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Distribution and microhabitats of native and non-native gammarids (Amphipoda, Crustacea) in Brittany, with particular reference to the endangered endemic sub-species *Gammarus duebeni celticus*

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ABSTRACT

Aim To assess temporal changes in gammarid distribution in Brittany and microhabitat-use overlap between the endangered endemic *Gammarus duebeni celticus* Stock & Pinkster, 1970, the expanding natives *G. pulex* (Linnaeus, 1758) and *Echinogammarus berilloni* (Catta, 1878), and the introduced *G. tigrinus* Sexton, 1939.

Location Brittany and adjacent regions in western France.

Methods The spatial and temporal patterns in distribution of gammarids at the scale of Brittany were studied using 351 sites. Longitudinal distributions (from the source to the estuary of the river) and microhabitat-use (substratum type and water velocity) were also considered in selected rivers.

Results At the regional scale, all species occurred together less often than expected statistically, with significant deviations from expected for *G. pulex* vs. both *G. duebeni celticus* and *G. tigrinus*, and for *E. berilloni* vs. both *G. duebeni celticus* and *G. tigrinus*. However, at the microhabitat scale, *E. berilloni* occurred significantly more often than expected with the endemic *G. duebeni celticus*, and this appears to be due to similar substratum and water velocity preferences, although at both the regional and microhabitat scales *E. berilloni* prefers wider streams than *G. duebeni celticus*. This study reveals a decline in the endangered *G. duebeni celticus* since 1970.

Main conclusions The longitudinal and local distributions of *G. duebeni celticus*, and the higher-than-expected co-occurrence of the species with *G. pulex*, suggest that the decline of the endemic species may be due to changes in the environment and/or interference from native *G. pulex*, which is expanding its range in Brittany. The results are discussed as regards to the consequences for regional biodiversity.

Keywords

Biodiversity, biogeography, endangered species, freshwater fauna, Gammaridae, historical biogeography, species replacement.

INTRODUCTION

Freshwater ecosystems are rich in biological diversity, but are amongst the most threatened by climate change and human activities such as land use, river regulation, pollution and over-

exploitation (Naiman *et al.*, 1995; Meyer *et al.*, 1999; Dudgeon, 2000; Lake *et al.*, 2000). Even in cases where biodiversity does not decrease *per se*, aquatic fauna can suffer from homogenization (i.e. an increase in the similarity of biota over time) due to the introduction of non-native species, the

extirpation of native species (especially endemics), and habitat alteration, which can facilitate the former two processes (Rahel, 2002; Devin *et al.*, 2005).

Temporal changes in the distribution of aquatic invertebrates in most regions of the world have generally received less study than those of fishes (e.g. Penczak & Kruk, 2000) and Amphibia (e.g. in Asia, Dudgeon, 2000), and information about species extinctions or even inventory lists are lacking for most inhabitants of rivers and streams (Palmer *et al.*, 2000). This is not the case for Gammaridae (Crustacea, Amphipoda) of Brittany, where three extensive studies were performed during the late 1960s and the early 1990s (Pinkster *et al.*, 1970; Gras & Maasen, 1971; Stock, 1993). These studies recorded three species of freshwater gammarid of which two are widely distributed over Western Europe in general, i.e. *Gammarus pulex* (Linnaeus, 1758) and *Echinogammarus berilloni* (Catta, 1878). Also recorded was *Gammarus duebeni celticus* Stock & Pinkster, 1970, which is a distinct sub-species endemic to Western Brittany and Ireland (Pinkster *et al.*, 1970; Stock & Pinkster, 1970; Dennert, 1975; Costello, 1993). The decline of *G. d. celticus* in Ireland has been attributed to the introduction of two continental invaders *G. pulex* and *G. tigrinus* and the resulting interaction (Dick *et al.*, 1990; Dick, 1996; MacNeil *et al.*, 2003), even though *G. d. celticus* and *G. pulex* occur together in some parts of their native ranges (e.g. Brittany). Elsewhere in Europe, introductions of Gammaridae [e.g. *G. tigrinus*, and *E. ischnus* (Stebbing, 1899)] and Pontogammaridae like *Dikerogammarus villosus* (Sowinsky, 1894) have been found to coincide with local extinctions of native Gammaridae (Pinkster *et al.*, 1992; Dick & Platvoet, 2000; Devin *et al.*, 2003; Jazdzewski *et al.*, 2004; Wawrzyniak-Wydrowska & Gruszka, 2005), though habitat alteration is likely to be a contributing factor (Rahel, 2002). The consequences of these environmental changes can be dramatic for the gammarids, as suggested in some locations by the predatory and interference effects of introduced *G. pulex* (Kelly *et al.*, 2003).

In light of the apparent overlap in Brittany of the distributions of an endemic gammarid (*G. d. celticus*), two expanding natives (*G. pulex* and *E. berilloni*) and a non-native gammarid (*G. tigrinus*), the aims of the present study were to assess the temporal change in gammarid distribution at the regional scale and to determine whether a relationship exists in their respective population trends. The specific objectives were to: (1) estimate the rate of invasion of Brittany by non-native species and compare this with other European countries; (2) evaluate the changes in the distribution of native expanding species since 1970; and (3) assess the extent of habitat use overlap between *G. d. celticus* and the other gammarid species.

STUDY SITE, MATERIAL AND METHODS

Brittany encompasses an area of 32,588 km² in western France, with the eastern limit corresponding to a line between the River Loire estuary to the south and the Bay of Mont St Michel to the north (Fig. 1). This part of France consists of two geological sections: two broad coastal granite bands in the north and south and a central band of schist. The Brittany

climate is oceanic temperate, with high precipitation (1400 mm year⁻¹ in the western, coastal part and 700 mm year⁻¹ in the eastern part). Low soil permeability promotes a very dense hydrographical network, which consists of about 28,130 km of rivers and streams. Maximum altitude is 384 m, with a very patchy landscape consisting of woodlands, pastures and agricultural plots.

Temporal changes in gammarid distribution were examined initially at 21 locations along the western limit of *G. pulex*'s distribution using published data from 1969 (Pinkster *et al.*, 1970) and 1992 (Stock, 1993). Recent changes in gammarid population distributions were assessed annually over a period of 8 years (from September 1997 to August 2001, and again in March 2005) at three sites: two locations in the River Aulne, one upstream at Lohuec (48°42' N, 3°54' W) and one downstream at Landeleau (48°26' N, 3°60' W); and a third site in the River Elorn at Plouedern (48°48' N, 4°23' W). Eight samples were taken in these three sites using a quantitative Surber net sampler (0.05 m² with 500- μ m mesh size) in different habitats as described in the French IBGN standardized protocol (AFNOR, 1992).

The spatial distribution of gammarids was examined at three spatial scales.

1. Regional: 351 sites were sampled in 256 rivers between September 2003 and March 2005 with a highest distance of 13 km between sites. Gammarids were sampled with a hand net (500- μ m mesh size) to collect at least 30 individuals at most sites, but with a minimum of 10 individuals in poorly populated sites. At each sampling site, substratum type, water velocity (*V*) and river channel width (*W*) were measured, with the latter two variables categorized by class as follows: water velocity in cm s⁻¹ ($V \leq 5$; $5 < V \leq 25$; $25 < V \leq 50$; $50 < V \leq 75$; $V > 75$); channel width in m ($W \leq 1$; $1 < W \leq 5$; $5 < W \leq 10$; $W > 10$).

2. Longitudinal: between four and six sites from the source to the estuary (where salinity was $< 1 \text{ g L}^{-1}$) were sampled along three rivers (Trieux, Couesnon and Vilaine; Fig. 1) at the most populated habitat, i.e. leaf litter (to remove any risk of between-site variability), using a hand net sampler.

3. Mesohabitat scale: 18 samples were collected at two sites where three gammarids species (i.e. *G. pulex*, *G. d. celticus* and *E. berilloni*) exist in sympatry: the River Trieux at Pommerit le Vicomte (48°62' N, 3°14' W), which is a 4th order stream, with a mean channel width of 25 m and elevated water velocity; the Goaz Col Stream at Plougonver (48°46' N, 3°37' W), which is a slow-flowing second order stream of 1.5 m mean width. Samples at each of two sites were taken in triplicate from each of five habitats (litter, aquatic vegetation, boulder and pebbles), with one sample taken in each water velocity (low, medium or high) in the pebble habitat, using a quantitative Surber net sampler (0.05 m² with 500- μ m mesh size).

4. Microhabitat scale: at eight sites where two or three species co-occurred, gammarids were collected separately in litter, vegetation and pebbles with two current velocities for pebbles.

Biogeographical analyses were undertaken using ArcGIS v9.0 (<http://www.esri.com>) to draw the species distributions and to

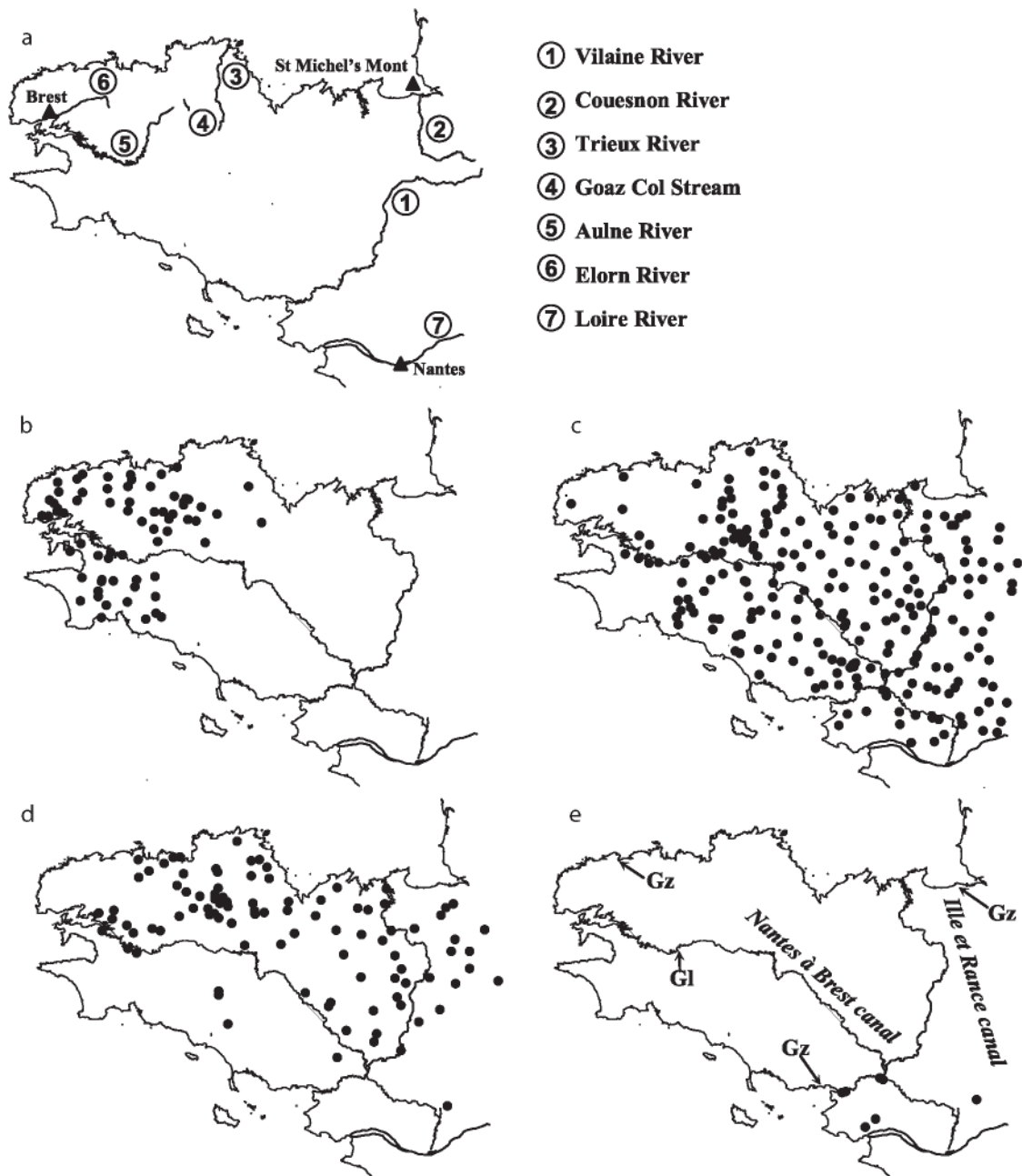


Figure 1 Study area (a) and distributions in Brittany (between September 2003 and March 2005) for gammarid species: (b) *Gammarus duebeni celticus* ($n = 68$); (c) *G. pulex* ($n = 247$); (d) *Echinogammarus berilloni* ($n = 110$); (e) *G. tigrinus*, with arrows to indicate the sites where *G. lacustris* (Gl; Châteauneuf du faou, 48°24' N, 3°6' W) and *G. zaddachi* (Gz; River Couesnon estuary, 48°59' N, 1°51' W; River Loch estuary, 47°69' N, 2°98' W; Flèche Stream, 48°37' N, 4°16' W; Montafilan Stream, 48°54' N, 2°21' W) were found.

compute distance between sites. Electivity indices (preferences/avoidances) were calculated at the catchment scale (stream width) and at the microhabitat scale (width, substratum type and water velocity) as the difference between the frequency of a species in the group of samples associated with a given category of environmental variable and the frequency of that species in all the samples. Values approaching + 0.5 indicate preference and those approaching - 0.5 indicate avoidance. Deviations from the expected frequencies of gammarid occurrence with environmental categories, and of co-occurrence between gammarid

species, were tested for using chi-squared (χ^2) analysis, except where expected values were < 5, when the Fisher Exact test was used. At sites where the gammarid species *G. pulex*, *G. d. celticus* and *E. berilloni* existed in sympatry, differences in species density with respect to the substratum and water velocity were tested for using one- and two-way analysis of variance (ANOVA). Statistical tests were performed using Statistica 6 software (Statsoft™, Tulsa, OK, USA), StatViewSE+Graphics™ (Abacus Concepts Inc., San Francisco, CA, USA) and STATA™ (StataCorp LP Inc., College Station, TX, USA).

RESULTS

At the regional scale (Fig. 1), six gammarid species were observed: five native species (*G. d. celticus*, *E. berilloni*, *G. lacustris* Sars, 1863, *G. pulex* and *G. zaddachi* Sexton, 1912), and one non-native species (*G. tigrinus*), which was first recorded in Brittany in the present study. Three of these species were widely distributed (Fig. 1b–d), whereas *G. lacustris* has been found at only one location, *G. zaddachi* at only four locations and non-native *G. tigrinus* at only eight locations (Fig. 1e), situated in south-eastern Brittany between the River Loire estuary and the River Vilaine estuary. At this regional scale, all of the gammarid species occurred together less often than expected (Table 1). Statistically significant deviations from expected co-occurrence (i.e. ‘avoidance’) were observed for *G. pulex* vs. *G. d. celticus* and *G. pulex* vs. *G. tigrinus* as well as for *E. berilloni* vs. *G.d. celticus* and *E. berilloni* vs. *G. tigrinus*. At the microhabitat scale (Table 1), *G. pulex* also occurred less often than expected with other species, but the associations were statistically significant with *E. berilloni* and the non-native species *G. tigrinus*. Whereas, the association between *E. berilloni* and *G. d. celticus* switched from avoidance to preference (i.e. higher-than-expected co-occurrence); this resulted from the fact that, in the sites where both species co-occurred, *E. berilloni* was present in all the microhabitats sampled. The association between *G. pulex* and *G. d. celticus* switched from very significant to non-significant avoidance between the regional and microhabitat scales; therefore, when only sites containing these two species were considered, they were found to occur together significantly more often than expected (Fisher exact, $P = 0.006$). A lower-than-expected co-occurrence of *E. berilloni* and *G. tigrinus* was observed at both regional and microhabitat scales.

The longitudinal and local distributions of *E. berilloni* and *G. pulex* in the three studied rivers followed different but reciprocal patterns (Fig. 2). Along the River Trieux, *G. pulex* decreased from the source to the estuary, whereas *E. berilloni* increased and became dominant after 15 km from the source (Fig. 2a). The same pattern was observed in the River Couesnon, with a decrease of *G. pulex* after 30 km (Fig. 2b). In the River Vilaine, *G.*

Table 1 Associations between gammarid species (Gp = *Gammarus pulex*, Gd = *G. duebeni celticus*, Gt = *G. tigrinus*, Eb = *Echinogammarus berilloni*) at regional (351 sampling locations) and microhabitat scales (256 sampling points) in Brittany, with significantly lower-than-expected (LTE) and greater-than-expected (GTE) co-occurrences indicated for $P < 0.05$ (*) and $P < 0.0001$ (**) for χ^2 analysis.

	Regional scale			Microhabitat scale		
	Eb	Gd	Gt†	Eb	Gd	Gt†
Gp	LTE	LTE**	LTE*	LTE*	LTE	LTE**
Eb	–	LTE**	LTE*	–	GTE**	LTE*
Gd	–	–	LTE	–	–	GTE

†The Fisher Exact test was used due to expected values being < 5 .

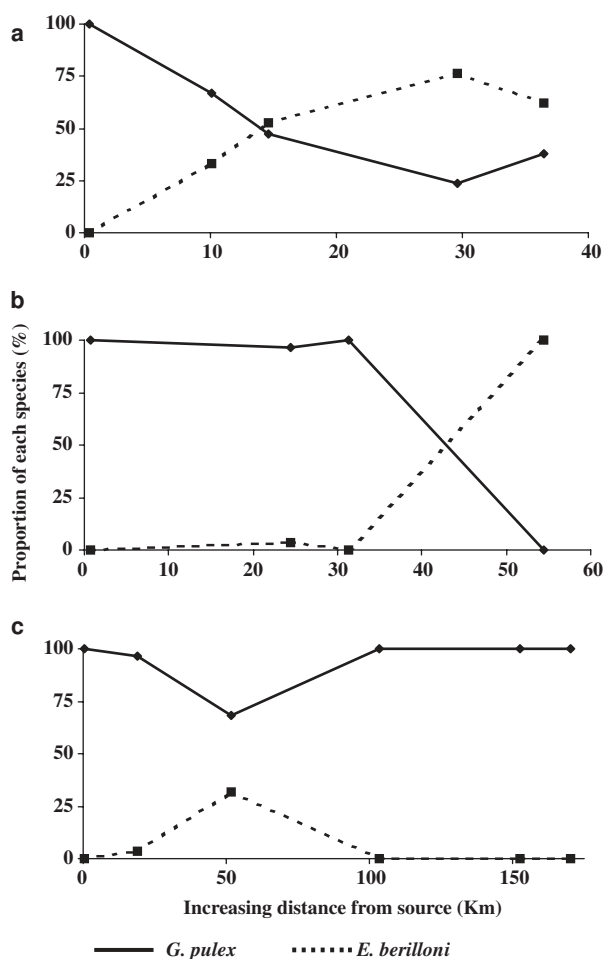


Figure 2 Longitudinal range of relative proportions (%) of *Gammarus pulex* and *Echinogammarus berilloni* in three rivers according to the distance from source: (a) in the River Trieux, (b) in the River Couesnon, and (c) in the River Vilaine (December 2004 and February 2005).

pulex decreased upstream for 50 km as *E. berilloni* increased, but the latter species disappeared after 100 km (Fig. 2c).

The preferences of the four species for stream channel width varied between regional and microhabitat scales (Fig. 3), with statistically significant deviations from expected (preference/avoidance) at the regional scale observed in *G. d. celticus* and *G. tigrinus* only. *Gammarus duebeni celticus* avoided wider streams, and the preference for narrow water courses was also observed at the microhabitat scale, where vegetation substrata and elevated water velocities were preferred. However, *G. tigrinus* preferred wider water courses at both regional and microhabitat scales (Fig. 3), with preference for lentic waters but no apparent preference for substratum type. *Gammarus pulex* showed a non-significant preference for wide rivers at the regional scale, but this was not observed at the microhabitat scale (Fig. 3) where wider water courses and elevated water velocity were significantly avoided, although no substratum preferences were observed. In *E. berilloni*, a weak (non-significant) preference for wide water courses at the

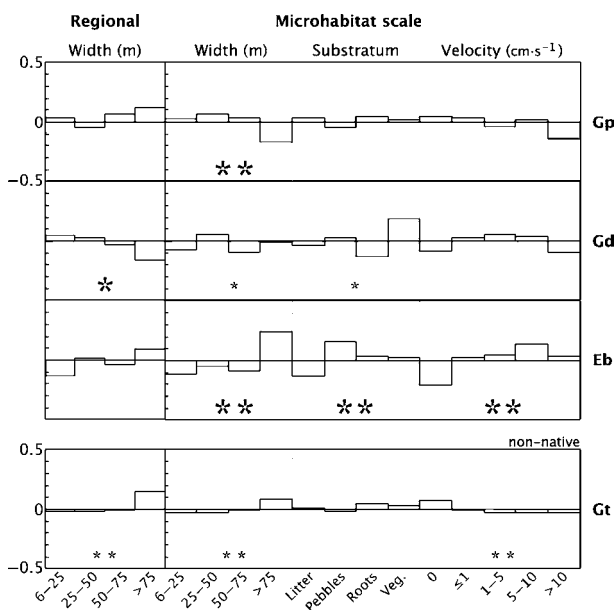


Figure 3 Habitat preferences at the regional scale (river width) and microhabitat scale (river width, substratum type and water velocity) for *Gammarus pulex*, *Echinogammarus berilloni*, *G. duebeni celticus* and *G. tigrinus*, calculated as the difference between the frequency of a species in the group of samples having that category of environmental variable and the frequency of that species in all the samples. Values approaching $|t|0.5$ indicate preference (+) or avoidance (-), with significant deviations from expected ($*P \leq 0.05$; $**P \leq 0.001$) given for chi-squared (large asterisks), or Fisher Exact tests (small asterisks).

regional scale became stronger (significant) at the microhabitat scale, along with significant preferences for pebble substrata and elevated water velocities.

At the mesohabitat and microhabitat scales, gammarid densities varied significantly between substratum characteristics (Fig. 4a, Table 2), with similar patterns observed in both rivers: densities of *G. pulex* were significantly higher in litter and macrophytes, whereas densities of *E. berilloni* were significantly higher in pebbles and boulders (Fig. 4a) and those of *G. d. celticus* were significantly higher in aquatic vegetation (Fig. 4a). In pebble substrata (Fig. 4b), the density of *E. berilloni* varied significantly with water velocity (Table 3), but with reversed patterns in the two rivers: the density of *G. pulex* significantly increased with velocity in the River Trieux and that of *G. d. celticus* decreased with velocity in Goaz Col Stream (Table 3).

Finally, in rivers where *G. pulex* and *E. berilloni* lived in sympatry (Fig. 5), the proportion of *G. pulex* was significantly higher in litter substratum (Tukey's HSD test $P = 0.046$), whereas *E. berilloni* was more abundant in pebbles (Tukey's HSD test $P = 0.046$). No significant differences ($P = 0.841$) in gammarid proportions were observed for pebble substrata between high and low current velocities.

When the temporal changes were considered at the regional scale (Fig. 6), *G. d. celticus* has regressed from east to west, over part of the eastern limit of its distribution, by 10 km (8.1 % of its current distribution) over the last 36 years. First, at the four sites where *G. pulex* and *G. d. celticus* co-occurred in 1969 (Pinkster *et al.*, 1970), only one had *G. d. celticus* in 2005. Secondly, in 2005 *G. pulex* was the only gammarid observed at

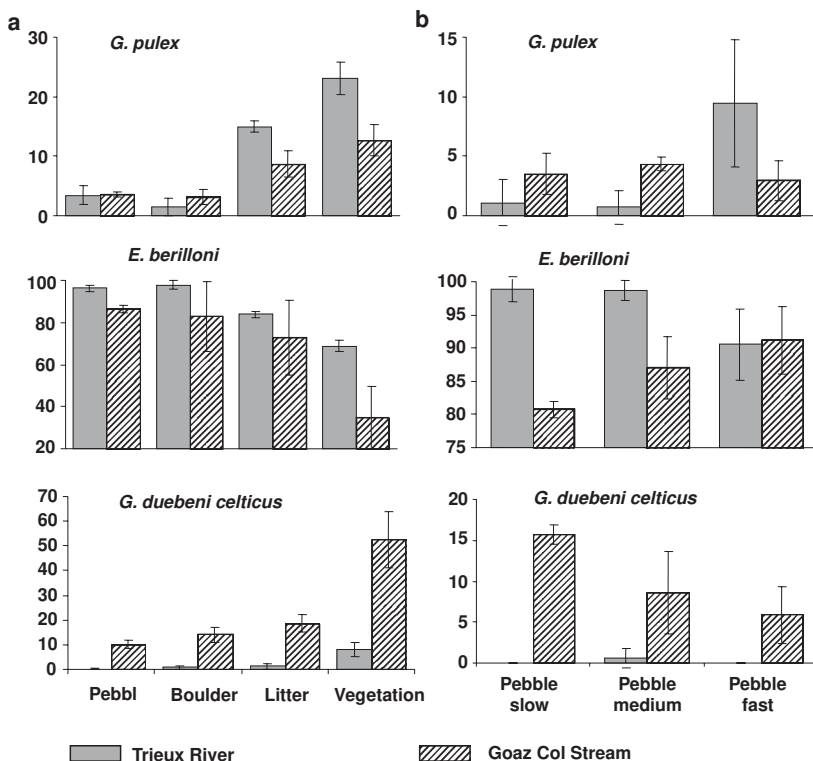


Figure 4 Density (individuals m^{-2}) of *Gammarus pulex*, *Echinogammarus berilloni* and *G. duebeni celticus* on a mesohabitat scale at the River Trieux in October 2004 and Goaz Col Stream in March 2005. Density of gammarids in (a) four types of substratum and (b) three classes of current velocities over pebbles.

Table 2 Results (*F*-test and *P*-values) of one-factor ANOVAS and Tukey's HSD tests (following the ANOVAS) comparing relative abundance of the three species according to the substratum types in the River Trieux and Goaz Col Stream (see Fig. 4a for details).

River	Tested factor	<i>Gammarus pulex</i>	<i>Echinogammarus berilloni</i>	<i>Gammarus duebeni celticus</i>
Trieux River	ANOVA			
	d.f.	15	15	15
	<i>F</i>	20.39	34.71	11.15
	<i>P</i> -values	< 0.001	< 0.001	< 0.001
	Tukey's HSD test			
	Pebble × boulder	n.s.	n.s.	n.s.
	Pebble × litter	0.026	0.017	n.s.
	Pebble × vegetation	< 0.001	< 0.001	0.002
	Litter × boulder	0.009	0.007	n.s.
	Litter × vegetation	n.s.	0.004	0.003
Vegetation × boulder	< 0.001	< 0.001	0.006	
Goaz Col stream	ANOVA			
	d.f.	15	15	15
	<i>F</i>	17.67	77.25	73.88
	<i>P</i> -values	< 0.001	< 0.001	< 0.001
	Tukey's HSD test			
	Pebble × boulder	n.s.	n.s.	n.s.
	Pebble × litter	0.045	0.027	n.s.
	Pebble × vegetation	< 0.001	< 0.001	< 0.001
	Litter × boulder	0.025	n.s.	n.s.
	Litter × vegetation	n.s.	< 0.001	< 0.001
Vegetation × boulder	< 0.001	< 0.001	< 0.001	

Table 3 Results (*F*-test and *P*-values) of one-factor ANOVAS comparing the density (individuals m⁻²) of the three species according to the current velocity (*V*) over pebbles in the River Trieux and Goaz Col Stream (see Fig. 4b for details).

River	Variable	<i>Gammarus pulex</i>	<i>Echinogammarus berilloni</i>	<i>Gammarus duebeni celticus</i>
Trieux River	Velocity in pebbles			
	d.f.	6	6	6
	<i>F</i>	7.66	7.00	0.70
	<i>P</i> -values	0.017	0.021	0.528
Goaz Col stream	Velocity in pebbles			
	d.f.	6	6	6
	<i>F</i>	0.70	4.96	6.04
	<i>P</i> -values	0.534	0.053	0.036

seven of the twelve sites where *G. d. celticus* was the only gammarid in 1969. These seven sites were located upstream of sites where *G. pulex* was sampled in 1969.

When temporal changes were considered at the river scale, different patterns were observed (Fig. 7). At the upstream site on the River Aulne, where *G. pulex* and *E. berilloni* co-occurred, their relative proportions changed little between 1997 and 2005 (with 3.1% coefficient of variation for *G. pulex* and 12.9% for *E. berilloni*; Fig. 7a). At the downstream site on the River Aulne, *G. pulex*, *G. d. celticus* and *E. berilloni* co-occurred from 1997 to 1999. After 1999, the relative abundance of *G. pulex* had increased, whereas that of *E. berilloni* had decreased slightly and that of *G. d. celticus* decreased to zero by 2000 (Fig. 7b). A much stronger pattern was observed in the River Elorn (Fig. 7c), where a sharp decrease in the proportion of *G. d. celticus* coincided with a sharp increase in *G. pulex* since 1997.

DISCUSSION

Changes in the gammarid assemblages of Brittany over the last 30 years have coincided with the introduction of a non-indigenous species (*G. tigrinus*) as well as shifts in the distributions and densities of native species (*G. pulex* and *G. d. celticus*). In this study, the first observation of the distributions of rare native species in Brittany (*G. lacustris* and *G. zaddachi*) did not allow us to draw conclusions about their evolution. It is notable that the distribution of the endemic *G. d. celticus*, a glacial relict that colonized Ireland and Brittany during a glacial optimum when the English Channel was dry (Dennert, 1975), was previously restricted to the western part of Brittany and Ireland (Hynes, 1954). Two opposing hypotheses have been proposed for the current dynamics of the freshwater populations of *G. duebeni* (Hynes, 1954; Sutcliffe, 1967): (1) that *G. d. celticus* colonized freshwater during the

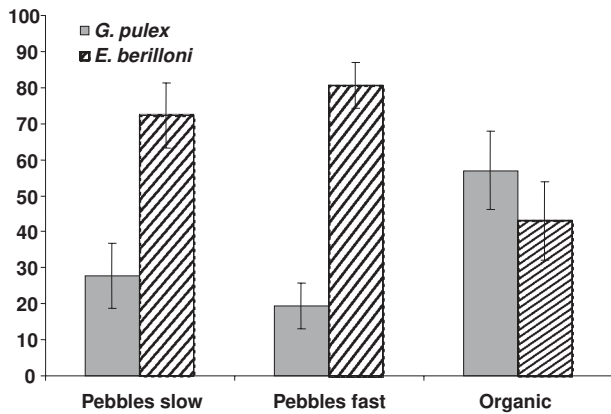


Figure 5 Relative abundance (%) of *Gammarus pulex* and *Echinogammarus berilloni* according to habitat types at 29 locations in Brittany sampled between September 2004 and March 2005. Organics samples consisted of litter and aquatic vegetation. Pebbles were sampled locations with slow ($\leq 30 \text{ cm s}^{-1}$) and fast water velocity ($> 30 \text{ cm s}^{-1}$).

glacial period and was formerly widespread in most Western Europe before being eliminated from freshwater through competition with *G. pulex* (Hynes, 1954); or (2) that the species is a recent colonizer of freshwaters that has gradually extended its range inside the continent (Sutcliffe, 1967). Whilst favouring Hynes' hypothesis, Pinkster *et al.* (1970) and Stock (1993) were unable to provide supporting evidence due to the absence of historical references (Pinkster *et al.*, 1970) and/or significant changes in the recent distribution of the two species (Stock, 1993).

Our results support Hynes' hypothesis, demonstrating both potential microhabitat co-exploitation and a regression in the range of endemic *G. d. celticus*. At the microhabitat scale, the omnipresence of *E. berilloni* at sites occupied by *G. d. celticus*, combined with the positive association between *G. d. celticus* and *G. pulex* at sites where the two co-occur, suggests that either *G. pulex* is merely creating itself a niche in areas vacated by *G. d. celticus* when it is displaced by *E. berilloni*, or the expanding natives *G. pulex* and *E. berilloni* are working commensally to displace the endemic species. The regressions in range of *G. d. celticus* in Brittany (Fig. 6) resemble that reported in Ireland (Costello, 1993; Dick, 1996), and neither



Figure 6 Temporal changes in the distribution of *Gammarus duebeni celticus* (a) and *G. pulex* (b) in Brittany. The circles correspond to sites at the limit of the gammarid distribution observed by Pinkster *et al.* (1970) in 1969 (open circles) and sites at the limit of their actual distributions (filled circles). The continuous line corresponds to the actual distribution of gammarids and the dotted line to their distribution between 1969 and 1992.

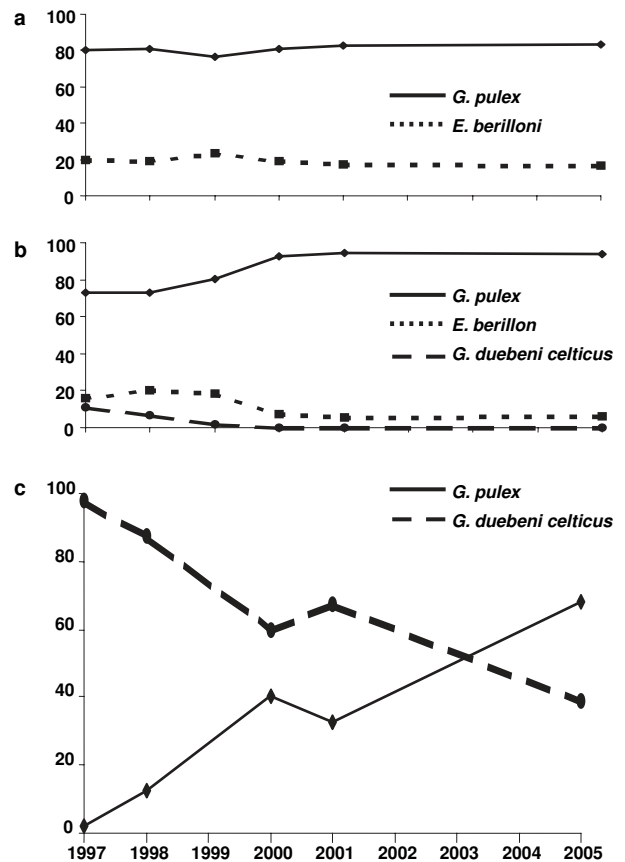


Figure 7 Temporal change in the proportions (%) of gammarids in three stations since 1997: (a) an upstream site in of the Aulne River; (b) a downstream site in the River Aulne and (c) in the River Elorn.

appears to be a recent process. Indeed, the presence of *G. d. celticus* at an isolated site on the River Trieux, outside of the known eastern limit of the species (Pinkster *et al.*, 1970), suggests that this species had a wider distribution in Brittany in the past.

The mechanism for range regression of *G. d. celticus* in Brittany remains unclear, as microhabitat preferences suggest limited overlap (i.e. potential competition for resources) between the endemic and the native species. The native *E. berilloni* had a significant positive association with

G. d. celticus (Table 1), but rather different microhabitat preferences (Fig. 3) – *E. berilloni* preferred pebble substrata in wide, faster-flowing rivers, which contrasts with the preference of the endemic *G. d. celticus* for vegetation in narrow, moderate-flowing water courses. The decline of the endemic *G. d. celticus* may be the result of other human-induced impacts (e.g. river regulation and organic pollution) which have intensified in Brittany over the last 100 years. For example, *G. d. celticus* is known to be more abundant in well oxygenated, good quality water (MacNeil *et al.*, 2001a,b, 2004), but the species' water velocity preferences appear to be quite broad, although it avoids lentic and fast-flowing waters (Fig. 3). This could suggest an adaptation for variable river discharge, which is one of the features of water courses that is lost when rivers are regulated. Moreover, the increase of intensive livestock farming and cultivation in Brittany since 1971 has had an adverse effect on water quality in Brittany except in the Armorique National Nature Park (French Water Agency, <http://www.eau-loire-bretagne.fr/>), where adverse impacts of agricultural activities have been limited and no decline in *G. d. celticus* was observed.

Another contributory factor in the regression of *G. d. celticus* in Brittany may be the interaction with *G. pulex*, such as already proposed for England and Ireland (Dick *et al.*, 1990). In the present study, the replacement of *G. d. celticus* by *G. pulex* was observed at sites where the two species had co-occurred in 1969, or where *G. pulex* had occurred in the downstream part of the rivers (Pinkster *et al.*, 1970). We also observed a concurrent disappearance of *G. d. celticus* and appearance of *G. pulex* in the rivers Aulne and Elorn since 1995. One possible explanation for the decline in *G. d. celticus* could be the combined effect of the overlap of the microhabitat of the endemic with that of *E. berilloni* (Table 1) and the emerging omnipresence of *G. pulex*, which appears to be a microhabitat generalist (Fig. 3) and a predator (as males) on moulted females of *G. d. celticus* (Dick *et al.*, 1990, 1999; Dick, 1996). The colonization of ten new sites by *G. pulex* during the last 10 years at the western limit of the species' distribution may have been facilitated by two factors. First, the Nantes à Brest canal, which transects the former range of *G. d. celticus*, is an invasion pathway already colonized by *G. pulex* (Pinkster *et al.*, 1970), which is now expanding into the canal's tributaries. Secondly, new isolated populations of *G. pulex* may have been randomly established in the western coastal rivers through accidental transport by waterfowl or anglers.

Of particular note in the present study was the appearance of *G. tigrinus*, a euryhaline North American species with wide water quality tolerances (Pinkster, 1975) that has not previously been reported for Brittany (Pinkster *et al.*, 1970; Gras & Maasen, 1971). The *G. tigrinus* population in south-eastern Brittany is restricted to an area between the Vilaine and the Loire estuaries (Fig. 1) and appears to have no natural connection with other European populations. This non-native species was probably introduced accidentally by ships, which visit large harbours (Nantes and Arzal) in this part of France from other European countries where *G. tigrinus* has become

established (i.e. England, Germany, Netherlands and Poland) or from North America, where *G. tigrinus* is native. Ship traffic has been identified as the dispersal mechanism for *G. tigrinus* now established in several harbours in the Netherlands (Pinkster *et al.*, 1992), Ireland, England (Gledhill *et al.*, 1993) and the Baltic sea (Szaniawska *et al.*, 2003; Jazdzewski *et al.*, 2004). Invasions elsewhere in Europe by *G. tigrinus* have been dramatic, with evidence of native species being eliminated by the invader (Pinkster *et al.*, 1992). The occurrence of *G. tigrinus* at these few locations of south-eastern Brittany (Fig. 1e) may explain the current absence of *G. pulex* and *G. zaddachi*, which were present at these locations in 1970 (Gras & Maasen, 1971). The exclusion of *G. pulex* by *G. tigrinus* was often attributed directly to their relative reproductive outputs and resistance to water pollution (Hynes, 1955; Chambers, 1977; Pinkster *et al.*, 1977, 1992). However, a high reproductive output alone would not be sufficient for *G. tigrinus* to out-compete *G. pulex* reproductively (Dick, 1996), and therefore it is likely that some interspecific interaction (competition and predation) is involved. In view of its high environmental plasticity, *G. tigrinus* is likely to invade most of the lentic waters of Brittany, expanding from its current distribution in the River Vilaine to the west via the Nantes à Brest canal and to the north via the Ille et Rance canal. However, because *G. tigrinus* prefers large and slow-flowing rivers, the species' distribution within river catchments may not extend to the upstream river stretches, where native Gammaridae currently exist.

In conclusion, the current distribution of gammarids in Brittany appears to result from the combined influences of environmental change (in particular river regulation) and of two colonization processes: a post-glacial colonization by the European native species *G. pulex* and a recent invasion by the introduced, North American, species *G. tigrinus*. The consequences of these factors could be very different. *Gammarus tigrinus* is likely to be restricted to the downstream part of large rivers and where it is expected to interact with *G. pulex* and *E. berilloni*, and perhaps also *G. zaddachi* in estuarine areas. Even if all of these species may be eliminated by *G. tigrinus*, then the most apparent direct effect on the regional biodiversity would be the loss of *G. zaddachi*, as the other two species are post-glacial invaders. However, the indirect effect of *G. tigrinus* invasion would be the restriction of *G. pulex* to mid- and upstream stretches, potentially accentuating the pressure that *G. pulex* may already be exerting on the threatened endemic *G. d. celticus*. In addition to regular monitoring of gammarid distributions in Brittany, future research should focus on the interspecific interactions between, and the relative water quality tolerances of, *G. pulex* and *G. d. celticus* in the rivers of Brittany.

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