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PRIMARY RESEARCH PAPER

Alien molluscs affect the composition and diversity of native macroinvertebrates in a sandy flat of Lake Neuchâtel, Switzerland

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Abstract The spread of alien molluscs is a serious threat to native biodiversity in fresh waters. Alien freshwater molluscs may deplete the resources of native species and alter the physical structure of the habitat through their shell mass. These changes might have both positive and negative effects on native community members. We investigated the native macroinvertebrate community in relation to the densities of four alien mollusc species (*Corbicula fluminea*, *Dreissena polymorpha*, *Potamopyrgus antipodarum* and *Lithoglyphus naticoides*) in a sandy flat of Lake Neuchâtel, Switzerland. The habitat examined was dominated by these alien mollusc species. The abundance of the alien molluscs did not directly impact the native community assembly. However, *C. fluminea* and *D. polymorpha* influenced the composition and diversity of native macroinvertebrates by transforming the sandy substratum into a partly hard substratum habitat. Substantial differences in community composition between shallow (<3.5 m) and (≥5 m) deep sites were recorded. At shallow sites, the abundance of *D. polymorpha* was significantly reduced as a result of depth-selective feeding of ducks. A controlled shell decay study revealed that shells of alien molluscs (*C. fluminea*, *D. polymorpha*) persist for a longer period in the sediment than those of native molluscs. Consequently, shells of alien molluscs have a long-lasting impact by modifying the sandy habitat. This form of ecosystem engineering favours the occurrence of several native taxa, but is disadvantageous for other taxa with specific habitat requirements, and thus can be regarded as an indirect impact of competition.

Keywords Alien species · Lake littoral · Macroinvertebrates · *Corbicula fluminea* · *Dreissena polymorpha* · Ecosystem engineer · SCUBA-diving

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Introduction

Invasive species often reduce the local biodiversity and probably will influence the global biodiversity in the future (Sala et al., 2000; Nentwig, 2007). Interactions between invasive and native species, including competition, predation and transmission of diseases and parasites can change natural communities (Mooney et al., 2005). Invasive species may also function as ecosystem engineers by altering abiotic and/or biotic factors of habitats or by creating novel habitats, and

thereby facilitating native species (Jones et al., 1997; Gutierrez et al., 2003).

Freshwaters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems (Dudgeon et al., 2006). Besides of pollution, destruction or degradation of habitat and flow modification, the invasion of non-native species is a major threat to native freshwater biodiversity (Strayer, 1999). One of the most important groups of freshwater invaders includes molluscs that suspension-feed on phytoplankton and seston, graze on periphyton, or browse on vascular plants (Strayer, 2010). Furthermore, invasive molluscs may act as ecological engineers by creating large amounts of shells (Gutierrez et al., 2003; Sousa et al., 2009). This shell material can persist for a long time after the molluscs die, providing habitat for other organisms, especially in soft sediments (Strayer & Malcom, 2007), and playing an important part in cycling of CO_2 and Ca^{2+} (e.g. Green, 1980; Chauvaud et al., 2003).

In the past decades, European inland waters have been increasingly affected by the colonisation of non-native molluscs, causing significant changes in aquatic communities (Strzelec, 2000; Mörtl & Rothhaupt, 2003; Baur & Schmidlin, 2007; Gergs & Rothhaupt, 2008; Sousa et al., 2008a). For example, the invasion of the zebra mussel, *Dreissena polymorpha* (Pallas 1771), influenced the abundance of sediment bacteria, caused both benthic algal blooms and declines in native unionid mussel and fish populations as well as changes in physical and chemical attributes that define the habitat for all resident species (Higgins & Vander Zanden, 2010).

Populations with high densities of the Asian clam *Corbicula fluminea* (O. F. Müller 1774) caused modest to dramatic declines in phytoplankton and seston (Leff et al., 1990; Phelps, 1994). Strayer (1999) assumed that large numbers of unionid sperm, glochidia, and newly metamorphosed juveniles might be ingested in dense populations of *C. fluminea*. In contrast to the zebra mussel, *C. fluminea* actively disturbs the sediment by pedal feeding. Thus, high densities of *C. fluminea* may reduce both habitat quality and food supply for native macroinvertebrates (Hakenkamp & Palmer, 1999). On the other hand, a short-term field experiment in the Lake Constance demonstrated that valves of *C. fluminea* enhanced the density of the mayfly *Caenis* spp. on soft substrate and that living clams hindered juvenile *C. fluminea* with a chemical cue from settling in close proximity to reduce intraspecific competition (Werner & Rothhaupt, 2007, 2008). Furthermore, a laboratory experiment showed that valves of *C. fluminea* increased the abundance of benthic invertebrates in poorly structured sediment (Werner & Rothhaupt, 2008). However, there are still huge gaps in our understanding of how *C. fluminea* impacts native benthic invertebrate communities in natural freshwater bodies.

Corbicula fluminea is nowadays one of the most abundant mollusc species in many European lowland lakes and rivers, often co-occurring with other alien species and interacting with the native community (Schmidlin & Baur, 2007; Sousa et al., 2008b; Werner & Rothhaupt, 2008; Müller & Baur, 2011). The clam colonised lake Neuchâtel, Switzerland, in 2003 (P. Stucki, personal communication). In this lake, three other alien molluscs occur: *D. polymorpha* (first recorded in 1976; Pedroli, 1978), and the snails *Potamopyrgus antipodarum* (J. E. Gray 1843; first recorded in 1978; Crozet et al., 1980) and *Lithoglyphus naticoides* (C. Pfeiffer 1828; first recorded in 1998; CSCF, 2010).

We examined the native benthic macroinvertebrate community in relation to the densities of these four alien molluscs in a sand flat of the littoral zone of Lake Neuchâtel with the assumption that alien molluscs influence native communities. We also conducted a field experiment to assess the decay rate of empty shells of different mollusc species. In particular, we addressed the following questions:

(1) How frequently and in which density do the alien molluscs *C. fluminea*, *D. polymorpha*, *P. antipodarum*, and *L. naticoides* occur in the sandy flat in Lake Neuchâtel?
(2) Do alien species influence the community assembly of native benthic macroinvertebrates?
(3) Do the four alien molluscs act as ecosystem engineers by providing shells with a low decaying rate as additional hard substratum and thus facilitate other macroinvertebrate taxa?

Materials and methods

Study area

Lake Neuchâtel (surface area: 217.9 km^2, mean depth: 64.2 m) is a pre-alpine, calcareous, mesotrophic lake

situated at the foot of the Jura Mountains in Western Switzerland. Its drainage area covers ~2,670 km^2. The littoral zone covers 26.5% of the area of Lake Neuchâtel and sand flats constitute a significant part of this zone (Sollberger, 1974). Both the field survey and the shell decay assessment were conducted in a shallow sandy section of the littoral zone at the south-eastern shore of Lake Neuchâtel near the port of Portalban (46.922 N, 6.949 E). The study area measured about 600 m × 500 m and is situated in close proximity of a bird and wetland reserve of national importance.

Field survey

Using SCUBA-diving, benthic macroinvertebrates were collected from the sandy substratum in an area of about 0.3 km^2 on five occasions. On each occasion, 10–14 sampling sites, arranged at distances of 30–50 m along 600-m long transect lines running perpendicular to the shore line, were considered. The survey was conducted on the following dates: 20 May 2007 (2 transects, each with 12 sampling sites), 21 October 2007 (2 transects, each with 10 sampling sites), 24 May 2008 (1 transect with 14 sampling sites), 18 October 2008 (1 transect with 14 sampling sites), and 16 May 2009 (1 transect with 13 sampling sites). For each of the 85 sampling sites, we measured shore distance, water depth, cover of submerged vegetation (a semiquantitative estimate), type of sediment and organic matter of the sediment and determined the geographical coordinates using GPS (Garmin Geko 201). However, because of the strong inter-correlation of environmental variables (shore distance and water depth) and of the low variation in the remaining variables, we used only water depth in the data analyses. The water depth ranged from 0.73 to 22.14 m ($N = 85$).

At each of the 85 sites, macroinvertebrates were collected using a circular metallic frame (radius: 11 cm, 7 cm high). The frame was pressed by hand into the sandy substratum and the topmost 5 cm of the bottom material was transferred into a bag with a mesh size of 2.0 mm using a small shovel. Three of these subsamples were collected at each sampling site. Macroinvertebrates were labelled, preserved in 75% ethanol and then returned to the laboratory for examination.

Macroinvertebrates were later identified to the lowest taxonomic level possible using the keys of Schwab (1995), Grabow (2000), and Tachet et al. (2006) for various invertebrate groups, Glöer & Meier-Brook (1998) and Glöer (2002) for Mollusca, Neubert & Nesemann (1999) for Hirudinae, Lechthaler & Stockinger (2005) for Trichoptera and Studemann et al. (1992) for Ephemeroptera.

Assessment of shell decay rate

We measured the relative decay rate of shells [(initial shell weight − final shell weight)/initial shell weight] over 1 year in five mollusc species co-existing in Lake Neuchâtel: two native gastropods (*Bithynia tentaculata* [Linnaeus 1758], *Valvata piscinalis* [O. F. Müller 1774]), one alien gastropod (*P. antipodarum*) and two alien bivalves (*C. fluminea*, *D. polymorpha*). We used shells from living animals sampled in the field survey near Portalban. The animals were killed in 75% ethanol. The soft bodies were removed from the shells and the shells were air dried. We constructed water-resistant "litter" bags measuring 8 cm × 9 cm using window screening with a mesh size of 2.0 mm. We placed either 7 shells of *B. tentaculata* (mean shell height: 9.2 mm), 7 shells of *V. piscinalis* (4.1 mm), 10 shells of *P. antipodarum* (4.2 mm), 10 valves of *C. fluminea* (mean valve length: 18.0 mm) or 10 valves of *D. polymorpha* (15.4 mm) in single bags. The total weight of shells or valves in each bag was measured to the nearest 0.01 mg before the bag was sealed. For each species 20 bags were used (in total 100 bags). Bags were fixed with a rope and metallic sticks on the sandy substratum (>30 cm apart from each other) at water depths of 1 m (20 bags), 6 m (40 bags) and 8 m (40 bags). We placed bags into the field on 24 May 2008 and retrieved them on 16 May 2009. We carefully removed the shells from the bags and cleaned them. Air-dried shells were reweighed. In total, we recovered 89 of the 100 bags initially exposed.

The water of Lake Neuchâtel was supersaturated with $CaCO_3$ in 2007–2009 (total hardness $CaCO_3$: 2.78–144 mg l^{-1}; Ca^{2+}: 2.0–56.2 mg l^{-1}; pH: 8.0–8.5; SCPE Neuchâtel, Service de la protection de l'environnement; www.les3lacs.ch; 2007–2009).

Statistical analyses

Macroinvertebrates from the three subsamples at each sampling site were pooled resulting in 85 samples for

data analyses. Raw data (number of individuals recorded for each species) from each sample were used in all analyses. Altogether 23,342 individuals were assigned to a species or a higher taxonomic group. On all five sampling occasions molluscs were the most abundant group (74.8–88.5% of the individuals collected, grand mean = 82.4%). We therefore examined seasonal differences (May vs. October) in the abundance of molluscs and the remaining macroinvertebrate taxa. Because the proportion of molluscs and that of the remaining taxa did not show any significant differences between the samples collected in May and October ($\chi^2 = 2.47$, df = 1, $P = 0.12$), we pooled the samples from different sampling seasons for community analyses. The frequency distribution of sampling sites in relation to water depth was bimodal. Consequently, based on water depth, sampling sites were assigned to two groups: shallow sites with a depth < 3.5 m [$N = 71$ sites (83.5%), mean depth 1.90 m, range 0.73–3.34] and deep sites with a depth ≥ 5 m [$N = 14$ sites (16.5%), mean depth 8.94 m, range 5.00–22.14 m].

Analysis of similarities (ANOSIM; Clarke, 1993) was used to test community-based separation of samples collected at shallow and deep sites. ANOSIM is a non-parametric multivariate analysis that compares the mean of the ranked similarities within and between water depth groups based on R values. R ranges from -1 to $+1$. An R value of 1 indicates that the most similar sites belong to the same depth group. $R = 0$ indicates that sites with high and low similarities occur in equal frequencies in both depth groups, whereas an R value of -1 shows that the most similar sites belong to different depth groups. ANOSIM was run using the Bray-Curtis dissimilarity index (Podani, 2000) with 999 permutations.

Indicator species analysis (INDVAL; Dufrene & Legendre, 1997) was run to identify characteristic taxa of shallow and deep sites, respectively. Analysis of variance using distance matrices (called ADONIS in *R*), referred to also as "permutation MANOVA", "non-parametric MANOVA" (Anderson, 2001; McArdle & Anderson, 2001) or "multivariate regression analysis of distance matrices" (Zapala & Schork, 2006), was used to test how alien mollusc taxa influence community similarity of native taxa [for further details see Zapala & Schork (2006) or Oksanen et al. (2009)]. For the distance matrices, we used the Bray-Curtis dissimilarity index with 999 permutations.

Generalised linear models (GLM) with Poisson distribution were used to test how the four most abundant alien taxa (see result: *D. polymorpha*, *C. fluminea*, *P. antipodarum* and *L. naticoides*) influence the numbers of native taxa, native individuals, protected taxa, protected individuals, taxa with sand preference, individuals with sand preference, native taxa with hard bottom preference and native individuals with hard bottom preference. The application of Poisson distribution was necessary because of the many zeros in the response variables. The abundances of the four alien taxa were $\log(x + 1)$ transformed to decrease the impact of extreme values. Overdispersion was tested following Wetherill and Brown (1991). If abundance data were not overdispersed then the final model was selected based on Akaike's Information Criterion (AIC). If data structure showed overdispersion, we fitted quasi-poisson models and model selection was performed manually. We used each alien mollusc species as an independent variable in model building. To get reliable mathematical models, we ran GLMs for variables with data from at least 10 species occurrences. In cases with fewer occurrences, the impact of alien molluscs on native protected species and sand-preferring taxa at deep sites was not tested.

To take into account size differences among alien mollusc species and potential effects of empty mollusc shells on the native community, we expressed the abundance of the four alien molluscs in the GLMs in four different ways: (A) numbers of living individuals, (B) shell weight of living individuals, (C) shell weight of living and empty (dead) individuals, and (D) shell weight of empty (dead) individuals.

To estimate the shell mass at each sampling site, we used the mean shell weight of each species measured in the shell decay study (see below), multiplied by the corresponding numbers of individuals per m^2. *L. naticoides* was not considered in the shell decay study. We therefore calculated its shell weight following the protocol used in the shell decay study.

The relative shell decay rate was calculated based on the pre- and post-experimental weight of shells in each bag. To compare shell decay rates, a nested linear model was fitted to the data with the relative shell decay rate as response variable and with type of origin (native vs. alien) and taxon (*B. tentaculata*, *V. piscinalis, C. fluminea*, *D. polymorpha* and *P. antipodarum*, nested with the type of origin) as

categorical predictors next to water depth and individual shell weight as continuous predictors. We started with the full model and simplified it based on AIC. For all analyses, we used the R statistical computing environment (R Development Core Team, 2009). ANOSIM and analysis of variance using distance matrices (=ADONIS) were calculated using the *vegan* package (Oksanen et al., 2009), for testing overdispersion the *qcc* package (Scrucca 2004), and for INDVAL (Dufrene & Legendre, 1997) the *labdsv* package was used (Roberts, 2010).

Null models are frequently used to elucidate assembly rules or a set of mechanisms (e.g. competition) that lead to non-random patterns in multispecies assemblages (Gotelli & Graves, 1996; Ulrich, 2004). Null models are adequate tools for detecting biotic interactions based on distributional data of taxa. However, these models are based on the assumptions that there are no differences among habitat characteristics, no influence of the biogeographical and evolutionary history of the samples, and that only biotic interactions and chance variation are responsible for the community patterns observed (Gotelli & Graves, 1996; Ulrich, 2004). In this study, most of these requirements were fulfilled because sampling was restricted to a relatively homogenous (sandy) habitat limited in space (0.3 km^2) and time (sampling period < 2 years). Tests of null models were originally developed for presence/absence data in studying species communities (Gotelli, 2000). Recent advances allow an examination of null models for data sets with species abundances (Ulrich & Gotelli, 2010). We used the standardised number of "abundance checkerboard" (CA_{ST}) to identify possible competitive interactions between native taxa. CA_{ST} represents an abundance analogy of "checkerboard" distributions (Diamond, 1975), a distribution pattern where species pairs never co-occur together (Ulrich & Gotelli, 2007). CA_{ST} varies between 0 (indicates no competition) and 1 (indicates strong competition). To test whether a calculated CA_{ST} value comes from a chance event or reflects real competition, we compared the calculated CA_{ST} values with a null distribution using IT null model algorithm (Ulrich & Gotelli, 2010) based on 100 random assemblages. The IT algorithm reassigns all individuals randomly to matrix cells with probabilities proportional to the totals of observed row and column abundances until total abundances are reached for each row and column. The IT algorithm shows a low Type I error rate compared to other algorithms (Ulrich & Gotelli, 2010).

First, we run our null models for both shallow and deep sites separately. To elucidate the possible impact of the four alien species (*C. fluminea*, *D. polymorpha*, *L. naticoides* and *P. antipodarum*) within depth level, sampling sites were further divided into two groups: (1) sampling sites with low abundance of alien species (abundance of the alien species was less than the median of their total abundance at the depth level), and (2) sampling sites with high abundance of alien species (abundance of alien species was equal to or larger than the median of their total abundance). We compared the raw abundance checkerboard values and their relative positions compared to the generated null distributions. Null models were run using CoOccurrence software (Ulrich, 2006).

Results

Taxa richness and abundance

We found 45 taxa among the 17,929 individuals collected at shallow sites and 36 taxa among the 5,413 individuals at deep sites (Table 1). The alien bivalve *C. fluminea* was the only species occurring at all shallow (71) and deep (14) sampling sites. Further taxa with high frequencies of occurrence were *Pisidium* sp. (shallow sites: 95.8%; deep sites: 85.7%), *D. polymorpha* (93.0%; 100%), Oligochaeta (93.0%; 92.9%) and *P. antipodarum* (91.6%; 78.6%). ANOSIM analysis confirmed the separate handling of shallow and deep sites, because the communities at either depth were distinct ($R = 0.175$, $P = 0.012$). Analysis with only native taxa showed a similar separation by depth ($R = 0.162$, $P = 0.042$).

Indicator species analysis identified *Spongilla lacustris* (Linnaeus 1758) as the single indicator species for shallow sites (indicator value [IV] = 0.45, $P = 0.006$), whereas deep sites were characterised by 14 indicator taxa. The alien bivalve *D. polymorpha* had the highest indicator value (IV = 0.77, $P = 0.007$) at deep sites, followed by *V. piscinalis* (IV = 0.46, $P = 0.001$), *Asellus aquaticus* (Linnaeus 1758; IV = 0.43, $P = 0.001$) and *Gyraulus albus* (O. F. Müller 1774; IV = 0.41, $P = 0.001$).

The abundances of mollusc individuals in relation to all individuals sampled were almost identical at

Table 1 Frequency of occurrence of the identified macroinvertebrate taxa (number of sites), mean density (±standard error) and maximum density of individuals in shallow (<3.5 m) and deep (≥5 m) littoral sites near Portalban in Lake Neuchâtel

Group	Taxon	Shallow sites (<3.5 m; $N = 71$)			Deep sites (≥5 m; $N = 14$)			Type of origin[a]	Protection status[b]
		Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}	Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}		
Porifera	*Spongilla lacustris***	32 (45.1)	na	na	0 (0.0)	0.0 (0.0)	0.0	N	n
Hydrozoa	*Hydra viridissiama*	7 (9.9)	10.0 (5.5)	343.2	5 (35.7)	42.1 (15.5)	528.0	N	n
Turbellaria	Turbellaria indet.**	1 (1.4)	0.1 (0.1)	8.8	2 (14.3)	18.2 (7.3)	246.4	N	n
	Dugesia sp. (cf. *D. tigrina*)**	0 (0.0)	0.0 (0.0)	0.0	2 (14.3)	3.1 (1.1)	35.2	A	n
Oligochaeta	Oligochaeta spp.	66 (93.0)	215.2 (25.3)	968.0	13 (92.9)	226.9 (30.5)	941.6	N	n
	Branchiura sowerbyi	11 (15.5)	1.9 (0.5)	17.6	1 (7.1)	0.6 (0.3)	8.8	A	n
Hirudinae	*Erpobdella* sp.**	23 (32.4)	12.2 (2.8)	123.2	6 (42.9)	8.8 (1.6)	52.8	N	n
	*Alboglossiphonia heteroclita***	7 (9.9)	3.2 (1.6)	105.6	6 (42.9)	8.2 (1.4)	35.2	N	n
	*Glossiphonia complanata***	2 (2.8)	0.3 (0.2)	8.8	4 (28.6)	5.7 (1.4)	44.0	N	n
	Helobdella stagnalis	29 (40.9)	11.8 (2.6)	96.8	9 (64.3)	17.6 (2.6)	88.0	N	n
Gastropoda	*Bithynia tentaculata***	37 (52.1)	25.5 (7.9)	554.4	10 (71.4)	30.2 (4.4)	149.6	N	n
	Lithoglyphus naticoides	44 (62.0)	19.0 (3.6)	184.8	7 (50.0)	13.8 (2.2)	52.8	A	n
	Potamopyrgus antipodarum	65 (91.6)	470.0 (74.5)	3264.8	11 (78.6)	257.1 (28.0)	748.0	A	n
	Valvata piscinalis	3 (4.2)	1.5 (1.0)	70.4	7 (50.0)	17.6 (2.7)	79.2	N	n
	Radix auricularia	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Radix balthica	3 (4.2)	0.6 (0.3)	17.6	3 (21.4)	1.9 (0.4)	8.8	N	n
	Lymnaea stagnalis	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Gyraulus albus	4 (5.6)	3.4 (2.6)	193.6	7 (50.0)	15.7 (3.4)	114.4	N	n
	Gyraulus crista	1 (1.4)	0.1 (0.1)	8.8	3 (21.4)	3.1 (0.8)	26.4	N	3
	Planorbis carinatus	2 (2.8)	0.5 (0.4)	26.4	0 (0.0)	0.0 (0.0)	0.0	N	3

Table 1 continued

Group	Taxon	Shallow sites (<3.5 m; $N = 71$)			Deep sites (≥5 m; $N = 14$)			Type of origin[a]	Protection status[b]
		Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}	Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}		
Bivalvia	*Sphaerium corneum*	0 (0.0)	0.0 (0.0)	0.0	1 (7.1)	0.6 (0.3)	8.8	N	n
	Pisidium spp.	68 (95.8)	232.8 (31.0)	1460.8	12 (85.7)	143.9 (18.3)	413.6	N	n
	*Corbicula fluminea**	71 (100.0)	515.6 (65.9)	3599.2	14 (100.0)	404.8 (76.3)	2657.6	A	n
	*Dreissena polymorpha***	66 (93.0)	586.0 (99.7)	5368.0	14 (100.0)	1963.0 (192.4)	5473.6	A	n
Bryozoa	*Cristatella mucedo*	2 (2.8)	0.3 (0.16)	8.8	5 (35.7)	52.2 (14.0)	396.0	N	n
Crustacea	*Dikerogammarus villosus***	16 (22.5)	2.4 (0.5)	17.6	5 (35.7)	11.9 (2.2)	61.6	A	n
	*Gammarus pulex***	1 (1.4)	0.1 (0.1)	8.8	2 (14.3)	1.3 (0.4)	8.8	N	n
	Asellus aquaticus	0 (0.0)	0.0 (0.0)	0.0	6 (42.9)	34.6 (8.9)	299.2	N	n
Coleoptera	*Donacia* sp.	4 (5.6)	1.2 (0.8)	61.6	0 (0.0)	0.0 (0.0)	0.0	N	n
Diptera	Chironominae**	50 (70.4)	44.0 (7.7)	308.0	12 (85.7)	65.4 (6.4)	184.8	N	n
	Orthocladiinae**	8 (11.3)	1.0 (0.3)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Tanypodinae	3 (4.2)	0.5 (0.3)	17.6	6 (42.9)	6.9 (1.5)	52.8	N	n
	Ceratopogonidae	8 (11.3)	1.5 (0.6)	35.2	2 (14.3)	2.5 (0.7)	17.6	N	n
Ephemeroptera	*Centroptilum luteolum*	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	4
	Cloeon dipterum	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
	Caenis macrura	9 (12.7)	3.8 (1.9)	140.8	1 (7.1)	1.3 (0.5)	17.6	N	n
	Caenis horaria	12 (16.9)	6.8 (3.9)	290.4	3 (21.4)	2.5 (0.6)	17.6	N	n
	Caenis luctuosa	7 (9.9)	2.6 (1.3)	96.8	1 (7.1)	0.6 (0.3)	8.8	N	n
	*Ephemera vulgata**	2 (2.8)	0.3 (0.2)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	3
	*Ephemera lineata**	15 (21.1)	5.1 (1.7)	114.4	1 (7.1)	0.6 (0.3)	8.8	N	1
	*Ephemera danica**	13 (18.3)	4.1 (1.3)	61.6	0 (0.0)	0.0 (0.0)	0.0	N	4

Table 1 continued

Group	Taxon	Shallow sites (<3.5 m; $N = 71$)			Deep sites (≥5 m; $N = 14$)			Type of origin[a]	Protection status[b]
		Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}	Frequency of occurrence (%)	Mean density ind. m^{-2} (±se)	Maximum density ind. m^{-2}		
Lepidoptera	*Acentria ephemerella*	4 (5.6)	0.7 (0.4)	17.6	0 (0.0)	0.0 (0.0)	0.0	N	n
Odonata	*Ischnura* sp.	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n
Trichoptera	*Athripsodes cinereus*	48 (67.6)	22.8 (3.1)	140.8	7 (50.0)	21.4 (4.1)	132.0	N	n
	Ceraclea dissimilis	0 (0.0)	0.0 (0.0)	0.0	2 (14.3)	1.3 (0.4)	8.8	N	n
	Mystacides azureus	13 (18.3)	2.6 (0.8)	52.8	3 (21.4)	10.1 (2.7)	88.0	N	n
	Oecetis lacustris	14 (19.7)	2.5 (0.6)	26.4	1 (7.1)	2.5 (1.0)	35.2	N	n
	*Molanna albicans**	17 (23.9)	5.5 (1.4)	52.8	3 (21.4)	4.4 (1.3)	44.0	N	n
	Agraylea multipunctata	1 (1.4)	0.1 (0.1)	8.8	0 (0.0)	0.0 (0.0)	0.0	N	n

The origin (native or alien) and protection status are also indicated

na not assessed

* High preference for sandy microhabitats (Tachet et al., 2006)

** High preference for hard microhabitats (Tachet et al., 2006)

[a] Type of origin: *N* native, *A* alien

[b] Duelli (1994): *n* not on the red list, *1* prone to extinction (=endangered based on IUCN categorisation), *3* endangered (=vulnerable based on IUCN categorisation), *4* potentially endangered (=rare based on IUCN categorisation)

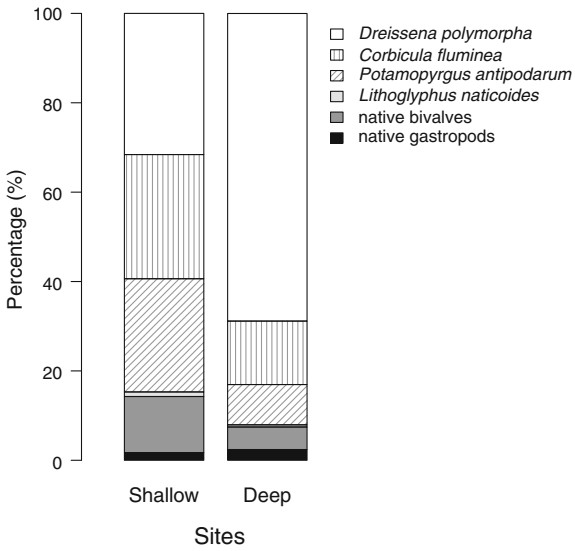

Fig. 1 Relative distribution of mollusc individuals (%) among alien and native taxonomic groups at shallow (<3.5 m, $N = 14{,}969$ individuals) and deep (≥5 m, $N = 4{,}437$) sites in Lake Neuchâtel

shallow and deep sites (83.5 vs. 83.8%). However, the composition of gastropods and bivalves was different: gastropod individuals accounted for 28.1% of all molluscs at shallow sites, but only for 11.9% at deep sites ($\chi^2 = 494.2$, df $= 1$, $P < 0.001$). This difference was mainly a result of depth-dependent differences in the abundance of *P. antipodarum*, *D. polymorpha, C. fluminea* and *Pisidum* sp. (Fig. 1). Among native gastropods, only *B. tentaculata* reached more than 1% of the total mollusc abundance (shallow sites: 1.4%, deep sites: 1.1%). The percentage of alien mollusc individuals was larger at deep sites (92.5%) than at the shallow sites (85.7%, $\chi^2 = 144.6$, df $= 1$, $P < 0.001$).

The overall density of all macrobenthic taxa averaged 2,222 individuals m^{-2} at shallow sites and 3,402 individuals m^{-2} at deep sites. Bivalves contributed 1,334 and gastropods 521 individuals m^{-2} at shallow sites. At deep sites bivalves showed an even higher abundance (2,512 ind. m^{-2}; gastropods: 339 ind. m^{-2}).

The bivalve *D. polymorpha* showed the highest density of individuals of the taxa collected. The median density of *D. polymorpha* was higher at deep sites than at shallow sites (290 individuals m^{-2} versus 1,835 individuals m^{-2}, two-sided two-sample Wilcoxon test: $W = 793.5$, $P < 0.001$). The maximum density of *D. polymorpha*, however, did not differ between shallow and deep sites (5,368 vs. 5,474 individuals m^{-2}). Similarly, the median density of *C. fluminea, P. antipodarum* and *L. naticoides* did not differ between shallow and deep sites (*C. fluminea*: 352 vs. 189 ind. m^{-2}: $W = 654$, $P = 0.064$; *P. antipodarum*: 150 versus 194 ind. m^{-2}: $W = 536.5$, $P = 0.644$; *L. naticoides*: 8.8 vs. 0.5, $W = 550$, $P = 0.518$).

Six species found at shallow sites are on the red list of Switzerland (*Gyraulus crista* [Linnaeus 1758], *Planorbis carinatus* [O. F. Müller], *Centroptilum luteolum* [Müller 1776], *Ephemera vulgata* [Linnaeus 1758], *Ephemera lineata* [Eaton 1870] and *Ephemera danica* [Müller 1764]; Duelli, 1994). Only two of them were found at deep sites (*G. crista, E. lineata*; Table 1).

Impact of alien molluscs on community structure

Six of the taxa recorded at the shallow sites were alien (*Branchiura sowerbyi* [Beddard 1892], *L. naticoides*, *P. antipodarum*, *C. fluminea*, *D. polymorpha* and *Dikerogammarus villosus* [Sowinsky 1894]). In addition to these six species a further alien species (*Dugesia tigrina* [Girard 1850]) was found at deep sites.

Analysis of variance using distance matrices (ADONIS) revealed that the changes in the abundance of the four alien species explain 20.0% of the variation of the native community at shallow sites and 50.8% of that at deep sites. At shallow sites, *C. fluminea* and *L. naticoides* were the best explanatory variables, whereas at deep sites the abundance of *D. polymorpha* and *L. naticoides* explained most (Table 2).

Generalised linear models identifying the effects of alien molluscs indicated that the number of aliens had a positive impact on most of the response variables at shallow sites (Table 3). Exceptions were a negative influence of *L. naticoides* on the number of native individuals with hard bottom preference at shallow sites, and of *C. fluminea* on the numbers of invertebrate individuals with sand preference and on the number of protected individuals. Similar results were obtained at shallow sites when the abundance of the few alien species was expressed by the weight of living animals (approach B; Table 3). Considering shell weight of both living and dead animals as independent factor, GLMs revealed similar but less pronounced effects at shallow sites, but *L. naticoides* had a negative impact on the numbers of native taxa and *P. potamopyrgus* negatively influenced the

Table 2 Summary of the analyses of variance using distance matrices testing the effect of alien taxa on the native community similarity (ADONIS)

Alien taxa	Shallow sites						Deep sites					
	Df	SS	MS	F	R^2	*P*	Df	SS	MS	F	R^2	*P*
Lithoglyphus naticoides	1	0.94	0.94	5.26	0.064	**0.001**	1	0.53	0.53	3.08	0.168	**0.012**
Potamopyrgus antipodarum	1	0.40	0.40	2.25	0.027	**0.031**	1	0.31	0.31	1.80	0.099	0.086
Corbicula fluminea	1	0.90	0.90	4.98	0.060	**0.001**	1	0.11	0.11	0.62	0.034	0.724
Dreissena polymorpha	1	0.73	0.73	4.05	0.049	**0.002**	1	0.66	0.66	3.80	0.208	**0.006**
Residuals	66	11.85	0.18		0.800		9	1.56	0.17		0.492	
Total	70	14.82			1		13	3.18			1	

Significant results are in bold

number of individuals with hard bottom preference (approach C, Table 3). Using the weight of empty shells as predictor variable (approach D), *C. fluminea* kept the positive influence on most native groups but lost the negative influence on the native protected and sand-preferring individuals while empty shells of *P. antipodarum* enhanced the number of native taxa with sand preference.

Most remarkably is the positive influence of *D. polymorpha* on the number of native invertebrate individuals, and on both the numbers of native taxa and taxa with hard bottom preference at deep sites in the first three approaches. In the fourth model (approach D), only *P. antipodarum* had a positive impact on both the number of native individuals and the number of hard bottom preferring taxa (Table 3).

Considering the null model of random patterns of species assemblage, CA_{ST} values of 0.015 were obtained for shallow sites and 0.035 for deep sites. At shallow sites, the expected values were 0.015 (lower and the upper limits of the 95% confidence intervals of the null assemblages were 0.014 and 0.017) and 0.021 (0.015 and 0.026) for deep sites. This indicates that the impact of competition structuring the benthic macroinvertebrate community is moderate and differs among depths. The comparison with the null distributions showed that the macroinvertebrate community at shallow sites was randomly organised, whereas the community at deep sites may be partly structured by competitive interactions. High abundance of each alien species increased only moderately the competition in the community as indicated by the standardised number of abundance checkerboard (Fig. 2).

Total shell mass and shell decay rates

The total shell mass of living and dead individuals of the six most abundant mollusc species amounted to 700.9 g m^{-2} at shallow sites and 1,275.0 g m^{-2} at deep sites in Lake Neuchâtel (Table 4). The four alien species (*C. fluminea*, *D. polymorpha*, *P. antipodarum*, *L. naticoides*) contributed to 98 and 97% of the total shell mass at shallow and deep sites, respectively. Considering single species, *C. fluminea* contributed to 69 and 37% of the total shell mass at shallow and deep sites. The corresponding figures for *D. polymorpha* were 27 and 59%. The shells of these two invasive clams constituted more than 95% of the organic hard substrate on the sandy bottom of the lake and thus changed the habitat characteristics for benthic organisms.

Considering the shell decay study, model selection removed the factors taxon (within origin) and water depth, and left the factors origin (native or alien) and shell weight in the minimal adequate model (Table 5). The analysis revealed that shells of the studied alien species have a significantly slower relative decay rate than those of native species (mean loss in 1 year: *C. fluminea* 2.3%, *D. polymorpha* 10.0%, *P. antipodarum* 10.9%, *B. tentaculata* 20.0%, and *V. piscinalis* 21.9%; Table 5, Fig. 3) and that shell weight has a marginally negative effect on the relative decay rate (Table 5; Fig. 4). Thus, the bigger and heavier alien molluscs *C. fluminea* and *D. polymorpha* lost less shell material within 1 year than smaller native molluscs (Fig. 4).

Table 3 Minimal adequate models showing the influence of the alien *D. polymorpha*, *C. fluminea*, *P. antipodarum*, and *L. naticoides* on the numbers of native taxa, native individuals, protected taxa, protected individuals, taxa with sand preference, individuals with sand preference, native taxa with hard bottom preference and native individuals with hard bottom preference

Dependent variable	Factor	Shallow sites						Deep sites					
		A			B	C	D	A			B	C	D
		Estimate	se	*P*				Estimate	se	*P*			
N. of native taxa	*Corbicula fluminea*	**0.100**	**0.040**	**0.015**	+	+	+						
	Dreissena polymorpha	**0.211**	**0.026**	**<0.001**	+	+		**0.250**	**0.077**	**0.001**	+	NS	NS
	Potamopyrgus antipodarum											NS	+
	Lithoglyphus naticoides					−							
N. of native individuals	*Corbicula fluminea*	**0.345**	**0.086**	**<0.001**	+	+	+						
	Dreissena polymorpha	**0.288**	**0.059**	**<0.001**	+	+		**0.411**	**0.645**	**0.003**	+	+	
N. of protected taxa[a]	*Corbicula fluminea*	−0.274	0.181	0.130	NS	NS		na					
	Dreissena polymorpha	**0.253**	**0.114**	**0.027**	NS	+		na					
	Lithoglyphus naticoides				NS			na					
N. of protected individuals[a]	*Corbicula fluminea*	**−1.074**	**0.287**	**<0.001**	−	−		na					
	Dreissena polymorpha	**0.277**	**0.138**	**<0.001**	+	+		na					
	Potamopyrgus antipodarum	**0.405**	**0.153**	**0.010**				na					
	Lithoglyphus naticoides				+			na					
N. of taxa with sand preference[b]	*Dreissena polymorpha*	0.191	0.108	0.076	+	NS		na					
	Potamopyrgus antipodarum						+	na					
	Lithoglyphus naticoides	**0.405**	**0.177**	**0.022**	+	+		na					
N. of individuals with sand preference[b]	*Corbicula fluminea*	**−0.632**	**0.130**	**<0.001**	−	−		na					
	Dreissena polymorpha	**0.278**	**0.079**	**<0.001**	+	+		na					
	Potamopyrgus antipodarum	**0.311**	**0.087**	**<0.001**	+			na					
	Lithoglyphus naticoides	**0.439**	**0.130**	**<0.001**	+	+		na					
N. of native taxa with hard bottom preference[c]	*Corbicula fluminea*	**0.145**	**0.058**	**0.016**	+	+	+						
	Dreissena polymorpha	**0.188**	**0.038**	**<0.001**	+	+		**0.386**	**0.156**	**0.013**	+	+	

Table 3 continued

Dependent variable	Factor	Shallow sites						Deep sites					
		A			B	C	D	A			B	C	D
		Estimate	se	*P*				Estimate	se	*P*			
	Potamopyrgus antipodarum												+
N. of native ind. with hard bottom preference[c]	*Corbicula fluminea*	**0.531**	**0.126**	**<0.001**	+	+	+						
	Dreissena polymorpha	**0.474**	**0.081**	**<0.001**	+	+							
	Potamopyrgus antipodarum					−	−						
	Lithoglyphus naticoides	**−0.456**	**0.179**	**0.013**	−								

The abundance of alien molluscs was expressed in four different ways (indicated by capitals): A, number of living individuals; B, shell weight of living individuals; C, shell weight of living and dead individuals (empty shells) and, D, shell weight of dead individuals (empty shells). Effect size (Estimate), standard error (se) and significance value (*P*) are presented for approach A (significant effects are in bold). For the approaches B–D symbols indicate significant positive (+), negative (−) or non-significant (NS) effects. At deep sites GLMs were not run for protected and sand-preferring taxa because these groups consisted of less than 10 individuals (see "Materials and methods" section). Dependent variables which did not enter the model are not listed

[a] Protected taxa following Duelli (1994)

[b] Sand preference following Tachet et al. (2006), taxa with a preference value of 5 were considered

[c] Hard bottom preference following Tachet et al. (2006), taxa with preference values of 4 and 5 were considered

Discussion

This study shows that the benthic macroinvertebrate community in a sandy flat of the littoral zone of Lake Neuchâtel is dominated by a few alien mollusc species (*C. fluminea, D. polymorpha, P. antipodarum*). Our analyses suggest that the composition and diversity of native macroinvertebrates are influenced by the abundances of alien molluscs which transform sandy substratum into a partly hard substratum habitat. However, patterns strongly depend on the water depth at the sampling sites. Null-model analysis testing the impact of alien molluscs on community assembly suggests that shallow sites are randomly organised, whereas deep sites are influenced by competitive interactions among native community members. Our shell decay study also shows that valves and shells of the studied alien species persist for a longer period in the sediment than those of native species, and consequently have a longer lasting impact through habitat modification than those of native mollusc species. These findings indicate that alien mollusc species have a profound impact on native macroinvertebrates by changing habitat characteristics of the sandy bottom.

Nowadays, numerous freshwater habitats are dominated by alien taxa (Ricciardi & MacIsaac, 2000; Tittizer et al., 2000; Wirth et al., 2010), and in many cases by alien molluscs (Karatayev et al., 2003; Lewin & Smolinski, 2006; Sylvester et al., 2007; Nalepa et al., 2010). Similarly, Lake Neuchâtel has recently been invaded by the alien molluscs *D. polymorpha*, *C. fluminea*, *P. antipodarum* and *L. naticoides*. We found substantial differences in the composition of benthic macroinvertebrates between shallow (<3.5 m) and deep (≥5 m) sites of a sandy flat. The depth-related difference in the density of alien species was most pronounced in *D. polymorpha*, which could be the result of the water depth depending feeding behaviour of diving ducks (Werner et al., 2005; Keller & Burkhardt, 2010). Diving ducks have to manage their feeding costs and energy budget (de Leeuw et al., 1999). Consequently, they prey first upon the easily reachable mussels (*D. polymorpha*) at shallow sites before they exploit deeper sites. This foraging pattern fits our observations that the density of *D. polymorpha* was lower at shallow than at deep sites and that mainly small (1-year-old and younger) *D. polymorpha* individuals occurred at shallow sites, whereas at deep sites

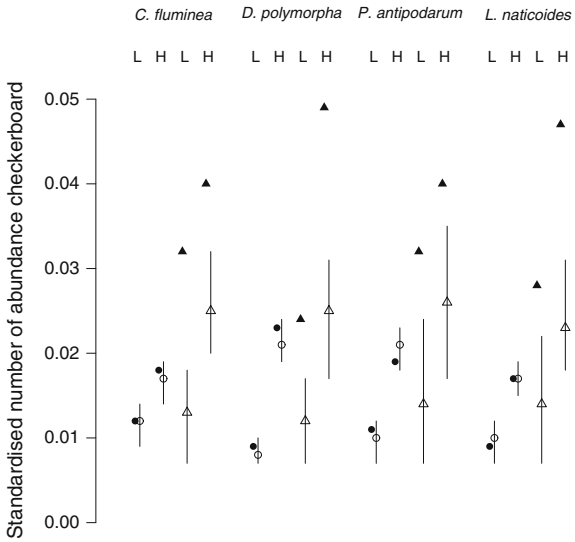

Fig. 2 The impact of low (L) and high (H) abundance of four alien species (*C. fluminea, D. polymorpha, P. antipodarum* and *L. naticoides*) at shallow (*circles*) and deep (*triangles*) sites on the standardised number of abundance checkerboard (*filled symbols*) and its comparison with random species assemblages (*open symbols* show expected mean values and whiskers the 95% confidence intervals). Standardised number of abundance checkerboard reflects the strength of competition within the community structure

several years old individuals dominated. Similarly, the zebra mussel showed a decline in abundance of 95% at shallow sites (1 and 3 m) in Lake Constance following the feeding of ducks over one winter (Werner et al., 2005). Interestingly, duck do not feed on *C. fluminea*, which has thicker valves than *D. polymorpha* and lives buried in the upper layer of sand (Schmidlin & Baur, 2007).

Several studies suggest that alien species generally have a negative impact on native communities (Strayer, 1999, 2010; Rahel, 2002; Arndt et al., 2009). However, Botts et al. (1996) demonstrated in a field experiment that *Dreissena* species can change the physical structure of sandy habitats which in turn may lead to increased densities of native species. Similarly, short-time experiments showed that several native macroinvertebrate taxa may benefit from the presence of *C. fluminea* in sandy habitats (Werner & Rothhaupt, 2007, 2008). Sousa et al. (2009) reviewed the eco-engineering effects of alien bivalves, including *C. fluminea* and *D. polymorpha*. Both bivalves cause a decrease in turbidity and an increase in light penetration in the water column because of filter feeding. The increase in light and visibility may enhance macrophyte growth. Interstices between clams and mussels provide refuge from predators to other invertebrates and shells can be colonised by algae, freshwater sponges, gastropods, amphipods and other invertebrates. Moreover, alien mussels might provide additional sources by biodeposition (Mitchell et al., 1996; Mörtl & Rothhaupt, 2003). Our results are in agreement with the above mentioned studies showing that alien molluscs might have both positive and negative effects on native communities. We should note, however, that the biological explanation of the negative impact of *L. naticoides* (revealed by GLMs) is rather challenging because the species was present only in low density.

The results of ADONIS support both views: alien mollusc species influence the structure of the native macroinvertebrate community in a sandy flat of the littoral zone of Lake Neuchâtel. The relationships between the abundance of the four alien mollusc species and native community variables suggest a positive effect on the native community structure. Thus, habitat transformation by increasing the amount

Table 4 Total shell mass (in g m^{-2}) of living and dead individuals of four alien and two native mollusc species at shallow (depth <3.5 m) and deep (depth 5.0–22.4 m) sites in Lake Neuchâtel

Species		Shallow sites			Deep sites		
		Living	Empty	Living + empty	Living	Empty	Living + empty
Corbicula fluminea[a]	Cf	314.5	165.8	480.3	246.9	221.6	468.5
Dreissena polymorpha[a]	Dp	137.1	53.9	191.0	459.3	289.2	748.5
Potamopyrgus antipodarum[a]	Pa	2.2	14.2	16.4	1.2	20.0	21.2
Bithynia tentaculata	Bt	0.4	8.6	9.0	0.5	4.8	5.3
Valvata piscinalis	Vp	0.0	2.2	2.3	0.4	29.2	29.5
Lithoglyphus naticoides[a]	Ln	1.3	0.6	1.9	0.9	1.1	2.0

[a] Alien species

Table 5 Summary of the minimal adequate model of the effects of origin (native vs. alien) and shell weight on the decay rate of mollusc shells

Factor	Estimate	se	*t* value	*P*
Intercept	21.267	2.164	9.830	<0.001
Origin (alien)	−9.659	3.353	−2.881	0.005
Weight	−14.151	7.767	−1.822	0.071

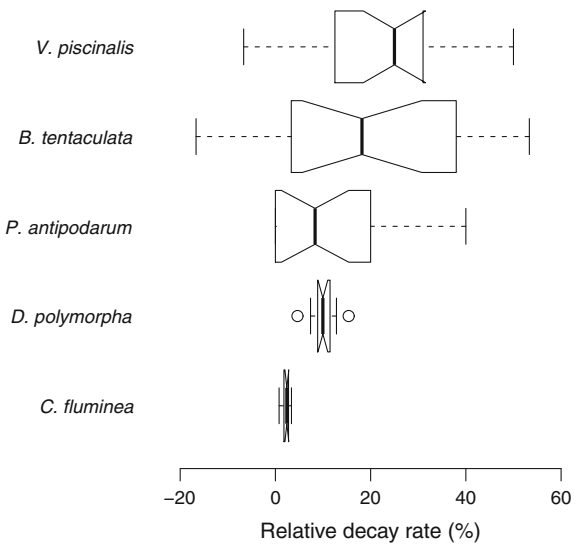

Fig. 3 Relative decay rate of shell material of three alien (*C. fluminea, D. polymorpha, P. potamopyrgus*) and two native (*B. tentaculata*, *V. piscinalis*) molluscs in Lake Neuchâtel

of hard substratum in the sand flat might be advantageous for several native taxa, but it might be disadvantageous for other taxa adapted to the conditions of sandy habitat. Indeed, *C. fluminea* was found to have a negative impact on the number of individuals with sand preference and on the number of protected species. This negative effect of a species on other species through habitat modification (i.e. ecosystem engineering) can be regarded as way of indirect competition (Gonzalez et al., 2008). The differential impact of *C. fluminea* and *D. polymorpha* can be explained by their different habitat use (burrowing vs. surface dwelling, e.g. Schmidlin & Baur, 2007; Higgins & Vander Zanden, 2010). Our findings support the use of trait-based analyses in invasion ecology (Townsend & Hildrew, 1994; Statzner et al., 2008; Ordonez et al., 2010) and its applications in

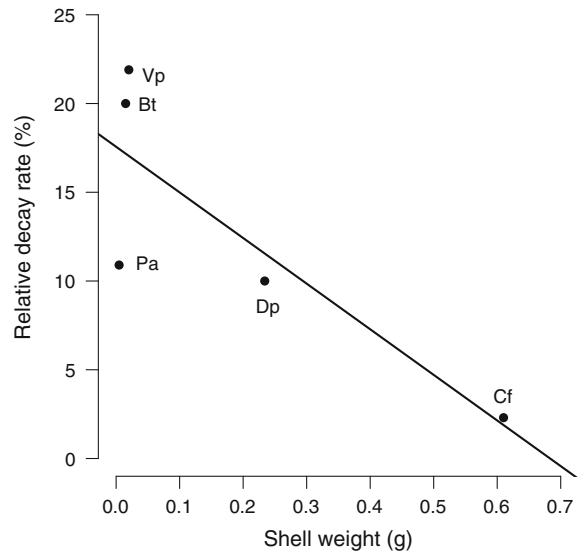

Fig. 4 Relative decay rate of shell material in five species of freshwater molluscs, averaged over all retrieved bags, as a function of mean shell weight of each species ($r^2 = 0.70, n = 5$, $P = 0.077$) in Lake Neuchâtel. Bt, *B. tentaculata*; Cf, *C. fluminea*; Dp, *D. polymorpha*; Pa, *P. antipodarum*; Vp, *V. piscinalis*. Full species names are given in Table 4

conservation issues because most sand-preferring native taxa are threatened in Switzerland (Table 1).

Alien species can transform a competitively structured native community into a randomly organised one (Sanders et al., 2003). Our null-model analysis showed that native benthic macroinvertebrate communities were structured randomly at shallow sites. At deeper sites, however, competition was important in structuring the community. At both depths, these patterns were not influenced by any of the alien mollusc species examined. Consequently, water depth per se has a stronger effect on the native community assembly than the four alien species. We assume that this difference between shallow and deep sites comes from the difference in the abundance of *D. polymorpha* caused by duck feeding (see above). However, stochastic and demographic processes might also influence the abundance of analysed taxa (Gotelli & McCabe, 2002).

The relative shell decay rates (2.3–21.9% of the initial shell mass per year) recorded in this study are similar to the values measured in other molluscs in the U.S.A. (Strayer & Malcolm, 2007). We found that the relative shell decay rate of alien mollusc species is slower than that of native ones. This means that the shells of alien species persist for a longer period in and

on the sediment, and consequently, have a long-lasting impact on the community structure through modification of the habitat.

It is important to note that some factors may restrict the generalisation of our conclusions. First, our samples deal with the topmost 5 cm of the sediment only. Consequently, the patterns observed might be different by applying other sampling techniques paying more attention to animals living deeper in the sediment (Waringer, 1987). Second, we used bags with a mesh size of 2 mm for handling samples. In other studies, sampling devices with a mesh size of 1.2 mm or even smaller have been applied (Carter & Resh, 2001). Consequently, the size distribution of macroinvertebrates sampled in our study might be biased slightly towards taxa with larger bodies.

In summary, our study showed that a sandy flat of the littoral zone of the Lake Neuchâtel is seriously invaded by alien mollusc species. The observed patterns suggest that the existence of these mollusc species (*D. polymorpha*, *C. fluminea*, *P. antipodarum* and *L. naticoides*) and their empty shells transform the sandy habitat into a more structured habitat with some hard substratum. This effect favours the occurrence and abundance of several native taxa, but it is disadvantageous for a limited number of taxa with specific habitat requirements. This study is to our knowledge one of the first which demonstrates depth-dependent impacts of alien species on the native community of a freshwater lake. These findings call the attention to the careful examination of the impact of alien ecosystem engineers to native communities, because negatively impacted taxa might have a high conservation value.

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