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Research article

Consumption of amphipods by littoral fish after the replacement of native *Gammarus roeseli* by invasive *Dikerogammarus villosus* in Lake Constance

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Abstract

The Ponto-Caspian amphipod *Dikerogammarus villosus* (Sowinski) invaded Lake Constance, Central Europe (47°39'N, 9°18'E,) in 2002 and within four years had colonized the entire littoral zone of the upper lake basin, replacing the formerly dominant species *Gammarus roeseli* Gervais. Fifteen fish species were sampled from six littoral sites in the upper lake basin in 2005 and 2006, and their stomach contents were compared with samples taken prior to the replacement of *G. roeseli* by *D. villosus*. Three zoobenthivorous fish species (European eel *Anguilla anguilla* (L.), Eurasian perch *Perca fluviatilis* L., and burbot *Lota lota* (L.)), which had regularly consumed *G. roeseli*, included *D. villosus* immediately into their diet in similar proportions. Shifts in amphipod consumption have thus not been detected, whereas effects of the invasive amphipod on the macrozoobenthos community, which on their part might affect the food base of littoral fish, require detailed study.

Key words: burbot, eel, perch, stomach contents, Lake Constance

Introduction

Lake Constance, the second largest lake at the northern fringe of the European Alps (47°39'N, 9°18'E, 536 km^2; 273 km shoreline length; 48 km^3 volume; Figure 1), is increasingly colonized by alien aquatic species. Although immigration into the lake from the River Rhine is hindered by a 23 m high waterfall, situated about 30 km downstream of the lake, several aquatic invasive species have recently colonized the lake via unknown immigration routes (LfU 2005).

One of the first invaders was the zebra mussel *Dreissena polymorpha* (Pall), which appeared during the 1960s and has colonized the entire lake in high densities, providing the food base for thousands of overwintering birds (Werner et al. 2005). Non-native ruffe *Gymnocephalus cernuus* (L.) was first detected in the 1980s (Dussling and Berg 2001) and established a large population shortly thereafter (Rösch and Schmid 1996), and at about the same time the spiny cheek crayfish *Orconectes limosus* (Rafinesque) started to spread in the lake (Hirsch 2007). Other alien species like the freshwater jellyfish

Craspedacusta sowerbyi (Lankester), the turbellarian *Dugesia tigrina* (Girard), the signal crayfish *Pacifastacus leniusculus* (Dana), or the Chinese mitten crab *Eriocheir sinensis* Milne-Edwards are found occasionally (LfU 2005).

The most successful invader during the last decade, however, has been the Ponto-Caspian amphipod *Dikerogammarus villosus* (Sowinsky) (Mürle et al. 2004). It was first detected in autumn 2002 at two isolated sites. During the following years, the littoral macrozoobenthos community was monitored twice per year at around 160 sites in Upper Lake Constance (ULC) and at 35 sites in Lower Lake Constance (see http://www.neozoen-bodensee.de/projekt/neozoen-monitoring). By the summer of 2006, *D. villosus* had colonized the entire 186 km shoreline of ULC (Table 1). Colonisation of Lower Lake Constance, which is connected to ULC via a riverine stretch of 4 km length, began in summer 2006, and by spring 2007 *D. villosus* had spread along the entire southern shoreline (cf. http://www.neozoen-bodensee.de/aktuelles).

The introduction of *D. villosus* into Lake Constance was most likely through human activities (transport of leisure boats among drainage systems, aquarium trade, fish transport, or others), as the species was not present up to 150 km downstream of the lake at the time of its appearance in the lake. The rapid dispersal in the lake within five years is attributed to the species' high mobility. *D. villosus* is known to be an aggressive predator and a strong competitor in macrozoobenthos communities (Dick et al. 2002; Kinzler and Maier 2004; Kley and Maier 2003). In Lake Constance, *D. villosus* has indeed largely replaced *Gammarus roeseli* Gervais, the formerly most abundant gammarid in the lake, which on his part had only spread in Lake Constance in the 1970s replacing the formerly dominant *Gammarus lacustris* Sars (LfU 2005). *D. villosus*, however, has not extirpated *G. roeseli* so far (Table 2). Both gammarids are probably able to coexist in the littoral zone of Lake Constance, utilizing different microhabitats (Hesselschwerdt, Limnological Institute, University of Constance, pers. comm.) Because amphipods are an important food source for many zoobenthivorous fish, we examined whether the proportion of amphipods in their diet had changed following replacement of the native amphipod by the alien species.

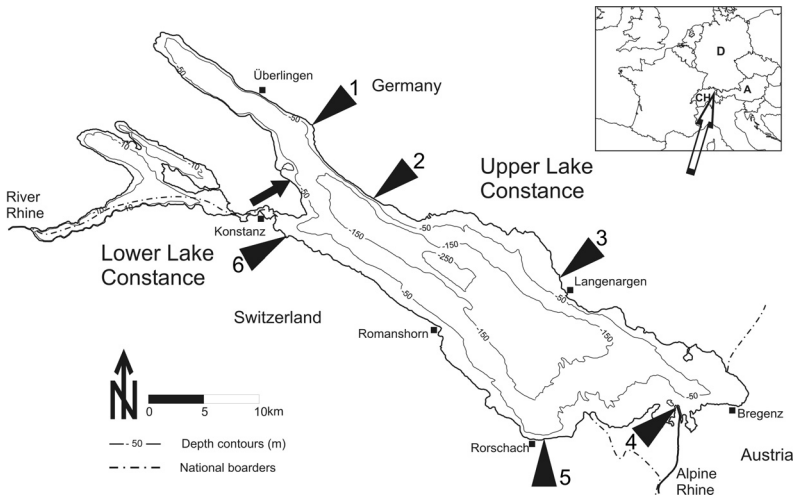

Figure 1. Sampling sites in Upper Lake Constance. Routine sampling site for macrozoobenthos and benthivorous fish sampled in 2000-2004 (arrow), and six additional sites sampled in 2005 and 2006 (triangles)

Material and Methods

After *D. villosus* had invaded the lake, a monitoring programme was started and fish were sampled from six different littoral sites in ULC in the years 2005 and 2006 (Figure 1, Table 1). Samples of perch taken in 2004 at our routine sampling site were included in the analysis. Fish stomach contents were compared with those from fish sampled at our routine sampling site in the years 2000, 2001, and 2003, i.e. before *D. villosus* invaded the lake and colonized the entire littoral zone. The fish were sampled by electro-fishing, beach seining, and with gill nets of small

Table 1. Coordinates (WGS84) of sampling sites in Upper Lake Constance (cf. Figure 1), which were monitored for the establishment of *D. villosus* and from where fish samples for stomach content analysis were taken in 2005 and 2006. Month and year indicate the time when *D. villosus* had become established at that site

Routine site	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
47°41.52'N 09°12.09'E	47°45.00'N 09°11.80'E	47°42.02'N 0915.20'E	47°36.10'N 09°31.50'E	47°31.20'N 09°38.60'E	47°28.90'N 09°31.50'E	47°37.60'N 09°15.85'E
Oct 2004	Nov 2004	Oct 2003	Oct 2004	Feb 2006	Feb 2006	Feb 2006

Table 2. Abundance of *G. roeseli* and *D. villosus* (individuals · m^{-2}) at two sampling sites in Upper Lake Constance assessed at 40 cm water depth before and after *D. villosus* became established at these sites

Sampling site	Time interval	*G. roeseli*	*D. villosus*
Routine site	09/1999 – 01/2003	279.0	0
	04/2005 – 09/2006	21.2	103.2
Site 2	05/2002 – 09/2002	104.0	0
	09/2005 – 09/2006	0	181.3

mesh sizes (from 6 to 20 mm, knot to knot). They were killed with an overdose of anaesthetic, injected with 10% formaldehyde solution into the body cavity to inhibit further digestion of food items, and stored in 5% formaldehyde solution. Subsequently, fish were measured for total length (TL) and weighed, their stomach contents removed and determined to the lowest taxonomical level possible. Only those species that had consumed at least some gammarids (apart from other zoobenthos prey and zooplankton or fish) were considered for analysis. Zoobenthos prey were measured under a dissecting microscope for conversion of length into biomass according to standard length-weight regressions (Baumgärtner and Rothhaupt 2003), or our own regression in the case of *D. villosus*, $y = 0.0016\ x^{3.2441}$, where y = dry weight and x = body length (Schleuter 2007). Finally, stomach content composition was expressed as percent dry weight. Since we focused on the relative contributions of the two amphipod species to the zoobenthos diet of fish, ingested fish were not considered in these calculations as they accountted for extremely variable proportions (0–95%) in the fish's diet.

Results

A total of 15 fish species were sampled and their stomach contents analysed (Table 3). Only four species had consumed amphipods: burbot *Lota lota* (L.), European eel *Anguilla anguilla* (L.), Eurasian perch *Perca fluviatilis* L. and non-native ruffe. Ruffe, however, was not considered in the diet analysis because the species rarely consumed amphipods and continued to feed predominantly on chironomid larvae and pupae, as they did prior to the arrival of *D. villosus* (Schleuter and Eckmann 2008).

G. roeseli almost completely replaced by *D. villosus* in the diet of Eurasian perch and of burbot. Perch is known to undertake an ontogenetic diet shift, whereby intermediate size classes pass through a benthivorous stage. Perch were even more abundant in our samples than ruffe, but only samples from August/September were suitable for this analysis as the fish were either zooplanktivorous or piscivorous most of the time (Schleuter and Eckmann 2008). In August 2003, when *D. villosus* had not yet replaced *G. roeseli* at our routine sampling site (cf. Figure 1), the stomachs of perch ranged 5–13 cm TL (age-classes 0 and 1) and contained 46 % *G. roeseli* and no *D. villosus* (Table 4). In August 2004, however, after *D. villosus* had fully colonized the littoral zone at our routine sampling site, perch contained on average 54 % *D. villosus* and only 2 % *G. roeseli* in their stomachs (Table 4).

Table 3. Fish species sampled from six littoral sites in Upper Lake Constance in 2005 and 2006. Total number of individuals sampled (Total) and number of individuals that contained amphipods in their stomach are indicated for each species

	9 / 2005		6 / 2006	
Fish species	Total	Amphipoda	Total	Amphipoda
Bleak *Alburnus alburnus* (Linnaeus, 1758)	18	0	104	0
Common bream *Abramis brama* (Linnaeus, 1758)	17	0	1	0
Bullhead *Cottus gobio* Linnaeus, 1758	1	0	1	0
Burbot *Lota lota* (Linnaeus, 1758)	85	51	82	36
Chub *Squalius cephalus* (Linnaeus, 1758)	39	0	8	0
Dace *Leuciscus leuciscus* (Linnaeus, 1758)	34	0	8	0
European eel *Anguilla anguilla* (Linnaeus, 1758)	20	4	37	27
Eurasian perch *Perca fluviatilis* Linnaeus, 1758	917	0	432	1
Roach *Rutilus rutilus* (Linnaeus, 1758)	10	0	7	0
Ruffe *Gymnocephalus cernua* (Linnaeus, 1758)	495	7	536	2
Stone loach *Barbatula barbatula* (Linnaeus, 1758)	9	0	0	0
Threespine stickleback *Gasterosteus aculeatus* Linnaeus, 1758	0	-	5	0
Brown trout *Salmo trutta* Linnaeus, 1758	5	0	0	2
Pikeperch *Sander lucioperca* (Linnaeus, 1758)	8	0	6	0
Silver bream *Blicca bjoerkna* (Linnaeus, 1758)	0	-	1	0

Table 4. Benthivorous fish from the littoral zone of Upper Lake Constance (cf. Figure 1) inspected for the consumption of amphipods. The mean percentage contributions in terms of dry weight of the two amphipod species, *Gammarus roeseli* and *Dikerogammarus villosus,* of other zoobenthos prey and of zooplankton, to stomach contents (excluding fish) are indicated

	Perch		Burbot					Eel
Sampling date	Aug 2003	Aug 2004	Jun 2000	Sep 2000	Jun 2001	Sep 2005	Jun 2006	Jun 2006
Sampling site	routine	routine	routine	routine	routine	6 sites	6 sites	6 sites
Sample size	35	85	10	10	27	85	82	37
TL min-max (cm)	5–13	5–13	12–16	7–11	10–16	4–22	9–22	10–48
% *G. roeseli*	46	2	32	84	35	3	3	2
% *D. villosus*	-	54	-	-	-	69	63	87
% other zoobenthos	33	33	68	16	65	28	34	11
% zooplankton	21	11	0	0	0	0	0	0

Discussion

In the present study, we focused on the potential of an invading, partly carnivorous macrozoobenthos species to affect the food choice of zoobenthivorous fish. Of particular interest from a fisheries management point of view is how an invader might alter littoral fish production.

If the invader possesses morphological and/or behavioural defences against fish predation, then it might not be readily included into the diet of zoobenthivorous fish. Consequently, as the invader consumes a certain portion of the benthic production, the energy flow from zoobenthos to fish could be reduced; this effect is more likely to be pronounced where the invader displaces a native species but does not take its important role as prey for a native fish species. This scenario did not take place during the replacement of *G. roeseli* by *D. villosus* in ULC, because the invader was almost instantaneously included into the diet of zoobenthivorous fish. In perch, *D. villosus* accounted for a similar pro-

portion in the diet as did *G. roeseli* prior to the invasion. In burbot, the consumption of amphipods increased, in two out of three cases, after the invasion. A similar pattern was observed during the invasion by *D. villosus* and other zoobenthos species of the River Rhine, where the invaders were readily included in the diet of native fishes, with *D. villosus* appearing to be a preferred prey (Rey et al. 2004).

Still, the energy flow to zoobenthivorous fish can be modified by *D. villosus* in at least two ways. As the invader is partly carnivorous and may prey e.g. on native *G. roeseli* (Kinzler and Maier 2004), a formerly important prey item for littoral fish, the trophic transfer efficiency in the littoral zone might be reduced by the incorporation of an additional trophic link into the food web. On the other hand, when the invader uses food sources that would otherwise not be available to fish, a greater share of the benthic production could be made available for fish, thereby increasing the overall fish production in the littoral zone. It would, however, be extremely difficult to measure these indirect effects of the invasive amphipod on the fish assemblage through the assessment of fish community structure or production. Therefore, possible impacts of the invader on the benthic community, primarily on prey items for zoobenthivours fish, need to be studied.

In summary, five years after *D. villosus* was first detected in ULC, the species has colonized the entire shoreline and the southern shoreline of LLC as well, replacing, but not extirpating, the native species *G. roeseli* almost completely. The invader was included immediately into the diet of zoobenthivorous fish. No marked effects on zoobenthivorous fish have so far been observed, but more subtle influences are possible, which require detailed study.

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