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Research Article

Invasive freshwater snails provide resource for native marine hermit crabs

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Abstract

Invasive species can have significant direct and indirect impacts on native biota. Here, we conducted a survey of two invasive freshwater snail species (*Melanoides tuberculata* and *Tarebia granifera*) in Tobago and assessed the effects on shell use by native marine hermit crab populations (*Clibanarius tricolor* and *C. vittatus*). Abundant in freshwater, numbers of empty shells at the mouth of a river in Charlotteville (Northeast Tobago) increased from 75 to 800 m^{-2} after heavy rains in the wet-season of June 2012. Subsequent sampling of a nearby rocky shore revealed that the freshwater shells were occupied by 70.2% of hermit crabs. Mimicking a flood event, the experimental planting of marked alien freshwater shells showed that 20.3% of hermit crabs exchanged their marine shell for a freshwater shell. Similarly, a laboratory shell-choice experiment showed that *C. tricolor* hermit crabs changed shells repeatedly, and that 22.2% occupied a freshwater shell rather than a marine shell. Overall, due to the numeric abundance of freshwater shells and the compulsive shell changing behaviour of *Clibanarius* spp., the ongoing invasion of freshwater gastropods in the Caribbean may change the shell use patterns and population dynamics of the native hermit crabs.

Key words: invasive species; *Melanoides tuberculata; Tarebia granifera;* Caribbean hermit crabs; *Clibanarius* spp.; shell use

Introduction

Invasive species can have dramatic impacts on native biota and ecosystem functioning (White et al. 2006). Typically these effects are negative due to their ability to competitively exclude native biota, for example via the introduction of novel diseases (Strauss et al. 2012). Less common is the notion that introduced species could also offer a resource to the receiving community. For instance, the introduction of rabbits in Australia provided prey items for the native wedge-tailed eagles *Aquila audax* (Latham, 1802) (Sharp et al. 2002). On an ecosystem scale, the introduction of the Asian hornsnail [*Batillaria attramentaria* (Sowerby I, 1855)] on the mudflats of Northeast Pacific has been reported to positively impact communities as the empty shells were used by two native hermit crab species (*Pagurus* spp.) and the shells provided a hard substrate for epibiont species (Wonham et al. 2005). Suitable shells afford hermit crabs protection from predators and can also lead to increased reproductive success (Hazlett 1981). Shells cannot be obtained from living gastropods and empty shells are typically acquired through intra- and interspecific fighting between crabs (Fotheringham 1976). The arrival of empty shells can initiate a series of hermit crab shell moves in a phenomenon known as a 'vacancy chain' (Briffa and Austin 2009). If the novel resource is both plentiful and perceived to be valuable, this could significantly alter the shell use, reduce shell-crowding, and alter hermit crab fitness (e.g. Lewis and Rotjan 2009). This is particularly true for hermit crabs inhabiting unsuitable shells (damaged or small sized), which are more prone to predation (e.g. Robbins and Bell 2004).

The Caribbean has been invaded by several non-native freshwater snail species, including *Melanoides tuberculata* (Müller, 1774) and *Tarebia* granifera (Lamarck, 1822). Both snails are deposit feeders that prefer to feed on algae and diatoms. Originally from East Africa and Asia, respectively, both species were introduced accidentally into the Caribbean in the 1940s due to the aquarium trade (Pointier and Giboda 1999). In the 1960s, they were introduced intentionally in many Caribbean countries as competitors of *Biomphalaria* snails, vectors for schistosomiasis disease (Pointier and Giboda 1999). However, *M. tuberculata* and *T. granifera* were subsequently found to have introduced parasites and new diseases into the habitats they colonized (Pointier and Giboda 1999; Tolley-Jordan and Owen 2008). The first report of *M. tuberculata* in Trinidad dates from late 1970's (Bacon et al. 1979), but the snail was not found in Tobago until 1996 (Bass 2003). The exact timing of the introduction of *T. granifera* in Trinidad is unknown, but it is thought to have occurred about 20–30 years ago (Snider 2001) and this species has not been previously documented in Tobago. Both species are likely to benefit from predator release in their invasive range (Keane and Crawley 2002), which, in combination with their reproductive biology (i.e. parthenogenesis and short generation time), could explain their rapid population expansions.

Although *M. tuberculata* and *T. granifera* are restricted to freshwater, they are prone to being washed downstream during heavy downpours. Since these gastropods cannot tolerate prolonged exposure to salinities above 25 psu (Bolaji et al. 2011), their mortality results in an influx of empty shells to the marine environment. Once in the sea, however, their empty shells could be a valuable resource for hermit crabs such as *Clibanarius tricolor* (Gibbes, 1850) and *C. vittatus* (Bosc, 1802). *Clibanarius* is a genus of omnivorous hermit crabs in the family Diogenidae which mostly prey on small animals and scavenge carrion (McLaughlin and Türkay 2012). Although this genus contains the only hermit crab species known to spend its life in freshwater, the two focal species of this study, *Clibanarius tricolor* and *C. vittatus* are restricted to the marine environment. Both species appear to be shell-limited (Fotheringham 1976), and their behaviour centres on the acquisition of new shells, as is evidenced from the daily movement of *C. tricolor* (see Hazlett 1981), and the attraction of *C. vittatus* to areas where gastropods are preyed upon (Rittschof et al. 1990).

In the present work, we analysed the distribution and extent of the invasion of *M. tuberculata* and *T. granifera* in Tobago and focused on the effect of this early-stage invasion on the shell use of two native hermit crab species (*C. tricolor* and *C. vittatus*). The natural inflow of empty freshwater shells was monitored and manipulation experiments were performed to assess their impact on the shell utilization patterns of intertidal populations of the two hermit crabs on the rocky shore of Charlotteville (Northeast Tobago).

Methods

Survey of invasive snail distributions across Tobago

To assess the distribution of *T. granifera* and *M. tuberculata* in Tobago, 39 catchments and major rivers around the island were surveyed during June 2012 (Figure 1). At each of these sites, densities were estimated by counting the number of snails in four randomly assigned quadrats (0.5 m × 0.5 m). Snail species density was expressed as mean (± SE) per m^2.

Assessment of the effects of freshwater invasive species on the shell occupation by hermit crabs

Estimates of snail and hermit crab densities

Hermit crabs were observed inhabiting freshwater snail shells for the first time along Charlotteville rocky shore in Tobago (19°19.541'N, 60°32.946'W) in June 2012. To determine the effects of freshwater snail shell influx to the shore, the densities of *T. granifera* and *M. tuberculata* were recorded before and after a downpour event (9^{th} and 17^{th} June 2012, respectively) using quadrats at 121, 133 and 143 m from the river mouth. Within each quadrat, all snail shells were counted, including those underneath rocks. The species of snail of each shell was recorded, along with whether or not it was occupied by a snail or hermit crab (*Clibanarius tricolor*, *C. vittatus*). *Calcinus tibicen* were also present but these hermit crabs were rare, and the adult of this species is generally too large to occupy the freshwater shells.

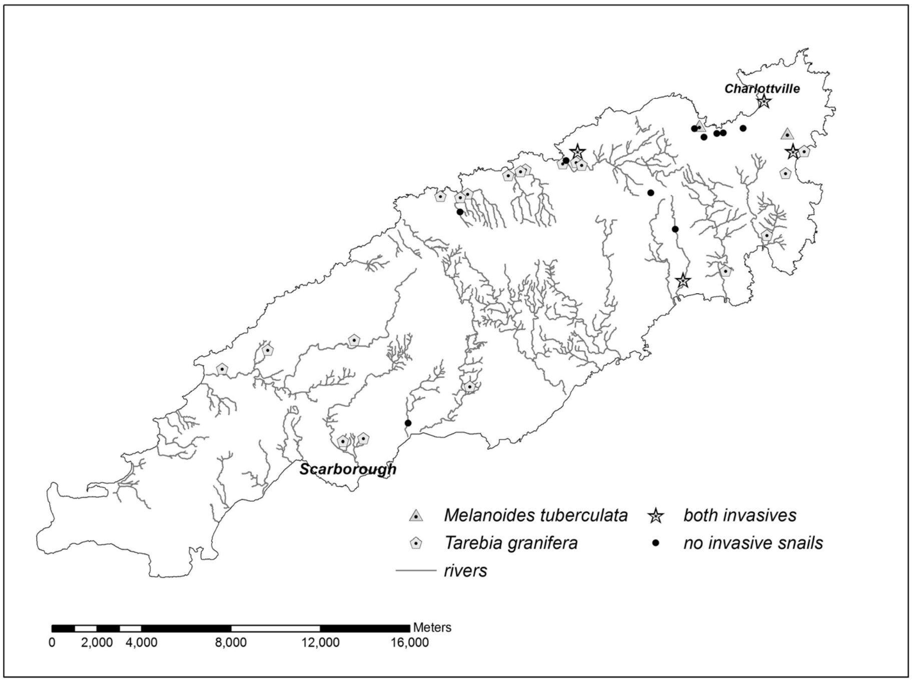

Figure 1. Map of Tobago showing the main rivers and sampling sites where either *Melanoides tuberculata, Tarebia granifera*,both species or no invasive freshwater snail species were found in June 2012.

Wild mark-recapture experiment

A total of 999 empty freshwater snail shells of *T. granifera* were marked with nail polish. Marked shells were placed at three sites where empty *T. granifera* shells were not present, at low tide on 18 June 2012 (333 shells per site; each site marked with a different colour) and re-captured 24h later. The number of re-captured marked shells was tallied within a 2.25 m^2 area (nine 0.5 m × 0.5 m quadrats) around the release point and shells and hermit crabs were recorded as above.

Individual shell choice experiment

Shell choice of the hermit crab *C. tricolor* was analysed experimentally on 12–13 June 2012. *C. tricolor* (n=40) occupying the marine snail shell, *Supplanaxis nucleus,* were collected from the rocky shore at Charlotteville. To induce a shell change, the hermit crab shell was damaged by removing 2 mm around the circumference of the operculum and 1 mm of the shell apex. To provide empty shells for the choice experiment, 40 *S. nucleus* were removed from their shells by boiling in water and removing the body with forceps, and a further 40 empty *T. granifera* shells were collected from Charlotteville River. Each hermit crab was size matched with an empty *S. nucleus* and *T. granifera* shell within ±2.0 and ±6.0 mm length and ±2.5 and ±3.0 mm operculum diameter, respectively, and placed individually within a plastic pot (4.5 cm dia.) with sand substrate. Every hour for 10 h the shell occupied by each *C. tricolor* individual was recorded (i.e. original damaged (*S. nucleus*), freshwater (*T. granifera*) or marine (*S. nucleus*) shells).

Statistical analyses

The population density of invasive snails was compared to that of native gastropods using a Mann-Whitney test, and the variance in density between populations of invasive and native snails was analysed with a Levene's test. Shell occupancy was analysed using Chi-square tests and binomial mass function. Changes in the steepness of the cline of the proportion of hermit crabs in freshwater shells relative to the distance to the river mouth was analysed using a Binary logistic regression. Mann-Whitney tests were used to analyse the increase in density of freshwater shells after the rains. All tests were performed in Minitab 12.1.

Results

The survey of 39 riverine sites around Tobago (Figure 1) revealed the presence of one or both invasive snail species at 29 (74.4 %) sites (*Tarebia granifera*: n=22; *Melanoides tuberculata* n = 2; both species: n=5). Where present, the mean ± SE abundance of the invasive species, 59.9 ± 16.6 individuals m^{-2}, was significantly higher than that of all native freshwater gastropods combined (9.87 ± 5.09 individuals m^{-2}), (Mann-Whitney test: W=190.5, $P = 0.004$). Across colonised sites, the variance in density of the invasive gastropods was significantly higher than that of their native counterparts (Levene's Test: $t = 12.106$, $P = 0.002$). These data suggest that the invasive snails can reach a much higher carrying capacity than the native gastropods.

Both invasive species were observed in Charlotteville in an unnamed river circa 100 m from the rocky shore occupied by intertidal hermit crabs. The mean ± SE number of empty freshwater snail shells in the river mouth was found to increase more than ten-fold after a period of heavy rain, i.e., from 75 ± 19.4 m^{-2} to 800 ± 219 m^2 (Mann-Whitney test: $W = 15.0$, $P = 0.012$) (Figure 2). In both sampling periods, the majority of the empty snail shells (~97 %) were *T. granifera* with just a small number of *M. tuberculata* shells. Many shells appeared to be washed into the sea, and the resulting inflow of shells onto the rocky shore caused a significant change in the proportion of *Clibanarius tricolor* and *C. vittatus* hermit crabs occupying freshwater snail shells. Before the rains, 19.4 % (19 out of 98) of hermit crabs occupied a freshwater shell compared to 70.2 % (1068 out of 1522) after the rains ($\chi^2 = 107.557$, d.f. = 1, $P < 0.001$) (Figure 2). The number of empty marine shells before the rains (1 out of 99) also increased significantly to 57 out of 783 (7.2 %) after the rains (binomial test: $P = 0.005$), which suggests that the availability of a large number of freshwater shells resulted in hermit crabs exchanging their marine shell for a freshwater one.

The proportion of hermit crabs occupying freshwater shells declined steeply (30 % per meter) with distance from the river mouth (Binary logistic regression: mean (5–95 %CI) Odds Ratio = 0.70 (0.65–0.76), $Z = -8.92$, $P < 0.0001$) (Figure 3). As a consequence, the relative ratio of shell types occupied by hermit crabs changed markedly across the transect (Figure 4).

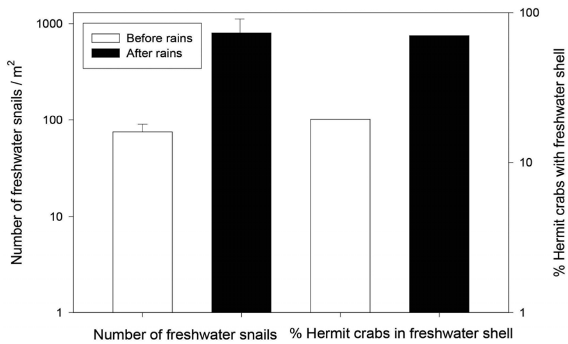

Figure 2 Mean (± SE) number of freshwater snails (*Tarebia granifera* and *Melanoides tuberculata*) per square meter in the river mouth, and the mean percentage of hermit crabs in freshwater shells found in three quadrats at 121, 133 and 143 m from the river mouth before (open bars) and after (solid bars) the rains.

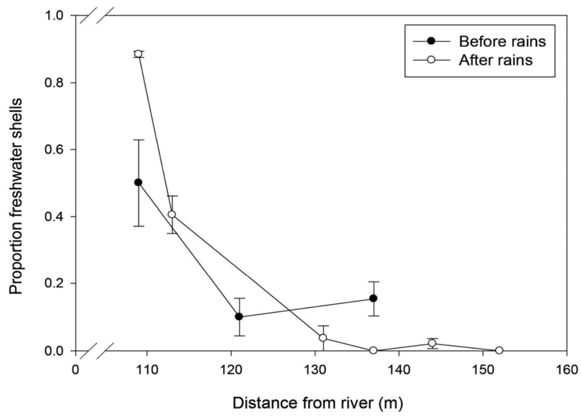

Figure 3 The proportion of hermit crabs (mean ± SE) in freshwater shells observed on the rocky shore relative to the distance from the river mouth before and after heavy rains. Only quadrats with > 15 hermit crabs are shown. The largest change in shell utilization is observed near the river mouth.

In a mark-release-recapture experiment, there were no unoccupied marine shells before the empty freshwater shells were planted. Twenty-four hours after the release, 62 (18.6 %), 115 (34.5 %) and 91 (27.3 %) of marked shells were recaptured at the three sites, of which the majority were occupied by either a *C. tricolor* or *C. vittatus* hermit crab (51 (82.3 %), 49 (42.6 %) and 42 (46.2 %) at the three replicate release-sites). Combining the three release sites, a total of 142 hermit crabs occupied freshwater shells, compared to 558 in marine shells, showing that 20.3 % of all hermit crabs at the three release

Table 1. Number of marine shells occupied and unoccupied by hermit crabs, and percentage of empty marine shells after experimental release of 999 empty freshwater shells on the Charlotteville rocky shore, Tobago, recorded 19 June 2012.

Marine shell species	Occupied	Unoccupied	%Unoccupied	Total
Supplanaxis nucleus (Bruguière, 1789)	278	11	4	289
Cerithium eburneum (Bruguière, 1792)	106	3	3	109
Tegula excavata (Lamarck, 1822)	48	19	28	67
Tegula fasciata (Born, 1778)	38	13	25	51
Nerita tessellata (Gmelin, 1791)	27	5	16	32
Oliva sayana (Bruguière, 1789)	16	0	0	16
Thais haemastoma floridana (Conrad, 1837)	15	1	6	16
Mitrella ocellata (Gmelin, 1791)	11	0	0	11
Littorina meleagris (Potiez & Michaud, 1838)	6	0	0	6
Modulus modulus (Linnaeus, 1758)	5	0	0	5
Unidentified green marine sp.	0	3	100	3
Astraea caelata (Gmelin, 1791)	2	1	33	3
Cittarium pica (Linnaeus, 1758)	2	0	0	2
Pisania pusio (Linnaeus, 1758	1	0	0	1
Stigmaulax sulcata (Born, 1778)	1	0	0	1
Purpura patula (Linnaeus, 1758)	1	0	0	1
Epitonium novangliae (Couthouy, 1838)	1	0	0	1
Columbella mercatoria (Linnaeus, 1758)	0	1	100	1

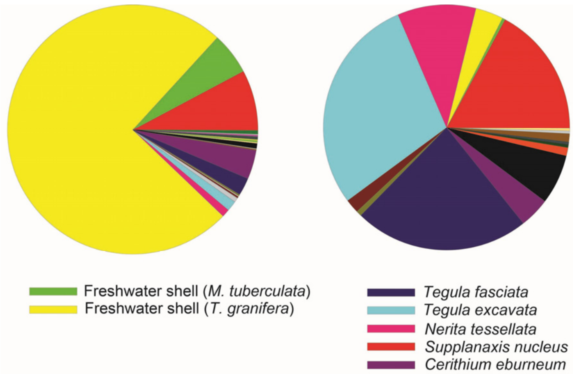

Figure 4. Pie charts showing the shell types across two rocky shore transects, one 109–130m distance from the river mouth (left) and the other 131–163m from the river mouth (right) after rains. Here, *Tegula fasciata* and *T. excavata* are most often exchanged, while *Supplanaxis nucleus* are less often exchanged for a freshwater shell, which is consistent with the proportion of unoccupied shells found after the release experiment (see Table 1).

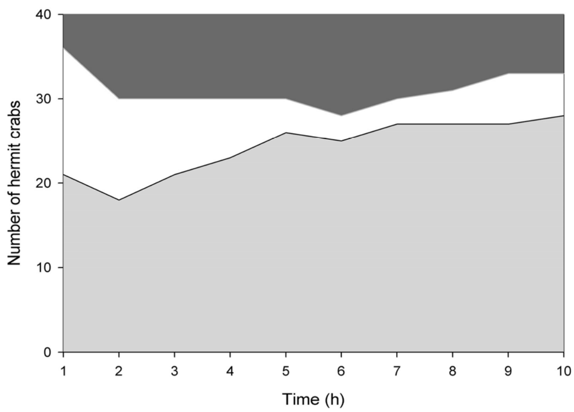

Figure 5 The number of hermit crabs occupying freshwater shells (*Tarebia granifera*), their original damaged shells (*Supplanaxis nucleus*), or a new marine shell (*S. nucleus*) over a 10h shell-choice experiment. Undamaged marine shells were significantly more preferred than the size-matched freshwater shell or the damaged shell.

sites had exchanged their marine shell for a (marked) freshwater shell. Based on the ratio of empty versus occupied shells after experimental release, some types of marine shells were significantly more likely to be exchanged for a freshwater shell than others ($\chi^2 = 62.058$, d.f.= 4, $P < 0.001$) (see Table 1). For example, the shells of *Tegula excavata* and *T. fasciata* were significantly more often discarded (28 and 25 %, respectively), while shells of *Supplanaxis nucleus* were among the shell types being vacated less often (4 %) (Table 1; Figure 4; for shell size data see Appendix 1).

During the shell choice test, 55% of *C. tricolor* individuals changed shells more than once (mean ± SE number of shell changes = 1.93 ± 0.27) during the 10 h experimental period (overnight). The hermit crabs were most often found in the new native marine shell (60.8 %), while 17.0 % remained in their (experimentally) damaged shell, and 22.2 % moved to the freshwater *Tarebia granifera* shell (Figure 5).

Discussion

Here, for the first time we record the presence of *Tarebia granifera* in Tobago and map its distribution and density, along with another invasive freshwater gastropod, *Melanoides tuberculata*. Both snails are now widespread across the island, although several rivers have yet to be colonized (Figure 1). The wide range of densities observed suggests that many populations have yet to reach carrying capacity. Of the 10 sites where *M. tuberculata* has been found previously (Bass 2003), six were revisited and the presence of *M. tuberculata* confirmed in three of these locations, while *T. granifera* alone was found in the remaining three sites. Long-term studies suggest that alone, both species are capable of attaining relatively stable populations over long periods of time in their invasive habitat (Pointier and Giboda 1999). Where both species occur together, this may not be the case: *T. granifera* has been shown to displace *M. tuberculata* from some sites in Martinique (Facon et al. 2005). The discrepancy between the findings of Bass (2003) and the present study suggests that *M. tuberculata* may also be displaced by *T. granifera* in Tobago. Further efforts should be made to continue monitoring this recent invasion as both *T. granifera* and *M. tuberculata* have the potential to outcompete native snail species (Pointier and Giboda 1999), and the interactions between the two invasive species has received little attention.

A field study on the rocky shore of Charlotteville, Tobago showed that the density of shells from these invasive freshwater snails increased more than ten-fold after a period of heavy rain in June 2012. This inflow resulted in a significant change in the proportion of *Clibanarius tricolor* and *C. vittatus* hermit crabs occupying freshwater shells, particularly near the river mouth. Experimental release of freshwater shells initiated a similar change in hermit crab shell occupancy, and shell choice experiments in the laboratory showed that although hermit crabs prefer marine shells, a considerable proportion moved into freshwater shells.

Shell preference is known to vary between hermit crab species (Tricarico et al. 2009), and it has often been related to shell weight, thickness and resistance to wave action (e.g. Arce and Alcaraz 2011). Although our experiment showed that *C. tricolor* does not generally prefer freshwater over marine shells, the inflow and high availability of freshwater shells significantly altered the shell use in both *C. tricolor* and *C. vittatus* populations 24 h after their release. So rather than a preferred shell choice, the high uptake rate of freshwater shells might be a density effect.

Given that empty shells are usually rare, and that inhabited shells are damaged over time or become too small as crabs grow, this compulsive changing of shells may be an adaptive behaviour (e.g. Robbins and Bell 2004). Judging by the repeated change of shells in the shell-choice experiment in the laboratory, and the large number of empty marine shells on the rocky shore, the inflow of a large number of freshwater shells appears to initiate a 'vacancy chain' wherein the availability of empty shells results in a chain reaction of shell exchanges (Briffa and Austin 2009).

Previous studies on *Clibanarius* spp. revealed that shell usage is not directly related to empty shell availability, suggesting that crabs have other selection criteria (Nakim and Somers 2007). Given the present results, however, it seems that high availability of shells from *T. granifera* and *M. tuberculata* does play an important role. Compared to some marine shells, these freshwater shells may also confer other advantages, such as morphometric fit of the shell to the hermit crab (see e.g. Lawal-Are et al. 2010), and the preference of hermit crabs for lighter shells that facilitate mobility (Argüelles-Ticó et al. 2010).

Although the relationship between hermit crabs and shell resources is complex (e.g. Robbins and Bell 2004), in the current invasion scenario the abundance of freshwater shells appears to have a marked effect on the biology of hermit crabs. In a similar scenario, the introduction and establishment of the Asian hornsnail *Batillaria attramentaria* in a mudflat ecosystem in the Northeast Pacific has had a dramatic effect on that community. These snails provide substrate for eelgrass, other snail species, as well as shells for hermit crabs *Pagurus* spp. (Wonham et al. 2005). The ongoing invasion and population expansion of *T. granifera* and *M. tuberculata* in Tobago, and probably elsewhere in the Caribbean, has the potential to alter hermit crab population dynamics in the adjacent marine environment. This will have long-term consequences for their population viability and demography (Lewis and Rotjan 2009) and is likely to have community-wide effects (e.g. Wonham et al. 2005).

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References

Arce E, Alcaraz G (2011) Shell use by the hermit crab *Calcinus californiensis* at different levels of the intertidal zone. *Scientia Marina* 75: 121–128, http://dx.doi.org/10.3989/scimar.2011.75n1121

Argüelles-Ticó A, Álvarez F, Alcaraz G (2010) Shell utilization by the hermit crab *Clibanarius antillensis* Stimpson, 1862 (Crustacea Anomura) in intertidal rocky pools at Montepio, Veracruz, Mexico. *Tropical Zoology* 23: 63–73

Bacon PR, Jaikaransingh E, Seeberan G (1979) Notes on some freshwater molluscs from Nariva Swamp, Trinidad. *Living World Journal of the Trinidad and Tobago Field Naturalists' Club* 1979: 14–15

Bass D (2003) A survey of freshwater macroinvertebrates in Tobago. *Living World Journal of the Trinidad and Tobago Field Naturalists' Club* 2003: 64–68

Bolaji DA, Edokpayi CA, Samuel OB, Akinnigbagbe RO, Ajulo AA (2011) Morphological characteristcis and salinity tolerance of *Melanoides tuberculata* (Muller, 1774). *World Journal of Biological Research* 004: 2

Briffa M, Austin M (2009) Effects of predation threat on the structure and benefits from vacancy chains in the hermit crab *Pagurus bernhardus*. *Ethology* 115: 1029–1035, http://dx.doi.org/10.1111/j.1439-0310.2009.01687.x

Facon B, Jarne P, Pointier JP, David P (2005) Hybridization and invasiveness in the freshwater snail *Melanoides tuberculata*: hybrid vigour is more important than increase in genetic variance. *Journal of Evolutionary Biology* 18: 524–535, http://dx.doi.org/10.1111/j.1420-9101.2005.00887.x

Fotheringham N (1976) Populations consequences of shell utilization by hermit crabs. *Ecology* 57: 570–578, http://dx.doi.org/10.2307/1936441

Hazlett BA (1981) The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics* 12: 1–22, http://dx.doi.org/10.1146/annurev.es.12.110181.000245

Keane RM, Crawley MJ (2002) Exotic plant invastions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164–170, http://dx.doi.org/10.1016/S0169-5347(02)02499-0

Lawal-Are A, Uwadiae RE, Owolabi OR (2010) Shell selection of the hermit crab *Clibanarius africanus* (Aurivillus, 1898) (Decapoda: Diogenidae) in the Lagos lagoon: Aspects of behavioural and bio-ecology of benthos. *World Rural Observations* 2: 70–78

Lewis SM, Rotjan RD (2009) Vacancy chains provide aggregate benefits to *Coenobita clypeatus* hermit crabs. *Ethology* 115:356–365, http://dx.doi.org/10.1111/j.1439-0310.2009.01626.x

Nakim M, Somers M (2007) Shell availability and use by the hermit crab *Clibanarius virescens* along the eastern Cape Coast, South Africa. *Acta Zoologica Academiae Scientiarium Hungaricae* 53: 149–155

McLaughlin P, Türkay M (2012) *Clibanarius* Dana, 1852. In: World Paguroidea and Lomisoidea database. Accessed through: World Register of Marine Species

Pointier JP, Giboda M (1999) The case for biological control of snail intermediate hosts of *Schistosoma mansoni. Parasitology Today* 15: 395–397, http://dx.doi.org/10.1016/S0169-4758(99)01517-3

Rittschof D, Kratt CM, Clare AS (1990) Gastropod predation sites: the role of predator and prey in chemical attraction of the hermit crab *Clibanarius vittatus. Journal of the Marine Biological Association of the United Kingdom* 70: 583–596, http://dx.doi.org/10.1017/S0025315400036602

Robbins BD, Bell SS (2004) Relationships between a hermit crab and its shell resource: spatial patterns within a seagrass dominated landscape. *Marine Ecology Progress Series* 282: 221–227, http://dx.doi.org/10.3354/meps282221

Sharp A, Gibson L, Norton M (2002) The breeding-season diet of wedge-tailed eagles (*Aquila audax*) in western New South Wales and the influence of Rabbit Calcivirus Disease. *Wildlife Research* 29: 175–184, http://dx.doi.org/10.1071/WR00077

Snider SB (2001) Towards a movement ecology: Modeling the behavioral response of invasive snails to resources and competition. PhD thesis. North Carolina State University, USA, 121 pp

Strauss A, White A, Boots M (2012) Invading with biological weapons: the importance of disease mediated invasions. *Functional Ecology* 26: 1249–1261, http://dx.doi.org/10.1111/1365-2435.12011

Tolley-Jordan LR, Owen JM (2008) Habitat influences snail community structure and trematode infection levels in a spring-fed river, Texas, USA. *Hydrobiologia* 600: 29–40, http://dx.doi.org/10.1007/s10750-007-9173-3

Tricarico E, Bertocchi S, Brusconi S, Chessa L, Gherardi F (2009) Shell recruitment in the hermit crab *Clibanarius erythropus. Journal of Experimental Marine Biology and Ecology* 381: 42–46, http://dx.doi.org/10.1016/j.jembe.2009.09.001

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. *Diversity and Distributions* 12: 443–455, http://dx.doi.org/10.1111/j.1366-9516.2006.00265.x

Wonham M J, O'Connor M, Harley C (2005) Positive effects of a dominant invader on introduced and native mudflat species. *Marine Ecology Progress Series* 289: 109–116, http://dx.doi.org/10.3354/meps289109

Supplementary material

The following supplementary material is available for this article:

Appendix 1. Size of the marine snail shells utilized by *Clibanarius tricolor* and *C. vittatus* hermit crabs in the current study.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2013/Supplements/AI_2013_vanOosterhout_etal_Supplement.pdf