Long-term biomonitoring of invertebrate neozoans in Lake Geneva

Autor(en): **Lods-Crozet, Brigitte**

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Long-term biomonitoring of invertebrate neozoans in Lake Geneva

Brigitte LODS-CROZET[1]

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Abstract

*Exogenous species often influence native biocenoses and potentially alter native community structure or facilitate other species. We investigated the quantitative expansion and depth distribution of a well-established gammarid (*Dikerogammarus villosus*) since 2004 and of two more recent neozoans (*Chelicorophium curvispinum, Corbicula fluminea*) at two locations in Lake Geneva.* D. villosus *shows a high inter-annual and depth variability since 2004 (mean 103.2 ± 70.7 ind. m²) between 0 and 5 m, almost excluding the native gammarid (*Gammarus pulex/fossarum*) from these littoral habitats. This displacement of indigenous species to greater depths induced a niche partitioning between* D. villosus *and other gammarid species.* C. curvispinum *presented an exponential trend over the last two years (> 10 000 ind. m² in 2012 on the eastern site) while the colonisation of* C. fluminea *was relatively slow (max. 135 ind. m²), probably limited by an unsuitable stony substratum in the littoral zone. Our results confirmed the numerical expansion of non-indigenous species in Lake Geneva representing up to 40 % of the benthic invertebrate richness and up to 95 % of the abundance. This constant increase in exogenous species contributed to a homogenization of the freshwater fauna in the littoral habitat, mainly driven by a biodiversity loss and an increase of suspension feeders.*

Keywords: Dikerogammarus, Chelicorophium, Corbicula, *Switzerland, invasive species, depth*

Résumé

Monitoring à long-terme des invertébrés néozoaires du Léman. – *Les espèces exogènes influencent souvent les biocénoses indigènes et peuvent potentiellement modifier la structure des communautés ou faciliter l'écologie de certaines espèces. Nous avons suivi l'expansion quantitative et la répartition bathymétrique d'une espèce de gammaridé (*Dikerogammarus villosus*) bien établi depuis 2004 et de deux néozoaires plus récents (*Chelicorophium curspinum, Corbicula fluminea*) dans deux sites du Léman.* D. villosus *montre une grande variabilité interannuelle et bathymétrique depuis 2004 (moyenne 103.2 ± 70.7 ind. m²) entre 0 et 5 m de profondeur, excluant presque totalement l'espèce indigène (*Gammarus pulex/fossarum*) des habitats littoraux. Ce déplacement vers les plus grandes profondeurs de l'espèce native induit une séparation des niches écologiques entre ces deux espèces.* C. curvispinum *présente une expansion exponentionnelle au cours des deux dernières années (> 10 000 ind. m² en 2012 sur le site côté est), tandis que la colonisation de* C. fluminea *est relativement lente (max. 135 ind. m²), probablement limitée par un substrat caillouteux en zone littorale peu propice à son installation. Nos résultats confirment l'expansion numérique des espèces non indigènes représentant un maximum de 40 % de la richesse des invertébrés benthiques et jusqu'à 95 % de l'abondance. Cette augmentation constante en espèces exogènes contribue à une homogénéisation de la faune aquatique du littoral qui est principalement liée à une perte de biodiversité et un accroissement des invertébrés filtreurs.*

Mots-clés: Dikerogammarus, Chelicorophium, Corbicula, *Suisse, espèces invasives, profondeur*

1. Introduction

Benthic invertebrate communities in the Swiss lakes are changing because of the arrival of a constant stream of mainly Ponto-Caspian and Asian species (Lods-Crozet and Reymond 2006, Schmidlin *et al.* 2012a, 2012b, Steinmann 2008). After the major invasion of the mussel *Dreissena polymorpha* in the sixties and the more inconspicuous arrival of species such as *Branchiura sowerbyi, Girardia tigrina, Potamopygus antipodarum, Haitia (Physella) acuta* and *Gyraulus parvus* later (Juget 1967,

[1] *Direction Générale de l'Environnement – Protection des eaux, Boveresses 155, CH-1066 Epalinges, Switzerland.*
E-mail corresponding author: brigitte.lods-crozet@vd.ch

Crozet et al. 1980, Lods-Crozet et al. 2013), Lake Geneva was colonised at the beginning of the XXI[e] century by new Ponto-Caspian crustacean species: *Dikerogammarus villosus* in 2002 (Bollache 2004), *Hemimysis anomala* in 2007 (Lods-Crozet *et al.* 2013, Golaz & Vaïnölä 2013) and *Chelicorophium curvispinum* in 2010 (Lods-Crozet *et al.* 2013). In addition, the Asian clam *Corbicula fluminea* was first recorded in 2008.

In many European countries, invasions of Ponto-Caspian species have been facilitated by habitat alteration, caused by the previous settlement of *D. polymorpha* and helping subsequent invasions, and eventually leading to an "invasional meltdown" (sensu Simberloff and Von Holle 1999, Gallardo and Aldridge 2013). In recent years, densities of non-indigenous species are increasing rapidly in lakes (e.g. Bollache et al 2004; Ciutti et al. 2011; Mürle et al. 2003; Schmidlin *et al.* 2012a, 2012b) and their expansion is considered a threat to the native fauna of the invaded ecosystems.

Lake Geneva, the largest lake in Western Europe has benefited from substantial historical biological data since the end of the XIX[e] century. The need to document the risk represented by alien species is a priority for the International Commission for the water protection of Lake Geneva (CIPEL) and environmental authorities and agencies all around the lake.

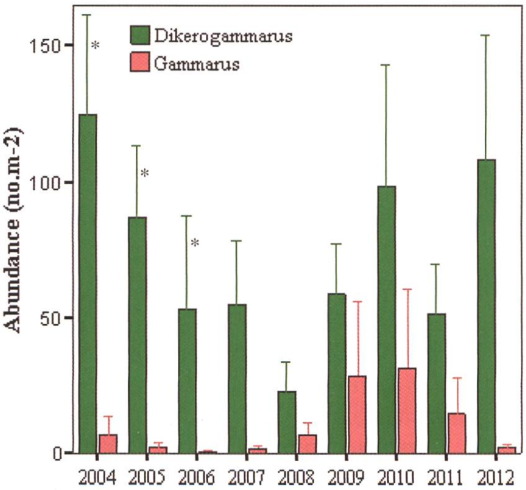
The objectives of this paper are to analyse the expansion of the well-established *D. villosus* and the present status of two more recent invaders: *Corbicula fluminea* and *Chelicorophium curvispinum* and to assess the risk of the impact of these non-native species on the invertebrate community structure.

2. Study sites and methods

The first site studied was located at «Rivaz gare (RG)» (46°28'10"N; 6°47'05"E) along the littoral zone on the Swiss side of Lake Geneva (between Lausanne and Vevey) at a depth of 0-13 m. Substratum was composed of grain size 0.2-5 cm at a depth of 0-0. 50 m. Cobbles with a diameter of 5-20 cm could be found down to a depth of 5 meters. At greater depth (10 m) a sandy/muddy bottom predominated. The 0.5-5 m depths were colonized by aquatic plants (*Zannichellia palustris* L., *Potamogeton crispus* L., *P. pectinatus* L., *P. perfoliatus* L. and *Myriophyllum spicatum* L.). There was an average 15% slope.

A second study site was added in 2010 to the monitoring program to increase the database on neozoans and to follow their spatial spread. It was situated 20 km west of Lausanne (Saint-Prex - SP - 46°28'75"N; 6°27'75"E) along the shore line at a depth of 0-10 m. Cobbles with a diameter of 5-20 cm fromed the main substratum between 0-5 m. At depths greater than 5 m, a predominance of sandy/muddy bottom occurred. The 0.5-7 m depths were colonized by aquatic plants (*Zannichellia palustris* L., *Potamogeton crispus* L., *Myriophyllum spicatum* L. and Characeae). The slope There was an average 5% slope. The site, located on a cape, was more exposed to the wind than RG. In both sites, the stony and sandy substratum was covered by *Dreissena polymorpha* shells at depths greater than 1 m.

RG has been monitored since 2004 and SP since 2010, once a year in late autumn. Invertebrate fauna was collected at six different depths (0.5, 1.0, 2.5, 5.0, 10.0, 13.0 m). The deepest station (13 m) was added in 2006. Surber-type bottom sampler was used



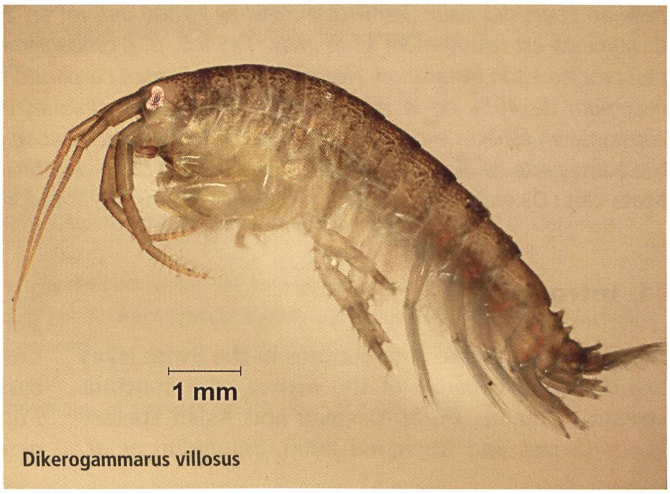


Fig. 1. Temporal changes of mean abundance (no. m^{-2} *± standard error) of* Dikerogammarus villosus *and* Gammarus pulex / G. fossarum *at "Rivaz gare" site in Lake Geneva. *: the differences between abundances are significant for* $p < 0.05$.

by a SCUBA diver and eight replicates (30 x 30 cm; 0.72 m^2 total sampled surface area; 300 µm mesh size) were taken till 2008. A modified protocol (modified Surber-type bottom sampler) was then applied to optimize the sorting time (five replicates 25 x 25 cm; total sampled surface area: 0.3215 m^2) at each depth to provide an overall sample. The bulk of amphipods and non-indigenous clams were sorted under stereomicroscope. For the 2009 and 2012 material, all the macroinvertebrate fauna was taken in account.

Abundance was calculated by depth and date. For Gammaridae, body length was determined (from the tip of the rostrum head to the base of the telson). The proportion of males / females was also calculated for each depth/date at the RG site. Trends in richness and abundance of non-native species in the macroinvertebrate communities were analysed using the Taxonomic Contamination Index (TCI) and Abundance Contamination Index (ACI) (Panov et al. 2009). TCI = Rnis / Rt *100, where Rnis is the total number of non-indigenous species, while Rt is the total number of identified species. ACI is the relative abundance of non-indigenous species in a sample.

Inter-annual variability of the two gammarids (*Dikerogammarus villosus, Gammarus pulex/fossarum*) at each site was performed using nonparametric Kruskal-Wallis tests. Differences between abundances of the two gammarids per year were tested by means of nonparametric Mann-Whitney *U*-tests. Data was considered statistically significant at $P < 0.05$. All statistical analyses were performed with SPSS 14.0.

3. Results

3.1. Dikerogammarus villosus *monitoring*

Dikerogammarus villosus was found from the lake shore to a depth of 10 m, colonizing either stony substratum or *Dreissena* aggregates of muddy sediments. Only a few individuals (max. 8 ind. m^{-2}) were found at greater depth (10 m) at RG site, but in greater number at SP site (max. 165 individuals m^{-2} at 10 m). Mean abundance per year (Fig. 1) varied between 124.7 ± 36.5 ind. m^{-2} in 2004 and 22.7 ± 11.0 ind. m^{-2} in 2008 at RG site but differences are not significant (Kruskal Wallis test, P = 0.43). At SP site, mean density per year of *D. villosus* was two times higher (Fig. 2), ranging between 313.3 ± 122.2 ind. m^{-2} in 2010 and 105.1 ± 40.3 ind. m^{-2} in 2012 and also not significantly different (Kruskal Wallis test, P = 0.22). The native species, *Gammarus pulex/fossarum* complex, common and abundant before the beginning of XXI^e century in every stony bottom in the littoral zone (i.e. 250 ind. m^{-2} before 1990, Lods-Crozet, unpublished data) was totally excluded from the upper littoral in the beginning of 2000. They were found almost exclusively at greater depths than *D. villosus*, between 5 and 13 m, with maxima not exceeding 175 ind. m^{-2} at RG site and 195 ind. m^{-2} at SP in 2010 (Fig. 1 and 2).

Mean abundances of *G. pulex/fossarum* per year were significantly lower at RG site between 2004 and 2006 (Fig. 1) and at SP site between 2010 and 2012 (Fig. 2) than those of *D. villosus* (Mann-Whitney *U*-tests, $P < 0.05$).

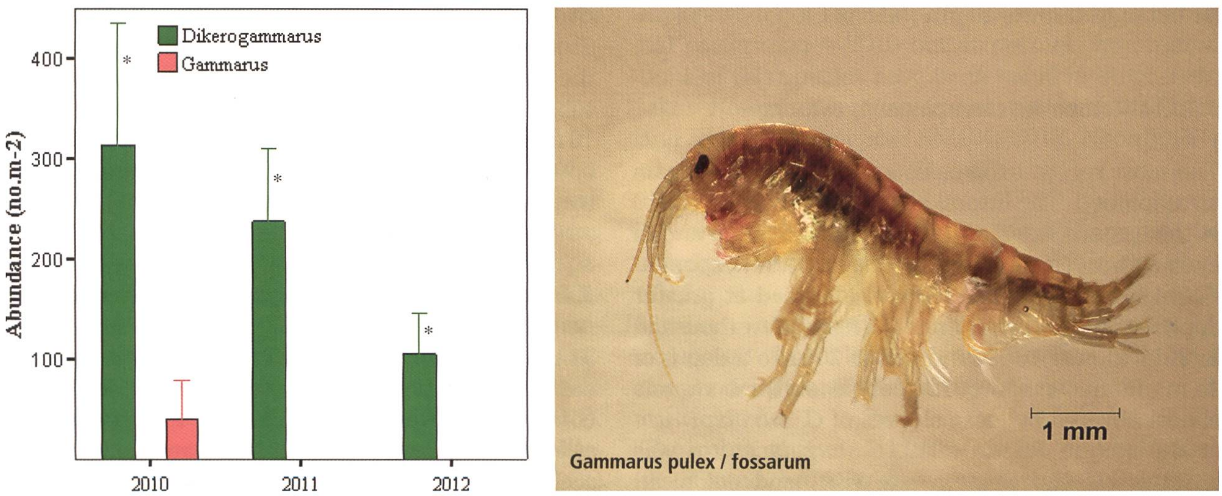
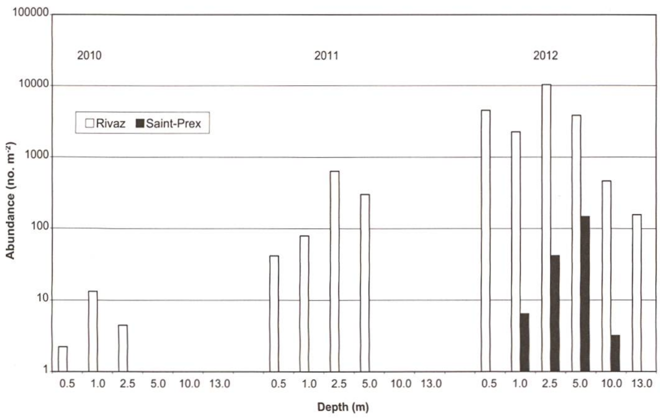


Fig. 2. Temporal changes of abundance (no. m^{-2} ± standard error) of Dikerogammarus villosus *and* Gammarus pulex / G. fossarum *at "Saint-Prex" site in Lake Geneva. *: the differences between abundances are significant for* $p < 0.05$.

Table 1. Abundance (no. m^{-2}) of males (M), females (F) and sex-ratio (M/F) in the Dikerogammarus villosus *population at station Rivaz (RG).*

Depth (m)		2006	2007	2008	2009	2010	2011	2012	M/F mean ± SD
0.5	M	26	13	7	53	22	45	90	
	F	21	36	3	38	40	61	192	
	M/F	1.27	0.35	2.50	1.41	0.56	0.74	0.47	1.04 ± 0.76
1	M	100	25	35	36	69	22	32	
	F	119	35	21	62	196	38	74	
	M/F	0.84	0.72	1.67	0.57	0.35	0.58	0.43	0.74 ± 0.44
2.5	M	0	28	3	31	38	29	70	
	F	22	28	10	33	158	70	141	
	M/F	0.00	1.00	0.29	0.93	0.24	0.41	0.50	0.48 ± 0.37
5	M	0	64	33	38	11	22	32	
	F	11	97	24	64	49	29	26	
	M/F	0.00	0.66	1.41	0.59	0.23	0.78	1.25	0.70 ± 0.51



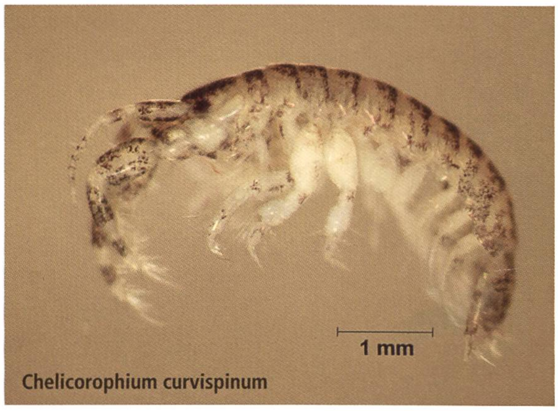


Fig. 3. Temporal changes of abundance of Chelicorophium curvispinum *at "Rivaz gare" site (white boxes) and "Saint-Prex" site (black boxes) at different depths in Lake Geneva*

A predominance of females of *D. villosus* was observed across depth and years (Table 1). The male / female proportion in the population was quite similar but only at lower depth (0.50 m).

3.2. Chelicorophium curvispinum *monitoring*

The most recent exogenous species was once again an amphipod. The littoral colonization began in 2010 in the eastern site (RG) down to 2.50 m deep and in low numbers (max. 13 ind. m^{-2}) (Fig. 3). An exponential increase in abundance and a spread at greater depths was observed thereafter, from a few thousand in 2011 to over 10000 ind. m^{-2} in 2012 to a depth of 13 m. In december 2012, cobble substratum was almost covered by loose sleeves of *C. curvispinum* at the station RG. In 2012, *C. curvispinum* was observed at the western site (SP) and colonized stony/sandy bottoms to a depth of 10 m with a maximum of 147 ind. m^{-2} at 5 m deep.

3.3. Corbicula fluminea *monitoring*

Observed for the first time in 2008 near the Rhône river inflow (Le Bouveret beach), populations of C. *fluminea* expanded across the lake and arrived on the northern shores in 2012. Limited to sandy/muddy substratum and at depths comprised between 5 and 10 m in Rivaz station, the species colonized also stony bottoms at SP station (Fig. 4). The maximum abundance was found at 5 m in RG (135 ind. m^{-2}).

3.4. *Assessment of the risk for indigenous invertebrates*

34 taxa were found in 2012 with 50 % of species present in both stations. Total taxa richness at RG site is comprised between 10 and 19 taxa, with a maximum at 5 and 13 m deep (Table 2). Neozoan species (TCI) accounted for 10 to 40 % of the richness depending on depth. Five neozoan species were present: 3 mollucs (*Potamopyrgus antipodarum, Corbicula flu-*

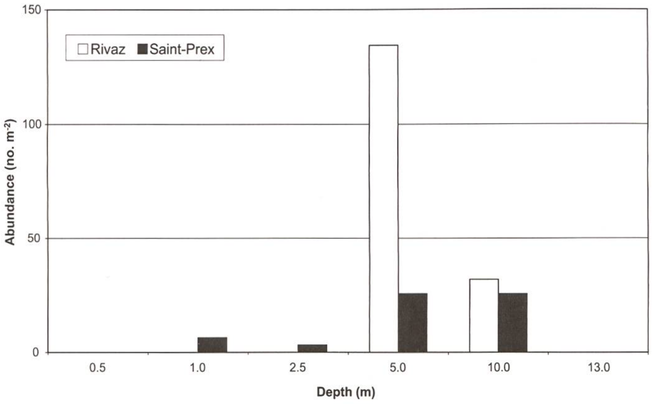


Fig. 4. Abundance of Corbicula fluminea *at "Rivaz gare" site (white boxes) and "Saint-Prex" site (black boxes) in 2012, at different depths in Lake Geneva.*

minea and *Dreissena polymorpha*) and 2 amphipods (*Dikerogammarus villosus, Chelicorophium curvispinum*). However, the neozoan abundance (ACI) contributed to 95.5% of the total invertebrate abundance at 0.50 m and decreased with depth; *Dreissena polymorpha* and *Chelicorophium curvispinum* were the main contributors.

A similar pattern was observed on the second site (SP), but with a lower total richness (range 8-17 taxa; TCI: 25-36%) and total abundance (max. 7546 ind. m^{-2}). The abundance contamination index (ACI) ranged from 82% at lower depths to 7.3% at the deepest station. *Dreissena polymorpha, Potamopyrgus antipodarum* and *Dikerogammarus villosus* were the most abundant species.

Indigenous crustacean (*Gammarus pulex/fossarum* complex, *Asellus aquaticus*) were absent from the upper littoral zone and colonized only depths below 10 m and only in low numbers for *Gammarus*.

4. Discussion

Since the sixties, an accelerated flow of neozoan have been observed in Lake Geneva. A yearly monitoring program was initiated in 2004 to document the spatial extent of *Dikerogammarus villosus* (Lods-Crozet and Reymond 2006) and later of other non-indigenous species as *Corbicula fluminea, Hemimysis anomala, Chelicorophium curvispinum* (Lods-Crozet *et al.* 2013, Golaz & Vaïnölä 2013). Three exogenous species (*D. polymorpha, D. villosus, C. fluminea*) present in Lake Geneva (Table 2) are included in the list of the100 most problematic invasive alien species in Europe (DAISIE webSite). *D. villosus* populations showed a fluctuating abundance pattern since 2004, in term of depth distribution. In Lake Geneva, the arrival of *D. villosus* has induced changes in distribution and abundance of indigenous gammarids and similar patterns were observed, e.g. in Lake Markermeer, the Netherlands (Noordhuis *et al.* 2009), Lake Constance, Germany (Gergs *et al.* 2011) or Lake Garda, Italy (Ciutti *et al.* 2011). Replacement of species is expected because of the rapid decrease in native gammarid populations. Other studies showed that, though locally and temporarily excluded, none of the native or naturalized gammarids disappeared completely (Guy *et al.* 2005). The female-biased sex ratio observed over the years and at different depths was also observed in a river population (Devin *et al.* 2004).This process could be advantageous for the species, because it increased the reproductive capacity of the population.

Chelicorophium curvispinum, the most recent and rapid invader of Lake Geneva has shown an exponential pattern since 2010 but at present, no observations of this species have been made in other Swiss lakes. However, the species is abundant in the Rhône and Rhine catchments (ANEBO 2013, Noordhuis *et al.* 2009).

As constrast to the rapid expansion of *Corbicula fluminea* in Lake Neuchâtel in 2003 (Schmidlin *et al.* 2012a), the slower spread in Lake Geneva was probably due to a non optimum littoral substratum, mainly composed of cobbles. The species was only found at deeper depths and in relatively low numbers.

The zebra mussel, a Ponto-Caspian species widely distributed throughout western Swiss lakes since the sixties, has frequently been attributed to driving invasional meltdowns (Simberloff 2006, Gallardo &

Site			Rivaz						Saint-Prex				
	Depth (m)	1st obs.	0-0,5	1	2,5	5	10	13	0-0,5	1	2,5	5	10
Dugesidae								13					
Planariidae					3								
Valvata	*piscinalis (O.F. Müller, 1774)*					13		38					
Potamopyrgus	*antipodarum (Gray, 1843)*	1978	48	19	666	237	10			416	438	141	6
Haitia (Physella)	*acuta Draparnaud, 1805*	1971											3
Bithynia	*tentaculata (Linnaeus, 1758)*			3		13	6	6					
Radix	sp.				3								
Radix	*balthica (Linnaeus, 1758)*				29	26		6			6.4		3
Gyraulus	*albus (O.F. Müller, 1774)*					3		3					
Gyraulus	sp. (juveniles)		3	6	6		3						
Ancylus	*fluviatilis (O.F. Müller 1774)*			6	6	3			16	86	214	64	
Anodonta	*anatina (Linnaeus, 1758)*				6		10	6				10	6
Sphaeriidae				10	275	26	10	74		96	96	131	198
Corbicula	*fluminea (O.F. Müller, 1774)*	2008				134	32			6	3	26	26
Dreissena	*polymorpha (Pallas, 1771)*	1962	2970	1152	6099	806	320	1043	1194	3648	3334	2694	262
Oligochaeta			51	58	499	611	3648	2093	189	803	669	899	237
Glossiphonia	sp.					3	26	19					
Helobdella	*stagnalis (Linnaeus, 1758)*				6	3	83	67		10	35	16	10
Erpobdella	*octoculata (Linnaeus, 1758)*			6	10	51	333	157			3		
Asellus	*aquaticus (Linnaeus, 1758)*						531	608				3	13
Gammarus	*pulex/fossarum (Linnaeus, 1758) / Koch,1835*						6	6					
Dikerogammarus	*villosus (Sowinsky, 1894)*	2002	278	112	221	54			221	176	109	35	
Chelicorophium	*curvispinum Sars, 1895*	2010	4573	2253	10317	3882	464	157		6	42	147	3
Baetidae				3									
Caenis	sp.		186	64	54	29	282	10	48	67	294	1203	237
Ephemera	*danica Müller, 1764*								3		10	3	
Orthotrichia	sp.				10								
Hydroptila	sp.		38	3	3	3							
Tinodes	*waeneri (Linnaeus, 1758)*		13	13			3		26	48	6	6	
Ecnomus	*tenellus (Rambur, 1842)*							3					
Limnephilinae										3			
Athripsodes	*cinereus (Curtis, 1834)*									3		22	
Mystacides	*azurea (Linnaeus, 1761)*					6	13	19				29	13
Chironomidae			80	74	26	3	1530	1146	29	144	269	2115	3094
		Total abundance (no. m^{-2})	8240	3782	18240	5907	7309	5475	1725	5514	5530	7546	4112
		Total richness	10	15	18	19	18	19	8	14	15	17	14
		Neozoan abundance (no. m^{-2})	7869	3536	17302	5114	826	1200	1414	4253	3926	3043	301
		Neozoan relative abundance ACI (%)	95.5	93.5	94.8	86.0	11.3	21.9	82.0	77.1	71.0	40.3	7.3
		Neozoan richness	4	4	4	5	4	2	2	5	5	5	5
		Neozoan relative richness TCI (%)	40	27	22	26	22	10	25	36	33	29	36

Aldridge 2013). This was confirmed by the large contribution of three Ponto-Caspian species in Lake Geneva (*D. polymorpha, D. villosus, C. curvispinum*) in terms of relative abundance, in the widespread stony substratum of Lake Geneva. The competition for space and food and the predation mechanisms induced, shifts in the benthic invertebrate communities and leads to biodiversity loss for native species. These trends can be seen as driving the homogenization of the zoobenthic compartment of Lake Geneva.

In Switzerland, even though the Rhine basin is a prominent highway for the dispersal of aquatic invasive species, others routes such as canals, ballast water during boat transport, fisheries, aquarium activities also contribute to concrete ways of expanding neozoans. Lake Constance was the first lake concerned by the spread of Rhine species (ANEBO 2013). Similar exogenous invasions were patent in other large lakes of the Swiss Plateau, with the large expansion of *Dikerogammarus villosus* in Lake Constance (ANEBO 2013), Lake Zürich (Steinmann 2008) and of *Corbicula fluminea* in Lake Neuchâtel (Schmidlin *et al.* 2012a). In the Southern Alps, Lake Garda was invaded by *D. villosus* at the same time as Lake Geneva and earlier by *C. fluminea* (Ciutti *et al.* 2011). The presence of an almost continuous stony littoral substratum could be a facilitating factor for the rapid dispersion of *D. villosus* and *C. curvispinum*, although drift was shown to be the main mechanism in both species (Noordhuis *et al.* 2009). Moreover, it was discussed by Gergs *et al.* (2011) that amphipods benefited significantly from *Dreissena polymorpha* biodeposits, a previous invader from the sixties and now assimilated as a naturalized species. Karatayev *et al.* (2009) concluded that the ongoing spread of non-indigenous species not only affects biodiversity but also strongly shifts communities toward greater tolerance to organic pollution and increases the number of collectors-filterers, thereby enhancing benthic pelagic coupling in aquatic ecosystems with high densities of invaders.

It is known that economic development and globalisation of trade have resulted in the strong expansion of exogenous species but other non-exclusive explanations have also been suggested. To explain such a success of invaders in the Swiss lakes via the Rhine pathway, it was hypothezied by Devin and Beisel (2008) and Uehlinger *et al.* (2009) that high invasiveness of the river Rhine may also be related to the presence of vacant niches. The native fauna diversity of the river is rather low in comparison to rivers in south-eastern biogeographic regions. The Alps formed a barrier that reduced the accessibility from southern refuges during Pleistocene glaciations. This enhanced species extinction and impeded or delayed re-colonization from these refuges after the last glacial period (Devin and Beisel 2008, Uehlinger *et al.* 2009).

Lake Geneva was also colonized by the pelago-benthic mysid, *Hemimysis anomala*, first observed in the lake during the autumn 2007 (Lods-Crozet *et al.* 2013, Golaz & Vaïnölä 2013). It spread fast across Lake Geneva and three years later it was also reported in another large lake, 60 km north (Lake Neuchâtel; P. Stucki, pers.comm.).

The impact on native fauna was obvious on the native gammarid *Gammarus pulex/fossarum* complex. Its seems also that densities of *Asellus aquaticus*, triclads, leeches and trichopteran larvae of *Tinodes waeneri, Ecnomus tenellus* have dropped considerably over the last two decades at depths exploited by the invasive gammarids (Lods-Crozet *et al.* 2013), as was observed in the Netherlands (Noordhuis *et al.* 2009). However, the importance of the recovery from eutrophication of Lake Geneva must not be underestimated as an explanation for the reduction of littoral invertebrates during the same period.

The current invasion corridors and future developments of the European network of inland waterways continue to supply the active and passive dispersion of exogenous species towards Lake Geneva and other Swiss lakes. Several potential exogenous species, already established in the Rhine and/or Lake Constance can be expected in the near future. Appropriate risk assessment tools are required at the national level to address ecological and socio-economic risks and also to promote monitoring programs, propose preventive measures and management options but also to balance negative and positive ecological impacts of these changes.

In conclusion, the continuous spread of new exogenous species in lakes is one of the most important direct driver of biodiversity loss, contributing to potentially affect the functioning of Lake Geneva. The number of exogenous species increases constantly often in high abundance, contributing to a homogenization of the invertebrate communities. The implementation of a long-term monitoring program, initiated to follow the invasion of a single

Table 2. Abundance and richness of the zoobenthic fauna at the two sample sites in late autumn 2012. Non-indigenous species are underlined in orange and year of first observation (1st obs.) is given. ACI: Abundance Contamination Index; TCI: Taxonomic Contamination Index.

species, *Dikerogammarus villosus*, was relevant to explore quantitative changes and bathymetric distribution of neozoan among the invertebrate assemblages.

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