

## Role of behaviour in biological invasions and species distributions; lessons from interactions between the invasive *Gammarus pulex* and the native *G. duebeni* (Crustacea: Amphipoda)

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### Abstract

In attempting to understand the distributions of both introduced species and the native species on which they impact, there is a growing trend to integrate studies of behaviour with more traditional life history/ecological approaches. The question of what mechanisms drive the displacement of the fresh-water amphipod *Gammarus duebeni* by the often introduced *G. pulex* is presented as a case study. Patterns of displacement are well documented throughout Europe, but the speed and direction of displacement between these species can be varied. From early studies proposing interspecific competition as causal in these patterns, I review research progress to date. I show there has been no evidence for interspecific competition operating, other than the field patterns themselves, a somewhat tautological argument. Rather, the increased recognition of behavioural attributes with respect to the cannibalistic and predatory nature of these species gave rise to a series of studies unravelling the processes driving field patterns. Both species engage in 'intraguild predation' (IGP), with moulting females particularly vulnerable to predation by congeneric males. *G. pulex* is more able both to engage in and avoid this interaction with *G. duebeni*. However, several factors mediate the strength and asymmetry of this IGP, some biotic (e.g. parasitism) and others abiotic (e.g. water chemistry). Further, a number of alternative hypotheses that may account for the displacement (hybridization; parasite transmission) have been tested and rejected. While interspecific competition has been modelled mathematically and found to be a weak interaction relative to IGP, mechanisms of competition between these *Gammarus* species remain largely untested empirically. Since IGP may be finely balanced in some circumstances, I conclude that the challenge to detect interspecific competition remains and we require assessment of its role, if any, in the interaction between these species. Appreciation of behavioural attributes and their mediation should allow us to more fully understand, and perhaps predict, species introductions and resultant distributions.

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### Introduction

Even although the 'father' of invasion biology, Charles S. Elton, warned us in 1958 of the dangers of invasive species as 'ecological explosions', fifty years later we find that the rate of arrival of new species has actually accelerated in many areas (e.g. Ricciardi, 2006). Invasive species are recognised as drivers of population (local/regional) and global extinctions of native species (see Ricciardi, 2004; Clavero and Garcia-Berthou, 2005) and are thus major determinants of species distributions at multiple spatio-temporal scales (Lockwood, 2007). Elton's descriptions of the spread of invasive species have been formalised mathematically in modern volumes (see Shigesada and Kawasaki, 1997) and many of the ecological processes and impacts of invasives are understood. A more recent emerging field, however, has been the integration of behavioural traits into studies seeking to understand and predict invasive species success and impacts on natives (Holway and Suarez, 1999; Dick and Platvoet, 2000; van Riel *et al.*, 2007; Bollache *et al.*, 2008). It is the purpose of this paper to give a case study of

how appreciation of behavioural traits, and their mediation by abiotic and biotic factors, can lead to greater understanding and, perhaps, prediction of invasive and native species distributions in space and time.

I briefly review studies over the past 50 years or so that have sought to unravel the processes behind the patterns of displacement of the freshwater amphipod *Gammarus duebeni* by *G. pulex*. Both are considered as native to Europe, but the latter has been introduced by man into many areas, particularly islands. This study system is ideal for the present endeavour; while the field patterns are historically as well as contemporarily well documented, the scientific journey to understanding the processes behind shifting distributions moved from the purely life history/ecological to the behavioural. In addition, many early anecdotes of behavioural traits of these species were subsequently examined in rigorous experiments and the traits found to be causal in the displacement patterns. Further, Elton (1958) himself comments on this system, reporting on HBN Hynes' experimental introductions of *G. pulex* into the Isle of Man, where *G. duebeni* is also found (see Dick *et al.*, 1997) and states that 'the only place where both occur living together is the Isle of Man,

where possibly the balance is in the process of change' and that, as with other examples of invader/native interactions, 'the complete unravelling of any of these relationships will be an interesting but often very difficult task'. While I cannot claim the complete unravelling of this story, I can show that significant advances have been made when the appreciation of the animals' behaviour was combined with study of their ecology.

### Field patterns of the native and invader

In 1955, HBN Hynes wrote that 'on the whole, when *G. pulex* has been present on any land mass for a considerable time *G. duebeni* is completely absent from fresh water'. This has been largely true for *G. d. celticus*, the recognised freshwater form of *G. duebeni* (see Stock and Pinkster, 1970; Rock *et al.*, 2007). However, *G. duebeni* has persisted long-term in some French rivers (Dunn, 1995; Stock, 1993; Piscart *et al.*, 2007), the Isle of Man (Dick *et al.*, 1997; MacNeil *et al.*, in press) and Irish rivers, even 50 years after deliberate introduction of *G. pulex* into Ireland by fishermen (Strange and Glass, 1979; Dick *et al.*, 1990a, 1994; MacNeil *et al.*, 2001a). Indeed,

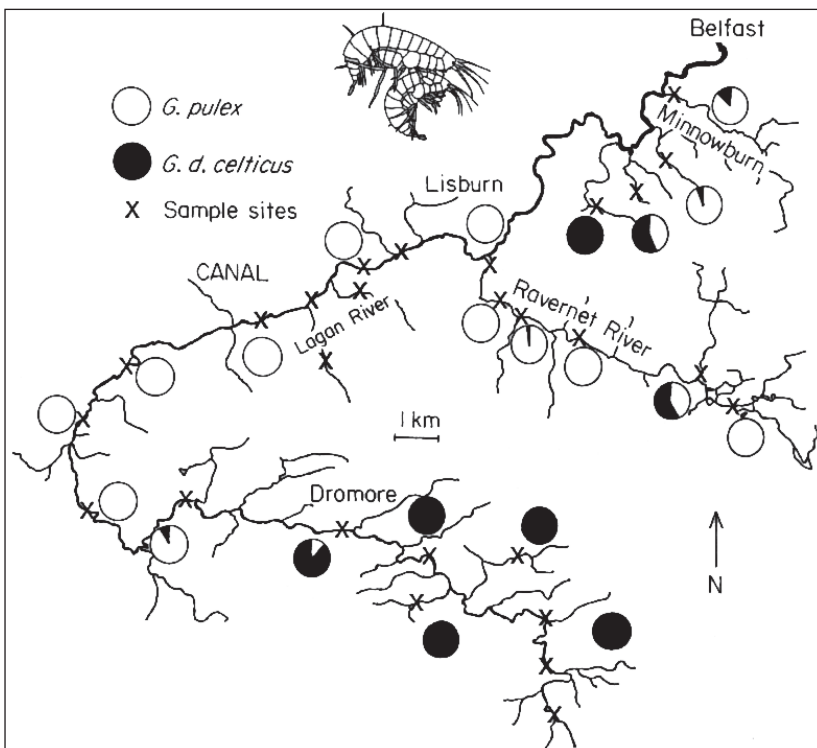


Fig. 1. Typical invasion pattern by *Gammarus pulex* (here, the River Lagan, N. Ireland; see Dick *et al.*, 1990a, 1994). *G. duebeni* is rapidly replaced in lower sections, with short reaches of often temporary co-occurrence further upstream. *G. duebeni* appears able to withstand invasion in the uppermost reaches.

the accepted uni-directionality of *G. pulex* ousting *G. duebeni* has been challenged, such as with the disappearance of *G. pulex* from a few Irish river sites and their re-colonisation by *G. duebeni* (Dick *et al.*, 1994), some failed introductions of *G. pulex* into Isle of Man streams populated with *G. duebeni* and the disappearance of *G. pulex* after many years co-occurring with *G. duebeni* in one such stream (Dick *et al.*, 1997; MacNeil *et al.*, in press).

Figure 1 shows a typical pattern of invasion by *G. pulex*, whereby *G. duebeni* is rapidly replaced in lower stretches of rivers and streams, there are some points of contact where the species co-occur for some time but usually (although not always) eventually becoming pure *G. pulex*, while some upper stretches of stream remain pure *G. duebeni* for decades (see also Pinkster *et al.*, 1970). In addition, along the shores of Ireland's Loughs, such as L. Neagh and L. Beg, all possible combinations have been found of *G. duebeni* and *G. pulex* and the N. American invaders *G. tigrinus* and *Crangonyx pseudogracilis* (Dick, 1996; MacNeil *et al.*, 2001a). Further, this pattern, while constant at the scale of whole lakes, is very dynamic over time at the scale of individual patches or sites, with 82% of sites changing in their amphipod community structure between summer and winter (i.e. over 5 months; MacNeil *et al.*, 2001a). Thus, the drive has been not only to understand the displacement of *G. duebeni* by *G. pulex*, but also elucidate factors which speed up, slow down or even reverse this pattern and illuminate mechanisms of co-existence of these species at various spatio-temporal scales.

### Linking processes with patterns

When an invasive species arrives and native species decline, there may be several causative mechanisms acting alone or in concert. Where the invader is a known predator and directly consumes natives, which is a rather obvious interaction, the cause is often then clear, such as with introduced predatory fish in Panama (Zaret and Paine, 1973) and snakes on Guam (Fritts and Rodda, 1998). In some circumstances, disease or parasites are transmitted from invader to native, again often relatively easily observed, such as from introduced to native sturgeon (Dogiel *et al.*, 1958) and similarly with crayfish, squirrels and others (see Prenter *et al.*, 2004). Hybridization can be the causative mechanism of

displacement, such as with crayfish (Perry *et al.*, 2001) and birds (Munoz-Fuentes *et al.*, 2007). Where invader and native are taxonomically and/or trophically similar, interspecific competition is often inferred or assumed. The evidence for invader/native competition may be good (e.g. zebra mussels and native bivalves; Strayer and Smith, 1996; Ricciardi *et al.*, 1998), however, competition is both much more difficult to 'observe' or detect and subject to alternative explanations, requiring rigorous experimental assessment (see Schoener, 1983; Petren and Case, 1996). Overlap in diets or 'niches' were popular ways of inferring competition (see Lawlor, 1980), with natives and invasives often compared in this way (e.g. Gee and Young, 1993). The advent of stable isotope analyses may have strengthened conclusions as to competition and invaders' impacts on trophic relationships (e.g. Vander Zanden *et al.*, 1999; van Riel *et al.*, 2006; Karlson *et al.*, 2007), however, alternative mechanisms may be untested or overlooked. Indeed, my readings of the literature on the displacement of *G. duebeni* by *G. pulex* often found the term 'competition' used rather loosely as an assumption that it must be occurring since the species were closely related and of the same 'functional feeding group' (see MacNeil *et al.*, 1997 for critique of FFG).

Hynes (1954) investigated the generally mutually exclusive distributions of *G. duebeni* and *G. pulex* and concluded that this pattern 'indicates that competition occurs between the species', but also reports that in his laboratory, when the species were placed together, there seemed to be no 'mutual interference'. Later, Hynes (1955) alludes to competition among *Gammarus* species as causal in their distribution patterns and reasons that the higher 'biotic potential' (yearly offspring production of a typical female) of *G. pulex* may explain why it is an 'ecologically dominant species'. The 'biotic potential' argument is rather contradicted in the paper since Hynes calculated that *Crangonyx pseudogracilis* has a biotic potential at least 10 times greater than *G. pulex*, but the former does not 'dominate' the latter, indeed quite the reverse (see also Dick, 1996; MacNeil *et al.*, 2000). Hynes (1955) does, however, suspect that it is 'possible that [*G. pulex*] has some other ecological advantage which offsets its lower reproductive rate, but this is not at present apparent'. Our studies subsequently showed that *G. pulex* is an effective predator of *C. pseudogracilis* (Dick, 1996; MacNeil *et al.*, 1999).

The theme of competition among *Gammarus* species and a link with differences in reproductive output were pursued by the Dutch. Pinkster *et al.* (1970) assumed that *G. duebeni* was in 'strong competition with' a number of other *Gammarus* species including *G. pulex*, and indeed assert that, because the two species were rarely found together, 'these data clearly reveal that there must be a strong interspecific competition between *G. duebeni* and *G. pulex*'. Pinkster also favoured the link between reproductive output and competition, stating that 'its [*G. duebeni*] reproductive capacity is too low to compete successfully with the other species now present' (Pinkster *et al.*, 1992). However, this argument fails to articulate which resources may be subject to competition, if the resources are limited in supply, the mechanisms of differential use of those resources (simple exploitation and/or interference), or any measurements of the fitness effects of 'competition'. Further, no alternative interspecific interactions were hypothesised or tested. However, Dennert (1974) purports to experimentally examine interspecific competition among *G. pulex*, *G. d. duebeni* and *G. d. celticus*. Whilst a good introduction to the definition of competition is provided, the experiments do not actually test for competitive effects (under resource limitation) on major components of fitness (i.e. principally growth, reproduction, and mortality), but focus solely on survival rates. No indication is given of any resources supplied in such a way that they are limiting, a pre-condition for the operation of competition, as described by the author himself. The author does, however, admit that the interspecific interactions among such species could be competitive and/or predatory. Nevertheless, the paper does not provide convincing support for the operation of interspecific competition. Further, nothing is said of the fate of dead *Gammarus* in experimental aquaria, whether they died and the cadavers remained in the tanks or, as in the (closely monitored) similar experiments of Dick *et al.* (1999), animals were lost from the tanks due to predation between the species, which was actually observed.

Finally on this point of 'biotic potential', there are mixed conclusions recently as to whether high fecundity is a typical characteristic of invasive gammarids and their success in displacing native gammarids (see Devin and Biesel, 2007; Grabowski *et al.*, 2007). Certainly, there are cases where invaders with high fecundity have displaced those with lower fecundity, for example, *G. pulex* (see Hynes, 1955)

and *Dikerogammarus villosus* (see Pockl, 2007) have done so, but some highly fecund species, such as *Crangonyx pseudogracilis* (see Dick *et al.*, 1998) have not. What is more important in my view, is understanding the mechanism(s) of interaction (if any) between invader and native and asking if differences in reproductive output contribute to this process. For example, species that are stronger intraguild predators (see below) and have high reproductive output relative to natives may be more likely to displace native species.

Even in the face of evidence to the contrary, for decades many authors stuck to the perceived wisdom that *Gammarus* were shredders of leaves and that carnivory was a lesser life-style, with actual predation observed but rather ignored as to its implications. Hynes (1954 and references therein) noted cannibalism and the predation of other taxa by *G. pulex* and *G. duebeni*, while Pinkster (1970) and Dennert (1974) recognised cannibalism of juveniles in *G. duebeni*. Indeed, the cannibalistic nature of *Gammarus* was seen as a nuisance to their study rather than as a *bona fide* intraspecific interaction (see Dick, 1995; MacNeil *et al.*, 2003b) that foretold of an interspecific predatory nature both towards other *Gammarus* species and other invertebrate groups. A review by MacNeil *et al.* (1997) challenged the perceived 'functional feeding group' classification of *Gammarus* spp. as 'shredders' and finally demonstrated that predation was a fundamental part of the feeding repertoire of species such as *G. pulex* and *G. duebeni*. That review also highlighted the growing evidence that *Gammarus* species engaged in 'intraguild predation', or IGP, a phenomenon that is associated with cannibalism (see Polis *et al.*, 1989), since a propensity for the killing and eating of conspecifics is easily transferred to congeners and other related taxa. Indeed, IGP in *Gammarus* species was identified by Meijering (1972) and Goedmakers and Roux (1975), although the term IGP was not used, rather, the term 'cannibalism' was used to describe killing and consumption in both intra- and interspecific contexts.

While the experiments of Meijering (1972) and Goedmakers and Roux (1975) brought intra- and interspecific pairings of male and female *Gammarus* spp. together, the context was attempts to understand the systematic relationships and mating isolating mechanisms among the species, rather than the effects of interspecific interactions on distributions and abundances. It was similar experiments, this



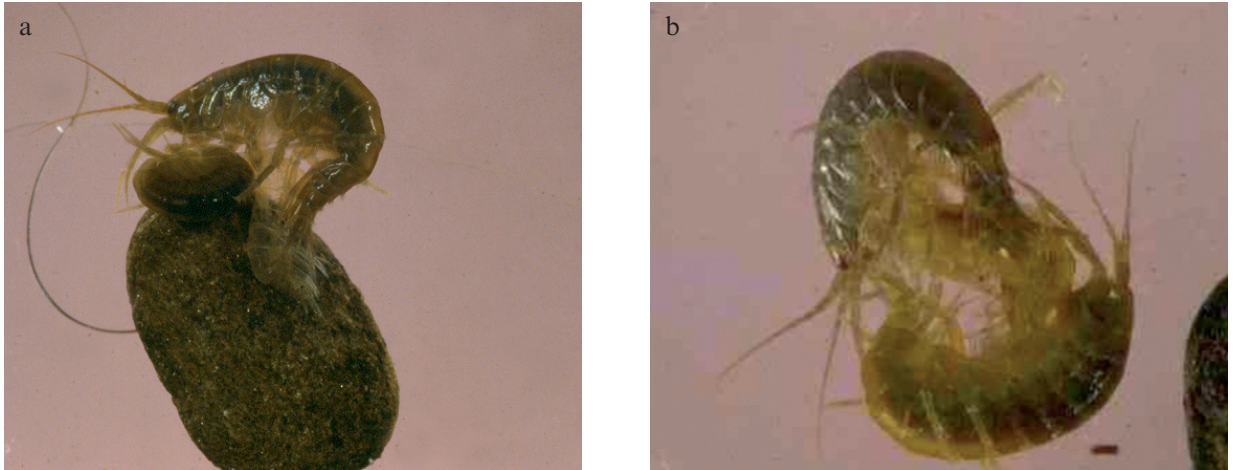


Fig. 2. (a) A male *G. duebeni* holding a female in precopula. Note the female has just shed her exoskeleton, which remains partly attached to her. (b) The same pair a few minutes later, the guarding male now attempting to wrestle the female from the grip of an attacking male *G. pulex* (bottom animal). The female was almost entirely consumed by both males once the male *G. pulex* had begun to feed on her.

time in the context of mate choice and mating decisions, that brought Dick *et al.* (1990b) to realise that differential predation by males on moulting female congeners might be a mechanism explaining the displacement of *G. duebeni* by *G. pulex* (see Fig. 2).

A series of papers examined this hypothesis at a range of experimental scales and resolutions. For example, simple one-on-one experiments (e.g. Dick *et al.*, 1993; Dick, 1996) were supplemented by examinations of the dynamics of laboratory simulations of invasions in large aquaria (e.g. Dick *et al.*,

1999; MacNeil *et al.*, 2004a) and field experiments (e.g. MacNeil *et al.*, 2004b). All pointed to the mutual nature of IGP between *G. pulex* and *G. duebeni*, but to the superiority of the former over the latter in both avoiding this interaction and impacting on the other species (see Fig. 3).

Further, behavioural assays revealed that one of the causes behind this pattern is the inherently more aggressive nature of *G. pulex* (Dick *et al.*, 1995). This results in males of this species killing and consuming more guarded, moulting female *G. duebeni* than in the reciprocal interaction, and *G. pulex* is also a more aggressive defender of its mates (see Fig. 3 and Dick *et al.*, 1995).

Experiments in both the laboratory and field, alongside behavioural assays and mathematical modelling (e.g. Dick *et al.*, 1993), all supported the hypothesis that differential IGP largely explained the displacement of *G. duebeni* by *G. pulex*. But, as detailed earlier, the field patterns varied spatially and temporally and indeed, on occasion, were the reverse of the normal displacement of *G. duebeni* by *G. pulex*, and co-existence of the species can occur for many years. Explanations were sought and several lines of investigation proved illuminating. First, we hypothesised that parasitism may mediate IGP between these species (see Parasitism review by Prenter *et al.*, 2004). In a series of field, laboratory and mathematical modelling studies, it was shown that microsporidian and acanthocephalan parasites

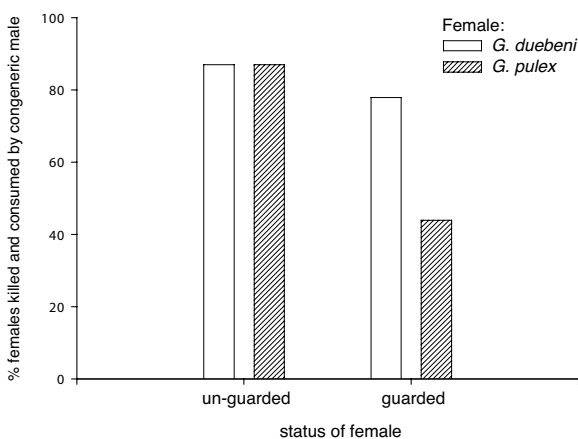


Fig. 3. Percentage of moulting female *G. duebeni* and *G. pulex* killed and consumed by male congeners in experiments where the females were either un-guarded or guarded by male conspecifics (see Dick *et al.*, 1993).

altered the strength and asymmetry of IGP between the species and could thus determine the speed of replacement (MacNeil *et al.*, 2003b, c, d; 2004a). Further, parasitism can theoretically have a ‘keystone’ effect on IGP interactions, enhancing the range of conditions under which IGP systems can persist and species come to co-exist (Hatcher *et al.*, in press). Second, while we know that lower water quality, particularly with regards to oxygen levels, aids the replacement of *G. duebeni* by *G. pulex* (MacNeil *et al.*, 2004b), we further hypothesised that some feature of water chemistry (other than oxygen) in higher reaches of streams may also mediate the strength of IGP and this appears to be the case (Piscart *et al.*, unpublished data). Essentially, both *G. pulex* and *G. duebeni* females survive and moult equally well in aerated water taken directly from stream reaches of *G. pulex* only, mixed *G. pulex/G. duebeni* and *G. duebeni* only. However, while the invader was always a more effective predator of congeners than the native, this asymmetry became significantly weaker as we moved from ‘invader water’ through ‘co-existence water’ to ‘native water’ (Piscart *et al.*, unpublished data). We can thus now understand why *G. pulex* slows in its advance upstream and its replacement of *G. duebeni* and why indeed this progress may be entirely halted. Further, if the as yet unidentified constituent(s) of water that shift the balance of the IGP interaction can sometimes lead to that balance tipping in favour of *G. duebeni*, this may explain the occurrence of reversals in the displacement pattern. This is clearly now a research challenge, although determining what chemical constituents are causal in the above patterns will be a difficult task.

Finally, I have criticised other workers for not testing alternative hypotheses concerning the process(es) behind the patterns of displacement of *G. duebeni* by *G. pulex*, and I should mention several further points in this regard. We have tested for interspecific precopulation and hybridization between these species, and found no evidence to support this mechanism (Dick and Elwood, 1992). Nor did we find evidence for transmission of parasites between the species (MacNeil *et al.*, 2003c). As for the operation of interspecific competition, despite my protestations above, I have not embarked on empirical study of its existence/operation. However, I point the reader to several modelling papers (Dick *et al.*, 1993; Dick and Platvoet, 1996; MacNeil *et al.*, 2004a) which all indicate the same phenomenon.

That is, interspecific competition is a weak interaction relative to IGP, such that even a bias towards *G. duebeni* as being a superior competitor over *G. pulex* might not have any bearing on the outcome of interactions between the species where IGP is asymmetrical. However, that *G. duebeni* might have some competitive superiority came to light recently, when we found that the ‘functional response’ of *G. duebeni* towards prey was significantly higher than that of *G. pulex* (Bollache *et al.*, 2008). On balance, therefore, I favour investigation of the operation of interspecific competition between these species, as it is clear that IGP could be finely balanced when mediated by biotic and abiotic factors. Thus, small differences in competitive ability may play a role in determining the outcome of interactions between the species and hence their distribution patterns. Once we attain ‘the complete unravelling of (...) these relationships’ (Elton, 1958), we may be in a position to not only understand the distributions of invader and native, but predict from behavioural traits and their mediation the results of new introductions.

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