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Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with native benthic fauna

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Abstract

Biological invasions are regarded as a major threat to native ecosystems, yet studies investigating the interactions of invaders with native biota under field conditions are rare. Whilst many invaders are present only in low densities, it is often the effects of high densities that are of particular concern. We manipulated densities of the invading New Zealand aquatic snail *Potamopyrgus antipodarum* within an Australian stream to test the relationships between relatively high and low densities of the invading snail and other benthic fauna. Two experiments were carried out: the first experiment investigated the relationship between *P. antipodarum* and benthic fauna colonising within a short period of six days, the second looked at the effects after six days of high *P. antipodarum* densities on resident benthic fauna. In both experiments, there was no evidence of a negative relationship between densities of *P. antipodarum* and native fauna. On the contrary, both experiments showed a positive relationship between *P. antipodarum* densities and those of some common native fauna. In the second experiment invader densities were positively correlated with total number of native taxa, as well as with total densities and the densities of common invertebrates. Coprophagy is suggested as a possible mechanism by which increase in *P. antipodarum* could facilitate increase in native fauna. The results of this work strongly suggest that the effects of an invader can include indirect effects on the trophic dynamics of an ecosystem.

Introduction

Biological invasions have been recognised as a major form of global change (Sala et al. 2000). Invading species can have a multitude of effects, including dramatic changes to whole ecosystems, to disturbance regimes, and negative interactions with native species (Mack and D'Antonio 1998; Strayer 1999; Strayer et al. 1999). Freshwater systems are suggested to be particularly prone to invasions by alien species (Lodge et al. 1998), as they are utilised intensively by people in ways that maximise opportunities for spread and establishment of invaders (Griffiths et al. 1991).

Invaders can become pests, as they dramatically increase in population densities in their new environment. It is at this stage that their effects on native ecosystems can be most severe (Williamson 1996), yet their potential effects on organisms other than closely related species or commercially important species are rarely investigated (Simberloff and Stiling 1996). Furthermore, given the risks of manipulating invaders *in situ*, studies that are realistic in their approach to determining ecological effects of biological invaders

are rare. Most commonly, effects of invaders are invoked to explain observed changes in native biota occurring simultaneously with an observed invasion. A major drawback of this approach is the number of possible, equally satisfactory, explanations that may involve a multitude of factors not necessarily associated with the invasion.

Experimental manipulations, with treatments including and excluding invaders, can provide a stronger basis for developing hypotheses in relation to the effects of invaders, albeit only at the spatial and temporal scales of the experiment. However, field experiments involving the introduction of an invader into an area where it has not been found before, defeat the practical purpose of identifying the potential effects of an invader prior to its impact. Risk assessments for biological control introductions use laboratory experiments as the first step for determining potential negative effects of an introduction (Vermeij 1996; Thomas and Willis 1998). Yet, laboratory experiments can be misleading, as it is impossible to reconstruct field conditions at the appropriate scales. Furthermore, dispersal of the invader in its new environment usually cannot be considered in laboratory situations (Simberloff and Stiling 1996).

Experimental manipulations of field densities, rather than presence or absence, address questions related to the effects of sudden increases in population densities of invaders. Such population explosions can occur shortly after the new arrival of a species (e.g. the zebra mussel, *Dreissena polymorpha*, invasion of North America: Strayer 1999), but may also occur after a species has been present in low densities for long periods of time (Williamson 1996). Manipulations of sedentary organisms can be done at small scales and have been successfully used to demonstrate, for example, increases in benthic macroinvertebrates and organic matter associated with the presence of live zebra mussels in Lake Eire, USA (Stewart et al. 1998). For mobile organisms, such as the invading crayfish, *Orconectes rusticus*, *in situ* cages allowed Lodge et al. (1998) to increase local densities in a lake that otherwise had only low abundances of this predator.

We also took the approach of manipulating field densities of an invader, the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae), to examine relationships with native macroinvertebrates. *Potamopyrgus antipodarum*, a small, parthenogenic, omnivorous, gastropod, from New Zealand, was first recorded in south-eastern Australia around 1870 (Ponder 1988). This species invaded England and continental Europe at a similar time (Hubendick 1950; Boettger 1951). More than 100 years later, in 1987, *P. antipodarum* were first found in rivers in the United States (Bowler 1991; Langenstein and Bowler 1991). In Australia, there has been concern that *P. antipodarum* could be directly competing with native hydrobiids (Ponder 1988, 1994), but no one has examined the potential of this snail to affect other native, aquatic invertebrates. In the United States extremely high densities of *P. antipodarum* in the Snake River have led to the suggestion that *P. antipodarum* could also affect other native, non-molluscan fauna by direct competition (Strayer 1999), presumably for food and space.

Similar to Lodge et al. (1998) an area with very low densities of *P. antipodarum* was selected to allow field manipulations of densities without running the risk of introducing the invader to a new area. However, in contrast to Lodge et al. (1998), treatments did not need to be fully enclosed in cages to contain high densities of the invader. Instead, the experimental substrata mimicked natural field conditions by allowing native benthic fauna relatively unrestricted access. Nevertheless, it was anticipated that individuals of *P. antipodarum* would eventually disperse and thus the experiments were run only over a relatively short time period. The aims of the experiments were to determine whether changes in native fauna were associated with high densities of *P. antipodarum* relative to areas with low densities of this invader, rather than investigate temporal aspects of this interaction.

Methods

Study site

The study was carried out in a stony-bottomed, approximately 8 m wide and 50 m long section of the Tarra River, a small, unregulated stream in south-eastern Australia (38°28′ S, 146°32′ E), with an average depth of 30 cm and relatively unpredictable flows (Cowell's indices based on 18 years of flow data: contingency = 0.15, constancy = 0.21, predictability = 0.37, refer to Gordon et al. 1992). Riparian vegetation consisted predominantly of native vegetation within the Tarra–Bulga National Park. A dirt track running along side the stream and a small caravan park ca. 1 km upstream of the site represented the only potential disturbances to the site. Background to this study was provided by

density samples taken over the same spatial scale as the experimental substrates (20 cm × 20 cm), at approximately quarterly intervals between September 1994 and August 1996. Density samples confirmed that *P. antipodarum* were the only snails present, always occurred in low densities and native fauna colonising the experimental substrates reflected that of the surrounding streambed. Further downstream of the study site, *P. antipodarum* occurred in high enough numbers to provide a reliable source for collecting individuals to add to the experiments. The experiments were carried out between 17 February and 16 May 1996.

Design of experimental units

Wire baskets, 20 cm × 20 cm × 10 cm deep, were used as experimental units. The sides and bottom of each basket were covered with fine-meshed curtain material (mesh size approximately 0.2 mm) to prevent snails from being washed out of the baskets before they emerged from their shells after they had been added to the baskets. Otherwise no attempts were made to restrict *P. antipodarum* to the baskets, in the hope that minimal manipulation would also result in minimal disturbance of colonising stream invertebrates. A pilot study showed that, when 200 *P. antipodarum* were added to each of five baskets, densities were still high (ca. 199 snails) the following day.

One rock was added as the dominant substratum to each basket. The rocks were collected from a downstream area and were scrubbed and dried on the banks of the stream for three weeks prior to the first experiment. Each rock filled its basket as much as possible, without extending above the rim of the basket. Rock surface areas ranged from 443 to 928 cm^2, as determined by the method of Doeg and Lake (1981).

Experimental procedure

Flow was measured above each basket when it was placed in the stream, using a Marsh McBirney flow meter (mean flow = 0.15 m/s). Depths to the top (mean depth = 0.24 m) and bottom (mean depth = 0.37 m) of the rocks were also measured at this time. There were no differences between treatments in current velocity above the baskets at the beginning of the experiments (ANOVA: P always greater than 0.225) nor in the depth to the top of each rock and bottom of each basket (ANOVA: P always greater than 0.315).

The number of *P. antipodarum* added to the high-density treatments at the beginning of both experiments (200) was based on average densities over 15 months recorded from two nearby rivers that were dominated by *P. antipodarum*. No snails were added to the low-density treatments as *P. antipodarum* densities were naturally low at the experimental site and it was assumed that only few *P. antipodarum* would colonise the experimental rocks and baskets from the surrounding area.

Baskets were sampled in two stages: first the rock was scrubbed into a net (mesh size 0.3 mm) and the contents of the net were preserved. Then the remainder of the basket was emptied into the net and the basket was scrubbed out. Snails were relaxed by addition of some menthol crystals and then preserved in 70% ethanol.

Experiment 1: effects of high P. antipodarum *densities on colonising fauna*

On 17 February 1996, one scrubbed and dried rock was placed into each of 40 baskets. We added 200 *P. antipodarum*, which had been collected early on the same day, to each of the high-density treatments, and then all baskets were placed at random locations into the stream. Ten replicates per treatment were sampled at two subsequent times, day 1 (18 February 1996) and day 6 (23 February 1996).

Experiment 2: effects of high P. antipodarum *densities on resident fauna*

Twenty baskets with rocks were placed into the stream at random locations on 26 March 1996, 6.5 weeks prior to the addition of *P. antipodarum*. Previous work showed that around four weeks are adequate for recolonisation of small patches in stony streams by aquatic macroinvertebrates (Lake and Doeg 1985; Doeg et al. 1989; Downes et al. 1998). On 10 May 1996, 200 snails were added to the randomly assigned high-density treatments by placing the snails into the baskets *in situ* and covering the basket briefly with a mesh-covered lid. This procedure allowed the snails, which had withdrawn into their shells during handling, time to re-emerge from their shells. The low-density treatments were treated similarly (the rock was tapped with forceps similar to the actions required to add snails, and the lid was briefly put onto the basket) to control for any effects of the physical procedure of establishing the high-density treatment. Ten replicates per treatment were sampled on day 6 (16 May 1996).

Laboratory procedure

All invertebrates were sorted and identified using current keys (Hawking 1994; Smith 1996; Dean and Suter 1996; Cartwright 1997; Dean 1997; StClair 1997; Jackson 1998) and with reference to voucher specimens (Department of Biological Sciences, Monash University). Water mites, oligochaetes and the chironomid subfamily Tanypodiinae, as well as individuals from other groups that were too small or too damaged to be identified were grouped at a higher taxonomic level.

Results

Experiment 1: effects of high P. antipodarum *densities on colonising fauna*

As *P. antipodarum* were not prevented from leaving the baskets during the experiments, differences in *P. antipodarum* densities between treatments were compared to check that treatments were maintained. *Potamopyrgus antipodarum* densities were significantly higher in the high-density treatment than in the low-density treatment (Table 1), but in contrast to the pilot study, final densities were lower and more variable in the high-density treatment relative to the initial conditions of 200 snails per basket (high-density treatment: mean = 97 snails per basket, SE = 14.4; low-density treatment: mean = 5 snails per basket, SE = 1.1).

Table 1. Analysis of variance showing that 'high-density' and 'low-density' *P. antipodarum* treatments were maintained in both experiments. All variables transformed by ($\log_e$(Number + 0.001)).

Source	Mean square	*F*-ratio	*P*
Experiment 1			
Day	7.215	1.204	0.280
P. antipodarum density	201.220	33.568	<0.001
Day × *P. antipodarum* density	26.893	4.486	0.041
Residual	5.994		
Experiment 2			
P. antipodarum density	11.614	17.469	0.001
Residual	0.665		

A total of 42,309 invertebrates, belonging to 133 taxa, colonised 40 experimental baskets during the six days of the experiment. Most (26,125 individuals) were chironomids, in particular *Thienemaniella* (10,265), 'small chironomids' (4103 individuals), and *Polypedilum* (2965 individuals). Simuliids were also common, but again most were too small to be identified (5616 'small simuliids', 4726 *Austrosimulium furiosum*). Overall, colonising fauna showed little response to high densities of *P. antipodarum* (Figure 1a; Analysis of Similarities, Clarke and Warwick 1994: $P = 0.70$, global $R = -0.028$), except for a significant, but weak positive correlation of *P. antipodarum* densities with total densities of native macroinvertebrates on day 6, with *Polypedilum* on day 1 and with 'small Leptoceridae' on day 6 (Figure 2).

Experiment 2: effects of high P. antipodarum *densities on resident fauna*

Positive correlations of native invertebrates with *P. antipodarum* were more common and more pronounced in the second experiment (Table 2). Total

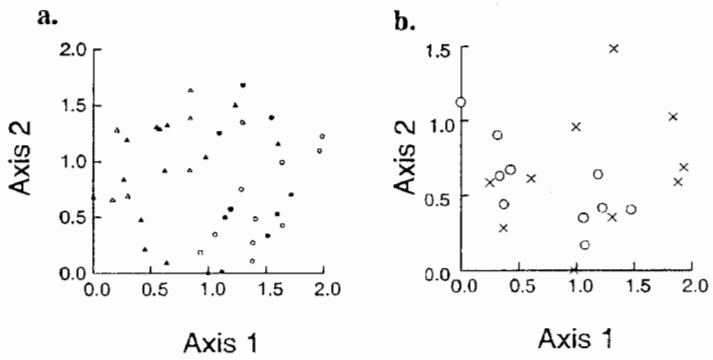

Figure 1. Relationship between samples based on assemblage structure displayed by non-metric multidimensional scaling (20 random starts, maximum of 200 iterations). (a) Experiment 1: effects of *P. antipodarum* on colonising fauna, minimum stress in 2 dimensions = 0.094. Δ = day 6, high-density treatment; ▲ = day 6, low-density treatment; ○ = day 1, high-density treatment; ● = day 1, low-density treatment. (b) Experiment 2: effects of *P. antipodarum* on resident fauna, minimum stress in 2 dimensions = 0.068. × = high-density treatment, ○ = low-density treatment.

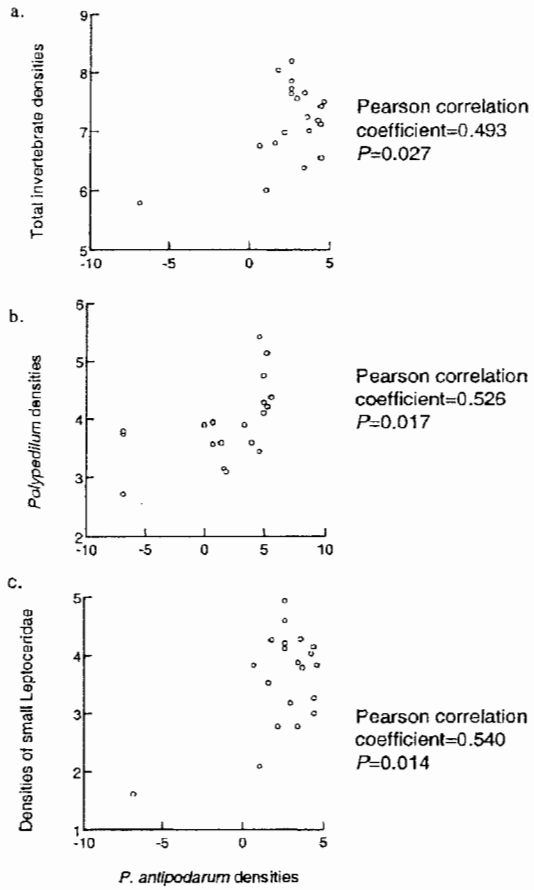

Figure 2. Experiment 1: effects of *P. antipodarum* on colonising fauna. Correlation between *P. antipodarum* and (a) total densities on day 6, and densities of (b) *Polypedilum* on day 1 and (c) 'small Leptoceridae' on day 6. All densities are transformed as $\log_e(\text{Number} + 0.001)$.

number of taxa, total abundances of native fauna and five of the ten most common taxa showed a strong positive correlation with numbers of *P. antipodarum* (Figure 3, Table 2). Three of the ten most common taxa in experiment 1 were also common enough in experiment 2 to be analysed and were also positively correlated with *P. antipodarum* abundances (Table 2): densities of *Polypedilum*, 'small Leptophlebiidae' and 'small Caenidae' increased with increases in *P. antipodarum* densities in both experiments.

The fauna, 13,319 invertebrates of 139 taxa, was dominated by 'small Caenidae' (2053) and 'small Leptoceridae' (1465), as well as four taxa of chironomids (1012 *Zavreliella*, 894 'small Tanypodinae', 653 *Rheotanytarsus* and 403 *Polypedilum*), Baetidae sp. EPA3 (324), 'small Leptophlebiidae' (641) and *Tamasia* caddises (380). In terms of assemblage structure, some high-density substrates separated from low-density substrates in ordination space (Figure 1b), but overall analysis of similarities (Clarke and Warwick 1994) did not show a significant difference between treatments ($P = 0.32$, global $R = 0.014$). Similar to the first experiment, snails were lost from the initial 200 snails per basket in the high-density baskets (high-density treatment: final mean = 72 snails per basket, SE = 18.1; low-density treatment: mean = 14, SE = 2.7), but again treatments were maintained with a significant difference between high- and low-density treatments (Table 1).

Table 2. Experiment 2: effects of high *P. antipodarum* densities on resident fauna. Correlations between actual *P. antipodarum* densities and total number of taxa, total number of invertebrates, abundances of the 10 most common invertebrates in experiment 2 (denoted by C2) and the abundance of taxa common in experiment 1, but not amongst the 10 most common taxa of experiment 2 (denoted by C1). All variables transformed by $(\log_e(\text{Number} + 0.001))$.

	Pearson correlation coefficient	*P*
Total taxa	0.530	0.016
Total numbers	0.739	<0.001
^{C2}Small Caenidae	0.608	0.004
^{C2}Small Leptophlebiidae	0.705	0.001
^{C2}Baetidae sp. EPA3	−0.380	0.098
^{C2}Small *Notalina*	0.370	0.108
^{C2}*Tamasia*	0.436	0.055
^{C2}Oligochaeta	0.720	<0.001
^{C2}*Zavreliella*	0.571	0.008
^{C2}*Polypedilum*	0.551	0.012
^{C2}*Rheotanytarsus*	0.422	0.064
^{C2}Tanypodinae	0.438	0.053
^{C1}*Thienemaniella*	0.617	0.004
^{C1}*Tanytarsus*	0.556	0.011
^{C1}Small chironomids	0.754	<0.001

Discussion

Successful invaders can affect ecosystems in numerous ways, depending on their structural and functional roles within the invaded environment. Competition with native species for resources, such as food and space, are just one, potentially negative, effect of invading species. High densities of an invader can physically change the recipient environment: for example, the high densities of *D. polymorpha* that settle on any hard

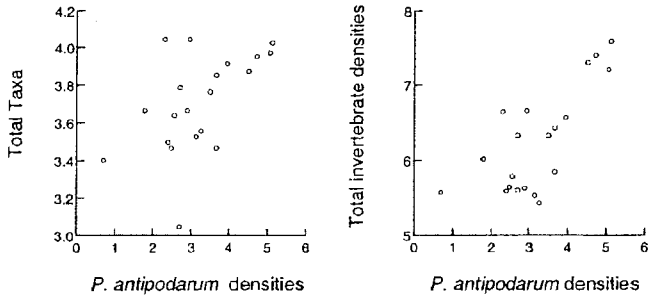

Figure 3. Experiment 2: relationship between changes in densities of resident fauna (total number of taxa, total number of individuals) with changes in *P. antipodarum* densities. All densities are transformed to $\log_e$(Number + 0.001).

surface in aquatic systems do not only directly affect native fauna, (e.g. by initially taking up all available space for settlement), but can also potentially provide additional habitat space (Wisenden and Bailey 1995; Ricciardi et al. 1997; Stewart et al. 1998). Invaders can change trophic dynamics of an ecosystem, as demonstrated by the strong trophic cascades resulting from the introduction of brown trout (*Salmo trutta*) to New Zealand streams (Flecker and Townsend 1994; McIntosh and Townsend 1996; Huryn 1998).

Despite the recognition of the potential ecological importance of biological invasions in their recipient environment, the effects of invaders are rarely studied under realistic conditions. The recognition of potential density-dependent effects provides an avenue for experimentally testing the effects of invaders under field conditions (e.g. Lodge et al. 1998). This approach was taken in the present study to investigate the short-term effects of the aquatic, invading snail, *P. antipodarum*, on native stream macroinvertebrates in southern Victoria, Australia. The open nature of the substrata employed in this study provided a realistic context of a dynamic stream environment and native fauna collected in the experiment reflected that of the surrounding environment. However, manipulations of field densities were restrictive in that densities could only be manipulated for short periods of time and over small spatial scales and conclusions drawn from these experiments apply only to these scales.

The first experiment was put in the general context of the colonisation of denuded substrates. Small scale disturbances that result in eliminating fauna from small patches are common in streams and these patches are generally rapidly recolonised (Boulton et al. 1988; Lake 1990; Downes et al. 1998), with *P. antipodarum* being amongst the earliest colonisers (Quinn et al. 1998). By providing bare patches with and without relatively high densities of *P. antipodarum*, the first experiment examined the response of colonising native fauna to areas that were already occupied by *P. antipodarum*. The second experiment was less likely to mimic naturally occurring stream processes, as adult *P. antipodarum* were added at one point in time to fully colonised substrata. Nevertheless, alien species already present in low densities can show relatively sudden increases in density (Williamson 1996) and it is feasible that other resident fauna show behavioural responses.

Contrary to expectations of negative relationships between the invader and native fauna, a consistent, positive correlation between native macroinvertebrate fauna and *P. antipodarum* was found at the temporal and spatial scales of our experiments. In particular, densities of common taxa increased with increases in *P. antipodarum* densities. For colonising fauna, the correlation between relatively high *P. antipodarum* densities and total number of native invertebrates was significant only after six days of colonisation and overall response patterns were weak. The positive relationship between densities of the invader and that of common native fauna was stronger when *P. antipodarum* were added to fully colonised surfaces. In particular, increases in the numbers of dominant species of chironomids and small individuals of chironomids, caddises and mayflies were significantly correlated with increases in *P. antipodarum*.

The identities of the taxa that showed a positive correlation with *P. antipodarum* densities suggest coprophagy as one plausible explanation for the observed patterns. Young instars of stream invertebrates may rely heavily on detritus as a food source, and may benefit from the presence of an invader that

can improve the quality of available detritus by feeding on it and excreting it in a more digestible form (Brendelberger 1997; Constantini and Rossi 1998). Molluscs, especially gastropods, are well known to have enzymes to digest complex carbohydrates, notably cellulases as well as chitinases (Calow and Calow 1975). Thus, *P. antipodarum* may be capable of digesting not only the cellulose but also the chitin from fungi and insects present in detritus. Faeces produced by the snails, along with mucoproteins and mucopolysaccharides in the mucus, may be high quality food for grazing and deposit-feeding stream detritivores (Shepard and Minshall 1981; Wolf et al. 1997), boosting the abundance of these animals. Similar mechanisms have been suggested as facilitating increases in macrobenthos associated with zebra mussel beds in the American Great Lakes and the Hudson River (Griffiths 1993; Stewart and Haynes 1994; Roditi et al. 1997; Stewart et al. 1998; Strayer et al. 1999). Snail mucus could also contribute indirectly to increasing food by trapping microalgae and bacteria, a process that has been observed in intertidal limpets (Connor and Quinn 1984; Connor 1986; Herndl and Peduzzi 1989). However, fresh *P. antipodarum* mucus trails observed in an aquarium lost their adhesive properties within only a couple of hours (pers. obs.).

Whilst some invading species have caused direct dramatic reductions in some native species (Civeyrel and Simberloff 1996; Vermeij 1996), other, less obvious effects have rarely been investigated. The mere presence of the invader is not the only factor that could influence native fauna. Invading species become part of the recipient biota and as such contribute to the processes in these systems. As the densities of the invaders change, their contributions to these processes also change. For example, increases in local densities of a particular species can change the relationship between different trophic levels, depending on whether the invader facilitates or competes with other species. Field density manipulations can contribute to the investigations of effects of changing densities of invaders on native fauna. Effects that are related to the mere presence of an alien species of course cannot be inferred from density manipulations. Furthermore, any experimental manipulations will only relate to current environmental conditions and cannot address previous dramatic effects, such as past extinctions of native species following biological invasions. Nevertheless, we have illustrated that local experimental field manipulations of an invader can contribute to the development of hypotheses about its interactions with native fauna. Ultimately, our understanding of biological invasions requires a range of scientific approaches applied at a range of spatial and temporal scales, including small-scale, experimental field manipulations.

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References

Boettger CR (1951) Die Herkunft und Verwandtschaftsbeziehungen der Wasserschnecke *Potamopyrgus jenkinsi* E.A. Smith, nebst einer Angabe über ihr Auftreten im Mediterrangebiet. Archiv für Molluskenkunde 80: 57–84

Boulton AJ, Spangaro GM and Lake PS (1988) Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance: an experimental approach. Archiv für Hydrobiologie 113: 551–576

Bowler PA (1991) The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the Middle Snake River, southern Idaho. In: Pister EP (ed) Proceedings of the Desert Fishes Council, Vol XXI (Twenty-First Annual Symposium), pp 173–182. Desert Fishes Council, Bishop, California

Brendelberger H (1997) Coprophagy: a supplementary food source for two freshwater gastropods? Freshwater Biology 38: 145–157

Calow P and Calow LJ (1975) Cellulase activity and niche separation in freshwater gastropods. Nature 255: 478–480

Cartwright D (1997) Preliminary guide to the identification of late instar larvae of Australian Ecnomidae, Philopotamidae and Tasimiidae (Insecta: Trichoptera). Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 10, Thurgoona, Australia

Civeyrel L and Simberloff D (1996) A tale of two snails: is the cure worse than the disease? Biodiversity and Conservation 5: 1231–1252

Clarke KR and Warwick RM (1994) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, UK

Connor VM (1986) The use of mucous trails by intertidal limpets to enhance food resources. Biological Bulletin 171: 548–564

Connor VM and Quinn JF (1984) Stimulation of food species growth by limpet mucus. Science 225: 843–844

Constantini ML and Rossi L (1998) Competition between two aquatic detritivorous isopods – a laboratory study. Hydrobiologia 368: 17–27

Dean JC (1997) Larvae of the Australian Hydrobiosidae (Insecta: Trichoptera). Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 11, Thurgoona, Australia

Dean JC and Suter PJ (1996) Mayfly nymphs of Australia: a guide to genera. Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 7, Thurgoona, Australia

Doeg T and Lake PS (1981) A technique for assessing the composition and density of the macroinvertebrate fauna of large stones in streams. Hydrobiologia 80: 3–6

Doeg T, Lake PS and Marchant R (1989) Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Australian Journal of Ecology 14: 207–220

Downes BJ, Lake PS, Schreiber ESG and Glaister A (1998) Habitat structure and regulation of local species diversity in a stony, upland stream. Ecological Monographs 68: 237–257

Flecker AS and Townsend CR (1994) Community-wide consequences of trout introduction in New Zealand streams. Ecological Applications 4: 798–807

Gordon ND, McMahon TA and Finlayson BL (1992) Stream Hydrology: an Introduction for Ecologists. Wiley, Chichester, UK

Griffiths RW (1993) Effects of Zebra Mussels (*Dreissena polymorpha*) in shallow water of northeastern Lake Erie. In: Nalepa TF and Schloesser DW (eds) Zebra Mussels. Biology, Impacts and Control, pp 415–437. Lewis Publishers, Boca Raton, Florida

Griffiths RW, Schloesser DW, Leach JH and Kovalak WP (1991) Distribution and dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. Canadian Journal of Fisheries and Aquatic Sciences 48: 1381–1388

Hawking JH (1994) A preliminary guide to keys and zoological information to identify invertebrates from Australian freshwaters. Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 2, Thurgoona, Australia

Herndl GJ and Peduzzi P (1989) Potential microbial utilization rates of sublittoral gastropod mucus trails. Limnology and Oceanography 34: 780–784

Hubendick B (1950) The effectiveness of passive dispersal in *Hydrobia jenkinsi*. Zoologiska Bidrag från Uppsala 28: 493–504

Huryn AD (1998) Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. Oecologia 115: 173–183

Jackson J (1998) Preliminary guide to the identification of late instar larvae of Australian Calocidae, Helicophidae and Conoesucidae (Insecta: Trichoptera). Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 16, Thurgoona, Australia

Lake PS (1990) Disturbing hard and soft bottom communities: a comparison of marine and freshwater environments. Australian Journal of Ecology 15: 477–488

Lake PS and Doeg TJ (1985) Macroinvertebrate colonization of stones in two upland southern Australian streams. Hydrobiologia 126: 199–212

Langenstein S and Bowler PA (1991) On-going macroinvertebrate analysis using the biotic condition index and the appearance of *Potamopyrgus antipodarum* (Gray) in Box Canyon Creek, southern Idaho. Proceedings of the Desert Fishes Council, Vol. XXI (Twenty-First Annual Symposium) pp 183–194. Desert Fishes Council, Bishop, California

Lodge DM, Stein RA, Brown KM, Covich AP, Brönmark C, Garvey JE and Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology 23: 53–67

Mack MC and D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13: 195–198

McIntosh AR and Townsend CR (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108: 174–181

Ponder WF (1988) *Potamopyrgus antipodarum* – a molluscan coloniser of Europe and Australia. Journal of Molluscan Studies 54: 271–285

Ponder WF (1994) Australian Freshwater Mollusca: conservation priorities and indicator species. Memoirs of the Australian Museum 36: 191–196

Quinn GP, Lake PS and Schreiber ESG (1998) A comparative study of colonisation by benthos in a lake and its outflowing stream. Freshwater Biology 39: 623–635

Ricciardi A, Whoriskey FG and Rasmussen JB (1997) The role of the Zebra Mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences 54: 2596–2608

Roditi HA, Strayer DL and Findlay S (1997) Characteristics of zebra mussel (*Dreissena polymorpha*) biodeposits in a tidal freshwater estuary. Archiv für Hydrobiologie 140: 207–219

Sala OE, Chapin III S, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff LeR N, Sykes MT, Walker BH, Walker M and Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774

Shepard RB and Minshall GW (1981) Nutritional value of lotic insect feces compared with allochthonous materials. Archiv für Hydrobiologie 90: 489–491

Simberloff D and Stiling P (1996) Risks of species introduced for biological control. Biological Conservation 78: 185–192

Smith BJ (1996) Identification keys to the families and genera of bivalve and gastropod molluscs found in Australian inland waters. Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 6, Thurgoona, Australia

StClair RM (1997) Preliminary guide to the identification of late instar larvae of Australian Philorheithridae, Calamoceratidae and Helicopsychidae (Insecta: Trichoptera). Cooperative Research Centre for Freshwater Ecology, Identification Guide No. 12, Thurgoona, Australia

Stewart TW and Haynes JM (1994) Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. Journal of the Great Lakes Research 20: 479–493

Stewart TW, Miner JG and Lowe RL (1998) Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic

matter production and shell-generated habitat. Journal of the North American Benthological Society 17: 81–94

Strayer DL (1999) Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society 18: 74–98

Strayer DL, Caraco NF, Cole JJ, Findlay S and Pace ML (1999) Transformation of freshwater ecosystems by bivalves: a case study of zebra mussels in the Hudson River. Bioscience 49: 19–27

Thomas MB and Willis AJ (1998) Biocontrol – risky but necessary? Trends in Ecology and Evolution 13: 325–329

Vermeij GJ (1996) An agenda for invasion biology. Biological Conservation 78: 3–9

Williamson M (1996) Biological Invasions. Chapman & Hall, London, 244 pp

Wisenden PA and Bailey RC (1995) Development of macroinvertebrate community structure associated with the Zebra Mussel (*Dreissena polymorpha*) colonization of artificial substrates. Canadian Journal of Zoology 73: 1438–1443

Wolf B, Zwick P and Marxsen J (1997) Feeding ecology of the freshwater detritivore *Ptychoptera paludosa* (Diptera, Nematocera). Freshwater Biology 38: 375–386