

Long-term population fluctuations of the exotic New Zealand mudsnail *Potamopyrgus antipodarum* and its introduced aporocotylid trematode in northwestern France

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Abstract Long-term studies of invasive populations are rare, which is unfortunate because important aspects of their dynamics may only be detected over long term. For instance, invasive populations can experience substantial population declines, or even crashes, sometime after their introduction and invasion. *Potamopyrgus antipodarum* (Caenogastropoda) is a successful invader, and is rarely parasitized in introduced areas. In France, the snail is parasitized as first intermediate host by only one trematode species (*Aporocotylid* sp. I), native to the snail's home range, New Zealand. Here, we examined the dynamics of the

molluscan assemblage in a French stream on a 14-year interval (2000–2004 and 2009–2013), focusing on this introduced host-parasite association. Overall, *P. antipodarum* was numerically dominant (90.80%) among molluscs, also including sphaeriid clams (9.12%) and pulmonate snails (0.08%). However, during the last monitoring period, we found a substantial population decline of *P. antipodarum*, potentially driven by environmental change, such as decreased water temperature and depth, and possibly competitive interactions with sphaeriids, which became numerically dominant (56.34%). *P. antipodarum* was the only mollusc found infected and only by *Aporocotylid* sp. I. Interestingly, despite low monthly prevalence (from 0 to 1.52%) and snail host population decline, the *P. antipodarum*-aporocotylid relationship appeared to be persistent over time.

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Introduction

Long-term studies of species invasions are relatively rare. This is unfortunate, because although invasive species do undergo periods of rapid population growth and spread [when we deem them “invasive” (Kolar & Lodge, 2001)], they can then strongly fluctuate in

abundance over time, and sometimes even spontaneously collapse (Simberloff & Gibbons, 2004; Strayer et al., 2006; Simberloff, 2013 for reviews). Hence, the preponderance of short-term studies of introduced species will not provide the full understanding of the impacts of invasive species. The demographic success of invasive species can be affected by many factors such as abiotic stresses due to environmental change (e.g., drought, pollution), impacts of parasitism (by parasites introduced after the host introduction and/or native parasites acquired after introduction), and other interactions (Simberloff & Gibbons, 2004; Strayer et al., 2006; Simberloff, 2013 for reviews).

The freshwater snail, *Potamopyrgus antipodarum* (Gray, 1843) (Caenogastropoda), is a globally invasive species, which is a member of the largely Australasian family Tateidae [previously a subfamily of the Hydrobiidae, but now recognized as being a separate family (Zielske et al., 2011; Wilke et al., 2013)]. Native to New Zealand, *P. antipodarum* has invaded streams and lakes of most of the world's continents including Australia, Europe, America, and Asia (Alonso & Castro-Díez, 2012; Collado, 2014). Its introduction on these different continents likely has multiple independent origins, but has involved only a small number of parthenogenetic clones (e.g., Hughes, 1996; Jacobsen & Forbes, 1997; Städler et al., 2005; Hoy et al., 2012). In Europe, only two haplotypes have been reported to date: “t” and “z.” The most widely distributed is haplotype t, which appears to be a generalist in fresh waters, whereas haplotype z is restricted to brackish waters (Städler et al., 2005). As for many invasive species, the successful spread of *P. antipodarum* is at least partly explained by inadvertent human introductions, but also by the snail's mode of reproduction (i.e., ovoviviparity and parthenogenesis), wide physiological tolerances (e.g., euryhalinity), efficient dispersal, and enemy release (predators, parasites) (Alonso & Castro-Díez, 2008, 2012 for reviews). In its native range, *P. antipodarum* is first intermediate host for as many as 20 species of highly host-specific trematodes (Hechinger, 2012), which, as parasitic castrators, generally can substantially impact host populations (e.g., Lafferty, 1993; Gérard, 1997, 2001; Negovetich & Esch, 2008). In contrast, in Europe, populations are rarely parasitized. Previous studies in France and Poland revealed that *P. antipodarum* was infected as first intermediate host by only a

single trematode species and at very low levels ($\leq 0.48\%$ in France, 0.007% in Poland) (Gérard & Dussart, 2003; Gérard & Le Lannic, 2003; Gérard et al., 2003; Zbikowski & Zbikowska, 2009). This trematode was reported for the first time in 1999 in western France (Gérard et al., 2003), where *P. antipodarum* was first recorded in 1912 (Lucas, 1965). DNA sequence analyses indicate that the trematode from French *P. antipodarum* corresponds to *Aporocotylid* sp. I (sensu Hechinger, 2012), a New Zealand blood fluke with a two-host life cycle that infects fishes as final hosts (Gérard et al., 2017). Both in New Zealand and in Europe, the average prevalence of *Aporocotylid* sp. I in *P. antipodarum* is very low (0.07%), suggesting that this trematode probably does not regulate native or introduced snail host populations (Gérard et al., 2017).

Here, we investigate the long-term population dynamics of *P. antipodarum* and its aporocotylid parasite in a French stream over a 14-year period, with intensive sampling during 2000–2004 [just after the first record in 1999 of the parasite in the same region (Gérard et al., 2003)] and 2009–2013 (10 years after). We had three aims. First, we sought to better understand temporal fluctuations of the introduced population of *P. antipodarum* in relation with abiotic and biotic conditions. Therefore, we examine the temporal fluctuations of two major abiotic parameters; water temperature, which is crucial for ectotherms such as molluscs and which can correlate with other physicochemical parameters, and depth, which reflects the availability of habitat/space resources. We also examine the long-term dynamics of the whole molluscan assemblage, which may include potential competitors with the invasive snail. Second, we wished to observe whether there was a delayed regulation or even a crash of the invasive mudsnail following its introduction. Third, we sought to examine details of parasitism by the introduced aporocotylid parasite in the *P. antipodarum* population. Gérard et al. (2017) presented limited information concerning the parasite's prevalence, using pooled samples from this same dataset. Here, we reported higher-resolution details of the prevalence of *Aporocotylid* sp. I in *P. antipodarum* throughout the entire 14-year time period, and we examined the occurrence of parasitic trematodes (including *Aporocotylid* sp. I) in the rest of the molluscan assemblage.

Materials and methods

Study site

We conducted monitoring in a fourth-order oligotrophic stream (Le Petit Hermitage, in Ille-et-Vilaine, eastern Brittany, France, 48°32'N, 1°34'W) draining a 10 ha-catchment area in a riparian wetland at an altitude of ca. 20 m above sea level (see Clément et al., 2002; Lefebvre et al., 2004; Gruau et al., 2004 for site details). Stream flow is characterized by a base-flow period from June to November (mean monthly discharge $\leq 40 \text{ L s}^{-1}$), and a high-flow period from December to May ($> 40 \text{ L s}^{-1}$). Stream substratum is primarily schist, consisting mainly of fine gravel and coarse sand. We measured physicochemical variables in May 2003 (Supplementary Table). Water had medium calcium levels (10–40 mg/l Ca^{2+}), known to provide the most favorable conditions for freshwater molluscs (Dussart, 1976, 1977).

Sample collection and measurements

To ensure a standard search effort, the same person (CG) sampled molluscs at 62 different dates on a 14-year interval during two broad time periods. The early period included June 2000–September 2004, with monthly samples collected in June 2000–June 2001, March 2002–June 2002, September 2002, March–May 2003, May 2004, and September 2004. The later period included April 2009–May 2013, with monthly samples in April 2009–March 2012, and March 2013–May 2013. On each occasion, we measured water temperature ($^{\circ}\text{C}$) and maximum water depth (cm). Then, we trawled a pond-net (nylon mesh: 1 mm, square aperture: $0.5 \times 0.5 \text{ m}$) from the surface sediment through the water column for three minutes along a 20 m long \times 2 m wide area, as in previous studies (Blanc & Gérard, 2001; Gérard & Dussart, 2003; Gérard et al., 2009). We carefully examined the contents in tap water in the laboratory, and we counted and identified all the molluscs, following Glöer & Meier-Brook (1994), to the species level for gastropods and to the family level for bivalves. We measured the shell size of each gastropod to the nearest 0.1 mm, but we only measured bivalve size in March 2003, May 2004, and September 2004. We dissected each mollusc under a stereoscopic microscope to detect infection by larval trematodes

(sporocysts or rediae, and cercariae) and to record sex for gonochoristic species (i.e., *P. antipodarum*). When present, parasites were observed alive under light glass coverslip pressure using bright-field and phase-contrast microscopy.

We dissected females of *P. antipodarum* with shell height $\geq 2.5 \text{ mm}$ to count the number of brooded embryos in March, April, and May 2002 (1008 females), in May 2004 (69), and in March, April, and May 2013 (37). Fecundity was not investigated in females $< 2.5 \text{ mm}$ because the smallest size of gravid females from the stream was previously shown to be about 3.0 mm (Gérard & Poullain, 2005).

We noted the general occurrence of other macroinvertebrates in the pond-net contents without specific identification in March–April 2002, September 2002, and March–April–May 2013; no obvious changes occurred between dates. Macroinvertebrates were classified to the following taxonomic groups: Erpobdellidae, Glossiphoniidae, Lumbriculidae, Conchostreca, Gammaridae, Ephemeroptera, Trichoptera, Zygoptera, Heteroptera, Coleoptera, and Chironomidae. We also recorded some vertebrates throughout the whole 14-year study, including one lamprey *Lampetra planeri* (Bloch, 1784) (Petromyzontidae) and three juvenile stone loaches *Nemacheilus barbatulus* (Linnaeus, 1758) (Balitoridae) in September 2002, and one yellow eel *Anguilla anguilla* (Linnaeus, 1758) (Anguillidae) in September 2009.

Statistical analysis

We report central tendencies as the mean \pm 95% confidence interval (CI). We describe parasitism by prevalence (number of hosts infected with a particular parasite species/number of examined hosts) (Bush et al., 1997). For prevalence, we calculated CI using the score method (Newcombe, 1998).

We performed analyses using R software (R Core Team, 2014). We analyzed temporal variation of the *P. antipodarum* population using a linear model (LM) based on generalized least squares (GLS) to take into account temporal autocorrelation (autoregressive process of order 1) [R package nlme (Pinheiro et al., 2017)]. The number of individuals was \log_e transformed, and the independent variables were time [number of months since the first sampling date, i.e., from 0 (June 2000) to 139 (March 2012)], monitoring period (June 2000–June 2001, March 2002–

September 2004, April 2009–March 2012), water depth, and the interaction between time and monitoring period. The monitoring period of March 2013–May 2013 (3 months) was not included in analyses because it is composed of only three data points. Water temperature was not considered because preliminary analyses showed that it was clearly correlated with time (Spearman correlation: $r = -0.398$, $S = 55,536$, $P = 0.001$) and water depth (Spearman correlation: $r = -0.456$, $S = 57,817$, $P < 0.001$), whereas water depth was not correlated with time (Spearman correlation: $r = -0.142$, $S = 45,356$, $P = 0.270$). We used a Wald test to assess significance of each term of the model and least square means (LSMeans) for post hoc analyses [R package lsmeans (Lenth, 2016)]. When there was a significant interaction between time and monitoring period, we tested the slope of the *P. antipodarum*–time relationship against the null value for each monitoring period. When there was a significant effect of monitoring period, we computed the LSMean abundance and 95% CI of *P. antipodarum* at the middle point of each monitoring period in order to control for possible trends over time within periods. The three CI were Bonferroni-adjusted and examined for overlap.

We analyzed the abundance of Sphaeriidae (\log_e -transformed) in the exact same way as for the abundance of *P. antipodarum*. We tested the general relationship between these two abundances (*P. antipodarum* and Sphaeriidae) independently of the time period using a Pearson correlation test.

Due to the high proportion of zeroes and the very low non-zero values in parasite prevalence and abundance data, it was not possible to fit a proper model on these data, and so we performed no statistical analysis.

We analyzed the fecundity of *P. antipodarum* using a likelihood-ratio test based on a generalized linear model (family: negative binomial, link: \log_e) where the independent variables were the female's size treated as an ordinal factor with five levels: 2.5–2.99, 3.0–3.49, 3.5–3.99, 4.0–4.49, and 4.5–4.99 mm), sampling year (2002, 2004, and 2013), month nested in year (March, April, and May), and the female size \times year interaction. We tested the relationship between the mean monthly fecundity and the total number of *P. antipodarum* sampled the same months using a Pearson correlation test.

We compared mean monthly water temperature between monitoring periods (June 2000–June 2001, March 2002–September 2004, April 2009–March 2012) using an ANOVA based on an LM. We chose mean monthly temperature in order to take into account that temperature was not consistently monitored among the three periods. We applied the same procedure to water depth.

Differences were considered statistically significant at $P \leq 0.05$.

Results

Temporal fluctuations of temperature and depth

Temperature, which varied from 0 to 17°C during the whole study, was different between the three monitoring periods according to the LM model ($F_{2,15} = 27.93$, $P < 0.0001$) (Fig. 1a). Specifically, temperature was significantly lower during the last monitoring period (April 2009–March 2012, $6.4 \pm 0.4^\circ\text{C}$) compared to both the first (June 2000–June 2001, $9.0 \pm 0.4^\circ\text{C}$) and second periods (March 2002–September 2004, $11.7 \pm 0.7^\circ\text{C}$), and temperature was also different between these two periods (Fig. 1a).

Maximal water depth, which varied from 10 to 70 cm during the whole study, was also different between the three monitoring periods according to the LM model ($F_{2,15} = 15.70$, $P < 0.0001$) (Fig. 1b). Specifically, depth was significantly higher during the first period (June 2000–June 2001, 41.4 ± 2.1 cm) compared to both the second (March 2002–September 2004, 28.6 ± 3.7 cm) and third periods (April 2009–March 2012, 25.3 ± 2.1 cm), which were not different from each other (Fig. 1b).

Temporal fluctuations of *P. antipodarum* and its life history characteristics

Potamopyrgus antipodarum abundance showed strong periodicity, with positive autocorrelation being strongest at time intervals of 1–2 months and about 1 year (10–13 months). The LM-GLS model revealed no significant effect of depth on *P. antipodarum* abundance ($F_{1,52} = 2.83$, $P = 0.098$), but a significant effect on abundance of time ($F_{1,52} = 89.38$, $P < 0.0001$), monitoring period ($F_{2,52} = 18.99$,

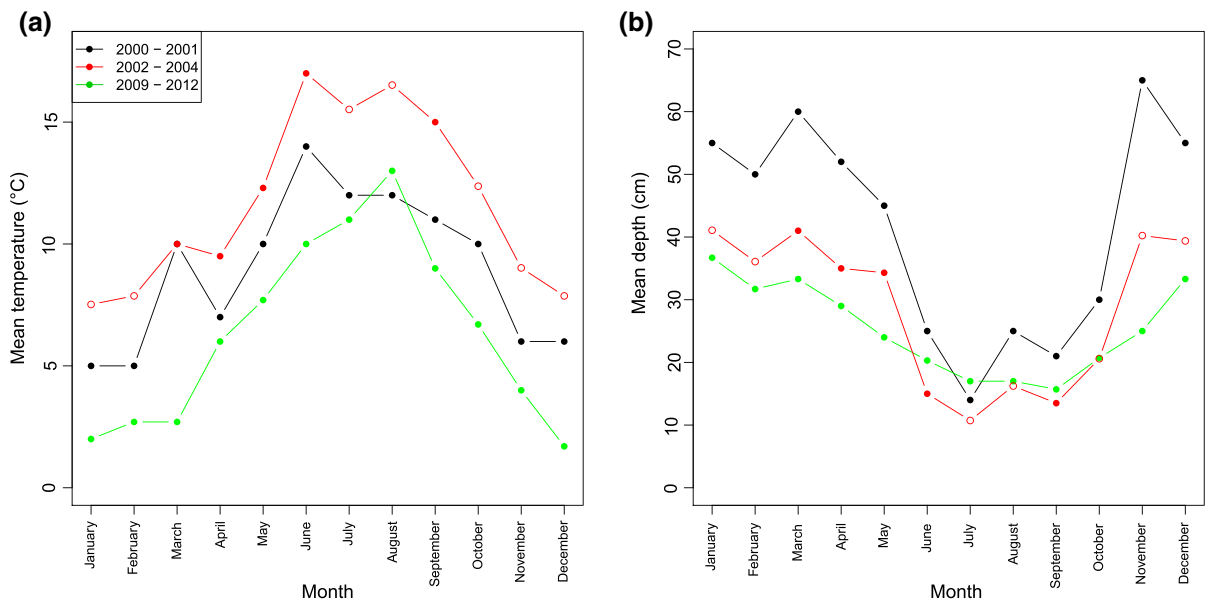


Fig. 1 Temporal fluctuations of (a) water temperature and (b) maximal water depth in the French stream (Le Petit Hermitage) during the three monitoring periods included in

$P < 0.0001$), and their interaction ($F_{2,52} = 3.51$, $P = 0.037$). The mean abundance of snails was significantly different between the three monitoring periods. Indeed, it was sixfold higher during the second period [March 2002–September 2004, back-transformed LSMeans (95% CI): 1,992 (1021–3886) snails] compared to the first period [June 2000–June 2001, 319 (154–664) snails], and 87-fold higher compared to the third period [April 2009–March 2012, 23 (15–36) snails] (Fig. 2a). Moreover, we observed a significant temporal trend of the snail population only during the first monitoring period, with a tenfold increase in population size from June 2000 to June 2001 ($t_{52} = 2.42$, $P = 0.019$) (Fig. 2a). No male *P. antipodarum* was encountered.

According to the GLM, the number of embryos per female significantly increased with shell size ($\chi^2 = 818.90$, $df = 4$, $P < 0.0001$), and did so similarly in each year fecundity data were taken (2002, 2004, and 2013) ($\chi^2 = 10.50$, $df = 7$, $P = 0.162$) (Table 1). The GLM also revealed a significant increase of fecundity from March to April ($\chi^2 = 48.24$, $df = 4$, $P < 0.0001$) (Table 1). Moreover, the mean number of embryos per female was significantly different between 2002, 2004, and 2013 ($\chi^2 = 10.36$, $df = 2$, $P = 0.006$). Specifically, in

statistical analyses, i.e., June 2000–June 2001, March 2002–September 2004, and April 2009–March 2012. Full circles are observed values, empty circles are predicted values

2002 and 2004, the mean embryo number per female, respectively 15.25 ± 0.79 and 16.87 ± 2.86 , was significantly lower than in 2013, i.e., 27.78 ± 7.59 (Table 1). Despite there being a hint that fecundity was highest when *P. antipodarum* density was lowest (Table 1), no correlation was found between the mean monthly fecundity and the *P. antipodarum* abundance ($r = -0.21$, $t_5 = -0.47$, $P = 0.657$). Additionally, *P. antipodarum* populations consistently had adults (individuals > 3 mm), with new snail recruitment at several points throughout the year, and two or even three generations were observed in most months but without obvious period of recruitment [Supplementary Fig. Relative size-frequency distributions from June 2000 to September 2004 (a), and from April 2009 to May 2013 (b)].

Molluscan assemblage and overall parasite prevalence

A total of 29,865 molluscs were collected during the study, among which 90.80% (27,118) were *P. antipodarum*. The other mollusc species corresponded to Sphaeriidae (9.13%), a family of Bivalvia [namely, *Pisidium* spp. Pfeiffer, 1821 and *Sphaerium corneum* (Linnaeus, 1758)], and to Pulmonata (0.07%)

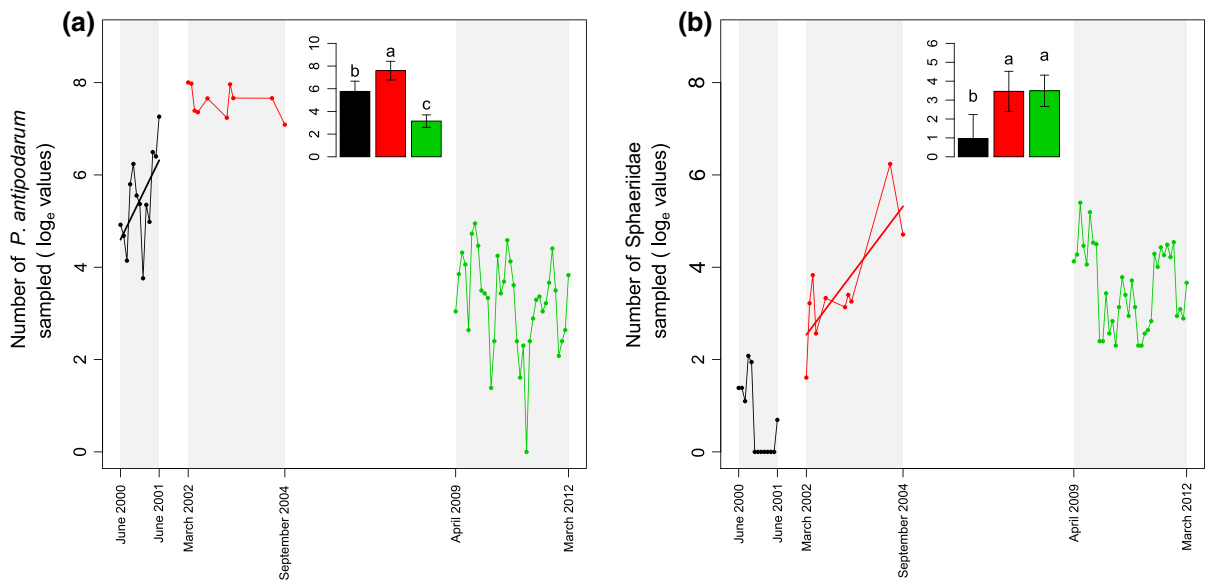


Fig. 2 Temporal fluctuations of (a) *P. antipodarum* abundance (\log_e -values) and (b) Sphaeriidae abundance (\log_e -values) in the French stream (Le Petit Hermitage) during the three monitoring periods included in statistical analyses, i.e., June 2000–June 2001, March 2002–September 2004, and April 2009–March

2012. Sample sizes are indicated in Table 2. Different letters (*a*, *b*, *c*) in bar plots indicate statistically significant differences between monitoring periods. When a statistically significant relationship between mollusc abundance and time was found, this is represented by the corresponding regression line

belonging to five families (Acroloxidae, Ancyliidae, Lymnaeidae, Physidae, and Planorbidae) (Table 2). All the pulmonate snails were juveniles according to their shell size, and included 14 individuals of *Planorbis planorbis* (Linnaeus, 1758), two individuals of *Ancylus fluviatilis* Müller, 1774 and *Aplexa hypnorum* (Linnaeus, 1758) and one individual of *Acroloxus lacustris* (Linnaeus, 1758), *Physa heterostropha* (Say, 1817), and *Radix ovata* (Draparnaud, 1805). Mean species richness of gastropods (seven species in total) over the 62 sampling dates of the study was very low: 1.23 ± 0.13 species.

Despite its high overall relative abundance (90.80%), *P. antipodarum* was numerically dominant only during the first broad time period (June 2000–June 2001, March 2002–September 2004) when it comprised 96.81% of mollusc individuals. In contrast, during the second time period (April 2009–March 2012, March 2013–May 2013), *P. antipodarum* represented only 43.51% of all encountered molluscs, and the Sphaeriidae become the numerically dominant taxon, with 56.34% relative abundance (Table 2). However, no significant relationship was found between the abundance of *P. antipodarum* and the

abundance of Sphaeriidae (Pearson correlation: $r = 0.14$, $t_{57} = 1.11$, $P = 0.272$).

Potamopyrgus antipodarum was the only molluscan species found parasitized (Table 2) and, as reported by Gérard et al. (2017), it was only infected by the trematode species *Aporocotylid* sp. I, with an overall prevalence of 0.09% (CI 0.06–0.14%). Below, we report details on the temporal fluctuations of prevalence.

Temporal fluctuations of Sphaeriidae

Sphaeriidae abundance showed strong periodicity, with positive autocorrelation being strongest at a time interval of 6 months. The LM-GLS model demonstrated a significant and negative effect of depth ($F_{2,52} = 10.23$, $P = 0.002$), and a significant effect of time ($F_{1,52} = 10.49$, $P = 0.002$), monitoring period ($F_{2,52} = 8.36$, $P = 0.0007$), and time x period interaction ($F_{2,52} = 3.82$, $P = 0.028$). The abundance of Sphaeriidae was also higher during the two last monitoring periods [March 2002–September 2004, back-transformed LSMean (95% CI): 31 (13–74) bivalves; April 2009–March 2012, 32 (16–64) bivalves] compared to the first [June 2000–June

Table 1 Mean number (\pm CI) per size class and maximal number (Max) of embryos per female of *P. antipodarum* (Pa) in the French stream Le Petit Hermitage in 2002 (March, April, May), 2004 (May), and 2013 (March, April, May)

Size classes (mm)	2002		2002		2004		2013		2013	
	March	April	May	Mean number/ year	May	May	March	April	May	Mean number/ year
2.5–3.0	0.88 \pm 0.40	4.64 \pm 1.43	–	2.01 \pm 0.58	0.90 \pm 1.14	–	0.00 \pm 0.00	3.00 \pm 38.12	–	1.00 \pm 2.57
3.0–3.5	7.11 \pm 1.01	11.82 \pm 1.38	9.67 \pm 12.50	7.53 \pm 0.93	8.60 \pm 6.56	–	–	24.00 \pm 25.41	7.00 \pm 4.79	10.40 \pm 6.31
3.5–4.0	16.54 \pm 1.13	16.05 \pm 1.97	20.84 \pm 2.17	17.03 \pm 0.94	21.03 \pm 3.26	14	14	–	30.67 \pm 5.13	28.29 \pm 7.14
4.0–4.5	26.68 \pm 1.96	22.77 \pm 3.74	34.33 \pm 1.89	29.60 \pm 1.39	25.33 \pm 5.07	–	–	39.00 \pm 50.82	54.91 \pm 9.25	52.46 \pm 8.47
4.5–5.0	–	–	43.18 \pm 4.56	43.18 \pm 4.56	–	–	–	38	–	38
Mean number/month	12.51 \pm 0.83	12.97 \pm 1.56	29.15 \pm 1.74	15.25 \pm 0.79	16.87 \pm 2.86	2.80 \pm 7.77	2.80 \pm 7.77	24.29 \pm 15.03	33.76 \pm 9.59	27.78 \pm 7.59
Number of Pa dissected	726	129	153	1,008	69	5	5	7	25	37
Max	48	41	61	61	40	14	14	43	74	74

– means that no snails were found in this size class

2001, two (0–6) bivalves] (Fig. 2b). Moreover, we observed a significant temporal trend only during the second monitoring period with a 27-fold increase of Sphaeriidae from March 2002 to September 2004 ($t_{52} = 2.84, P = 0.006$) (Fig. 2b).

Temporal fluctuations of *Aporocotylid* sp. I

The monthly prevalence of *Aporocotylid* sp. I infecting *P. antipodarum* varied from 0.00% (CI 0.00–0.13%, $n = 2871$) in April 2003 to a maximum of 1.52% (CI 0.65–3.50%, $n = 330$) in September 2000 (Fig. 3). The abundance of infected *P. antipodarum* per monitoring period decreased over time, whatever the total abundance of *P. antipodarum* (Table 2). However, the overall prevalence of infection did not significantly vary between monitoring periods, given the generally overlapping 95% CI calculated on the prevalence data [June 2000–June 2001 prevalence = 0.32% (0.19–0.52%), March 2002–September 2004 prevalence = 0.04% (0.02–0.08%), April 2009–May 2012 prevalence = 0.07% (0.01–0.41%), March–May 2013 prevalence 0% (0.00–5.07%)].

Discussion

Molluscan assemblage in Le Petit Hermitage

We recorded seven species of gastropods (the caenogastropod *P. antipodarum* and six pulmonates) and two taxa of bivalves belonging to Sphaeriidae in Le Petit Hermitage during the whole study. However, the diversity was very low over time (1.2 ± 0.1 gastropod species per sampling date) as was the mean abundance of most species ($\leq 0.2 \pm 0.2$ individuals of each pulmonate species per sampling date). The molluscan assemblage in the study site was characterized by a high dominance of the exotic mudsnail *P. antipodarum*, especially during the period of 2000–2004 (97%). By the period of 2009–2013, the relative abundance of *P. antipodarum* decreased to 44% of the molluscan assemblage, which was then dominated by Sphaeriidae (56%). These cosmopolitan bivalves are very common and abundant in Europe, occurring in all types of running and still waters (Boycott, 1936; Dussart, 1979; Holopainen & Jónasson, 1989). Interestingly, while Sphaeriidae were rare

Table 2 Molluscan assemblage (total abundance, A, and relative abundance, A%) in the French stream Le Petit Hermitage from June 2000 to May 2013 according to the monitoring period (NMS = number of monthly samples per period)

	<i>P. antipodarum</i>		Pulmonata		Sphaeriidae		Total	NMS
	A	A%	A	A%	A	A%		
Jun 2000–Jun 2001	4,713 (15)	99.45	4 (0)	0.08	22 (0)	0.46	4,739	13
Mar 2002–Sep 2004	20,941 (9)	96.23	12 (0)	0.06	808 (0)	3.71	21,761	10
Apr 2009–Mar 2012	1,392 (1)	43.66	0 (0)	0.00	1,796 (0)	56.34	3,188	36
Mar 2013–May 2013	72 (0)	40.68	5 (0)	2.82	100 (0)	56.50	177	3
Total	27,118 (25)	90.80	21 (0)	0.07	2,726 (0)	9.13	29,865	62

See the sampling dates for each monitoring period in “Materials and methods”. Number of infected individuals is indicated in parenthesis

(3%) in Le Petit Hermitage during the period of 2000–2004, they were abundant (~ 50% of the molluscan assemblage) at the same time in a nearby pond (about 50 m away), which was connected to the stream during the flood season and where *P. antipodarum* has never been recorded (Blanc & Gérard, 2001; Gérard et al., 2009; Gérard, pers. obs.). We rarely found pulmonates, all native species, in the stream during the study (0.07%) and, when encountered, they were always juveniles. Most of these individuals probably originated from the above mentioned nearby pond, where most of the pulmonate species were commonly recorded and abundant (Blanc & Gérard, 2001; Gérard et al., 2009; Gérard, pers. obs.). Environmental conditions in Le Petit Hermitage appeared unfavorable for these pulmonates compared to the pond (Blanc & Gérard, 2001; Gérard et al., 2009), whereas they seemed to become favorable for Sphaeriidae based on their dominance during the period of 2009–2013.

Temporal fluctuations of abundance and fecundity of *P. antipodarum*

Change in the dynamics of the *P. antipodarum* population was evident during our 14-year field investigation. After an exponential growth, the introduced population strongly declined before the last monitoring period and the snail abundance was about 14-fold lower compared to its initial abundance. Given the long history of the *P. antipodarum* invasion in France [over 100 years, first recorded in 1912 (Lucas, 1965)], we cannot know whether the dynamics we documented in Le Petit Hermitage reflect periodic

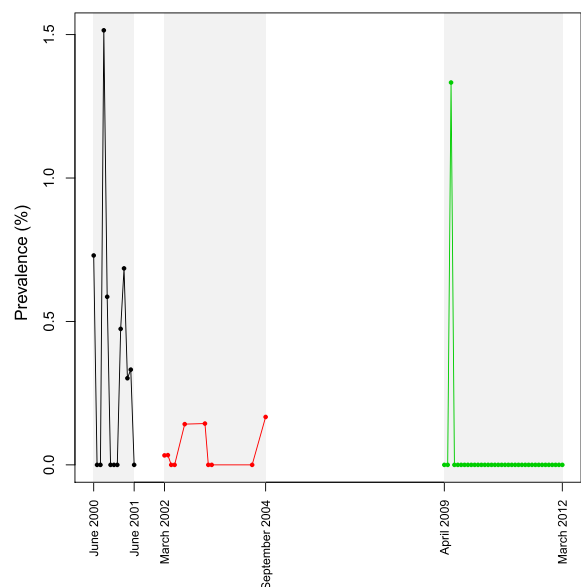


Fig. 3 Temporal fluctuations of *Aporocotylid* sp. I prevalence (%) in the French stream (Le Petit Hermitage) during the three monitoring periods included in statistical analyses, i.e., June 2000–June 2001, March 2002–September 2004, and April 2009–March 2012. Sample sizes are indicated in Table 2. Note that, despite temporal fluctuations, prevalence was always low ($\leq 1.52\%$) throughout the monitoring periods

cycling of a long-established population (Ricklefs & Miller, 2005), or a post-invasion “boom and bust,” similar to that described for *P. antipodarum* in a North American California stream, 7 years after its first report there (Moore et al., 2012). According to relatively short-term (< 5 years) demographic studies, population dynamics of *P. antipodarum* in invaded ranges can be unstable, with unexplained rapid increases and sudden extinctions (e.g., Dorgelo,

1987; McMillan, 1990; Dahl & Winter, 1993; Levri et al., 2008; Cross et al., 2011; Dorgelo et al., 2014). These extinctions, for which the causes remain unknown, occur despite the generally large physiological tolerance characterizing the small number of clones that have invaded most of the world's continents, particularly the generalist clone (haplotype t) from European fresh waters (e.g., Hughes, 1996; Jacobsen & Forbes, 1997; Städler et al., 2005; Hoy et al., 2012), which probably occurs in our study site.

In Le Petit Hermitage, the absence of male *P. antipodarum* indicates that the population was exclusively composed of parthenogenetic females. The lack of sexual reproduction is consistent with what is seen for introduced *P. antipodarum* from Europe, Australia, and America, where males are rare or completely absent (e.g., Wallace, 1978, 1985; Hughes, 1996; Schreiber et al., 1998; Gérard et al., 2003; Gaino et al., 2008; McKenzie et al., 2013; Collado, 2014).

The number of embryos per female *P. antipodarum* in Le Petit Hermitage increased from March to May in each year, and also increased with snail size, as previously demonstrated (e.g., Winterbourn, 1970; Gérard & Poullain, 2005; Gaino et al., 2008; McKenzie et al., 2013). Females were reproductively mature at shell height from 2.5 to 3.0 mm, with up to 74 embryos in the largest females. These results are also consistent with observations for other introduced populations, which mature at size between 2.5 and 3.5 mm, and have maximum brood size ranging from 60 to 89 embryos (e.g., Strzelec & Serafinski, 1996; Gaino et al., 2008; McKenzie et al., 2013).

Based on the size-frequency distributions (Supplementary Fig.), both adult and newly recruited, growing *P. antipodarum* were present throughout the year, but without obvious, constrained periods where most recruitment occurred. In general, parthenogenetic forms of *P. antipodarum* produce offspring throughout the year, with seasonal fluctuations in reproductive output depending on the clonal population considered and environmental conditions such as temperature, hardness (dissolved calcium), phosphorus level, food availability, and population density (e.g., Winterbourn, 1970; Dussart, 1977; Dahl & Winter, 1993; Schreiber et al., 1998; Neiman, 2006, 2013; Tibbets et al., 2010; McKenzie et al., 2013). Females in Le Petit Hermitage had a higher fecundity in 2013 when population densities were low (from 12 to 48 snails sampled per month) than in 2002 and 2004 when

densities were very high (from 1,623 to 2,993 snails per month), although no significant correlation was found between monthly embryo number per adult female and snail abundance. If the high fecundity in 2013 represents fecundity during the last monitoring period (2009–2012), it would indicate that higher mortality rates, not lower birth rates, are what drove population density down. However, it is possible that 2013 represented recently increased individual fecundity preceding the beginning of a new population increase. According to Neiman (2006), a nearly twofold increase in the embryo number per female was observed in low versus high density populations maintained in the laboratory with similar food availability, suggesting that reproductive output may be influenced by intraspecific competition. In contrast, the reproductive output of *P. antipodarum* was much higher in high versus low density conditions in other experiments with no food limitation (Neiman et al., 2013), as also observed in the Italian Topino River (Gaino et al., 2008). Thus, further investigations are needed for a more comprehensive view of the complex connections between environmental quality, resource availability, density, and fecundity of parthenogenetic females, and how they may influence the population dynamics of *P. antipodarum*.

What possible environmental changes may influence the dynamics of *P. antipodarum*?

Despite the difficulty of identifying the causes of *P. antipodarum* population decline in Le Petit Hermitage, we explore two potential explanations.

First, the snail abundance may have been negatively influenced by changing abiotic conditions, such as the substantial decrease in water temperature and depth. Indeed, mean water temperature decreased about 3°C between the first and the last monthly monitoring periods (2000–2001 and 2009–2012), and very low winter temperatures (0–5°C) were frequently observed during 2009–2012 (vs. 2000–2001). Such temperatures (0–5°C) have been associated with lower performance and population densities of *P. antipodarum* in a Danish estuary (Europe) and the Silver Creek watershed (Idaho, USA) (Siegismund & Hylleberg, 1987; Moffitt & James, 2012a, b). In fact, temperature is generally considered to drive *P. antipodarum* dynamics even if temperature tolerance may vary between invasive clones (Gangloff, 1998;

Kerans et al., 2005). Temperature is one of the most significant physicochemical variables positively related to *P. antipodarum* density, as demonstrated in 15 European sites from North West England and the French Bay of Mont St. Michel (including Le Petit Hermitage) (Dussart, 1977; Gérard & Dussart, 2003) and in two California (USA) lakes (Bennett et al., 2015). Hence, it is possible that the temperature decrease explains the substantial decrease in *P. antipodarum* population abundance observed over the 14-year time period.

In addition to the temperature decrease, the water depth decreased by almost half from 2000–2001 to 2009–2012, resulting in a reduced water volume and a more restricted habitat area. In general, the increase in predator pressure and interspecific competition related to the restricted habitat size during drought leads to the elimination of most freshwater gastropods, and new generations typically appear after the water level rises again (Dudgeon, 1983; Gérard, 2001). In small Mediterranean streams characterized by seasonal droughts and floods, *P. antipodarum* populations are generally incapable of achieving very high densities, and this has been attributed mainly to harsh hydrologic conditions (Múrria et al., 2008). In conditions of much deeper depths (≥ 10 m), as in the North American Great Lakes, the density of *P. antipodarum* is influenced by water depth and highest densities occurred between 15 and 25 m, no individuals being detected at less than 13 m and at more than 40 m (Levri et al., 2008). Hence, it is possible that in the shallow studied stream, the water depth (habitat area) decrease may have combined with lower temperatures to negatively influence *P. antipodarum* abundance, explaining its longer-term decline.

Secondly, it is possible that *P. antipodarum* may have been negatively affected by sphaeriid bivalves, or vice versa. Some studies (e.g., Kerans et al., 2005; Hall et al., 2006; Moore et al., 2012) have shown negative interactions between *P. antipodarum* density (and/or biomass) and those of native macroinvertebrates. In a North American California stream for instance, as *P. antipodarum* populations rose and fell, the abundance of native grazing herbivores crashed and then recovered (Moore et al., 2012). In our study, sphaeriid bivalves were rarely recorded during 2000–2001, corresponding to the period of increasing abundance of *P. antipodarum*. Then, sphaeriid abundance rapidly increased about 27-fold from 2002 to 2004, and high abundance

was maintained in 2009–2012 and until the end of the study in 2013, coinciding with the decline of the *P. antipodarum* population. Even if no direct relationship was found between the abundance of Sphaeriidae and *P. antipodarum*, the increase of Sphaeriidae may have amplified the decline of *P. antipodarum* or may have resulted from the decline. Indeed, competitive interactions both for space and nutrients probably occur between them, given their great ecological and physiological similarities. Occurring in a great variety of lotic and lentic waters, Sphaeriidae inhabit the bottom (mud, sand) or bury in the substratum, and often climb up plants (Boycott, 1936; Dussart, 1979; Holopainen & Jónasson, 1989; Dillon, 2004; Korniuschin, 2007), as is also observed for *P. antipodarum* (Alonso & Castro-Díez, 2008, 2012 for reviews). To feed, Sphaeriidae filter phytoplankton, bacteria, and particulate organic matter from the water column (Vaughn & Hakenkamp, 2001; Dillon, 2004; Korniuschin, 2007 for reviews). Interestingly and unlike most other bivalves, they also remove bacteria and organic detritus from the sediment by filtering interstitial water and pedal deposit feeding (i.e., a form of deposit feeding using cilia on the foot to collect buried organic matter) (Vaughn & Hakenkamp, 2001 for review). *P. antipodarum* is a generalist feeder, simultaneously a deposit-feeder, grazer and detritivore, which uses periphytic algae (e.g., green algae, diatoms), bacteria, and detritus, and thus, the same resources as many other macroinvertebrates found in the French stream, including Sphaeriidae (Fenchel, 1975; Haynes & Taylor, 1984; Schreiber et al., 1998; Kerans et al., 2005). Because food limitation is shown to be a primary source of negative density-dependence for *P. antipodarum* (Fenchel, 1975; Neiman et al., 2013), potential decrease of resource availability (not only food but also space) possibly induced by the increased abundance of Sphaeriidae may have contributed to the decline of *P. antipodarum* in Le Petit Hermitage. Hence, further studies are warranted to carefully examine the extent to which competition occurs between *P. antipodarum* and sphaeriids. Such studies might use biomass as a currency, instead of abundance, which could be important given that the sizes of these taxa can substantially differ (e.g., *P. antipodarum* is usually ~ 2 –5 mm length, whereas *S. corneum* can be ~ 10 –12 mm) (Glöer & Meier-Brook, 1994).

We may explain the increased abundance of Sphaeriidae by them responding positively to

changing environmental conditions, as is documented elsewhere. For instance, the great temporal fluctuations of Sphaeriidae (both *Pisidium* and *Sphaerium*) observed in a Danish Lake through a 34-year investigation were possibly due to eutrophication and food availability (Holopainen & Jónasson, 1989). In Le Petit Hermitage, the increase of Sphaeriidae may be related to the substantial decrease of water depth because sphaeriid density was negatively influenced by water depth. More precisely, the rapid increase of sphaeriid abundance from 2002 to 2004 (about 27-fold), followed by consistently high abundance from 2009 to the end of the study, coincided with the lower water levels in Le Petit Hermitage (29 cm in 2002–2004 and 25 cm in 2009–2012 vs 41 cm in 2000–2001). Our results are consistent with the gradual reduction of *Pisidium* spp. abundance in the North American Ottawa River as depth increased beyond 50 cm (Kilgour & Mackie, 1988). Moreover, Sphaeriidae can survive both temporary air exposure and freezing of the sediment they inhabit (Jurkiewicz-Karnkowska & Zbikowski, 2004; Kubíková et al., 2011), yet may perform poorly at increased temperatures [e.g., the declines of *Pisidium amnicum* in the French Saône and Iberian Minho Rivers during heat waves (Mouthon & Daufresne, 2008; Sousa et al., 2011)]. This all suggests that the substantially lower mean and minimum water temperatures and lower depths may have favored the population performance of Sphaeriidae in Le Petit Hermitage, and disfavored the population performance of *P. antipodarum*.

To conclude, both water temperature and depth decrease, and competitive interactions between *P. antipodarum* and Sphaeriidae may contribute to explain the longer-term decline of *P. antipodarum* in Le Petit Hermitage. Other environmental factors, not studied here, may have also contributed to this decline. For instance, microcystins (hepatotoxic cyanotoxins) known to induce the decline of molluscan assemblages in stagnant waters subject to recurrent cyanobacterial blooms (e.g., Gérard et al., 2008) were previously detected in tissues of *P. antipodarum* from Le Petit Hermitage despite the absence of cyanobacteria (Gérard et al., 2009). The large, long-term population drop of *P. antipodarum* in Le Petit Hermitage is similar in magnitude to the decrease documented by Moore et al. (2012) for invasive *P. antipodarum* in a North American California stream. Although the drivers of that population crash are also not known,

the collapse strongly influenced the impacts of the invasive snail on the surrounding ecosystem (Moore et al., 2012). The extent to which such strong fluctuations in population size and impacts occur for *P. antipodarum* more broadly in Europe is unknown given the lack of other long-term data sets on the abundance of this invasive species.

Temporal fluctuations of *Aporocotylid* sp. I prevalence in *P. antipodarum* and number of infected snails

Despite the decreasing abundance of *P. antipodarum* in Le Petit Hermitage, the aporocotylid prevalence did not significantly vary between the monitoring periods and appeared to remain stable over the 14-year study with a mean prevalence of 0.09% and a maximal monthly prevalence of 1.52%. Both the occurrence of a single parasite species in the introduced mudsnail and the low prevalence of this parasite are in accordance with the Enemy Release Hypothesis, namely that the success of introduced species is at least partly driven by them having relatively low levels of overall parasitism (Torchin et al., 2003). The low prevalence of *Aporocotylid* sp. I in Le Petit Hermitage is also consistent with that observed in Poland (Zbikowski & Zbikowska, 2009). Interestingly, this specific parasite (*Aporocotylid* sp. I) also has similarly low prevalence in populations of *P. antipodarum* in the native range (New Zealand) (Gérard et al., 2017). As Gérard et al. (2017) noted, this pattern is also consistent with the general pattern characterizing invasive parasites, where, for those few parasites that make it to an invaded range with their host, there is no general tendency for prevalence to change compared to that in the native range (Torchin et al., 2003). However, the persistence of this host-parasite association in Le Petit Hermitage may be threatened, at least in the long term, if there is a real decline of the host population. Indeed, as the snail host population strongly declined during the study period, so did the number of snails infected by *Aporocotylid* sp. I in Le Petit Hermitage (15 in 2000–2001, nine in 2002–2004, one in 2009–2012, and no infected snails in 2013). Although no infected *P. antipodarum* were detected after June 2009 [i.e., 10 years after the first record in the same region (Gérard et al., 2003)], we cannot infer that the parasite is no longer present. It is possible that the parasite is still present because the low abundance of the snail during that time period

(2009–2013) translated into lower sample sizes compared with the early part of the temporal study (2000–2004). Hence, although we dissected 1,321 snails after June 2009 (from July 2009 to May 2013), the low overall prevalence of the parasite (0.09%) means that we had a 30% chance of missing it [$(1 - 0.0009)^{1321} = 0.30$]. In any case, the population size of *Aporocotylid* sp. I decreased (assuming the river site reflected the broader population) and it remains an open question how much of this drop was driven by the decline in *P. antipodarum* abundance, or by other factors, including those involving the parasite's unknown final host fish in New Zealand, as well as in Europe (Gérard et al., 2017).

Conclusion

In summary, we document a substantial population decline for the invasive *P. antipodarum* in a French stream, indicating that the ecological impacts of this invader have changed over time. This population decline was potentially driven directly or indirectly by documented environmental changes in water temperature and depth and competitive interactions with sphaeriid clams. Further studies are needed to (i) confirm what mechanisms underlie negative density-dependence in *P. antipodarum*, (ii) determine whether the population decline of *P. antipodarum* is more widespread, and (iii) understand how the population collapse has influenced the impacts of this invader on species in the surrounding communities, including the dynamics of its “co-invasive” aporocotylid parasite.

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Compliance with ethical standards

Conflict of interest All of the authors read and approved the paper that has not been published previously nor is it being considered by any other peer-reviewed journal. The authors declare that there are no conflicts of interest.

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