment×Depth	2, 89	2.602	0.080	
Treatment	1, 89	4.694	**0.033**	wave < control
Depth	2, 89	0.605	0.548	
Treatment×Depth	2, 89	3.114	0.049	

Wave measurement

Both methods of measuring waves, i.e. using the acoustic Doppler velocity meter and measuring the gypsum dissolution rate, showed a distinct depth dependency of increasing wave exposure from the deepest to the most shallow depth (Table 4). The gypsum dissolution rates significantly differed between treatment and depth, but also the interaction of treatment and depth (all $p < 0.001$, Table 4). Not surprisingly, the effect of wave propagation and dissipation was significantly higher with increasing water depth (Table 4, with post-hoc comparison Tukey's HSD). The dissolution rates of gypsum spheres were significantly lower in the control mesocosm than in the wave mesocosm at either depth. Solving the interaction of depth and treatment in separate analyses of gypsum dissolution clearly revealed that depth dependency is restricted to the wave mesocosm ($df_{2,12}$, $F_{678.75}$, $p < 0.001$) and was not significant in the control mesocosm ($df_{2,12}$, $F_{0.735}$, $p = 0.500$). A detailed technical and methodological description of the wave machine as well as wave measurement, propagation and dissipation of waves in the mesocosm will soon occur (Scheifhacken, Klahold & Hofmann submitted).

The produced mesocosm turbidity measured as gypsum dissolution rate are clearly in a similar range of regular field conditions at 0.4-m depth (Table 4). Wave exposure differed during the few exemplified samplings at the three lake sites ($df_{2,50}$, $F_{158.6}$, $p < 0.001$) and week of exposure ($df_{4,50}$, $F_{101.1}$, $p < 0.001$ weeks: 5=4<4=2<3<1) as well as the interaction of both ($df_{8,50}$, $F_{10,47}$, $p < 0.001$; all comparison with Tukey's HSD). However, the northern sites S2, S3, S5 are generally more exposed than the sites at the southwestern shore S1, S4 (Table 4, separate ANOVAs).

Periphyton content

The periphyton content [mean (± SE)] was higher at the beginning of the experiments [24.4 (± 3.1) mg cm^{-2} organic matter and 2.8 (± 0.6) mg cm^{-2} ash-free dry mass] than at the end of the experiments [10.5 (±1.5) mg cm^{-2} organic matter and 1.8 (± 0.2) ash-free dry mass in the wave mesocosm, and 15.2 (±1.2) mg cm^{-2} organic matter and 2.2 (0.2) mg cm^{-2} ash-free dry mass in the control mesocosm]. The upper two depths differed significantly, with lower values in dry weight at 0.2-m depth than at

0.4-m depth (permanent waves, $F_{6.34}$, $df_{4, 36}$; $p = 0.008$) and between the treatments (periodic waves, $F_{12.57}$, $df_{4, 36}$; $p = 0.002$, wave < control). However, the lowest values of ash-free dry mass recorded [1.8 (± 0.2) mg cm^{-2}] still provide sufficient organic matter for snails to feed upon (N. Scheifhacken, unpublished data), and are higher than results of Lake Constance previously published (lowest values of 0.4 mg cm^{-2}; Fink 2005).

Table 4: Results of turbidity measurement and 2-way ANOVA statistics in wave and control mesocosms and 3, 5 lake sites S1-S5 respectively. Results of gypsum dissolution are compared with results obtained with the acoustic Doppler velocity meter (ADV) in the mesocosm. The mesocosm waves were permanent, and 3 bar pressure was applied. The main effects were compared in a post-hoc comparison with Tukey's HSD with sequential Bonferroni adjustment.

	Gypsum dissolution — mesocosm			**ADV**
Treatment	**Water depth (m)**	**mean (g h^{-1})**	**SE**	**Velocity (m s^{-1})**
	0.20	1.545	0.015	0.150–0.200
Wave	0.40	1.018	0.029	0.055–0.100
	0.80	0.429	0.017	0.060–0.080
	0.20	0.233	0.010	-
Control	0.40	0.227	0.006	-
	0.80	0.221	0.002	-
	2-way ANOVA – Gypsum dissolution mesocosm			
Source	**$d_{eff, err}$**	**F**	**p-value**	**Post-hoc**
Treatment	1,24	554.813	<0.001	control < wave
Depth	2,24	4037.852	<0.001	0.2 m < 0.4 m < 0.8 m
Interaction	2,24	519.043	<0.001	

	Gypsum dissolution — field [mean ± SE (g h^{-1})]				
			samplings		
site	**1**	**2**	**3**	**4**	**5**
S4	0.921 ± 0.023	0.316 ± 0.083	0.616 ± 0.022	0.521 ± 0.115	0.492 ± 0.013
S1	1.114 ± 0.008	0.501 ± 0.018	0.733 ± 0.013	0.549 ± 0.062	0.462 ± 0.008
S5	1.741 ± 0.036	1.222 ± 0.013	1.208 ± 0.019	0.768 ± 0.079	0.685 ± 0.011
S3	—	—	—	—	0.708 ± 0.019
S2	—	—	—	—	1.034 ± 0.039
	2-way ANOVA – Gypsum dissolution field				
df; F	$df_{2,11}$; $F_{318.9}$	$df_{2,6}$; $F_{93.3}$	$df_{2,9}$; $F_{287.5}$	$df_{2,12}$; $F_{2.4}$	$df_{4,20}$; $F_{109.2}$
p-value	p<0.001	p<0.001	p<0.001	p=0.138	p<0.001
Post-hoc	S4<S1<S5	S4=S1<S5	S4<S1<S5	S4=S1=S5	S1=S4<S5=S3>S2

Discussion

To date, studies on the growth rates and behavioural traits of freshwater gastropods in relation to wave exposure are very limited. Only qualitative field observations of *Lymnaea stagnalis* (Arthur 1982) and *Potamopyrgus jenkinsi* and *Theodoxus fluviatilis* (Schernewski 2000) have been published. In contrast, the importance of physical constraints on marine gastropods has been widely recognised (e.g. Atkinson & Newbury 1984; Brown & Quinn 1988; Trussell 1997; Jenkins & Hartnoll 2001; Rios-Jara *et al.* 2004).

In the present study, the common freshwater pulmonate snail *R. ovata* clearly responded to wave-induced turbulence by reducing its grazing and movement, as compared to the calm control conditions. The retreated snails are forced to stop their ingestion completely under such turbulent conditions (P. Fink, Konstanz, personal communication). This observation is strongly supported by the results from the growth experiment, specifically in the permanent wave condition. After two weeks of exposure to permanent waves, a high mortality at the upper two water depths (0.2- and 0.4-m depth) was observed. Furthermore, this mortality was accompanied by negative growth rates at both water depths. At 0.8-m depth, the snails could remain within the wave mesocosm, but the growth was still significantly lower than in the control mesocosm. Owing to the experimental constraints, I can only assume that snail activity at 0.8-m depth remains lower than the control, but should presumably also be higher than at the upper two depths. Negative shell growth partly reflects the systematic error of the measuring tools. The snails measured were alive, and since retreated individuals probably cannot be positioned exactly in the same sitting conditions than measured before, hence, the angle from the basal lip to the apex might vary slightly. Furthermore, the transparent outer mantle edge is difficult to separate from the calciferous material on living snails, and snails might also reabsorb the mantle edge at least partly under unfavourable conditions. Negative shell length has also been observed by others (Fink & Von Elert 2006).

In a feeding experiment, Brendelberger (1997b) demonstrated that the closely related (or conspecific, see Methods) snail *R. peregra* can still grow (24–30% of the control) and survive for 11 weeks with low-quality food, which was simulated by offering faeces. His experiments also revealed that *R. peregra* voluntarily and regularly fed on its own faeces, which still contained living cells of green algae and diatoms and were rich in bacteria after gut passage. In the experiments, coprophagy might suit as a supplementary food source in the controls, but this potential food source was probably suspended by waves and was thus not available to snails. However, I demonstrated sufficient periphyton supply even under the most-exposed conditions after each week of permanent wave exposure (N. Scheifhacken, unpublished data). Fink (2005) recorded the lowest periphyton biomass in Upper Lake Constance from June to July 2003 (2.8 µg cm^{-2} chlorophyll *a* and 0.4 mg cm^{-2} ash-free dry mass). He concluded that food quantity was not limited, which corresponded with the calculations of Stelzer & Lamberti (2002), who documented for the lotic freshwater gastropod *Elimia livescens* (which is a very efficient grazer) that only 0.1 mg ash-free dry mass cm^{-2} would remain on substrate surfaces even with limiting quantities. Nevertheless, in the permanent wave experiment, most individuals could not survive at the upper two depths for more than two weeks, thus indicating either a high energy consumption necessary to remain within the wave zone, e.g. to remain attached (Denny 1994), or direct lethal effects of wave turbulence. As demonstrated by Brendelberger (1997b), low-food stress alone was not severe enough to cause high mortality rates after only two weeks in his laboratory experiments. In the experiments, growth rates remained suppressed at the upper depth of 0.2 m in the wave mesocosm compared to the control, even with mild disturbances, i.e. periodic waves, and all individuals survived at either depth.

The results of the activity experiment and the simultaneously recorded place of residence also indicate that snails were able to move on stones, altering their position throughout the wave exposure. Brendelberger (1994) measured the movement of *R. peregra* in the laboratory and obtained a mean speed (± SE) of 2.1 cm min^{-1} (± 0.3). P. Fink (personal communication), however, observed maximum crawling speeds of approximately 20 cm min^{-1}. *L. peregra* is also able to move several meters a day (Jarne & Delay 1990). Interestingly, *R. ovata* individuals did not clearly avoid exposed sites or prefer if exposed to waves such places with food supply. However, micro-scale flow or turbulence patterns around the concrete stones were not measured. Therefore, the sheltered and current categories should be treated with caution. Nevertheless, the observed avoidance of periphyton tiles with wave exposure still remains apparent.

Food selectivity of *R. ovata* (and related species) has been controversially discussed in the literature. Several authors found evidence for an active food selection in laboratory (Brendelberger 1995, 1997a; Fink 2005) and in field experiments (Lodge 1986), but contrasting findings based on gut content analyses of *R. peregra* have been also presented by Reavell (1980), who observed a high variety of digested algae and other components, including detritus.

Growth rates (mm d^{-1}) of *R. ovata* (and related species) in standardised laboratory experiments presented in literature differ considerably. Fink (2005) found maximum growth rates of juvenile *R. ovata* of 0.22 mm d^{-1} and 0.12 mm d^{-1} with high and low quantities of nutrient-saturated green algae (*Ulothrix fimbriata*), respectively. In contrast, Brendelberger (1997a) described 0.051 mm d^{-1} and 0.013–0.023 mm d^{-1} in juvenile *R. peregra* as high and intermediate growth rates, respectively. The observed growth rates (0.089–0.103 mm d^{-1} in controls) are intermediate compared to both of these laboratory studies, but in contrast to these studies, older individuals (shell length approximately 11 mm instead of 4 mm) were used, which generally have lower growth rates (P. Fink, personal communication; Brendelberger 1995; Rios-Jara *et al.* 2004). Therefore, a sufficient food and nutrient supply in the experiments can be assumed. Also a decrease in growth rates in the controls from the first (permanent wave) to the second (periodic wave) experiment was observed, which indicates a seasonality of the growth rates. This can be interpreted as a suppressed growth prior to reproduction (see Brendelberger 1995).

Dussart (1987) investigated the effects of water flow on the detachment of some pulmonate freshwater gastropods, including *L. peregra,* in relation to shell profile, body mass, and foot area. The maximum velocity endured reported by Dussart (1987) is 0.86 m s^{-1}, compared to maximal currents of 0.10–0.25 m s^{-1} measured in the present study. However, *L. peregra* remained attached for a long time (1200 s at maximum flow rate) irrespective of its shell size. This confirms the present results, i.e. snails remained attached under all applied wave conditions. However, the ability to adhere to the substratum has been found to be positively related to snail foot size (Dussart 1987). This has been also demonstrated for marine gastropods (e.g. Atkinson & Newbury 1984; Trussell 1997; Hohenlohe 2003). Tenacity has been demonstrated to be directly proportional to foot area, but did not increase isometrically with shell height in two *Littorina* species, resulting in a lower tenacity/drag ratio for larger individuals (Hohenlohe 2003). However, a larger foot or shell size might also be disadvantageous with respect to overall metabolic costs and the amount of energy left for reproduction. Locomotion itself is attributed with a high energy cost because of pedal mucus production (Denny 1980).

Several marine gastropods have greater shell lengths at protected shores than at exposed shores (Brown & Quinn 1988; Trussell 1997); squat shell shape (Trussell 1997) or larger shell diameter (Rios-Jara *et al.* 2004) at exposed shores has also been documented. Furthermore, differences in shell size or growth rates can be related to shore height for some marine taxa (Hobday 1995; Tanaka *et al.* 2002). The relative importance of wave action *vs.* genetic determination was investigated by some authors using tagged snails reciprocally transferred between sites (Brown & Quinn 1988; Trussell 1997) or into laboratory flow tanks (Trussell 1997, 2002). The total wet mass of three species (*Collisella digitalis*, *Collisella scabra*, and *Nucella emarginata*) increased at protected sites (34, 43, and 9.5%, respectively) and decreased at exposed sites (2, 2.7, and 1%, respectively) over 2.5 months (Brown & Quinn 1988). Trussell (1997) found the variation in foot size in wave-exposed snails (*Littorina obtusata*) less flexible than that of protected conspecifics, which produced larger foot sizes when raised in high velocity flumes than controls growing at their native protected shores. In contrast, snails initially exposed to waves showed no change in foot size irrespective of rearing under high or low velocity conditions thereafter. In a second study, Trussel (2002) presented evidence that both flow velocity and source of population influenced growth (shell length, thickness, mass; tissue mass), with greater growth rates in low-flow environments than in high-flow environments. Furthermore, the growth of the wave-exposed population exceeded the growth of the sheltered population, irrespective of the flow treatment. The greater growth potential was particularly evident at low velocity. The counter gradient variation in growth rates was interpreted by Trussel (2002) as a selection for fast-growing genotypes in wave-exposed habitats to compensate limitations on foraging time and therefore energy availability for growth under increased hydrodynamic stress. This is supported by the findings of Jenkins & Hartnoll (2001), who investigated the food supply, grazing activity, and growth rates of the limpet *Patella vulgata* with respect to wave exposure. Grazing activity was twice as high at the exposed shore, with lower food supply than at the sheltered site, but growth rates did not differ between exposed and sheltered shores.

As a consequence of the results obtained in the present study and the published mechanism of various marine snail taxa, a further focus on growth rates, survival success, and body mass increase of *R. ovata* under ambient field conditions and under different hydrodynamic conditions is suggested in future studies. The shell form differences between the freshwater snails *R. peregra* and *R. ovata* have been discussed with respect to their specific habitat preferences. Wullschleger & Ward (1998) argues that the aperture expansion in *R. ovata* allows a larger foot, which is advantageous for remaining attached in turbulent environments. Lam & Calow (1988) found significant differences in shell shape and size between lotic (> 0.3 m s^{-1}) and lentic (<0.04 m s^{-1}) habitats for *L. peregra*, but they excluded individuals from intermediate habitats, such as slow-flowing streams and wave-swept shores. Similar observations have been made with a *Lymnaea stagnalis* population in a wave-swept freshwater environment (Arthur 1982). Wullschleger & Jokela (2002) demonstrated also a wide plasticity in shell morphology between *R. ovata* and *R. peregra* from four populations, which converged into similar phenotypes in the laboratory after two generations, yet the reproductive traits remained different. In the present study, only individuals from site S1 (intermediate exposure status) were used and exposed to mesocosm conditions to which they should have been adapted. Similar turbidity ranges as produced in the mesocosm were regularly recorded in field (Table 4) and are also known from other studies (Chapter 5, Pabst 2005; Pabst *et al.* accepted). Differences in growth rates, mean shell size, and timing of the reproduction cycle of *R. ovata* within differently exposed natural habitats cannot be solved here, but I plan on addressing these points in future studies.

In the present study, the field abundance of *R. ovata* was highest at site S1, which is exposed to intermediate wave action, compared to the more exposed sites S2, S3, and especially S5, and to the more sheltered site S4 (Table 4, Bäuerle *et al.* 1998). At site S4, the extreme amount of fine, silty sediment on top of the cobblestones paralleled by locally high drift and accumulation rates of finer sediments may contribute to unfavourable conditions for periphyton growth and snail distribution (N. Scheifhacken, unpublished data). But in contrast to the more-exposed sites, S2, S3 and especially S5, site S1 might contain an optimal periphyton/sediment ratio (Storey 1970; James *et al.* 2000b). Higher sediment incorporation into peripython increased the grazing rate and assimilation efficiency of the snail *Potamopyrgus antipodarum* at similar oligotrophic field conditions in New Zealand (James *et al.* 2000b). We would expect from field observations (N. Scheifhacken, L. Peters, unpublished data) that silt content is generally reduced at the exposed site and in combination with slope, fetch length, and effective wave exposure, this is presumably lowest at site S5, the site with the lowest abundances of *R. ovata*. In contrast to the present results, some marine gastropods are generally found in higher abundances at the exposed site (Brown & Quinn 1988). Brönmark (1988) argues that snail distribution might be strongly determined by vertebrate predation while others found no evidence for such influential biotic interaction in Upper Lake Constance (Baumgärtner 2004; Chapter 4, 5).

The *P. antipodarum* grazing rate is variable at various depths. The rate is generally greater at 2-m than 10-m depth and varies from 0.09 to 0.37 µg chlorophyll *a* per snail per day, but tends to be highest in concentrations above 4 µg cm^{-2} (James *et al.* 2000b). A variety of studies have focused on the percentage of periphyton removed, which ranges from 37 to 78% for various snail taxa (Rounick & Winterbourn 1983; Lowe & Hunter 1988; Lamberti *et al.* 1995). James *et al.* (2000b) argued that *P. antipodarum* might search for more valuable food sources measured as chlorophyll *a* content at low grazing rates rather than enhance feeding rates. *R. ovata* is capable of compensatory feeding. The snails increased their food consumption up to three-fold when confronted with high amounts of low-quality food in a laboratory experiment (Fink 2005). However, laboratory results are based on single algae cultures with nutrient enrichments or depletions, and are thus only restrictedly comparable to the natural periphyton layer. In contrast to Fink (2005), Stelzer & Lamberti (2002) did not find food-quality effects in a stream outdoor mesocosm experiment with snail *Elimia livescens* fed on high quantities of semi-natural periphyton of unknown taxa composition. Following the assumptions of Fink (2005) that *R. ovata* might be capable of chemotactic and behavioural responses to detect and deplete food sources efficiently in its naturally patchy environment, similar mechanisms can be assumed in outdoor mesocosms.

However, the present study reveals that hydrodynamic constraints and the total energetic costs of individual snails in a turbulent environment also influence the exploitation rate of the periphyton food source by *R. ovata*. In summary, the growth and activity of *R. ovata* was strongly influenced by hydrodynamic turbulences, as shown in the outdoor mesocosm wave experiment. A similar pattern can be assumed to be relevant under ambient conditions at lake littoral zones, hence contributing to the observed field distribution. In consequence, the distribution pattern of this species is expected to rely on an annual mean wave exposure gradient either directly owing to restrictions in growth and reproduction success and/or indirectly owing to substrate composition and food supply altered by wind abrasion or sediment accumulation and food supply (Cattaneo 1990; Chapter 6).

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Chapter 4

Trophic interaction between littoral benthic communities and the two competitors perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) under contrasting wave exposure

Nicole Scheifhacken with Diana Schleuter

Summary

The predation effects of perch (*Perca fluviatilis* L.) and ruffe (*Gymnocephalus cernuus* (L.)) on the eulittoral benthic community in Upper Lake Constance was examined in enclosure experiments. In single and mixed fish species set-ups effects of intraspecific and interspecific competition were studied under field conditions. Cages were deployed at two sites with contrasting wave exposure, exposed and sheltered.

We found strong effects of site and sampling date on benthos abundances and composition, but only weak predation effects based on size-selective counts. Total benthos abundances, taxa density, and stomach contents of perch and ruffe were higher at the exposed site. Additionally, the benthic community structure differed between sites and was reflected in the composition of the fish diet. Surprisingly, higher abundances of most benthic taxa and size classes were found at the end of the experiment in all treatments. We assume a low accessibility of benthic organisms to fish predators, which are in general restricted to the upper substrate layer. Benthos revealed strong inherent processes on both temporal and spatial scales, which seemed to mask predation effects. We assume a bottom-up control of the studied benthos community–fish predation system.

We found evidence that interspecific competition between native perch and the recently introduced ruffe influences the foraging success and consumption rates of both fish species. Under conditions of interspecific competition, niche overlap of the two species decreased significantly at both sites. The outcome of competition, however, strongly depended on the study site. At the more sheltered site with more limited food resources, intraspecific competition masked the effects of interspecific competition. At the exposed site with higher benthos abundances, ruffe was the superior competitor.

Keywords: Competition, enclosure, fish, macroinvertebrates, predation

Introduction

Predator–prey interactions in freshwater systems have been widely studied. The effects of fish on macrobenthic prey communities are highly complex and diverse, and the results and conclusions drawn from studies on the predatory impact differ. Strong effects of fish predation in the littoral zone on invertebrate abundance or biomass or both have been observed (Crowder & Cooper 1982; Mittelbach 1988; Gilliam *et al.* 1989; Diehl 1995; Dahl & Greenberg 1999). Other authors found diverse results: Gilinsky (1984) found variable predation effects in different macroinvertebrate groups, dependent on sampling dates. Others, e.g. Hershey (1985), only detected predation effects when macrophytes were absent. Cobb & Watzin (1998) found that predation effects were only significant at high predator density for three of six prey taxa. No top-down control of benthic communities by fish were found by, e.g. Thorpe & Bergey (1981), Hanson & Legget (1986), Culp *et al.* (1991), and Baumgärtner (2004). Also highly selective preying on only few specific taxa (Gilinsky 1984; Brönmark 1994) and size-selective consumption by fish has been documented frequently (Crowder & Cooper 1982; Mittelbach 1988; Butler 1989; Gilliam *et al.* 1989; Macchiusi & Baker 1991; Peckarsky *et al.* 2001). However, while some authors claim a size selectivity of predatory fish for large organisms (Gilinsky 1984; Mittelbach 1988), others found fish to prefer small organisms (Hershey 1985; Macchiusi & Baker 1991).

Various reasons for these controversial results have been proposed. Prey availability could be the main factor that influences predator success (Boisclair & Leggett 1985), and can be altered by habitat complexity, for instance by vegetation stands (Crowder & Cooper 1982; Werner *et al.* 1983; Gilinsky 1984; Diehl 1992), either through lower perceptibility of prey organisms (Gilinsky 1984), restricted manoeuvrability of predators (Winfield 1986), or altered behavioural patterns of specific prey taxa (McCollum *et al.* 1998). The behaviour, morphology, and even life history traits of invertebrates can be altered in response to chemical cues released by potential predators (Crowl & Covich 1990; Culp *et al.* 1991; Arnqvist & Johansson 1998; Baumgärtner *et al.* 2002, 2003; Kolar *et al.* 2002; Peckarsky *et al.* 2002), but also depend on specific fish taxa and fish density (Baumgärtner *et al.* 2002; Kolar *et al.* 2002). The common amphipod *Gammarus roeseli*, for instance, displayed predator avoidance behaviour only in preconditioned water of burbot (*Lota lota*) and crucian carp (*Carassius carassius*), but not of juvenile perch (*Perca fluviatilis*) (Baumgärtner *et al.* 2002). In a similar study by Kolar *et al.* (2002) amphipods (*Gammarus pseudolimnaeus*) decreased their activity more pronouncedly in the presence of ruffe (*Gymnocephalus cernuus*) than of yellow perch (*Perca flavescens*).

In addition to food availability, also competition between predators can influence their diet composition and consumption rate (Hanson & Leggett 1986; Bonesi *et al.* 2004; Dieterich *et al.* 2004a, b; Schleuter & Eckmann 2006). Eurasian perch (*Perca fluviatilis*), and ruffe (*Gymnocephalus cernuus*), introduced in the 1980s (Roesch & Schmid 1996), are common littoral fish species in Lake Constance (Fischer & Eckmann 1997a; Reyjol *et al.* 2005) and are assumed to be competitors for macroinvertebrates. Perch undergo an ontogenetic diet shift from zooplankton, through zoobenthos to fish (Collette *et al.* 1977; Thorpe 1977; Persson 1986; Radke & Eckmann 2001). Ruffe is usually described as an effective benthivorous generalist with a diverse diet (Collette *et al.* 1977; Hölker & Thiel 1998; Kangur *et al.* 1999).

Various aspects of intraspecific and interspecific competition for food of perch and ruffe have been evaluated in several laboratory studies (Bergman & Greenberg 1994; Savino & Kolar 1996; Fullerton *et al.* 1998, 2000; Dieterich *et al.* 2004a, b; Schleuter & Eckmann 2006). Dieterich *et al.* (2004a), for instance, focused on the influence of competition on food consumption over different substrate types. When food was provided on bare and mussel-covered stones, perch out-competed ruffe (Dieterich *et al.* 2004b). In a further study (Dieterich *et al.* 2004b) compared the influence of food availability and found that perch consumed more benthic food than ruffe under conditions of high food supply; however, with low food supply, perch consumed much less, whereas ruffe consumption remained high on fine sediments. The authors concluded that under natural conditions with limited food resources, ruffe will forage efficiently over fine sediments and perch over coarse sediments.

In the study of Fullerton *et al.* (1998) on the influence of competition on prey selection of the two species, perch and ruffe chose a wider range of prey organisms in mixed species experiments. In single species experiments, both species selected mainly soft-bodied taxa, e.g. *Chironomus* and *Chaoborus*, whereas in mixed species experiments, they also included less-preferred prey taxa, e.g. *Gammarus,* with intermediate body types, i.e. sclerotized but without shell or cases. Bergman & Greenberg (1994) could show in mesocosm studies, that under the presence of roach (*Rutilis rutilus*) perch and ruffe growth rates decreased with increasing ruffe density, and perch switched to less-preferred food items, whereas ruffe's diet composition remained constant.

The structure of the littoral zone of Lake Constance is highly variable and the shallow area is exposed to strong hydrodynamic forces. These forces, however, are still widely ignored as a potential factor influencing benthic or fish communities in freshwater as compared to marine habitats. In a comparative study marine littoral fish production was highly correlated with benthic (crustacean) production rates and with sea grass biomass as a structural component, but was negatively correlated with wave exposure measured as fetch (Edgar & Shaw 1995). Furthermore, hydrodynamics influence predator–prey interaction in marine (Weissburg & Zimmer-

Faust 1993; Powers & Kittinger 2002) and lotic freshwater habitats (Lancaster *et al.* 1990; Peckarsky *et al.* 1990; Hansen *et al.* 1991; Lancaster 1996) and recent studies indicate the importance of hydrodynamics in structuring lake littoral benthic communities. Growth rates and activity of the common littoral snail *Radix ovata* are strongly suppressed under experimental wave conditions (Chapter 3). Furthermore, the distribution pattern of a variety of macrobenthic species seems to rely on the hydrodynamic disturbance history of the sites (Chapter 6, Scheifhacken *et al.* 2007).

In the present study, we analysed whether the littoral benthic community of Lake Constance is top-down or bottom-up controlled and whether the benthic communities at two sites with different wind and wave exposure have an impact on the competitive outcome of the two competing fish predators perch and ruffe. We hypothesised, that i. benthic abundances and biomass are top-down controlled, and expected alterations in size structure and community composition as a result of predatory impact, ii. we assumed fish predation to be influenced by competitive interactions and that iii. both, predatory impact and competitive interactions are influenced by two study sites with different wave exposure.

Methods

Study site

The experiments were conducted in Upper Lake Constance, a large, oligotrophic (10 µg P l^{-1} during spring circulation) pre-alpine lake in central Europe, with a surface of 473 km^2, a mean depth of 101 m, and a maximum depth of 254 m. Westerly winds prevail throughout the year, with a second less-dominant peak of easterly winds especially in winter (Bäuerle *et al.* 1998). The littoral zone in Lake Constance is defined as the upper 10 m and is restricted to less than 10% of the total lake area (Wessels 1998). Along the 186-km shoreline of Upper Lake Constance, the littoral zone varies greatly, e.g. in width, sediment composition, and wind exposure, resulting in a highly variable benthic community. We chose two representative study sites: site 1 near Konstanz (Litoralgarten 47°41’26.668’’N, 9°12’18.355’’E) on the south-western shore is more sheltered against wind and ferry- and leisure-boat-induced waves owing to its geomorphologic structure and slope; the littoral zone is broad, strong wind events are rare, and the substrate consists of cobble stones loosely embedded within fine sediments with a sparse macrophyte cover of *Chara* spp. and is thus quite heterogeneous (Schmieder *et al.* 2004). Site 2 near Meersburg (47°41’37.249’’N, 9°16’11.660’’ E) on the north-eastern shore is highly exposed to westerly winds and ferry- and leisure-boat-induced waves (Bäuerle *et al.* 1998). The shore is narrow, the substrate consists mainly of coarse stones, and macrophytes are lacking above 5 m (Schmieder *et al.* 2004).

Experimental design

The experimental design involved two factors with two levels each, fish species (perch and ruffe) and competition (interspecific and intraspecific) plus a control treatment without fish. Three cages each were stocked with either perch or ruffe or both species or no fish (control), i.e. 12 cages were randomly deployed in a block design. Experiments started at site 1 on July 13. 2004. The cages were removed after one week, cleaned, and then exposed for one week at site 2 starting July 21. We know from previous studies, that site differences strongly superimpose such minor time displacements of one week (Chapter 6, Scheifhacken *et al.* 2007).

Each cage consisted of a steel frame (1.0×0.8×0.4 m) covered with 0.8-mm mesh gauze, which allowed water to flow through the cage, but prevented large-and medium-sized macroinvertebrates and fish to enter or leave. The bottom was open to allow fish access to the sediment. The top cover could be opened for benthos sampling and fish removal and had an additional opening with bayonet coupling (18-cm diameter) for fish stocking. The cages were set by scuba divers at a water-depth of 1.0 m along a transect, with 1.5 m between the cages. The cages were anchored in the sediment with 40-cm pegs at each corner. The bottom edges were sealed with sand-filled sacks of 90 cm length and 20 cm diameter placed on the outside and covered with pebbles. Before fish were introduced into the cages, divers sampled benthos (see next section) and removed any fish or crayfish from the cage bottom with a dip net; the top cover was then immediately closed. Minor perturbations of benthos by divers are likely, but all cages were treated alike, and fast resettlement and uniform redistribution within cages was visually observed.

Benthos

Benthos was quantitatively sampled (25 cm×25 cm, A_o = 625 cm^2) by scuba divers using a suction sampling device as developed and described by Baumgärtner (2004) and Mörtl (2003). All substrates or macrophytes within the sample frame were transferred into a hand net (200 µm) while the pump run continuously. This minimised the escape of mobile organisms and allowed further sampling of the upper fine sediment layer. Invertebrates and suspended sediment were retained within a filter inlet (200 µm) and then added to the hard substrate fraction. Benthos in the cages was sampled immediately before fish were introduced into the cages. The sampled area was covered with concrete stones to mark the position and compensate for substrate removal. Benthos was re-sampled at the end of the experiment after fish removal. Benthos outside of the cages at the same depth stratum were sampled to detect natural predation pressure and cage effects.

All samples were brought to the laboratory and processed immediately. Coarse stones were carefully brushed and rinsed within a bowl (200 µm) to remove attached invertebrates, which were stored in 70% ethanol. Fine sediments were repeatedly floated to suspend all invertebrates in the water column. Invertebrates were identified to the species level when possible or to the nearest taxonomic level using a dissection binocular (10× magnification), counted, and classified into three size classes (small, medium, and large) according to values of (Baumgärtner & Rothhaupt 2003) and standard determination literature. Values of unlisted taxa were based on our own extensive length/dry mass calculations, conforming to their methods.

Fish

The perch (8.5 ± 0.6 cm, mean ± SD) and ruffe (8.0 ± 0.9 cm) used in this study were caught in the lake with a lift net nine months before the experiments started and held in 300-l aquaria under a natural day/night cycle. At least two weeks before the experiment started, the fish were transferred to 500-l outdoor tanks for acclimatisation to natural light intensities. To provoke a competitive situation and to ensure a high predation pressure, we used high fish densities (Gilinsky 1984;

Hanson & Leggett 1986; Cobb & Watzin 1998), i.e. 10 perch or 10 ruffe or 5 perch plus 5 ruffe per cage.

Cages were stocked with fish by gently placing the fish into a Plexiglas tube that protruded the water surface and was docked to the additional opening in the top cover. The fish immediately swam downwards into the cage. The tube was removed, and the opening was sealed with a cap. At the end of the experiment, fish were removed late in the morning to ensure that the visual predator perch had time to feed and that the food ingested by ruffe during the night still remained in the stomach (D. Schleuter, personal observation). A frame with a 4-mm mesh net was placed around the cage. The top of the cage was opened, and the fish were removed by electrofishing. The fish were anaesthetised with a lethal concentration of 1,1,1-trichloro-2-methyl-2-propanol-hemihydrate (2 g/l). Formalin (10%) was injected into the body cavity to conserve the stomach contents; the fish were then stored in 4% formalin. In the laboratory, stomachs were removed and prey items were identified to the family or genus level. Insect larvae and amphipods were grouped into three size classes as described above. For the calculation of the stomach fullness (dry mass of stomach content (mg)/ wet mass of fish (g)) dry mass of prey organisms was calculated using length dry mass regressions of Baumgärtner & Rothhaupt (2003). Calculations for unlisted taxa were based on our own extensive length/dry mass calculations, conforming to their methods.

Data analysis

Total benthos abundance, taxa density, diversity parameters, dominant taxa abundances, and size classes were examined with repeated measurement MANOVA, with site and treatment as factors (Bonferroni-corrected). Variances were stabilised with log(x+1) transformation and tested for homogeneity with the Levene test. Tukey HSD post-hoc tests were applied when significant effects were detected. For all multivariate calculations, the statistical package SPSS 13.0 was used.

Predation effects on benthos community composition and fish stomach contents were examined with non-metric multidimensional scaling (nMDS) using the PRIMER 6b software package (Clarke & Warwick 2001). Benthos data were log(x+1) transformed to enhance the contribution of less-abundant taxa to overall community composition. Benthos from stomach contents, however, were computed as original data because the same order of magnitude was found in all samples (Clarke & Warwick 2001). Data were displayed in nMDS plots using the Bray-Curtis index for sample similarity calculations. A priori defined groups (site, treatment, and for benthos samples, also date) were tested with ANOSIM permutation statistics against random distribution. Species contribution was analysed using the SIMPER routine. The BVSTEP procedure was used to detect the influential prey items in stomach contents. With this procedure, the smallest possible species subset whose Bray-Curtis similarity matrix correlates at least at $\rho = 0.95$ (Spearman correlation coefficient) with the similarity matrix for the full set of species was determined.

Stomach fullness within sites was compared with one-way ANOVA and students-t as post-hoc test (Program JMP 4.0), if variance and normal distribution could be stabilised with log(x+1) transformation. Otherwise, the Kruskal-Wallis test was utilised. Sites were compared using the t-test or the Kruskal-Wallis test.

The selectivity of fish for prey items was calculated using Strauss' preference index (Strauss 1979): $L_i=r_i-p_i$, where r_i is the ratio of food type i in the diet and p_i the ratio in the environment. Negative values represent avoidance or inaccessibility, whereas positive values indicate preference for a prey type. Values above 0.20 or below –0.20 were considered as preference and avoidance, respectively.

Results

Benthic community abundance

The total benthic community abundance (mean ± SE per sample unit) pooled over both sampling dates and all sites was 4594 (± 398) (range 921–18,942) individuals. The number of taxa was 19 ± 0.4 (mean ± SE) out of a total of 47 species or higher taxonomic groups. The most abundant taxa were small non-definable Chironomidae larvae (795 ± 86), followed by older larval stages of Chironominae (524 ± 59), Trichoptera *Tinodes waeneri* (298 ± 33), Ephemeroptera *Caenis* spp. (105 ± 13), Oligochaeta (100 ± 16), Orthocladiinae (84 ± 9), Ostracoda (81 ± 27), *Gammarus* spp. (57 ± 10), Tanypodinae (56 ± 13), *Dreissena polymorpha* (19 ± 4), and *Dikerogammarus villosus* (19 ± 4) (Fig. 1); for further details see Table 1. Benthic Cladocera (309 ± 71) were only counted at site 1, after recognising this taxon from stomach contents of perch and ruffe as an unexpected important food source. As a trend, lower abundances of benthic Cladocera were found at site 2, but quantification for site 2 was not possible hereafter. However, the rank order of most of the taxa differed between sites and sampling dates. A variety of insect larvae, mainly of caddisflies and mayflies, and other invertebrates such as snails and leeches also regularly occurred, but in low numbers. Few taxa were exclusively found at one site: at site 1, *Micronecta* spp., *Hydroptila* spp. *Gammarus roeseli*, and *Stagnicola corvus*; and at site 2, *Goera pilosa*, *Sericostoma personatum/flavicorne*, and *Riolus* spp.

Table 1: Species contribution to benthos community composition, average similarity at site 1 and site 2 per sampling unit (25×25 cm). The Simper routine in PRIMER was used. *SD* standard deviation, cut off by >90%.

Species	**Average similarity (%)**	**Average abundance N**	**Average similarity (%)**	**SD**	**Contribution (%)**	**Cumulation (%)**
			Site 1 – Litoralgarten, Konstanz			
Chironominae	49.23	597.3	23.5	2.3	47.8	47.8
Chironomidae non det.		266.6	7.2	1.2	14.6	62.4
Tinodes waeneri		97.6	5.9	0.9	12.0	74.3
Tanypodinae		95.3	3.4	1.5	6.9	81.2
Ostracoda		145.1	2.5	0.8	5.0	86.2
Orthocladiinae		60.2	2.4	1.4	5.0	91.2
			Site 2 – Meersburg			
Chironominae	79.12	1324.2	39.7	7.8	50.1	50.1
Chironomidae non det.		499.2	13.8	5.0	17.5	67.6
Tinodes waeneri		450.1	11.6	3.3	14.6	82.2
Tanypodinae		188.9	4.5	2.3	5.6	87.8
Ostracoda		161.6	4.0	1.9	5.1	92.9

Benthos — site effects

Total abundance, number of taxa, species richness and diversity (except eveness), and most of the dominant single taxa revealed clear site differences with significantly lower abundances at site 1 than at site 2 (Table 2, Appendix). Exceptions were Ostracoda, Ephemeroptera without *Caenis* spp., Tanypodinae, and medium-sized Chironominae, which had significantly higher abundances at site 1.

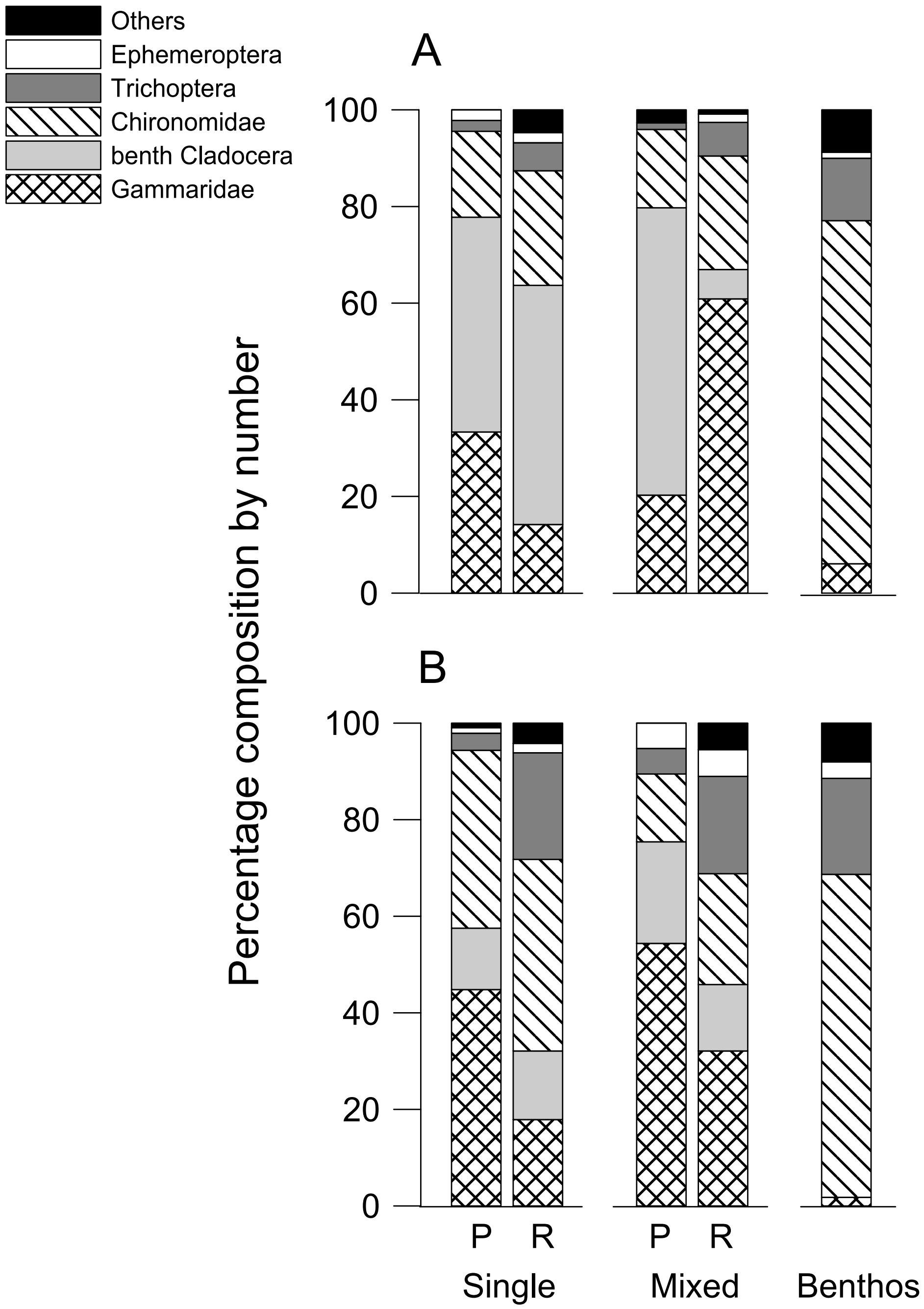

Figure 1: A, B Proportion of the main prey types found in fish stomachs and in the benthic community. **A** Site 1, Litoralgarten, Konstanz. **B** Site 2, Meersburg. *P* perch, *R* ruffe.

Benthos — date effects

Most taxa showed a significant date effect, with surprisingly higher abundances in general on the second sampling date. However, significantly lower abundances of *Tinodes waeneri* (small), *Dikerogammarus villosus* (small), *Caenis* spp. (large), and Orthocladiinae (small) were found on the second sampling date (Appendix).

Benthos — treatment effects

Significant treatment effects were only found for two taxa: small non-definable Chironomidae (cageless control / cage control p = 0.027) with higher values in cageless control samples, and large individuals of *Tinodes waeneri*. The latter showed significantly higher abundances in the cages stocked with only perch than in the mixed species cages (p = 0.003), the unstocked cages (p = 0.019), and the cageless controls (p = 0.005), but hardly not in the cages stocked with only ruffe (p = 0.067).

Benthos — interaction effects

Significant treatment by site or treatment by date interactions were found for the following taxa within specific size classes: *T. waeneri* (large), *Caenis* spp. (medium), Tanypodinae (all sizes), Orthocladiinae (small), Chironomidae non-definable (small), Chironominae (large), and Ephemeroptera with and without *Caenis* spp. (see Table 2). At site 2, significantly lower abundances of large individuals of *T. waeneri* were found in the cageless control and in the mixed species cages than in cages stocked with only perch (p = 0.016 and p = 0.047, respectively). Significantly fewer individuals of small Orthocladiinae were found in cages stocked with perch than in cageless controls (p = 0.037). Medium-sized *Caenis* spp. larvae were in lower abundances in cages stocked with ruffe than in cageless controls (p = 0.036). In cages stocked with perch, lower abundances were found than in cageless controls, but the difference was marginally not significant (p = 0.063).

Table 2: Results of repeated-measurement MANOVA on total benthos abundance, number of taxa, diversity and dominant taxa (sum), including three size classes of most taxa. All data were log(x+1) transformed, except taxa and diversity. S1 site 1, Litoralgarten, Konstanz; S2 site 2, Meersburg; D1 experimental start, week 1, D2 experimental end, week 2. Categories: C unstocked cages, N external controls, R ruffe only, P perch only, M (mixed) perch and ruffe together. Only significant results ($p < 0.05$) are shown. Values of the taxa sum are printed in bold.

		Date	Site	Treatment	Date × treatment	Site × treatment	Date × site	Date × site × treatment	Post hoc	
Abundance	N		0.007						S1<S2	
Number of taxa	S		<0.001				0.001		S1<S2	
Species richness	D		0.003				<0.001		S1<S2	
Shannon diversity	H'_{loge}	<0.001	0.002		0.019				S1<S2; D1<D2	
Pielou’s evenness	J'	0.045					0.007		D1<D2	
Chironominae	sum									
	large		0.027		0.004			<0.001	S1<S2	
	medium		0.002						S2<S1	
	small				0.029					
Orthocladiinae	sum		**<0.001**						**S1<S2**	
	small	0.019	<0.001		0.035			0.033	S1<S2; D2<D1	
Tanypodinae	sum		**<0.001**						**S2<S1**	
	large				0.007			0.009		
	medium		<0.001						S2<S1	
	small		<0.001		0.013		0.031		S2<S1	
Chironomidae non det.	sum	**0.017**	**<0.001**						**S1<S2; D1<D2**	
	small	0.009	<0.001	0.032	0.018	0.041	0.030	0.013	S1<S2; D1<D2	C<N p=0.027
Tinodes waeneri	sum	**0.009**	**<0.001**		**0.010**				**S1<S2; D1<D2**	
	large		<0.001	0.003		0.013			S1<S2	M=N=C=R<R=P
	medium		<0.001						S1<S2	
	small	0.003	<0.001		0.015		0.037		S1<S2; D2<D1	
Trichoptera excl. *Tinodes*	sum	**0.015**	**0.004**				**0.009**		**S1<S2; D1<D2**	
Caenis spp.	sum	<0.001	<0.001		0.050		0.009		S1<S2; D1<D2	
	large	0.002	<0.001				0.001		S1<S2; D2<D1	
	medium		0.025		0.003	0.021	0.019	0.025	S1<S2	
	small	<0.001	<0.001				0.017		S1<S2; D1<D2	
Ephemeroptera excl. *Caenis*	sum	**0.013**	**<0.001**				**0.001**	**0.048**	**S2>S1; D1<D2**	
Dreissena polymorpha	sum	**<0.001**	**<0.001**						**S1<S2; D1<D2**	
	large									
	medium	<0.001							S1<S2	
	small	<0.001	0.002				0.004		S1<S2; D1<D2	
Gastropoda	sum	**0.001**							**S1<S2**	
Dikerogammarus villosus	sum									
	large		0.001						S1<S2	
	medium		<0.001						S1<S2	
	small	0.033							D2<D1	
Gammarus non det.	small	0.021	0.045						S1<S2; D1<D2	
Oligochaeta	sum		**<0.001**						**S1<S2**	
	large		<0.001						S1<S2	
Ostracoda	sum	**0.003**	**0.001**						**S2<S1; D1<D2**	

Benthos — nMDS

Benthos assemblages based on abundance data for both sites combined, with site and sampling date as factors, are shown in Fig. 2A. To enhance visibility, the effects of treatments and sampling date are displayed separately for each site in Fig. 2 B, C. Benthos composition showed clear site differences (Global $R = 0.748$, $p < 0.001$) and also weak, but significant differences between sampling dates at site 1 and site 2 ($R = 0.324$ and $R = 0.366$, respectively, both $p < 0.001$, treatment data pooled) compared to random distribution (range –0.12 to 0.24). Benthos communities showed considerably higher variability between samples at site 1 than at site 2 (Fig. 2A). Average similarity between all samples was lower at site 1 (49%) than at site 2 (79%). Comparison of the two sites revealed a dissimilarity of 37% on average (Table 1). Chironomidae contributed 48% of total abundances at site 1 and 50% at site 2 (Fig. 1), but total abundance was two-fold higher at site 2 (Table 1).

Treatment effects were tested separately for each site and date. However, none of the combinations showed any effect compared to random distribution at both sites (site 1, site 2: Global $R = 0.214$, $R = 0.222$, range of random distribution -0.30 to 0.30 site 1; 0.35 site 2).

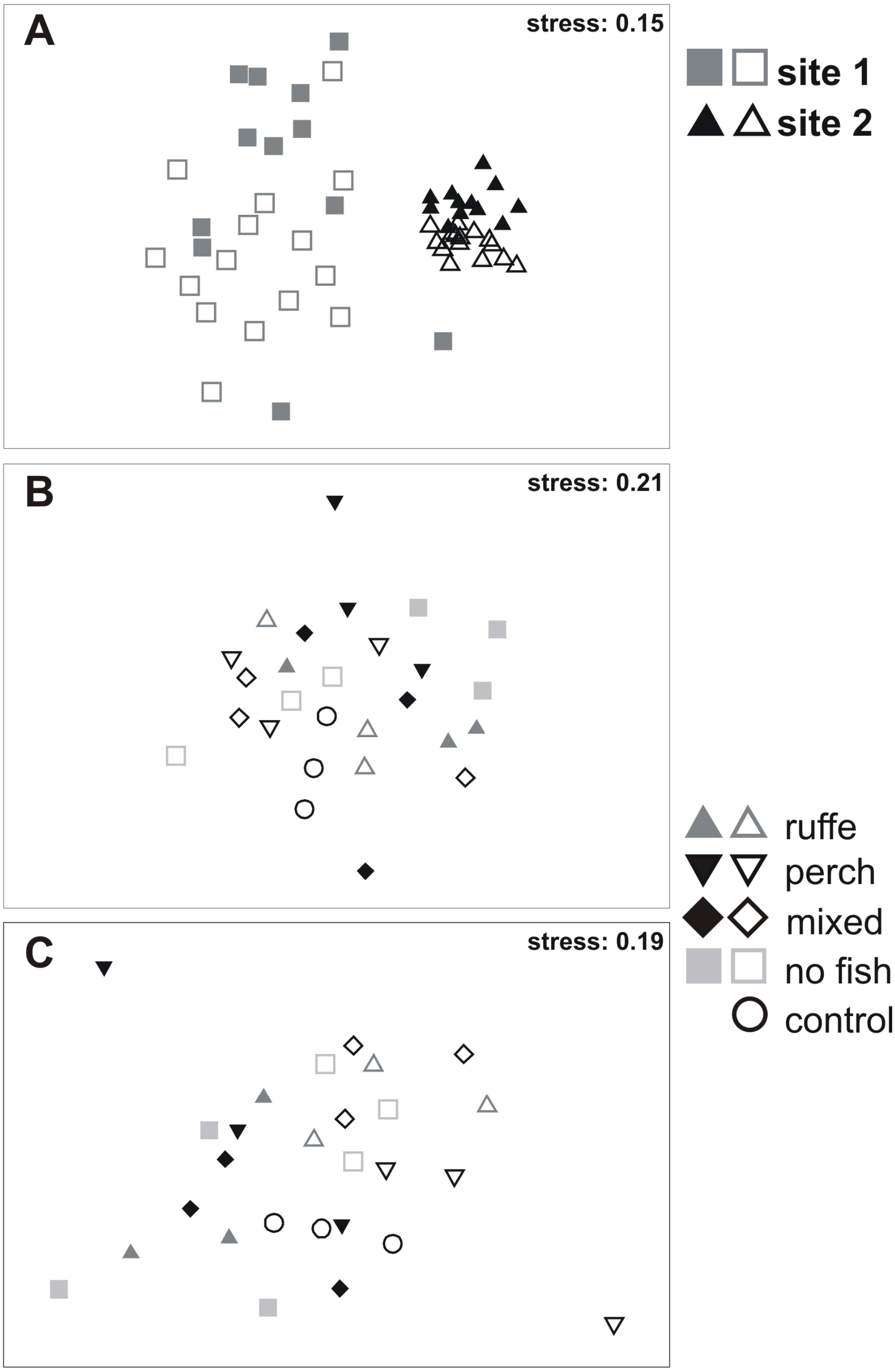

Figure 2: A–C NMDS of benthos community composition based on abundance data. **A** Sites 1 and 2 combined. The factors site and sampling date are highlighted. **B** Site 1, Litoralgarten, Konstanz. **C** Site 2, Meersburg. In **B** and **C** treatments are highlighted seperately. In **A–C**, sampling dates are indicated as follows: filled symbols, experimental start; open symbols, end of the experiment. All data are log(x+1) transformed and standardised to unit N; the Bray-Curtis similarity index was applied.

Fish

Owing to the high water turbidity at site 1, fish could barely be seen, and the escape of some fish could not be prevented. After three sampling rounds electrofishing was stopped. During the experiment at site 2, one cage stocked with both species was lifted by a storm so that the bottom edges were not completely sealed during the remaining days. Only two perch and one ruffe were recaptured, along with two eels that had invaded the cage. These were excluded from further analysis. Despite the adverse conditions, the overall recapture rate was high (> 60%), with the recapture success lower at site 1 (perch: 58%; ruffe: 38%) than at site 2 (perch: 73%; ruffe: 73%).

At site 1, perch and ruffe preyed mainly on small Gammaridae, benthic Cladocera, and Chironomidae (single species/ mixed species: perch 96%/96%, ruffe 87%/90%) (Fig. 1A). With interspecific competition, the proportion of benthic Cladocera in the diet of perch was higher (60% compared to 44%) and the proportion of small Gammaridae was lower (20% compared to 33%). For ruffe, in contrast, the proportion of Cladocera was higher with intraspecific competition (49% compared to 6%) and the proportion of small Gammaridae was lower (61% compared to 14%).

At site 2, both fish species preyed on types similar to those at site 1 (Fig. 1B). Perch preyed mainly on small Gammaridae, benthic Cladocera, and Chironomidae (single species/mixed species: 94%/89%). For ruffe, Trichoptera (22%/20%) accounted next to Gammaridae, benthic Cladocera and Chironomidae for the main prey types (91%/90%).

Both perch and ruffe ingested a higher proportion of insect larvae at site 2. Especially in the single species cages, more Chironomidae were consumed (site 1/site 2: perch: 18%/37%; ruffe: 24%/39%). The proportion of Ephemeroptera ingested was only slightly higher (up to 5%) at site 2 for both species. Perch consumed also a slightly higher proportion of Trichoptera at site 2 (single species/both species: 2%/1% compared to 4%/5%), but ruffe consumed up to a 15% higher proportion of Trichoptera at site 2 (6%/7% compared to 22%/20%).

With the nMDS and ANOSIM analysis no differences between stomach contents of perch and ruffe were found in cages stocked with only one species (Global $R = 0.125$; sample range –0.08 to 0.10; site 1: $R = 0.018$; site 2: $R = 0.097$)

(Fig. 3A, B). In the mixed species cages, however, food items consumed by perch and ruffe differed. The nMDS plot clearly divided perch and ruffe into two separate groups at both sites, even though the variability of stomach contents within one species was very high (Fig. 3C, D). The high variability was also reflected in the relatively low Global R value in ANOSIM (Global $R = 0.243$, sample range –0.16 to 0.22; site 1 $R = 0.374$, $p = 0.009$; site 2 $R = 0.275$, $p = 0.024$). However, when we removed the ruffe individual that did not consume small Gammaridae at site 1 (marked with an asterisk in Fig. 3C) from the analysis, the ANOSIM results were far more pronounced (Global $R = 0.846$, $p = 0.001$). No site differences in stomach contents were found for perch (single species: $R = –0.003$; mixed species: $R = 0.153$; Global R and range for single and mixed species see above). For ruffe, in contrast, differences between sites were more pronounced. In cages stocked only with ruffe, the differences were significant ($R = 0.233$, $p = 0.001$), and in cages stocked with both species, they were almost significant ($R = 0.212$, $p = 0.097$).

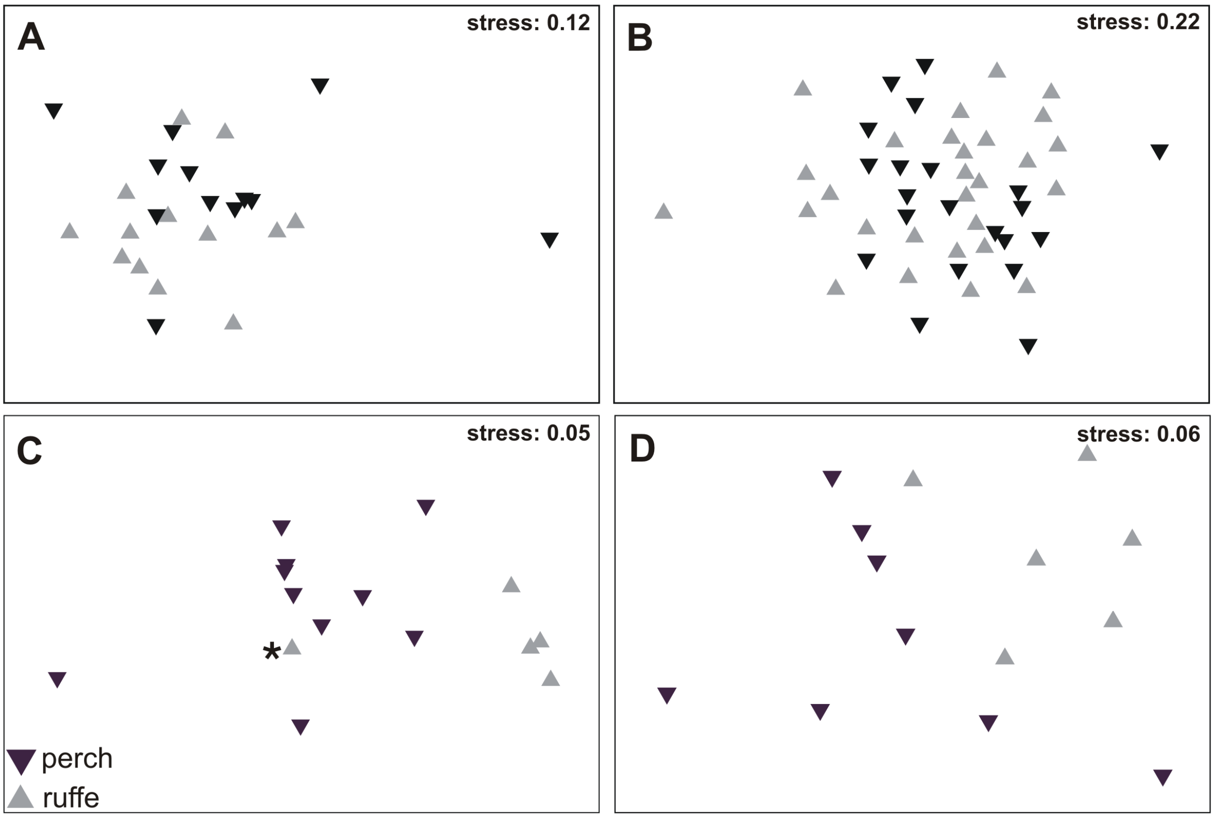

Figure 3: A–D NMDS plots of abundance of each prey type in the different size classes in the fish stomachs. The Bray-Curtis similarity index was applied. **A** Site 1, Litoralgarten, Konstanz, single species ; **B** site 2, Meersburg, single species; **C** site 1, Litoralgarten, Konstanz, mixed species; **D** site 2, Meersburg, mixed species. ***** in **C** marks the outlying data point of the ruffe stomach contents.

Gammaridae and benthic Cladocera were found to be mainly responsible for the differences in the mixed species treatment at site 1 (BVSTEP: $\rho = 0.973$, $p = 0.001$). At site 2, food items of different size classes were responsible for the documented differences in stomach contents (BVSTEP: $\rho = 0.955$, $p = 0.001$). Perch fed more on Gammaridae, benthic Cladocera, and small Trichoptera. Ruffe, in contrast, consumed more Chironomidae, especially of medium- and large-size classes, and medium-sized Trichoptera.

Stomach fullness as a proportion of body weight also differed between species and sites (Fig. 4). At site 1, stomach content was low for all fish and there were no differences between species and treatments (Kruskal-Wallis: df = 3, ChiSquare = 1.091, $p = 0.779$). At site 2, stomach fullness differed between species and treatments (ANOVA df = 3, F-value = 4.327, $p = 0.008$). Perch and ruffe did not differ in stomach fullness in the mixed species treatments. However, compared to the single species treatments, the stomach fullness in the mixed species treatment was lower for perch ($p < 0.05$) and higher for ruffe, resulting in a significant difference between stomach contents of perch and ruffe ($p < 0.01$). Significant differences in stomach fullness were detected only for ruffe between the two sites (single species: Kruskal-Wallis, $p = 0.012$; mixed species: t-test = 0.015).

Strauss' selectivity index indicated in most cases an indifferent feeding of both species on specific prey organisms (Table 3). However, at both sites, small insect larvae were avoided by ruffe and perch in all cages (rage: –0.21 to –0.59). At site 1, ruffe further avoided benthic Cladocera in the cages stocked only with ruffe (–0.22 ± 0.14), and positively selected small Gammaridae in the mixed species cages (0.35 ± 0.15). Perch, however, positively selected Cladocera in both, in the single species and in the mixed species cages (0.27 ± 0.12; 0.42 ± 0.29). At site 2, in contrast, ruffe preferred medium-sized insect larvae (0.25 ± 0.11; 0.24 ± 0.15). Perch avoided Oligochaeta in cages stocked only with perch (–0.20 ± 0.04) and positively selected small Gammaridae in cages stocked with perch only or with both fish species (0.46 ± 0.10; 0.45 ± 0.21).

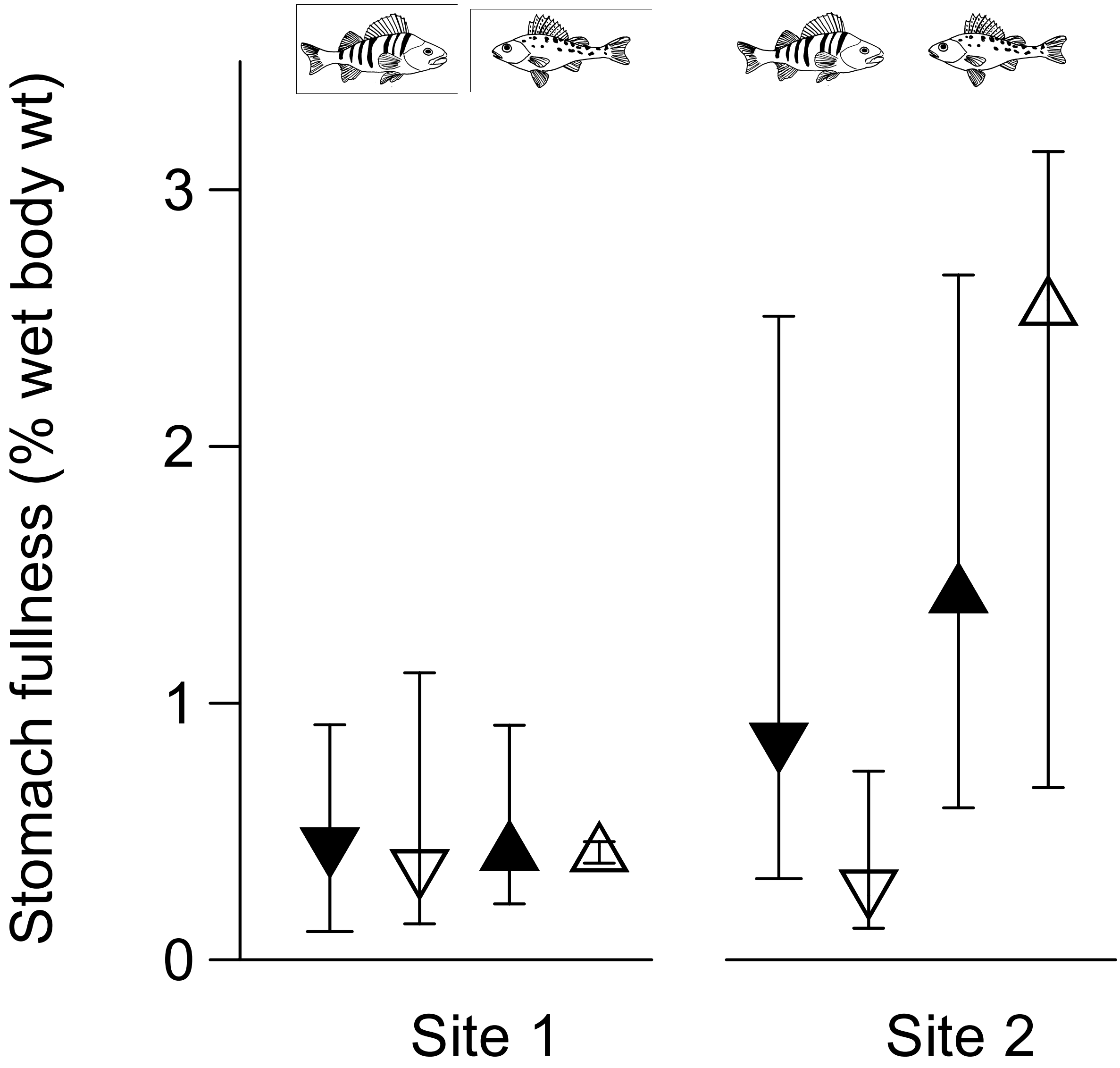

Figure 4: Median ± upper and lower quartile of the dry weight of the stomach contents relative to wet body weight. ▼perch single species, ▽ perch mixed species, ▲ ruffe single species, ∆ ruffe mixed species. Site 1: Litoralgarten, Konstanz; site 2: Meersburg.

Discussion

Spatial variability

Overall benthos abundance and species richness and diversity clearly differed between the two study sites. Total abundance, abundances of most of the dominant taxa, and diversity were higher at site 2. The documented site differences in benthos abundance and assemblage structure reflect the habitat and substrate preferences of some taxa. These patterns are at least indirectly caused by hydrodynamic processes, such as wave exposure and water-level fluctuations, which affect substrate composition and macrophyte and periphyton coverage. Orthocladiinae and the caseless caddisfly *Tinodes waeneri* had highest abundances at the exposed site 2, whereas, e.g. Chironominae, Tanypodinae, Ostracoda, and the amphipod *Dikerogammarus villosus* occurred more often at the more sheltered site 1. We also observed a considerably higher variability within benthos samples at site 1. We assume this is a result of a more patchy environment at site 1 modified by a less-frequent disturbance background compared to site 2. A fine sediment layer thereby results on top of hard substrates or between the shallow, developed macrophyte stands of *Chara* spp. Hence, the amount of interstitial refuges is higher at site 2 and seems to support higher abundances of benthos as well as number of taxa (Lewin *et al.* 2004). In a one-year comparison of shallow littoral sites, it was documented that benthic communities continuously differed between nearby shallow littoral sites with differing hydrodynamic regimes (Chapter 6, Scheifhacken *et al.* 2007).

The observed differences in benthos communities between sites resulted in differences in the diet of the fish. Stomach fullness relative to body mass was higher at site 2, except for perch in the mixed species cages. However, also differences in sediment composition and wave exposure could be other reasons for the differences in stomach fullness between the sites. High turbidity can reduce foraging success (Barrett *et al.* 1992; Utne-Palm 2004). Turbidity is higher at site 1 owing to the finer sediments, and this, along with lower benthos abundances at site 1, could be a reason for the lower stomach content of perch, which are optically oriented predators. Ruffe, in contrast, can feed in complete darkness using its sensory abilities (Janssen 1997; Schleuter & Eckmann 2006); therefore, turbidity is not likely an important factor. The higher stomach contents at site 2 can be attributed to higher energy requirements of both fish species in order to compensate for the higher metabolic costs within the exposed habitat, in addition to higher benthos abundances. However, the energy requirement of the fish under the different hydrodynamic conditions could not be determined in our experiments.

The higher abundance of Trichoptera (*Tinodes waeneri*) and the tendency of a higher abundance of the Ephemeroptera *Caenis* spp. in the benthos samples at site 2 were reflected in higher proportions in the diet composition of the fish, especially ruffe. These results provide evidence for a bottom-up control of the studied system.

Table 3: Selectivity of prey items (mean ± SD) using the preference index of Strauss (1979). Negative values represent avoidance or inaccessibility; positive values represent preference of prey items. Values exceeding 0.20 or falling below –0.20 are in boldface.

Group	Size	Ruffe single species	Ruffe mixed species	Perch single species	Perch mixed species
Site 1 – Litoralgarten, Konstanz					
Oligochaeta	small	0.04 ± 0.07	–0.00 ± 0.00	–0.02 ± 0.02	0.01 ± 0,02
Hirudinea	medium	0.06 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mollusca	medium	–0.03 ± 0.02	–0.02 ± 0.02	–0.03 ± 0.02	–0.01 ± 0.01
Insect larvae	small	**–0.21 ± 0.02**	**–0.38 ± 0.07**	**–0.39 ± 0.13**	**–0.47 ± 0.04**
Insect larvae	medium	0.06 ± 0.09	–0.09 ± 0.02	–0.05 ± 0.04	–0.12 ± 0.11
Insect larvae	large	0.03 ± 0.06	–0.05 ± 0.01	–0.02 ± 0.03	–0.02 ± 0.03
Gammaridae	small	0.16 ± 0.11	**0.35 ± 0.15**	0.07 ± 0.10	0.03 ± 0.04
Gammaridae	medium	0.12 ± 0.08	0.13 ± 0.16	0.18 ± 0.06	0.16 ± 0.15
Gammaridae	large	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cladocera	small	**–0.22 ± 0.14**	0.07 ± 0.07	**0.27 ± 0.12**	**0.42 ± 0.29**
Site 2 – Meersburg					
Group	Size	Ruffe single species	Ruffe mixed species	Perch single species	Perch mixed species
Oligochaetae	small	–0.13 ± 0.04	–0.07 ± 0.01	**–0.20 ± 0.04**	–0.07 ± 0.01
Hirudinea	medium	0.00 ± 0.00	0.01 ± 0.03	0.00 ± 0.00	–0.01 ± 0.00
Mollusca	medium	–0.02 ± 0.03	–0.06 ± 0.05	–0.03 ± 0.01	–0.06 ± 0.05
Insect larvae	small	**–0.37 ± 0.09**	**–0.59 ± 0.03**	**–0.54 ± 0.02**	**–0.57 ± 0.05**
Insect larvae	medium	**0.25 ± 0.11**	**0.24 ± 0.15**	0.09 ± 0.17	–0.02 ± 0.00
Insect larvae	large	0.02 ± 0.04	0.04 ± 0.03	0.01 ± 0.04	0.03 ± 0.07
Gammaridae	small	0.00 ± 0.08	0.14 ± 0.25	**0.46 ± 0.10**	**0.45 ± 0.21**
Gammaridae	medium	0.11 ± 0.02	0.12 ± 0.07	0.06 ± 0.06	0.03 ± 0.05
Gammaridae	large	0.01 ± 0.00	0.02 ± 0.03	0.01 ± 0.02	0.00 ± 0.00

Predation and date effects

Although fish density was higher in enclosures than in external natural habitats, only weak predation effects of perch and ruffe for some benthic taxa were detected. Predation effects relied exclusively on a specific taxa or size-class abundance at one of the two sites, but predation had no effects on species composition at either site. This clearly contradicts our hypothesis of expected strong predation effects resulting from a high density fish stocking and the findings of other authors (Crowder & Cooper 1982; Mittelbach 1988; Gilliam *et al.* 1989; Dahl & Greenberg 1999). However, our results support the findings of others, who found only moderate or transitory predation effects on benthic communities by yellow perch (Cobb & Watzin 1998), roach and perch (Okun & Mehner 2005), cyprinids (Chapter 5), and burbot (Baumgärtner 2004).

A seasonal taxa-specific process was indicated by a pronounced size-class shift from large- to medium- or small-sized individuals, which occurred equally for some taxa in all cages. Within one week, the benthos community at both sites changed clearly and significantly. Several taxa increased in density throughout the experiment, e.g. non-definable Chironomidae (small), *Caenis* spp. (small, sum), and zebra mussel *Dreissena polymorpha* (small, sum), whereas others decreased, e.g. *Tinodes waeneri* (small), *Caenis* spp. (large), Orthocladiinae (small), and *Dikerogammarus villosus* (small) (Table 2). Thus, we found a strong spatial pattern in benthos abundance and a weak but significant temporal pattern in species composition (Fig. 2A). Some aquatic insects could have emerged, which would explain to some extent the lower abundance of large organisms at the end of the experiment, but not the increase of smaller size-classes. We rather assume drift effects in most cases to be responsible for the accumulation of small-sized individuals as a result of single high-wind events at both sites. In addition, the observed increase in zebra mussel abundance reflects early instar larvae that recently underwent metamorphosis. These taxa could probably immigrate because of the relatively large mesh size of our cages.

Size-selective feeding resulting in a shift in size structure of prey taxa was observed only within a few taxa and size classes. We expected a greater proportion of large-sized prey to be consumed by perch and/or ruffe within the enclosures (Gilinsky 1984; Mittelbach 1988). We indeed observed a negative selection of small insect larvae and Oligochaeta. In a comparison of the predation effects on benthos abundances between treatments with the fish stomach contents, however, the results revealed some discrepancies. We observed effects of fish stocking on some invertebrates, e.g. *T. waeneri* (large), *Caenis* spp. (medium), Chironominae (sum), Orthocladiinae (small), Tanypodinae (sum), and non-definable Chironomidae (small). The decrease of small insect larvae in some treatments, however, cannot be accredited to fish predation, as they were negatively selected after Strauss' selectivity index; other size classes and taxa, e.g. *T. waeneri* and *Caenis* spp., were neither positively nor negatively selected. Since stomach contents could only be sampled at the end of the experiment, we do not know whether the food ingested varied during the experiment.

Invertebrate predation might also have occurred and, as an uncontrolled factor, also might have contributed to variability. A variety of invertebrate predators prey on other invertebrates (Lancaster *et al.* 1991), mainly leeches (Elliot & Mann 1979), flatworms (Hansen *et al.* 1991), and Chironomidae (Macan 1977). Furthermore, several studies have shown that vertebrate exclosure leads to an increased invertebrate predation (Macan 1977; Crowder & Cooper 1982; Gilinsky 1984). Since the effects of fish stocking detected in this study were fine-scale effects, the results prove the importance of size-class differentiation in benthos impact surveys. The differences in total counts could only be seen if size-class counts were considered.

Both fish species consumed less food than expected, with some stomachs being empty and others containing only few prey organisms. Fish were recaptured in the late morning, the time of the day when the perch and ruffe stomachs are full (D. Schleuter, personal observation). We interpret the low stomach contents to be a result of low availability of benthic food sources, regardless of total benthos abundances, which were generally high and increased throughout the experiment.

Whether the benthos sampled corresponds to the benthos available for fish greatly depends on the sampling method used. Weak predation effects might have occurred on top of substrates, but were unlikely to be detected by a quantitative benthos sampling device. Since the suction sampler used here also samples the upper interstitial layer of finer sediment, the total abundance sampled is probably considerably higher and weak predation effects might have been overridden and hidden behind sample variances. However, other sampling methods provide other constraints. We opted for high precision and repeatability.

The benthos exploitation rate depends on differences between potential and available food within the upper layer of soft sediment (mainly at site 1) and on top of hardsubstrates (both sites) or within the sparse *Chara* spp. stands (exclusively at site 1). A much smaller proportion of food is visible and therefore truly available for foraging fish. Several factors might influence detection and consumption rates, such as colour, contrast, or activity of the prey organism (Macchiusi & Baker 1991; Utne-Palm 2004), specific fish preference, specific size selection, reactive distance, or gape restriction (Werner & Hall 1974; O'Brien *et al.* 1976; Schael *et al.* 1991; De Vries *et al.* 1998; Mehner *et al.* 1998; Bremigan *et al.* 2003; Krebs & Turingan 2003). Boisclair & Leggett (1985) assumed that only 1% of total benthos biomass is actually available for fish consumption. They found evidence in their comparative study of 21 temperate lakes that daily and annual fish consumption rates of zoobenthos within the upper 5 m of the littoral zone were significantly lower than the reported benthic production/biomass ratios. The probability of successful prey capture should increase linearly with the total biomass of fish and benthos (Hanson & Leggett 1986). We found evidence for such an increased fish consumption rate at site 2, which in both species except perch in the mixed species treatment had total benthos abundance and consumption rates that were higher than at site 1. The high amounts of ingested benthic Cladocera (especially at site 1), which are considered as low-quality food (Hanson & Leggett 1986) further support the hypothesis of low benthos availability. Hanson and Leggett (1986) documented that the amount of consumed food items eaten by yellow perch (*Perca flavescens*) decreased with increasing perch density and led to an increased ingestion of inferior food. In their study, perch consumed 30–50% microcrustaceans when placed under high intraspecific competition, i.e. twice the natural density, and only <1% when reared at low or natural densities.

Strauss' selectivity index should provide further indications of food availability. In our study, small insect larvae and Oligochaeta were negatively selected; small Gammaridae, in contrast, were positively selected. In the study of (Fullerton *et al.* 1998), however, soft-bodied organisms, e.g. Chironomidae, were the favoured diet of both perch and ruffe and were preferred over more sclerotized organisms, i.e. Gammaridae. We therefore attribute our results to low availability of the small soft-bodied organisms, which might live buried in the sand or in the interstitial layer, rather than to active avoidance and on the other hand to the better availability of the small Gammaridae, which move over the sediment.

The predation effects found were weak and diverse and, in comparison to the stomach contents of the fish, only slightly conclusive. Inherent processes of the benthic community probably masked potential predator effects. The low availability of the benthos to predators also made it difficult to detect predatory impacts and leads to the assumption of a bottom-up controlled community. According to Pierce & Hinrichs (1997), there is a difference between systems in which a new fish is introduced and the maintenance of an already existing community. This could explain why some authors did not find differing impacts with differing fish density (Gilliam *et al.* 1989). Post & Cucin (1984), for instance, observed dramatic changes in the benthic community of Little Minnow Lake after introduction of yellow perch. In our experiments, however, we used fish that have co-inhabited the littoral benthic community of Lake Constance for the past 20 years. This could explain why we did not find predatory impacts, even though we used a high fish density.

Competition between perch and ruffe

We found clear evidence for interspecific competition between perch and ruffe for benthic food resources under in situ conditions. Effects of competition between the two species have only been observed under standardised laboratory conditions to date (Kolar *et al.* 2002; Dieterich *et al.* 2004a, b; Schleuter & Eckmann 2006). In our experiments, in the single species treatments , no significant difference between the diets of perch and ruffe were found after nMDS analysis. In the mixed species treatments, in contrast, niche overlap decreased, which is what we would expect under competitive conditions (Bergman & Greenberg 1994; Fullerton *et al.* 1998; Bonesi *et al.* 2004). However, the diet of the fish within the treatments varied greatly. Therefore, Global R values were lower than expected from the nMDS plots, where each species clearly formed its own group in the cages stocked with both species. If outlying points were removed, the Global R reached high values.

Interspecific competition had strong effects on stomach fullness at site 2. Stomach fullness did not differ between perch and ruffe in cages stocked with a single species. However, in the mixed species cages, the stomach fullness of perch was lower, while that of ruffe was higher. Perch might have been restricted by interference competition, both intraspecific (Schleuter & Eckmann 2006) and interspecific (Savino & Kolar 1996; Schleuter & Eckmann 2006). At site 1, no differences in stomach fullness between species or treatments were found. This could be caused by the more limited food source at site 1, thereby generally causing very low stomach contents for both species within both treatments, with a high proportion of benthic Cladocera in the stomach contents (Hanson & Leggett 1986). The high intraspecific competition at site 1 probably superimposed the effects of interspecific competition. However, we would have expected a higher competitive ability of ruffe at site 1, and of perch at site 2 (Dieterich *et al.* 2004a). Furthermore, ruffe should be able to detect prey more easily in the more turbid water at site 1 because of its sensitive lateral line organ (Eiane *et al.* 1997; Janssen 1997; Schleuter & Eckmann 2006); on the other hand, the use of this organ could restrict foraging success in water with high hydrodynamic action, as at site 2. Additional in situ studies are necessary to further elucidate the influence of these variables on the outcome of competition between the two species.

Conclusions

We analysed the impact of fish predation on the benthic community of Lake Constance and found hardly any differences between cages stocked with fish and the unstocked controls. However, we found a clear effect of sampling date, with most invertebrate taxa and size classes having higher abundances at the end of the experiment, and differences between the two experimental sites. At site 2, the site exposed to westerly winds and ferry- and leisure-boat-induced waves, benthos abundances were generally higher, as well as the proportion of Trichoptera and Ephemeroptera. These differences between sites were clearly reflected in the stomach contents of perch and ruffe. Relative to body mass, stomachs were fuller at site 2 and contained a higher proportion of Trichoptera and Ephemeroptera. The results lead to the assumption that predation effects on benthos is minor and can be ignored in comparison to inherent benthos seasonal shifts. Therefore, benthos is not likely to be controlled by top-down processes. However, the opposite can be presumed for fish that are likely to be mediated by bottom-up effects of benthos availability. Our results support the findings of others, who found only moderate or transitory predation effects on benthic communities by yellow perch (Cobb & Watzin 1998), roach and perch (Okun & Mehner 2005), cyprinids (Chapter 5), and burbot (Baumgärtner 2004).

We also found clear indications for competition between perch and ruffe: In the cages stocked with a single species, no differences between the diet of the two species were found. In cages stocked with both species, in contrast, niche overlap of perch and ruffe decreased. The effects of competition on stomach fullness depended on the study site. At site 1, the stomach fullness was generally low and no difference between species or treatments was found. At site 2, the stomach fullness of perch decreased with interspecific competition, while that of ruffe increased.

We conclude that the benthic community at both study sites is bottom-up controlled rather than top-down controlled. A top-down control might only be relevant in systems that have not previously experienced fish predation (Post & Cucin 1984). In systems adapted to fish predation, predation effects are not pronounced enough to alter underlying benthic community structures. On the basis of the present study for perch and ruffe and a comparable study for juvenile cyprinids in similar habitats (Chapter 5) we agree with the assumption of Cobb & Watzin (1998) that this is a common pattern for temperate littoral zone communities.

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Appendix: Total abundance, number of taxa, diversity, and dominant taxa (mean ± SE) per sampling unit (Ao = 625 cm^2) pooled for both sampling dates and sites and differentiated between sites (*S1* site 1, Litoralgarten, Konstanz; *S2* site 2, Meersburg) and week.

	Total		Site 1				Site 2			
			Week 1		Week 2		Week 1		Week 2	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Abundance, N	4594	398	3282	691	4955	1269	5294	224	4721	283
Number of taxa, S	19.3	0.4	16.4	0.9	19.1	0.7	22.2	0.6	19.5	0.3
Species richness, D	2.2	0.0	1.9	0.1	2.2	0.1	2.5	0.1	2.2	0.0
Pielous evenness, J'	0.6	0.0	0.6	0.0	0.6	0.0	0.6	0.0	0.6	0.0
Shannon diversity, H'_{loge}	1.7	0.0	1.6	0.0	1.6	0.0	1.7	0.0	1.8	0.0
Chironomidae non.det.	795.4	85.8	174.2	45.9	340.5	122.9	1423.8	95.8	1244.6	64.9
Chironominae	523.7	59.4	505.1	124.3	671.1	176.6	493.5	38.3	415.4	61.7
Alonidae	308.6	71.4	939.9	204.4	359.1	89.8	-	-	-	-
Tinodes waeneri	298.4	32.5	137.0	25.3	66.0	14.3	595.6	41.1	422.1	34.9
Caenis spp.	105.0	12.6	12.6	4.1	77.0	17.2	100.7	12.8	210.4	20.3
Oligochaeta	100.3	15.6	14.9	4.7	9.2	4.0	200.6	32.0	179.5	25.0
Orthocladiinae	84.1	9.0	67.1	18.9	54.6	12.4	136.7	17.9	85.0	17.2
Ostracoda	81.4	26.8	60.8	38.0	212.6	84.0	15.0	4.3	20.0	3.7
Gammarus non det.	57.3	9.7	37.3	16.9	87.8	29.8	38.9	5.8	57.6	9.9
Tanypodinae	55.5	12.7	71.5	13.4	114.4	40.1	14.6	2.7	16.6	2.5
Dreissena polymorpha	19.4	3.7	6.1	3.3	20.2	9.5	9.8	2.3	37.0	7.1
Dikerogammarus villosus	19.3	3.6	32.9	12.4	20.4	7.8	17.1	1.8	8.9	1.4
Chironomidae non det. P.	12.2	1.7	9.0	3.1	11.8	3.5	16.5	4.6	11.7	2.0
Pisidium spp.	8.4	1.4	6.6	2.4	13.4	3.9	6.6	2.1	6.3	1.4
Radix ovata	4.6	1.3	0.3	0.2	1.3	0.9	9.8	3.5	7.4	3.4
Leptoceridae non det.	4.4	0.9	0.0	0.0	1.1	1.1	10.2	2.5	6.7	1.4
Trichoptera non det.	4.2	2.0	7.4	6.1	1.0	1.0	5.0	4.8	4.1	3.6
Athripsodes atterimus	4.0	1.3	2.4	1.7	11.2	4.1	1.1	0.3	0.5	0.2
Acari	2.7	1.4	11.0	5.7	0.0	0.0	0.0	0.0	0.9	0.6
Polycentropus flavomaculatus	2.5	0.7	2.1	1.6	0.2	0.2	5.6	2.2	2.8	0.8
Centroptilum luteolum	2.5	0.8	2.0	1.0	5.9	2.6	1.9	0.9	0.0	0.0
Mystacides spp.	1.7	0.6	1.3	1.2	3.8	1.7	1.4	1.2	0.2	0.1
Bezzia spp.	1.6	0.7	0.2	0.2	5.1	2.5	0.1	0.1	0.3	0.3
Erpobdella octoculata	1.4	0.3	0.7	0.4	0.1	0.0	2.4	0.8	2.3	0.7
Coryoneura spp.	1.1	0.5	0.0	0.0	2.1	1.2	0.2	0.2	1.9	1.2
Ecdyonurus dispar	1.1	0.4	0.0	0.0	0.1	0.1	4.3	1.5	0.6	0.2
Bithynia tentaculata	1.1	0.3	0.5	0.4	0.6	0.3	3.0	1.0	0.7	0.6
Micronecta spp.	1.0	0.4	0.9	0.6	3.1	1.4	0.0	0.0	0.0	0.0
Planorbis spp.	0.8	0.3	0.0	0.0	0.0	0.0	1.7	0.8	1.7	0.9
Gammarus roeseli	0.6	0.3	0.4	0.3	1.9	0.9	0.0	0.0	0.0	0.0
Hydroptila spp.	0.5	0.3	0.0	0.0	1.9	1.1	0.0	0.0	0.0	0.0
Trichoptera pupae	0.4	0.4	0.2	0.2	1.5	1.3	0.0	0.0	0.0	0.0
Gyrinidae/Dytiscidae larvae	0.2	0.2	0.0	0.0	0.9	0.9	0.0	0.0	0.0	0.0
Sericostoma pers./flavic.	0.2	0.2	0.0	0.0	0.0	0.0	1.0	1.0	0.0	0.0
Potamopyrgus antipodarum	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4
Goera pilosa	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1	0.1
Gyraulus albus	0.1	0.1	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0
Radix peregra	0.1	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Ceraclea spp.	0.1	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Acentria ephemerella	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Turbellaria	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1
Riolus spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1
Odonata non det.	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Ephemera danica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Ecnomus tenellus	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
Stagnicola corvus	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0

Chapter 5

No evidence for top-down control of macroinvertebrates by juvenile cyprinids under contrasting hydrodynamic regimes in the littoral zone

Nicole Scheifhacken with Petra Klahold and Stefan Stoll

Summary

The predation effects of juvenile cyprinids (bream, dace) on macroinvertebrates were studied in an enclosure experiment at three differently wind exposed sites and compared with samples from fish exclosures and natural controls. Fish cages were stocked with both species of age classes 0+ and 1+. Both cyprinid species consumed considerable amounts of benthos and were well fed throughout the experiment. However, contrary to our expectations, we found no evidence for top-down effects on macroinvertebrate abundance, biomass, or community composition independent from direct wind exposure effects of the sites. Significant site differences were detected and a strong seasonal shift at all sites occurred within benthos communities, which is interpreted as an indirect result of hydrodynamic processes that alter substrate and benthos abundance and community composition.

Résumé: *Les effets de la prédation de juvéniles de cyprinidés (brème, vandoise) sur les macroinvertébrés ont été étudiés dans des enclos expérimentaux, localisés à trois sites différents, et comparés à des échantillons récoltés dans des enclos sans poissons et dans des sites témoins naturels. Les enclos expérimentaux contenaient des poissons des deux espèces (classes d'âge 0+ et 1+). Les deux espèces de cyprinidés ont consommé de grandes quantités de benthos et étaient nourries à satiété tout au long de l'expérience. Nous n'avons cependant pas trouvé d'effets « top down » évidents sur l'abondance de macroinvertébrés, leur biomasse ou la structure de leur communauté, indépendamment des effets directs imputables au caractère clos des sites. Toutefois, des différences significatives entre les sites ont été mises en évidence et un changement saisonnier marqué des communautés de benthos a été observé. Ces résultats ont été interprétés comme des effets indirects de processus hydrodynamiques altérant le substrat et l'abondance et la structure des communautés de benthos.*

Keywords: benthos, dace, bream, wave exposure, enclosure, predator-prey interaction

Introduction

Predator-prey interactions of benthivorous fish on macroinvertebrates in freshwater systems have been widely studied. Contrasting results on the effects of fish predation on macrobenthic communities have been documented, ranging from strong predation effects (e.g. Crowder & Cooper 1982; Gilinsky 1984; Gilliam *et al.* 1989; Diehl 1992; Brönmark 1994) to moderate (Cobb & Watzin 1998) or no effects (Thorpe & Bergey 1981; Culp 1986; Hanson & Leggett 1986). When predation occurs, vertebrate predators tend to selectively remove specific prey taxa (Gilinsky 1984; Brönmark 1994) or size classes (Gilliam *et al.* 1989; Peckarsky *et al.* 2001), and often concentrate on large size classes only (Mackay 1979; Diehl 1988; Mittelbach 1988; Diehl 1992).

Macrophytes tend to reduce prey vulnerability (Crowder & Cooper 1982; Gilinsky 1984; Diehl 1992). Habitat complexity can mask or obscure predation effects due to increased abundance and number of invertebrate taxa in vegetation stands by providing additional food or habitat resources (Gilinsky 1984). Competing invertebrate predators (Diehl 1995) or rapid recolonisation of epibenthic invertebrates (Gilliam *et al.* 1989; Chapter 2) can further mask fish predation. Therefore, predation is likely to affect only species with low colonisation abilities (Gilliam *et al.* 1989; Dahl & Greenberg 1999).

Many invertebrate species alter their behaviour, morphology, and life history in response to increased predation risk (e.g. Crowl & Covich 1990; Forrester 1994; Sih & Wooster 1994; McCollum *et al.* 1998; Peckarsky *et al.* 2001; Baumgärtner *et al.* 2002; Baumgärtner *et al.* 2003). Oligochaeta (Gilliam *et al.* 1989), amphipods (Baumgärtner *et al.* 2002, 2003) and snails (McCollum *et al.* 1998) reduce their activity above the sediment when the predator density is high. The visual or olfactory sensing of fish by snails can further inhibit reproduction and increase snail mortality (McCollum *et al.* 1998).

Cyprinids often dominate the fish fauna of lakes in the northern hemisphere, and are thus an important part of the food web (Fischer & Eckmann 1997a, b; Specziar *et al.* 1997; Driver *et al.* 2005). However, cyprinids are widely neglected in ecological studies probably because of the lack of commercial interest for most taxa, e.g. dace, chub, bream, and white bream. Juvenile cyprinids feed on a variety of benthic organisms (Mann 1974; Mackay 1979; Giles *et al.* 1990; Garner 1996; Specziar *et al.* 1997; Specziar 2002) and are therefore an important factor in the structuring of benthic communities. They also commonly feed on non-animal food, such as periphyton (Garner 1996), detritus, or macrophytes, e.g. *Chara* spp. (Horppila 1999) and especially during early ontogeny on zooplankton (Giles *et al.* 1990; Garner 1996; Vasek & Kubecka 2004).

The structure of the littoral of Lake Constance is highly variable and the shallow area strongly exposed to hydrodynamic forces. However, such forces are still widely ignored as potential factors influencing benthic or fish communities in freshwater compared to marine habitats. Furthermore, hydrodynamics were found to influence invertebrate predator–prey interactions in marine (Weissburg & Zimmer-Faust 1993; Powers & Kittinger 2002) and lotic freshwater habitats (e.g. Lancaster *et al.* 1990; Peckarsky *et al.* 1990; Hansen *et al.* 1991; Lancaster 1996).

We hypothesised that hydrodynamic forces are important physical parameters that likely mediate biotic interactions, e.g. benthos abundance as well as biomass, exploitation rate, and foraging success of fish. Hence, we examined the predatory impact of juvenile cyprinids on littoral macroinvertebrate abundance, diversity, and biomass in relation to the wave dynamics at three differently wind exposed sites. We specifically focused on benthic community composition, which is often ignored in enclosure experiments, but which might change as a result of predation pressure independently of single species abundance.

Methods

Study site

The study was conducted at Upper Lake Constance, which is the second largest oligotrophic, pre-alpine lake in central Europe (9°18' E, 47°39' N; surface area: 472 km^2; total volume: 47.6 km^3; max. depth: 254 m; mean depth: 101 m). All sites are at the southwestern shore of the lake. Westerly winds prevail throughout the year; intermittent peaks occur from the east at regular intervals (Huss 1975; Bäuerle *et al.* 1998). Furthermore, wave exposure arises from ferry and leisure boat traffic. Two of the sites were shallow ($S1_{shallow}$ and $S2_{shallow}$), and one was deep ($S1_{deep}$). The S1 sites (9°12'18.4'' E, 47°41'26.7'' N) are the most wind-exposed sites. The site S2 (9°10'53.2'' E, 47°42'35,9'' N) is protected from wind and ferry-generated waves by the Mainau Island. During the experimental period (July 26 to August 30, 2004), the water level continuously decreased by about 1 cm per day, resulting in an average water depth within the enclosures of 0.5–0.8 m at sites $S1_{shallow}$ and $S2_{shallow}$, and 1.7–2.0 m at site $S1_{deep}$. The littoral substrate at site $S1_{shallow}$ is dominated by coarse gravel and cobblestones (size range: 14.3–121.1 mm, mean ± SE: 32.2 mm ± 1.2, n = 360 single stones from four replicate samples) covered with a fine silty layer and loosely embedded within the finer sediment. Site $S1_{deep}$ contains sand material densely covered with submerged vegetation, mainly *Chara* spp. accompanied by a few individuals of *Potamogeton pectinatus*. Site $S2_{shallow}$ is sparsely vegetated, but is also dominated by a fine and silty substrate, and contains single stones (size range: 20–50 mm) as hardsubstrates.

The summer littoral fish community in Lake Constance is dominated by age-0+ cyprinids of the species chub, dace, and bream (Fischer & Eckmann 1997a, b) and recently also bleak (Reyjol *et al.* 2005 in press). Highest abundance, e.g. up to 55 ind./100 m^2 of 0+ chub, are found in the shallow most littoral areas below 50 cm water depth. Also age-0+ bream are often found in higher densities in shallow lake sites. This pattern changes, however, when sublittoral areas become vegetated by dense stands of submerged aquatic vegetation and bream move to deeper littoral areas (Fischer & Eckmann 1997a).

Enclosure experiment

Six enclosures at each site comprising three control enclosures (without fish) and three treatment enclosures (with fish) were randomly placed. Enclosures were made of 4-mm bar-mesh material, tightly fixed at the bottom to a square metal frame (1.4 x 1.4 m A = 2 m^2). Sealing between the substratum and the enclosure frame was done by deploying gravel substratum on the outsides of the enclosures, which were additionally stabilised by sandbags. The height of the enclosures was adjusted to the maximal water depth at each site during the experiment and emerged at least 50 cm above the water surface. The mesh material at the four upper ends of each enclosure was tightened and wired to wooden poles previously driven into the lake bottom at either edge of each enclosure. This construction allowed free water and surface wave flow through the enclosures. The 4-mm mesh size was chosen to ensure the emigration and immigration of benthos and plankton as well as sufficient flow-through during the experiment, thereby maximising the simulation of natural conditions. To prevent avian predation on the fish, all cages were covered with 20-mm mesh. Within all treatments, the cages were placed 1.5 m apart and parallel to the shoreline. They were placed by scientific divers and then left for one week to allow resettlement of the organisms.

Fish sampling

Dace [*Leuciscus leuciscus* (L.)] used in the experiment were obtained by beach seining or electric fishing in related habitats adjacent to the study areas. Common bream [*Abramis brama* (L.)] and white bream [*Blicca bjoerkna*] were either raised from spawn in the laboratory or purchased from a hatchery. Most of the age-1 bream were accidentally killed a few days before the start of the experiments because of a technical defect in the holding tank; therefore, white bream of the same size were used instead. This sister species is commonly associated with bream (Specziar 2002), has an almost identical body shape (S. Stoll and P. Klahold, unpublished data), and uses a very similar niche pattern (Specziar *et al.* 1997; Molls 1999). Furthermore, hybrids of the two species are well documented (Swinney & Coles

1982). We therefore assumed that age-1 white bream could adequately substitute for age-1 bream in the experiment.

All fish were kept in small groups in the laboratory for at least three weeks prior to the experiment to ensure their vitality. During this time, they were fed *ad libitum* with *Daphnia* spp. and chironomid larvae. Immediately before cage release, all fish were weighed (g wet weight), measured (fork length, lowest mm), and individually tagged with coded wired tags (Northwest Marine Technology) injected into the right cheek. The initial mean weight and fork length (± SD) of all taxa and age classes are given in Table 1. A total of 58 fish, containing 8 dace and 8 bream or white bream, age-1; and 12 dace and 30 bream, age-0 were placed in the enclosures. To provoke effects, the average stocking density in the enclosures was 29 ind. m^{-2} and therefore 20 times higher than *in situ*. We chose this higher density to intensify the predation impact.

Table 1: Average body mass (wet weight) (± SD), fork length (± SD), and gape size (± SD) of juvenile cyprinids in the cages at the beginning of the experiment and in the field. n = number of individuals per enclosure or field.

			Cage			**Field**		
Taxa	Age	Gape (mm)	n	Weight (g)	Fork length (mm)	n	Weight (g)	Fork length (mm)
Dace	0+	4.0 ± 0.7	12	1.0 ± 0.6	46.1 ± 10.9	11	1.4 ± 0.6	45.7 ± 8.7
Dace	1+	7.9 ± 1.1	8	9.0 ± 2.7	97.2 ± 8.9	21	21.5 ± 5.5	120.1 ± 11.2
Bream	0+	2.3 ± 0.7	30	0.13 ± 0.05	22.5 ± 2.2	3	2.4 ± 0.7	56.0 ± 5.3
White bream	1+	7.4 ± 1.2	8	17.1 ± 6.4	104.1 ± 11.8		-	-

The cages were checked daily, and attached algae were removed from the net material. Every ten days, two fish per species and size class were recaptured with a hand net to estimate growth rates and to determine the gut filling rate and content. Withdrawn fish were replaced by other fish of the same species and size class to maintain the species numbers. At the end of the experiments, all fish were removed by electric fishing and frozen for later determination of individual growth rates (Stoll *et al.* 2008). Parallel to the enclosure experiments, fish were caught at the three experimental sites with gill nets (6, 9, 12, 15 mm) to obtain gut filling and content data under *in situ* conditions. All caught fish were immediately killed with trichlor-2-methyl-2-propanol-hemihydrate (2 g l^{-1}), measured (fork length), weighed, and preserved in 4% formaldehyde for later gut analysis. For gut content analysis, the anterior loop, which contained the least-digested fraction, was removed, and its content was determined and counted to the lowest possible taxonomic level (see next subsection).

Benthos sampling

Benthos was quantitatively sampled (25×25 cm, $A_o = 625$ cm^2) by scientific scuba divers using a suction sampler as described in Baumgärtner (2004). All hard substrates or macrophytes from the sample area were transferred into a hand net (200 µm); the upper finer sediment layer was thereby carefully raised and suctioned with continuous pumping. The adjusted permanent suction current during sampling minimises the number of escaping mobile individuals. Suspensions and escaping organisms were retreated within a filter inlet (200 µm gaze), added to the hard substrate fraction, and processed in the laboratory. Samples were taken immediately before fish were placed in control and treatment cages and then again after one month. Additionally, natural controls were sampled within same depth strata to compare natural predation pressure and to detect cage effects at the end of the experiment.

All benthic samples were brought to the laboratory immediately after sampling and processed. The coarse substrate 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-µm sieve and preserved in 70% ethanol. Macroinvertebrates observed under a dissection binocular scope (10× magnification) were identified to the species level if possible or otherwise to the nearest taxonomic level and counted. The individuals were classified into three size classes for further biomass calculation. The body size parameter, e.g. head-capsule width or shell length, from a subsample of at least ten individuals per size class and taxon was measured to the nearest 0.01 mm using an image analysis system. Means were calculated for each size class; biomass was calculated as described by Baumgärtner & Rothhaupt (2003). The length and dry mass of the recently invaded amphipod *Dikerogammarus villosus* and the leeches *Erpobdella octoculeata* and *Glossiphonia complanata* were also calculated following the methods described in Baumgärtner & Rothhaupt (2003).

Wave exposure and abiotic parameters

Wind exposure was calculated from hourly mean wind data obtained from a nearby weather station (Egg, Konstanz) using fetch and the effective fetch equation (Hakanson 1977; Keddy 1982, 1984). Wave exposure was measured by deploying standard cylindrical sediment traps (n = 3 per site) throughout the experiment (see Bengtsson *et al.* 1990; Bloesch 1994, 1995; Douglas & Rippey 2000) and by determining dissolution rates of standardised gypsum spheres (3 times – 10 days of exposure, n = 5 per site) as described in detail in Chapter 2 (see also Petticrew & Kalff 1991; Angradi & Hood 1998; Porter *et al.* 2000). Temperature was continuously recorded with a StowAway® Onset datalogger at each site. Turbidity was measured using a Seapoint® turbidity Micromec® datalogger for 24 h on a calm weekday at each site to characterise wave action induced by ferries and leisure boats.

Statistical analyses

Benthos abundance data were examined with repeated measurement MANOVA with site and treatment as factors and Bonferroni corrected (Rice 1989). To stabilise variances, abundance data were log(x+1) transformed, except for number of taxa and the diversity parameters in the benthos data. Variance homogeneity was tested with the Levene test. Tukey post-hoc tests were used when significant effects were found. The non-parametric test was applied when variance heterogeneity persisted after transformation (Kruskal-Wallis test, pair-wise Mann-Whitney U-test). The statistical package of SPSS 13.0 was used for all uni- and multivariate analyses.

Experimental effects on species composition (assemblage data) were analysed for benthos abundance and biomass abundance [both log(x+1) transformed] and fish gut content (square-root-transformed) with non-metric multidimensional scaling (nMDS) plots using the PRIMER 6b software package (Clarke & Gorley 2001; Clarke & Warwick 2001). The Bray-Curtis index was used as a similarity matrix. The similarity of *a priori* defined groups (e.g. site, treatment, fish taxa, fish age-class) was tested against random distribution using the ANOSIM permutation statistics. Different transformations were necessary. Data sets with only few highly abundant taxa, e.g. benthos abundance and biomass abundance, were log(x+1) transformed to recognise less-abundant taxa in the assemblage; in other cases of more evenly distributed data sets (gut content), the data sets were square-root transformed.

Results

Wave exposure and temperature

The chosen sites differed in their exposure to waves during the experiment. The gypsum dissolution rates [mean ± SE (g/h)] were lowest at site $S2_{shallow}$ (0.31 ± 0.1), p<0.001), followed by site $S1_{deep}$ (0.59 ± 0.1) and highest at site $S1_{shallow}$ (0.76 ± 0.1). Highest dissolution occurred within the first sampling decade at all sites alike, no differences thereafter (MANOVA: site: $F_{2,29} = 587.8$, $p < 0.001$, time: $F_{2,29} = 13.7$, $p < 0.001$, site×time $F_{2,29} = 0.7$, $p = 0.573$). The calculated mean fetch and mean wind exposure at the S1 sites ($S1_{shallow}$ and $S1_{deep}$) were about eightfold and ninefold higher, respectively, than at site $S2_{shallow}$ (fetch: 14.9 and 1.8, respectively; wind exposure: 634.3 and 70.3, respectively).

Turbidity (mean ± SE) caused by ferries increased considerably at site $S1_{shallow}$ (22.7 ± 0.9 FTU) in the morning (9:30 am), with a peak in the afternoon (3:00 pm, 250 FTU) and remained at a high level until 8:00 pm. Almost no turbidity caused by boat activity occurred at the deeper site $S1_{deep}$ (2.9 ± 0.02 FTU), and only few events were recorded at site $S2_{shallow}$ (5.0 ± 0.08 FTU) within a 24-h period. Turbidity was therefore highest at the shallow site $S1_{shallow}$ followed by $S2_{shallow}$ and the deep site $S1_{deep}$ ($p < 0.001$, $Z = 765.7$, $df_{eff,\ err} = 2, 4292$, H-test, U-test).

The temperature (mean ± SE) increased during the first two weeks from 21.6 ± 0.4 °C to 24.6 ± 0.14 °C, declined rapidly in the second week to 18.4 ± 0.58 °C, and remained at the lower level until the end of the experiment, with an overall mean of 21.1 ± 0.28 °C. The mean and minimum temperatures were similar at all sites, but the maximum temperature and the daily amplitude differed between the sites, with highest amplitudes at site $S2_{shallow}$, followed by site $S1_{shallow}$, and lowest values at site $S1_{deep}$.

Benthic community abundance and biomass

The total abundance (mean ± SE per sample unit) was 6664 ± 1103 individuals pooled over both sampling dates and at all three sites. The maximal number of taxa was 55 (mean 17.7 ± 0.54). The most abundant taxon was the zebra mussel *Dreissena polymorpha* (4578 ± 1146), which also had the highest biomass values (3718 ± 937 mg per sample unit). All other taxa differed in their abundance *vs.*

biomass rank order (Tables 2 and 3). The next most abundant taxa were mayfly *Caenis* spp. (422 ± 63), Chironominae (407 ± 53), Ostracoda (380 ± 71), early instar Chironomidae non det. (291 ± 43), Oligochaeta (160 ± 34), Orthocladiinae (86 ± 14), caddisfly *Tinodes waeneri* (72 ± 12), *Pisidium* spp. (55 ±12), Tanypodinae (50 ± 5), *Bythinia tentaculata* (39 ± 10), *Dikerogammarus villosus* (24 ± 7), *Bezzia* spp. (21 ± 5), *Centroptilum luteolum* (18 ± 4), and Acari (10 ± 3). A variety of insect larvae and other invertebrates, including leeches, regularly occurred in low numbers. Some taxa were found exclusively at one site, e.g. *Bezzia* spp., Lepthophlebiidae, and *Ephemera danica* were found only at site $S2_{shallow}$. *D. villosus* was not found at site $S2_{shallow}$; *T. waeneri* was not observed at site $S1_{deep}$.

Date, site, and treatment effects with Bonferroni correction

Total abundance, diversity parameters (Shannon, Margalef, Evenness), and most of the dominant taxa except number of taxa and single taxa abundance of *T. waeneri*, Chironominae, *Pisidium* spp., and *B. tentaculata* showed significant date effects (Table 4). Most remarkably, the total abundance increased ($p < 0.001$) on the second sampling date at all three sites with highest values at site $S1_{deep}$ (Table 3; $S1_{shallow}$ 6-fold, $S2_{shallow}$ 1.7-fold, $S1_{deep}$ 9-fold). This pattern is primarily based on early-settlement *D. polymorpha* larvae; metamorphosis occurred on both sampling dates. Similar but less pronounced increased abundance data were observed for *Caenis* spp. and ostracods at all sites and for all three subfamilies of chironomids at site $S1_{shallow}$. Higher biomass values were not always found with higher abundance values (Table 3). For example, biomass values of *Caenis* spp. and full-grown chironomid larvae decreased throughout the experiment, whereas the abundances of first instar larvae increased. The number of taxa was lowest at the exposed site $S1_{shallow}$. Number of taxa was higher at site $S2_{shallow}$ than at site $S1_{deep}$. Species richness was similar at the exposed sites $S1_{shallow}$ and $S1_{deep}$, but significantly lower than at the sheltered site $S2_{shallow}$. Diversity and evenness indices were lowest at site $S1_{deep}$, higher at site $S1_{shallow}$, and highest at site $S2_{shallow}$.

Table 2: Benthos abundance (mean ind./unit ± SE), number of taxa, diversity, and mean dominant taxa abundance per site and sampling date. Sample unit 25 × 25 cm. A_o = 625 cm^2, all samples pooled. Parameters in **A** – including, in **B** - without *D. polymorpha* individuals.

		S1$_{deep}$ (exposed)				**S1$_{shallow}$ (exposed)**				**S2$_{shallow}$ (sheltered)**			
		26.07.2004		**30.08.2004**		**26.07.2004**		**30.08.2004**		**26.07.2004**		**30.08.2004**	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Abundance (N)	**A**	2317	*134*	21009	*1664*	1277	*217*	7516	*741*	1624	*176*	2768	*359*
No. of taxa (S)	**A**	18.4	*1.11*	15.6	*0.58*	13.2	*0.85*	16.1	*0.70*	20.2	*0.91*	21.9	*0.98*
Margalef species richness (d)	**A**	2.26	*0.14*	1.47	*0.06*	1.74	*0.12*	1.71	*0.09*	2.63	*0.14*	2.66	*0.08*
Shannon diversity (H'log e)	**A**	2.21	*0.02*	0.28	*0.06*	1.82	*0.05*	1.57	*0.06*	2.09	*0.06*	2.08	*0.04*
Pielou's evenness (J')	**A**	0.76	*0.01*	0.10	*0.02*	0.71	*0.01*	0.57	*0.02*	0.70	*0.02*	0.68	*0.02*
Shannon diversity (H'log e)	**B**	2.23	*0.15*	2.02	*0.07*	1.66	*0.13*	1.70	*0.09*	2.52	*0.18*	2.58	*0.58*
Pielou's evenness (J')	**B**	0.81	*0.02*	0.72	*0.04*	0.70	*0.01*	0.59	*0.02*	0.69	*0.02*	0.66	*0.02*
Dreissena polymorpha	1	715	*74.7*	20083	*1701.81*	36	*13.5*	3261	*643.2*	10.2	*3.7*	323	*109.1*
Chironominae	2	252	*19.7*	82	*32.1*	343	*64.1*	952	*136.9*	481	*76.9*	319	*57.2*
Orthocladiinae	3	236	*35.3*	42	*11.0*	34	*7.1*	43	*9.9*	50	*12.8*	86	*22.4*
Oligochaeta	4	203	*10.6*	28	*64*	2.8	*0.9*	8.4	*6.1*	285	*56.2*	432	*131.9*
Pisdium spp.	5	201	*8.4*	70	*19.3*	2.0	*1.0*	7.0	*2.3*	6.1	*2.7*	7.9	*4.2*
Chironomidae non det.	6	183	*17.4*	39	*11.5*	295	*50.3*	804	*93.3*	268	*38.4*	169	*54.4*
Dikerogammarus villosus	7	120	*12.5*	5	*1.6*	6.1	*2.3*	0.6	*0.2*	0.0	*0.0*	0.0	*0.0*
Bithynia tentaculata	8	112	*17.3*	92	*34.6*	0.3	*0.2*	0.6	*0.2*	0.1	*0.1*	1.8	*0.7*
Ostracoda	9	92	*11.0*	290	*69.3*	156	*43.3*	1051	*262.8*	49	*6.6*	453	*54.9*
Caenis spp.	10	78	*17.9*	200	*52.1*	213	*52.4*	1032	*158.2*	186	*26.0*	661	*104.9*
Tanypodinae	11	57	*11.3*	18	*4.3*	43	*4.0*	81	*10.5*	61	*9.9*	40	*12.0*
Radix ovata	12	7.0	*2.6*	1.8	*0.4*	0.1	*0.1*	0.0	*0.0*	0.4	*0.2*	2.8	*1.6*
Tinodes waeneri	13	0.0	*0.0*	0.0	*0.0*	128	*11.6*	201	*22.9*	71	*11.2*	56	*17.3*

Table 3: Benthos biomass (mean mg/unit ± SE) and dominant taxa biomass per site and sampling date. Sample unit 25 × 25 cm. A_o = 625 cm^2, all samples pooled.

		$S1_{deep}$ (exposed)				**$S1_{shallow}$ (exposed)**				**$S2_{shallow}$ (sheltered)**			
		26.07.2004		**30.08.2004**		**26.07.2004**		**30.08.2004**		**26.07.2004**		**30.08.2004**	
		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Biomass (b)		2018	*278.7*	18524	*1512.2*	170	*35.0*	3489	*514.4*	127	*5.1*	673	*158.0*
Dreissena polymorpha	1	819	*117.8*	18204	*1527*	34	*12.2*	2949	*581.5*	10.6	*3.3*	292	*98.6*
Dikerogammarus villosus	2	435	*70.2*	14.8	*4.4*	40	*11.6*	5.0	*2.6*	0.0	*0.0*	0.0	*0.0*
Bithynia tentaculata	3	371	*213.5*	60	*16.6*	1.9	*1.2*	1.9	*1.2*	0.9	*0.9*	4.0	*2.0*
Radix ovata	4	214	*84.2*	46	*9.5*	0.0	*0.0*	0.0	*0.0*	5.8	*3.8*	0.7	*0.4*
Ostracoda	5	38	*5.5*	120	*28.6*	64	*17.9*	434	*108.4*	20	*2.7*	186.7	*22.6*
Pisidium spp.	6	36	*1.6*	12.1	*3.3*	0.3	*0.2*	1.2	*0.4*	1.0	*0.5*	1.46	*0.7*
Orthocladiinae	7	11.8	*2.2*	1.4	*0.3*	1.0	*0.2*	1.7	*0.4*	1.6	*0.4*	2.5	*0.6*
Chironominae	8	8.1	*0.6*	4.8	*2.3*	9.9	*1.4*	22	*3.0*	10.8	*1.4*	6.8	*1.2*
Chironomidae non. det.	9	6.1	*2.1*	4.7	*2.3*	8.7	*1.0*	25	*4.0*	7.4	*1.93*	6.6	*2.8*
Tanypodinae	10	3.4	*1.0*	0.7	*0.3*	2.1	*0.2*	5.5	*0.7*	3.7	*1.0*	3.3	*0.9*
Caenis spp.	11	0.3	*0.2*	2.7	*1.3*	0.6	*0.2*	8.9	*1.0*	6.5	*0.9*	8.1	*1.8*
Oligochaeta	12	0.2	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.3	*0.1*	0.5	*0.2*
Tinodes waeneri	13	0.0	*0.0*	0.0	*0.0*	4.7	*0.8*	9.9	*2.0*	15.3	*3.0*	3.8	*1.2*

Also significant site differences were found for all taxa abundances, total abundance, number of taxa, diversity parameters, and biomass values (Table 4). However, the rank orders differed and were taxa dependent (Tukey post-hoc test). Overall abundance and biomass were lowest at site $S2_{shallow}$, higher at site $S1_{shallow}$, and highest at site $S1_{deep}$. The same rank order occurred for the amphipod *D. villosus* and the zebra mussel *D. polymorpha*. The latter comprised up to 96% of the overall abundance at site $S1_{deep}$ on the second sampling date, whereas it comprised only 31% at the start of the experiment. At the other two sites, *D. polymorpha* abundances were less pronounced, with lower values at sites $S1_{shallow}$ (3%; 43%) and $S2_{shallow}$ (0.1%; 12%) on both sampling dates. The site differences and rank orders of the abundance and biomass data were generally consistent.

The taxa abundance, total abundance, species diversity parameters, and biomass did not reveal any treatment effects in any combination (Tukey post-hoc test). Although *D. polymorpha* abundances (mean $\pm$ SE per sample unit) were somewhat lower in the fish enclosure on the second sampling date, especially at site $S1_{deep}$ (15425 $\pm$ 2260) than in the fish exclosure (22665 $\pm$ 1550) and cageless controls (22158 $\pm$ 3303), the lower abundances were not significant.

The date$\times$site interaction for overall abundance and biomass and for abundance and biomass of several taxa (e.g. *D. polymorpha*, *T. waeneri*, *Pisidium* spp., chironomids, *D. villosus*, and Oligochaeta), and for abundance of *Caenis* spp. was highly significant (Table 4). The treatment$\times$date interaction for total abundance and evenness was significant. The treatment$\times$date$\times$site interaction for total abundance and *D. polymorpha* abundance was weak. No significant treatment effects at any site on the last sampling date were found for these groups in treatment$\times$date (site) and in date (site)$\times$treatment analyses.

Table 4: Results of repeated measurement of MANOVA on benthos abundance and biomass, total and dominant taxa, number of taxa, and diversity. All data were log(x+1) transformed except taxa and diversity data. The effects of date, site, treatment and the interaction between them: date $\times$ site, date $\times$ treatement, date $\times$ site $\times$ treatment, site $\times$ treatement were tested and significant results displayed. Date ($df_{1,18}$) was significant ($p < 0.001$) in all measured metrics except in number of taxa (S), Chironominae, *Pisidium* spp. and *Tinodes waeneri* (both abundance and biomass), Oligochaeta, Chironomidae, Tanypodinae (biomass) and was therefore removed from the table. All other significant results are shown. Sites: S1d-$S1_{deep}$; S1s-$S1_{shallow}$; S2s-$S2_{shallow}$.

			Abundance			**Biomass**		
		$Df_{eff,err}$	F	p	Tukey post-hoc	F	p	Tukey post-hoc
Abundance (N)	Date×Site	2,18	64.56	<0.001		11.52	0.001	
	Date×Treatment	2,18	5.41	0.014		0.06	0.568	
	Site	2,18	40.00	<0.001	S2s<S1s<S1d	107.60	<0.001	S2s<S1s<S1d
Taxa (S)	Date×Site	2,18	8.835	0.002				
	Site	2,18	28.14	<0.001	S1s<S1d<S2s			
Species richness	Date×Site	2,18	12.04	<0.001				
Margalef (d)	Site	2,18	35.90	<0.001	S1s=S1d<S2s			
Shannon diversity	Date×Site	2,18	276.67	<0.001				
(H'log e)	Site	2,18	130.18	<0.001	S1d<S1s<S2s			
Pielou evenness	Date×Site	2,18	521.04	<0.001				
(J')	Date×Treatment	2,18	6.29	0.008				
	Site	2,18	105.05	<0.001	S1d<S1s<S2s			
Dreissena	Date×Site	2,18	5.98	0.010		6.3	0.008	
polymorpha	Site	2,18	40.09	<0.001	S2s<S1s<S1d	42.44	<0.001	S2s<S1s<S1d
Chironominae	Date×Site	2,18	16.78	<0.001		10.49	0.001	
	Site	2,18	23.62	<0.001	S1d<S2s=S1s	12.08	<0.001	S1d=S2s<S1s
Orthocladiinae	Date×Site	2,18	19.70	<0.001		35.46	<0.001	
	Date×Site×Treatment	4,18	5.89	0.003		1.84	0.165	
	Site	2,18	4.81	0.021	S1s=S2s<S2s=S1d	15.68	<0.001	S1s=S2s<S1d
Oligochaeta	Date×Site	2,18	11.31	0.001		11.40	0.001	
	Site	2,18	95.42	<0.001	S1s<S1d<S2s	23.40	<0.001	S1s=S1d<S2s
Pisidium spp.	Date×Site	2,18	6.78	0.006		12.94	<0.001	
	Site	2,18	31.87	<0.001	S1s=S2s<S1d	61.63	<0.001	S1s=S2s<S1d
Chironomidae	Date×Site	2,18	36.79	<0.001	S1s	10.11	0.001	
	Site	2,18	24.72	<0.001	S1d<S2s<S1s	11.34	0.001	S1d=S2s<S1s
Dikerogammarus	Date×Site	2,18	29.04	<0.001		15.16	<0.001	
villosus	Site	2,18	85.18	<0.001	S2s (0)<S1s<S1d	42.53	<0.001	S2s (0)<S1s<S1d
Ostracoda	Site	2,18	4.23	0.031	S1d=S2s<S2s=S1s	4.65	0.023	S1d=S2s<S2s=S1s
Caenis spp.	Date×Site	2,18	1.83	0.189		9.05	0.002	
	Site	2,18	15.84	<0.001	S1d<S2s=S1s	46.25	<0.001	S1d<S1s<S2s
Tanypodinae	Date×Site	2,18	26.94	<0.001		19.425	<0.001	
	Date×Site×Treatment	4,18	3.64	0.024		3.891	0.019	
	Site	2,18	3.50	0.052	S1d=S2s<S2s=S1s	4.84	0.021	S1d=S2s<S2s=S1s
	Date×Site	2,18	6.74	0.007		16.47	<0.001	
Tinodes waeneri	Date×Site×Treatment	4,18	5.98	0.003		2.26	0.103	
	Site	2,18	714.48	<0.001	S1d(0)<S2s<S1s	96.77	<0.001	S1d(0)<S1s=S2s

Benthos community composition (nMDS plots)

The abundance and biomass data of the benthos assemblages are shown in Figs. 1 and 2, respectively. Date effects were analysed separately for each site and were highly significant for abundance and biomass (Global R abundance/biomass: $S1_{shallow}$ R = 0.839 / 0.737; $S2_{shallow}$ R = 0.595 / 0.748; $S1_{deep}$ R = 0.819 / 0.922; all p = 0.001). Site $S2_{shallow}$ showed higher variances between replicates than the other two sites, which resulted in lower R values.

Benthos species composition (Fig. 1) and biomass (Fig. 2) clearly differed at all three sites (Global R = 0.913 and R = 0.785, respectively; both p = 0.001). In a pair-wise comparison of species assemblages based on abundance data ($S1_{shallow}/S2_{shallow}$ R = 0.797; $S1_{deep}/S2_{shallow}$ R = 0.990; $S1_{shallow}/S1_{deep}$ R = 0.922; all p = 0.001) and on biomass data, differences remain highly significant in all combinations ($S1_{shallow}/S2_{shallow}$ R = 0.606; $S1_{deep}/S2_{shallow}$ R = 0.934; $S1_{shallow}/S1_{deep}$ R = 0.798; all p = 0.001).

Treatment effects were tested separately for each site and date. No combinations revealed any effect in abundance (range Global R: $-0.148 \leq R \leq 0.152$) and in biomass (range Global R: $-0.193 \leq R \leq 0.152$) compared to a random distribution.

Fish gut content analysis

The mean gut fullness of bream (age class 0+, 68 % ± 5.0; age class 1+, 73 % ± 5.3) was lower than that of dace (age class 0+, 82 % ± 4.5; age class 1+, 87 % ± 4.1), and was higher in age class 1+ than in age class 0+ in both taxa (Fig. 3). However, the gut fullness differed significantly only between bream of age class 0+ and dace of age class 1+ (ANOVA $F_{3,581}$, $df_{3,136}$, p = 0.016). No other significant differences were found between sites for both taxa and age classes. Dace guts were usually more filled. Only a few individuals contained guts with less than 50% filled (age class 0+, 17.7%, age class 1+, 10.8%). No dace had completely empty guts. In contrast, three individuals (7.5%, out of 40) and one individual (3.4 %, out of 29) of bream of age classes 0+ and 1+, respectively, had empty guts. Less than half-filled guts were found in 25.0% of the bream of age class 0+ and in 25.5% of bream of age class 1+. Full guts were found in 58.8% of the dace of age class 0+ and in 70.3% of dace of age class 1+ (n = 34, 37 individuals respectively).

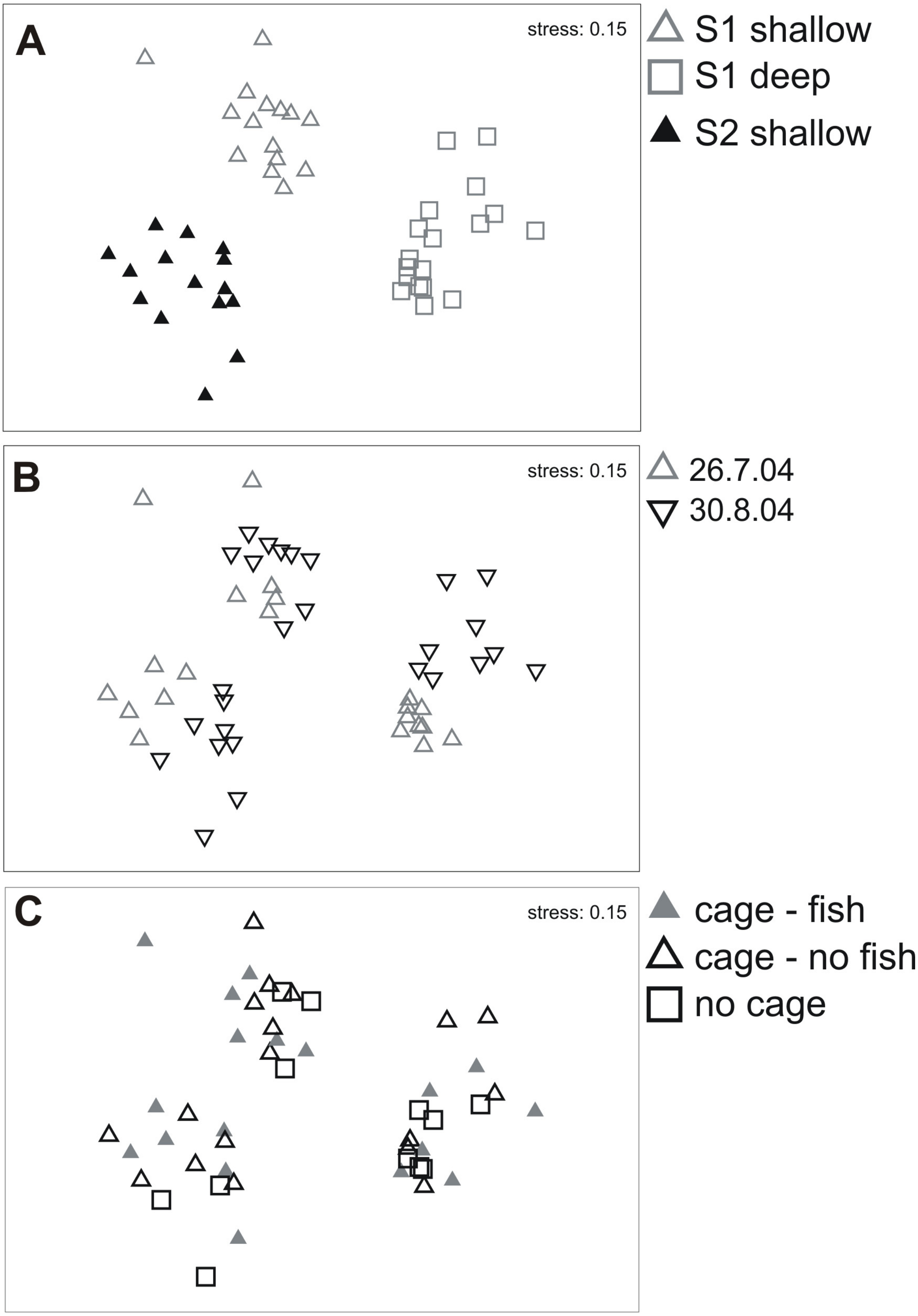

Figure 1: NMDS of benthos community composition based on abundance data. **A**: sites, **B**: sampling date, **C**: treatments are highlighted. Data are log(x+1) transformed, and the Bray-Curtis similarity index was applied.

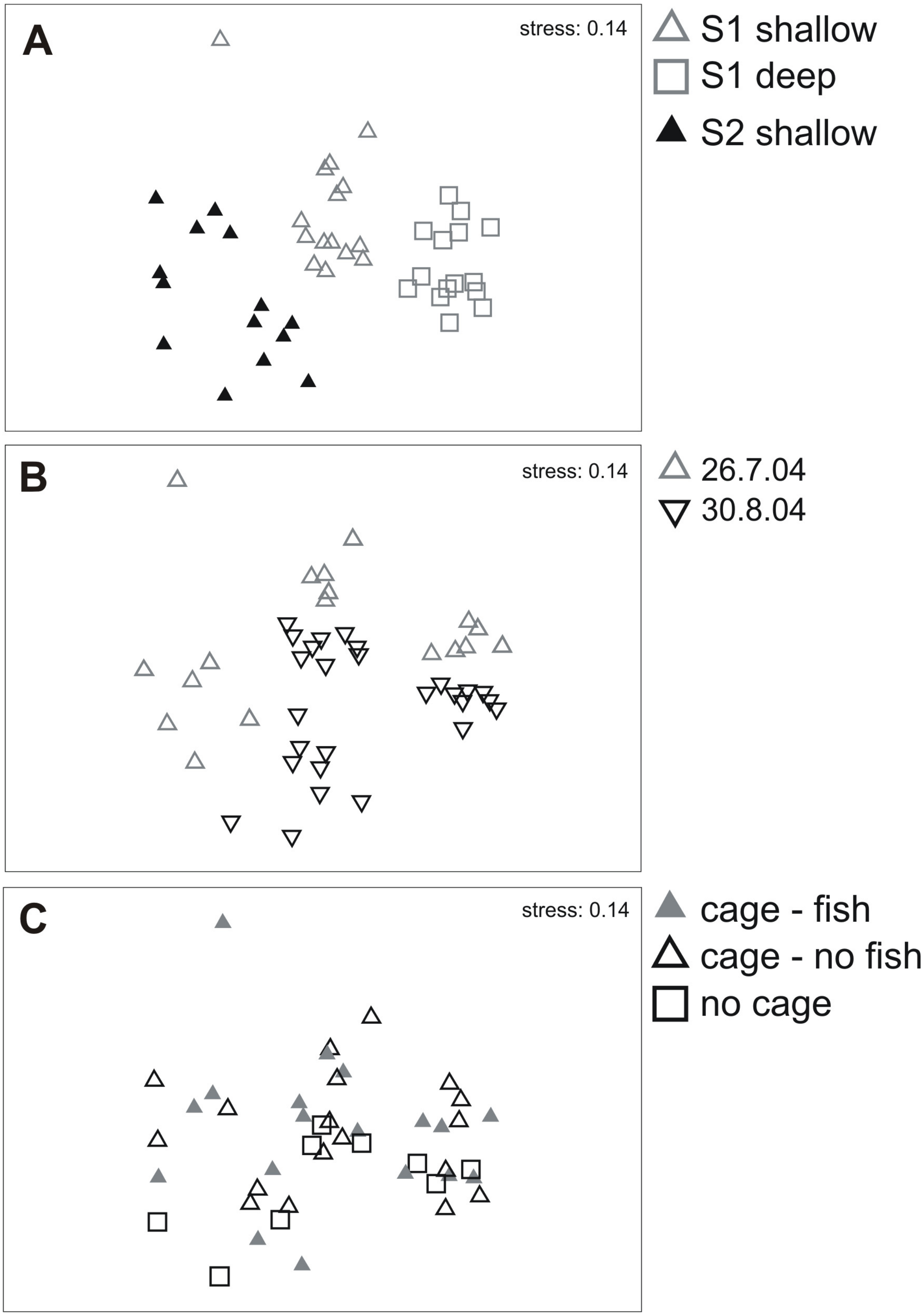

Figure 2: NMDS of benthos community composition based on biomass data. **A**: sites, **B**: sampling date, **C**: treatments are highlighted. Data are log(x+1) transformed, and the Bray-Curtis similarity index was applied.

The species composition found in the guts was less diverse than that of the natural substrate samples. Only 18 species or higher order groups were consumed (mean individuals ± SE), including the non-animal food macrophytic *Chara* spp. (3.4 ± 1.4) and filamentous algae (0.71 ± 0.71). Both cyprinid fish species most frequently consumed the benthic Cladocera (11.6 ± 2.3) and early-settlement larvae of *D. polymorpha* (11.0 ± 2.2). Other food items included a variety of insects, such as chironomids (all three subfamilies, pupae) and case-less and case-bearing caddisflies, as well as other taxa, such as amphipods (*Dikerogammarus villosus*), oligochaeta, and molluscs (*Pisidium* spp.). Five taxa were identified as the most important food items, i.e. explaining 95% of the variety, using the BVStep procedure of Primer6b (Rho = 0.964, $p = 0.001$): Cladocera, Orthocladiinae, Chironomiinae, diptera pupae, and *D. polymorpha*. Other than benthic Cladocera, none of the zooplankton taxa dominant in the field samples (nauplii, Rotatoria, *Bosminia* spp., cyclopoid, and copepods) were found within the fish guts (data not presented).

The diet of the 140 examined juvenile bream and dace differed significantly in the proportion of mean specific prey items consumed at all three sites and between fish taxa and age classes (Fig. 4; H-test, Table 5). The average number of consumed molluscs (mainly *D. polymorpha*), plankton, and macrophytes was highest at site

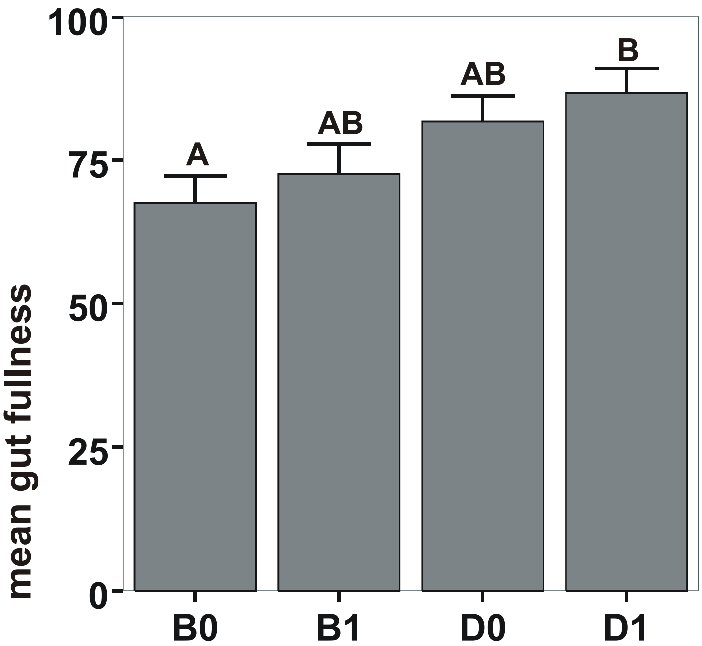

Figure 3: Mean gut fullness (± SE) of bream (B) and dace (D) at age classes 0+ (0) and 1+ (1). Values of gut filling status were visually obtained in 5% steps. Bars with different letters have significantly different means ($p < 0.05$).

S1$_{deep}$, lower at site S2$_{shallow}$, and lowest at S1$_{shallow}$, and the increased amount at the sites was similar for the three types of food items. Small amounts of other prey, i.e. gammarids (*G. roeseli*, *D. villosus*), dipterians (all subfamilies of chironomids, pupae) and a variety of other taxa, were also regularly included in their diet. Zooplankton was mainly consumed by bream; in age-class 0+ bream, zooplankton comprised 83.4% of the total diet (mean 11.8 $\pm$ 2.6), whereas in age-class 1+ bream, higher amounts of total plankton (34.9 $\pm$ 9.4) were consumed, but the proportion was lower (57.4%). In contrast, dace consumed plankton only occasionally (age class 0+: 4.1 $\pm$ 1.3, 1.56%; age class 1+: 2.0 $\pm$ 0.8, 0.06%); they consumed even less diptera, gammarids, and other taxa. Dace of both age classes (age class 0+: 15.7 $\pm$ 5.3, 59.4%; age class 1+: 11.7 $\pm$ 4.3, 37.9%) and bream of age class 1+ (19.3 $\pm$ 5.6, 31.7%) fed considerably on molluscs (mainly *D. polymorpha*). The largest proportion of food items in dace guts of age class 1+ consisted of macrophytes, mainly *Chara* spp. (12.9 $\pm$ 4.8 , 41.7%).

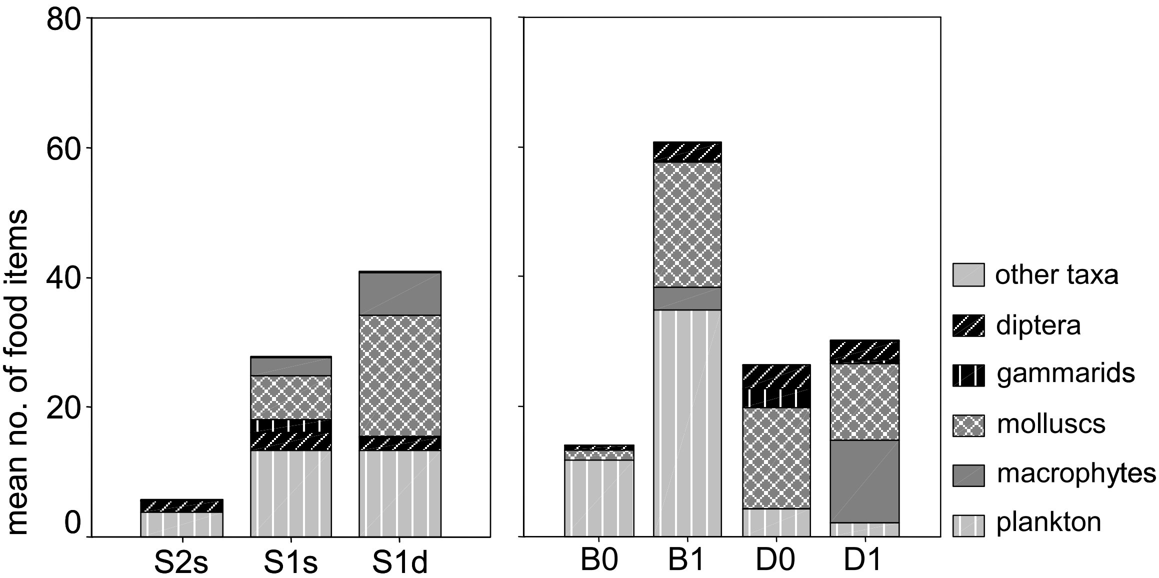

Figure 4: Average number and taxa composition of five dominant prey items in the guts of bream (B) and dace (D) at age classes 0+ (0) and 1+ (1). Sites: S1s, S1$_{shallow}$; S2, S2$_{shallow}$; S1d, S1$_{deep}$. All other taxa consumed were pooled within the category *other taxa*.

The consumption rates of the two fish species were determined from the gut contents (nMDS, Fig. 5). There were no specific differences in the species consumed between the sites (Global R = 0.002) or taxa (dace, bream: Global R = 0.153), summarised or differentiated between the two age classes. A pair-wise test was not significant when compared to random distribution (R = 0.158–0.301, ANOSIM, 2-way-crossed).

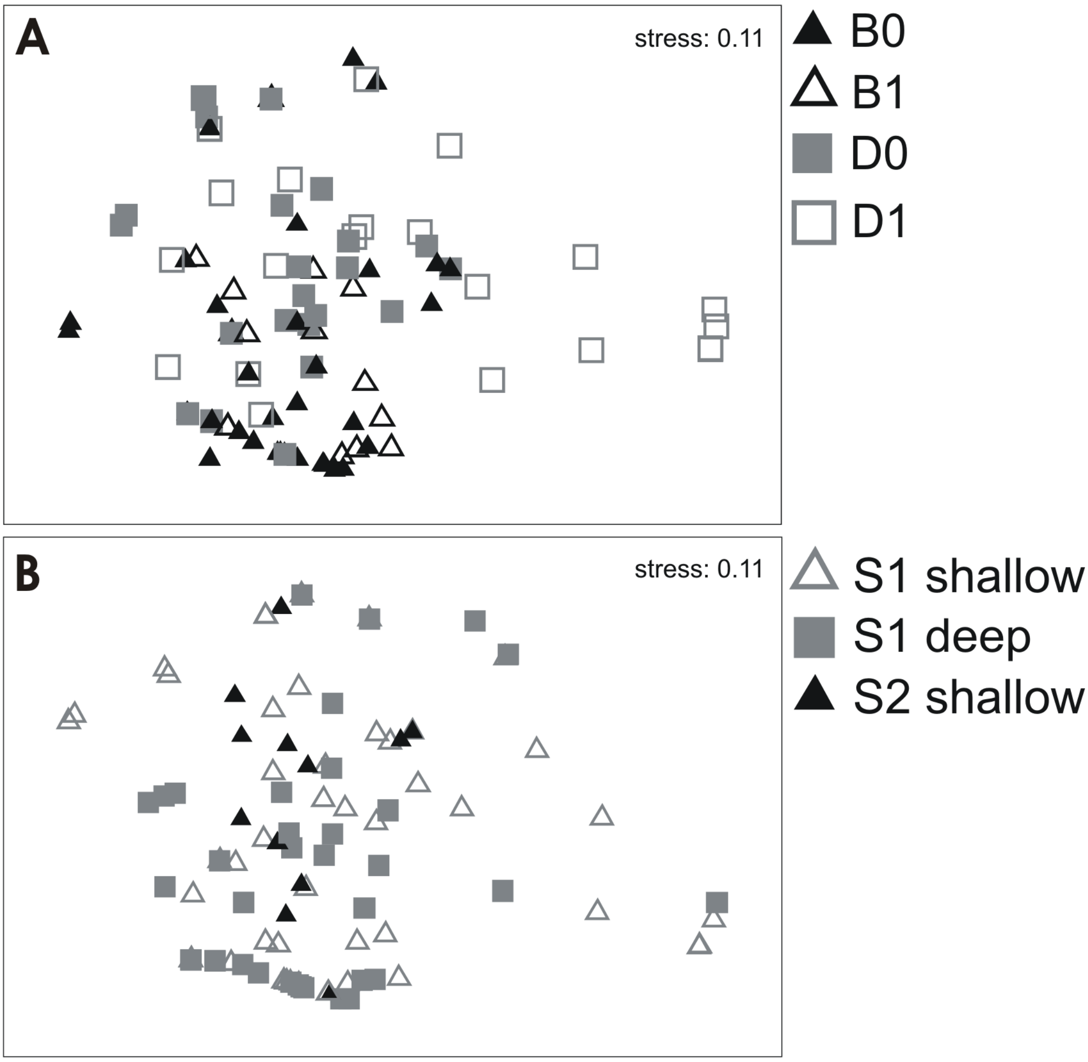

Figure 5: NMDS of benthos, plankton and macrophyte consumption within the gut content of juvenile cyprinids **A**: Dace (D) and bream (B). The gut content is highlighted for fish species (D, B) in their specific age class 0+ (0) and 1+ (1) therefore B0, B1, D0, D1). **B**: shows the differenciation of sites. Data are square-root transformed, and the Bray-Curtis similarity index was applied.

Discussion

Predation effects

In the experimental enclosures, the juvenile cyprinids (age classes 0+ and 1+) dace and bream consumed high amounts of macroinvertebrates, and their guts were generally well filled. Differences in feeding behavior specific to fish species and age class were observed. Juvenile bream consumed regularly zooplankton, which was only occasionally included in the diet of dace. Although fish density was higher in enclosures than in natural habitats, no predation effects of cyprinids on macroinvertebrate abundance, biomass, or species composition were detected at any of the enclosure sites. No differences in the prey in the gut content of the fish from the three sites were observed, regardless of the exposure status. The three sites chosen represent common habitat types within the upper littoral zone of Lake Constance. Our results indicate that macroinvertebrate abundances and assemblage structure are only marginally influenced, if at all, by predation by juvenile cyprinids. These results were surprising since they clearly contradicted our hypothesis.

Habitat complexity i.e. substrate structure, interstitial space or macrophyte coverage differed at the three sites. It was lowest within the most sheltered site, $S2_{shallow}$, which should contain the lowest number of refuges for invertebrates. Nevertheless, no increased predation effects were observed. Benthos abundance was generally high and increased throughout the experiment. We therefore assumed a sufficient nutrient supply for fish consumption. However, the benthos exploitation rate depends on differences between potential and available food within the upper layer of soft sediment ($S2_{shallow}$, $S1_{deep}$), on top of hard substrates ($S1_{shallow}$), or within macrophyte stands ($S1_{deep}$). Furthermore, a much smaller proportion is visible and therefore truly available for individual foraging fish. Several factors might influence detection and the consumption rates, such as prey colour, activity, contrast, specific fish preference (Schael *et al.* 1991; Mehner *et al.* 1998), reactive distance (Werner & Hall 1974), prey size (Hart & Gill 1992), gape restriction (De Vries *et al.* 1998; Bremigan *et al.* 2003; Krebs & Turingan 2003), and size selection (Hart & Gill 1992; Mehner *et al.* 1998; Rincon & Lobon-Cervia 1999). Boisclair and Leggett (1985) assumed that only 1% of the total biomass is truly available for fish consumption. They found evidence in their comparative study of 21 temperate lakes, that fish consumption rates of zoobenthos (daily, annual) within the upper 5 m of the littoral were significantly lower than reported benthic production/biomass ratios. The probability of successful prey capture should increase in a linear fashion with the total biomass of fish and benthos (Hanson & Leggett 1986). However, we did not observe such an increased fish consumption rate at the three sites in our study. On the other hand, the apparently high amounts of ingested macrophytes (mainly *Chara* spp.), which are interpreted as low-quality food by Horppila (1994), support the hypothesis of low benthos availability of Boisclair & Leggett (1985) also for Lake Constance.

Significant amounts of macrophytes similar to the amounts in our study were ingested by pumpkinseed fish (*Lepomis gibbosus*) (Hanson & Leggett 1986). The amount of inferior food (microcrustaceans) consumed by yellow perch (*Perca flavescens*) increased from <1% to 30–50% with increasing intraspecific competition, but the total amount decreased, and the total macroinvertebrate abundance and biomass was also unaffected by fish biomass (Hanson & Leggett 1986). In our study, the observed significant differences in consumed zooplankton and proportion of benthos between bream and dace could be interpreted as a result of competition, gape size restriction, or species- and age-specific food preferences. Possible effects of intraspecific and/or interspecific competition between the cyprinids chosen cannot be determined from our experiments, and we intend to study this issue in the future.

Vasek & Kubecka (2004) found the highest gut contents in bream in the afternoon and shortly before sunset. The bream in their study fed exclusively on zooplankton, but feeding on benthos at night instead of preying on zooplankton during the day has also been documented (Schulz & Berg 1987). Other seasonal and day-to-day changes in consumption rates have been documented for cyprinids (Horppila 1994; Specziar *et al.* 1997; Specziar 2002) and other littoral fish (Fischer & Eckmann 1997a, b; Baumgärtner 2004). The consumption rates in our study are based exclusively on daytime samples. Thus, we would assume a pattern similar to that reported by Horppila (1999), which would result in a higher predatory impact on benthos taxa than documented solely by our gut content analyses of the two taxa. Nevertheless, such a predatory effect was not detectable in benthos abundance, size structure, biomass, and taxa composition at all sites. In contrast to our hypothesis, we found no evidence that the wind exposure of sites alters the exploitation rates of benthic invertebrates by cyprinids. The fish-specific performances, growth rates (length and weight), and energy required to remain within the three habitats in relation the physical constraints are the focus of a parallel study (Stoll *et al.* 2008).

Our biomass data, which are based on size class counts, do not reveal size-selective feeding that would result in a shift in size structure of the prey taxa. We expected that cyprinids within the enclosures would consume a greater proportion of large prey, leaving higher proportions of less-favorable small prey as compared to fish exclosures. We observed a size shift of some invertebrates, e.g. *Caenis* spp., in the enclosures from a few large individuals to high numbers of early instar individuals. However, these sizes occurred in all treatments including fishless controls, which indicated a seasonal taxa-specific process. This is a good example of predation effects being masked by other community-inherent processes.

Cobb & Watzin (1998) observed predation effects of yellow perch only at high density. In our study, the stocking density of juvenile cyprinids might be too low to detect predation effects. However, it was approximately 20 times higher than *in situ*.

Weak predation effects might have occurred on top of substrates, but were not likely to be detected by the quantitative benthos sampling device used. The suction sampler also includes the upper interstitial layer of finer sediment within the entire sample. This probably increases the total abundance of the sample unit considerably, and weak predation effects might have been overridden and hidden behind sample variances. However, other sampling methods have other constraints, and we therefore opted for high precision and repeatability.

Fish exclosures are not necessarily predator free. A variety of invertebrate predators prey on other invertebrates (Lancaster *et al.* 1991), mainly leeches (Elliot & Mann 1979), flatworms (Hansen *et al.* 1991), and chironomids (Macan 1977). Such an increased effect of invertebrate predation has been observed in vertebrate exclosures (Macan 1977; Crowder & Cooper 1982; Gilinsky 1984). Crayfish (*Orconectes limosus*) predation on invertebrates has also been documented (e.g. Lodge *et al.* 1994; Charlebois & Lamberti 1996; Nystrom *et al.* 1996; Stewart *et al.* 1998a; Dorn & Mittelbach 1999), but could not be observed in our study.

Benthos seasonal patterns

We found a strong seasonal pattern in benthos abundance, biomass (Tables 2 and 3), and species composition (Figs. 1 and 2) at all three sites. Within one month, the benthos community at all three sites changed dramatically and highly significantly because of a strong seasonality in the life history of the major taxa. Several taxa increased in density throughout the experiment, e.g. *Caenis* spp., Ostracoda, Chironominae, and *D. polymorpha*. Mainly *D. polymorpha* dominated in the overall increased abundances. High numbers of tiny zebra mussel individuals that recently underwent metamorphosis were found at all sites, but predominantly at site $S1_{deep}$. Another temporal factor complicating the predation effect by cyprinids was the emergence of some aquatic insects, particularly mayflies (*Caenis* spp., Leptophlebiidae, *Ecdyonurus dispar*) and chironomids (Orthocladiinae, Tanypodinae). With the chosen experimental design, emergence rates cannot be quantified. We also assumed that the mesh size used allowed a continuous flux of invertebrates within the enclosures and exclosures, which would lead to consumed invertebrates being replaced by immigrating individuals of the same or other taxa. However, we found a complete community shift during the experiment in all treatments at all sites (Figs. 1 and 2).

Recolonisation rates of benthic invertebrates in lake littoral zones have rarely been studied (but see Quinn *et al.* 1998a, b; Chapter 2). Bare substrates left for recolonisation within same habitats, as in the present study, contained similar benthic assemblages after one month, but some taxa reached abundances as high as those of control samples within a few days (Chapter 2). In Chapter 2 fully colonised single stones had 479 ± 39 (mean ± SE) individuals per 300 cm^2. Considering the sample size in the present study of 625 cm^2, we would then expect approximately 1000 individuals on a plain substrate area of that size. Such an assumption completely disregards any interstitial spaces, which are found in natural environments, but estimates the amount of invertebrates potentially accessible to fish, which are usually restricted to foraging on the uppermost sediment layer. Hence, the number of macroinvertebrates available for the given sample size (6664 ± 1103, mean ± SE) was 6.7-fold higher than the number truly accessible for fish. The total cage size was 2 m^2, which would theoretically mean 31930 benthic individuals on top of the substrate compared to 213248 individuals within the upper substrate layer (Chapter 2).

In Chapter 2 I assumed intermediate recolonisation rates on stones with established periphyton and inorganic fine sediment layer. Abundances observed after two weeks of pre-colonisation were compared with abundances after one month. Within these two weeks, 333 individuals arrived in an area of 300 cm^2 (or 694 individuals in an area of 625 cm^2), which would result in 22200 individuals arriving per cage (2 m^2). If the mean benthos consumption rates (mean benthos individual per fish) of dace (age class 0+: 22.3, age class 1+:15.5) and bream (age class 0+: 2.3, age class 1+: 22.3) for the given number of fish (dace: 12 age class 0+, 8 age class 1+; bream: 30 age class 0+, 8 age class 1+) are considered, then approximately 639 individuals were consumed per day per cage. Furthermore, if an evacuation rate of one day and an equal consumption rate during the experiment are assumed, then approximately 19170 individuals were consumed per cage. This rather simple calculation clearly points out that the recolonisation rate is either slightly higher than or in a range similar to the consumption rate of juvenile cyprinids, which were stocked in densities 20 times higher than in the field.

In Chapter 2 I also documented differences in the recolonisation rate dependent on the hydrodynamic regime; highest rates were found at the dynamic study site. In the present study, we found further evidence that hydrodynamic processes might be a key factor in determining benthos community structure directly as well as indirectly. The increase in the settlement of early instar larvae of *D. polymorpha* strongly differed at the three sites; the abundance was highest at site $S1_{deep}$ (28-fold increase first to second sampling date), but the increase was in proportion highest at the most-exposed site $S1_{shallow}$ (90-fold increase), $S2_{shallow}$ (32-fold increase) (Table 2). Larval transport mediated by a wind-induced circulation pattern has also been observed in an estuarine shelf study (Xie & Eggleston 1999). Benthic recolonisation is considerably faster when the habitat structure, i.e. the organic or inorganic coverage on hard substrates, does not change, even after severe disturbances (Scheifhacken & Rothhaupt 2004).

Benthos site differences

The documented site differences in benthos abundance data and assemblage structure reflect the habitat, depth, and substrate preferences of some taxa. These patterns of, e.g. substrate composition, and macrophyte or periphyton coverage, are at least indirectly altered by hydrodynamic processes, such as wind, wave exposure, and water-level fluctuations.

From the results of this study, we conclude that predation effects on benthos are negligible compared to inherent benthos seasonal shifts and can be ignored. Furthermore, we found no evidence that hydrodynamic processes mediate the cyprinid–macroinvertebrate interaction. Therefore, benthos in this study is not likely controlled by top-down processes of cyprinids. However, the reverse can be presumed for fish constraints, which are likely mediated by bottom-up effects of benthos availability and accessibility. Our results support the findings of others, who found only moderate or transitory predation effects on benthic communities by yellow perch (Cobb & Watzin 1998) and burbot (Baumgärtner 2004). Baumgärtner (2004) repeated the experiments of burbot predation on benthos and obtained periodically varying effects. Cobb & Watzin (1998) also suggest that predation effects are not pronounced enough to alter underlying benthic community structures, and they assume that this is a common pattern for temperate littoral zone communities. We followed this assumption in the current study of juvenile cyprinids and in a study of perch and ruffe (Chapter 4).

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Chapter 6

Complex spatial and temporal patterns of littoral benthic communities interacting with water level fluctuations and wind exposure in the littoral zone of a large lake

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Summary

The spatial and temporal organisation of benthic invertebrate communities was studied in a large oligotrophic lake in central Europe. Three shallow littoral sites at 0.4-m depth were sampled monthly from May 2002 to April 2003. On a spatial scale, the benthic community composition at all sites and in all samplings significantly differed in both abundance and biomass. On a temporal scale, the benthic communities at all sites gradually changed each month; monthly samples always significantly differed, but samples from consecutive months were more similar to each other than to samples of non-consecutive months. The observed variability within benthic communities corresponded with changes in the abiotic parameters water level and wind exposure, but was best explained by short- and long-term fluctuations in the water level. Effects of wind exposure were most pronounced in the winter months, when high wind events most often occurred. However, wind effects were masked by stronger effects, such as water-level fluctuation within the shallow littoral zone, or diminished by parameters with opposite effects, e.g. slope *vs.* exposure. Wind-induced shear stress in the upper eulittoral zone directly influenced the abundance and biomass of the benthic community to a lesser extent. We conclude, however, that this stress alters habitats constantly (e.g. substrate composition, periphyton growth, resuspension *vs.* sedimentation) and is therefore the driving force for the reported permanent site differences. Furthermore, benthic communities were well adapted to frequent minor changes and also to regular major changes of their habitat, as bare substrates were rapidly recolonised within a month.

Keywords: macroinvertebrates, water-level fluctuation, wave exposure, slope, fetch, eulittoral zone

Introduction

The littoral zone plays an important role in the energy transfer of lake ecosystems (James *et al.* 2000a; Higgins *et al.* 2001; Tolonen *et al.* 2001; Vadeboncoeur *et al.* 2003) and affects various trophic levels within benthic coupled food webs. Even in large, deep, oligotrophic lakes, where littoral zones represent often a smaller portion of the entire lake area, this habitat can be a very limited resource for benthic invertebrate settlement and fish spawning and foraging.

A key role in energy transfer to upper levels is played by macroinvertebrates (Gilinsky 1984; Gilliam *et al.* 1989; Lindegaard 1994), but their community structure, population dynamics, habitat association, and trophic interactions are poorly understood. The structure of the benthic communities and the abiotic factors involved in the structuring are of special interest. Habitats in large lakes are altered and become heterogeneous through hydrodynamic processes and water-level fluctuations (Keddy 1982; Palomäki 1994; James *et al.* 1998), in addition to, e.g. trophy and water chemistry. Hydrodynamic processes strongly influence the size class structure of littoral sediments (Hakanson & Jansson 1983; Schmieder *et al.* 2004). The size class structure, the fine sediment layer on top of larger cobblestones, and the availability of interstitial refuges, i.e. the substrate composition, influence the occurrence of macroinvertebrates (Gjerlov *et al.* 2003) and benthic fish (Fischer 2000).

The benthic community structure is also influenced by wave action and water depth. Wave action at littoral sites strongly depends on the exposure to wind- or boat-generated waves, the frequency and duration of such events, and the lake morphology, such as slope, lake size, and wind fetch across the lake surface (e.g. Hakanson 1977; Hakanson & Jansson 1983; Cattaneo 1990; Petticrew & Kalff 1991; Rowan *et al.* 1992; Rasmussen 1993; Hamilton & Mitchell 1996; Rasmussen & Rowan 1997). On the horizontal scale, wave exposure at different sites can differ owing to their positions relative to the direction of the prevailing winds. Furthermore, the water level can fluctuate because of variations in inflow and outflow rates; this fluctuation can affect invertebrate (Palomäki 1994; Baumgärtner 2004), fish (Hunt & Jones 1972; Fischer & Eckmann 1997a), and macrophyte (Riis & Hawes 2002) productivity and community composition. On the vertical scale, hydraulic stress on organisms and substrate decreases with increasing water depth. The water depth intercorrelates with several abiotic factors, e.g. slope and substrate composition (Duarte & Kalff 1986; Petticrew & Kalff 1991; Rasmussen 1993; Rasmussen & Rowan 1997; Cyr 1998a; Schmieder *et al.* 2004), depth of light penetration and spectrum (Donohue *et al.* 2003), temperature (Baumgärtner 2004), and nutrients in the water column (Hamilton & Mitchell 1997). Various macroinvertebrate taxa (Brodersen 1995; Baumgärtner 2004; Stoffels *et al.* 2005), periphyton (Cyr 1998a, b), and macrophyte communities (Duarte & Kalff 1986) prefer specific water depths.

Mainly qualitative macrobenthic studies of Lake Constance in central Europe have been carried out both before (Muckle 1942) and during its period of eutrophication (Reiss 1968; Streit & Schröder 1978; Frenzel 1979). More recently, during its phase of re-oligotrophication, a few single samplings have been taken (Mauch 1996; Röck 1999). Because of the differences in trophic status of the lake, the studies are hardly comparable among each other and with present-day studies. To date, only a few quantitative macroinvertebrate studies in Lake Constance (Baumgärtner 2004; Mörtl 2003; Werner *et al.* 2005) and in other large oligotrophic lakes (Palomäki 1994; James *et al.* 1998; Stoffels *et al.* 2003, 2005) have been carried out. The studies were often limited to one or very few samplings per site or lake; this reflects the difficulties in quantitative sampling in lake littoral zones in general. Especially in large oligotrophic lakes, littoral zones are often steep and narrow. Sampling is restricted to arm length in the eulittoral zone unless scuba divers are available. Quantitative sampling in upper stony littoral habitats and in the infralittoral zone is also hampered by the lack of a unidirectional current, which does occur in lotic habitats. The substrates of lentic systems are comprised of grains ranging from fine sediment to cobblestones or gravel. This variation in grain size has obstructed the various attempt to standardise samplings and has hindered the development of a general sampling method.

In the present study, we wanted to assess the effect of potentially relevant environmental factors on the benthic community structure in Lake Constance. We expected wave exposure and water-level fluctuation to be the most influential abiotic forces structuring benthic communities. We further assumed that the upper eulittoral zone at 0.4-m depth would be the most susceptible to wave hydrodynamics and water-level fluctuations. We expected colonisation processes and species turnover to be strong innate community sources responsible for a large proportion of the observed high dynamics within benthic systems. Monthly samples were taken to study the seasonality on a scale finer than any studies published to date. We thereby expected to be able to distinguish potential environmental factors, i.e. wave exposure and water-level fluctuation, responsible for community variations and life-history-related factors of the benthic community. Here, we focus on spatial and temporal patterns in the community structure. Abundance, biomass, and diversity patterns will be presented in a subsequent paper.

Methods

Study sites

The study was conducted in the littoral zone of the large, oligotrophic, pre-alpine Upper Lake Constance in central Europe, with a surface of 473 km^2, a mean depth of 101 m, and a maximum depth of 254 m. Westerly winds prevail throughout the year, with a second, less-dominant peak from the east, especially in winter (Bäuerle *et al.* 1998). The littoral zone is restricted to less than 10% of the total lake area (Wessels 1998). Lake Constance drains parts of the European Alps, resulting in an annual water-level fluctuation of up to 2 m (Luft & Vieser 1990), with low levels in winter and high inflow rates after snowmelt in summer.

Along the 186-km shoreline of Upper Lake Constance, the littoral zone varies greatly in shore width, sediment composition, and wind exposure, among other factors. This results in an expectedly high variability of the benthic community. Therefore, we chose three representative study sites: Site Litoralgarten near Konstanz (47°41’26.668’’N, 9°12’18.355’’E) is situated at the south-western shore, which is more sheltered from wind-, ferry-, and leisure-boat-induced waves owing to the geomorphological structure and slope. Sites Meersburg (47°41’37.249’’N, 9°16’11.660’’E) and Immenstaad (47°39’46.808’’N, 9°20’50,093’’E) lie on the north-eastern shore and are highly exposed to westerly winds (Bäuerle *et al.* 1998), but differ in their specific fetch length (lower at site Meersburg than at site Immenstaad) and exposure to ferry- and leisure–boat-induced waves (higher at site Meersburg than at site Immenstaad). The slope of the sites differ: Meersburg, approximately 30%; Litoralgarten, approximately 19%; and Immenstaad, approximately 5%. The substrate at all three sites is composed of cobblestones loosely embedded within finer sediments. The fraction of fine sediment is higher at site Litoralgarten, and the mean grain size is significantly higher at site Meersburg. The shore at site Meersburg is narrow (15–25 m), and the sediment consists mainly of coarse stones. The littoral zone is broader at site Litoralgarten (50 m) and site Immenstaad (150–200 m). Strong wind events are more seldom at site Litoralgarten, and the sediment is more silty and sandy and thus more heterogeneous (Schmieder *et al.* 2004).

Sample collection and processing

Benthos was quantitatively sampled in the upper eulittoral zone (25×25 cm, A_o = 625 cm^2) at 0.4-m depth monthly from May 2002 to April 2003 at the three sites (four replicates each). We used the suction sampling device developed and described by Baumgärtner (2004) and Mörtl (2003), and modified the device for use in the eulittoral zone: the height of the side walls was increased to 50 cm aluminium frame with 200-µm gauze to minimise the risk of escape of mobile taxa. All hard substrates from the sampling area were transferred into a hand net while the pump was continuously running; this also minimised the number of escaping mobile individuals. Suspensions and escaping organisms were retained within a filter inlet (200-µm gauze) and then added to the hard substrate fraction. All substrates were brought to the laboratory after sampling and were processed immediately. Coarse stones were carefully brushed and rinsed within a basket (200 µm) to remove attached invertebrates, which were then preserved in 70% ethanol. Fine sediments were floated repeatedly to suspend all invertebrates in the water column. The suspension was decanted and filtered to isolate the organic fraction, which was then added to the coarse fraction and preserved. Invertebrates were identified to the species level if possible or to the nearest taxonomic level using a dissection microscope (10×magnification), counted, and classified into three size classes for later biomass calculations: small, medium, and large, according to Baumgärtner & Rothhaupt (2003) and standard determination literature. For taxa not listed therein, values were based on our own extensive length/dry mass calculations following the methods described by Baumgärtner & Rothhaupt (2003).

Abiotic parameters

Gauge data were permanently recorded at Konstanz Harbour and are available at http://www.wetteronline.de. We used the gauge level of the sampling date as an indicator and calculated five fluctuation parameters: differences in water level as compared to 1, 3, 7, 14, and 28 days prior to sampling. Littoral slope topography was taken from a topographical map on a computer screen (Geogrid Viewer 1:25,000). Bathymetric depths were related to the annual mean low-water level.

Hourly mean wind data (wind speed and direction) of the nearby weather station (Konstanz no. 2795) were obtained from the German Weather Service (DWD). Fetch and effective fetch were calculated using the equation given by Hakanson (1977) and the exposure level of sites (Keddy 1982, 1984). Wind data were delivered in 10° degree steps (36 compass bearings). We therefore adapted published fetch calculations to our finer wind data solution. The distance to the farthest point (km) at the opposite shore was determined for 36 compass bearings from a topographical map on a computer screen (Geogrid Viewer 1:25,000). The fetch lengths of each of these bearings were taken to calculate a mean fetch (F_m) using equation 1 (Hakanson 1977; Keddy 1982, 1984).

$$F_m = \sum f_i * \cos y_i / \sum \cos y_i \qquad \text{Eq. 1,}$$

where f_i is the distance of i degrees from bearing and y_i is the angle from the bearing in ±10° degree steps.

We distinguished three fetch variables. After calculating the maximum possible fetch length per site (F_{max}) and the maximum orthogonal fetch length (F_{ortho}) to the opposite shore, we summarised all measured fetch lengths per site for each of the determined 36 compass bearings within a variable fetch sum (F_{sum}). The fetch values, mean wind velocity at angle y_i (km h^{-1}), and percentage of days when wind was blowing from each of the 36 compass bearings over the experimental period were combined to calculate the annual mean exposure (E_m) of each site using equation 2 (Keddy 1982). Exposure level of sites was calculated similarly to water-level fluctuation for 3, 7, 14, 28 days prior to sampling.

$$E_{m\_} = \sum \text{mean velocity} * \text{percent frequency} * \text{fetch} \qquad \text{Eq. 2}$$

Benthos data treatment

Community structure of macroinvertebrates was analysed using log(x+1)-transformed abundance data. This transformation enhances the recognition of less-abundant taxa in their contribution to overall community structure. We tested for differences between sites, months, and the combination of both, depending on the spatial or temporal scale considered. The Bray-Curtis coefficient was applied for similarity measurement between replicates and plotted within non-metric multidimensional scaling graphs (nMDS, see Clarke 1993) using the PRIMER 5, 6b software package (Clarke & Warwick 2001). Replicates represent different combinations of pooled data in both analyses. We tested for differences among a priori defined groups (site, month, site and month) against random distribution using ANOSIM permutation statistics. For comparison of community structure among months, we assumed that communities might change from site to site; therefore, we separated this effect from month effects using two-way crossed ANOSIM (Clarke & Warwick 2001). The BVSTEP option within PRIMER was applied to search for the smallest subset within the similarity matrix (plotted as nMDS graphs) to describe the overall community pattern best, based on abundance data (stop criteria, Rho>0.95, delta rho<0.001, five restarts, step-wise search). The step-wise search is recommended for huge data sets, e.g. species communities analyses, whereas all possible combinations can be tested with the BIOENV procedure for smaller data sets, e.g. abiotic data. The variability of community samples on a specific scale was analysed using the SIMPER routine. This routine outlines the contribution of the most dominant taxa.

Abiotic parameter treatment

All measured and calculated environmental data (wind, slope, gauge parameter) were used in a normalised similarity matrix. A Euclidian distance coefficient was applied as a similarity coefficient suitable for abiotic variables with PRIMER software, again plotted as an nMDS graph. We used the BIOENV procedure within PRIMER (Clarke & Ainsworth 1993; Clarke & Warwick 2001) to search for the smallest subset of abiotic variables explaining the similarity matrix best (stop criteria, Rho>0.95, delta rho<0.001, five restarts, random search, all combinations). The spatial and temporal pattern of macroinvertebrate communities was then related to corresponding abiotic variables using the BIOENV procedure within PRIMER. The Spearman rank correlation (ρ_s) was applied for comparison of the two similarity matrices. The null hypothesis of 'no relation' between the two similarity matrices (Clarke & Ainsworth 1993; Clarke & Warwick 2001) was tested using a permutation procedure. The sample labels from one similarity matrix were permutated many times (at least 99), and the matching with the second similarity matrix was recalculated (ρ_s) every time. The null distribution of ρ was compared with distribution of ρ_s results.

Results

Community composition

The seasonal patterns of abundance and biomass data of the benthos communities were similar at all three sites (Fig. 1). Samples from May, June, August, and November 2002 differed most pronouncedly from other months and can be clearly separated from the other monthly samples from the respective sites. This separation is based on a higher variability of species composition within these months compared to samples (and replicates) from the other sampling dates (Fig. 1). The average similarity between all samples per site (months pooled) was highest at site Litoralgarten (56%), intermediate at site Immenstaad (41%), and lowest at site Meersburg (34%) (SIMPER routine, Table 1 A). Lowest monthly similarities (sites pooled) were obtained in August (32%), November (34%), June (38%), and May 2002 (46%), and highest monthly similarities were obtained in the winter months and in the spring months of 2003 (>70%) (Table 1 B).

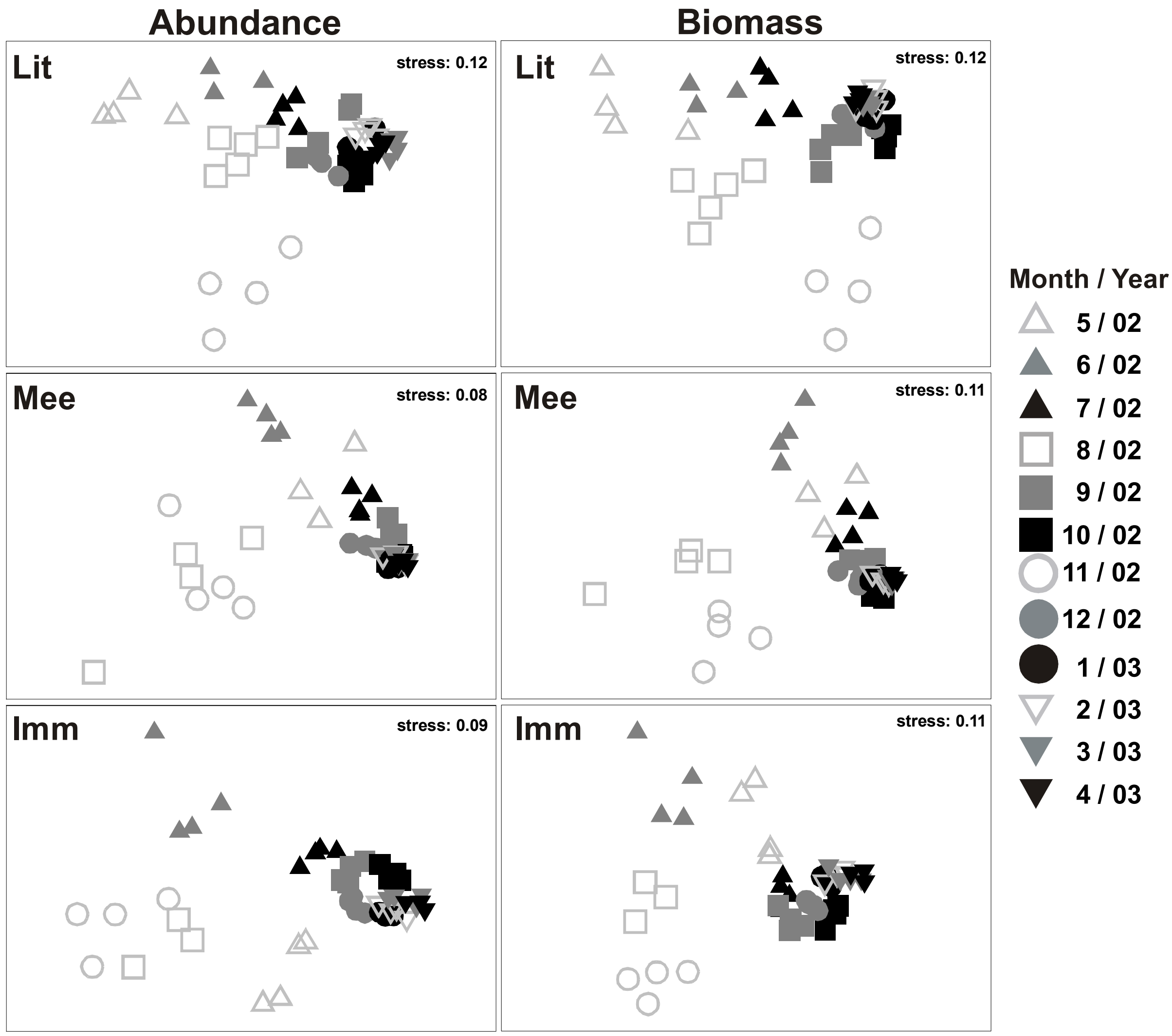

Figure 1: NMDS plots of monthly (May 2002 to April 2003) macroinvertebrate community data based on abundance and biomass, separately at sites Litoralgarten (Lit), Meersburg (Mee) and Immenstaad (Imm). Replicates are represented by same shaded symbols. All data are log(x+1) transformed, and the Bray-Curtis similarity index was applied.

Nevertheless, despite this strong noise, a significant linear seriation pattern in the species composition was observed, i.e. the benthic communities of consecutive months were more closely related in their species composition than those of non-consecutive months ($p < 0.001$, tested only for abundance). This pattern was most pronounced at site Litoralgarten ($R = 0.509$) than at the other two sites (Meersburg $R = 0.293$, Immenstaad $R = 0.350$).

Table 1: Results of Simper routine. Dominant taxa/species contribution to community similarity per sampling unit (A_o = 625 cm^2). **A**: For the site differences, data from all months are pooled, and the taxa are listed. Contribution was cut off at >90%. **B**: For the seasonal differences, data from all sites are pooled. SD: standard deviation.

	Average abundance	Average similarity	Similarity [SD]	Contribution [%]	Cumulative [%]
A			**Data pooled for months**		
Average similarity: 56.3			**Site Litoralgarten**		
Orthocladiinae	1381	17.2	1.9	30.5	30.5
Chironominae	1485	16.3	1.6	28.9	59.4
Chironomidae non. det.	437	5.0	1.8	8.9	68.3
Tanypodinae	343	3.8	1.7	6.8	75.1
Caenis spp.	275	2.7	1.0	4.8	79.9
Dreissena polymorpha	340	2.4	0.8	4.3	84.2
Tinodes waeneri	227	2.0	0.9	3.5	87.6
Corynoneura spp.	155	1.7	0.7	2.9	90.6
Average similarity: 34.2			**Site Meersburg**		
Orthocladiinae	1034	12.3	1.1	35.9	35.9
Chironominae	618	5.0	0.8	14.7	50.6
Caenis spp.	454	4.0	0.8	11.7	62.3
Dreissena polymorpha	474	3.6	0.7	10.6	72.9
Oligochaeta	121	2.0	0.6	5.9	78.7
Chironomidae non. det.	154	2.0	1.2	5.8	84.6
Ostracoda	59	0.9	1.2	2.5	87.1
Corynoneura spp.	139	0.8	0.2	2.4	89.5
Tinodes waeneri	178	0.8	0.4	2.2	91.6
Average similarity: 41.3			**Site Immenstaad**		
Orthocladiinae	806	13.6	1.4	32.9	32.9
Chironominae	732	7.1	1.0	17.2	50.2
Caenis spp.	610	6.4	1.0	15.5	65.7
Dreissena polymorpha	559	5.2	0.8	12.6	78.2
Chironomidae non. det.	124	1.7	1.2	4.1	82.4
Tanypodinae	154	1.7	1.0	4.0	86.4
Oligochaeta	120	1.4	1.2	3.4	89.8
Tinodes waeneri	90	1.1	0.9	2.6	92.4

B						**Data pooled for sites**						
Month/Year	May 02	Jun 02	Jul 02	Aug 02	Sep 02	Oct 02	Nov 02	Dec 02	Jan 03	Feb 0	Mar 03	Apr 03
Average similarity	46.0	37.9	55.9	31.4	59.8	72.5	33.5	63.7	70.7	70.8	71.2	75.1

Benthic community structure differed strongly among the sites (Fig. 2) when monthly data were plotted separately. These spatial variations persisted for all sampling dates. Replicates per site were more similar to each other than the samples from the other two sites within a specific month. Extreme differences of benthic community composition between sites and high similarities of replicates per site were found in June, July, and November 2002 and January 2003, which resulted in an overlapping of same site symbols in nMDS plots for these months and further in pronounced distances between site symbols (Fig. 2). Thus, the invertebrate community abundance (site Global $R = 0.964$) and biomass (site Global $R = 0.929$) structure varied significantly between sites and months (Global R: abundance $R = 0.797$, biomass $R = 0.751$; all $p = 0.001$) throughout the year compared to random distribution (site R range: abundance –0.16 to 0.18, biomass –0.08 to 0.12; months R range: abundance –0.08 to 0.13, biomass –0.16 to 0.16; two-way crossed ANOSIM analysis). The pair-wise comparison also revealed highly significant differences for all three site combinations (abundance $R > 0.910$, biomass $R > 0.850$, $p = 0.001$) and for all comparisons between months. In the latter, the differences of replicates per site and month were lower in samples obtained between January/February and March/April 2003 ($R = 0.490$, $R = 0.579$, respectively; both $p = 0.002$), reflected by the lower R values for abundance, which are, however, still significant. All other months showed R values greater than at least 0.723 (July/August 2002, February/March 2003) and mostly greater than 0.900 ($p \leq 0.002$), even when consecutive months were compared. The community composition per site completely changed within one month. A similar pattern was observed for biomass (Fig. 1). The less-pronounced community shifts were again observed in the winter and spring months (January/February: $R = 0.510$, $p = 0.001$; March/April 2003: $R = 0.425$, $p = 0.003$), compared to other pair-wise comparisons with R greater than at least 0.773 (August/November 2002, $p \leq 0.002$), or mostly greater than 0.900 ($p \leq 0.002$).

The step-wise search for the smallest subset to describe the overall community pattern best was based only on abundance data (pooled for all samples, sites, and months) because abundance and biomass data corresponded highly. BVSTEP selected 7 of 61 taxa: the zebra mussel *Dreissena polymorpha*, the mayflies *Caenis* spp. and *Centroptilum luteolum*, the caddisflies *Tinodes waeneri* and *Arthripsodes atterimus/cinereus*, the amphipod *Gammarus roeseli,* and the Chironominae subfamily ($R = 0.955$, $p < 0.001$, Spearman rank correlation, BVSTEP Primer). These taxa explained most of the overall community pattern (temporal and spatial variability in the complete pooled data set). These patterns are often based on dominant taxa (e.g. *Tinodes waeneri*, *Dreissena polymorpha*, *Caenis* spp. Chironominae; see Table 1), but not necessarily (all other above mentioned taxa).

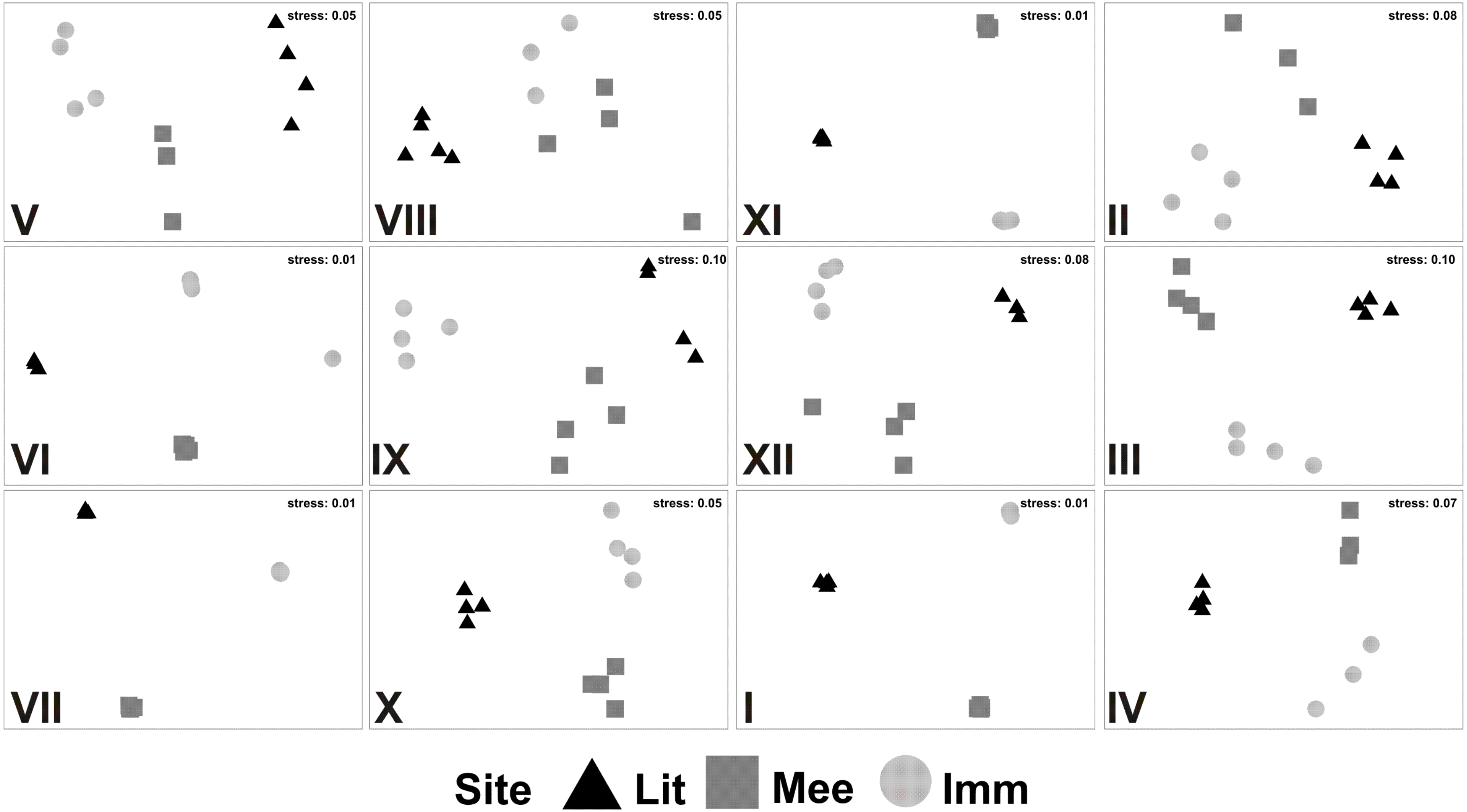

Figure 2: NMDS plots of macroinvertebrate communities at sites Litoralgarten (Lit), Meersburg (Mee) and Immenstaad (Imm). Each plot displays monthly samples taken at 0.4-m depth, starting in May 2002 (**V**) and ending in April 2003 (**IV**). Replicates for all sites greatly overlap in months VI, VII, XI 2002, and I 2003 and can hardly be distinguished, which symbolises a low variability between replicates. All data are log(x+1) transformed, and the Bray-Curtis similarity index was applied.

When all sites were separately compared (data structure beyond Fig. 1, see also Table 1, Appendix), the smallest subset was found for site Meersburg (5 taxa), in comparison to sites Immenstaad (8 taxa) and Litoralgarten (11 taxa) (all $R > 0.950$, $p < 0.001$). The importance of the caddisfly *Tinodes waeneri* remained, but it was accompanied by the leech *Erpobdella octoculata* for all sites. *Dreissena polymorpha* and *Caenis* spp. accounted only for the variability of sites Meersburg and Litoralgarten, whereas the mayfly *Centroptilum luteolum* was important at the two northern sites, Meersburg and Immenstaad. Furthermore, at site Litoralgarten, the distribution pattern of the snail *Radix ovata*, the caddisflies *Goera pilosa* and *Polycentropus flavomaculatus*, the dipterans *Bezzia* spp., the chironomid subfamily Orthocladiinae, and small non-determinable chironomids were important. At site Immenstaad, in addition, the overall abundance patterns were strongly reflected by the amphipod *Gammarus roeseli*, the leech *Helobdella stagnalis*, the caddisfly *Ceraclea* spp., Chironominae, and water mites. In contrast to the pooled data set as selected above, most of the taxa responsible for the monthly variability per site had lower abundances, and are thus not listed in Table 1.

Abiotic factors

Water level

The observed daily fluctuations of gauge level (Fig. 3) generally approximated the long-term average means recorded from 1950 to 2004 at Konstanz Harbour, with low levels in winter and high inflow rates after snowmelt in summer (min: 282 cm, max: 436 cm, range: 1.54 m). Exceptions occurred in winter 2002 and early spring 2003, when the water level considerably exceeded the long-term level by over 1 m. The water level usually fluctuated a few centimetres per day, but strongly increased in August 2002 (38-cm increase on August 12; 18-cm increase on August 13) within one day because of strong rains in the Alps. Other minor increases occurred in May/June 2002 (snowmelt in the Alps) and November 2002 (rain front in the Alps), with maximum increases of 20–33 cm within a week.

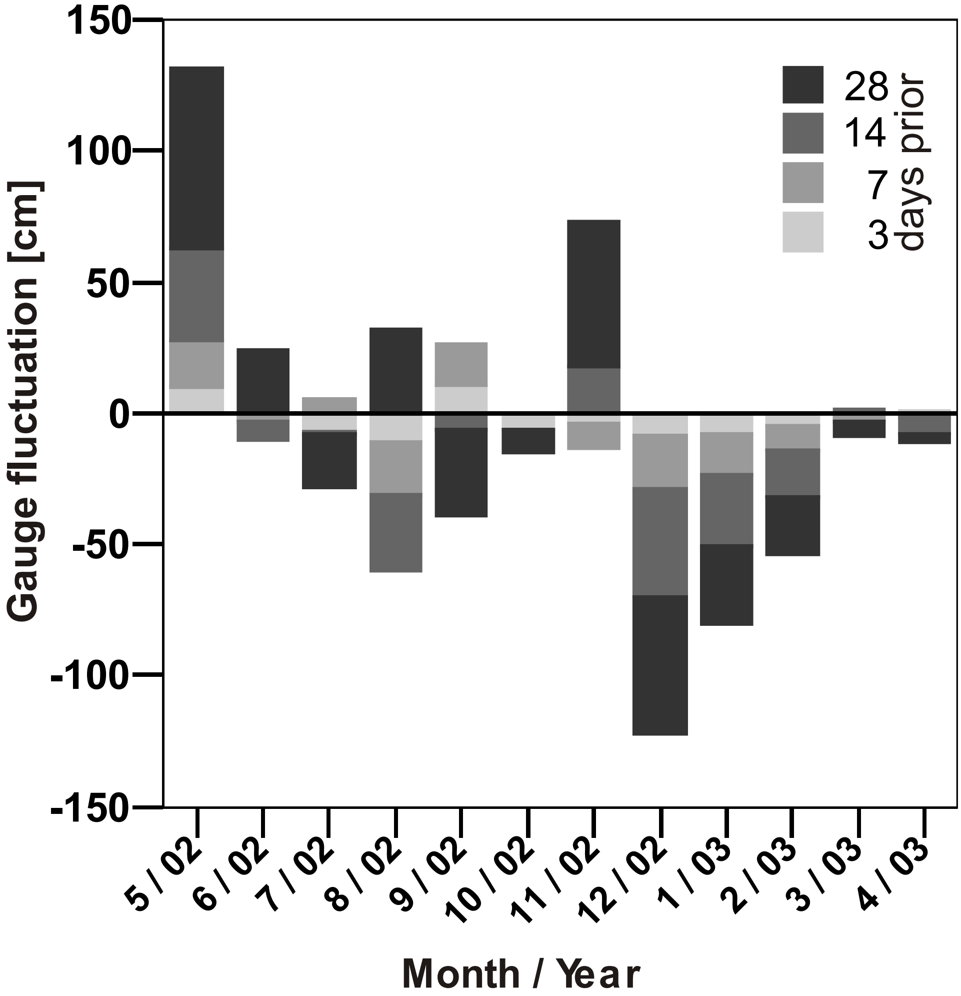

Figure 3: Gauge-level fluctuation at Lake Constance Harbour from May 2002 to April 2003 on 3, 7, 14, and 28 days prior to sampling. Data were obtained from http://www.wetteronline.de.

Wind field

As expected, the lake wind field was dominated by westerly winds (SW–NW) and also less-pronounced, easterly winds (NO–O) (Fig. 4). The mean (± SE) wind speed from May 2002 to April 2003 was 2.05 m s^{-1} (± 0.13). Low wind speeds of 1–2 on the Beaufort wind scale (Table 2, Fig. 4) were most common throughout the year and accounted for more than 80% throughout the year (Beaufort scale 1: 42.3%; 2: 40.3%). Less often, winds of 0 (1.3%), 3 (13.5%), and 4 (2.3%) on the Beaufort scale were recorded, and seldom, but regular storm events of 5–6 on the Beaufort scale occurred (5: 0.3%, and 6: 0.04%, respectively; Chi = 61.63, $df_{6,77}$ $p < 0.001$, H-test, Beaufort scale: 5, 6 < 4 $\leq$ 0, 3 < 1, 2; U-test). Wind fields $\geq$4 on the Beaufort scale

($5.4\ m\ s^{-1}$) occurred almost exclusively from the west (Fig. 4; 4 bft=229 h; 5 bft=28 h; 6 bft=4 h).

Table 2: Percentage of mean hourly wind speed counted, measured from May 2002 until April 2003, categorised within Beaufourt Scala (bft) 1-6 and differentiated between 12 directions in 30 degree steps.

Direction [°]	**0 bft** $0.0\text{-}0.2 ms^{-1}$	**1 bft** $0.3\text{-}1.5\ ms^{-1}$	**2 bft** $1.6\text{-}3.3\ ms^{-1}$	**3 bft** $3.4\text{-}5.4\ ms^{-1}$	**4 bft** $5.5\text{-}7.9\ ms^{-1}$	**5 bft** $8.0\text{-}10.7\ ms^{-1}$	**6 bft** $10.8\text{-}13.8\ ms^{-1}$
0-30	0.22	4.04	4.94	0.18	0.00	0.00	0.00
>30-60	0.12	3.86	7.41	3.49	0.05	0.00	0.00
>60-90	0.12	2.88	2.67	1.28	0.10	0.00	0.00
>90-120	0.05	4.10	2.71	0.05	0.00	0.00	0.00
>120-150	0.06	3.32	1.15	0.06	0.00	0.00	0.00
>150-180	0.03	2.37	0.91	0.00	0.00	0.00	0.00
>180-210	0.11	1.83	0.84	0.03	0.01	0.00	0.00
>210-240	0.13	1.97	2.57	1.03	0.26	0.05	0.01
>240-270	0.10	3.23	8.35	5.76	1.64	0.20	0.03
>270-300	0.10	5.99	5.93	1.48	0.24	0.03	0.00
>300-330	0.11	4.71	2.10	0.08	0.00	0.00	0.00
>330-360	0.14	4.02	0.70	0.02	0.00	0.00	0.00

The mean (± SE) monthly wind exposure (Fig. 5) was highest at Immenstaad (4094 ± 186), followed by Meersburg (2589 ± 79), and lowest at Litoralgarten (1996 ± 76; $F_{2,136} = 80.03$, $p < 0.001$). During the autumn and winter months (October 2002 to January 2003), both northern sites (Meersburg and Immenstaad) were highly exposed to westerly winds, more pronouncedly than during the rest of the year. However, during the late winter and spring months (February 2003 to April 2003), the south-western site Litoralgarten was more exposed to wind waves than the site Meersburg on the opposite, north-western shore owing to persistent north-easterly winds. Maximum wind speed was measured in January 2003 (10.3–14.2 $m\ s^{-1}$ from 230 to 250°), followed by October (9.5–11.1 $m\ s^{-1}$ from 230 to 270°), and November 2002 (7.3–9.4 $m\ s^{-1}$ from 230 to 250°).

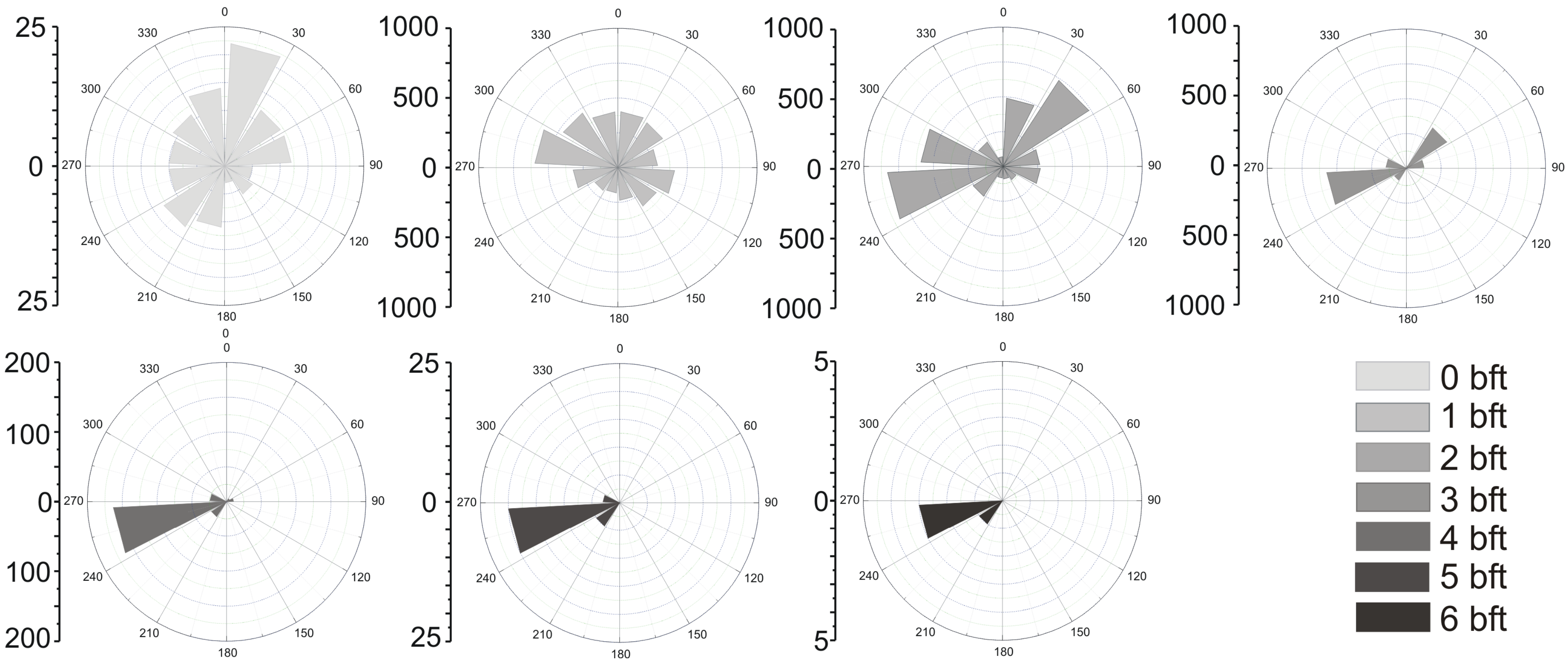

Figure 4: Wind speed (number of hours) on the Beaufort scale 0–6 (bft); from left first line (0 bft) to right second line (6 bft) increasing wind strength (0: 0.0–0.2 m s^{-1}, 1: 0.3–1.5 ms^{-1}; 2: 1.6–3.3 m s^{-1}; 3: 3.4–5.4 m s^{-1}, 4: 5.5–7.9 m s^{-1}; 5: 8.0–10.7 m s^{-1}; 6: 10.8–13.8 m s^{-1}) differentiated between 12 directions in 30° steps and displayed in polar plots.

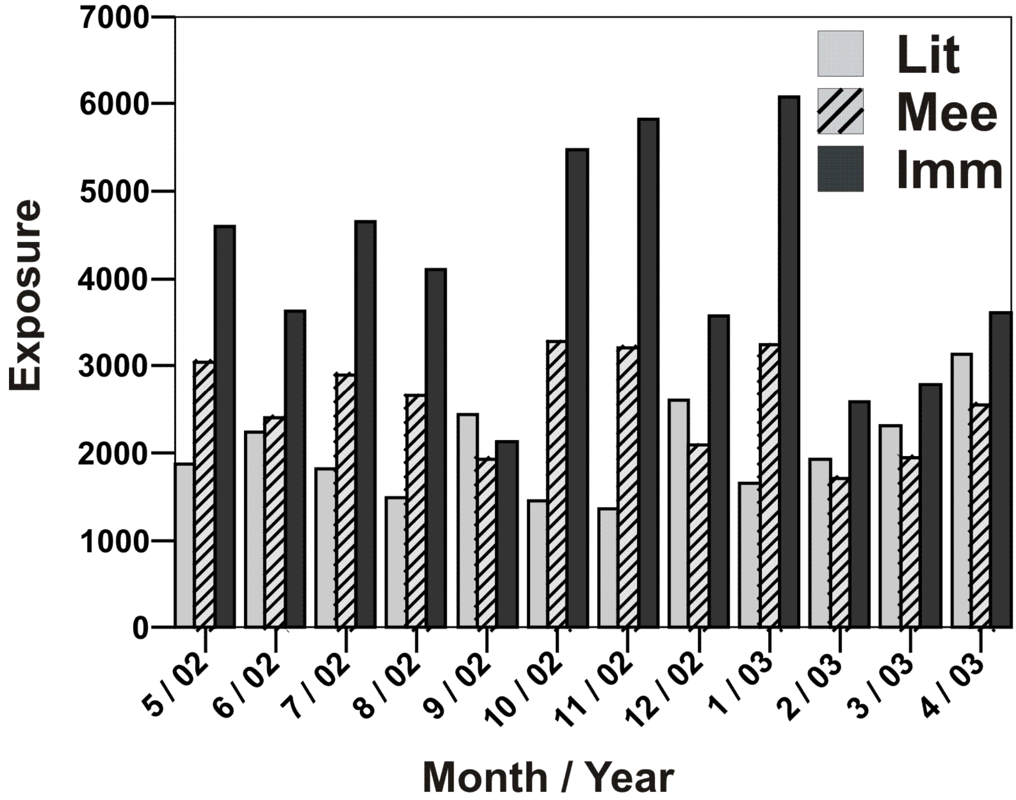

Figure 5: Mean monthly exposure of site (dimensionless), calculated after Keddy (1982).

The BIOENV procedure selected five variables from all measured and calculated abiotic parameters as the most influential within the similarity matrix displayed in Fig. 6 A, i.e. exposure 7 days prior to sampling, effective fetch, maximum fetch, and gauge level fluctuation 7 and 28 days prior to sampling ($R > 0.957$, $p < 0.001$). In the second-highest selection, effective fetch was replaced by slope ($R > 0.951$, $p < 0.001$). The site Immenstaad can be clearly separated from the other two sites by its abiotic characters (Fig. 6 A) (Global $R = 0.579$, $p < 0.001$); the difference is even more pronounced in a pair-wise comparison (Litoralgarten/Immenstaad $R = 0.802$, Meersburg/Immenstaad $R = 0.714$, all $p < 0.001$). The comparatively low global R can be explained by lower, but still significant differences between the sites Meersburg and Litoralgarten ($R = 0.264$, $p < 0.001$) compared to random distribution (range R –0.025 to 0.050).

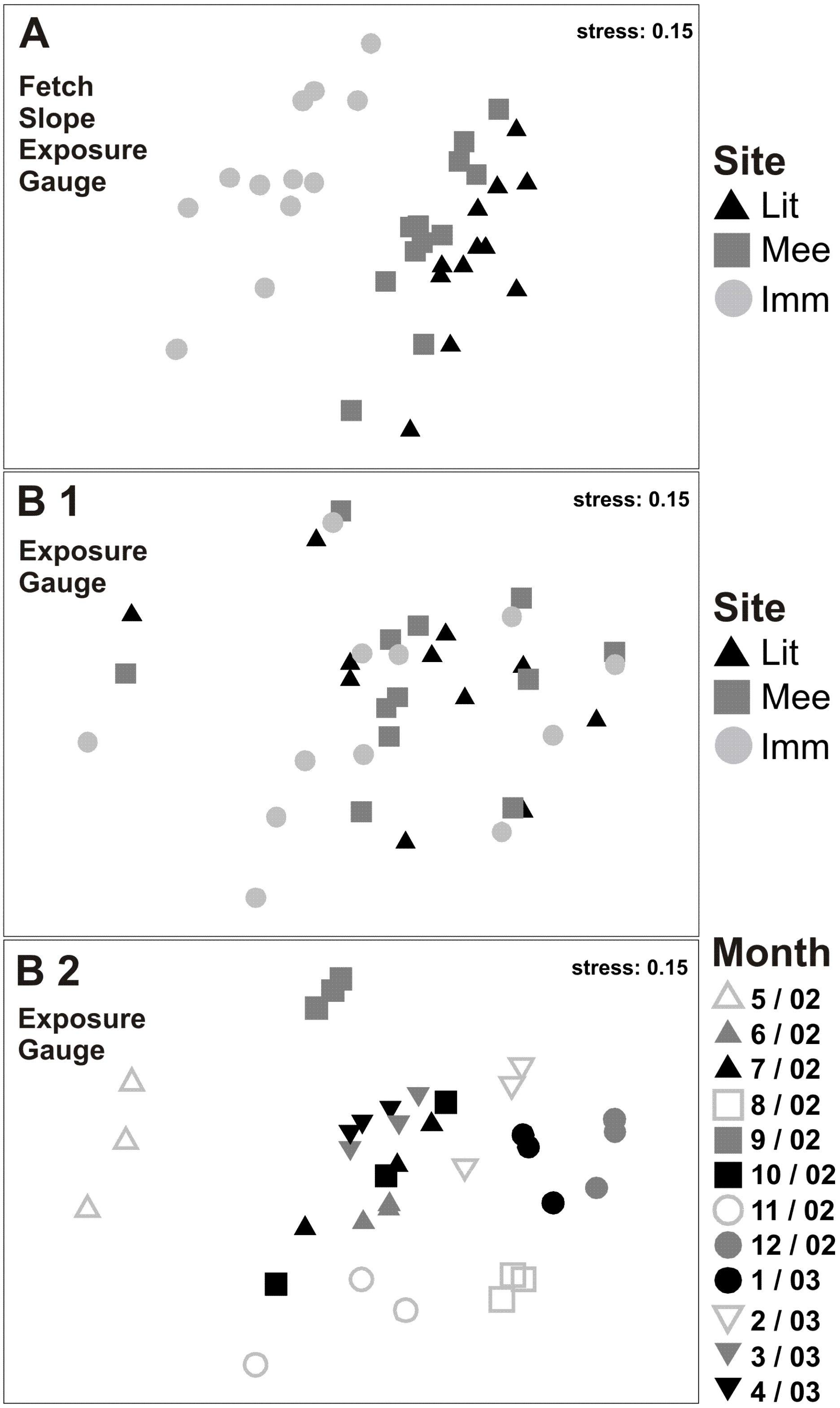

Figure 6: NMDS plot of all abiotic variables, including fetch, slope, exposure, and gauge (**A**), or exposure and gauge fluctuation only (**B1**, **B2**). Site differences of Litoralgarten (Lit), Meersburg (Mee), Immenstaad (Imm) are displayed in **A** and **B1**, whereas monthly differences are highlighted in **B2.** The same similarity matrix was used in B1 and B2. Replicates are represented by same shaded symbols. All data are normalised, and the Euclidian similarity index was applied.

By restricting abiotic variables to the most variable parameters, i.e. exposure and water-level fluctuation (excluding fetch, slope, and mean yearly exposure from the similarity matrix), the observed strong differences between sites disappear (Fig. 6 B1; $R = 0.076$, $p > 0.05$). In this case, however, the BIOENV procedure even more clearly selected short-term (1 day prior: gauge, 3 days prior: wind, gauge) and intermediate fluctuations (14 days prior: wind, gauge) as the most influential for explaining the similarity matrix based on both wind exposure and water-level fluctuation ($R > 0.960$, $p < 0.001$). A pronounced seasonal variability of exposure and gauge parameters was also observed (Fig. 6 B2). Several months are clearly separated from the other months (e.g. May, August, September, December, January), but monthly differences are significant in general (Global $R = 0.804$, $p < 0.001$, ANOSIM). In a pair-wise comparison, most months significantly differ in their specific abiotic variability (at least $R > 0.427$, but mostly $R > 0.736$, all $p < 0.001$). Non-significant exceptions are July/October, January/February, and March/April; the pairs October/February ($R = 0.325$, $p = 0.03$) and October/March ($R = 0.273$, $p = 0.05$) show only small differences.

Community–habitat relationship

We examined the community–habitat relationship on three different scales: 1) the entire lake community, 2) the entire lake community in selected months, and 3) single-site communities. The lake community was related to all single abiotic variables to examine their contribution in explaining the benthic variability. Furthermore, all abiotic variables were related to benthic community patterns in a separate analysis. Finally, only a combination of wind exposure (short- to long-term) and water-level fluctuation (short- to long-term) was compared with the benthic similarity matrix. For the third scale, we chose a subset of autumn-to-winter months (October 2002 to January 2003) that are usually highly susceptible to wind events and again examined the contribution of abiotic variables to explain the observed benthic variability.

In general, the benthic community based on abundance data revealed a strong relationship to gauge-level fluctuations both in the short term and the long term ($\rho_s = 0.586$, $p < 0.01$; 1-day, 3-day, and 28-day fluctuation, lake level at date of sampling). The additional combination with effective fetch ($\rho_s = 0.568$) or mean yearly exposure (ρ_s = 0.561) computed by BIOENV resulted in slightly lower matches. The variability of benthic communities based on biomass data was lower, but in a similar range, and is explained by abiotic variables (overall best match: ρ_s = 0.563 $p < 0.01$; 1-day and 28-day fluctuation, lake level at date of sampling). When slope (ρ_s = 0.560), effective fetch (ρ_s = 0.553), or exposure (ρ_s = 0.536) is added, slightly lower but still significant results ($p < 0.01$) were obtained.

Focusing on the site differences explained by abiotic patterns revealed the dominance of lake-level fluctuation, both in the short-term (1 day prior) and in the long-term (28 days prior). This dominance occurred at all sites to a similar extent and was significant, but was higher than the pooled data set (Litoralgarten ρ_s = 0.783, Meersburg ρ_s = 0.626, Immenstaad ρ_s = 0.685). The correlations of single variables were always lower than those of specific subsets, e.g. 1-day (ρ_s = 0.242), 3-days (ρ_s = 0.126), and 28-day fluctuation (ρ_s = 0.560), and lake level (ρ_s = 0.307) for the entire lake community. However, the mean monthly water-level fluctuation explained most of the observed variability of benthic samples within the complete year data set. All other variables (exposure, slope, fetch, short-term water-level fluctuation) were not correlated (ρ_s < 0.117) as single variables, but enhanced the overall correlation pattern, as shown for specific combinations.

The analysis of the autumn-to-winter months (October 2002 to January 2003) again showed that short- and long-term water-level fluctuations are highly influential (1, 3, and 28 days, lake level at date of sampling), but also showed that short-term wind exposure (3 days) accounted for the observed variability in benthic communities. All five variables resulted in a comparatively high correlation with the observed variability of benthic community samples (ρ_s = 0.739; $p < 0.01$) compared to the analysis of the entire year at all sites or the analysis of single sites.

Discussion

Spatial and temporal pattern of benthic communities

The benthic community composition exhibited a clear gradual monthly transition at all sites. Similar and significant temporal changes in community structure in abundance and biomass data occurred at all sites. Consecutive months were more similar than non-consecutive months, as expressed by a significant linear seriation pattern (Clarke *et al.* 1993; Clarke & Warwick 2001). This pattern occurred at all sites and indicates an underlying innate benthic seasonal process. However, the comparatively low seriation values, especially at sites Meersburg and Immenstaad, are presumably the result of the high variability of some months (see Fig. 1: May, June, July, August, November 2002; January 2003). In these months, the benthic communities exhibited greater variability in both replicates and samples than in the other months, and either high water-level fluctuations prior to sampling (May, August, November 2002) or strong wind events (October 2002, January 2003) or both (August, November 2002) occurred (Figs. 3, 5).

Some of the observed seasonal turnover in benthos abundances and biomass can be attributed to emergence or somatic growth of taxa (Statzner & Resh 1993; Petersson & Hasselrot 1994; Petersen *et al.* 1999; Banziger 2000). However, strong benthic community changes occurred mainly in late autumn to winter, and emergence is therefore unlikely to contribute greatly within this period. Other changes might be partly caused by predation effects of benthivorous fish. However, in contrast to the often-proposed strong effects of fish predation (e.g. Crowder & Cooper 1982; Gilliam *et al.* 1989; Diehl 1995), such influential top-down control was not supported by enclosure experiments carried out in Lake Constance for several fish taxa, such as cyprinids (Chapter 5), perch and ruffe (Chapter 4), and burbot (Baumgärtner 2004), but see Baumgärtner & Rothhaupt (2005).

In addition to the strong seasonal difference in benthic community composition, a more-pronounced and continuous site difference was observed throughout the year (Fig. 2). Even after severe disturbance, e.g. when the gauge level increases rapidly within a few days or high wind events occur, the community composition of the sites remain different. Strong site differences within benthic assemblages were also found in other studies carried out at Upper Lake Constance (Chapter 2, 4, 5) and in other oligotrophic lakes (James *et al.* 1998; Stoffels *et al.* 2003, 2005). Site differences in benthic communities are also reflected in the diet composition of native perch and introduced ruffe and the outcome of food competition between the two fish species (Chapter 4).

Communities response to habitat changes

In the present study, the detected high variability in the benthic community was correlated with the changes of abiotic parameters both spatially and temporally. Generally, gauge-level fluctuation was the dominant factor explaining most of the seasonal variation observed over the one year study period in the upper eulittoral zone of the three sites. Interestingly, both short- and long-term fluctuation accounted for the variation within the benthic communities of all three sites. A decrease of benthic biomass with increasing water-level fluctuation was observed by Palomäki (1994) within the 0–3-m depth zone in Finnish oligotrophic lakes. Baumgärtner (2004) and Mörtl (2003) also attribute some of the observed variation of drift-line samples to water-level fluctuation prior to sampling.

Surprisingly, we also found site differences in the correlation scores of short- and long-term water fluctuation, with highest scores at site Litoralgarten. This pattern presumably emphasises indirectly other abiotic factors, such as slope and/or exposure (e.g. Hakanson 1977; Cattaneo 1990; Petticrew & Kalff 1991), and is not a result of direct gauge-level fluctuation (see below).

The effects of wave exposure

Wave dissipation energy is highest within the sampled upper eulittoral zone (Arts 1994; Denny 1994; Denny *et al.* 2003). Bottom shear stress could account for direct damage and even mortality, influence growth rates (Brown & Quinn 1988; Chapter 3), or induce habitat alteration (Brodersen 1995; Death 1995; James *et al.* 1998; Norkko *et al.* 2002). However, drag force and survival of wind-wave or torrentially-swept organisms also depends on their body shape (Denny 1994).

Differences in community abundance, taxa occurrence, or diversity and their dependence on site exposure have often been discussed (Barton & Hynes 1978a; Lindegaard & Dall 1988; Burton *et al.* 2002), but have seldom been analysed. In one large-scale comparative analysis of stony habitats in Swedish lakes and streams, step-wise multivariate analysis showed that either lake surface or water velocity explained the observed benthic variances (Johnson *et al.* 2004). The authors interpret lake surface area as a proxy of the wave action that benthic communities experience, which will increase in parallel with lake size because of, e.g. fetch length.

The authors also stated that both wind-exposed lake shores and stream riffles are harsh habitats strongly characterised by the strength of water movement (roughly bi-directional in lakes and uni-directional in streams) and considered them as strong determinants of benthic communities that account for a significant amount of variation among sites. In the present study, the taxa reflecting most of the seasonal variability clearly differed between sites. For instance, the gastropod *R. ovata,* which had presumably the lowest mobility rates, strongly accounted for seasonal variability at the most-sheltered site Litoralgarten (BVSTEP selection, Appendix).

Catastrophic sediment deposition that destroys benthic communities is also likely after high wind events at lake sites, as demonstrated in an estuarine experiment (Norkko *et al.* 2002). Such effects should be particularly relevant at less-disturbed sites (e.g. site Litoralgarten), which contain larger amounts of fine sediments. Indeed, we observed adverse effects of sand deposition at a site that was not considered within this study. This site at the south-western shore in the upper eulittoral zone (0.2-0.8 m depth) has a very gentle slope. An area of approximately 100-m^2 at this site was completely covered with a several-centimetre layer of sand after exposure to a high north-easterly wind event (site Staad, N. Scheifhacken, personal observation). In the estuarine study of Norkko *et al.* (2002), the number of macroinvertebrates was reduced by more than 50% after 3 days and by more than 90% after 10 days of sediment deposition, irrespective of the thickness of the layer at four different depths. However, in contrast to the destructive effects, regular wind events can also act positively by dispersing fine sediment deposits. In the study of Norkko *et al.* (2002), a storm event occurred a month after the experimental deposition of sediment at the exposed site, eliminated all fine deposits, and allowed a rapid recolonisation of surficial sediments thereafter. At the site sheltered from wind, however, the experimental deposition of sediment resulted in a long-lasting habitat change (Norkko *et al.* 2002).

Characteristics of water-level fluctuations — consequences of decreasing water level

When water-level fluctuation is discussed, the decrease and increase of the water level must be considered separately because they represent different processes for benthic communities. We expect that decreasing water levels have predominately adverse effects on benthic communities. A slow decline presumably leads to an accumulation of benthic invertebrates into greater, still-flooded water depths, as is known for lotic habitats (Blinn *et al.* 1995; Williams & Smith 1996). Taxon-specific mobility constraints will restrict reaction time (Blinn *et al.* 1995; Matthaei & Townsend 2000a) and distance of movement (Erman 1986; Elser 2001). Furthermore, the timing of a pronounced decrease in the water level will influence the amount of negative effects on benthic communities depending on the taxa or life stage mobility at that particular time. However, even for comparatively immobile invertebrates, such as the snails *Radix* spp., the ability to move several metres a day has been reported (Brendelberger 1994). Interstitial habitats can also be used as refuges in times of short-term decreases in the water level (Dole-Olivier *et al.* 1997; Fowler 2002); but see also Palmer *et al.* (1992). A variety of organisms (e.g. Trichoptera, Ephemeroptera, Chironomidae, Gastropoda) have been observed in the upper 6 cm and predominantly in the uppermost 2 cm of a dry littoral zone (Baumgärtner 2004; Mörtl 2003). However, interstitial refuges seem to be utilised only by small taxa or early life stages of larger taxa (Dole-Olivier *et al.* 1997; Baumgärtner 2004; Mörtl 2003). Matthaei and Townsend (2000) have reported significantly lower total abundance, densities of the four most common taxa, and taxa richness in a dry flood plain of a small gravel stream than in samples taken the day before the flood event and concluded that invertebrates were able to leave drying gravel patches. However, they also documented a high proportion of trapped individuals (37%). The risk of desiccation, which would result in individual losses, might be partly reflected by generally lower biomasses and abundances in the upper eulittoral than in deeper water depths. This has indeed been reported for Lake Constance at the long-term average low-water line at one site (LWL: 2.61 m, Baumgärtner 2004; Mörtl 2003). However, at Lake Coleridge, a similar deep oligotrophic lake in New Zealand, highest abundances and biomass were restricted to greater depths (4 - 7.5 m, James *et al.* 1998). The combination of short-term air exposure with other adverse circumstances, such as subzero winter air or high wind events, might multiply benthic loss rates. Blinn *et al.* (1995) reported high losses of benthos biomass (90%) at exposed sites in a cobblestone river with regular fluctuating discharges after short-term (12 h) air exposure accompanied by freezing temperatures. This should be a typical situation at Lake Constance during winter months, when the water level gradually decreases (Luft & Vieser 1990) and was documented in the present study. However, we did not focus on this aspect during sampling.

Characteristics of water-level fluctuations — consequences of increasing water level

An increase in lake water level provides benthic communities with new habitats, i.e. settlement areas at various trophic levels (periphyton, benthos, crayfish, fish), including foraging and reproduction demands of fish. Unsilted hardsubstrates might be particularly favoured by a variety of benthic taxa. Therefore, in contrast to decreasing water levels, we expect benthos communities in general to benefit from increasing water levels. However, some negative short-term effects can occur for taxa with specific habitat demands (e.g. Heptageniidae), which might require new habitat sections after a pronounced increase in the gauge, as has been shown for lotic habitats after high discharges (Malmqvist & Englund 1996; Lancaster 1999). Previously well-adapted individuals are forced to seek new habitats after an increase in the water level. Fast recolonisation based on total abundances occur in lake littoral zones within a few days (Quinn *et al.* 1998a; Chapter 2), with similar recovery rates at the bottom and throughout the water column (Quinn *et al.* 1998). However, the recovery of benthic community structure on a single stone within undisturbed eulittoral sites is more complex and required 1–2 months to reach the control level in Lake Constance (Chapter 2). For lotic habitats, drift recolonisation is the dominant source of fast recovery (Matthaei *et al.* 1997; Englund & Hambrack 2004; Roll *et al.* 2005) and similar mechanisms are observed in lakes (M. Korn, personal communication). In contrast to decreasing lake water levels, the effects of increasing levels seem to be far more pronounced and presumably responsible for the observed low abundances and biomasses in the freshly submerged littoral areas (Appendix, Figs. 1, 2).

Wave exposure and water-level changes interacting with littoral topography

Littoral topography and exposure were responsible for the site differences based on abiotic variables (Fig. 6 A). These factors were also important in combination with gauge-level fluctuation related to benthic community variations. In the present study, higher correlation scores with benthic similarity matrices were obtained when slope or exposure variables were added than gauge variables scored alone. Both factors are also known to influence the substrate stability within the littoral zone (Rowan *et al.* 1992; Rasmussen & Rowan 1997; Cyr 1998a). Site Litoralgarten has an intermediate platform slope compared to the steeper site Meersburg or the comparatively gentle slope at site Immenstaad. For gauge variation, the distance between previously and newly flooded areas will be smaller on a steeper slope than on a very gentle littoral slope. Therefore, a lake-wide water-level increase should result in different extents of newly generated habitats on the vertical scale and thus areas available for benthic recolonisation.

Littoral slope in particular counteracts site exposure to wind- and boat-induced waves (Hakanson 1977; Hakanson & Jansson 1983; Duarte & Kalff 1986; James *et al.* 1998). The results presented (Fig. 6) support these published findings. Steeper slopes exhibit a greater substrate instability and accumulation of fine sediments into greater depths (Rowan *et al.* 1992; Rasmussen & Rowan 1997). Wave dissipation energy within the upper eulittoral zone is also higher at steep slope sites than at gentle slope sites (Arts 1994; Denny 1994; Denny *et al.* 2003). When unexpected high wind events occur, the varying distance to protected deeper depth zones on steep and gentle littoral slope sites might again be relevant for the survival of refuge-seeking organisms (Denny 1994).

Evaluating the effects of wind exposure and water-level fluctuation

In the present study, strong gauge-level fluctuations generally coincided with high wind events occurring within the same month; therefore, separating the two effects to explain the observed benthic community changes remains difficult. We expected wind and gauge variables to be the most influential and to alter other, unmeasured habitat parameters indirectly (e.g. substrate composition, sedimentation and resuspension frequencies). The strong influence of water-level variation on benthic community variability was prominent in all analyses (entire data set, single sites, winter months only). Strong wind events also partly accounted for the observed variability in benthic samples, as demonstrated by the BIOENV analysis of the winter months. At this time of the year, when high wind events occur most frequently, the overall correlation index between benthos communities and abiotic variables was highest (BIOENV, $\rho_s = 0.739$). We assume that wind events influence abundance and biomass variability only on the short term, when sites are directly exposed (e.g. storm Jeanette in October 2002, Scheifhacken & Rothhaupt 2003). Wind-speed-induced resuspension can thereby superimpose direct wind effects. Such effects also depend on slope gradients and the disturbance history of the sites. We assume that wind or wave disturbance indirectly influence benthic communities in altering habitat conditions permanently, which results in the observed permanent and persistent differences in benthos community composition between sites. This pattern presumably comprises both regular mild and irregular strong wind events. As mentioned, site differences were persistent throughout the year in the present study and also in other studies at Lake Constance (Chapter 2, 3, 4, 5). In contrast to these permanent site differences, our results suggest that gauge fluctuations contribute more than wind-induced disturbances to the observed monthly variations in the upper eulittoral zone. Furthermore, benthic communities presumably benefit overall from increasing water levels but suffer from decreasing water levels.

In summary, the results presented clearly reflect the high dynamics within benthic systems and therefore the importance of understanding the spatial and temporal organisation of benthic communities. The results also stress that quantitative samples taken once or twice a year are difficult to interpret in general, and even more with respect to possible underlying biotic or abiotic parameters. Water-level fluctuation and wind-induced exposure clearly contribute to the observed benthic community variability, but at different scales, intensities, and frequencies. The patterns are further complicated by littoral topography, as slope can both intensify and diminish the impact of both factors on benthic communities depending on the particular combination of factors.

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Appendix: Mean (± SE) abundance [ind./per unit] and biomass [mg/per unit] of 8 dominant taxa groups per month (total - sites pooled) and specified for sites and months. Sample unit was 25 x 25 cm, Ao = 625 cm^2.

		abundance								biomass							
		total		Lit		Mee		Imm		total		Lit		Mee		Imm	
month		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
5 / 02		1555	376	2940	392	1167	358	462	63	87	17	144	20	82	26	34	6
6 / 02		877	281	2288	176	241	60	456	113	44	13	107	8	15	4	25	7
7 / 02		1214	119	937	117	1705	80	1000	123	63	9	43	5	104	6	42	4
8 / 02		634	201	1405	101	39	23	142	43	29	9	63	4	2	1	7	2
9 / 02		1098	194	1941	20	956	62	397	23	57	10	102	2	45	3	22	1
10 / 02	**Orthocladiinae**	373	26	346	62	396	32	379	48	16	1	16	4	13	1	17	1
11 / 02		297	119	817	144	33	5	40	12	12	5	34	7	1	0	2	0
12 / 02		1637	195	1501	183	2232	334	1145	137	62	7	51	5	87	11	46	4
1 / 03		1197	84	1103	87	974	88	1513	100	51	5	43	5	38	3	71	5
2 / 03		1951	239	2622	377	2013	296	1234	129	142	14	156	20	180	22	100	8
3 / 03		988	168	535	64	1625	276	806	118	65	13	31	5	117	21	46	7
4 / 03		2554	159	2208	227	2902	208	2551	333	125	10	92	9	140	5	150	20
5 / 02		693	266	1789	128	38	7	87	25	18	6	43	5	1	0	4	1
6 / 02		527	272	1892	272	25	7	6	2	15	8	54	3	1	0	0	0
7 / 02		769	198	1674	88	314	114	319	26	31	7	61	4	12	5	18	1
8 / 02		230	77	525	39	5	2	40	16	7	2	15	1	0	0	1	1
9 / 02		565	105	897	244	478	38	320	35	18	4	31	8	14	1	8	1
10 / 02	**Chironominae**	1078	56	1204	122	983	99	1047	37	33	5	52	9	20	1	28	2
11 / 02		44	22	116	50	6	1	9	2	1	0	2	1	0	0	0	0
12 / 02		960	235	2008	221	236	36	897	171	27	7	55	12	6	2	26	5
1 / 03		1730	222	2401	313	921	214	1870	147	62	11	101	19	24	6	61	5
2 / 03		2329	382	3752	448	1476	339	1547	132	93	20	169	24	44	10	55	5
3 / 03		1831	333	1575	72	2375	955	1544	392	90	9	105	9	82	17	83	18
4 / 03		667	87	457	98	632	96	995	133	37	5	28	3	29	4	58	8
5 / 02		14	3	5	2	13	4	24	2	5	1	2	2	8	2	6	1
6 / 02		4	2	11	7	0	0	3	1	2	1	5	4	0	0	1	0
7 / 02		192	36	335	39	61	14	180	16	200	35	307	37	53	12	240	27
8 / 02		44	21	77	48	17	6	24	7	39	21	73	48	13	5	16	4
9 / 02		523	90	512	131	215	36	843	66	954	176	922	389	481	83	1458	158
10 / 02	**Bivalvia**	974	194	455	78	720	33	1747	313	1619	322	863	322	1237	212	2757	567
11 / 02		25	7	47	17	13	6	13	4	23	6	35	13	11	5	23	8
12 / 02		471	88	715	194	231	48	528	118	1693	363	2814	507	421	84	2125	394
1 / 03		808	85	1045	149	818	81	562	108	6154	1660	13001	2463	3657	361	1804	313
2 / 03		906	92	927	79	902	266	888	188	11148	2580	21410	2154	4760	1179	5675	648
3 / 03		756	169	136	16	1290	294	843	41	4919	870	1865	520	7663	1469	5230	489
4 / 03		935	201	118	22	1481	82	1295	139	6537	1220	2112	621	9100	880	9022	2104
5 / 02		4	1	0	0	4	1	7	3	9	3	2	2	23	7	6	3
6 / 02		4	2	12	7	1	0	2	0	31	19	97	61	9	6	4	2
7 / 02		5	1	4	3	3	2	7	1	30	15	1	1	13	10	76	35
8 / 02		1	0	1	1	0	0	3	1	3	3	0	0	0	0	12	11
9 / 02		39	11	87	13	12	4	19	4	818	286	2092	290	113	44	248	31
10 / 02	**Gastropoda**	44	11	88	14	10	3	35	6	715	203	1454	349	120	67	572	134
11 / 02		15	6	40	5	1	0	3	1	254	100	698	102	7	6	59	27
12 / 02		21	8	43	27	10	4	15	2	373	158	826	540	131	74	275	59
1 / 03		35	14	91	24	12	6	4	2	672	313	1967	487	40	36	10	4
2 / 03		16	7	42	10	1	1	2	0	309	152	841	252	0	0	9	0
3 / 03		22	6	48	6	2	1	15	6	345	141	976	136	17	6	42	6
4 / 03		22	5	30	5	4	2	37	8	243	84	557	99	5	4	144	4

Appendix continued

		abundance								biomass							
		total		Lit		Mee		Imm		total		Lit		Mee		Imm	
month		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
5 / 02		416	108	144	55	926	137	307	16	51	13	28	9	112	12	27	3
6 / 02		67	19	46	1	25	3	124	41	27	6	38	2	8	1	37	12
7 / 02		121	20	114	37	171	38	77	10	28	7	17	4	50	16	15	1
8 / 02		51	16	111	7	7	5	7	1	3	1	6	2	2	2	1	0
9 / 02		562	94	501	152	838	177	348	29	17	3	15	5	27	6	8	1
10 / 02	**Ephemeroptera**	599	51	586	56	467	86	744	72	24	3	31	6	19	4	20	2
11 / 02		4	1	6	3	4	1	4	2	1	1	3	1	1	1	0	0
12 / 02		268	40	383	78	140	16	310	46	22	5	44	7	17	4	11	1
1 / 03		527	126	338	101	165	15	1077	94	39	7	58	16	19	3	42	3
2 / 03		940	152	628	58	676	236	1451	210	61	7	71	6	40	10	68	16
3 / 03		1167	147	591	31	1245	142	1665	141	76	11	50	10	67	9	112	20
4 / 03		964	150	425	40	1211	191	1351	170	111	14	131	19	123	26	68	7
5 / 02		5	2	4	2	1	1	10	5	1	0	1	1	0	0	1	1
6 / 02		94	38	281	40	18	7	31	7	8	3	20	6	0	0	6	2
7 / 02		198	35	358	16	114	10	124	28	47	11	92	15	10	2	39	9
8 / 02		36	12	80	13	5	3	3	1	2	1	4	1	1	0	0	0
9 / 02		750	181	494	85	1548	150	208	12	24	3	25	9	30	4	16	2
10 / 02	**Trichoptera**	352	73	655	98	165	22	236	47	66	13	118	21	43	2	37	8
11 / 02		23	12	63	28	2	1	5	3	1	1	2	1	0	0	2	1
12 / 02		315	104	845	23	58	15	176	17	94	25	220	4	28	11	66	8
1 / 03		379	63	648	55	170	12	321	32	103	11	141	14	58	5	109	4
2 / 03		384	41	450	57	241	61	427	53	107	13	103	12	66	15	141	21
3 / 03		256	22	196	23	305	14	269	49	76	9	42	8	104	9	83	14
4 / 03		274	21	235	27	298	24	294	60	97	9	68	3	123	4	100	19
5 / 02		34	15	59	37	9	3	28	13	218	87	378	192	14	12	212	114
6 / 02		15	8	14	7	1	0	30	19	77	52	19	11	2	2	195	133
7 / 02		59	19	24	12	9	4	143	19	307	126	27	12	28	15	865	136
8 / 02		33	12	73	17	2	1	9	3	45	15	75	29	5	3	49	16
9 / 02		96	21	138	52	57	16	94	23	168	45	86	33	95	44	324	85
10 / 02	**Gammaridae**	70	9	46	7	103	14	61	7	113	20	53	6	187	33	100	10
11 / 02		53	12	70	24	16	4	75	18	69	14	71	12	22	6	112	24
12 / 02		65	14	29	5	110	26	48	6	117	31	66	38	203	65	68	11
1 / 03		28	4	33	7	13	3	37	6	43	7	51	9	26	6	53	17
2 / 03		39	7	52	6	39	19	26	9	81	19	117	14	95	55	35	16
3 / 03		15	2	16	1	18	4	12	3	29	4	28	2	37	9	21	5
4 / 03		57	9	48	7	54	8	73	33	38	10	29	7	19	3	73	31
5 / 02		38	13	58	33	49	18	11	4	16	6	24	14	20	7	4	2
6 / 02		37	24	128	69	4	1	1	1	15	10	53	28	2	1	1	0
7 / 02		84	25	167	57	56	13	28	6	34	10	69	24	23	5	11	2
8 / 02		35	10	66	15	18	6	4	3	14	4	27	6	7	3	2	1
9 / 02		182	41	277	100	180	53	89	8	75	17	114	41	74	22	37	3
10 / 02	**Ostracoda**	194	44	183	25	372	31	27	7	80	18	75	10	153	13	11	3
11 / 02		13	3	18	4	18	5	2	0	5	1	7	2	7	2	1	0
12 / 02		77	19	101	30	118	29	19	6	32	8	42	12	49	12	8	3
1 / 03		138	34	266	50	120	20	27	3	57	14	110	20	49	8	11	1
2 / 03		166	38	285	52	172	41	42	11	68	16	118	22	71	17	17	4
3 / 03		127	20	175	22	163	20	45	6	52	8	72	9	67	8	18	2
4 / 03		106	16	78	8	159	24	74	19	44	6	32	3	65	10	30	8

Chapter 7

Concluding remarks and perspectives

Study focus

In the previous chapters, I presented my investigations of the potential abiotic and biotic constraints on benthic communities in lake littoral zones. The underlying premise was that hydrodynamics, i.e. wave exposure, are a strong abiotic force likely to influence taxa occurrence as well as habitat parameters and to interfere with or mediate biotic interactions. This thesis furthermore clearly emphasises the importance of another abiotic factor — water-level fluctuations — for the benthic community within the upper eulittoral zone of unregulated pre-alpine lakes.

In an initial step, I focused on the colonisation abilities of macroinvertebrates under field conditions because the utilisation of new habitats seemed to be important in understanding the impact of abiotic disturbance processes (Chapter 2). To test the influence of wave exposure on various taxa under standardised conditions, we developed a new pneumatic wave machine and used it in an outdoor mesocosm to study the effect of common and realistic wave propagation and dissipation (Chapter 3). I chose the herbivorous snail *Radix ovata* as the study organism. This snail is widespread in many European lakes, and it often occurs with high abundance and biomass. Thus, compared to insect herbivores a pronounced grazing impact (Feminella & Hawkins 1995) and links to higher trophic levels (Nystrom *et al.* 1996; Werner *et al.* 2005) can be expected.

I particularly regarded biotic interaction with benthivorous fish as a potential source of benthic community variations. I expected this predator–prey relationship to explain a relevant proportion of the benthic abundance or biomass reductions and to alter diversity and community composition patterns. Therefore, the predation impact of the most abundant fish taxa, perch and ruffe, as well as cyprinids was tested in enclosures and exclosures in the field (Chapter 4, 5). In contrast to any studies on the impact of fish predation published to date, we additionally considered abiotic parameters, e.g. wave exposure, as a relevant factor likely to mediate the biotic interaction and chose study sites with contrasting hydrodynamic backgrounds.

Finally, I strongly regarded the natural dynamics of spatial and temporal variation of benthic communities as being important for background information on the system itself. Therefore, all experiments were accompanied by a one-year field study at three representative sites (Chapter 6). The benthic community patterns were related to the underlying abiotic changes: wind exposure at the sites and water-level fluctuations in the lake.

Main outcomes

This thesis clearly highlights the advantage of non-metric multidimensional statistics (e.g. nMDS, ANOSIM) over univariate or multivariate (ANOVA, MANOVA) statistics in investigations of complex benthic community patterns. The data from the colonisation study (Chapter 2) was processed in various ways and these methods of analysis were compared in detail. Colonisation processes were often exclusively studied using abundance or biomass data of dominant taxa only, neglecting the community structure. However, this can lead to false conclusions, as was shown for the recolonisation of bare single stones. The colonisation process, in terms of taxa abundance and occurrence, was completed within a few days (3–11 days), but the process was not complete in terms of community composition (31–73 days). Site differences were only detectable when treatment was directly compared to control stones per site, but not in a MANOVA analysis with site and days of colonisation as factors. Site differences were rather prominent at the beginning of the colonisation process and lasted longer, as shown with non-metric analyses (nMDS, ANOSIM).

This thesis further indicates the importance of manipulative studies in differentiating between factors that potentially explain the observed field distributions (Chapter 3). I manipulated waves with a newly developed new pneumatic wave machine to mimic realistic outdoor conditions. The growth rates and behavioural pattern of *R. ovata* depended on the hydrodynamic conditions applied. Interestingly, the impact of wave applications on snail individuals depended on the duration of the waves. Permanent wave application led to a surprisingly high mortality, whereas regular short-term wave applications allowed survival of snail individuals and reduced the growth rate only at some depths. The mesocosm results furthermore imply that other affiliated factors are influenced by wave action. For example, the periphyton food source of *R. ovata* is differently top-down controlled under turbulent or mild field conditions.

During these studies, in which it was shown that the occurrence of single taxa strongly differed among the various sites, a variety of related themes became apparent. Future studies in these areas would provide further insights into epibenthic communities. For instance, the growth patterns of *R. ovata* in the field under different hydrodynamic regimes and with varying periphyton/sediment ratios (dry mass/ash-free dry mass) at several sites would be a interesting point. A comparison of the size-class distribution at the differently exposed sites accompanied by a recording of the timing of the different life stages (e.g. reproduction) might be informative. Autecological or synecological studies would provide valuable insights into factors governing the distribution and population dynamics of other species. Promising target species are dominant or characteristic taxa in eulittoral zones, such as the mayfly *Ecdyonurus dispar*, the tube-building caddisfly *Tinodes waeneri*, the native amphipod *Gammarus roeseli,* and the recently established *Dikerogammarus villosus*. The interplay of other benthic communities, such as meiofaunal or periphyton assemblages with macroinvertebrates, particularly within different abiotic scenarios, should also be investigated in more detail in future studies.

In contrast to our expectations, we found no significant top-down control of benthivorous fish on macroinvertebrates in all mesocosm experiments, including short-term experimental manipulation with perch and ruffe and a long-term study with juvenile cyprinids, bream, and dace as predators (Chapter 4, 5). The results rather point towards a bottom-up control. The enclosure studies allowed restricted recolonisation of the benthos by using a fine mesh in the short-term study and almost unconstrained recolonisation by using a coarse mesh in the long-term study. Even with these differences in recolonisation possibilities, both experiments clearly revealed strong site differences in the benthic community for all parameters studied:

abundance (biomass, Chapter 5), diversity, and community composition. I interpret these results as a strong but indirect indication of different hydrodynamic situations. On the temporal scale, we documented significant differences between benthic communities, even after one week of exposure (Chapter 4), which implies a strong innate benthic variability in lake littoral zones. Interestingly, we found evidence of interspecific competition between perch and ruffe, with lower foraging success and consumption rates in both species. These effects also depended on the sites, with lower food availability at the sheltered site than at the exposed site. However, as the conflicting results of Baumgärtner (2004) and Baumgärtner & Rothhaupt (2005) on burbot predation in a similar, but also temporally repeated experimental manipulation in different years in the littoral zone suggest, consumption rates of fish can vary seasonally and cannot be ruled out without further results. Such experimental manipulations could also be used to focus further on consumption rates during various competitive situations with standardised wave regimes (wave machine, Chapter 3) and also with different substrate compositions (see Dieterich *et al.* 2004).

Quantitative benthos sampling, processing, and counting are extremely labour-intensive procedures. Therefore, the present field studies had to be restricted to representative sites in terms of exposure, substrate composition, and slope. Within the one-year field study (Chapter 6), the monthly sampling was restricted to one depth at three sites. However, to my knowledge, no other study has focused on such a fine-scaled seasonality in littoral communities. This time frame was primarily chosen to attribute community changes to underlying abiotic patterns and processes. As expected, on the temporal scale, benthic communities at all sites exhibited a gradual monthly transition. Surprisingly, a large amount of the observed variability of the benthic community could be related to short- and long-term water-level fluctuations. The effects of wind exposure were weaker than expected on a temporal scale within the year; gauge variability played a stronger role. The most pronounced effects of wind exposure were observed during the winter months, the time of the year when high wind events generally occur. On the spatial scale, however, the sites consistently differed in all months. This was at first surprising, but permanent site differences were also found in all other field and enclosure studies carried out (see Chapters 2, 4, 5). The results indicate that wave exposure is a main factor involved in altering habitat conditions at the sites constantly and thereby determines the specific benthic community composition. Furthermore, the results suggest that the slope of the sites interferes with both gauge-level fluctuation and wind exposure, but with opposite effects. When gauge levels decrease at sites with gentle slopes, great benthic losses can be expected if organisms are trapped on dry, exposed substrates. When gauge levels increase, vast areas of new habitats will arise, especially at sites with gentle slopes (Figs. 1, 2; see also Chapter 6). In contrast, the force of wave dissipation is diminished at shallow littoral sites more than at littoral sites with steep slopes (Arts 1994; Denny *et al.* 2003). These findings allow some general implications for defining disturbances in lakes or other habitats to be deduced (see also Figs. 1, 2).

General implications for disturbance processes and habitat or community evaluations

The strong seasonal and persistent spatial variability stresses the importance of long-term quantitative samplings in order to document and interpret alterations of benthic communities in water management or restoration projects and to differentiate between external effects and innate community processes. Such processes can depend on a variety of abiotic factors, but also on biotic interactions in some cases. The effects of larger geographical scales not addressed in the present study, need to be investigated in the future to be able to evaluate littoral communities of large, deep oligotrophic lakes in central Europe and to establish suitable survey schemes. This approach would allow an evaluation and comparison of macroinvertebrate community variance at similar lakes caused by regional-scale parameters rather than local-scale variables (see Johnson & Goedkoop 2002; Johnson *et al.* 2004). In a comparative study of Swedish lakes and streams, Johnson *et al.* (2004) stated that the among-site variance in benthic communities was best explained by habitat-scale characteristics rather than by ecosystem, riparian, catchment, geographic position, and ecoregion characteristics.

In applied and occasionally also in basic research studies, benthic samples are usually sampled once or twice a year, and then often not quantitatively. Sampling in lake littoral zones is usually restricted to the upper eulittoral zone, i.e. to arm-length sampling, and thus to an area highly susceptible to strong natural abiotic variations. Deceptive interpretations could thus arise when general questions are addressed, as is very common in applied studies. Such considerations should be taken into account in monitoring programmes at the local, state, federal, and international levels, e.g. the European Water Framework Directive. Such abiotic variations include strong water-level fluctuations, which could be a special feature of large unregulated lakes with high precipitation within its catchment area, i.e. pre-alpine lakes, and wave exposure, which is very likely a relevant factor for various lake types and sizes. Other relevant factors need to be identified for each system.

Even if the sampling effort is low or seasonal variations occur, mainly in applied studies, an extensive taxonomic analysis is often proposed. The authors particularly focus on historically interesting groups of taxa, such as mayflies, caddis flies, stoneflies, leeches, snails, and water beetles. A low taxonomic resolution of difficult groups, e.g. dipterans (chironomids, simulids), is often attained within the same study. The differences between economic and scientific constraints is indeed difficult to resolve, and similar restrictions apply also to the present study. When the analysis is restricted to a few samplings, I regard the focus on a few interesting benthic groups as misleading since the importance or occurrence of the few single or rare taxa might be overestimated. This problem is compounded when information about the local benthic community and the abiotic or biotic constraints is lacking. The autecological knowledge of most taxa and in particular of rare taxa, e.g. habitat constraints, niche parameters, and interactions with other taxa, is rather limited.

The field sampling of macroinvertebrates was restricted to shallow depths in our studies. I assume that invertebrate communities at deeper sites have a similar pattern of high spatial and temporal variability, even though wave exposure and gauge-level fluctuations have less influence below the long-term low-water line and benthic communities might generally benefit from less-severe alterations of habitat. This assumption is supported by earlier studies carried out at one site also included in the present studies, Litoralgarten in Upper Lake Constance (Mörtl 2003; Baumgärtner 2004). Highest abundance and biomass of macroinvertebrates were recorded at the long-term mean low-water line (Mörtl 2003; Baumgärtner 2004). Future studies will further provide essential insights into benthic communities and their governing forces (Scheifhacken, unpublished data).

At deeper sites, the availability of natural hard substrates, i.e. cobblestones, or ‘artificial’ hard substrates, i.e. *Dreissena polymorpha* shells (Stewart *et al.* 1998b; Mörtl & Rothhaupt 2003), might be of particular importance or a limiting factor in terms of total abundance, biomass, and diversity of benthic communities. The occurrence of macrophytes, which enhance the structural complexity, might be also relevant to understand benthic distribution patterns.

The recent new arrivals of exotic benthic taxa in Lake Constance — the amphipod *Dikerogammarus villosus* (Mürle *et al.* 2004) and the Asian clam *Corbicula fluminea* (Werner & Mörtl 2004) — probably have altered the benthic communities (e.g. Dick & Platvoet 2000; Hakenkamp *et al.* 2001). The consequences for the benthic communities and higher trophic levels, e.g. prey consumption by fish, will be evaluated in future studies. The present study was carried out prior to the introduction and massive expansion of *C. fluminea*, but *D. villosus* was present during the fish-benthos enclosure experiments (Chapters 4, 5, 2004, see also Mörtl *et al.* 2005). The results of the long-term study (Chapter 6) carried out before the introduction of *D. villosus* will be valuable for comparisons with future quantitative studies after its establishment.

Defining disturbance processes

Defining disturbances is very complex and difficult, because some of the environmental variability at the different scales is a fundamental part of a biological system. Therefore, communities can be expected to be well adapted to such changes within a specific range. Variables inherent to each system include general seasonal changes with subsequent shifts of various abiotic parameters (e.g. temperature, light intensity). In contrast, climatic changes that affect similar parameters can be regarded as disturbances. Both types of alterations of abiotic conditions can occur suddenly or gradually on temporal or spatial scales and therefore lead to different consequences for the affected community.

As a consequence, disturbance processes are defined very broadly and also inconsistently in the literature (for a review see Lake 2000; Shea *et al.* 2004). Definitions focus either on specific taxa or on the community level, e.g. mortality rates. Some authors concentrate on the amount of available resources, e.g. habitat parameter, space, or food availability. Another approach is to evaluate the nature of the force itself. Shea *et al.* (2004), for instance, defined disturbance as an event that alters niche opportunities. These events can destroy or remove biomass, shift nutrient availability, or alter organismic relationships and thus niche opportunities.

Alternatively, Townsend & Hildrew (1994) defined disturbance as a discrete event that removes organisms and leaves space or resources for other individuals of the same or other species. White & Picket (1985) concentrated also on the effects on the biota and their subsequent responses, whereas others characterised disturbance from the generated force (Lake 1990, 2000; Poff 1992). This clearly points out the importance of the scale regarded. The mechanism of force generation in lotic habitats is distinguished by Lake (2000) at three temporal scales of distinctiveness: **pulse** (short-term peak disturbance), **press** (sudden increase, but remains at a higher level afterwards), and **ramps** (steady increase over time, often accompanied by changes on a spatial scale). Most authors differentiate the disturbance attributes and focus on **frequency** (time since last event, disturbance history) and **intensity** or severity of the underlying force. However, **duration** (time which force lasts) and the spatial **extent** of the affected area are similarly important. The **predictability** of the damaging force is another important aspect. The scale could also include aspects of the time **phase of occurrence** of taxa traits (e.g. lifespan, resistant or sensitive life stages, merolimnic *vs*. hololimnic taxa) as well as of the disturbance force itself. The latter might be an exceptionally rare but catastrophic event with a low chance of genetic or evolutionary adaptability or a regularly occurring ‘misfortune’ with a great potential of the taxa to adapt. Habitat, taxa, population, and community levels require other characterisations or quantification strategies.

Quantification itself depends on the particular system investigated (wind speed, water depth, water level fluctuation, geographical position, human activities, etc.). A generalisation cannot be proposed. However, assuming three general classifications — low, medium, and high impact — for four characteristics of a disturbance parameter (frequency, intensity, duration, extent) will lead to 3^4=81 experimental units without any replication (see also Shea *et al.* 2004).

To complicate the situation even further, different sources of disturbances (e.g. wave exposure, water-level fluctuation) can occur in parallel and can either superimpose each other or conversely diminish the effects of a single factor. This interplay might be partly relevant only under the impression of a third factor, such as slope, as observed in the one-year field study presented here. Natural disturbances tend to vary at various axes simultaneously, which complicates standardised experimental analyses.

Transferring theories to the investigated ecosystem

In the present study, I showed the importance of waves and their implications as a disturbance parameter for benthic communities within Lake Constance, but often indirectly based on differences in benthic communities. Within large, deep, oligotrophic lakes, all three suggested mechanisms of force generation — pulse, press, and ramp (Lake 2000) — are likely and common, even if transitional in their occurrence and characteristics. For instance, regular short-term wave exposure generated by ferry boats are surely pulse disturbances, but wave exposure originating from high wind events, depending on their duration (ranging from a few days to weeks), could be regarded as either a pulse or a press event. However, a sudden accumulation of fine sediments after a high wind event represents a disturbance for benthic communities that extensively alters habitat conditions and leads to a different habitat situation, e.g. substrate composition (press). A similar situation applies to water-level fluctuations. Sudden increases in water level within a few days occur commonly (pulse). In contrast, steady increases and decreases over a longer seasonal period at Lake Constance (summer: high water level; winter: low water level) are also very common (press).

In the mesocosm wave exposure experiments (Chapter 3), I focused on the manipulation of the duration and frequency of applied waves and their implications on growth or behavioural patterns, but not on intensity or predictability. The extent of superimposed natural disturbance processes, including all above-mentioned parameters, are represented by the other experimental field studies (Chapters 2, 4, 5). A natural strong wind disturbance event (Scheifhacken & Rothhaupt 2003) and an experimentally induced severe disturbance (Scheifhacken & Rothhaupt 2004) have been studied previously. Both studies comprised different aspects of disturbance (extent, intensity, disturbance frequency and hence history) and their implications will be compared in an upcoming paper (Scheifhacken & Rothhaupt, in preparation).

Overview of disturbance patterns at Lake Constance

The Fig. 1 and Fig. 2 summarise the determined disturbance patterns for Lake Constance as an example and simplified overview. It also stresses the difficulties of handling parameters for experimental manipulations, when at least partly opposite effects for the benthic communities can be expected.

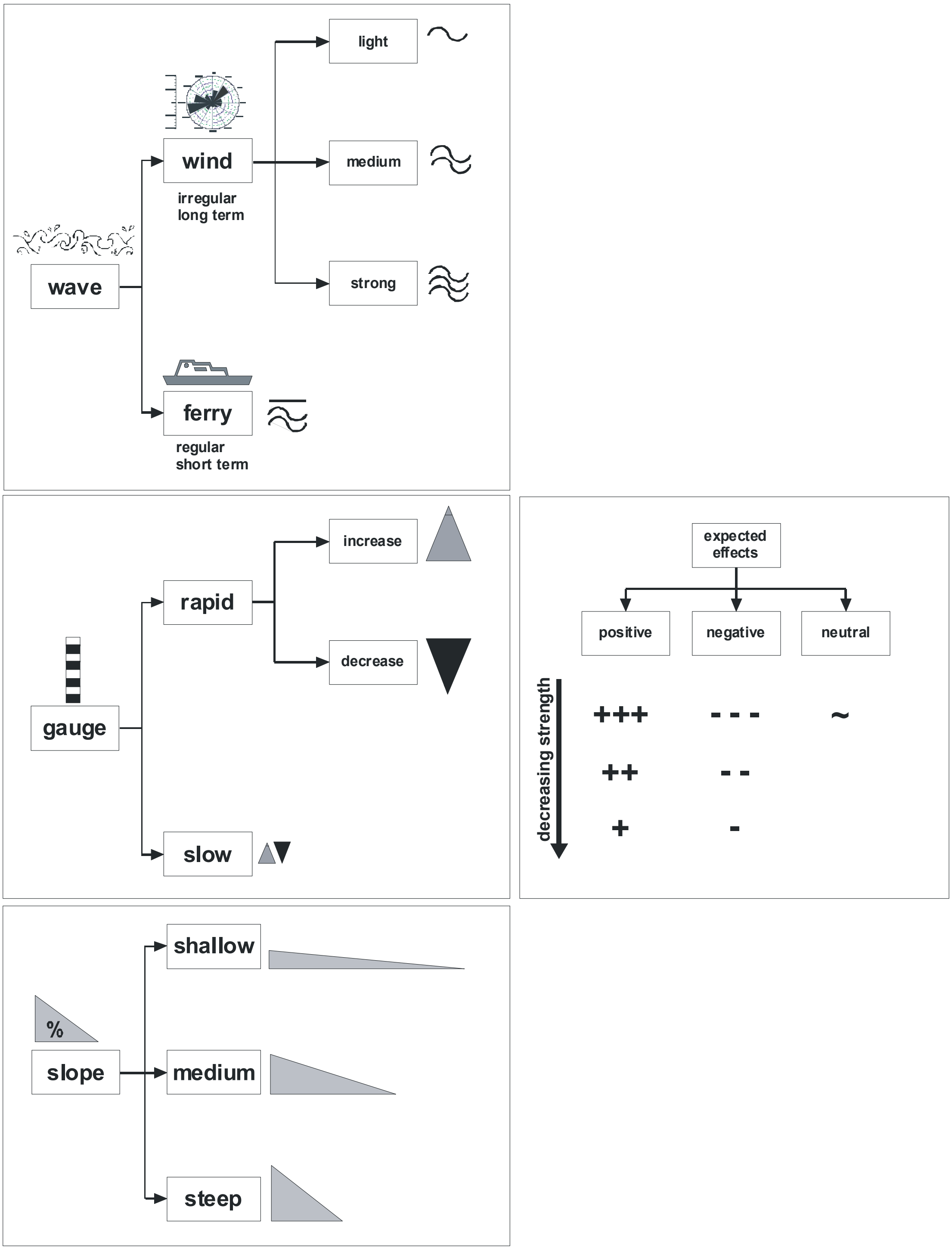

Figure 1: Conceptual framework of dominant abiotic parameters relevant within the studied environment, Upper Lake Constance. The indicated parameters wave exposure, gauge/water-level fluctuations, and slope in the boxes on the left are further differentiated into the assumed sub-classifications. The box on the right defines expected effects containing positive or negative values on a hypothetical three-step scale and also un-scaled neutral effects. All symbols, as defined in the figure, are also used in Fig. 2. See text for further details. Note that all definitions are not fixed or final, but are rather a rough simplification and a suggestion for future work.

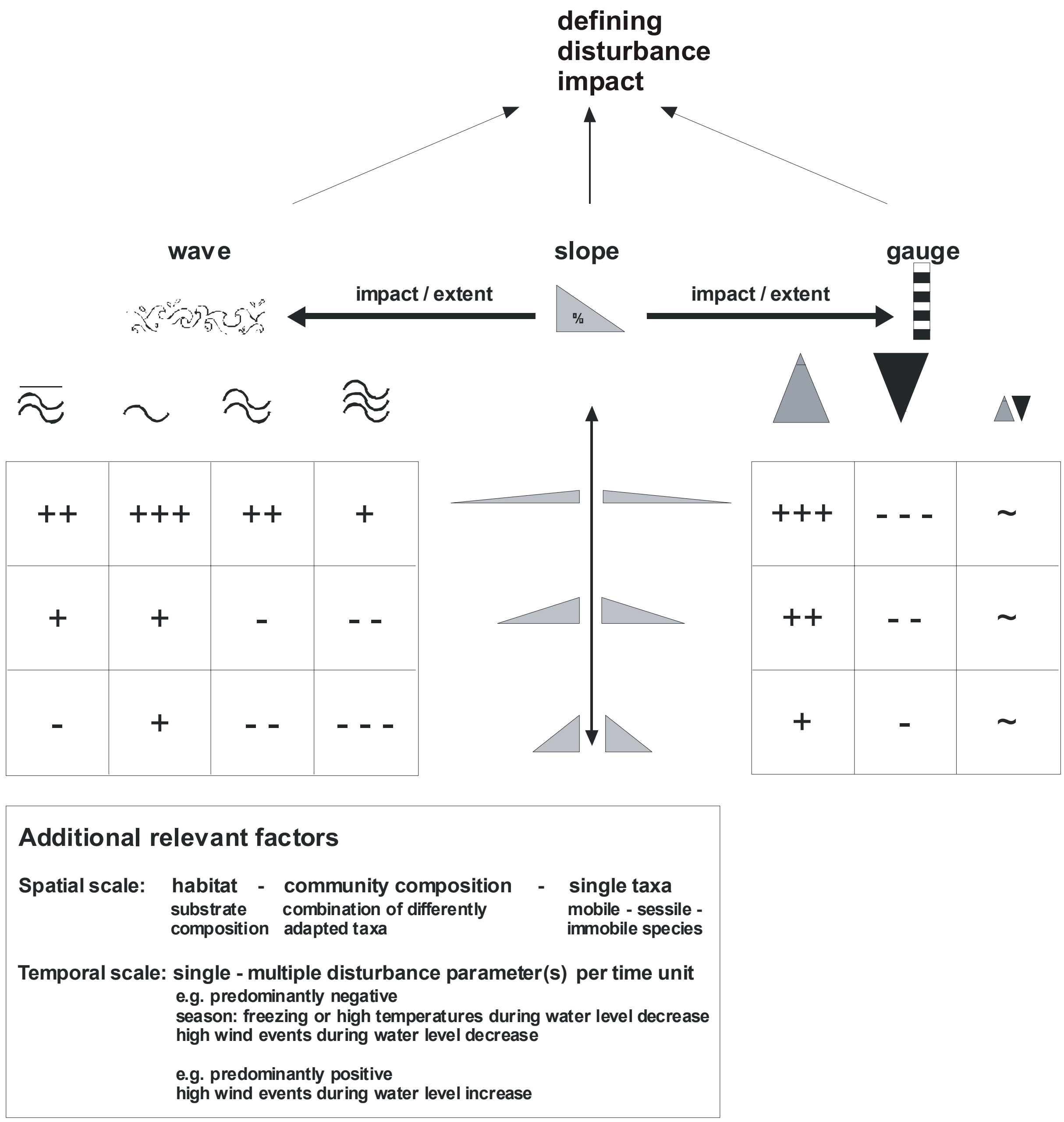

Figure 2: Conceptual overview of the three abiotic parameters wave exposure (left), gauge/water-level fluctuation (right), and slope (centre) and their expected interaction (impact effects: positive, negative, neutral) with benthic communities in sub-classifications, displayed as a contingency table. See **Figure 1** for symbols and their meanings. Slope in particular is vital. I hypothesise that different slope gradients are important and govern the outcome of single parameters and interfere with other parameters when occurring in parallel. Other additional relevant factors that might be of importance are listed at the bottom. See text for further details. Note that all definitions are not fixed or final and are rather a rough simplification to focus on opposing effects between parameters.

Other factors not displayed in Fig. 1, 2. might also apply and need to be recognised at other lakes as potential disturbance forces.

The 'Intermediate Disturbance Hypothesis' and its relevance for the present study

Abiotic disturbances and their implications for communities are often related to the assumptions arising from the 'Intermediate Disturbance Hypothesis' (IDH) established by Connell (1978). The theory states that highest diversities are found at intermediate disturbance levels (frequency, intensity); at lower disturbance levels, competitive species are expected to displace pioneer species, and at high disturbance levels, species with longer life cycles are excluded (Fig. 3). A surprisingly vast number of studies have dealt with these postulations to explain species coexistence in various habitats; the paper of Connell (1978) has been cited almost 2300 times to date (Web of Science, February 06). According to Shea *et al.* (2004), the approach used in many of the studies to test adaptability was unfortunately often restricted to a few aspects or was solely based on speculation based on the abundance or diversity data obtained from empirical or experimental studies. Shea *et al.* (2004) focused on recent results, but applied a general approach and covered various disturbance regimes in terrestrial or aquatic communities on a variety of scales (microcosm to landscape approach).

To date, the IDH has been used in a variety of aquatic and terrestrial habitats. Apart from examinations of coral reefs (e.g. Kilar & McLachlan 1989; Aronson & Precht 1995) and tropical rainforests (Molino & Sabatier 2001), the main focus for testing the hypothesis has been on marine habitats. Various studies focused on soft sediment communities (e.g. Austen *et al.* 1998; Frouin 2000; Widdicombe & Austen 2001; Garstecki & Wickham 2003) or on hard substrates, e.g. studies on macroalgae (Sousa 1979) and invertebrates (Lenz *et al.* 2004). Other studies centred on the stability of hard substrates in lotic freshwater habitats for invertebrates (Doeg *et al.* 1989; Townsend *et al.* 1997; Death 2002) and on epilithic algal diversity (Fayolle *et al.* 1998). In lake littoral zones, for example, the dependence of the diversity patterns of macrophyte communities on wind/wave exposure was investigated (Riis & Hawes 2003; see also reviews by Lake 2000, Roxburgh *et al.* 2004, and Shea *et al.* 2005). Similarly, in pelagic habitats, various studies focused on phytoplankton diversity (e.g. Sommer 1995; Flöder & Sommer 1999; Bertrand *et al.* 2004), including aspects of functional diversity (Weithoff 2003), as well as on zooplankton (Eckert & Walz 1998) and bacterial isolates (Beck 2000; Buckling *et al.* 2000, for a more general modelling approach, see Bartha *et al.* 1997; Collins & Glenn 1997; Wootton 1998).

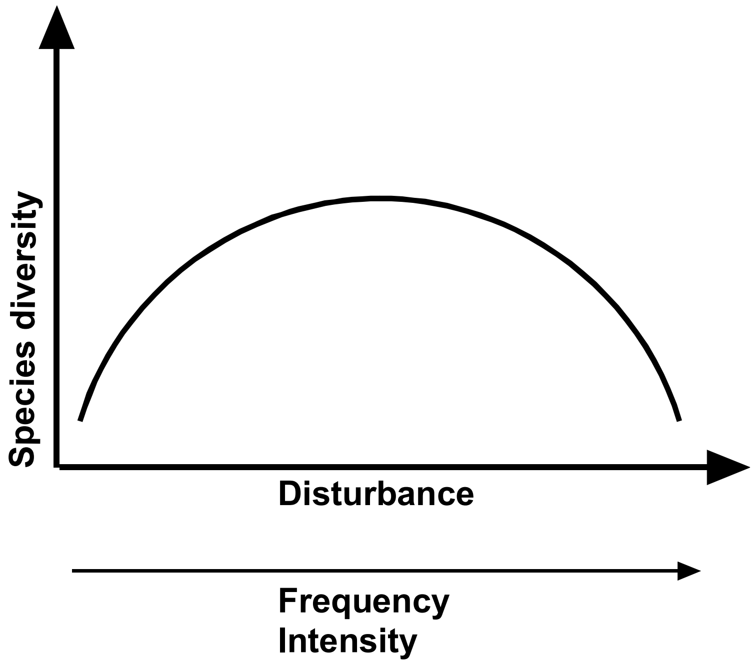

Figure 3: The unimodal relationship between the disturbance mechanism and species diversity based on the Intermediate Disturbance Hypothesis of Connell (1978); modified, see text for further details.

Besides the overwhelming agreement on this theory and its establishment in general ecology (Begon *et al.* 1990) and limnology textbooks (Lampert & Sommer 1993), the experimental results are still strongly inconsistent. Some results support the theory (e.g. Sousa 1979; Sommer 1995; Townsend *et al.* 1997) and others provide no evidence for its validity or applicability in the investigated context (e.g. Doeg *et al.* 1989; Garstecki & Wickham 2003). The lack of evidence in some studies is not surprising since, as I already presented, there can be difficulties in finding all relevant aspects of a physical disturbance. In the studies presented here, for example, there were conflicting disturbances factors of wave exposure and water-level fluctuation at different slopes (Figs. 1, 2). Furthermore, difficulties arise because of the general attributes of these disturbances, e.g. frequency, intensity, duration, extent, and predictability. Restrictions are necessary to be able to handle a workable amount within a particular experiment. When the IDH is applied, it must be decided whether all regarded disturbance factors are relevant and responsible for the recorded peculiarities. Despite these experimental difficulties in testing some aspects of disturbance patterns in the field or laboratory, the IDH increasingly forms the basis for studies of aquatic communities based on one or a few samplings at a few sites. The hypothesis at first appears to be simple but conclusive. However, after a closer look, it might also be deceptive, as the above-mentioned aspects of the disturbance features in the present study of lake littoral zones suggest.

It must be considered that the data used to form the basis of the IDH were gained in from tropical rain forests and coral reefs, i.e. communities dominated by sessile organisms. This might be one reason for the difficulties in finding patterns of the IDH for mobile organisms, as stated by Crandell *et al.* (2003) in their review on the effects of flooding on aquatic communities. Wootton (1998) also pointed out the difficulties in applying the IDH in multitrophic environments. In summary, I suggest that the IDH should not be applied generally to a few aspects and that a poor data set based on one or a few samplings should be avoided, if it is to be globally related. I follow Crandell *et al.* (2003) and Wootton (1998) in their advice to use more caution in applying this theory in general and also to consider other explanations beyond it.

Chapter 8

Summary

Littoral zones represent the most diverse, heterogeneous, and highly productive part of lakes (Wetzel 2001). Within this habitat, macroinvertebrates play a key role as they form an important link to other trophic levels. However, the mechanisms that structure benthic communities are far from being resolved. This lack of knowledge includes both abiotic and biotic constraints of benthic communities and their environment. The present thesis concentrates on various aspects of hydrodynamics, which are a major abiotic force within the upper eulittoral zone of large lakes, and the influence of wave exposure and disturbance history on macroinvertebrate occurrence and community patterns. This thesis includes results from standardised field and mesocosm experiments and from a field sampling.

I focused on the colonisation abilities of macroinvertebrates under field conditions, as the utilisation of new habitats is important to understand the affiliated mechanism of disturbance patterns in lake littoral zones (Chapter 2). The comparison of colonisation patterns at three sites exposed to different wind levels clearly showed the advantage of non-metric multidimensional statistics for investigating complex benthic community patterns. In terms of taxa abundance and occurrence, the colonisation process was completed within a few days (3–11 days), but finalisation of the community composition took longer (31–73 days). The site differences were only detectable when treatments were directly compared to control stones at each site, but not in a MANOVA, with site and days of colonisation as factors. Site differences were rather prominent at the beginning of the colonisation process and lasted longer, as shown with non-metric tools (nMDS, ANOSIM). The colonisation study

emphasises the importance of analysing the results with accepted statistical tools and points the risk of drawing misleading conclusions.

To study realistic scenarios of wave propagation and dissipation under standardised conditions, we developed a pneumatic wave machine for outdoor mesocosm application (Chapter 3, in cooperation with Petra Klahold). I restricted my studies to a key species, the very common and widespread herbivorous snail *Radix ovata.* The snail occurs in many European lakes, often in high abundance and biomass. Thus, a pronounced grazing impact of this species on its periphyton food source can be expected, and the snail itself is a valuable food source for other trophic levels. The results indicate that snail growth and behavioural traits depended on the applied wave impact, here expressed as the duration of wave exposure. The growth rate of *R. ovata* was strongly suppressed under constant wave application lasting for two weeks. This also resulted in a high mortality rate of snails in two of the three uppermost depths. In contrast, regular short-term wave application of equal strength caused only a growth suppression in the two uppermost depths, but no individuals were lost. I also documented a highly variable horizontal distribution of *R. ovata* at five different lake littoral sites. Highest abundances occurred at a site with medium disturbance history. Furthermore, the pneumatic wave machine proved to be an adequate tool for wave manipulation.

The present thesis involves two studies with emphasis on predator–prey interactions between benthivorous fish and their macroinvertebrate food source (Chapter 4, 5). Despite the direct impetus of fish on benthic variability, I assumed that wave exposure would interfere with or mediate such food web interactions. With this new approach, I expected to be able to differentiate between benthic invertebrate variability derived from a mere abiotic interference and the variability arising from biotic interactions, such as a strong predation pressure, under different disturbance conditions. We studied the impact of predation of the most abundant fish taxa in Lake Constance, perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*), as well as of juvenile cyprinids [dace (*Leuciscus leuciscus*), bream (*Abramis brama*, *Blicca bjoerkna*)] in enclosures and exclosures in the field. Two and three different study sites were chosen for perch/ruffe and cyprinids, respectively. The sites had contrasting hydrodynamics. Surprisingly, the expected and often proposed top-down control of fish on macroinvertebrates was not supported by our results. Instead, the results supported the opposite, bottom-up control. We documented the importance of food availability on the outcome of foraging success and consumption rates, particularly in the study of perch and ruffe. Furthermore, food availability strongly influenced the outcome of competition between perch and ruffe. Both fish–benthos interaction experiments also clearly revealed strong differences in benthic communities between sites for all presented parameters. I interpret this as indirect evidence of different hydrodynamic situations at these sites that presumably result in different benthic productivities or food availabilities on a longer time scale. However, we also documented a high temporal variability of benthic communities, with significant shifts in community structure occurring after one week of exposure. These results imply a strong benthic innate variability in the littoral zone and should be generally taken more into consideration when benthic communities in lake littoral zones are investigated.

The determination of benthic variability was the central focus of a one-year field study at three representative sites (Chapter 6). The understanding of the mechanism influencing the spatial and temporal patterns of benthic communities is an important background information on the system itself. Benthic community patterns obtained by monthly sampling were related to the underlying abiotic changes in wind exposure between sites and water-level fluctuations in the lake. This study clearly emphasises the importance of another abiotic factor – water-level fluctuations – for the benthic community structure within the upper eulittoral zone of unregulated pre-alpine lakes. The effects of wind exposure were most pronounced during the winter months, when high wind events occurred most often. However, wind effects were easily masked by water-level fluctuations in the upper eulittoral zone. The outcome of this interaction depended at least partly on another factor, the slope gradient of the investigated site. Slope can presumably both diminish and superimpose the effects of either wave exposure or water-level fluctuations. This likely interference should also be considered in future studies at Lake Constance.

In summary, the present thesis stresses the importance of hydrodynamics as a prevalent abiotic force within the upper eulittoral zone of large lakes. The potential of hydrodynamics to cause variability of communities needs to be considered in future studies. Both short- and long-term wave exposure result in a particular disturbance history of sites, which seem to be vital in determining macroinvertebrate occurrence and community patterns. However, water-level fluctuations are another abiotic factor in unregulated large lakes that alter benthic communities considerably. The present study also clarifies that abiotic processes can have both positive and negative effects on benthic communities. The results also suggest that slope, as a third prominent factor, considerably influences the outcome of wave and gauge impacts in either direction. This thesis stresses the importance of embedding benthic studies within larger contexts and collaborative research in order to understand the complex interplay of factors.

Chapter 9

Zusammenfassung

Uferzonen von Seen stellen einen vielfältigen, heterogenen aber auch sehr produktiven Lebensraum dar (Wetzel 2001). In diesem spielen insbesondere benthische Makroinvertebraten eine große Rolle, zum Beispiel über ihre verbindende Rolle zu anderen Trophieebenen in Nahrungsnetzen. Die Mechanismen, die die Struktur und Abläufe der benthischen Gemeinschaften maßgeblich beeinflussen, sind nach wie vor nicht zufriedenstellend aufgeklärt. Diese Wissenslücke umfasst sowohl abiotische als auch biotische Aspekte der Interaktionen, denen das Benthos in seiner Umwelt unterliegt. Der Schwerpunkt der vorliegenden Dissertation liegt in der Auseinandersetzung mit verschiedenen Aspekten der Hydrodynamik. Hydrodynamische Prozesse stellen eine sehr wesentliche abiotische Komponente in großen Seen dar, insbesondere im oberen eulitoralen Uferbereich. Auflaufende Wasserwellen entfalten hier ihre größte Kraftwirkung, was zum Beispiel über eine generelle Exponiertheit von Uferbereichen sowie die Häufigkeit der Störung bzw. – der Hintergründe im zeitlichen Verlauf beschrieben werden kann. Die damit verbundenen potentiellen Auswirkungen auf verschiedene Taxa sowie auf die Zusammensetzung der Benthoszönose selbst sind im Rahmen dieser Arbeit näher untersucht worden. Die Dissertation enthält mehrere experimentelle Untersuchungen im Freiland und unter Mesokosmosbedingungen sowie eine einjährige Freilandstudie.

Zu Beginn der Untersuchungen habe ich den Verlauf der Wiederbesiedlung neu entstandener Habitatinseln durch benthische Invertebraten an drei verschieden wellenexponierten Uferabschnitten untersucht (Chapter 2). Dabei handelt es sich um einen zum Verständnis von Störungsprozessen sehr wichtigen Mechanismus. Der

Vergleich der Besiedlungsabläufe an den drei Uferabschnitten verdeutlichte vor allem den Vorteil nichtmetrischer multidimensionaler gegenüber uni- und multivariater Statistik bei der Auswertung komplexer Zusammenhänge in der Benthosgemeinschaft. Hinsichtlich der Abundanz und Anzahl der Taxa ist die Wiederbesiedlung innerhalb von wenigen Tagen (3-11 Tage) abgeschlossen, nicht jedoch bezüglich der Zusammensetzung der Benthosgemeinschaft. Diese dauerte wesentlich länger (31-73 Tage). Der Besiedlungsverlauf auf den ausgebrachten Steinen war mit multivariater Statistik (MANOVA) nur im direkten Vergleich per Uferstelle nachweisbar (Faktoren: Uferbereich, Tage der Wiederbesiedlung). Die Unterschiede zwischen den Uferbereichen waren insbesondere zu Beginn der Wiederbesiedlung sehr groß. Sie ließen sich jedoch wesentlich länger mit den nichtmetrischen Methoden (nMDS, ANOSIM) statistisch nachweisen. Diese Studie weist ferner darauf hin, dass auch mit anerkannten statistischen Werkzeugen und Methoden erzielte Ergebnisse permanent hinterfragt werden sollten, um eine Fehlinterpretation zu vermeiden.

Um realistische Szenarien von Wellenpropagation und –dissipation unter standardisierten Bedingungen untersuchen zu können, haben wir eine pneumatische Wellenmaschine für den Außenanlagenbetrieb entwickelt (Chapter 3, in Kooperation mit Petra Klahold). Aus Gründen des Arbeitsumfanges musste die Anwendung vorerst auf eine wichtige Schlüsselart beschränkt werden. Hierzu wurde die sehr häufige und weit verbreitete herbivore Schnecke *Radix ovata* ausgewählt. Diese Art kommt in Europa in vielen Seen vor, häufig auch in hohen Abundanzen oder Biomassen. Daher kann von einem sehr ausgeprägtem Fraßdruck dieser Art auf ihre Nahrungsressource dem Periphyton ausgegangen werden. Ferner bildet sie selbst eine wichtige Verbindung zu anderen Nahrungsnetzebenen. Die Ergebnisse zeigen, dass das Wachstum der Schnecken sowie ihre Verhaltensweisen bei der Nahrungsaufnahme von der Wellensituation, der sie ausgesetzt waren, abhängig war. Die Stärke der Wellenexposition wurde über die Dauer der Anwendung manipuliert. Die Wachstumsraten waren stark eingeschränkt, wenn die Schnecken der permanenten turbulenten Situation für zwei Wochen ausgesetzt waren. Die dauerhafte Exposition führte zusätzlich zu hohen Sterblichkeitsraten in den oberen zwei von drei untersuchten Wassertiefen. Im Gegensatz dazu war eine regelmäßige Kurzzeitturbulenz gleicher Stärke wesentlich weniger beeinträchtigend. Unter diesen

Bedingungen konnten alle Schnecken den experimentellen Zeitraum von zwei Wochen überleben, das Wachstum war jedoch auch hierbei in den beiden obersten Wassertiefen eingeschränkt. Weiterhin zeigten die Freilandaufsammlungen eine sehr ungleichmäßige Verteilung der Art im Bodensee. Die höchsten Schneckenabundanzen wurden an einem mittel exponierten Uferabschnitt erzielt. Insgesamt erwies sich die entwickelte Wellenmaschine als ein sehr geeignetes Instrument zur Wellenmanipulation.

Die Dissertation beinhaltet weiterhin zwei Studien, die sich mit Räuber-Beute-Interaktion zwischen benthivoren Fischen und ihrer benthischen Nahrungsressource beschäftigen (Chapter 4, 5). Neben dem durch die Fische verursachten Fraßdruck und seinen Auswirkungen auf die Variabilität der benthischen Lebensgemeinschaft, sollte die Beeinflussung der biotischen Interaktion durch die an den Standorten wirksame Hydrodynamik untersucht werden. Dieser neue bisher unbeachtete Aspekt sollte ermöglichen, zwischen benthischer und der durch biotische Interaktionen verursachten Variabilität unterscheiden zu können, beides jedoch in Hinblick auf verschiedene abiotische Störungsszenarien. Hierfür wurden der Fraßdruck für die am häufigsten im Bodensee vorkommenden Fischarten, Flussbarsch (*Perca fluviatilis*) und Kaulbarsch (*Gymnocephalus cernuus*), sowie Döbel (*Leuciscus leuciscus*) und Brachsen (*Abramis brama*, *Blicca bjoerkna*) experimentell in Enclosure/Exclosure Käfigen unter Freilandbedingungen getestet. In der Barsch-Studie wurden zwei Uferbereiche, und in der Weißfisch-Studie drei verschiedene Uferbereiche untersucht, die sich jeweils hinsichtlich ihrer Wellenexposition unterschieden. Überraschenderweise konnten wir die erwartete und oft vorrausgesagte top-down Kontrolle der Fische auf das Benthos nicht nachweisen. Im Gegenteil, unsere Ergebnisse legen einen umgekehrten Zusammenhang von bottom-up Kontrolle nahe. Die Verfügbarkeit von Nahrung spielt offensichtlich eine große Rolle bei der erfolgreichen Nahrungssuche und Aufnahmerate durch die Fische. Dies zeigt sich insbesondere bei der Barsch-Studie. Die Nahrungssituation beeinflusste außerdem die Konkurrenzsituation zwischen Flussbarsch und Kaulbarsch. In beiden Experimenten zur Fisch-Benthos-Interaktion zeigten sich deutliche Unterschiede in der Benthosgemeinschaft für alle berücksichtigten Parameter. Dies lässt sich als indirekter Nachweis verschiedener Störungshintergründe dieser Uferbereiche werten. Als Konsequenz lassen sich daraus betrachtet über einen längeren Zeitraum auch verschiedene Produktivitäten und Nahrungsverfügbarkeit für andere Trophieebenen ableiten. Aber auch eine hohe zeitliche Dynamik wurde in beiden Untersuchungen deutlich. Signifikante Veränderungen der Zusammensetzung der Benthosgemeinschaft erfolgten bereits nach einer Woche. Diese Ergebnisse zeigen eine außerordentlich hohe Dynamik innerhalb der litoralen benthischen Gemeinschaft, die auch für zukünftige Untersuchungen berücksichtigt werden sollte.

Die Bestimmung der benthischen Dynamik war ein wesentlicher Punkt in der Feldstudie in drei verschiedenen Untersuchungsgebieten über einen Zeitraum von einem Jahr (Chapter 6). Das Verständnis der Mechanismen, die die räumliche und zeitliche Variabilität der litoralen Benthosgemeinschaft beeinflussen, ist eine wichtige Hintergrundinformation über das System selbst. Die monatlichen Benthosproben an den verschiedenen Uferstellen wurde zusammen mit den ebenfalls dokumentierten abiotischen Veränderungen, Windexposition und Wasserstandsschwankungen untersucht. Die Ergebnisse dieser Studie weisen sehr deutlich den hohen Einfluss von Wasserstandsänderungen auf die Benthosgemeinschaft in großen unregulierten Seen nach. Der Einfluss von Windexposition war insbesondere in den Wintermonaten ausgeprägt und deutlich. Während dieser Zeit treten stärkere Windereignisse besonders regelmäßig auf. Windeffekte werden jedoch auch leicht durch andere stärkere Effekte wie Wasserstandsschwankungen, die ebenfalls für die oberen litoralen Uferbereichen relevant sind, überlagert und verdeckt. Zusätzlich zeigte diese Studie, dass ein weiterer Faktor, das Ufergefälle, an den Auswirkungen von Windexposition und Wasserstandsschwankungen beteiligt ist. Das Ufergefälle kann vermutlich die Effekte von beiden Parametern sowohl abmildern als auch verstärken. Dieser Zusammenhang sollte bei weiteren Untersuchungen im Bodensee berücksichtigt werden.

Zusammenfassend weist die vorliegende Arbeit die Bedeutsamkeit von hydrodynamischen Störungen als einen der vorherrschenden abiotischen Faktoren in großen Seen nach. Die möglicherweise daraus resultierende Variabilität der Benthosgemeinschaft sollte auch in zukünftigen Studien mitbetrachtet werden. Sowohl kurzzeitige als auch längerfristige Wellenexposition können zu einem bestimmten Störungshintergrund von Uferbereichen führen, die offenbar eine wesentliche Komponente und Ursache für das Auftreten von verschiedenen Arten und die Zusammensetzung der Benthosgemeinschaft ist. Wasserstandsschwankungen sind jedoch in großen unregulierten Seen eine weitere Ursache für Veränderungen in der benthischen Gemeinschaft. Die vorliegende Arbeit zeigte außerdem, dass beide abiotische Faktoren sowohl positive als auch negative Auswirkungen haben können. Jedoch hängen die Auswirkungen von Wellenexposition und Wasserstandsschwankungen vermutlich von einem weiteren Faktor, dem Ufergefälle ab. Hier sind zum Teil gegenläufige Wechselwirkungen zu erwarten. Weiterhin zeigte diese Studie, dass die Einbettung benthischer Fragestellungen in einen größeren interdisziplinären Kontext sehr wichtig ist, um die komplexen Zusammenhänge und Interaktionen verstehen zu können.

Chapter 10

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Record of achievement / Abgrenzung der Eigenleistung

Chapter 2, 3	Results, design, and sample processing described in these chapters were exclusively performed by myself or under my direct supervision. The development of the pneumatic wave machine was part of a cooperation project with Petra Klahold (SFB 454, C2)
Chapter 4, 5	I contributed to design, field sampling and sample processing for both experiments and exclusively analysed the collected data (chapter 5) and the benthos data (chapter 4), and also contributed to the written elaboration. Both experiments are the result of cooperation projects within SFB 454 (C1 and A1, chapter 4; C2 and A1, chapter 5).
Chapter 6	I contributed to design, field sampling and sample processing for the survey and exclusively analysed the collected data.

Publications

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Schleuter D. & Scheifhacken N. (in preparation): Predation effects of two competitive fish species Eurasian perch and ruffe on littoral benthic communities: the influence of study site and competition.

Scheifhacken N., Klahold P., Stoll S. & Fischer P. (in preparation): Predator prey interaction between juvenile cyprinids and the benthic community in the littoral zone of a large pre-alpine lake.

Scheifhacken N. & Rothhaupt K.-O. (in preparation): Colonisation patterns of macro-invertebrates at three differently exposed lake sites.

Scheifhacken N., Fiek C. & Rothhaupt K.-O. (in preparation): Linking spatial and temporal patterns of macroinvertebrates to underlying abiotic constraints in lake littorals: water level fluctuation *vs*. wave exposure.

Scheifhacken N. & Rothhaupt K.-O. (in preparation): Comparison of experimental and natural severe disturbances in lake littorals and their implications for the benthic community.

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