

A review of the ecology and conservation of *Placostylus* (Mollusca: Gastropoda: Bulimulidae) in New Caledonia

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Abstract

Land snails of the genus *Placostylus* Beck, 1837 are found only in the Western Pacific, from the Melanesian Plateau to New Zealand. While the ecology of the New Zealand *Placostylus* species is generally well known, having been studied for more than 20 years, and there is some published information on the one species of *Placostylus* from Lord Howe Island, there is very little published information on the six New Caledonian species. These New Caledonian taxa are all endangered, but their conservation is hampered by a lack of information about the life-history, biology and ecology especially relating to *Placostylus bondeensis*, *P. eddystonensis*, *P. scarabus* and *P. caledonicus*. The data that is available comes mostly from studies on the two remaining species - *P. fibratus* and *P. porphyrostomus*. Here we review what is known of the activity patterns, growth rates, life-histories, habitat use, nutrition, movement patterns and causes of population decline in these two species and collate the available information from the limited and mostly unpublished literature. The two species are threatened in different ways - *Placostylus fibratus* is favoured as food, and as a result, has been over-collected from the wild, while *P. porphyrostomus* is threatened by habitat modification and destruction, and by predation by introduced rodents. We make several recommendations for the conservation of New Caledonian *Placostylus* which ultimately may depend on the work we describe here on captive breeding and management. Translocations to predator-free sanctuaries coupled with augmentation of existing populations may be necessary to maintain populations of these species in the wild.

Etat des connaissances sur l'écologie et la conservation des *Placostylus* (Mollusca: Gastropoda: Bulimulidae) de la Nouvelle-Calédonie

Résumé

Les escargots terrestres du genre *Placostylus* Beck, 1837 se rencontrent uniquement dans le Pacifique Sud-Ouest, depuis le Plateau Mélanésien jusqu'à la Nouvelle-Zélande. L'écologie des espèces de *Placostylus* de la Nouvelle-Zélande, étudiées depuis plus de 20 ans, est de relativement bien connue. Par contre, très peu de travaux ont été publiés sur les six espèces de la Nouvelle-Calédonie. La conservation de ces taxons, tous endémiques et menacés, est entravée par le manque de connaissances sur les traits d'histoire de vie, la biologie et l'écologie principalement pour *Placostylus bondeensis*, *P. eddystonensis*, *P. scarabus* et *P. caledonicus*. La plupart des informations disponibles proviennent des études réalisées sur les deux autres espèces, *P. fibratus* and *P. porphyrostomus*. Un état de la bibliographie récente sur plusieurs aspects de la biologie et de l'écologie de ces deux espèces (activité, croissance, reproduction, habitat, alimentation, mouvements et causes de disparition) est réalisé ici afin de compiler les connaissances à partir de la littérature disponible et non publiée de manière générale. *Placostylus fibratus*, très recherché pour la consommation humaine est collecté dans le milieu naturel, alors que *P. porphyrostomus* est menacé par la modification et la perte de son habitat naturel, et par la prédation par les rongeurs introduits. Enfin, différentes recommandations pour la conservation des *Placostylus* de la Nouvelle-Calédonie sont établies à partir des travaux d'élevage et des pistes de gestion discutés ici. La translocation d'espèces dans des réserves sans prédateurs, associée à l'augmentation des populations existantes peut être nécessaire à la survie des populations sauvages.

Key words: land snail, snail farming, conservation, Bulimulidae, biology, ecology

Introduction

The genus *Placostylus* Beck, 1837 belongs to the Bulimulidae (Gastropoda, Heterobranchia, Pulmonata), a widely dispersed snail family that is most numerous in South America and reaches its maximum diversity in Brazil (17 genera). A few genera extend north into the West Indies, Mexico, and the southern United States; others are found in Australia, New Zealand and Melanesia. The phylogeny of the Bulimulidae remains uncertain, but a South American radiation in the Mesozoic and Tertiary is suggested by the present distribution, comparative anatomy and fossil record (Solem 1959). *Placostylus* (subfamily Placostylinae) is found only in the Western Pacific, extending northwards from the tip of the North Island in New Zealand to Lord

Howe Island, Fiji, the Solomon Islands, Vanuatu and New Caledonia including the Loyalty Islands (Hedley 1892; Cockerell 1929; Solem 1959). The New Caledonian *Placostylus fibratus* (Martyn, 1789) is the type species of the genus (Chérel-Mora 1983). Molecular analysis suggests that the Lord Howe Island species and the New Zealand mainland taxa are sister groups, but that the Three Kings Islands taxon (off the northern tip of New Zealand) is independently derived, possibly from New Caledonian stock (Ponder *et al.* 2003). The New Caledonian species have typically been classified into two groups, namely *Leuchocharis* Pilsbry, 1900 and *Placostylus s. str.*, ranked as sections by Pilsbry (1901–1902) and as separate genera by Franc (1956).

The literature on the taxonomy of New Caledonian *Placostylus* abounds with more than 130 specific and infra-specific names (Crosse 1855a, 1855b, 1867, 1868, 1869, 1870, 1875, 1881, 1886, 1895; Gassies 1863, 1869, 1870, 1871, 1880; Brazier 1881, 1882; Pain 1955, 1958; Solem 1961). This multitude of taxa within New Caledonia is the result of the high degree of morphological variation in the shells (Solem 1959), and the tendency by early conchologists to describe taxa on the basis of just one or two individuals. Solem (1959) suggested that the New Caledonian species were monophyletic and all closely related, and that the shell divergences between the sections (or genera) represent minor habitat adaptations. More recent treatments have revised the species number downwards. Franc (1956) recognized 19 species, whereas Solem (1961) proposed 33 species. Starmühlner (1970) described the anatomy, the radula and the shell characteristics for seven species—*Placostylus albersi* Dautzenberg & Bouge, 1923, *P. caledonicus* (Petit, 1845), *P. duplex* (Gassies, 1871), *P. fibratus*, *P. goroensis* (Souverbie, 1870), *P. layardi* Kobelt, 1891 and *P. porphyrostomus* (Pfeffer, 1851). Using anatomical characteristics and analysis of shells from many populations collected all over New Caledonia and adjacent islands, Chérel-Mora (1982, 1983) recognized only four endemic species, each of them exhibiting very wide clinal geographic and ecological variation: *Placostylus fibratus*, *P. porphyrostomus*, *P. caledonicus* and *P. eddystonensis* (Pfeffer, 1855). Drs E. Neubert and P. Bouchet (MNHN, Paris; pers. comm. 2000; Neubert 2001) who are currently investigating the taxonomy and anatomy of New Caledonian *Placostylus*, suggest that six valid species and approximately twenty well defined geographic subspecies spread over the territory can be recognised in New Caledonia. In addition to the four species recognised by Chérel-Mora, *Placostylus scarabus* (Albers, 1854) and *Placostylus bondeensis* (Crosse & Souverbie, 1869), which were considered synonyms of *Placostylus caledonicus* by Chérel-Mora (1983), are recognized as valid species by Neubert (2001). Our observations in the New Caledonian dry forest since 1993, on *Placostylus porphyrostomus* in particular, show that further investigations on the systematics of New Caledonian *Placostylus* may still be warranted (Brescia and Pöllabauer 2004). Nevertheless, here we have adopted the classification of six species proposed by Neubert (2001).

The natural history of the New Caledonian *Placostylus* species remains poorly known and very little has been published on their behaviour, biology or ecology. In 1993, a study of the stock size and aspects of the biology and ecology of the two best known species of *Placostylus* (*P. fibratus* and *P. porphyrostomus*) was initiated (Pöllabauer 1994). This research is ongoing and is being expanded since all the New Caledonian species are considered at risk of extinction due to anthropogenic disturbances. Three species—*P. eddystonensis*, *P. fibratus* and *P. porphyrostomus*—are listed as vulnerable by IUCN (IUCN 2006). Very little is known of *P. caledonicus*; only one small population (estimated size ~200 individuals in 2004) is known from the North of New Caledonia (Koumac, “Three Creeks”), while *P. eddystonensis* seems to be the rarest species, with no living snails found in the last 10 years. The population status of *P. scarabus* and *P. bondeensis* has never been documented but our observations show that the

populations of these species are very restricted and found only in the far north of the main island and only in small patches of remnant forest.

Placostylus fibratus is the most polymorphic species and is found throughout New Caledonia, including the Loyalty Islands where a dwarf form occurs. This edible species is known as ‘the snail of the Isle of Pines’ (named after the coral island to the south of the mainland from which they are collected). Indeed, the only snails to be marketed commercially for consumption are those from this island. Control measures on the harvesting of these snails have been imposed by the local authorities charged with environmental protection. In parallel, conservation strategies such as off-site preservation as well as developing farming methods have been explored by the Institut Agronomique néo-Calédonien (IAC) since 1997 and will be described below.

Placostylus porphyrostomus is the most common species in sclerophyllous forests (Chérel-Mora 1983), which is the dominant vegetation type in dry areas on the west coast of the mainland (less than 1100 mm annual rainfall, mostly falling in three months of the year). This forest type is characterized by a high diversity of plant species. *Placostylus porphyrostomus* is also found on the Isle of Pines where it is sympatric with *P. fibratus*. It is also collected by locals for their own daily consumption but it is not commercially marketed. The sclerophyllous forest is currently the most threatened of the Caledonian biomes due to deforestation and habitat modification by feral ungulates (Programme Forêt Sèche 2007). A conservation programme with ten international, national and local partners (‘Programme Forêt Sèche’) has been recently initiated in an attempt to try to save this highly endangered biome and its associated specialised fauna and flora.

In this paper, we use the available literature and our own observations on many populations of each species to summarise what is known on the biology and the ecology of *P. fibratus* and *P. porphyrostomus*. For more than 10 years these two species have been the subject of research in New Caledonia because of their importance as food, which provides an economic imperative for their study. We assume here that the study of their biology will be indicative of the New Caledonian species generally, although we recognise the differences in the relative abundances in the species. We also review causes of the decline of the New Caledonian *Placostylus* in the wild and summarise the results of a captive breeding programme. Recommendations for the conservation of these species are given.

General state of knowledge

Life History

Published information about the life-history of New Caledonian *Placostylus* is very sparse. However, in this review we bring together information presented in a series of unpublished technical reports to government authorities in New Caledonia, particularly those concerning *P. fibratus* (Pöllabauer 1994, 1995; Brescia 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2007) and *P. porphyrostomus* (Brescia and Pöllabauer 2004, 2005). Some additional inferences can be made from studies on the New Zealand endemic *Placostylus* species (Choat and Schiel 1980;

Penniket 1981; Brook and Laurenson 1992; Sherley *et al.* 1998; Stringer *et al.* 2004) and on the one species of *Placostylus* on Lord Howe Island (Murphy and Nally 2004).

Distribution, habitat and diet

Placostylus fibratus, the most widespread species, inhabits all of the New Caledonian mainland, the Isle of Pines, and the Loyalty Islands. On the mainland, it is found in humid evergreen forests of the east coast; in the dry coastal forests of the west; and in the humid evergreen forests of the central mountain chain up to an altitude of 900 m from the north to the extreme south, where it occurs as a spectacular giant form weighing up to 100 g and measuring about 15 cm in shell height. *Placostylus porphyrostomus* is characteristic of the dry forests of New Caledonia (Chérel-Mora 1983). It is found in remnant patches of sclerophyllous forest along the west coast of the mainland, and does not occur in the wet forests of the island's interior. *Placostylus porphyrostomus* is sympatric with *P. fibratus* on the Isle of Pines. *Placostylus caledonicus*, occurs in the far north of the mainland, and inhabits dry coastal forests to an altitude of 500 to 600 m (Chérel-Mora 1983).

These snails appear to be relatively specific in their habitat requirements. *Placostylus fibratus* seems to be primarily associated with calcium-rich soil (Brescia 2001). On the Isle of Pines, opportunistic observations show that *P. fibratus* and *P. porphyrostomus* are attracted to and feed under trees with large canopies and/or with broad leaves such as fig and banyan trees (*Ficus* spp.), *Elaeocarpus hortensis* Guillaumin, 1931, *Meryta macrocarpa* Baillon, 1878, but also under the ferns *Asplenium nidus* Linnaeus, 1753 and *Microsorium punctatum* Copeland, 1929 (Pöllabauer 1995). Brescia (2000) found them preferentially under Pweu (*Ficus habrophylla* Bennett & Seeman, 1865) and Kohu (*Intsia bijuga* (Collebroke) Kuntze, 1891). Indigenous snail collectors on the Isle of Pines search preferentially for *Placostylus* under these trees, and also under Buniê (*Manilkara dissecta* var. *pancheri* (Baillon) Maas Geesteranus 1941) as they are known to be favoured by the animals. Juveniles (up to 1.5 cm in shell height) are often found up to 2 m from the ground on the foliage of the Jaanyi (*Codiaeum variegatum* Blume, 1825) (pers. obs.). *Placostylus* show a tendency to hide during daylight: Brescia (1997) found *P. fibratus* to be hidden during the day under dead leaves of the litter, under roots, coral rocks or fallen wood (82% of snails found, n=53) and very few (18%) were under no protection.

Very little data are available on the diet of New Caledonian *Placostylus*, but they are known to consume both fresh and fallen leaves of the species listed above. Adults and juveniles have also been seen grazing on algae and lichens on leaves and coral rocks (Pöllabauer 1995; pers. obs. F.B., and knowledge of locals from the Isle of Pines). After snails have been collected and just before they are marketed, women often feed them with the green leaves of Trüü (*Rivina humilis* Linnaeus, 1753, the Coral Bay), and also leaves of *Asplenium nidus* Linnaeus, 1753. When she studied the anatomy of *Placostylus*, Pöllabauer (1995) also found soil in the intestine.

In the dry forests of the mainland, the favoured habitat and environmental conditions have been described for *P.*

porphyrostomus by Brescia and Pöllabauer (2005). The snails appear to seek out areas with deep leaf litter, where the cover of understorey trees is high (> 75%). In general, they are found in shady places with low light levels (ca. 800 lux), and where environmental conditions are cooler (on average, 2–3°C less than points 1 m radius away from the snail). This suggests that snails use microhabitat variation to attain a more suitable environment (lower temperature and higher relative humidity) which may enable them to avoid desiccation during the drier daylight hours and during periods of low rainfall. Important components of the habitat of *Placostylus* of dry forests are the understorey trees of *Codiaeum peltatum* (Labillardière) Green (1986), *Carissa ovata* Brown 1810, and *Fontainea pancheri* (Baillon) Heckel 1870. In these forests the snails are generally found under leaf litter or close to fallen logs.

In New Zealand, Penniket (1981) found that the distribution and abundance of *P. ambagiosus* (Suter, 1906) and *P. hongii* (Lesson, 1830) in forest communities is also greatly influenced by the distribution of ground cover and local variation in leaf litter depth, and that older juveniles and adult snails feed on fallen leaves from broadleaf trees and shrubs. According to Brook and Laurenson (1992), the principal factors determining the within-colony distribution of the other New Zealand species *P. bollonsi* are the presence of broadleaf food plants and/or of a sheltered microhabitat that occurs under broadleaf litter or groundcover plants. Penniket (1981) suggested that there might be a minimum sized leaf under which a snail may find such a favourable microclimate.

On Lord Howe Island, Murphy and Nally (2004) found *P. bivaricosus* (Gascoin, 1854) under well-developed, moisture-retaining leaf litter in evergreen closed forest, often, but not exclusively, in the vicinity of Banyan Figs (*Ficus macrophylla columnaris* Moore & Mueller 1874). These authors also observed that *P. bivaricosus* was sparse or absent in areas developed as palm plantations, but mixed palm and broad-leaf forest provided good habitat.

Activity

Like most pulmonate land snails including other *Placostylus* species (Penniket 1981, Brook and Laurenson 1992, Murphy and Nally 2004), the New Caledonian *Placostylus* are nocturnal. Pöllabauer (1995) observed activity of *P. fibratus* between 7:00 pm and 6:00 am during the cool season and between 12:00 and 4:00 am during the warm season. She found that the peak of activity was between 2:00 and 3:00 am whatever the season (Figure 1), and that activity is negatively related to temperature ($r=-0.75$) and positively to humidity ($r=0.46$).

In observations of captive and wild populations over 24-hour periods during both the cool and warm seasons, Brescia *et al.* (1998) also found that *P. fibratus* is active between 7:00 pm and 6:00 am, but described two peaks of activity: one near 8:00 pm and another one between 3:00 am and 4:00 am. The intensity of activity appeared to be related to weather conditions, being greater during or following periods of rain. Overall, the activity levels were low—only 13 to 14% of the dark period of each 24 h comprised moving, feeding or sexual activities. Brescia (1997) found that during a week of observations in the field in July 1997, 19% (n=194) of snails showed no activity during that whole period.

Salas *et al.* (1997) and Brescia *et al.* (1998) found that, in captivity, between 6 and 50% of snails under observation remained inactive each night despite variation in temperature, humidity and lighting regimes. Hatchlings and

juveniles appear to be more active than sub-adults and adults (Pöllabauer 1995, pers. obs. F.B.).

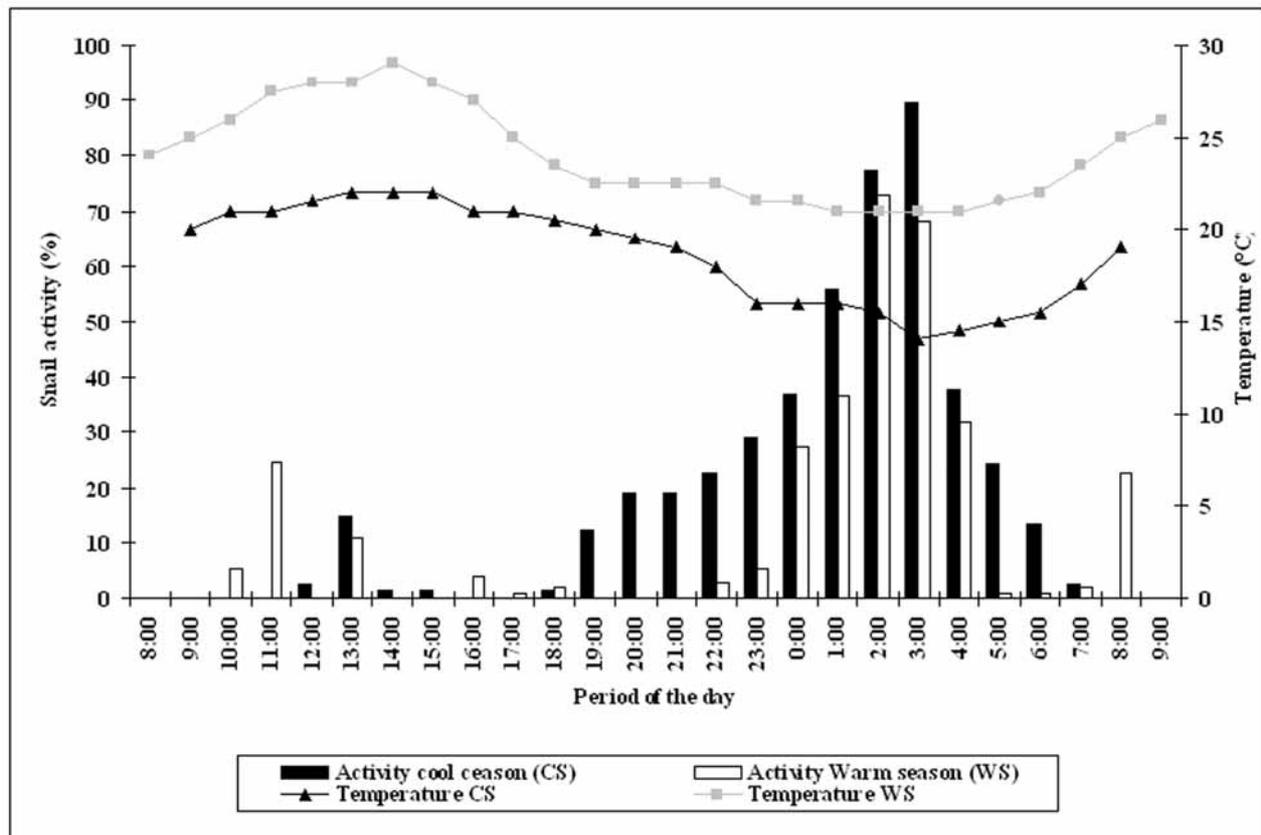


FIGURE 1. Daily activity patterns (defined as snails outside their shell showing locomotory and/or nutritional activities) of wild *Placostylus fibratus*, in Kaana, Isle of Pines, New Caledonia in the cool season (CS) (n=79) and warm season (WS) (n=109) (from Pöllabauer C. 1995. *L'escargot de l'île des Pins Placostylus fibratus, biologie, répartition, économie*. Service de l'Environnement, Province Sud. ISBN 2-9509343-0-7. Nouméa, Nouvelle-Calédonie).

Brescia (1997) observed *Placostylus* in captivity under controlled conditions by having the snails in a reverse light cycle—exposing them to daylight in their normal dark period—and showed that they appear fundamentally nocturnal and that a negative phototropism exists. Penniket (1981) suggested that the nocturnal behaviour of New Zealand *Placostylus* may serve as both a predator-avoidance mechanism and a strategy to avoid higher daytime temperatures and its drying effects.

Pöllabauer (1995) found seasonal differences in *P. fibratus* activity levels. At the beginning of the warm season (which runs from December to March), activity was found to be very low, with the majority of snails remaining inactive. When provided with a friable soil substrate during this season, the snails were found to burrow to cover their shell aperture, evidently as protection from desiccation. Even so, during extended dry periods, 30 to 45% loss of body weight due to desiccation was recorded. In the cool season (May to October), movement, reproduction and growth all resume.

Dispersal

Placostylus fibratus is a slow-moving animal and typically travels only about 1 m per night (Brescia 1997), although some adults have been observed to travel up to 20 m in a single night to lay eggs. The New Caledonian

Placostylus tend not to disperse far: tagged *P. porphyrostomus* and *P. fibratus* are regularly relocated in the same 10 x 10 m quadrat and mostly under the same shrub or tree over a year or more (Pöllabauer 1995; F. Brescia, pers. obs.; Brescia and Pöllabauer 2005). Penniket (1981) found that the New Zealand *Placostylus* also exhibited a very low rate of dispersal of about 1 to 2.8 m after six months and suggested that the snails may exhibit a homing behaviour, since some snails remain for several months in the same crevice or under the same tree. Penniket (1981) suggested that this strategy of low dispersal may be of selective value to an organism dependent on patchily-distributed resources in a heterogeneous environment, i.e. where preferred food trees and ground shelter are scattered within a mixed-forest association. By comparison, the introduced giant African snail *Achatina fulica* (Bowdich, 1822) has been observed traversing more than 50 m in a night (Van S. Greve 1981).

Life span and growth

Placostylus fibratus is a large snail and reaches 80–100 g when adult with a shell height of 9–15 cm. *Placostylus porphyrostomus* is smaller (7–8 cm in shell height, 45 g), and is characterised by the partial or total disappearance of the periostracum from the shell when adult (Figure 2).



FIGURE 2. Morphological differences between the New Caledonian endemic snails *Placostylus fibratus* (bottom) and *Placostylus porphyrostomus* (middle), and the introduced snail *Achatina fulica* (top).

Placostylus fibratus reaches maturity at five years and, based on a prediction of shell growth rates, it is suggested that they may live 15 years and attain 11.7 cm shell height (Pöllabauer 1995). Once maturity is reached, the increase in shell height stops, but thickening of the peristome continues (Pöllabauer 1995). Adult *P. fibratus* are thus characterised by a shell with a thickened apertural lip (more than 4 mm) which is also strongly correlated with the maturity of the genital tract ($r = 0.70$ for female organs and $r = 0.60$ for male organs) (Pöllabauer 1995).

The first study of growth rates of New Caledonian *Placostylus* in the wild used a Von Bertalanffy model fitted to mark-recapture data of 708 individuals of *P. fibratus* on the Isle of Pines (Pöllabauer 1995). The fitted model $H_{\infty}(1 - \exp^{-K(t-t_0)})$ predicts the height of the shell as a function of the animal's age (yr), where K is the rate of growth, set at 0.22 yr^{-1} and H_{∞} , the maximal possible shell height, set to 11.7 cm. This model recognises that shell height growth slows as maturity is approached. *Placostylus fibratus* generally exhibited slow growth rates during this study. In the dry year of 1994, growth rates (shell height increments) were only in the order of 5 to 19 mm per annum. However, it appears that *P. fibratus* exhibits great plasticity in growth rates and is able to respond to favourable environmental conditions—one marked individual grew from a shell height of 2.4 cm to reach maturity at 9.6 cm over the course of a single year (Pöllabauer 1995).

In a comparative study of growth under natural and artificial conditions, Brescia (2004) estimated mean growth rates of 18 mm shell height per annum in 30 juveniles of *P. fibratus* monitored in forest habitat on the Isle of Pines between February and June 2004. In captivity over the same period, when snails were fed an artificial diet (see below), animals in the same age class had mean growth rates about 2.5 times higher (44 mm shell height per annum). No information exists on the longevity and growth rate in other New Caledonian *Placostylus*.

Parrish *et al.* (1995) re-captured alive in 1991 snails that had been first marked in 1979, and suggested that the

New Zealand species *P. hongii* and *P. ambagiosus* may live to 20 years or more. *Placostylus hongii* have survived in captivity for more than five years (Penniket 1981), and in a recent growth study, Stringer *et al.* (2004) suggested that *P. hongii* may live at least 10 years and possibly more than 30 years, supporting the conclusions of Choat and Schiel (1980). In discussing New Zealand *Placostylus*, Penniket (1981) suggested that the long lifespan in these animals may be a strategy to compensate for living in environments where recruitment to the breeding population may be irregular and variable. The rate of increase in shell length for *P. hongii* varied from 6 to 25 mm per year in juveniles with shells < 38 mm in height, but slowed when adults reached maturity. Subsequently, the lip thickness increased about 0.1 to 0.4 mm per year but this growth rate varied considerably between individuals. In a study of size-frequency of *Placostylus bollonsi caperatus* Powell, 1948 from Wet Bay on Great Island (Three Kings Islands), Brook and Laurensen (1992) indicated an increase in shell length of about 25–30 mm per year, and that snails attain adult size at about 3 years old. The growth rate and lifespan of *P. bivaricosus* in Lord Howe Island are unknown (Murphy and Nally 2004).

Reproduction

Placostylus, like all pulmonates, are hermaphroditic and so all individuals are potentially capable of producing eggs. In the field, egg laying in New Caledonian species has been observed to occur primarily during the cool season, but the reproductive season of *P. fibratus* on the Isle of Pines can extend until October (Pöllabauer 1995). Clutches of 25 to 450 eggs are deposited in nests formed in depressions in the soil. These nests are generally located near coral blocks or close to tree roots in a friable humus-rich soil. Pöllabauer (1995) observed egg-laying progress at a rate of about 17 eggs per hour, followed by about 20 to 30 min of rest. The interval between laying and hatching was between 15 and 21 days. The egg-laying behaviour of *P. fibratus* kept in captivity, under semi-natural conditions, was similar to the field behaviour noted above, though here it was possible to observe that individuals can produce eggs several times per year (observed range 1 to 4 clutches). Eggs were produced at similar times of the year to snails in the wild (Brescia 1999 to 2005). Clutches averaged 205 eggs (SD=84; n=103, range 13 to 515). The eggs are oval in shape and off-white in colour, with a thin calcareous shell. Egg size varies from 3.6 to 4.4 mm × 5.5 to 6.7 mm, and their weight varies from 0.8 to 100 mg (67.7 mg on average, n=164). Brescia (2002) found no consistent variation in egg size or numbers of eggs per clutch among snails from different geographic origins on the Isle of Pines. However, as seems general for pulmonates (Tompa 1984; Heller 2001), egg size varies according to animal size—the larger the parent, the larger the egg and the larger the hatchling.

The interval between laying and hatching varies from 10 to 45 days in captivity (average 22 days), and is strongly dependent on ambient temperature—high temperatures (25 °C) hasten hatching to about 10 days. The hatching success in captivity is now in the order of 70% and at emergence, shell height varies between 4.4 and 7.2 mm, and the weight of the living animal between 23 and 94 mg. Hatchlings have

been observed to stay within or near the nest for several days but after that exhibit a strong tendency to climb on the walls of the enclosures. This behaviour can be reduced by the addition of a thick layer of leaf litter to the soil surface. In the wild, on Isle of Pines, hatchlings and juveniles (up to 15 mm in shell length) are often found climbing on shrubs and small trees such as the juvenile form of *Meryta* sp. (2 m high) or the fern *Asplenium nidus* (pers. obs.).

Mating has rarely been observed in New Caledonian *Placostylus*. One case involving *P. fibratus* was observed in June 2002 (F. Brescia & C. Pöllabauer, pers. obs.), with copulation lasting eight hours.

The reproductive biology of the New Zealand taxa appears similar to that of *P. fibratus*. *Placostylus hongii* and *P. ambagiosus* reach sexual maturity at 3–5 years. Mating appears to be triggered by climatic conditions in these species, and probably occurs every year except in periods of drought. Mating can last 10 hours or more and snails may mate several times with several different mates. Twenty to thirty eggs are laid in a nest and egg size varies from 5.7 mm long by 5.3 mm wide to 6.6 mm by 5.4 mm (Penniket 1981). Brook and Laurenson (1992) mentioned that *P. bollonsi* lays a smaller number of relatively large eggs (12.5–18.0 mm long). The temporal variability in abundance of eggs observed suggests that egg laying by *P. bollonsi* is seasonal, occurring in spring and/or early summer, with most eggs hatching by late summer (Brook and Laurenson 1992; Penniket 1981; Parrish *et al.* 1995). Hatching occurs after 6–15 weeks in these species, and the hatchlings spend an unknown period living in trees and shrubs up to 4 m above the ground where they are believed to graze on algae on leaf surfaces. The development of this arboreal behaviour by *Placostylus* hatchling snails may be a response to environmental (temperature) gradients by which snails seek lower temperatures at higher elevations (Penniket 1981).

On Lord Howe Island, *P. bivaricosus* lays small clutches of eggs in the soil beneath leaf litter, probably during the warmer months. Hatchling snails possess shells about 6.7 mm in length and 5 mm in width. Hatchling and juvenile mortality is high (Murphy and Nally 2004).

Population structure and population decline

All the species of New Caledonian *Placostylus* appear to have previously been more abundant and widespread than they are today, judging by historical records and by the frequent presence of old shells in forests, indicating former populations where no living snails exist today (Pisier 1985; Pöllabauer 1995; Brescia and Pöllabauer 2005; Philippe Bouchet, pers. comm. 1999).

Few data are available on the population structure of New Caledonian *Placostylus*. Density estimates have been made for *P. fibratus* on the Isle of Pines for the period 1995 to 2004 (Pöllabauer 1995, 2002; Brescia 2004, 2005), and for *P. porphyrostomus* in a few patches of dry forest on the mainland (Brescia and Pöllabauer 2004, 2005). The populations of *P. porphyrostomus* that remain appear far more scattered and isolated than populations of *P. fibratus*; this situation is largely due to the high level of fragmentation of dry forest compared to the situation of the humid forests of the Isle of Pines (see below). Densities of live snails and empty shells vary from 0.025 to 0.18 per m² (live) and 0.15 to 0.18 per m² (empty shells) for *P. fibratus* on the Isle of

Pines (Brescia 2004), and from 0.009 to 0.115 per m² (live) and 0.073 to 0.74 per m² (empty) for *P. porphyrostomus* in mainland dry forests (Brescia and Pöllabauer 2005). Generally empty shells are more common (66% for *P. fibratus* and 85% for *P. porphyrostomus*) than live snails since empty shells can persist for many years on the forest floor. Adult-sized animals predominate amongst both the live snails (62% for *P. fibratus* and 78% for *P. porphyrostomus*) and the empty shells (94% for *P. fibratus* and 82% for *P. porphyrostomus*). For both species, recently-hatched or juvenile snails are rarely found in the field. Moreover, when they are found, a high proportion of hatchlings and non-hatched eggs are usually dead, suggesting that the eggs and hatchlings are very susceptible to desiccation or predation.

The populations of New Caledonian *Placostylus* species show a similar structure to those of the New Zealand taxa shown by Choat and Schiel (1980); Penniket (1981), and Stringer *et al.* (2004). In New Zealand, *Placostylus* occur primarily as small and widely isolated populations. These populations appear to be maintained by a pool of large and long-lived adults (Choat and Schiel 1980) which produce many juveniles each with a low expectancy of reaching adult size. For *P. bollonsi*, Brook and Laurenson (1992) show that at least 60% of hatchlings fail to attain adulthood. This high juvenile mortality may be a natural feature of the population dynamics of *Placostylus* and one that is not conducive to rapid population recovery, but it is possible that it is the result of a novel additional source of mortality that may have driven the populations into decline. Brook and Laurenson (1992) suggest that recruitment to the adult population, which is always uncertain, depends on favourable conditions of climate and habitat. The long life of adults may provide some buffering against this uncertainty. Penniket (1981) suggests that a low proportion of empty adult shells relative to live snails would be the first indication that a population is recovering.

According to the criteria of Molloy *et al.* (2002), the New Zealand *P. hongii* is classified as 'Range Restricted', and *P. ambagiosus* is classified as either 'Nationally Critical' or 'Nationally Endangered', depending on the subspecies (Hitchmough *et al.* 2007). These rankings reflect range and population sizes and vulnerability to decline. In terms of density estimates, New Zealand and Lord Howe Island *Placostylus* are evidently much more abundant than seen in New Caledonian populations of *P. fibratus* and *P. porphyrostomus*. Mean densities of live adults and juveniles of *P. hongii* on the Poor Knights Islands was variously estimated at 0.78/m² (Stringer *et al.* 2004), 1.9/m² (Choat and Schiel 1980) and 8.1/m² (Penniket 1981). For *P. bollonsi*, Brook and Laurenson (1992) recorded densities of between 2–6/m² in local patches, but overall mean densities ranged from 0.15 to 0.35 /m². On Lord Howe Island, *P. bivaricosus* occurred at an average density of 0.24 live adults and 0.33 live juveniles per square metre, with localised densities of up to two live animals per square metre in patches of good microhabitat (Murphy and Nally 2004). These figures are around 5 to 10 times higher than densities found for either *P. fibratus* or *P. porphyrostomus* in New Caledonia.

Reasons for the decline of New Caledonian *Placostylus*

The reasons for the decline of New Caledonian *Placostylus* snails are now fairly clear. Habitat destruction or

modification, human harvesting for consumption, and predation by introduced species are all contributing factors.

Habitat modification and destruction

Since the New Caledonian *Placostylus* are found only in native forests, their range and abundance are strongly influenced by the removal and degradation of this vegetation type. The vegetation of New Caledonia has been considerably modified since human arrival ca. 3,500 years ago, with over 50% of the original vegetation cover lost through deforestation. Losses have been acute for humid forest with only 30% (3,900 km²) remaining (Jaffré *et al.* 1997). Nonetheless, it is the dry sclerophyllous forests that have been most severely deforested with the current distribution of this vegetation only a relic of its original extent: 4,500 km² of dry forest once occupied the western coast, whereas today barely 45 km² (1%) remains (Programme Forêt Sèche 2007). Forest clearance for agriculture, mining, urbanisation, and losses through bush fires are the main reasons for this serious decline in forest cover. Accentuating the problem is the heavy fragmentation of the remainder which now comprises 238 small and isolated patches ranging from 0.25 ha to 200 ha. In addition, these forests are heavily infested with invasive plants such as the autochthonous Gaïac (*Acacia spirobis* Labillardière 1825) and the allochthonous Lantana (*Lantana camara* Linnaeus 1753). This phenomenon has seriously jeopardised the regeneration and indigenous composition of the forest. Moreover, the forests are severely affected by ungulates such as the introduced rusa deer (*Cervus timorensis russa* Blainville, 1822), feral pigs (*Sus scrofa* Linnaeus, 1758), cattle (*Bos primigenius taurus* Bojanus, 1827) and to a lesser extent goats (*Capra aegargrus* Erxleben, 1777), which browse the understorey and leaf litter. The activity of these animals destroys or highly modifies the habitat of native taxa such as *Placostylus* by reducing litter mass and changing the microclimate at ground level (raising temperatures, decreasing humidity, and increasing exposure to light). Forest destruction and its modification are thus considered the main factors contributing to the decline in New Caledonian *Placostylus*. Some populations are already extinct, others on the verge of extinction. The risk of extinction is particularly acute for *P. porphyrostomus* which inhabits the sclerophyllous forests. Among rainforest inhabitants, *P. caledonicus* is known only from one extant population, and *P. eddystonensis* is thought to be already extinct.

Over-collection for human consumption

Placostylus are an important part of the Melanesian culture and tradition on the Isle of Pines, and are used for various purposes including food and jewellery as well as for their medicinal properties (e.g. a snail stock is drunk by pregnant women to improve lactation). It is also a traditional food: today in some families, boiled snails are still eaten two or three times a week and represent an important source of protein. *Placostylus fibratus* and the sympatric species *P. porphyrostomus* are both collected and consumed by Kuniés (Pöllabauer 1994; Lepoutre 1999; Brescia 2004, 2005). *Placostylus fibratus*, the largest and most widely distributed of the New Caledonia *Placostylus*, is the species most favoured for human consumption. However, only those

populations on the Isle of Pines are sufficiently abundant to sustain harvesting, primarily by the Kunié people. The smaller *P. porphyrostomus* is only consumed by locals and is not marketed commercially.

Placostylus fibratus progressed from a gastronomic speciality in the Isle of Pines to a delicacy in Nouméa (the New Caledonian capital) around 1950 (Pisier 1985). The export to Nouméan restaurants and supermarkets continued until 2000 when the sale of *P. fibratus* on the mainland was prohibited by the authority in charge of the environment in a bid to reduce the number harvested. Snail-harvesting for consumption from the natural populations on the Isle of Pines progressively increased and reached 48 tonnes (about 700,000 snails) in 1993 (Pöllabauer 1995) and the export of the snails became an important economic activity for the island inhabitants, assessed at US \$180,000 annually. About 70 Kunié families representing approximately 250 people were involved in harvesting the resource (Lepoutre 1999). Snails were collected mainly by local women. They were then bought from the collectors by two main preparers of the snails (ca. US\$ 0.30 per snail), and cooked like European *Helix* 'à la Bourguignonne' (with butter, garlic and parsley). Only adult *Placostylus* were collected for consumption, that is to say, snails with a thick aperture lip (> 4 mm).

During the last decade, at the request of Kuniés worried about the growing scarcity of the resource, a variety of scientific studies have been undertaken to improve the knowledge of *Placostylus* and to develop a sustainable management regime (Pöllabauer 1995, 2002; Brescia 1997, 1999, 2000, 2001, 2002, 2003, 2004, 2005; Brescia *et al.* 1998). A survey on the Isle of Pines was conducted from 1995 to 2004 to estimate the status of the *Placostylus* resource in the wild. Each year, *Placostylus* were searched for in about 140 randomly located, 100 m² quadrats. New quadrats were established for each survey and searched only once. In 2004, the total population of *P. fibratus* (adults and juveniles) on Isle of Pines was estimated at 4.6 ± 0.6 million (Brescia 2004). Snails of marketable size represented nearly 60% of the population; the remainder were mainly sub-adults. Preliminary results show that the population remained quite stable between 1993 and 2004 (Brescia 2005). Thus, the different control measures adopted during the period, such as setting-up of a collection period outside of which harvest was prohibited, and the prohibition of export out of Isle of Pines from 2001, appeared to have been effective at reducing the number of snails collected annually and thus stabilising the populations.

To assess the annual harvest of adult *Placostylus* from the Isle of Pines, regular surveys of Kunié families, restaurants, and the two main snail processors have been conducted regularly since 1993 (Pöllabauer 2002; Brescia 2004, 2005). The results suggest that since the 2001 prohibition of export, the number of *Placostylus* collected from the forests on the Isle of Pines has been only about half of that collected during the period 1995–2000 which Pöllabauer (2002) estimated as 200,000 to 250,000 snails harvested annually. Harvesting from the natural populations since 2003 is estimated to be around 120 000 adult *P. fibratus* per annum. In 2003, 60,200 snails were marketed in restaurants of Isle of Pines. The annual collection by Kuniés for their own use was about 50,000 snails, with *P. fibratus* accounting for about 99% of the harvest and *P.*

porphyrostomus making up the remaining 1%.

Thirty to fifty years ago *P. porphyrostomus* were also harvested from sclerophyllous forests on the mainland, largely for consumption, but this has now largely ceased. However, recently (2002), during a two day search, more than 200 *P. porphyrostomus* were collected for food by local residents from a 270 ha patch of sclerophyllous forest (a classified priority area), where the total snail population is evaluated at about 60,000 (Brescia and Pöllabauer 2005). The collectors were unaware of the status of the species on the mainland. Every now and then, reports of collections of the giant form of *P. fibratus* from the south of the mainland, and of the dwarf form of *P. fibratus* on the Loyalty Islands (particularly from Maré) are made (F. Brescia pers. obs.). On these occasions, the snails appeared in the local markets.

Pig and rodent predation

Introduced mammals such as feral pigs and rodents appear to also contribute to the decline of New Caledonian *Placostylus* populations. As well as destroying native vegetation and disturbing the leaf litter, feral pigs are predators of *Placostylus* (Pöllabauer 1995; Brescia 2004, 2005; Brescia and Pöllabauer 2005). They eat both large juveniles and adults. On the Isle of Pines, Brescia (2001) observed that in areas where pigs are present, *Placostylus* abundance was only half that of areas without pigs. Pigs are locally abundant on the Isle of Pines but their effects are even more important in sclerophyllous forests of the mainland since *Placostylus* populations there are restricted to small and isolated patches and therefore more vulnerable to this pressure.

In sclerophyllous forests, it has been found that rodents (Polynesian rats *Rattus exulans* (Peale, 1848), ship rats *R. rattus* (Linnaeus, 1758), and house mice *Mus musculus* (Linnaeus, 1758) also eat juvenile *Placostylus* up to 5 cm shell height (Brescia and Pöllabauer 2005). Rodent-damaged *Placostylus* shells are easily identified as rodents typically remove a broad spiral band of shell from one or more whorls starting from the aperture lip (Figure 3). Pig-damaged shells are also usually easily recognised since they typically break the shells into several large pieces. In 2004, during a search of thirty two 10 m x 10 m quadrats in three patches of sclerophyllous forest, 17 adults of *P. porphyrostomus* and 12 large juveniles and sub-adults were found along with 130 empty shells that showed evidence of rodent predation (Brescia and Pöllabauer, 2005). Similarly, Brescia (2007) found that in a mark-recapture study in sclerophyllous forests, up to 81% of shells on the ground in 20 m x 20 m permanent quadrats had been predated by rodents. On both the Isle of Pines and in the sclerophyllous forests, piles of up to 100 empty rodent-damaged shells are frequently found in rat caches. Rodent-damaged *Placostylus* shells are often more abundant than similarly damaged shells of the invasive giant African snail *Achatina fulica* suggesting a possible preference for the native snails. Mice have been recorded eating entire *Placostylus* egg clutches under semi-natural captive conditions on the Isle of Pines (Brescia 2004). Thus rodents appear to be potentially very harmful to *Placostylus* populations as they systematically eat eggs, hatchlings and juveniles which compounds the already high natural mortality rates of hatchling and juvenile size classes. The combined effect may greatly reduce recruitment to adult size.

In New Zealand, predation by introduced pigs, rodents, and birds has also been implicated in the decline of the *Placostylus* species there, along with habitat destruction and modification by farming and burning (Penniket 1981; Parish *et al.* 1995; Sherley *et al.* 1998).



FIGURE 3. Rodent-damaged *Placostylus* shells are easily identified by the broad spiral band of shell removed from one or more whorls.

Other threats

In 1972 the herbivorous giant African snail *Achatina fulica* (Achatinidae) was introduced to New Caledonia. Since then, it has become a pest in agricultural areas and a potential competitor of *Placostylus* in native forests. In response, as has occurred elsewhere in the Pacific, two carnivorous land snails, *Euglandina rosea* (Férussac, 1821) and *Gonaxis quadrilateris* Preston, 1910, were introduced in 1974 as biological control agents for African snails. Only *E. rosea* has established in New Caledonia but its distribution remains very localised (Maré Island and some northern areas of the mainland). Neither *E. rosea* nor *G. quadrilateris* are specialist predators of the African snail (Clarke *et al.* 1984; Griffiths *et al.* 1993), and in Hawaii their introduction was blamed for the extinction of several arboreal native snail species (Hadfield and Miller 1992). Gargominy *et al.* (1996) consider that these two species are likely to be significant threats to the native New Caledonian malacofauna. *E. rosea* may already have been responsible for the decline of some *Placostylus* populations in the far north of New Caledonia and Maré Island since where *E. rosea* has established the *Placostylus* populations have become locally extinct (pers. obs.).

Since the giant African snail and *Placostylus* share the same microhabitat, it is also possible that competition may also adversely affect *Placostylus* populations, but this hypothesis has not yet been directly tested.

Pöllabauer (1995) suggests that on the Isle of Pines, the presence of an indigenous carnivorous snail *Ouagapia inaequalis* (Pfeiffer, 1854) may further threaten *Placostylus* recruitment. She frequently observed up to 2–3 of these egg predators within *Placostylus* egg clutches, and noted that they have the potential to destroy all the eggs in a clutch. Brescia (2001) recorded a predation rate on clutches of 56% (n=42) on the Isle of Pines. On average, 4.6 ± 2.7 *O. inaequalis* were present per clutch in this survey.

The little fire ant, *Wasmannia auropunctata* (Roger, 1863), was recorded for the first time in New Caledonia in 1972 and has subsequently spread rapidly and invaded a wide array of habitats on the mainland, the Isle of Pines, and the Loyalty Islands. It is now found in both rainforest and sclerophyllous forest. It has been shown that when the little fire ant is present, a disruption of the native litter ant fauna and herpetofauna occurs in both types of New Caledonian forest (Jourdan *et al.* 2001). Nevertheless, as far as *Placostylus* are concerned, observations in the field on the Isle of Pines and in sclerophyllous forest suggest that little fire ant may have a net positive impact by controlling ground beetle (Carabidae) populations which are known predators of landsnails, or by influencing the spatial distribution of rodents. As evidence, we have generally found juvenile *Placostylus* in higher abundance where these ants are also present, though it is possible that little fire ants and juvenile *Placostylus* have similar habitat preferences and this positive association is an incidental consequence.

Conservation

Legal aspects

In 1994, a law was passed by the South Province Assembly of New Caledonia (Délibération 50–94/APS) that regulated the collection and the transportation of *P. fibratus* on the Isle of Pines. It became illegal to collect snails from 1st May to 30th September (during the breeding season), and illegal to transport live snails out of the Isle of Pines at any time (only cooked snails could be sent to restaurants and supermarkets on the mainland).

In 2000, the Assembly revised the law (Délibération 26-2000/APS), adding an amendment that allowed the collection of *Placostylus* throughout the year on the Isle of Pines but the prohibition of export to the mainland became applicable to both live and cooked snails. Cooked snails from the Isle of Pines thus could only be eaten in restaurants and by locals on the island but not at all on the mainland. As noted previously, this reduced the number of adult *Placostylus* collected on the island two-fold (to around 100,000 snails per year). No restrictions currently exist on the collection of *Placostylus* on the New Caledonian mainland.

Captive breeding

In parallel with passing of laws that control the numbers of *Placostylus* harvested from the wild, the Institut Agronomique Néocalédonien (IAC) has been actively developing farming methods. Captive breeding of snails may help to allow the exploitation of the resource to continue (a topic of great concern for inhabitants of Isle of Pines) by supplementing or replacing the harvest from the wild, as well as facilitating the preservation of natural populations. Successful farming of snails may also enable the re-stocking of small populations of *Placostylus* in areas where they are now rare or extinct.

A successful farming method has now been developed for *P. fibratus* following many years of trials (Brescia, 1997, 1998, 1999, 2000, 2001; Brescia *et al.* 1998). The initial attempts were not encouraging and it appeared that these snails were going to be very difficult to maintain in captivity.

Salas *et al.* (1997) recorded a 90% mortality rate of hatchling snails, a very slow growth rate of juveniles, a very high mortality rate (nearly 70%), and almost no breeding in captive snails. However, studies of *Placostylus* ecology and behaviour in natural conditions and further studies in captivity under semi-natural and regulated conditions enabled us to significantly improve our understanding of the snail's needs. This led to refined handling methods through systematic testing of alternative farming methods.

Placostylus are now maintained in plastic boxes with an artificial substrate of coco-fibre compost supplemented with calcium carbonate. Humidity is maintained by daily watering. A thick layer of leaves (papaya, banana) is used as a cover to maintain moisture, to reduce the light reaching the snails, and to limit the climbing behaviour of hatchlings. An artificial diet has been developed as a substitute to the natural diet of decaying forest leaves. Different artificial diets were tested and the growth and reproduction performance measured. Eventually, we decided to vary the diet to suit the different age classes of snails. Adult and juvenile snails are fed a dry mix of cereal flour (80% of dry weight) supplemented with calcium carbonate (20%). Hatchlings are fed a more energy-rich powder of cereal flour (50%) and calcium carbonate (20%) supplemented with milk powder (30%). A large number of feeding dishes and water-troughs are set out in different areas of the enclosures to improve access for these relatively sedentary snails.

To maximise the reproductive productivity, adult snails are collected from the forest during the breeding season and maintained in captivity under the conditions described above, with a stocking rate limit of 5 kg/m². At the start of these trials in 1995, only about 0.16 egg clutches per adult per year was obtained. Now, we achieve more than 10 times this (1.5 to 2.7 egg clutches per adult per year). About 72% of adult snails lay at least one clutch per year in captivity. Each day, egg clutches are collected from the enclosures and placed in a nursery on a substrate of humid coco-fibre/soil mix. Hatching under these conditions occurs after 10 to 45 days. Survival of the hatchlings to one month in the nursery now approaches 70% (in earlier farming attempts it was only 10%); and 68% of juveniles now survive to eight months. The best growth rates of juveniles are obtained when the stocking rates are maintained at a low level, around 1.5 to 2.0 kg/m². Adult size (and sexual maturity) in captivity is reached in two years under these conditions, compared with five years in the wild (Pöllabauer 1995).

In New Zealand, the techniques needed for successful captive breeding have not yet been developed (Parrish *et al.* 1995). However, researchers at Massey University have managed to keep a small number of *Placostylus* adults in captivity until they laid eggs which were then successfully raised to adulthood (Stringer and Grant 1992).

Utility for conservation

It is now possible to produce New Caledonian *P. fibratus* and *P. porphyrostomus* en masse in captivity. This farming method has also been shown to work for several other New Caledonian *Placostylus* species (Brescia and Pöllabauer 2004, 2005). Growth rates have doubled since the earlier rearing trials but the relatively high cost of this method of production needs to be reduced in order for commercial farming to be viable. The next step in achieving

this economy may be to develop extensive or semi-extensive methods with enclosures set directly in the forest. We are currently trialling the transfer of the farming method to local Kuniés and adapting it to suit the sociological and economic realities of the Isle of Pines.

The supplementation of threatened New Caledonian *Placostylus* populations using captive rearing is now feasible and this may provide some security against extinction. Accordingly, snails from some of the most threatened populations of the sclerophyllous forests are now being maintained in captivity to complement the on-going management of natural populations. Conservation trials on re-introduction, supplementation and translocation are now conceivable using animals from captive breeding programmes. However, there is a need to demonstrate the subsequent survival of released snails in the wild. Equally important, is the development of a strategy and operational plan that addresses and maintains the genetic integrity of wild populations. Caution must be exercised before snails are released into the wild to make sure that the existing genotypes are not swamped with new introduction of potentially unsuited genotypes sourced from elsewhere.

Research needs and conservation recommendations

Since 1994, three New Caledonian *Placostylus* species —*P. eddystonensis*, *P. fibratus* and *P. porphyrostomus* have been registered as Vulnerable on the Red List of IUCN (IUCN 2006) but a revision now seems warranted. *Placostylus bondeensis* and *P. scarabus* have never been evaluated and thus are not listed. Taking into account the small geographic range of these species (less than 100 km², in some cases restricted to a single locality), the population declines evident due to loss of native forests (99% for dry forest and more than 70 % for humid forest), and the severe fragmentation of many of these populations, *P. caledonicus*, *P. bondeensis*, *P. scarabus* and *P. eddystonensis* should be revised to Critically Endangered. The status of *P. fibratus* should also be changed to Endangered, given the estimated population decline due to the habitat degradation and the levels of exploitation and other factors implicated in the population decline.

No recovery plan currently exists for any New Caledonian *Placostylus*. To develop such a plan, further research on the predation, population dynamics and genetic differentiation between populations and species is a priority.

The management of *Placostylus* in sclerophyllous forests to prevent further extinction of the most distinctive races or morphs is urgently needed. The conservation of existing colonies in the wild will require fencing to protect the snails from pigs and the habitat from browsing by introduced rusa deer. Some re-vegetation and restoration of dry forests to enhance the habitat for snails will also be helpful. The maintenance and amplification of the most threatened races in captivity must also be pursued and investigations into the possibility of translocations and population supplementation should continue. The monitoring of population trends of selected populations will then be needed to assess the success of these different management strategies.

There is a need for further research to expand our knowledge on the status of extant populations, and enable the identification of suitable habitat for the establishment of new

populations to enhance protection of critical areas. Rodent control programmes at priority key locations should assist the persistence and recruitment rates of remnant snail populations. Research into competition for food and habitat with the introduced giant African snail would also be useful, especially in areas where rodents are being controlled.

Further scientific collaboration between New Zealand and New Caledonia will be of great value for the conservation of the genus in both countries and on neighbouring islands. On the Isle of Pines, the monitoring of natural population stocks of *P. fibratus* over the whole island should be continued. The total annual harvest of adult snails for local consumption by Kuniés and for the market should continue to be measured and depending on the results, further regulation may be necessary. The ecological studies initiated by Brescia and Pöllabauer (Brescia 2004, 2005; Brescia and Pöllabauer 2004, 2005) on population dynamics through the recording of recruitment, fecundity, longevity and mortality and the loss of snails from rodent and pig predation will enhance our understanding of population trajectories. The ultimate plan for the conservation of *Placostylus* on the Isle of Pines will depend on the integration of all these data in a Population Viability Analysis (PVA), allowing predictions to be made of whether the population will remain viable under various harvesting scenarios. This is a high priority for the agencies in charge of the environment in their quest to develop regulatory measures that will achieve a sustainable use of the resource and to protect the species and the economic potential for Kuniés.

Environmental education aimed at Kuniés on the Isle of Pines, and land owners on the mainland where patches of dry forest remain should continue, advocating the necessity of protecting *Placostylus* snails as part of a natural heritage and/or an economic resource. Demonstrating the cultural meaning and economic importance of *Placostylus* to local communities would probably be more successful if the Kuniés were directly involved in recovery planning and actions. This kind of community-led action, if successful, could provide an exemplary case and stimulate further recovery efforts for other threatened New Caledonian invertebrates.

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