

Clinal variation in shell morphology of the freshwater gastropod *Potamopyrgus antipodarum* along two hill-country streams in New Zealand

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Abstract The extremely polymorphic gastropod *Potamopyrgus antipodarum* is widespread in freshwater habitats throughout New Zealand. This study describes morphological variation of *P. antipodarum* along two streams in Waikato (North Island, New Zealand), and explores relationships between morphology and selected environmental variables (temperature, conductivity, pH, flow, shade, vegetation). Along each stream, fully grown snails were collected at 11 sites extending from the source of flow to 1 or 1.5 km downstream. In both streams, shells increased in size and in one stream they also became more obese with distance from the source. Of the environmental variables assessed only flow, which increased downstream, was found to have potential influence on shell morphology. Larger snails have a larger foot and thus a larger attachment area and therefore may be able to withstand higher currents, despite having a higher Reynolds number resulting in increased drag on them relative to smaller individuals. Other studies have found that clines of morphological variation in lakes are apparently driven by the differential risk of infection by parasites. This can be excluded for the stream populations in this study, because parasitised individuals were absent at upstream sites, suggesting that similar morphological patterns may have entirely different causes.

Keywords flow; Gastropoda; morphology; polymorphism; *Potamopyrgus antipodarum*; Waikato

INTRODUCTION

In many species, body size and shape have been identified as important determinants of individual fitness. They can influence a number of life history traits including fecundity, competitiveness for resources and mating partners, longevity, and vulnerability to predation. Being large or small may entail both benefits and costs, which are often traded off against each other. Size and shape thus underlie, to varying degrees, both natural and sexual selection, and environmental as well as developmental constraints. The response of size and shape to environmental cues may be plastic (for reviews see Stearns 1992; Peckarsky et al. 2001).

The ovoviviparous freshwater gastropod *Potamopyrgus antipodarum* (Gray, 1843) is well known for its morphological variability in both size and shape. The extreme polymorphism is reflected in the fact that there are more than 20 synonyms for what is currently considered a single species (Winterbourn 1970; Ponder 1988). *P. antipodarum* occurs in practically all types of freshwaters as well as in brackish water estuaries. It is endemic to and abundant

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throughout New Zealand and has been introduced to Australia, Europe, and North America (Ponder 1988). There are two karyotypes. Diploid specimens reproduce through outcrossing, and triploid snails are all female and parthenogenetic (Philipps & Lambert 1990; Wallace 1992; Dybdahl & Lively 1995). *P. antipodarum* is intermediate host of 14 species of digenean trematodes (Winterbourn 1974; MacArthur & Featherston 1976).

This combination of attributes has rendered *P. antipodarum* an ideal model on which to test hypotheses of life history theory (e.g., Lively 1987; Jacobsen & Forbes 1997; Levri 1999; Negovetic & Jokela 2001). In this context, shell morphology has been investigated most rigorously. In two lakes, snails collected in shallow water were smaller than specimens from deeper habitats. Maturation at smaller size near the shore has been attributed to the higher risk of trematode infection rather than being a direct consequence of depth (Jokela & Lively 1995a,b; Jokela et al. 1999). *P. antipodarum* may also become wider with increasing depth (Jokela et al. 1997a). In addition, morphological variation along local transects showed spatial variation across localities within the same lake (Jokela et al. 1997a,b). Comparing clones and sexual individuals, Jokela et al. (1997a) concluded that morphological variation was due to genetic variation. However, in another study it was shown that infection of *P. antipodarum* with trematodes during an early stage of development decreased growth rate and resulted in smaller final size as well as increased likelihood of castration (Krist & Lively 1998). In general, trematodes may cause stunting (e.g., Moose 1963; Sousa 1983) or gigantism (e.g., Rothschild & Rothschild 1939; Ballabeni 1995) in gastropods, or have no effect on morphology at all (e.g., Meuleman 1972; Hughes & Answer 1982).

Apart from this parasite-induced variation, the variability of shell morphology in *P. antipodarum* is poorly understood. It has generally been noticed, though, that large and plump shells are typical of open waters while animals living in swamps and seepages are smaller and more slender. Snails in the latter habitats may also exhibit sexual dimorphism with males being smaller and narrower than females (Wallace 1992). The occurrence of spines formed by the periostracum appears to be induced by the environment, but the causes are unclear (Boycott 1929; Warwick 1944, 1969; Boettger 1949; Jokela et al. 1997a). The potential to develop shell ornamentation appears to have a genetic basis (Warwick 1944, 1969; Johnson 1981; Hauser et al. 1992), although this has been questioned by some authors (Winterbourn 1972; Réal 1973; Simpson 1976; Foltz et al. 1984).

Genetic variation within and among populations of *P. antipodarum* detected by allozyme electrophoresis is substantial (Philipps & Lambert 1989, 1990; Dybdahl & Lively 1995, 1996; Fox et al. 1996). Our present knowledge on shell morphology as summarised above as well as an observation that some morphs appear to be restricted in their geographic distribution (M. Haase unpubl. data) also suggest that genes controlling shell morphology vary spatially. Thus, environmental effects on morphology should be more evident on a small geographical scale where genetic variation is restricted. The present paper describes the change of shell morphology of *P. antipodarum* along two headwater streams in Waikato hill country, North Island, New Zealand, and explores relationships between morphology and environmental variables.

MATERIALS AND METHODS

Potamopyrgus antipodarum was collected from 11 sequential sites (A–K, sites A being the spring sources) along each of two streams west of Whatawhata (Waikato; for a description of the sampling area refer to Quinn et al. (1997) and references therein) on 9 May (Stream 1) and 6 June (Stream 2) 2002. Stream 1 is an unnamed tributary of the Kiripaka Stream, which drains into the Mangaotama Stream, and Stream 2 is an unnamed tributary flowing into the

Karakariki Stream. Both, Mangaotama and Karakariki empty into the Waipa River. The spring sources of Streams 1 and 2 are at 37°45.8'S, 175°03.5'E and 37°48.1'S, 175°04.6'E, respectively. Stream 1 emerges in natural broadleaved forest and reaches farmland at station 1F, about half-way along the study section, while Stream 2 originates in pasture and, from station 2F onwards, flows through remnants of natural forest, i.e., small patches of more or less open treeland. Geologically, the area is dominated by sand- and siltstone. Stream 2, however, emerges on limestone. Sites 1A–1G were each separated by about 100 m, 1H–1J followed in increments of 200 m, and 1K was 300 m downstream of 1J. The sites along Stream 2 were all separated by 100 m. Thus, this survey covered 1500 m along Stream 1 and 1000 m along Stream 2. Samples at each site were taken within a stretch of 5 m. Snails sitting on hard substrate (rocks, stones, wood, leaves) were picked individually with forceps. Nets (mesh width < 1 mm) were used to collect animals from soft substrate and vegetation. The parameters measured or semi-quantitatively estimated included: temperature, pH (Standard pH Scan 2, Eutech Instruments), conductivity (TDSscan WP 3, Eutech Instruments), flow (0 = none, 1 = weak, 2 = moderate, 3 = strong), shade (1 = none, 2 = partial, 3 = full), surrounding vegetation (1 = natural forest, 2 = forest remnant, 3 = farmland).

The first 20 fully grown snails that fell out of each sampling vial were selected for analysis. *P. antipodarum* has determinate growth coinciding with sexual maturity, which is indicated by the formation of a continuous and thickened apertural lip. A few samples contained less than 20 mature individuals. Five parameters were measured under a dissecting microscope equipped with an ocular micrometer: shell height, shell width, width of the body (= penultimate) whorl, aperture width, and number of whorls (counted to the nearest eighth of a whorl). In addition, the shape parameter shell height/shell width was calculated. Two morphotypes, smooth and spiny, were distinguished. After measuring, shells were dissolved in diluted hydrochloric acid to investigate the soft body. The specimens were sexed, examined for the presence of parasites (trematodes), and females were checked for the presence of sperm in their seminal receptacles and eggs in their brooding pouches. Receptacles containing sperm have a shiny appearance. In doubtful cases, the contents of receptacles were examined under a microscope. Parasitised snails were excluded from the analysis because of the stunting effects of trematodes on shell shape (Krist & Lively 1998). The presence of allosperm was taken as indication for outcrossing and, thus, being diploid, assuming that parthenogenetic females do not mate.

The distribution of shell measurements was inspected by eye. Even after transformation most variables were not normally distributed and their variances were non-homogeneous. Therefore, the statistical analysis had to be restricted to non-parametric procedures. Mann-Whitney U tests (testing for sexual dimorphism at each site), Kruskal-Wallis tests (differences of shell variables along each stream), Spearman rank correlations (relating morphological and environmental variables to distance from spring source), and Wald-Wolfowitz runs (testing whether the sequence of morphological measurements along the streams was random) using medians as cutpoints were computed using SYSTAT version 10 (SPSS 2000). Minimum spanning trees based on Euclidean distances calculated from z-transformed medians of shell variables were calculated in SYN-TAX 5.02 (Podani 1993). Because of the exploratory character of this study, multiple tests were not Bonferroni-corrected.

RESULTS

The percentage of males at all 22 sites ranged from 7.1 to 60% (Fig. 1). In only 27 out of 132 pairwise comparisons (Mann-Whitney U tests) of the shell variables were males smaller than females. Therefore, both genders were pooled in all following analyses. Twenty-seven

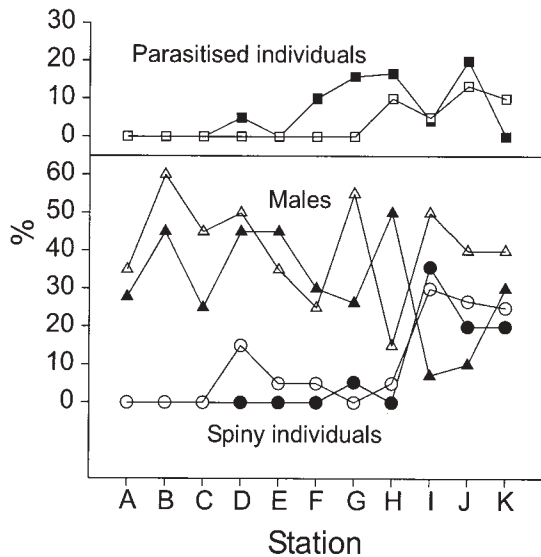


Fig. 1 Frequencies of spiny individuals, males and parasitised individuals along Stream 1 (black symbols) and Stream 2 (open symbols).

(11.0%) of 246 females had empty seminal receptacles. Of these, 22 were not brooding eggs, i.e., were not reproducing at the time of collection. This suggests that parthenogenetic, triploid strains were absent from both streams.

The proportion of parasitised individuals (0–20%) was relatively low, especially in Stream 2 (Fig. 1). In Stream 2, parasitism increased with distance from the origin (Spearman rank correlation $r_s = 0.829$, $P = 0.002$) and showed a similar trend in Stream 1 ($r_s = 0.582$, $P = 0.061$). Interestingly, many females infected by trematodes had mated, as indicated by the presence of sperm in their receptacles, despite being unable to reproduce due to castration caused by the parasites. Similarly, spiny individuals were absent in the upper parts of the streams and increased in frequency further downstream (Stream 1: $r_s = 0.787$, $P = 0.004$; Stream 2: $r_s = 0.756$, $P = 0.007$; Fig. 1). All spiny animals in Stream 1 were females including the subadult snails not included in the analyses.

Kruskal-Wallis tests rejected the null hypothesis of equal medians for all six shell variables along each stream ($P < 0.05$ in all cases) (Fig. 2, 3; Table 1). Patterns differed slightly between the streams. In Stream 1 shells became more obese, as indicated by the decreasing ratio of height/width, and had fewer whorls downstream, but their size did not change. However, the latter was largely an effect of sample 1H, which clearly falls out of the trend for an unknown reason. After its exclusion, all measurements except shell height significantly increased with increasing distance from the spring (Table 1). Wald-Wolfowitz runs yielded similar results. Over all 11 stations, only the sequences of number of whorls and the shape parameter were non-random ($P = 0.005$). After removal of data from 1H the tests for the size variables also became significant ($P < 0.05$). The minimum spanning tree (Fig. 4A) illustrates the gradual change of shell morphology along Stream 1 and also identifies sample 1H as outlier.

In Stream 2, shells increased in size and number of whorls, but the shape remained constant as expressed by Spearman rank correlations with distance from the spring (Table 1) and by Wald-Wolfowitz runs ($P = 0.004$ for measurements and whorl count; $P = 0.102$ for the shape parameter). At first glance, the pattern given by the minimum spanning tree (Fig. 4B) seems to be less clear than that for Stream 1. However, the samples from the upper

Table 1 Spearman rank correlations of medians of shell variables and environmental variables for Stream 1 above diagonal and Stream 2 below. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; + symbols have analogous meaning and indicate correlations which became significant after exclusion of station 1H (note that the coefficients are those for the entire dataset); C, conductivity; D, distance from spring source; aw, aperture width; bw, body whorl width; sh, shell height; sw, shell width; T, temperature; veg, surrounding vegetation.

	sh	sw	aw	bw	sh/sw	w	D	C	T	pH	flow	shade	veg
sh	—												
sw	0.933***	—											
aw	0.959***	0.956***	—										
bw	0.966***	0.966***	0.993***	—									
sh/sw	-0.276	-0.460	-0.420	-0.463	—								
w	0.909***	0.869**	0.828**	0.816**	-0.051	—							
D	0.934***	0.917***	0.970***	0.966***	-0.301	0.837***	—						
C	-0.954***	-0.928***	-0.977***	-0.968***	0.346	-0.831**	-0.993***	—					
T	-0.633*	-0.613*	-0.651*	-0.623*	0.225	-0.577	-0.664*	0.671*	—				
pH	-0.798**	-0.813**	-0.845**	-0.863**	0.116	-0.834**	-0.880***	0.839**	0.348	—			
flow	0.338	0.340	0.338	0.338	-0.405	0.311	0.337	-0.373	-0.173	-0.275	—		
shade	0.518	0.521	0.518	0.518	-0.388	0.562	0.516	-0.520	-0.664*	-0.395	0.479	—	
veg	-0.784**	-0.698*	-0.796**	-0.779**	0.253	-0.660	-0.839	0.844**	0.837**	0.614*	-0.327	-0.731*	—

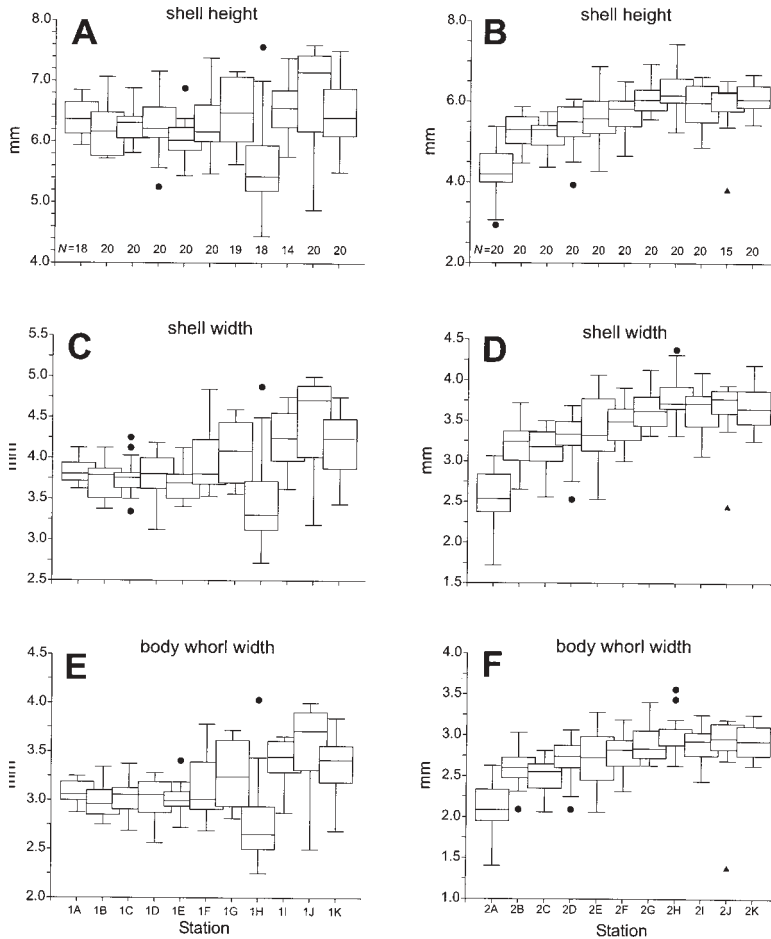


Fig. 2 Box-plots of shell variables along Stream 1 (A, C, E) and Stream 2 (B, D, F). **A, B**, shell height; **C, D**, shell width; **E, F**, body whorl width. The line within each box represents the median, the height of the box the interquartile range (25–75% quartile). T-lines extending from the box indicate adjacent values, i.e., the range of data up to 1.5 times as large as the interquartile range. Circles indicate mild outliers (values that are under three times the interquartile range from the 25 and 75% quartiles), triangles severe outliers. *N* = number of specimens.

and lower halves of the stretch investigated still group together. In contrast to samples from further downstream, the sequence of samples 2A–2E almost perfectly reflects the geographic order with a large distance separating 2A from the rest. Thus, the minimum spanning tree seems to reflect the increase of the shell size variables and whorl count, which follow a saturation curve with slight oscillations above and below the plateau of the downstream samples.

The course of temperature was opposite in the streams and, not surprisingly, paralleled by and correlated with vegetation and shade. Conductivity and pH remained more or less constant along Stream 1 while significantly decreasing, conductivity drastically, in Stream 2.

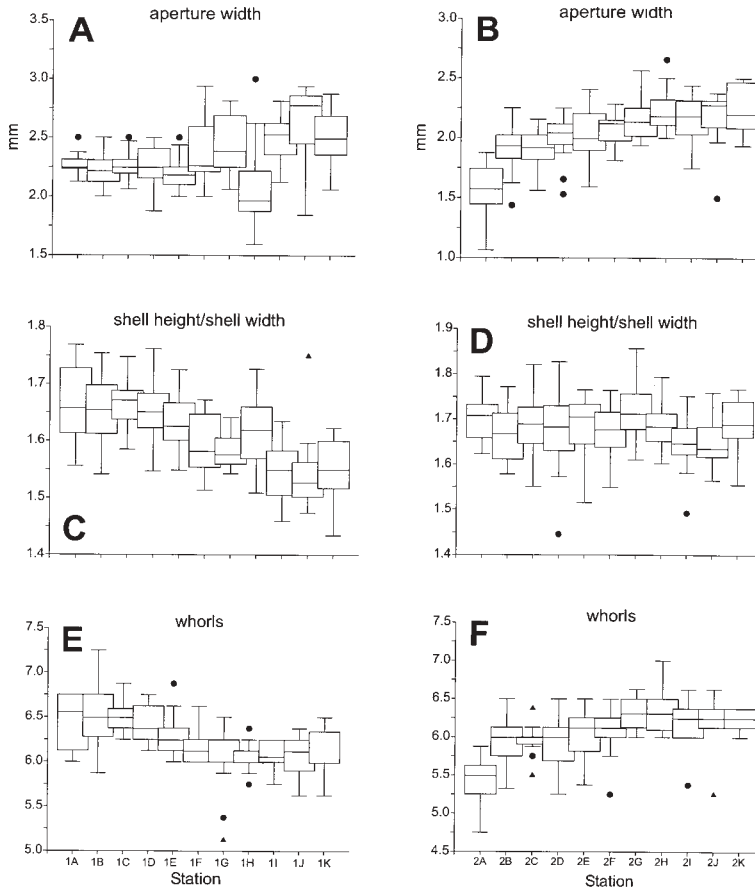
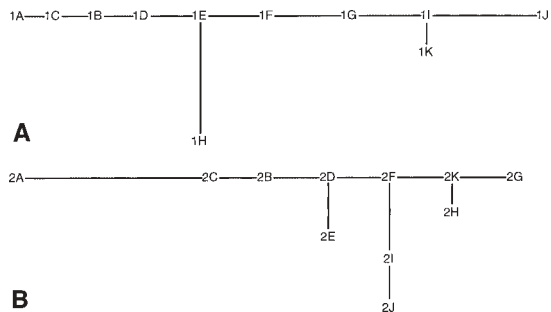


Fig. 3 Box-plots of shell variables along Stream 1 (A, C, E) and Stream 2 (B, D, F). **A, B**, aperture width; **C, D**, shell height/shell width; **E, F**, number of whorls.

Fig. 4 Minimum spanning trees based on Euclidian distances calculated from z-standardised medians of shell variables. Branch lengths are proportional to distances. **A**, Stream 1; **B**, Stream 2.



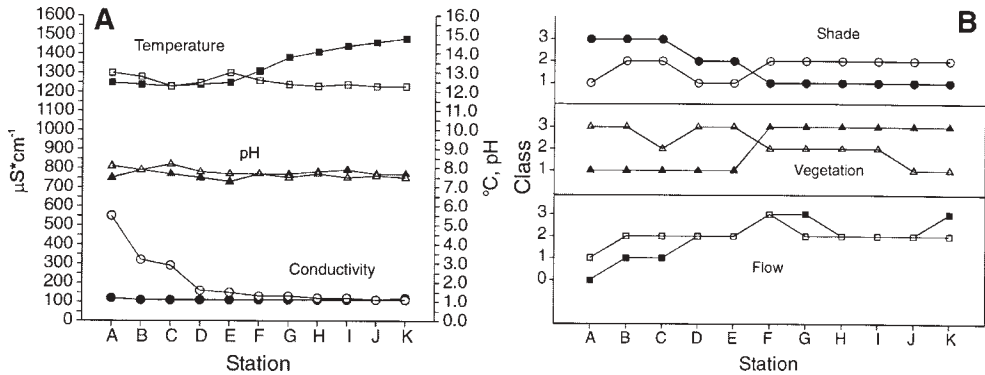


Fig. 5 Variation of environmental variables along Stream 1 (black symbols) and Stream 2 (open symbols). **A**, conductivity, pH, and temperature; **B**, flow class, surrounding vegetation type and degree of shade. Flow: 0, none, 1, weak, 2, moderate, 3, strong; vegetation: 1, natural forest, 2, forest remnants, 3, farmland; shade: 1, none, 2, partial, 3, full.

The increase of flow was significant only in Stream 1 (Fig. 5). These analyses were again based on Spearman rank correlations summarised in Table 1.

Over all 11 stations in Stream 1, only shell shape and number of whorls were correlated with temperature and inter-correlated environmental variables (see above). Also, shell and aperture width were correlated with temperature. Excluding station 1H improved most coefficients, rendering several significant. In Stream 2, flow and shade did not show any relationship with shell morphology. Practically all shell variables except for the shape parameter were correlated with the remaining highly inter-correlated environmental variables (Table 1). The frequency of spiny individuals increased with increasing temperature ($r_s = 0.790$, $P = 0.004$) and decreasing shade ($r_s = -0.642$, $P = 0.033$) towards the farmland (variable “vegetation”; $r_s = 0.671$, $P = 0.024$) along Stream 1 whereas in Stream 2 this frequency was inversely related to conductivity ($r_s = -0.759$, $P = 0.007$) and pH ($r_s = -0.613$, $P = 0.045$).

DISCUSSION

In both streams, shell size increased with increasing distance from the spring reaching a plateau in Stream 2 within 1 km of the spring. Shells became more obese in Stream 1 while shape remained constant along Stream 2. These findings are largely in accordance with the more general and large-scale observations of Wallace (1992), but demonstrate that there are local differences.

Although temperature, shade, and vegetation were correlated with shell variability along both streams, it is unlikely that these variables were the major determinants of morphological change, since these variables displayed opposite trends along the streams. It seems plausible to assume that the pattern of temperature change along these streams, recorded on single days in late autumn, reflects the pattern at other times of the year, perhaps with even increased differences during summer. However, the dependence of growth and final size on temperature needs to be tested in the laboratory. Similarly, conductivity and pH were unlikely to be important factors determining the observed changes in morphology, because their patterns differed considerably between the streams, leaving flow as the only estimated environmental

variable showing similar spatial correlations at both sites. Although flow class clearly increased along both streams, increase was significant only in Stream 1. In Stream 2 it reached a more or less constant level much earlier, which is probably why no significant increase was found over the whole stretch investigated. In addition, it has to be taken into account that *P. antipodarum* avoids strong currents by moving into more sheltered habitats (Holomuzki & Biggs 1999, 2000; see also Jowett et al. 1991). At stations with very strong current, snails were found mainly on the bank at the water line and in the riparian vegetation hanging into the water. This was especially so for young specimens (pers. obs.). Thus, the estimates of stream flow provided here were certainly quite gross, but it nevertheless appears to be reasonable that *P. antipodarum* would increase in size and, as in Stream 1 where flow was stronger, also in obesity with increasing flow. Larger and wider animals have a larger foot and thus a greater attachment area and may therefore better withstand stronger currents (cf. Dussart 1987), despite having a higher Reynolds number (Statzner & Holm 1989). This hypothesis, which can be tested experimentally, is supported by the observation that in a spring near Waitomo with high discharge large adult *P. antipodarum* were found on the exposed sides of rocks whereas small adults sat underneath (pers. obs.). Richards et al. (2001) also reported larger specimens from habitats with higher water velocities. However, they failed to state whether their samples included young individuals or only adults as in the present study.

An alternative or additional hypothesis explaining the increase in size could be the increase in nutrients available along streams. Dorgelo & Leonards (2001) showed that growth rate of *P. antipodarum* depends on food quality. Unfortunately, they could not provide data on final size. In the area of Whatawhata, pasture streams carry significantly more nutrients than streams in native forest (Quinn et al. 1997). The gradient in nutrient concentration should thus be pronounced along Stream 1, which emerges in forest. Also along Stream 2, nutrient concentration would be expected to increase, at least until reaching the forest remnants at station 2F (cf. Quinn & Stroud 2002). The appearance of spiny animals further downstream might also be due to higher nutrient concentration. This would at least be in accordance with similar observations made by Boettger (1949). Alternatively, spines might serve as spoilers, reducing drag, and their formation may be flow-related (Dussart 1987). These hypotheses could be tested in laboratory experiments.

Parasitised specimens were found only at downstream stations, probably because the water has to become deep enough to be accessible to the final hosts, fish and water fowl. Contrary to lake populations, where snails exposed to a higher risk of getting infected by trematodes matured at smaller size (Jokela & Lively 1995a,b; Jokela et al. 1999), risk of parasite infection apparently did not play a role in shaping shells along the streams investigated. The parasitised and consequently castrated females with allosperm in their receptacles must either have mated prior to infection or have mated despite being sterile. This would mean that the snails either do not perceive that they or, from the males' perspective, their partners are parasitised, or that there are other benefits to mating that outweigh the lost investment of resources and risks that mating entails.

That practically all females had mated before collection and that the majority of those which had no sperm reserves did not brood strongly suggests that there were no clonal strains present. Only if triploid females mate despite reproducing parthenogenetically does this assumption not hold, which would raise similar questions as for the mated parasitised females. Thus, considering the sex ratios found in the present study, the frequency of males in a population is not an appropriate predictor of the frequency of diploid females, as has been applied by previous authors in populations with both karyotypes, provided the above conclusion is correct.

Considering that clonal snails have a much higher reproductive success than outcrossing specimens (Jokela et al. 1997b), a mixture of one or more clones and diploid individuals would most probably have resulted in non-normal distribution of shell characters, because clones express only a small fraction of the phenotypic spectrum present in a population of outcrossing specimens (Jokela et al. 1997a). However, if the conclusion derived from female sperm reserves is correct, the presence of clones could not be the reason for the observed distributions. It is more likely that the non-normal distributions were a consequence of the dynamics of passive dislodging of smaller individuals downstream and active upstream movement reported for *P. antipodarum* and other gastropods (Haynes et al. 1985; Wallace 1992; Hurn & Denny 1997). This suggests that there is gene flow along the streams, which further suggests that the clinal variation of morphology observed is a phenotypic response rather than due to selection.

This study has demonstrated distinct spatial clines in morphology of *P. antipodarum* that were apparently related to flow but not to parasitism and other environmental variables. It appears to be reasonably safe to state that morphological patterns found in streams and lakes can be very similar yet may have entirely different causes. Several factors leading to these patterns require laboratory testing. However, it is evident from this work that complex longitudinal gradients in shell morphology may be present in genetically coherent populations.

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