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Predation by invasive *Platydemus manokwari* flatworms: a laboratory study

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Abstract: *Platydemus manokwari* de Beauchamp, 1963 is an invasive flatworm found on islands in the tropics, especially in the Pacific Ocean. It has been implicated in the decline of several snail populations, including the extinction of some *Partula* species. Its predatory behaviour was investigated to quantify predation rates and elucidate climatic influences. This laboratory study of the invasive flatworm confirms earlier reports that *P. manokwari* is a generalist predator of snails. It prefers small prey and avoids species defended by copious mucus, chemical defences or a tough integument. Prey are found by following damp mucus trails up to 15 h old. Flatworm activity is limited by temperature and humidity, with peak feeding at 24–30ºC and 85–95% humidity. This determines the geographical spread of the species and probably also the effectiveness of arboreal predation. Aboveground air circulation leads to drying, reducing the ability of the flatworms to locate trails and remain active high off the ground. Local climatic factors may dictate how significantly *P. manokwari* affects snail populations.

Keywords: *Platydemus manokwari*, ecology, invasion biology, snails, diet, invasive species

INTRODUCTION

Human impacts on the natural environment have intensified greatly since the 17th century. These impacts have not been uniformly distributed and island ecosystems are under particular pressure, as their small size and isolation increases the threats they face (Keppel et al. 2014). Principal threat factors are habitat loss, invasive species, and climate change. Habitat loss has affected different systems in varying ways, depending on topography, climate, and biodiversity. As a result, some islands still retain significant areas of important habitats, mainly in uplands. Most of these are no longer occupied by all of the original biota due to the impacts of invasive species. They affect all habitats to some extent and were considered the most significant threats in the past, now with the added complication of climate change (Wood et al. 2017).

Island land snails have particularly high extinction rates associated with invasive species, with the introduced predatory snail *Euglandina rosea* being directly responsible for one third of extinctions (Régnier et al. 2009). The significance of this threat is illustrated by the decline of the Pacific island tree snail family Partulidae, which lost 80% of species in the late 20th century (Gerlach 2016). All introduced populations of *Euglandina* have since declined (Gerlach 2016), but surviving partulid populations are now additionally threatened by introductions of the New Guinea flatworm *Platydemus manokwari* de Beauchamp, 1963.

Platydemus is suspected to have eliminated *Euglandina* from Guam in the Marianas (Kerr 2013) and the Bonin islands (Ohbayashi et al. 2005). The replacement (either directly or indirectly) of *Euglandina* by *P. manokwari* may alter the conservation prospects for many island snails. Consequently, there have been some field studies of the flatworm's ecology in the Bonin islands (Sugiura 2009; Sugiura & Yamaura 2009) and some laboratory studies (Kaneda et al. 1990, 1992; Ohbayashi et al. 2005; Sugiura 2009, 2010; Iwai et al. 2010).

In the Bonin islands, *P. manokwari* is known to be a major predator of ground snails, particularly small ones, but being able to kill all sizes, sometimes by gregarious attacks (Sugiura 2009, 2010). The invasive flatworms also prey on earthworms, woodlice, other flatworms (although not feeding cannibalistically) and nemertean ribbon worms (Ohbayashi et al. 2005). Most of the prey are located by following mucus trials (Iwai et al. 2010). Predation has been recorded at least 2 m above ground, but on trees the predation rate is reduced relative to ground predation (Sugiura & Yamaura 2009). Part of the success of introductions of this species follows from its extremely rapid development, taking just 24–27 days between egg laying and sexual maturity, when these hermaphrodites can lay eggs every 7–10 days (Kaneda et al. 1990), with an average juvenile production rate of 3.8 per week (derived from data in Kaneda et al. 1990). They can also regenerate from fragments (becoming reproductive after 2 weeks), but this does not appear to be used as a normal reproductive strategy (Kaneda et al. 1990). The only limitations on the species that have been identified are low temperatures; it has been estimated that ambient temperatures of 10ºC are too low for population establishment due to a lack of reproduction and increased mortality (Kaneda et al. 1992; Sugiura 2009). *Platydemus* is also reported to be vulnerable to seawater (Ohbayashi et al. 2005). All this suggests that most tropical land-snail habitats are vulnerable to *P. manokwari*, although invasion at higher altitudes may be slow. The species has recently extended its range, also to continental areas (Justine et al. 2014, 2015).

This laboratory study aimed to evaluate the potential impacts of the invasive flatworm *P. manokwari* on prey species and the likelihood of its future range expansion.

MATERIAL AND METHODS

Animal origin and general experimental conditions

Initially, 30 adult *Platydemus manokwari* were obtained from the Society Islands of Huahine and Raiatea. These were reared in plastic boxes measuring 3 cm × 10 cm

× 15 cm (with 2 flatworms each) or 10 cm × 15 cm × 20 cm (5–20 flatworms each). Every box was lined with wet tissue paper and contained half a plastic flowerpot as a shelter. Boxes were kept at 22ºC, except when experiments included investigation of temperature effects, as other researchers used 24ºC (Kaneda et al. 1990) or 25ºC (Ohbayahsi et al. 2005; Sugiura 2009; Iwai & Sugiura 2010). A light/dark cycle of 14/10 h was used, with low light intensity. Varying numbers, species, and sizes of snails were added to the boxes as sources of food in different experiments (Table 2). Boxes were cleaned and the tissue paper replaced every 2–3 days. During cleaning and the experiments, flatworms were manipulated as little as possible. Where handling was inevitable, round-tipped forceps were used to minimise the risk of damage. Observations concerned predatory behaviour, dietary preferences and consumption rates, trail following as well as effects of salinity, temperature, and humidity on activity and feeding.

Observations of predatory behaviour

During experiments, the details of hunting and predation events were recorded, both in isolation and when many flatworms were present. In all observations the flatworms were assigned to size categories according to their relaxed length (0-10 mm, 11-20 mm, >20 mm). The randomness of searching during predation was studied by placing a flatworm in a 1 m^3 clear Perspex arena on top of a heat mat, with a base of wet paper and a water reservoir to maintain saturated conditions. Prior to the experiment, the flatworm had been starved for a week. The box containing the flatworm was transferred to the experimental arena and the lid removed, allowing the flatworm free movement. When movement was observed, the trail of the flatworm was traced on the opposite side of the Perspex after the worm had moved away but the trail was still visible, thus avoiding any disturbance from vibration. In the analysis of randomness, the worm's trail was divided into 20-mm (flatworm body length) sections and the orientation of the sections was assigned to a 10º sector relative to the direction of movement in the previous section. Thus movement in a straight line would be recorded as a deviation of no more than 10º to the left or right.

Dietary preferences and consumption rate

Experiments offering different snail species to *Platydemus* lasted 24 h each and used live specimens of 11 species (Table 2). In addition, a single fresh dead *Partula rosea* × *varia* was offered along with 5 live *Cornu aspersum* (O. F. Müller, 1774) (Helicidae). The proportion of available prey consumed was recorded. In other consumption rate experiments, 5–10 *Cornu aspersum* of different sizes were kept with flatworms and the number of items consumed was recorded. All prey items were weighed on digital scales to the nearest 0.01 g.

Trail following

Experimental trails were formed by allowing a snail to crawl over a sheet of Perspex. The trail was traced on the underside of the sheet with a marker pen, providing a visual marker that was undetectable by the flatworm. A flatworm was placed near the trail, perpendicular to it and trail following was determined to have taken place when a flatworm contacted the trail and changed direction to move along the trail. Experiments were carried out with trails left to dry or kept in a fully moisture-saturated environment. Trails were used fresh or after varying lengths of time (1, 2, 6, 15, 19, 21, and 24 h).

Movement rate

The rate of movement was assessed when trail following was recorded by measuring (in mm) the length of trail covered in 10 s. This was repeated 10 times for 5 different worms.

Salinity

Flatworms were placed in an arena formed by a sheet of damp paper surrounded by concentric rings of paper soaked in different solutions of salt water. Their response to these salinity zones was categorised as active (normal behaviour) or avoided (turned away from contact).

Temperature and humidity

Boxes of flatworms were kept at different temperatures (14, 18, 20, 22, 24, 26, 34ºC) and relative humidity (85–100%, with experimental reductions to 74% lasting no longer than 1 h) and the rates of survival and feeding were recorded. Temperature and humidity were recorded with digital thermometers/hygrometers (to the nearest 0.1ºC and 1% humidity).

Statistical analysis

The significance of results was evaluated using the analysis of variance (ANOVA) for consumption rates of different prey species and sizes, and Student's *t* tests for comparisons of trail following under different conditions.

RESULTS

Predatory behaviour

Observations of predation showed that *Platydemus manokwari* killed and consumed prey by crawling onto the shell and immobilising the prey by wrapping around it (Fig. 1). Fluids (presumably containing enzymes) were secreted onto the prey. At that point, the prey either retracted into the shell or tried to crawl away. Within approximately 1 min (Table 1) the prey had ceased movement, and fluid production (probably including mucus from the prey) had increased. Flatworms stayed with the prey for several hours, after which time most of the body had been ingested. Where several flatworms were kept together, daylight feeding by one flatworm coincided with activity by another worm on 20% of occasions ($N = 50$). In contrast, when activity was observed during daylight without feeding, more than one flatworm moving simultaneously was recorded on only 6% of observations ($N = 50$).

The movement of starved flatworms searching for food was not consistent with undirected random movement at the scales examined. Once a direction of movement had been established, worms did not deviate their path by more than 10º for 7 body

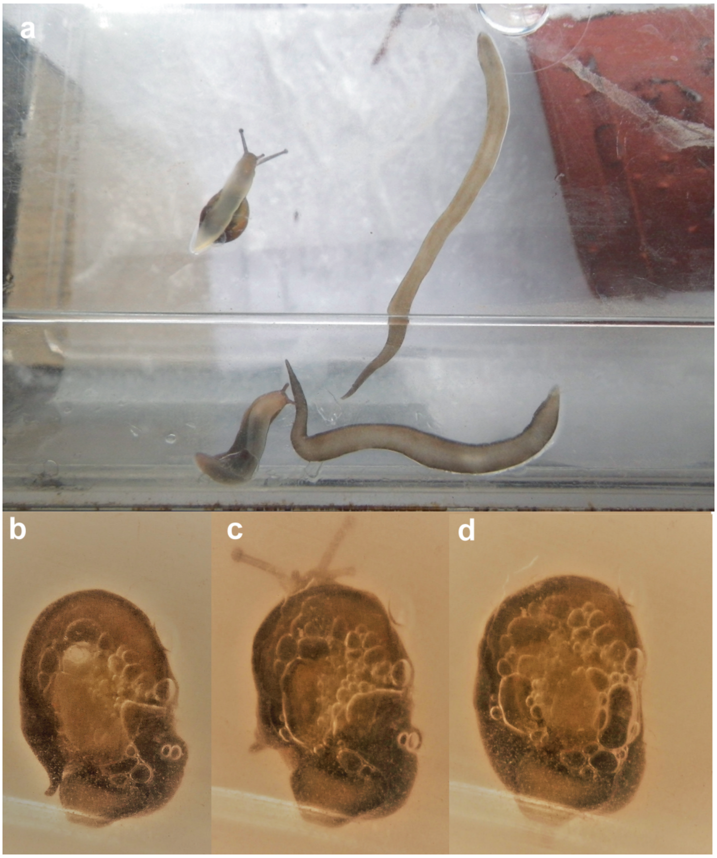

Fig. 1. *Platydemus manokwari* predatory behaviour: (a) two flatworms hunting on one *Deroceras laevis* and one *Cornu aspersum* on the underside of the lid; the shelter can be seen in top right of the photograph; (b–d) *Platydemus* attacking the same *C. aspersum*, seen from the underside: (b) flatworm wrapping around its prey (anterior part of the flatworm can be seen at lower left), mucus appears to be mainly produced by the prey; (c) prey attempting to escape, the flatworm now tightly enclosing the prey; (d) prey subdued and now being digested

Table 1. Duration of components of predatory behaviour of *Platydemus manokwari* (10–20 mm long) on *Cornu aspersum* of 0.2–0.3 g body weight

Behaviour	Prey active (N = 20)	Prey inactive (N = 20)
Contact to immobilisation	40±6.5 s	-
Immobilisation to fluid secretion	19±10.7 s	28±8.4 s
Digestion	235±23 min	243±31 min

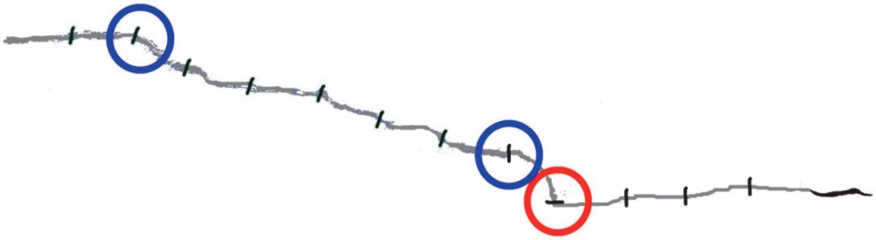

Fig. 2. Example of the direction taken by a foraging *Platydemus*. Trace of the trail shown in grey (flatworm at the right end of the trail), flatworm body length marked as perpendicular black bars; the flatworm at the upper end of the trail. Blue circle marks points with at least a 15º change in direction; red circle – 90º change in direction at a prey trail

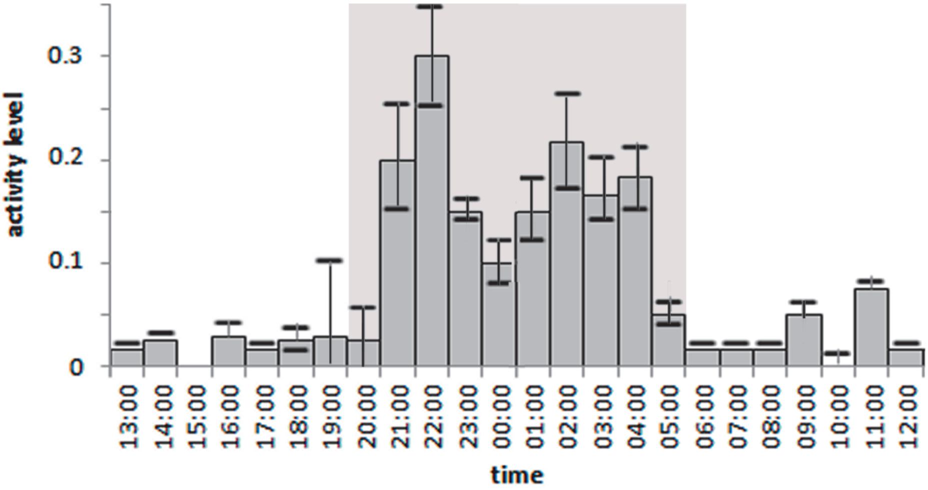

Fig. 3. Activity levels at 22ºC and 95% humidity shown as the proportion of flatworms active (*N* = 60). Dark hours shaded. Standard errors of the mean shown

lengths (mean 6.5 body lengths, approximately 130 mm) and over 20 body lengths (400 mm) the mean deviation was 15º (*N* = 50). Marked changes in direction were almost always a result of crossing a prey trail (25–90º deviation on 93% of interactions, *N* = 30) (Fig. 2). In the absence of prey trails, such large changes in direction occurred only 5% of the time (*N* = 50). Thus foraging is not a random movement in this species, at least over relatively short distances.

Foraging activity was recorded throughout the day and night but was significantly greater at night (Fig. 3).

Dietary preferences and consumption rates

All the snail species used in this study were consumed except *Leptinaria unilamellata* and *Paropeas achatinaceum* (Table 2), both of which produced copious frothy mucus when attacked. Carrion was also consumed, with 5 flatworms showing a preference for feeding on dead *Partula rosea* × *varia* despite the presence of live *Cornu aspersum*. In contrast, very few slugs were consumed (only one *Deroceras laevis*). Consumption rates of the prey species did not differ significantly (Table 3), although the overall percentage of consumption varied from 6% (*Deroceras laevis*) to 40% (*Ovachlamys fulgens* and *Subulina octona*).

Table 2. Consumption of the tested gastropod prey species by *Platydemus manokwari* (most of them alive, except for carrion of *Partula rosea* × *varia*, marked with *)

Prey snails	N	Eaten	Prey slugs	N	Eaten
Cornu aspersum (Helicidae)	180	61	*Deroceras laevis* (Limacidae)	18	1
Diastole conula (Helicarionidae)	40	10	unidentified Philomycidae	8	0
Elasias apertum (Achatinellidae)	30	6	unidentified Veronicellidae	12	0
Leptinaria unilamellata (Subulinidae)	20	0			
Ovachlamys fulgens (Helicarionidae)	20	8			
Paropeas achatinaceum (Subulinidae)	20	0			
Subulina octona (Subulinidae)	20	8			
Trichia hispida (Helicidae)	30	6			
Partula rosea × *varia* (Partulidae)*	1	1			

Table 3. ANOVA of consumption of different species of live gastropods by *Platydemus manokwari*

Sources	SS	df	MS	*F*	*p*
Between groups	44.083	1	44.083	1.762	0.214
Within groups	250.167	10	25.017		
Total	294.25	11	26.75		

Consumption rates were affected by temperature and humidity (see below). At 24ºC the mean predation rate was 0.40±0.11 snails per day, with a mean prey weight of 0.140±0.001 g. The average daily consumption rate was 0.056 g. The maximum prey size was 0.36 g. The proportions of prey categories eaten were significantly affected by the size of both predators and prey, with most consumption on smaller prey and by larger predators (Fig. 4; Table 4).

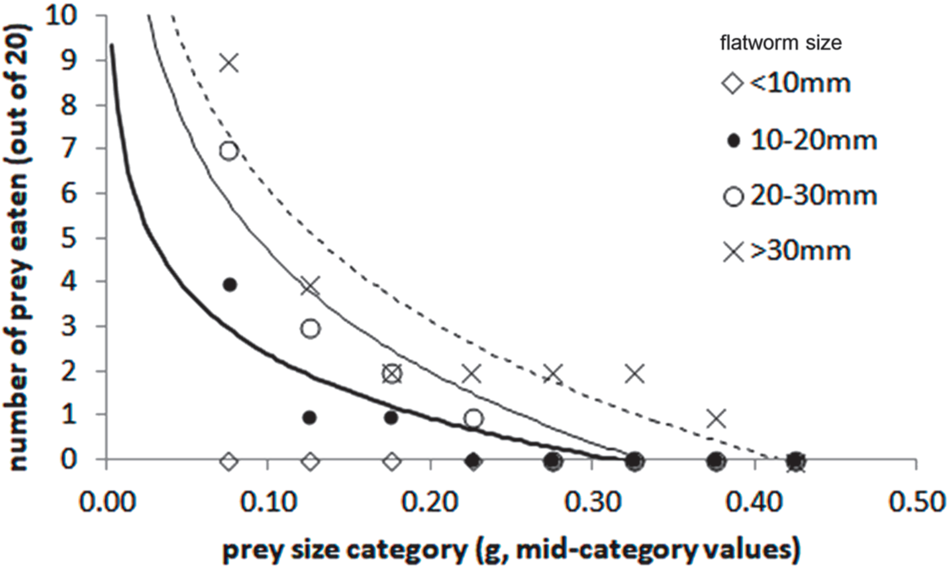

Fig. 4. Proportions of different-sized *Cornu aspersum* consumed by different-sized predators (*N* = 20 for each combination); lines show the response of each predator size category as log-linear regressions for visual purposes only

Table 4a. ANOVA of prey killed in each size category by different-sized *Platydemus manokwari*

ANOVA	SS	df	MS	*F*	*p*
Prey size	74.219	7	10.603	6.425	0.0004
Predator size	33.594	3	11.198	6.785	0.0022
Error	34.656	21	1.650		
Total	142.469	31	4.596		

Table 4b. Regression statistics of prey killed in each size category by different-sized *Platydemus manokwari*

Predator	R^2	*F*	***p***	Equation	***p***	
					intercept	slope
> 30 mm	0.795	19.396	0.007	y=-1.539–2.485ln(x)	0.114	0.007
21–30 mm	0.902	45.763	0.001	y=-2.759-2.647ln(x)	0.004	0.001
11–20 mm	0.723	13.437	0.015	y=-1.020-0.956ln(x)	0.040	0.015
≤ 10 mm	-	-	-	-	-	-

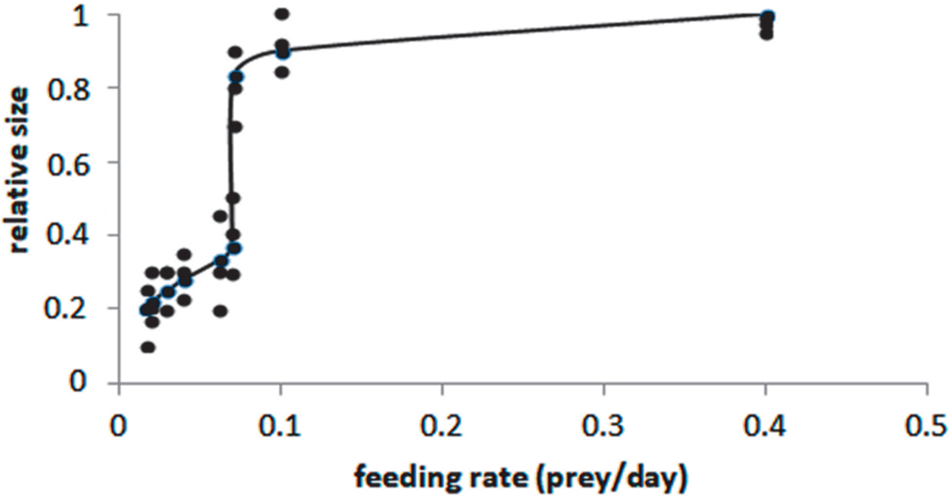

Fig. 5. Relative size change in flatworms affected by feeding rates; rates differ between experimental data (0.05-0.12 prey/day) and rearing data (high consumption rates of 0.40 prey/day). The curve shows moving average of the data, highlighting the rapid size change below 0.1 prey/day

Table 5. Trails ($N = 10$ for each combination) followed by *Platydemus manokwari* in wet and dry conditions, depending on trail age

Trail age (h)	Dry	Wet
0	10	10
1	0	10
2	0	9
6	0	9
15	0	7
19	0	0
21	0	0
24	0	0

Without feeding for 9 days, the flatworms shrank (Fig. 5) but regained their original size 3 days after feeding.

Trail following

Experimental trails were detected by flatworms only if fresh or in a moisture-saturated environment for up to 15 h (Table 5). Wet trail following was significantly correlated with trail age [full data ($N = 30$): Pearson's $t = -5.924$, $p = 0.002$; 0–15 h only ($N = 20$): $t = -4.577$, $p = 0.045$].

Movement rate

Mean movement rate was 0.33±0.003 mm s^{-1} (N = 30) for adults measuring 25–30 mm. Their speed of movement when foraging without prey present and when following trails (0.34±0.003 mm s^{-1}, N = 30) were not significantly different (t = 0.531, p = 0.597).

Salinity

When 10 flatworms were placed in an arena surrounded by paper rings soaked in different concentrations of salt water, they avoided salinity equivalent to sea water, whereas a salinity of 0.164‰ reduced activity to half, and no significant activity was observed at 0.08‰ (Fig. 6).

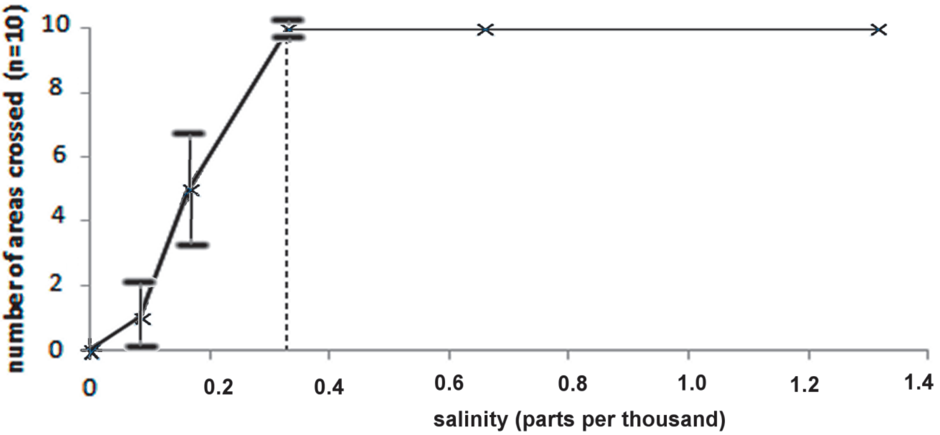

Fig. 6. The effect of salinity on movement of 10 different flatworms (salinity of sea-water marked with a dotted line), standard errors shown

Table 6. Temperature effects on survival of *Platydemus manokwari*

Day	Night	N	14-day survival	Notes
14	12	10	4	
18	12	10	7	
22	22	10	10	
24	22	10	10	
30	22	10	10	
34	34	2	0	both inactive after 30 min, but when transferred to 22ºC after 30 min one resumed activity

Temperature

Temperatures in the range of 18–30ºC showed no mortality effects, but 34ºC seemed to be a lethal temperature, and increased mortality occurred below 18ºC (Table 6).

Humidity

Little activity was recorded when relative humidity was above 96% (Fig. 7). Predation did not occur outside the humidity range of 84–96%, and maximum predation rates were only recorded at 90–94% humidity. In the humidity range of 74–84%, all worms were active, but no feeding occurred, and mortality was very high within 24 h of exposure to lower humidity.

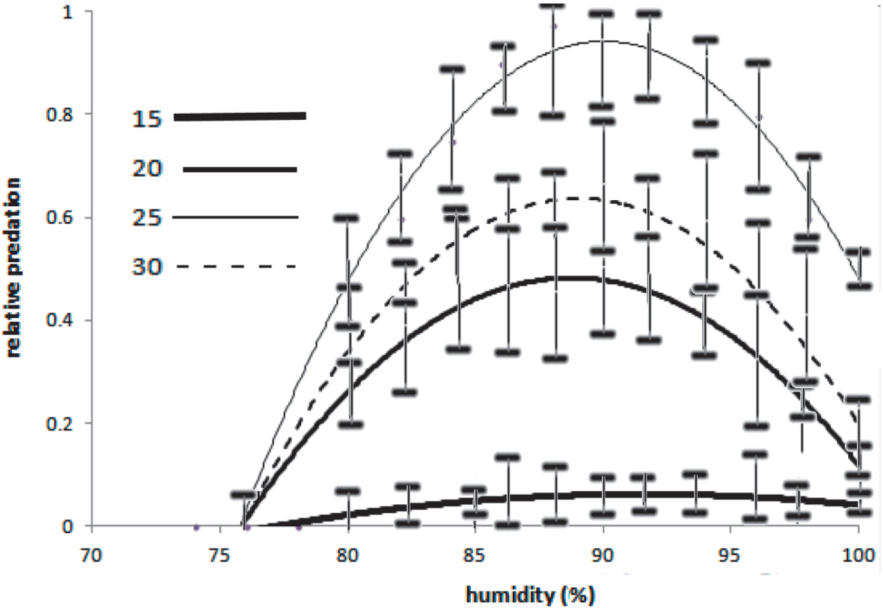

Fig. 7. Combined effects of temperature and humidity on relative predation rates (predation rate relative to the maximum value recorded). Polynomial regressions shown for temperatures between 15–30ºC. No predation was recorded at 10ºC and 35ºC. Standard errors are shown

DISCUSSION

Platydemus manokwari activity is limited by temperature and humidity. This species is able to survive at 12–30ºC according to the present study (which did not test temperatures < 12ºC), and its reproduction is restricted to above 15ºC (SUGIURA 2009). According to the cited study, adult survival is reduced at 14ºC (3% mortality in 14 days) and is further compromised at 10ºC (23% mortality). Predatory activity is also affected by these temperatures, with no feeding at 10ºC, 48% of adults feeding at 14ºC, 97% at 18ºC, and all feeding at 22–26ºC (Sugiura 2009). These calculations are also supported by field data, although weather station data may not reflect the microclimate precisely (Sugiura 2009).

The aversion of *P. manokwari* to saline conditions, observed in this study, may restrict its colonisation of coastal habitats. These data suggest that *P. manokwari* is able to invade all tropical lowland forest habitats, although there may be some locally unsuitable areas (due to altitude or habitat type).

The present study confirms previous reports that *P. manokwari* is a generalist predator of snails and slugs. The only gastropod prey that are not consumed are too large, too thick-skinned (Veronicellidae, although relatively small veronicellids can be killed, see Tan (2017); or groups of flatworms may kill adults – T. Coote pers. comm.), or produce defensive mucus (e.g. *Leptinaria unilamellata* and *Paropeas achatinaceum*) or chemicals (Philomycidae). *Platydemus* attacks by wrapping its body around the prey, which prevents escape. This is not normally possible with slugs, which explains the lower predation rate. Next, the flatworms release enzymes onto their prey before ingesting. These enzymes also digest part of the shell, leaving a distinctively thinned shell. This is not apparent in thicker-shelled snails but makes other shells very fragile (e.g. *Ovachlamys fulgens* and juvenile *Cornu aspersum*).

As with *Euglandina, P. manokwari* locates its prey by following mucus trials. It apparently lacks the capability to determine the direction of travel of its prey (Iwai et al. 2010). Although this suggests that trail following would only result in a 50% attack frequency, flatworms that failed to find a snail at the end of the trail then changed direction (Iwai et al. 2010), which could result in an attack frequency close to 100%. The success rate of these attacks, however, is not known.

The observations that feeding by one flatworm increases the activity of others may result from the flatworms being stimulated by chemicals released during predation: either the predator's enzymes or the prey's defensive mucus. If only large prey are present in the vicinity and flatworm densities are high, this may result in several flatworms attacking the same prey item in the 'gang attacks' reported by Mead (1963) and observed experimentally by Ohbayashi et al. (2005) and Sugiura (2010).

Predation by individuals is most frequent on snails weighing less than 0.18 g (Sugiura 2009) although prey up to 47 g can be killed (Kaneda et al. 1990). This size range covers most of the species living on the islands colonized by *Platydemus* (e.g. *Partula tohiveana* total weight 1.4 g, body weight 0.96 g – S. Aberdeen pers. comm.), although predation would probably be limited on most species. A newly established *P. manokwari* population can be expected to prey on the relatively small, easily killed species first, and consuming larger species (such as *Partula*) when other species had been over-exploited. Experimental demonstration of *Platydemus* feeding on relatively large *Lissachatina fulica* (Kaneda et al. 1990) involved flatworms up to 100 mm (exceptionally 120 mm) long. No flatworms of that size were available in the present study. The largest specimen located in the Society Islands was 40 mm long (relaxed length, reaching 60 mm when fully extended; pers. obs.) and none of the captive stock increased in length beyond this size. Specimens of *P. manokwari* from other localities have been in a similar size range (e.g. 50–80 mm in the Philippines according to Kawakatsu et al. 1992, and typically 40–50 mm in Australia, with the longest measured being 75 mm when fully extended – L. Winsor pers. comm.). The exceptional sizes cited by Kaneda et al. (1990) may be a result of captive rearing allowing maximal longevity and growth. In field conditions such sizes seem to be rare, although hypothetically they could be achieved in newly established populations where prey are highly abundant. This would be likely to be followed by high levels of predation on small and then large prey, with subsequent collapse of prey populations, which would be expected to be associated with reduction in flatworm size. Thus, although experimental data show high predation rates on small prey only, it is possible that *Platydemus* could cause collapse of populations of relatively large snails.

Predation by *P. manokwari* can occur at least 2 m above ground, but is reduced by 58% at 0.5 m and at least 63% at 1 m (Sugiura & Yamaura 2009). Extrapolating these limited data suggests that arboreal predation will be insignificant over 2.5 m above ground. This arboreal behaviour is limited by the presence of prey trails, temperature, and humidity. As trails are only followed if wet and less than 15 h old, the rate of drying is crucial for their prey finding ability. Accordingly, *Platydemus* may be relatively ineffective predators of arboreal snails in dry conditions (due to low rainfall, seasonal drying or local effects, such as strong, drying winds). Even in areas with such conditions, the flatworms are likely to persist at very low densities, as they can survive for extended periods without feeding (85 days for hatchlings and at least a year for adults, according to Kaneda et al. 1990). In permanently damp areas (humidity frequently over 85%), *Platydemus* predation levels would be expected to be high, as appears to have been the case in the Bonin islands (Chiba 2003; Ohabayashi et al. 2005; Sugiura et al. 2006).

Published data and the present study demonstrate that *P. manokwari* is an effective predator of snails, especially of small individuals. In the early stages of invasion, when flatworm numbers are very high, there could be substantial impacts on larger prey. These impacts will be most pronounced on terrestrial snails, with arboreal species suffering lower predation levels. In comparison to *Euglandina rosea*, invasion by *Platydemus* may result in declines of small ground-living species but lower predation on high canopy species. This significantly alters the dynamics of predator-snail interactions in the islands concerned.

Further spread of these inconspicuous, fast-breeding flatworms seems inevitable. It will be limited by climatic factors, restricting them to areas of high humidity within a temperature range of 15–30ºC. This makes most tropical islands vulnerable as well as parts of the continental tropics and subtropics. The appearance of this species in Florida (Justine et al. 2015) is therefore a major concern.

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