Captive rearing and biology of the endangered giant land snails *Placostylus ambagiosus* and *P. hongii* (Pulmonata: Bulimulidae)

I.A.N. Stringer and E.A. Grant

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ABSTRACT

Rearing of the land snails *Placostylus ambagiosus paraspiritus*, *P. a. michiei* and *P. hongii* in captivity was investigated as a conservation management option for establishing new populations of these threatened animals. Snails were kept in the laboratory with mostly karaka, *Corynocarpus laevigatus*, leaves as food. Snails were exposed to differing frequencies of handling, crowding conditions and given different substrates in which to lay eggs. Less frequent disturbance resulted in better survival in *P. ambagiosus*. Both *P. ambagiosus* and *P. hongii* laid clutches of 1–84 similarly sized eggs buried up to 2 cm deep, but the species appeared to have different substrate size preferences. *Placostylus ambagiosus* kept singly or in pairs grew larger than those in the wild. Crowding reduced growth rate, increased mortality and resulted in smaller adults. Captive-bred adult *P. ambagiosus* lived for 3.3–11.4 y: one adult *P. hongii* lived for 2.6 y and another lived for 4.6 y before being translocated onto an island. Both *Placostylus ambagiosus* and *P. hongii* can be successfully reared in captivity, in the laboratory, and large numbers of snails can potentially be produced, albeit with substantial costs. Although potentially risky for augmenting existing populations, these protocols may enable the establishment of new populations of these snails.

Keywords: growth rate, lifespan, egg, incubation, oviposition preference, *Placostylus*, land snail

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1. Introduction

Two of the three species of *Placostylus* land snails (Pulmonata: Bulimulidae) found in New Zealand, *P. ambagiosus* and *P. hongii*, survive tenuously on the mainland because of habitat loss, habitat modification by introduced mammals and predation by mammals. They now occur mostly in small scattered remnant populations which are vulnerable to extirpation from accidental fire or predation (Powell 1979; Parrish et al. 1995; Brook 2002). The risk of such accidental extinction can be reduced by increasing the number of populations through translocation, but removing sufficient individuals to ensure that translocations succeed may be detrimental to small source populations. One solution is to remove some snails and rear them in captivity in sufficient numbers to establish new colonies (e.g. Coote et al. 2004). We do not advocate using captive-bred snails to supplement an existing population unless there is no other option because of the possibility that a novel pathogen could be contracted in captivity and introduced to the wild population (Cunningham & Daszak 1998).

No method for rearing these species of *Placostylus* has been published despite four previous attempts, and few details of the methods used previously survive. We therefore investigated captive rearing these snails a fifth time. We used *P. hongii* from a large population on Aorangi Island, Poor Knights Islands, *P. a. paraspiritus* from near Cape Maria van Diemen, and *P. a. michiei* from Surville Cliffs near North Cape. Both populations of *P. ambagiosus* numbered several thousand individuals when snails were removed for captive breeding (Parrish et al. 1995).

1.1 THE STUDY ANIMALS

Both species of *Placostylus* have large (maximum length 60–95 mm) heavily calcified shells with a brown periostracum. Growth is determinate and the shell stops elongating when the aperture edge splays outward and thickens to form a distinctive lip or varix. The main predators are rats (*Rattus norvegicus, R. rattus*), mice (*Mus musculus*), birds (probably *Turdus philomelos*) and pigs (*Sus scrofa*). Rodents and birds prey on juvenile snails but the varix or the weight of the adult snail confers some protection to adults against them. Pigs prey on large juvenile and adult snails (Parrish et al. 1995). *Placostylus hongii* is now classified as 'range restricted' by Hitchmough et al. (2007) because many thousands occur on the Poor Knights Islands whereas elsewhere, only remnant populations survive—along the east coast of the mainland from Whangaroa to Whangarei and on some nearby islands. *Placostylus ambagiosus* occurs in small scattered populations at the end of the Aupouri Peninsula and on Motuopao Island off Cape Maria van Diemen. Six of the eight described subspecies of *P. ambagiosus* and a further eight populations that have not been described as subspecies are classified as 'nationally critical', the highest level of threat, by Hitchmough et al. (2007). Three subspecies, including *P. a. paraspiritus* and *P. a. michiei,* are classified as 'nationally endangered', the

second highest level of threat, by Hitchmough et al. (2007). There are now perhaps 2000 *P. a. michiei* whereas the other populations range from < 50 to probably < 500 individuals (Brook 2002). In addition, a few *P. a. pandora* survive on Motutakupu Island, in the Cavalli Island group, after they were translocated there by the now defunct New Zealand Wildlife Service in 1984 (Parrish 1989).

1.2 CONSERVATION AND PREVIOUS ATTEMPTS AT CAPTIVE BREEDING

Attempts to protect some of the populations of both *Placostylus ambagiosus* and *P. hongii* included intermittent rodent poisoning of the sites where they occurred since September 1982 (New Zealand Wildlife Service file WIL 33/2/6) and September 1985 (Wildlife Service file WIL 33/5/35), respectively, and by fencing off nine areas where snails were present (each < 1 ha) at the end of the Aupouri Peninsula between 1990 and 2000. These exclosures were designed to exclude pigs and other livestock to protect a nucleus of snails that could re-colonise the surrounding areas should snails in them be killed.

Both *P. ambagiosus* and *P. hongii* have previously been kept in captivity on four different occasions. The first was by N. Douglas who kept at least three *P. a. keenorum* in captivity at his home in Waiuku. This was before *Placostylus* species were protected by the Wildlife Act 1953 so no permit or documentation was required. However, Penniket (1981) reported that one adult kept by N. Douglas survived for 3.5 y, and there are two references in a file of the New Zealand Wildlife Service (file 33/5/37) that two juveniles kept by N. Douglas had almost become adult after 3 y in captivity in January 1982, and that two snails and some eggs were still alive in January 1985. N. Douglas was interviewed by G.H. Sherley (Department of Conservation, DOC) in 1988, who recorded that the snails were kept in a cage 230 mm wide × 840 mm long × 280 mm high. It had a glass front and was ventilated by an area of fine gauze in one of the walls. The snails were fed washed green and yellow karaka (*Corynocarpus laevigatus*) leaves, and the soil was kept moist with water. Snails that hatched in December 1978 took 2.2 y to reach a shell length of c. 53 mm and 4 y to become adult (G.H. Sherley, DOC, pers. comm. 2006).

Penniket (1981) kept at least 16 *P. hongii* in captivity and provided some information on their movements, choice of food plant leaves and the growth rates of seven juveniles over c. 0.5 y. These snails were collected from the Poor Knights Islands in April 1979 and kept in 'terraria' at Auckland University. There are no details on the rearing method or how long the snails survived.

The New Zealand Wildlife Service collected specimens of four subspecies of *P. ambagiosus* in March and May 1982 and kept them segregated according to subspecies in outdoor cages (c. 1 m × 1 m × 1 m) at the Fish & Wildlife Station, Kerikeri, Bay of Islands. The notes relating to how many snails were taken are confusing and contradictory, and there is uncertainty about the identity of one subspecies collected—recorded as '*P. a. watti*' but the location given was Surville Cliffs, where *P. a. michiei* occurs (Table 1). It is also possible that

snails were collected on only one occasion rather than on two because the numbers found on each occasion were similar. Once in captivity at Kerikeri, Bay of Islands, these snails were supplied with leaf litter once a month. All surviving snails and their progeny were released (each subspecies on a different island) onto three of the Cavalli Islands and one of the Simmonds Islands in 1984 (Wildlife Service files 33/2/6, 33/5/37, 33/5/70).

M. Meads (Department of Scientific and Industrial Research, pers. comm. 1990) attempted to breed from two *P. a. michiei* in captivity after collecting them on 15 February 1990 (DOC file FAU 502 02, 20/2/1990). Few details are available but the snails apparently died within 1 y. The snails were kept in a large aquarium with a glass lid. Gaps of 3–4 mm at the ends of the lid provided ventilation. The aquarium was initially filled with soil to a depth of 8 cm but this was replaced with 3 cm of sandy soil. The aquarium was originally kept outside at the Division of Scientific and Industrial Research, Taita, Hutt Valley, and then kept under a karaka tree at Meads' home at Pukerua Bay (G.H. Sherley, DOC, pers. comm. 2006).

TABLE 1. NUMBERS OF *Placostylus ambagiosus* SNAILS TAKEN INTO CAPTIVITY AT KERIKERI BY THE NOW DEFUNCT NEW ZEALAND WILDLIFE SERVICE. (24–27 MARCH COLLECTION REPORTED BY W. GLENTWORTH ON 31 MARCH 1983; 17–22 MAY COLLECTION REPORTED BY R. ANDERSON ON 23 MAY 1983.)

DATE	SUBSPECIES	NO. COLLECTED	DETAILS
24–27 March 1983	*P. a. watti / michiei*	16	Taken from Surville Cliffs
	P. a. pandora	9	Taken from Pandora
	P. a. keenorum	9	Taken from Spirits Bay
17–22 May 1983	*P. a. watti* (?)	6	No location given
	P. a. whareana	16	No location given
	P. a. pandora	16	No location given
	P. a. michiei (?)	9	No location given

2. Methods

2.1 SOURCE OF SPECIMENS

Five groups of snails were removed from the wild for rearing. The first group comprised four adult *Placostylus ambagiosus paraspiritus* and the second comprised four adult *P. a. michiei*, all collected on 1 and 2 May 1991 from Cape Maria van Diemen and from Surville Cliffs, respectively. A small juvenile *P. a. paraspiritus* (P9) was discovered 39 d after it was collected unintentionally amongst leaf litter included for transport with those adults. The third group, of nine medium-sized juvenile *P. a. paraspiritus* and two adults, was collected on 19 October 1992; the fourth group, of nine *P. hongii*, was collected from Aorangi Island, Poor Knights Islands, on 10 November 1992; and the fifth group, of three *P. hongii*, was collected from a small islet near Fanal Island, Mokohinau Islands, on 14 November 1996 by Brook & McFadden (1998).

The snails were kept segregated according to subspecies and, in the case of *P. hongii,* island of origin. All snails collected from the wild were measured and weighed at intervals. Snails that hatched were not handled until they were almost mature except for the first three *P. a. paraspiritus* to hatch and one *P. hongii* from the Poor Knights Islands. This was because our primary aim was to develop a captive-breeding method rather than to follow the snail's growth, and it was believed that repeated frequent handling could reduce the growth rate or cause increased mortality.

2.2 IDENTIFICATION OF INDIVIDUAL SNAILS

Individual identifying numbers were engraved through the periostracum of shells >20 mm long with a portable engraver ('Arlec', Dick Smith Electronics). Numbers were positioned near the aperture lip of adult shells or near the junction between whorls on juvenile shells where they could not be overgrown by later whorls. For added security, the prefixes 'P', 'M', 'H' and 'F' were used for *Placostylus ambagiosus paraspiritus*, *P. a. michiei, P. hongii* from the Poor Knights Islands, and *P. hongii* from the Mokohinau Islands, respectively.

The terms 'adult' and 'juvenile' are used herein in an operational way following Johnson & Black (1991) because some snails may become reproductively active well before they acquire a varix (e.g. Williamson 1976; Solem & Christensen 1984; Staikou & Lazaridou-Dimitriadou 1990; Lazaridou-Dimitriadou 1995).

2.3 REARING

2.3.1 Rearing conditions

Snails were kept in a temperature-controlled laboratory with a constant photoperiod of 14 h L : 10 h D except for four of the first two groups of snails collected. These were briefly kept in cages outside. The temperature in the laboratory was controlled by a domestic heat pump air-conditioning unit (Carrier 9, Carrier Corp., Farmington, USA) which produced small temperature fluctuations (< 1°C) many times per hour and slower weekly to monthly fluctuations. These resulted in the room experiencing a mean minimum temperature of 16.0 ± 0.9°C (± SD) and a mean maximum temperature of 18.5 ± 1.1°C. The electricity supply failed on eight occasions resulting in the temperature falling below 15°C on three occasions and exceeding 20°C on five occasions. Snails were exposed to these temperature extremes for less than 1 week on each occasion. No meterological readings were made while snails were in cages outside.

The insides of the aquaria were usually thoroughly wetted using a spray of fine water droplets from an atomiser each time leaves were added, on average once a week. If leaves already in the aquaria were dry, they were thoroughly moistened as well. Distilled water was used until January 1994 and tap water was used thereafter.

2.3.2 Rearing containers

One juvenile (P9) was initially kept for 113 d in a 600-ml glass jar ('Agee' preserving jar) covered with fine nylon bolting silk (mesh 0.6 mm) after it was first found. It was then kept in one of the large glass aquaria (see below). All other snails kept in the laboratory were housed in transparent plastic food containers (All-purpose box, Click Clack Ltd., Palmerston North) or in glass aquaria.

Two sizes of food container were used: 164 mm long × 102 mm wide × 64 mm high, and 209 mm long × 144 mm wide × 77 mm high. Both had close-fitting plastic lids with 12 evenly spaced holes (2.5 mm diameter) drilled in them for ventilation. The small plastic containers were used to house some newly hatched snails while some larger juvenile snails were temporarily housed in the large plastic containers. After being collected, single *Placostylus ambagiosus paraspiritus* were kept in three large plastic containers for 0.7 y and a pair were kept in another for 1.1 y before they were transferred to aquaria. Six *P. hongii* were kept in two large plastic containers (three in each) from when they were collected until they died 1.1–2.3 y later. Another large plastic container was used to keep 47 small juvenile *P. a. paraspiritus* before they were transferred to two small aquaria in groups of 22 and 27.

The two sizes of glass aquaria used were: 450 mm long × 280 mm wide × 315 mm high and 1080 mm long × 500 mm wide × 330 mm high. Rubber moulding was applied around the openings of the aquaria to provide a close fit with the lids. The lids consisted of a 4-cm-wide frame of particleboard, rebated to form a push-fit into the rubber moulding on top of the aquarium, with fine nylon bolting silk (mesh 0.6 mm) stretched across it. Four small aquaria were used to hold pairs of the first eight snails collected. Later, one aquarium

was used to hold one snail (P23) until it was 4.6 y old and the other three were used to keep pairs of large juvenile or adult *P. a. paraspiritus*. A fifth small aquarium was obtained to hold three *P. hongii* collected from Fanal Island and their progeny. Two large aquaria were used to keep eight *P. a. paraspiritus* collected from the wild and their progeny (P9, P14, P16, P18 and P11, P12, P19, P20). Initially, snail P9 was moved into a large aquarium when it was still a juvenile and snails P19 and P20 were housed in the other large aquarium after being collected. The other snails were added later (from large plastic containers) when they had developed into either large juveniles or adults. A third large aquarium was used to keep the four largest *P. hongii* collected from the Poor Knights Islands (H1–H4) and their progeny. Subsequent transfers of *P. a. paraspiritus* were made between aquaria to replace snails that had died.

Humidity within the aquaria was regulated by altering the proportion of mesh covered with plastic film. When the mesh was completely covered, condensation appeared on the inside of the aquarium walls and many newly hatched snails survived but fungi proliferated on the leaves. By decreasing the area covered by plastic film, fungal growth could be minimised but the number of small snails that survived was reduced. A layer of fine river gravel (particle diameter 2–8 mm) 20–40 mm deep lined the bottom of each container and water was added as necessary to keep the water level 10–20 mm below the surface of the gravel.

Snails kept outside were housed in two cages (1 m × 1 m × 1 m) with wooden frames and glass sides. The top was a closely-fitting lid made of wood and 70% shade cloth and there was no cage floor. The cages were located in a garden out of direct sunlight and the bottom edges were buried c. 2 cm into the ground.

2.3.3 Measurements

Laboratory balances (± 0.01 g or ± 0.001 g accuracy as appropriate) were used to weigh snails, and callipers (± 0.02 mm accuracy) were used to measure the maximum length of the shells and the thickness of the varix. The varix was measured at its midpoint and parallel to the shell surface at intervals > 1 y. Shells of newly hatched snails were not measured until 1 d or 2 d after emergence, because snails became active when handled, making it difficult to measure the delicate shells without damaging them. All measurements are presented as ± 95% CI unless stated otherwise.

The mass and maximum shell length of each snail collected from the wild in May 1991 was usually measured every 2–4 d or 7 d ('frequently'; 14 and nine occasions, respectively) whereas snails collected in 1992 were usually measured at intervals of 7–8 d or 13–15 d ('less frequently'; 16 and 101 occasions, respectively). The 1992 snails were weighed on each occasion, while shell lengths were measured less frequently. Once a varix had formed, the shell almost ceased increasing in length, so snails were measured at intervals of 39–112 d (mean 69 d).

2.3.4 Food and maintenance

Freshly fallen leaves of broadleaf plants were supplied as food. Most leaves were added at 6–8 d intervals (58.5% of occasions to *Placostylus ambagiosus paraspiritus* and 68.9% of occasions to *P. hongii*). Leaves were fed to the snails at intervals greater than 14 d on only 5% of occasions (maximum interval: *P. a. paraspiritus* 25 d, *P. hongii* 22 d.). Until 1994, karaka (*Corynocarpus laevigatus*; 98% of occasions), kohekohe (*Dysoxylum spectabile*; 2.7% of occasions), kawakawa (*Macropiper excelsum*; 1.1% of occasions) and other species (mahoe, *Melicytus ramiflorus* and hangehange, *Geniostoma rupestre*; 4.9% of occasions) were provided. After 1994, karaka was provided exclusively. Leaves were washed in running tap water up to February 2001 but were not washed after that.

2.4 TESTING NUMBERS OF EGGS LAID IN SUBSTRATES OF DIFFERING PARTICLE SIZE

The preference for egg-laying substrate was examined by counting the numbers of clutches and eggs found in three substrates of different-sized particles. The substrates used were sand (particle diameter: 0.5–< 2 mm), fine gravel (2–< 4 mm) and coarse gravel (4–< 8 mm). These were prepared by sifting the raw substrate through a series of Endicott sieves. Tests were done in one large aquarium for each species, and each aquarium contained a mixture of snails of all ages. In each aquarium, each substrate was presented in three plastic ice-cream containers (170 mm × 170 mm area) cut to the depth of the gravel in the aquarium. The nine containers were then arranged in a randomised Latin square occupying one end of the aquarium. Test substrate was filled to the top of each container so as to be flush with gravel elsewhere in the aquarium. The test substrates were carefully excavated and the eggs counted on three occasions after being left undisturbed for 0.8–2.3 y (Table 2). Each substrate was washed after it was examined and then presented once more in a new randomised Latin square. Considerable cross-contamination occurred between substrates during the experiments (Table 3).

TABLE 2. DATES FOR EGG-LAYING SUBSTRATE PREFERENCE EXPERIMENT. ALL REMAINING *Placostylus hongii* WERE TRANSLOCATED TO MATAKOHE/LIMESTONE ISLAND, WHANGAREI, ON 5 AUGUST 2002.

	Placostylus ambagiosus paraspiritus	*Placostylus hongii*
Start date	14 Mar 1998	18 Mar 1998
Dates when eggs were counted	20 Jul 2000	20 Jul 2000
	8 Oct 2002	12 Dec 2002
	7 May 2004	
Total period (y)	6.15	4.56

TABLE 3. PERCENTAGE COMPOSITION BY MASS OF THREE SUBSTRATES WITH DIFFERENT-SIZED PARTICLES AT THE END OF THE OVIPOSITION EXPERIMENT, TOGETHER WITH THE TOTAL MASS OF EACH SUBSTRATE. INITIALLY SUBSTRATES WERE 100% OF THEIR RESPECTIVE PARTICLE TYPE.

		MESH SIZE (mm)					TOTAL MASS
		<2	2–4	4–8	8–16	>16	(g)
Placostylus ambagiosus paraspiritus	Sand	30.1%	57.1%	4.3%	4.6%	1.8%	3901.6
	Fine gravel	5.2%	67.2%	24.8%	2.5%	0.1%	4059.9
	Coarse gravel	7.8%	23.5%	40.2%	19.4%	8.8%	3573.3
Placostylus hongii	Sand	32.2%	57.1%	4.3%	4.6%	1.8%	3901.6
	Fine gravel	5.4%	67.2%	24.8%	2.5%	3.8%	4059.9
	Coarse gravel	1.6%	16.9%	45.1%	26.4%	1.7%	3573.3

2.5 ANALYSIS

The growth rate of *Placostylus ambagiosus paraspiritus* was determined with a mixed effects model in S Plus (v5.1, Insightful Corp., Seattle). A minimum adequate model was obtained from measurements of maximum shell length up to 90% of adult shell length. The remaining 10% of final shell growth was not included because this varied too much between snails.

Egg laying preference was analysed using Chi-squared tests on the total numbers of clutches or eggs summed over the entire experimental period.

3. Results

3.1 REARING *Placostylus ambagiosus*

3.1.1 First attempt at maintaining snails in captivity

The first four adult *Placostylus ambagiosus paraspiritus* (P1–P4) and four adult *P. a. michiei* (M1–M4) collected from near Cape Maria van Diemen and Surville Cliffs, respectively, were measured two or three times a week. Their masses initially increased to a maximum of 9–27% greater than the initial mass after 40–61 d in captivity, then declined, until the snails died after 82–166 d in captivity (Fig. 1, Table 4). These snails were initially kept together in pairs in small aquaria until they started losing weight. When this occurred, the aquaria were cleaned and new gravel was provided. Two snails of each subspecies were transferred to cages outside once the others had died. These changes had no apparent beneficial effects except that two snails (P2, M1) showed slight transitory increases in mass after one of their transfers. All snails eventually died (Fig. 1).

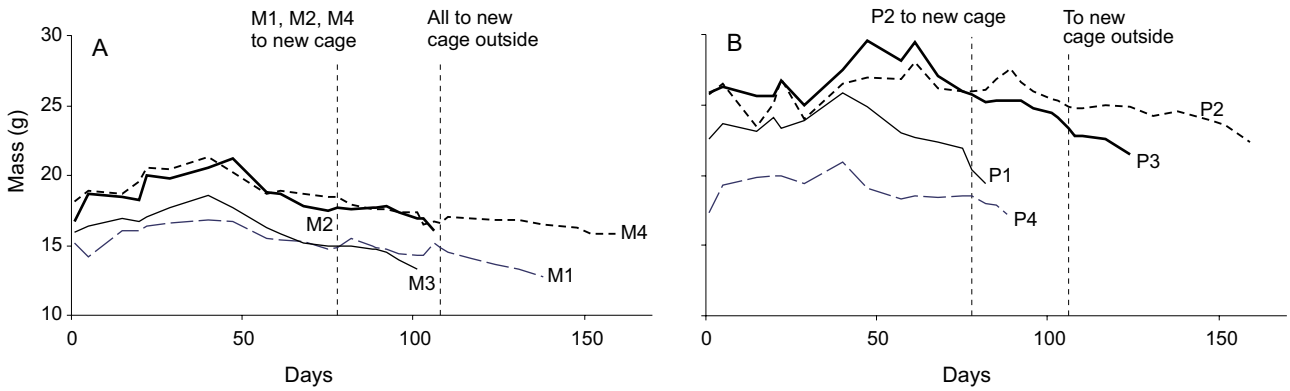

Figure 1. Change in body mass of adult snails in captivity. A. Four *Placostylus ambagiosus michiei*. B. Four *P. a. paraspiritus*. All snails were collected from the wild on 1 May 1991.

TABLE 4. CHANGES UNDERGONE BY FOUR ADULT *Placostylus ambagiosus paraspiritus* AND FOUR ADULT *P. a. michiei* SNAILS IN CAPTIVITY. VALUES ARE MEANS WITH RANGES IN BRACKETS.

	P. a. paraspiritus	*P. a. michiei*
Maximum shell length (mm)	68.8 (64.8–72.4)	63.7 (59.7–67.2)
Initial mass (g)	22.9 (17.3–25.9)	16.4 (15.1–18.1)
Maximum percentage increase in mass	114% (109%–120%)	118 (111–127)
Time to maximum mass (days captive)	47 (40–61)	42 (40–47)
Mass at death: percentage initial mass	89% (83%–99%)	88% (84%–96%)
Mass at death: percentage max. mass	76% (73%–82%)	74% (72%–76%)
Time of death (d in captivity)	113 (82–159)	127 (101–166)

When found, snail P9 had a maximum shell length of 11.4 mm and most of its subsequent increase in shell length was almost linear except when the snail was small and when it was approaching adult size. These changes gave the growth curve of shell length a slightly sigmoidal shape, whereas the increase in mass was strongly sigmoidal (Fig. 2A & B). However, the relationship between log-mass and log-shell length was approximately linear until shell growth ceased and then mass continued to increase (Fig. 2C). During growth, the mass usually underwent small (1.9–4.6%/d) daily fluctuations except when the snail was transferred from a small aquarium to a large one. At that point (123 d after collection), its mass first diminished at a rate of 29.7%/d, then increased again by 8.4%/d (130 d after collection) before stabilising again at a mean daily increase of 1.6%/d. No reduction in mass occurred before the lip of the shell aperture started to splay outward. This snail reached a mean mass of 50.8 ± 0.7 g during the the last year of its life.

The area around P9's genital aperture became slightly prominent and lighter in colour after 1.18 y in captivity, and after 1.43 y in captivity the lip of the shell aperture started splaying outwards, the first indication that the varix was starting to form. The varix became fully developed within c. 30 d of that time. Three other snails (from the third group collected) were introduced into the aquarium with snail P9—snail P16 when P9 had been in captivity for 1.91 y, and snails P14 and P18 when P9 had been captive for 3.20 y.

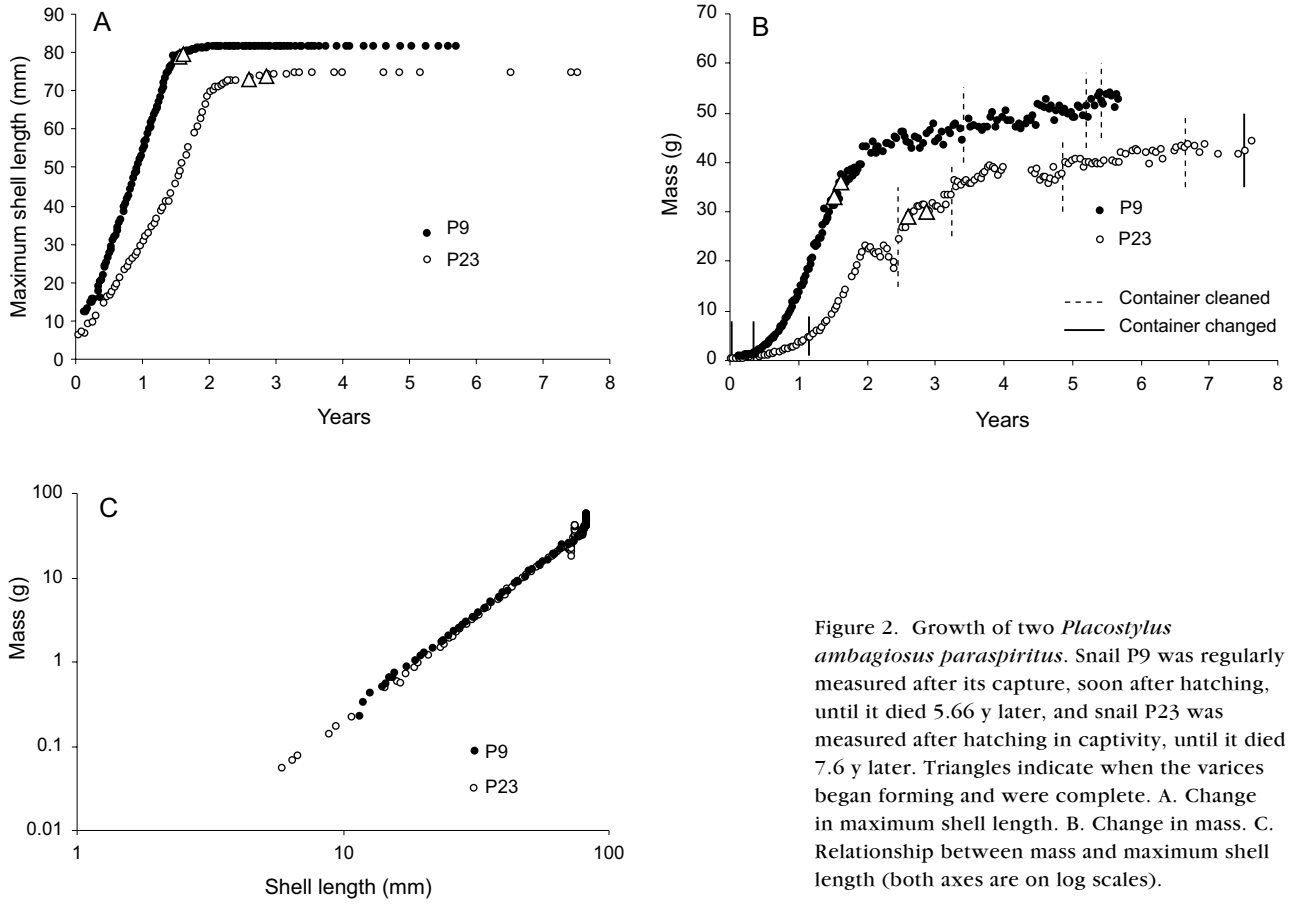

Figure 2. Growth of two *Placostylus ambagiosus paraspiritus*. Snail P9 was regularly measured after its capture, soon after hatching, until it died 5.66 y later, and snail P23 was measured after hatching in captivity, until it died 7.6 y later. Triangles indicate when the varices began forming and were complete. A. Change in maximum shell length. B. Change in mass. C. Relationship between mass and maximum shell length (both axes are on log scales).

Snail P9 dug holes and trenches intermittently for up to 119 d after snail P16 was introduced and eggs were observed under snail P9 when it had been captive for 2.45, 2.60 and 3.20 y.

Snail P9 grew to a shell length of 81 mm and became the largest of all snails that were reared. It died 4.1 y after becoming adult, after living for a total of 5.7 y in captivity.

3.1.2 The second attempt at rearing snails in captivity

The snails of the third group of *Placostylus ambagiosus paraspiritus* collected from near Cape Maria van Diemen (11 individuals) were usually measured at intervals of a week or more. The two adults P19 and P20 lived for 3.4 y and 4.2 y, respectively, and the nine juveniles (P10–P18) all matured into adults and lived for 4.2–8.5 y (mean 7.0 ± 1.2 y) (Table 5).

Both adults initially gained weight (maximum percentage of initial mass: P19, 36.3% after 30 d; P20, 14.5% after 23 d) then lost it, reaching minima 51–58 d after capture. Mass then increased a second time until, by c. 70 d after capture, the snails' masses were fluctuating about their long-term averages (P19, mean 21 g, range 18–23 g; P20, mean 25 g, range 23–27 g) (Fig. 3). The masses of both snails diminished slowly over a period of more than a year before they died. When last weighed, snail P19 was 6% lighter than when it was collected, and snail P20 was 4% heavier.

TABLE 5. LIFE HISTORY DATA FOR *Placostylus ambagiosus paraspiritus* (n = 9) COLLECTED AS JUVENILES FROM NEAR CAPE MARIA VAN DIEMEN ON 19 OCTOBER 1992. DURATION OF THE JUVENILE PERIOD IS FROM THE DATE OF CAPTURE. SNAILS WERE CONSIDERED ADULT WHEN A COMPLETE VARIX WAS FIRST OBSERVED. THE PRE-OVIPOSITION PERIOD IS FROM WHEN A COMPLETE VARIX WAS FIRST OBSERVED TO WHEN A SNAIL WAS FIRST FOUND ON EGGS.

SNAIL	TOTAL TIME IN CAPTIVITY (y)	JUVENILE (y)	AGE AT START OF VARIX (y)	TIME FOR VARIX TO DEVELOP (y)	ADULT LIFESPAN (y)	PREOVI-POSITION PERIOD (y)	DATE AT DEATH	MAX SHELL LENGTH (mm)
P10	7.2	1.9	1.1	0.7	5.4	–	25 Jan 2000	73.4
P11	6.6	1.1	0.9	0.2	5.5	2.3	9 Jul 1999	77.2
P12	4.2	1.0	0.9	0.2	3.3	–	24 Jan 1997	73.3
P13	8.5	1.6	1.1	0.5	6.9+	1.7	Still alive	75.1
P14	4.6	1.1	–	–	3.5	–	20 May 1997	76.8
P15	7.5	1.6	1.1	0.5	5.9	2.6	9 Jul 2000	69.9
P16	7.8	0.8	–	–	7.0+	–	Still alive	72.9
P17	8.5	1.4	1.1	0.3	7.1+	1.6	Still alive	74.4
P18	7.7	0.9	–	–	6.8	–	Aug 2000–Dec 2001	73.5

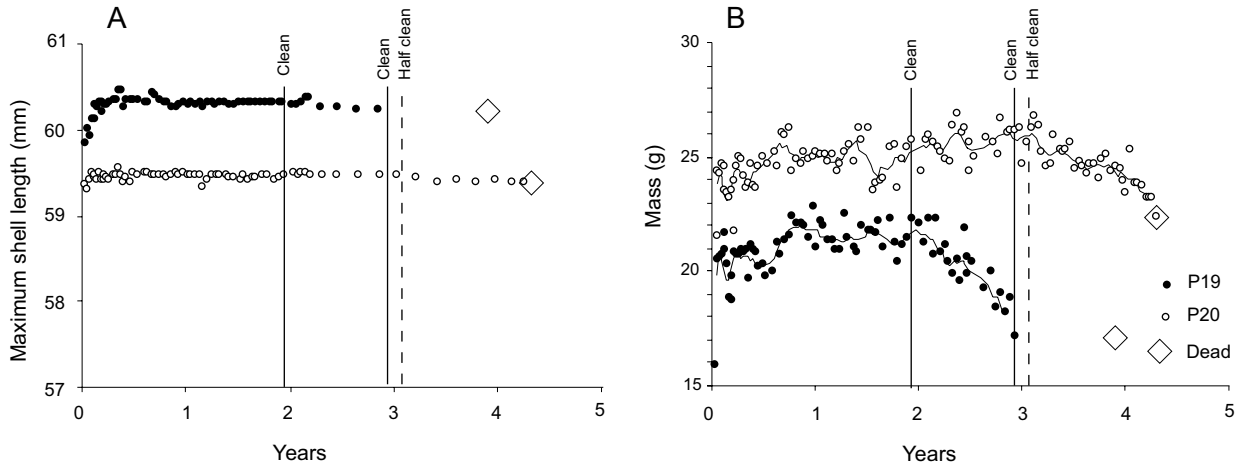

Figure 3. Change in maximum shell length (A) and mass (B) of two adult *Placostylus ambagiosus paraspiritus* (P19 and P20) in captivity, following their capture. Vertical lines indicate when all (solid line) or half (dashed line) of the gravel in their aquaria was cleaned and the lines give 5-point running averages of mass.

All nine juvenile snails showed similar growth patterns (Fig. 4), except that the masses of two of them (P10, P17) underwent temporary decreases just before the varix developed (Appendix 1). Their growth rates averaged 0.11 ± 0.01 mm/d (range 0.09–0.14 mm/d) until their shells reached 90% of adult length. Thereafter, they took a further 0.13–0.61 y to reach 99% of their final adult lengths. Their varices took 0.13–0.73 y to develop. These snails all grew into large adults (maximum shell length 74 ± 1.7 mm) (Fig. 4, Table 5).

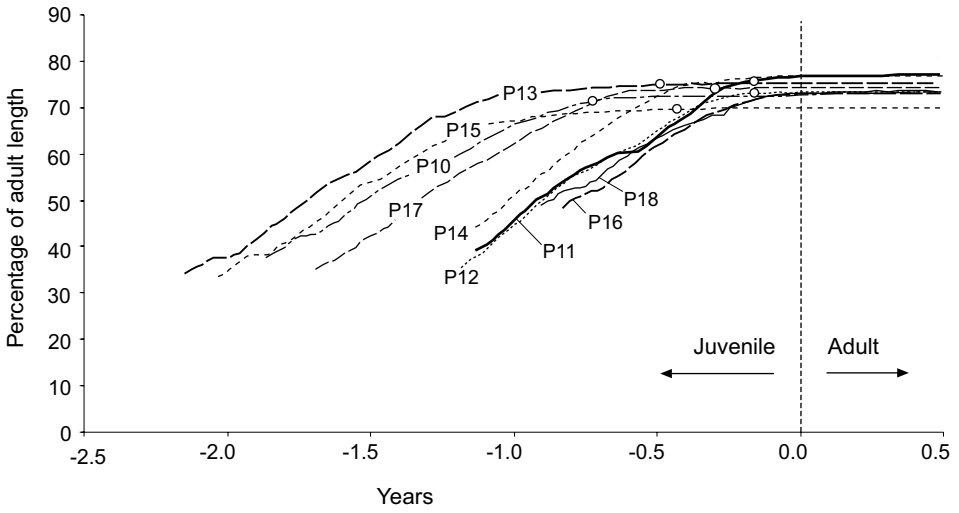

Figure 4. Growth in maximum shell length of 19 *Placostylus ambagiosus paraspiritus* in captivity after collection from Cape Maria van Diemen. Growth curves are shown in relation to when the varices became complete (vertical line at time 0). Circles indicate when the shell aperture started to splay outward at the start of varix formation.

Once snails P10–P17 became adult, their masses varied from –26% to 16% about a 7-point running average (minimum –10.3 ± 1.7%; maximum 10.0 ± 1.1%; ± SE, $n = 11$). In addition, many snails showed increases in mass after their aquaria were cleaned (Fig. 5).

3.1.3 Eggs

Eggs were laid either singly or in clutches of up to 70 (median 34.5 eggs, $n = 14$ clutches). They varied in shape from almost spherical (length:width ratio 1.05) to ovoid (length:width ratio 1.56), but averaged 5.3 mm long × 4.4 mm wide, with a mass of 0.6–0.7 g (Tables 6 and 7). The holes in which they were laid were covered over with gravel but occasionally the uppermost eggs were partly visible. Often a nest of eggs was marked by a slight depression

TABLE 6. DIMENSIONS OF 40 EGGS OF *Placostylus ambagiosus paraspiritus* RANDOMLY SELECTED FROM NUMEROUS BATCHES OF EGGS THAT HAD DIED FROM DESICCATION.

	MAX. LENGTH (mm)	MAX. WIDTH (mm)	LENGTH:WIDTH RATIO
Mean	5.32	4.40	1.21
SD	0.32	0.20	0.10
Range	4.82–6.40	3.84–4.82	1.05–1.56

TABLE 7. MASS (g) OF NEWLY LAID EGGS OF *Placostylus ambagiosus paraspiritus*.

DATE MEASURED	20/10/92	27/11/92	29/7/94	4/8/94
Mean	0.056	0.070	0.062	0.063
SD	0.009	0.011	–	–
n	5	10	66	47

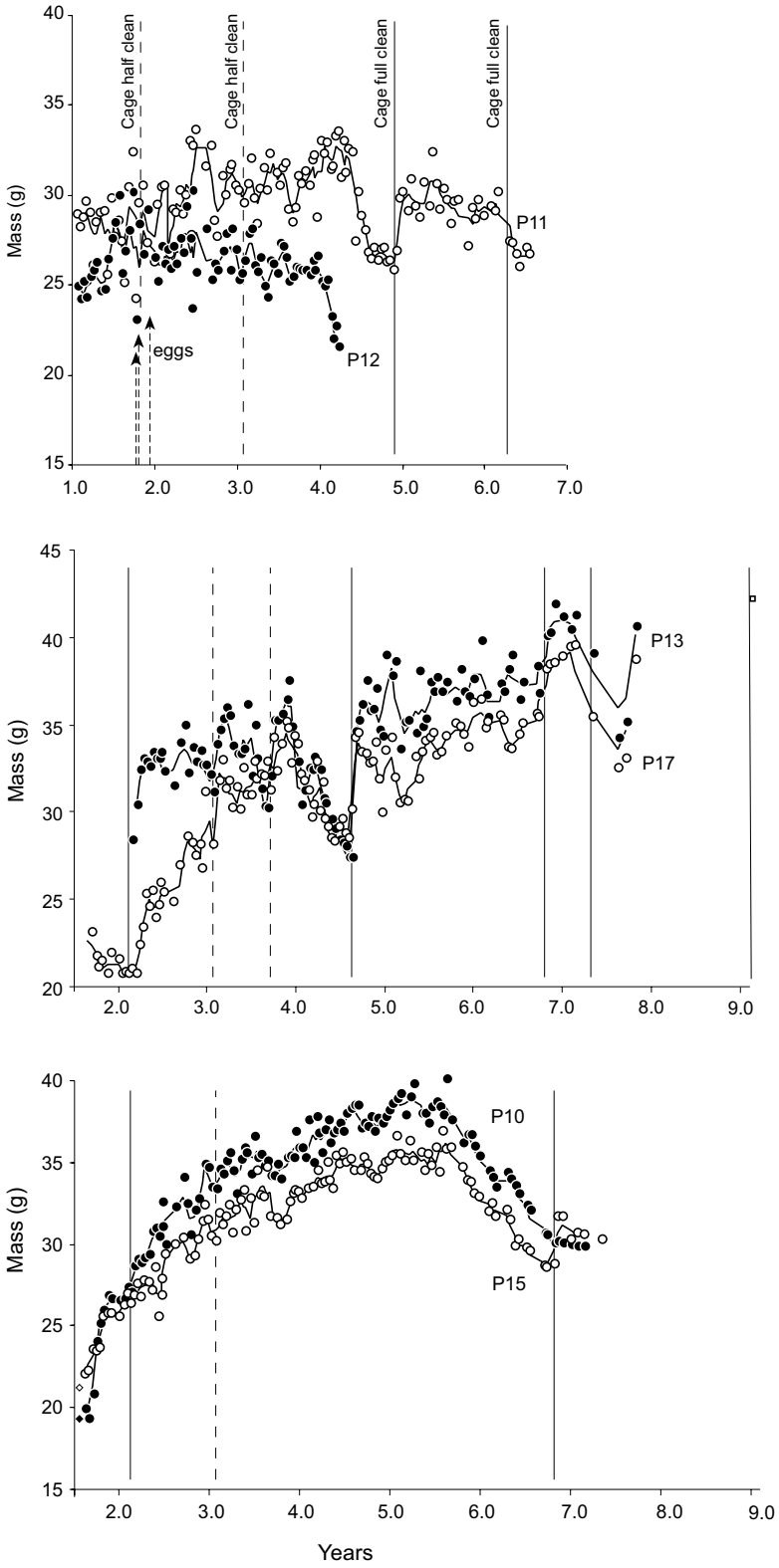

Figure 5. Changes in mass of six adult *Placostylus ambagiosus paraspiritus* in relation to when all (solid vertical lines) or half (dashed vertical lines) of the gravel in their aquaria was cleaned. The snails hatched in captivity and were kept together until they became adults, at which point they were housed as one pair per aquarium. Time (*x*-axis) is given from when the snails emerged as hatchlings; lines give 3-point running averages; arrows indicate when batches of eggs were found.

in the surface of the substrate. On two occasions, snails were found above holes containing eggs and on four occasions over holes without eggs. All holes were up to 2 cm deep and 1–1.5 cm in diameter. The diameters of the holes were narrower than the diameters of the shells so, presumably, the snails had used the foot to excavate them rather than using the shell as a plough.

3.1.4 Egg laying and incubation period

Only one estimation of the incubation period was made when, by chance, the first clutch of 38 eggs was found in a large aquarium containing only two adult snails (P19 and P20) on 20 November 1992. A slight depression in the gravel was observed and the eggs were gently excavated, counted and returned. Newly hatched snails were seen amongst the leaves and gravel 46 d later, and some appeared on the glass sides of the aquarium over the next 2 d (Fig. 6).

The substrate in this aquarium was not examined carefully for evidence of egg laying after the first clutch of eggs was found, but eggs were observed opportunistically on three later occasions during the following 3 y (Fig. 6). Hatchling snails were observed on the walls of the aquarium on 16.6% of occasions, whereas larger juveniles (> 6 mm shell length) were observed on the glass on 0.9% of occasions. Hatchling snails were also frequently observed on the leaves in the aquarium but these were recorded only when a second clutch of eggs hatched. On that occasion (5 March 1993), 15 hatchlings were on the leaves and ten were on the aquarium walls. No exact incubation period is available because the date when the eggs were laid is not known.

3.1.5 Substrate particle size preference for oviposition

A total of 142 intact eggs and 26 dead hatchling snails were found when all nine containers of test substrate were carefully excavated. These eggs and hatchlings occurred in too few clutches for any substrate preference to be demonstrated (four clutches in sand, three each in fine and coarse gravel) although, overall, significantly more eggs were laid in gravel (39.4% in fine gravel, 40.8% in coarse gravel) than in sand (19.7%) ($\chi^2 = 11.9$, $P = 0.003$). Significantly more dead hatchlings ($n = 20$) were found in coarse gravel than in either sand or fine gravel ($n = 3$) ($\chi^2 = 22.2$, $P > 0.001$) suggesting that hatchlings may have been trapped by heavier particles of gravel.

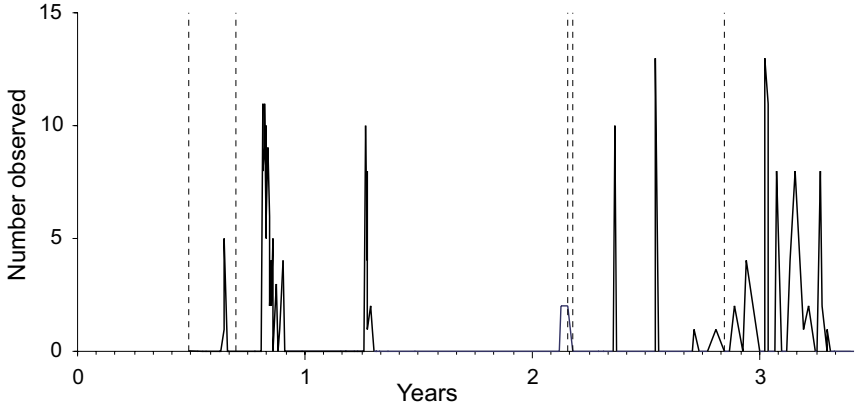

Figure 6. Numbers of hatchling snails of *Placostylus ambagiosus paraspiritus* observed on the glass of an aquarium originally containing two adult snails (P19 and P20). The dotted lines indicate when eggs were observed.

3.1.6 Snails that developed in captivity

Six hatchlings from eggs laid by P19 and P20 were weighed the day after they emerged (0.043 ± 0.008 g). These had a maximum length of 5–6 mm but the snails were still too active for their shells to be measured accurately. Five were still alive and less active 8 d after emerging, and had a mean maximum shell length of 5.9 ± 0.2 mm. Their mean mass had increased to 0.051 ± 0.007 g. Four of these snails died within 85 d and the survivor (P23) was kept isolated so that it would not be confused with other small snails while its growth was followed (Fig. 2). Its shell increased in length approximately linearly at a rate of 0.090 ± 0.007 mm/d (mean of a 5-d running average for 70–109 d) until it was 2.1 y old. Increase in shell length then diminished progressively to 0.01 mm/d until P23 reached an age of 2.6 y, when a slight outward splaying of the lip of the shell, at the anterior end of the aperture, was observed. The varix thickened to become fully developed c. 0.27 y later, and the shell subsequently increased very little in length (< 0.005 mm/d), but eventually reached a maximum length of 74.3 mm. More specifically, the varix thickened from 6.35 mm to 8.40 mm over 3.53 y, an increase of 32.3%, while the maximum shell length increased a total of 0.19% or 0.14 mm over that time. This snail steadily gained mass to reach 22.7 g by the end of its second year of life, then 0.6 y prior to the varix beginning to form, its mass began to decrease slowly, reaching a maximum of 18.0 g 0.2 y before the beginning of varix formation. This was followed by a rapid recovery first, with the snail attaining a mass of 24.1 g 28 d later and then 29.07 g when the varix began to form (Fig. 2). Its mass then continued to increase slowly while fluctuating 5.5–6% about a 7-point running average.

Snail P23 laid 15 eggs while it was kept by itself for 4.6 y as an adult, but none of these eggs hatched. The white area around its genital opening, however, became visible when it was 2.7 y old, before its varix developed. This snail lived for a further 3.9 y after other snails were introduced to its aquarium. Its total lifespan after hatching was 11.4 y (Table 8).

Two other snails (P24, P25) were followed intermittently some time after they hatched (Fig. 7). These snails originated from a community aquarium, so their dates of emergence after hatching are unknown. They were transferred together into an aquarium without other snails once measuring commenced. They grew in length at approximately uniform rates (shell length increase:

TABLE 8. LIFE HISTORY DATA FOR *Placostylus ambagiosus paraspiritus* REARED ENTIRELY IN CAPTIVITY. SNAILS WERE CONSIDERED ADULT WHEN A COMPLETE VARIX WAS FIRST OBSERVED.

SNAIL	JUVENILE (y)	AGE AT START OF VARIX (y)	TIME FOR VARIX TO DEVELOP (y)	LIFESPAN AS ADULT (y)	TOTAL LIFESPAN (y)	MAXIMUM SHELL LENGTH (mm)
P23	2.9	2.5	0.4	8.6	11.4	74.3
P24	–	–	0.6	6.6	–	74.4
P25	–	–	0.9	6.1	–	69.7

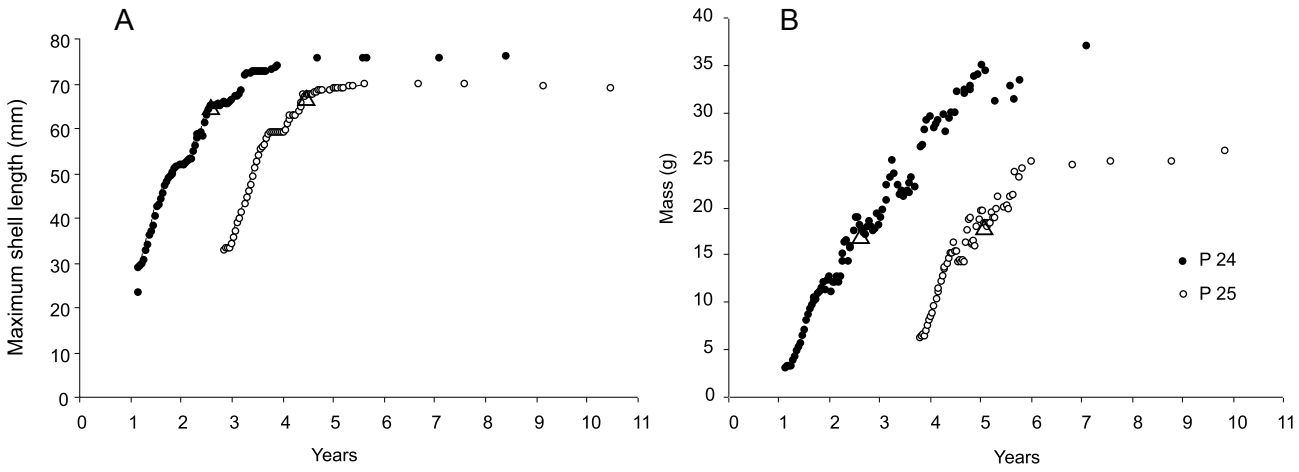

Figure 7. Changes in maximum shell length (A) and mass (B) of two *Placostylus ambagiosus paraspiritus* (P24, P25) that hatched in captivity. The hatching dates are unknown and the graphs have been separated along the *x*-axis arbitrarily. Triangles indicate when the varices started to form.

P24, 0.08–0.11 mm/d; P25, 0.05–0.13 mm/d) until the edges of their shells began to splay outward at the start of varix formation (Table 8). However, on two occasions prior to this, the growth of both snails slowed and almost ceased when the aquarium required cleaning, when the snails were 3.3–3.8 y old and again when they were 4 y old. On both occasions, normal growth resumed immediately after the aquarium had been cleaned. Once the varix began to form, further growth in shell length ceased in snail P25, but snail P24 underwent a further growth spurt when it was between 4.7 y and 4.8 y old. During this period its shell increased in length by 0.14 mm/d with the result that the final shell had a ridge (the first varix) separated by 4.5 mm from the final varix. P24 was the only snail that developed two varices. Furthermore, in both snails, on the second occasion when growth slowed, a notch formed at the edge of the shell aperture where this joins the previous whorl, and no periostracum was deposited at this point, leaving an area of white ostracum. After the gravel had been cleaned, the notch disappeared and periostracum began forming again, but periostracum was never deposited over the area of bare ostracum. Snails P24 and P25 lived for 6.6 y and 6.1 y, respectively, after the final varices developed (Table 8).

The rates of increase in mass of both P24 and P25 diminished on both occasions when their shell growth slowed down, and their masses showed only minor reductions around the times when their varices formed (Fig. 7). A substantial decrease in mass followed the growth spurt (in length) that snail P24 underwent following the formation of its first varix (Fig. 7).

Other snails that hatched were reared in community aquaria and were not followed individually as they developed. A total of 22 became adult with mean shell lengths of 60.7 ± 2.2 mm (range 54.2–74.2 mm). Nineteen of these were reared in a large aquarium with snails that were collected as juveniles from the field. Here, the density of snails with shell lengths > 30 mm varied from 216 cm^2/snail to 900 cm^2/snail. These snails were not measured during their development. However, periodic measurements were taken of shell lengths from snails in two small aquaria containing higher densities of snails

(Fig. 8). These snails, originally six newly hatched juveniles, were transferred with a clutch of 47 eggs to a new aquarium in June 1994. Forty-seven snails were still alive on 21 December 1995, at which point they were transferred into two new aquaria containing 20 and 27 snails (densities being 63 cm^2/snail and 46.7 cm^2/snail, respectively). The group of 27 snails all died within 6.5 y, before becoming adults, whereas 13 of the group of 20 snails survived and became adults by 6.5 y. Three of these were still alive 4.1 y later when this study ended.

3.2 REARING *Placostylus hongii*

3.2.1 Snails collected from the Poor Knight Islands

Two of three snails collected as adults (H1, H2) were still alive after 7.1 y in captivity but both died during the next 0.2 y. The third adult (H3) survived in captivity for 6.3 y but was then translocated onto Matakohe/Limestone Island, in Whangarei Harbour. The largest juvenile collected (H4) began developing a varix after 24 d in captivity and became adult with a fully developed varix after a further 0.2 y. This snail then lived for a further 2.6 y in captivity. All six of the remaining smaller juveniles (H5–H10) died before becoming adult, and only one (H5) grew to approximately adult size (Fig. 9, Table 9). The growth rates of the shells of these six juveniles decreased before they died, and all showed increases in shell length of less than 0.5 mm during the last 0.2–0.6 y of their lives (Fig. 9).

On only one occasion were the three adult snails weighed at intervals of about 2 weeks before and after their aquarium was cleaned. This occurred after the snails had been in captivity for 3.7 y, and the masses of all three snails subsequently increased slightly over the following 3 months (H1, 2.9%; H2, 2.5%; H3, 6.8%).

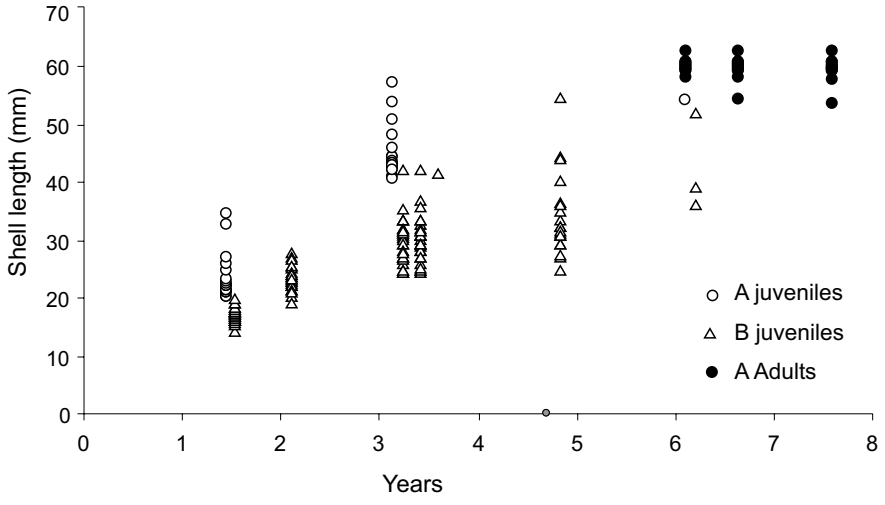

Figure 8. Growth of *Placostylus ambagiosus paraspiritus* snails kept in crowded conditions. All 47 snails were kept together until aged 4.7 years, then they were moved into separate aquaria. A = 20 snails, density of 1 snail/49.3 cm^2; B = 27 snails, density of 1/36.5 cm^2. Maximum shell lengths are shown only for live snails.

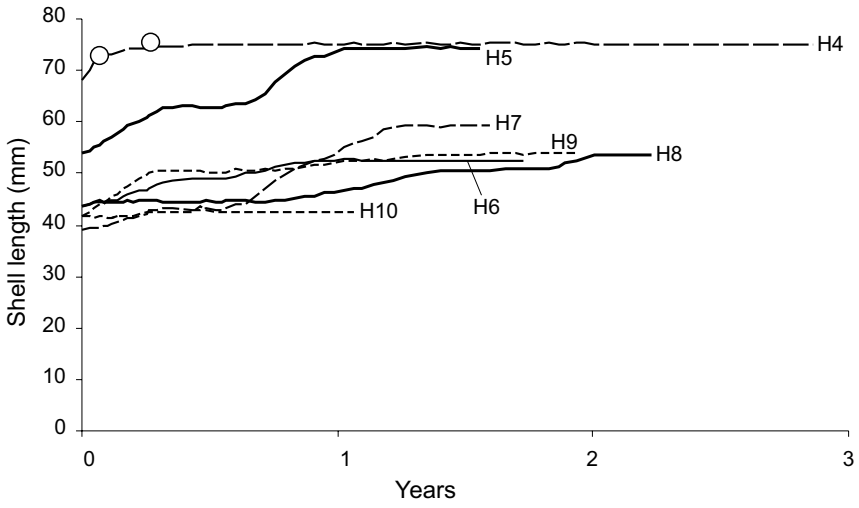

Figure 9. Changes in maximum shell length of seven *Placostylus bongii* snails after collection from the Poor Knights Islands. Circles indicate the start and completion of varix development.

TABLE 9. LIFESPANS OF *Placostylus bongii* IN CAPTIVITY COLLECTED FROM AORANGI ISLAND, POOR KNIGHT ISLANDS, IN NOVEMBER 1992.

SNAIL	SURVIVAL (y)	PERCENTAGE INCREASE IN MAX. SHELL LENGTH	STAGE AT DEATH
H1	7.22	0.1	Adult
H2	7.22	0.7	Adult
H3	9.10	1.6	Adult
H4	2.86	9.4	Juvenile/adult
H5	1.56	27.7	Juvenile
H6	1.73	17.2	Juvenile
H7	1.60	34.0	Juvenile
H8	2.23	18.1	Juvenile
H9	2.00	22.7	Juvenile
H10	1.06	2.1	Juvenile

3.2.2 Snails collected from the Mokohinau Islands

Two of three *Placostylus bongii* collected from the Mokohinau Islands were adult (F1, F2) with maximum shell lengths of 69.0 mm and 65.5 mm, respectively, and the third (F3) was a large juvenile 66.9 mm long. The latter became an adult in 0.5 y with a shell length of 68.05 mm. It died after an adult life of 4.5 y. Snails F1 and F2 died after 4.1 y and 3.4 y of captivity, respectively. The mean masses of all three snails, as adults, were similar (F1, 27.0 g, range 23.7–30.3 g; F2, 26.5 g, range 23.9–29.3 g; F3, 26.3 g, range 21.8–30.2 g) and they varied by up to 3.9 g from their mean adult masses. All three snails showed an increase of 3.8–5.3 g immediately after their aquaria were cleaned for the first time, 2.8 y after capture.

3.2.3 Eggs

All eggs were laid either singly or in groups buried up to 2 cm deep in the gravel. When the gravel in the aquarium holding snails from the Poor Knights Islands was carefully excavated on one occasion, five single eggs were found together with eight clusters containing 8–84 eggs (median 24.5 eggs). Eggs

laid by snails that originated from the Poor Knights Islands varied from almost spherical (length:width ratio 1.08) to an elongated ovoid (length:width ratio 1.24), and averaged 5.1 mm long × 4.3 mm wide (Table 10). These were not weighed, but 12 eggs laid by Mokohinau Islands' snails while in transit had a mean mass of 0.051 ± 0.007 g (range 0.033–0.075 g) (these eggs were not measured). Only numerous broken eggs were found when the gravel in the aquarium holding snails from the Mokohinau Islands was examined so no data were obtained on egg dimensions or clutch size.

3.2.4 Egg laying and incubation period

The first few eggs laid by adult *Placostylus hongii* collected from the Poor Knights Islands were found on 16 and 25 February 1993 and were detected by the presence of either visible eggs (three clutches) or a depression on the surface of the gravel (one clutch). Careful excavation of the gravel at the depression exposed the top layer of eggs. Apart from the uppermost eggs, the other eggs in all these clutches were left disturbed, so the following egg counts are not totals per clutch: 16 February, one clutch, 6 eggs observed; and 25 February three clutches, 7, 2, and ten eggs observed). Hatchlings appeared on the sides of the aquarium 45–75 d later, with the highest number ($n = 75$) being visible on the last day (Fig. 10). The first ten of these first newly hatched snails had a mean maximum shell length of 5.1 ± 0.2 mm and a mean mass of 0.042 ± 0.003 g.

TABLE 10. DIMENSIONS OF 35 EGGS OF *Placostylus hongii* RANDOMLY SELECTED FROM NUMEROUS BATCHES OF EGGS LAID BY SNAILS THAT ORIGINATED FROM THE POOR KNIGHTS ISLANDS.

	MAX. LENGTH (mm)	MAX. WIDTH (mm)	LENGTH:WIDTH RATIO
Mean	5.13	4.35	1.18
SD	0.19	0.13	0.04
Range	4.76–5.60	4.02–4.57	1.08–1.24

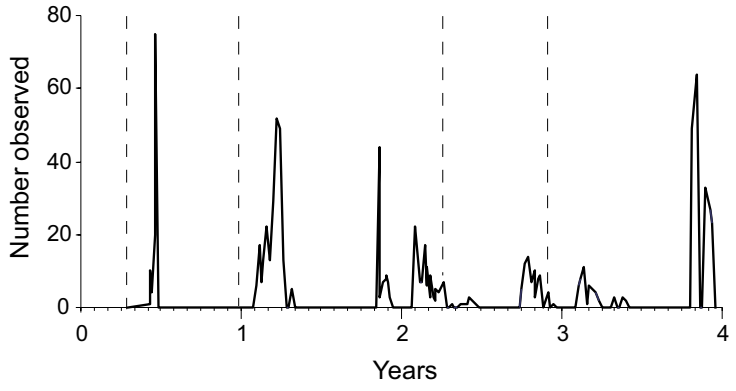

Figure 10. Numbers of hatchlings of *Placostylus hongii* observed on the glass of an aquarium containing three adult snails (H1, H2, H3). Dotted lines indicate when eggs were observed. Snails were collected from the Poor Knights Islands.

No further careful searches were done in the aquarium containing the snails from the Poor Knights Islands for indications of recent egg laying, although newly laid eggs were observed opportunistically on three later occasions (Fig. 10). Overall, hatchlings were observed on the glass of the aquarium housing the three adult snails on 27.2% of occasions when the aquarium was checked, and larger juveniles (shell length > 6 mm) were observed on the glass on 4.7% of occasions (Fig. 10).

The timing of egg laying of snails collected from the Mokohinau Islands was not recorded and no records were made of the numbers of juveniles that rested on the glass aquarium walls.

3.2.5 Substrate particle size preference for oviposition

A total of 350 intact eggs and 59 dead hatchling snails were found when testing preferred substrate particle size. Significantly more eggs were laid in sand (54.8%) than were laid in fine or coarse gravels (22.0% and 23.1%, respectively) ($\chi^2 = 73$, $P > 0.001$) but these were in too few clutches to demonstrate any preference for particle size (four clutches in both sand and fine gravel, two clutches in coarse gravel). There was no significant difference between the numbers of dead hatchlings found between the substrates (sand 16, fine gravel 22, coarse gravel 21; $\chi^2 = 1.05$, $P > 0.59$).

3.2.6 Snails that hatched in captivity (Poor Knights Island origin)

Juvenile *Placostylus hongii* found on the aquarium walls weighed 0.042 ± 0.003 g (n = 10) and had a maximum shell length of 5.1 ± 0.2 mm. Most that had hatched before September 1994 died before their shells had doubled in length. Up to this date, the glass aquarium walls had been regularly cleaned; juvenile survival increased only after green alga were allowed to grow on the glass. Clear tracks through the algae showed where juveniles had grazed.

The development of only one *P. hongii* (H11) was followed in detail although the date when it hatched in captivity was not known (Fig. 11). This snail was transferred to a new aquarium on 9 September 1994 when its shell was 14.1 mm long. It took 2.3 y from when it was first marked for its shell to reach a length of 66.6 mm, and then its growth slowed abruptly, the snail taking a further 0.4 y to reach a length of 67.3 mm. At this stage, the snail had a fully developed varix: the date when the varix first started to develop was not recorded. After the varix had formed, the shell increased in length very slowly to reach a maximum of 67.5 mm after a further 4.6 y in captivity. The mass of this snail increased, with fluctuations, to reach a maximum of 24.6 g 2.5 y after hatching, and then it declined to 21–24 g over the next 0.4–0.5 y before increasing to its final mean weight of 25.8 g. As an adult, its mass fluctuated up to 2.8 g about the mean. This snail was released onto Matakohe/Limestone Island on 5 August 2002.

All other snails that had been reared entirely in captivity were alive on 17 December 2001, at which time they were measured and weighed and had individual identification numbers engraved on their shells (H12–H24; Table 11). Ten were still alive on 5 August 2002 at the end of this study and were

translocated onto Matakohe/Limestone Island in the Whangarei Harbour. The group comprised three adults (H11, H13, H14) and seven juveniles (H16–H21, H23).

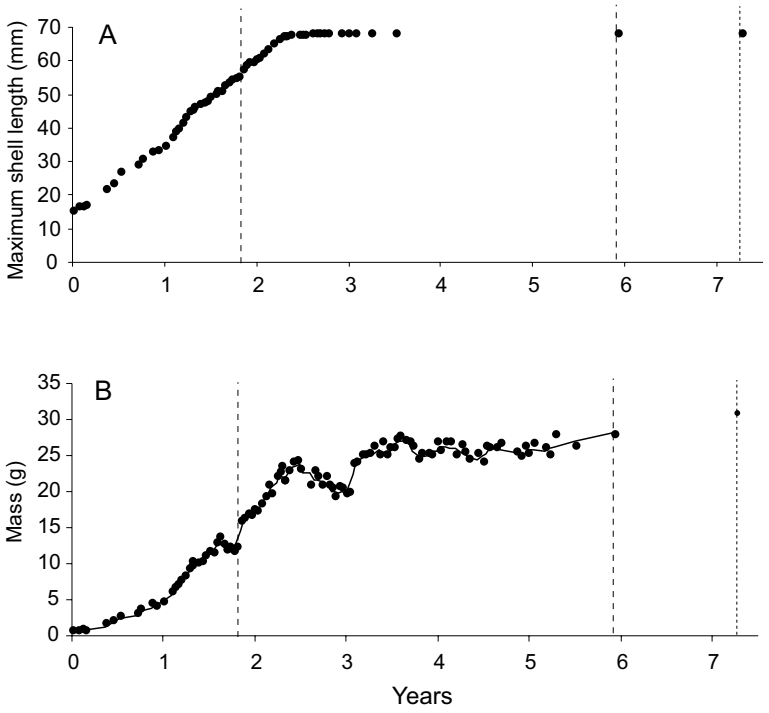

Figure 11. Change in maximum shell length (A) and mass (B) of a *Placostylus bongii* snail (H11) that hatched in captivity. The hatching date is unknown so time is given from when the snail was separated from other snails. Vertical bars indicate when the aquarium was cleaned, and a 3-point running average for mass is shown.

TABLE 11. DIMENSIONS OF CAPTIVE-BRED *Placostylus bongii* ON 17 DECEMBER 2001.

SNAIL	LENGTH (mm)	MASS (g)	VARIX THICKNESS (mm)	STAGE
H11	67.48	30.78	3.21	Adult
H12	63.32	25.31	2.23	Adult
H13	65.99	28.56	2.32	Adult
H14	67.47	30.39	3.40	Adult
H15	67.45	25.02	1.77	Adult
H16	65.25	26.56	–	Juvenile
H17	61.25	21.65	–	Juvenile
H18	54.95	15.11	–	Juvenile
H19	59.26	19.21	–	Juvenile
H20	42.40	8.71	–	Juvenile
H21	52.63	14.06	–	Juvenile
H22	48.83	12.17	–	Juvenile
H23	59.36	18.06	–	Juvenile
H24	65.13	19.39	2.51	Adult

4. Discussion

4.1 REARING CONDITIONS

4.1.1 Choice of rearing conditions

Temperature, moisture and photoperiod are the three most important environmental factors that influence growth in most terrestrial pulmonates, although a variety of other factors listed by Egonmwan (1991) and Hommay et al. (2001) may also affect the growth of some land snails. These three major factors are also reported to influence activity and food intake in *Placostylus fibrosus* in New Caledonia and thereby directly affect the growth of this species (Salas et al. 1997). In the present study of *P. ambagiosus* and *P. hongii*, temperature and photoperiod were kept as constant as practicable, at approximate mean summertime values for the northernmost part of New Zealand (New Zealand Meteorological Service 1983). The intention was to maximise growth of the snails. However, as well as directly affecting growth, temperature can have an inverse relationship with the time to maturation, lifespan and adult size in some pulmonates (Hommay et al. 2001) or it can have a positive relationship with adult size in other land snails (Wolda 1970; Oosterhoff 1977). Fluctuating temperatures may also result in faster growth compared with predictions from results of snails kept at constant temperatures (South 1982) but a variable temperature facility was not available for the present study. Photoperiod's influence on growth rate has been reported as negligible in some snails, and it has been documented as influencing reproductive maturation and the onset of dormancy in others (Cook 2001; Elmslie 2001; Gomot de Vaufleury 2001; Hommay et al. 2001). Photoperiod may also interact with temperature so that, for example, long-day photoperiods may increase growth rates already elevated by high temperatures or may compensate for the negative effects of low temperatures on reproductive output in some snail species (Gomot de Vaufleury 2001).

In general, we kept the humidity as high as practicable while minimising periods of lower humidity to reduce fungal growth on the leaves provided as food. This was done because high humidity and whether rain has fallen recently affects many aspects of land snail behaviour, including feeding, and erratic growth can result if suitable conditions occur only intermittently (Solem & Christensen 1984; Baba 1985; Goodfriend 1986).

4.1.2 Effects of rearing conditions on *Placostylus ambagiosus paraspiritus*

The conditions under which *Placostylus ambagiosus paraspiritus* was reared suited the species, as evidenced by the snails' relatively rapid growth and, when reared at low densities, by the larger size of their shells. Thus, shells of adults reared individually (maximum shell length: P9, 81.0 mm; P23–P25, 69.7–74.3 mm) (Table 8) or in groups of 2–4 snails (69.9–77.2 mm) (Table 5) were larger than those of their conspecifics in the field at Cape Maria van Diemen (63.2 ± 0.6 mm; $n = 333$). The latter occur at densities of up to

54 snails/m^2 (IANS, pers. obs.). In contrast, snails that were reared from eggs and later kept in groups of 20 and 27 (density 159 snails/m^2 and 214 snails/m^2, respectively) matured with smaller shell lengths (60.7 ± 2.2 mm) than those reared singly or in small groups of up to four, and they were even slightly smaller than those at Cape Maria van Diemen. The snails raised in groups of 20 and 27 also took longer to mature than snails kept in pairs or the single snail kept alone, as discussed below. It appears that the presence of other snails *per se* has no effect because one snail kept by itself (aquarium area 0.54 m^2) had a similar shell length to a pair (P24, P25) that was reared together (aquarium area 1250 cm^2).

Unlike *P. hongii* discussed below, *P. a. paraspiritus* did not need to eat the green algal material that grows on the glass walls of the aquaria in order to mature (see below) because field-collected *P. a. paraspiritus* matured when kept in aquaria with clean walls. However, newly hatched *P. a. paraspiritus* did move up onto the glass walls and clearly ate the algae when it was available. These hatchlings appeared to spend a much shorter time on aquarium walls than did newly hatched *P. hongii* and this corroborates, to some extent, field observations: newly hatched *P. ambagiosus* were observed on vegetation above ground on only one occasion (G.R.Parrish, G.H. Sherley, DOC, pers. comm. 1991) whereas newly hatched *P. hongii* are often seen on the undersides of leaves of shrubs and trees (Choat & Schiel 1980; Penniket 1981; Stringer et al. 2004).

The shells of snails kept in aquaria that had not been cleaned for prolonged periods developed scars or deformities, and growth rates diminished. Any of the causes, detailed below, that affect the growth of other snails, such as a build up of waste material or mucus, may have affected the growth rates of these snails.

4.1.3 Effects of rearing conditions on *Placostylus hongii*

The initial conditions under which the field-collected *Placostylus hongii* were reared were clearly unsuitable because only the largest field-collected juvenile matured, whereas six smaller field-collected juveniles died before their shells had increased more than about one-third of their initial lengths. Survival of this species, however, improved once green algal material was allowed to grow on the glass walls of the aquaria. Newly hatched snails clearly ate this, as did larger juveniles, but the latter only occasionally moved over the glass walls. This species is more arboreal than *P. ambagiosus* when newly hatched in the wild, as mentioned above. However, no large juveniles or adults of either species have ever been reported as being found any where other than on the ground in the wild (Choat & Schiel 1980; Parrish et al. 1995; Penniket 1981; Stringer et al. 2004).

4.2 EGGS AND INCUBATION PERIOD

Egg clutches of both *Placostylus ambagiosus* and *P. hongii* contained similar numbers of eggs, the eggs of both species were of similar size, and the hatchlings emerged from the ground a similar length of time after

oviposition. The incubation periods for *P. a. paraspiritus* and *P. hongii* have not been recorded previously, but Penniket (1981) noted that two clutches of *P. hongii* eggs ($n = 101$), collected from the Poor Knights Islands, hatched over a period of more than 82 d.

The numbers of eggs per clutch laid by captive snails in the present study had a greater range than reported for clutches found in the field. Choat & Schiel (1980) reported clutches of 20–55 eggs for *P. hongii* on the Poor Knights Islands, and Penniket (1981) noted that *Placostylus* commonly had clutches of 20–30 eggs (range 11–72 eggs), but he did not give separate information for *P. ambagiosus* and *P. hongii*. He did, however, note that the largest clutch of 72 eggs was found under two *P. hongii* that were side by side on Tawhiti Rahi Island, Poor Knights Islands. Stringer et al. (2004) also found a single nest of more than 68 eggs of *P. hongii* on the same island so it seems likely, as suggested by Penniket (1981), that some clutches may contain the eggs from more than one snail.

Placostylus a. paraspiritus can lay eggs without having mated, as evidenced by the single snail that was kept isolated until well after it had matured. None of these eggs hatched, which suggests that the snail had produced infertile eggs.

No clear preference for laying eggs in particles of different size was determined for either species, because dead hatchlings and too few clutches of eggs were found. However, the possibility that some clutches may actually contain eggs from more than one snail, as discussed above, suggests that the total numbers of eggs laid may provide some indication of preference. If this is the case, it does seem likely that *P. a. paraspiritus* prefers to lay eggs in gravel (particle size range 2–< 8 mm) whereas *P. hongii* prefers to lay eggs in sand (particle size range 0.5–< 2 mm).

4.3 GROWTH

Placostylus ambagiosus paraspiritus and *P. hongii* probably have similar growth patterns, although only one *P. hongii* was followed in detail and for only a short time after it had hatched in captivity. The latter snail showed an increase in shell length (mean 0.062 mm/d) that was lower than the growth rates of most individual *P. ambagiosus*, although the rate was still within the range for *P. a. paraspiritus*. All individuals of *P. a. paraspiritus*, except those kept at high densities as discussed below, grew at a similar, linear rate up until they had reached c. 90% of their final adult shell size, but they ended up with widely differing sizes of adult shells. Clearly, differences in adult size resulted from individual snails ceasing linear growth at different times, so there was no relationship between final adult shell size and the rate of growth, as reported for other land snails with determinate growth (Johnson & Black 1991). Almost identical growth patterns, except for the time scale, to those reported here for *Placostylus* occur in *Cepaea nemoralis* (Wolda 1970), *Archachatina marginata* (Plummer 1975), *Punctum pygmaeum* (Baur 1989) and many slugs (South 1992). Other examples that differ in only minor ways, such as the initial growth phase being slightly curved

instead of linear, are given by Severns (1981), Daguzan (1982), Staikou et al. (1988, 1990) and Lazaridou-Dimitriadou (1995). The general pattern for all of these snails is an initial growth phase, where the increase in shell length is approximately linear, followed by an intermediate phase characterised by decreasing growth rate, and a final phase where increase in shell length virtually ceases after a lip develops on the edge of the shell aperture. The reproductive organs mature, where this is known, during the intermediate growth phase, so it is possible that the reduction in mass that occurred during this phase in some *P. a. paraspiritus* and *P. hongii* may be related to this process (e.g. Williamson 1976; Solem & Christensen 1984; Staikou & Lazaridou-Dimitriadou 1990; Johnson & Black 1991; Lazaridou-Dimitriadou 1995). Although we did not sacrifice any of the reared snails to determine the maturation of reproductive organs, the appearance of a white area around the genital opening during the intermediate phase provides some circumstantial support that the reproductive organs may have been maturing.

Growth is usually sigmoidal in Mollusca (Wilbur & Owen 1964) and this pattern is reported for some pulmonate species and even for occasional individuals of species that normally have a linear initial growth phase (Baur 1989; Egonmwan 1991; Hommay et. al. 2001). However, the growth patterns described here for *P. a. paraspiritus* and *P. hongii* relate only to growth after the hatchlings appear above ground and we do not know how long the hatchlings remain underground or what their growth pattern is while they are underground. The time spent underground after hatching has not been documented for most pulmonates that bury their eggs, but it is known to vary from several days to 2–3 months in the few species for which this is recorded, and some hatchling snails are reported to grow while they are underground (Plummer 1975; Lazaridou-Dimitriadou 1995; Stringer et al. 2002).

The developmental periods for *P. a. paraspiritus* and *P. hongii* in captivity, from emergence after hatching to maturity, are relatively long for land snails, most of which become adult within 3 y in the field (Johnson & Black 1991, and references therein). This holds even when only the fastest developmental times are considered for *Placostylus* reared in small groups (2.5–4.4 y for *P. a. paraspiritus*; > 2.5 y for *P. hongii*). The juvenile periods for these species in the wild, however, are even longer: > 6 y for *P. a. paraspiritus* near Cape Maria van Diemen (Sherley et al. 1998), and > 3–6 y (estimated) for *P. hongii* on the Poor Knights Islands (Penniket 1981; Stringer et al. 2004). Two factors seem likely to account for a prolonged juvenile period in the wild. Firstly, it is unlikely that conditions are suitable for feeding every night, especially during dry periods in summer, in contrast to the situation in the laboratory. Secondly, wild snails usually occur in groups under suitable food plants, often at relatively high densities (maximum numbers: *P. a. ambagiosus,* 54 adults/m^2 given above; *P. hongii*, 10.7 adults/m^2) (Penniket 1981; Stringer et al. 2004), and crowding may delay their development to some extent as discussed above. However, data on the effects of density on growth are limited to *P. a. paraspiritus*. The single snail that was housed by itself in the laboratory (P23) developed the fastest (2.6 y; density of 8 snails/m^2) whereas others kept in groups of 20 and 27 (densities of 159 snails/m^2 or

214 snails/m^2, respectively) took, respectively, 3–6.5 y to become adult, or died within 6.5 y without becoming adults.

Both a reduction in size and a lengthening of the developmental period have been reported for other pulmonate species kept in crowded conditions, and it is the densities at which they are kept that appears to have a major influence on their development. This is variously reported among some terrestrial snails and slugs to affect growth (both stimulatory and inhibitory), individual variability, adult shell size, reproduction, activity, aggressive behaviour and cannibalism (e.g. Herzberg 1965; Williamson et al. 1976; Oosterhoff 1977; Cameron & Carter 1979; Egonmwan 1991; Foster & Stiven 1996; Lazaridou-Dimitriadou et al. 1998; Hommay et al. 2001). The ultimate cause of these effects, however, is not always clear. Suggestions include a build-up of waste material in the aquarium, feeding competition and unknown factors in the mucus of both conspecifics and other species of snail (e.g. Egonmwan 1991; Foster & Stiven 1996; Cook 2001; Hommay et al. 2001). In many of these studies, food was provided in excess, so other factors such as increased aggression due to crowding or chemical interactions were suggested as either affecting the consumption of food or directly affecting growth or reproduction. There is evidence that the negative effects of breeding snails at high densities may still occur, at least in some snails, even when waste material is prevented from accumulating by frequent cleaning (see review by Cook 2001).

4.4 LIFESPAN

The lifespans of laboratory-reared *Placostylus ambagiosus paraspiritus* and *P. hongii* confirm that these are long-lived snails. There are no published estimates for the lifespan of *P. a. paraspiritus* in the field, but estimates for *P. hongii* on the Poor Knights Islands vary from 10 y to 33 y and possibly longer (Choat & Schiel 1980; Stringer et al. 2004). Thus, at least for *P. hongii*, it seems likely that lifespan is reduced when snails are provided with relatively constant conditions that allow activity on most nights. In the wild, over 50% of the recorded lifespans for pulmonates are less than 2 y, with a maximum of 19 y (Cook 2001; Heller 2001).

5. Conclusions

Both *Placostylus ambagiosus* and *P. hongii* can be successfully reared in captivity, in the laboratory, and large numbers of snails can potentially be produced. This is, however, relatively expensive because of the long developmental period and because the snails should be kept at relatively low densities (otherwise their growth is slowed and they become small adults). Maintaining the snails in captivity requires little time on a weekly

basis—spraying the aquaria, collecting leaves and occasionally cleaning the gravel—but the overall investment in time is large given these species' long developmental periods.

Although frequent disturbance appeared to be one explanation for the early deaths of the first snails that were taken into captivity during this study, these species can certainly be handled at weekly intervals without apparent harm. This is evidenced by the few snails that were weighed and measured to follow their growth. The snails eventually became quite tame and readily emerged and moved about on the researcher's hands, provided that the hands were wet after being washed and thoroughly rinsed. Thus, although the present study provides minimal information on the growth and development of two species of *Placostylus*, it demonstrates that such research could be done in the future without deleterious effects on the snails.

6. Recommendations

We recommend the following procedures for rearing *Placostylus* in the laboratory:

1. Collect juvenile snails from the wild for captive-breeding because they have the lowest chances of survival in the wild where they are vulnerable to predation by rodents or birds owing to their long developmental period, and because juveniles survive better when taken into captivity. In addition, adult snails, although resistant to such predation, are best left in the parent population where they can continue to breed.
2. Provide large glass aquaria that are entirely enclosed, but with an area of fine gauze (mesh < 4 mm) for ventilation. Limit the numbers of snails in each aquarium: we suggest that each snail has a minimum area of c. 400 cm^2. Position the aquarium so it is well lit, but where it will not overheat in direct sunlight.
3. Use mixed gravel for a substrate with particles of 1–8 mm in diameter. Keep the substrate clean by removing well-rotted leaves and wash half of the gravel once a year, or more often if soil develops on top of the gravel. Allow green algae to grow on some sides of the aquarium for the hatchlings to eat. Try to keep a constant water level under the gravel to prevent eggs from flooding or drying out.
4. Provide the snails once a week with leaves that have fallen from a suitable food plant such as karaka, kohekohe, kawakawa or hangehange. Occasional, longer periods of up to 3 weeks between feeds appear to have no harmful effects. Allow the leaves to decay and turn brown and soft, but remove rotted leaves once they start matting together.
5. When providing leaves, thoroughly wet them, the aquarium sides and the substrate with a fine spray of tap water. Keep the humidity in the aquarium as high as practicable by alternating periods of high humidity

(covering the ventilation mesh with plastic film) with short periods of lower humidity (uncovering part of the mesh) so as to prevent excess fungal growth on the leaves.

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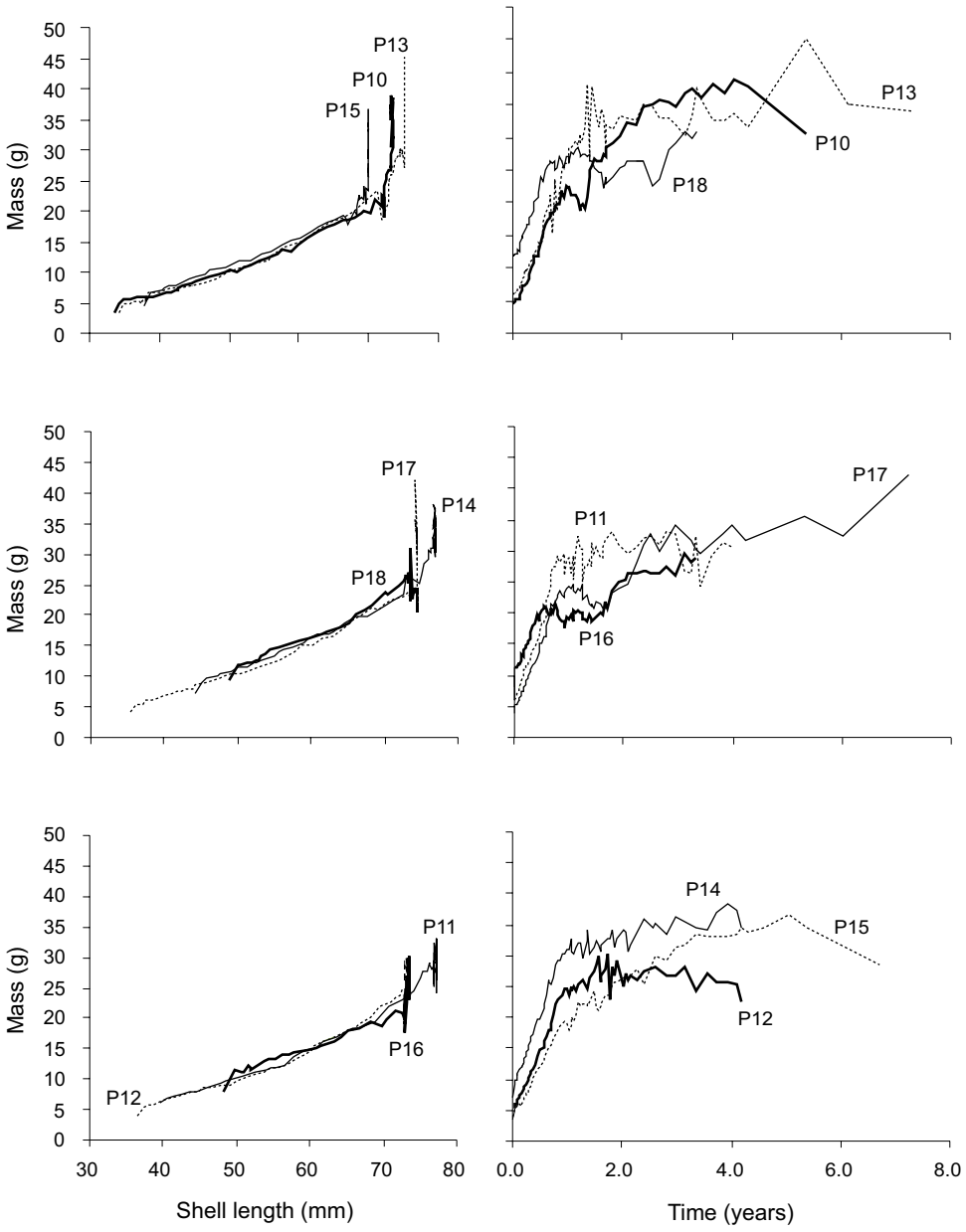
Appendix 1

CHANGE IN MASS AND MASS:LENGTH RATIO FOR INDIVIDUAL *Placostylus ambagiosus paraspiritus* KEPT IN CAPTIVITY (COLLECTED NEAR CAPE MARIA VAN DIEMEN, 19 OCTOBER 1992)



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