

High-resolution stable isotope profiles from shells of the land snail *Placostylus* reveal contrasting patterns between snails originating from New Zealand and New Caledonia

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ABSTRACT: The stable oxygen ($\delta^{18}\text{O}_{\text{shell}}$) and carbon ($\delta^{13}\text{C}_{\text{shell}}$) isotope ratios retrieved from the carbonate shell of terrestrial gastropods can be used as an environmental proxy and are thought to reflect dietary composition and ambient climatic conditions (e.g. precipitation amount, humidity, temperature). Here, we generate high-resolution isotopic profiles of nine modern land snails of the genus *Placostylus*, collected from two locations in New Caledonia and one location in New Zealand. We found that snails from New Zealand had, on average, higher $\delta^{18}\text{O}_{\text{shell}}$ values than their counterparts in New Caledonia, which surprisingly runs counter to the expected relationship based on the isotopic composition of rainwater between these two regions. Specimens from New Caledonia exhibit ephemeral decreases in their $\delta^{18}\text{O}_{\text{shell}}$ values, which could be linked to extreme precipitation events in this region, while snails from New Zealand have less variation in their $\delta^{18}\text{O}_{\text{shell}}$ values. Snails from New Zealand had, on average, slightly higher $\delta^{13}\text{C}_{\text{shell}}$ than their counterparts in New Caledonia, but a large difference in carbon isotopes was sometimes observed between snails collected at the same location. Most snails exhibit a temporal trend in their $\delta^{13}\text{C}_{\text{shell}}$ values, indicating potential shifts in diet through to maturity.

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KEYWORDS: Carbonate shell; *Placostylus*; southwest Pacific; stable isotopes; terrestrial gastropods

Introduction

Quantitative reconstructions of past climate rely on the use of climate proxies, where the physical or chemical properties of an archive are used to infer past environmental conditions (Evans et al., 2013). Biological archives from accretionary organisms, including skeletal carbonate produced by terrestrial and marine molluscs, provide a snapshot of the prevailing climate conditions under which the organism grew (Apolinarska et al., 2015; Jones and Quitmyer, 1996). Fossil land snails, in particular, have a wide range of applications to palaeoclimatic and palaeoenvironmental studies. Modern land snails have a broad geographic distribution and their shells are usually well preserved in Quaternary sediments (Goodfriend, 1992; Leng and Lewis, 2016). Taxonomic analyses of community assemblages have been used to produce qualitative palaeoenvironmental reconstructions (Brook, 1999a, 1999b; Moine et al., 2002), and analyses of chemical properties of fossil shells can provide quantitative proxies of past climate conditions (Goodfriend, 1992). Stable oxygen ($\delta^{18}\text{O}_{\text{shell}}$) and carbon ($\delta^{13}\text{C}_{\text{shell}}$) isotope composition comprise the most well understood geochemical properties of snail shells (Yanes et al., 2009). These isotope ratios can be used as proxies for past climate and provide insights into the diet of the organism, which can in turn provide insights into past vegetation assemblages (Gu et al., 2009; Stott, 2002).

The $\delta^{18}\text{O}_{\text{shell}}$ values obtained from snail carbonate are thought to mainly reflect the $\delta^{18}\text{O}$ signature of the water in the local environment, which is in turn controlled by a range of climatic factors (Fig. 1; Balakrishnan and Yapp, 2004; Baldini et al., 2007; Goodfriend et al., 1989; Goodfriend and Ellis, 2002; Lécolle, 1985; Yanes et al., 2017; Yapp, 1979). Correlations between climate variables and $\delta^{18}\text{O}_{\text{shell}}$ enables their use as a quantitative proxy for a range of climatic variables. However, the relationships between isotopic data and different environmental variables are spatially heterogeneous, inhibiting the application of a universal relationship (Yanes et al., 2019). The calcium carbonate of snail shells is produced by a precipitation reaction which takes place in the mantle (pallium) of the organism, with the oxygen component of the shell derived from the body water of the snails. In theory, $\delta^{18}\text{O}_{\text{shell}}$ is therefore controlled by the $\delta^{18}\text{O}$ of snail body water, in addition to the temperature at which the precipitation reaction takes place (Fig. 1; Urey, 1947). Flux balance models hypothesise a strong relationship between relative humidity and $\delta^{18}\text{O}_{\text{shell}}$ (Balakrishnan and Yapp, 2004). This has been confirmed in some empirical settings (Balakrishnan et al., 2005b; Zaarur et al., 2011) but, again, not universally (Magaritz et al., 1981). Studies investigating $\delta^{18}\text{O}_{\text{shell}}$ data from across a range of locations with significant geographical or elevation gradients have confirmed that $\delta^{18}\text{O}_{\text{shell}}$ generally follows the trend of oxygen isotopes in local precipitation ($\delta^{18}\text{O}_{\text{precip}}$), with varying relationships towards precipitation or

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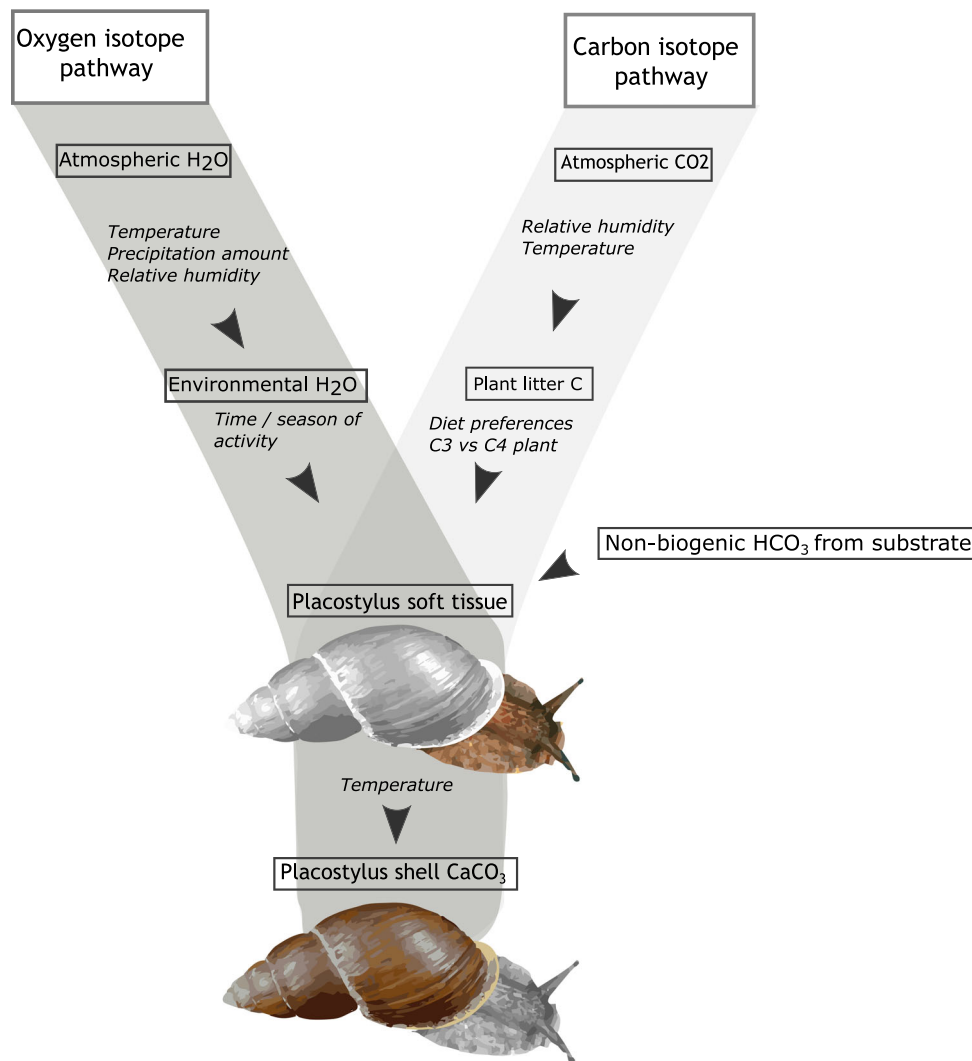


Figure 1. Schematic of the potential influences on final carbon and oxygen stable isotope composition of *Placostylus* shell. Pools of isotopes are framed, captions in italics indicate parameters affecting the isotope ratios at each step of the fractionation process. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3536)]

temperature (Bao et al., 2020, 2019; Amy L. Prendergast, Stevens, Barker, O'Connell 2015; Yanes et al., 2009).

The $\delta^{13}\text{C}_{\text{shell}}$ values of terrestrial gastropods are thought to be primarily influenced by snail diet, and in herbivorous land snails the $^{13}\text{C}/^{12}\text{C}$ shell ratio is correlated to the $^{13}\text{C}/^{12}\text{C}$ ratio found in dietary plants (Fig. 1; Balakrishnan et al., 2005a; Bao et al., 2018; Bing et al., 2012; Goodfriend, 1992; Goodfriend et al., 1989; Goodfriend and Magaritz, 1987; Yapp, 1979). Due to differences in metabolic pathways, C4 plants (e.g. tropical grass) typically have a higher $\delta^{13}\text{C}$ than C3 plants and therefore higher $\delta^{13}\text{C}_{\text{shell}}$ values are interpreted to reflect higher relative C4 plant intake when the snail's diet is mixed (Balakrishnan and Yapp, 2004; Wang et al., 2019). In non-tropical settings and situations where the diet of the snail does not include C4 plants, differences in $\delta^{13}\text{C}_{\text{shell}}$ can reflect differences in water use efficiency of the plants ingested by the snail (Diefendorf et al., 2010; Tibby et al., 2016). Changes in $\delta^{13}\text{C}_{\text{shell}}$ over large geographical areas representing a partition of plant community assemblages have been demonstrated (Colonese et al., 2014; Prendergast et al., 2017; Yanes et al., 2009), but high-resolution shell analyses have also revealed that changes in $\delta^{13}\text{C}_{\text{shell}}$ values can be associated with ontogenetic changes in snail diet (Baldini et al., 2007). In controlled experiments, positive correlations are observed between $\delta^{13}\text{C}_{\text{shell}}$ values and diet composition, with higher $\delta^{13}\text{C}_{\text{shell}}$ values for land snails fed with C4 plants (Metref et al., 2003; Stott, 2002). Aside from dietary carbon, other carbon sources for carbonate shell include

atmospheric CO₂ and direct ingestion of non-biogenic carbonate matter such as limestone (Yanes et al., 2012). It is not entirely clear how all these sources of carbon impact $\delta^{13}\text{C}_{\text{shell}}$ values. Studies relying on radiocarbon (^{14}C) have demonstrated the proportion of dietary carbon present in the carbonate shell of the snail seems to vary between species of snail or geographical area (Bing et al., 2012; Goodfriend and Magaritz, 1987; Pigati et al., 2010). Changes in $\delta^{13}\text{C}_{\text{shell}}$ values in fossil snails have the potential to provide insights about palaeodietary composition that can be used to infer changes in past plant community assemblages and climatic conditions (Balakrishnan et al., 2005a; Padgett et al., 2019; Yanes and Romanek, 2013). However, interpretations of $\delta^{13}\text{C}_{\text{shell}}$ remain complex and extending our contemporary understanding to fossil material requires extensive studies of modern specimens from the same geographical region.

The stable isotopic composition of land snails can either be obtained from whole-shell analyses or from serial samples along the axis of growth. The former reflects an average isotopic value over the lifespan of the snail, while the latter generates a high-resolution profile of isotopic variability that can permit interrogation of environmental relationships at a sub-annual resolution (Goodfriend, 1992; Yanes et al., 2012). In India, for example, high-resolution $\delta^{18}\text{O}_{\text{shell}}$ series from the invasive giant African snail, *Lissachatina fulica*, have been used to characterise details about monsoon season precipitation (Ghosh et al., 2017). In the Bahamas, high-resolution $\delta^{18}\text{O}_{\text{shell}}$ records of snails from the

genus *Cerion* are linked to decreased $\delta^{18}\text{O}_{\text{precip}}$ during the months with the highest rainfall (Baldini et al., 2007). Differences in $\delta^{18}\text{O}_{\text{shell}}$ values between snail species have received little attention, but comparisons of sympatric species indicate isotopic composition can differ significantly for snails of different ecology, size and ethology, with larger land snails showing consistently higher $\delta^{18}\text{O}_{\text{shell}}$ values than their smaller counterparts (Yanes et al., 2017).

To achieve reliable inferences about the past from fossil snail shell stable isotopes, analyses of modern specimens that compare stable isotopic composition with local environmental variability are necessary (Yanes et al., 2019). Here, we provide the first modern land snail stable isotope data ($\delta^{18}\text{O}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{shell}}$) for two regions of the southwest Pacific (New Zealand and New Caledonia). A protocol is developed to sample high-resolution isotopes from giant snail shells of the genus *Placostylus*. The stable isotope signal is compared with climatic variables, and differences in isotope composition between snails from two contrasting geographic locations and between sympatric species of snails are investigated.

Materials and geographic setting

Distribution and ecology of *Placostylus*

Placostylus is a genus of large terrestrial land snail endemic to the southwest Pacific. Extant species are found in the Solomon Islands, Fiji, Vanuatu, New Caledonia, Lord Howe Island and the north of New Zealand (Neubert et al., 2009). Quaternary fossil snail shell records are particularly abundant in the north of New Zealand (Brook, 1999b), and also exist at both Grande Terre and the Isle of Pines in New Caledonia (Neubert et al., 2009). Here, we focus on three species: *P. fibratus*, *P. porphyrostomus* and *P.*

ambagiosus. The ecology of these species has been extensively studied (Brescia et al., 2008; Parrish et al., 2014; Stringer et al., 2014). All three species are primarily nocturnal, usually burying themselves in leaf litter during the warmer daytime hours. Behavioural studies demonstrate that the New Caledonia species *P. fibratus* is most active during the cold season (May to October) and has a more limited activity (including reproduction) during the warmer wetter season (December to March) (Brescia et al., 2008). All three *Placostylus* species are believed to feed on fresh leaf litter, with their specific diet composition differing between geographical regions (Brescia et al., 2008; Parrish et al., 2014). Dispersal is very low based on tracking of individual New Caledonian *P. fibratus* and *P. porphyrostomus* found under the same tree or shrub for more than 12 months (Brescia et al., 2008). Similarly, *P. ambagiosus* in New Zealand tends to stay within the same area for most of its life (Stringer et al., 2018).

Geographical setting and sample collection

We sampled nine specimens of *Placostylus* from across three localities within two geographical regions in the southwest Pacific (New Zealand and New Caledonia; Fig. 2A, Table 1). The French territory of New Caledonia is comprised of several tropical islands located east of Australia (Fig. 2A, B). Land snails were live-collected from two locations in New Caledonia: Gadji (Fig. 2B, -22.5607°N , $167.4304805^{\circ}\text{E}$) on the Isle of Pines, and Forêt Nord (Fig. 2B, $-22.093459^{\circ}\text{N}$, $166.700256^{\circ}\text{E}$) on Grande Terre. The specimens from Gadji ($n=4$) were collected in April 2015 and belong to the species *P. fibratus* ($n=2$) and *P. porphyrostomus* ($n=2$). The specimens from Forêt Nord ($n=2$) belong to the species *P. fibratus* were collected between 2007 and 2012. The shells from New Zealand ($n=3$), belonging to the species *P. ambagiosus*, were donated by the Museum of New Zealand Te Papa Tongarewa

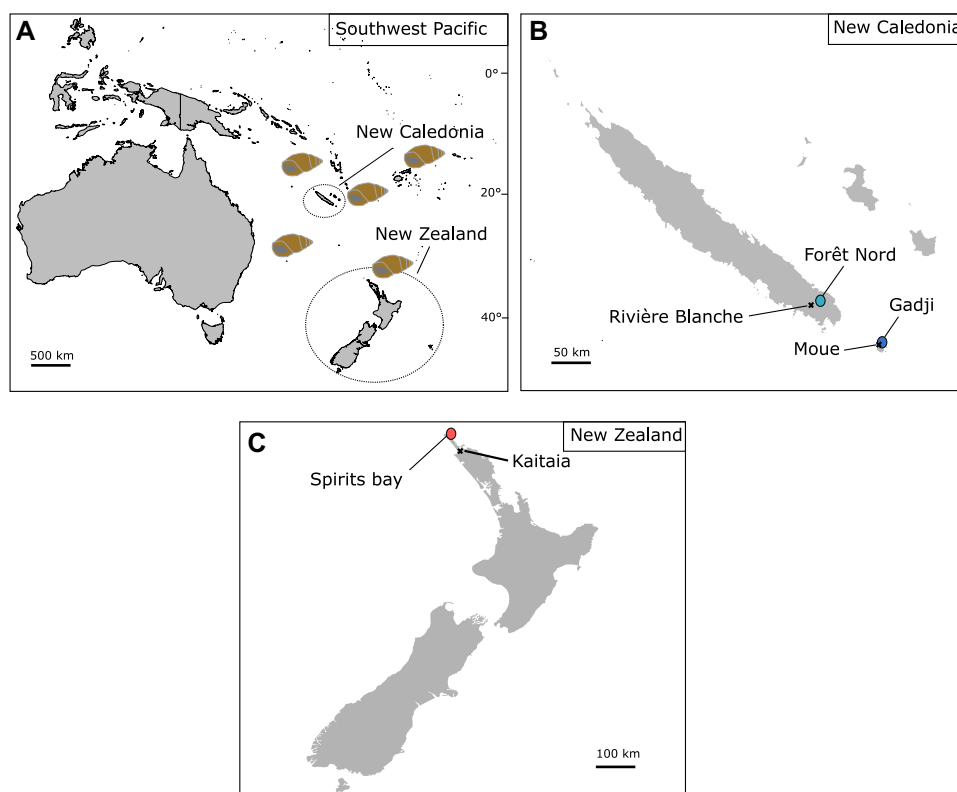


Figure 2. (A) Map of the southwest Pacific, indicating the geographical areas corresponding to New Zealand and New Caledonia, and the extant home range of *Placostylus* species. (B) Map of New Caledonia with sampling locations of *Placostylus* shells (coloured circles), and sampling location of meteorological data (black crosses). (C) Map of New Zealand with sampling locations of *Placostylus* shells, and sampling locations of meteorological data (black cross). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Table 1. Location and species information for the nine shells collected.

Shell ID	Species	Geographical region	Sampling site	Latitude (°N)	Longitude (°E)	Collection date
Forêt Nord 8-1 (FN81)	<i>Placostylus fibratus</i>	New Caledonia	Forêt Nord	-22.093	166.7003	2007–2015
Forêt Nord 8-5 (FN85)	<i>Placostylus fibratus</i>	New Caledonia	Forêt Nord	-22.093	166.7003	2007–2015
Gadji 11 (GA11)	<i>Placostylus porphyrostomus</i>	New Caledonia	Gadji	-22.561	167.43	April 2015
Gadji 13 (GA13)	<i>Placostylus porphyrostomus</i>	New Caledonia	Gadji	-22.561	167.43	April 2015
Gadji 04 (GA04)	<i>Placostylus fibratus</i>	New Caledonia	Gadji	-22.561	167.43	April 2015
Gadji 08 (GA08)	<i>Placostylus fibratus</i>	New Caledonia	Gadji	-22.561	167.43	April 2015
New Zealand 1 (NZ1)	<i>Placostylus ambagiosus</i>	New Zealand	Spirits Bay	-34.434	172.892	1949
New Zealand 2 (NZ2)	<i>Placostylus ambagiosus</i>	New Zealand	Spirits Bay	-34.434	172.892	1949
New Zealand 3 (NZ3)	<i>Placostylus ambagiosus</i>	New Zealand	Spirits Bay	-34.434	172.892	1949

and were live-collected in 1949 in Piwhane (Spirits Bay), located in the northernmost part of the North Island (Fig. 2C, -34.4338°N, 172.89167°E).

Climatological setting and meteorological data

New Caledonia

The climate of New Caledonia is tropical and characterised by high precipitation rates, high temperatures and constantly high humidity. Monthly meteorological data from New Caledonia spanning 2005 to 2021 were provided by Météo France (Fig. 3). The meteorological station of Moue on the Isle of Pines (-22.5898°N, 167.4521°E) is closest to Gadji and the Rivière Blanche Station on Grande Terre (-22.1326°N, 166.7263°E) is closest to Forêt Nord. Three variables were gathered from these stations: monthly cumulative precipitation (mm, MP; Figs 3A and 2D), mean monthly air temperature (°C, MMT; Figs 3B and 2E) and monthly mean humidity (%; MMH; Fig. 3C, F). An annual climatology with averaged monthly values was calculated for each variable with 95% confidence intervals over the timespan covered by meteorological stations (Fig. 3). Collectively, these records suggest that the seasonal precipitation and temperature cycles are in phase with one another, with a wet and warm season (December–April) followed by a colder and drier season (May–November). An outlier analysis was run on the monthly cumulative precipitation data (Chen and Liu, 1993) to capture anomalously high months of precipitation within the timespan over which the snails were collected (2007–2015). This revealed four anomalously high precipitation months in Moue (March and April 2008, January 2011 and July 2013; Fig. 3) and only two in Rivière Blanche (March 2013 and July 2013; Fig. 3D). Here these months of very high precipitation did not obviously match with any records of historical tropical storms in the region from the International Best Track Archive for Climate Stewardship (IBTrACS) database, suggesting that sources of high precipitation months can be various in the region, and not necessarily related to extreme punctual events. Overall, Forêt Nord receives more rain than Gadji, both during extreme events and on a regular basis (Fig. 3A, D). MMT oscillates from 18°C to 26°C for both locations with a maximum in February and minimum around July–August. MMH is almost constantly above 75% for both locations, and slightly higher during warmer months (December–April).

In New Caledonia, the isotope composition of rainwater has only been investigated for a two-year time period on Lifou, an island northeast of the New Caledonian archipelagos (Nicolini et al., 2016). The lowest oxygen and hydrogen isotope ratios in precipitation were recorded during the wet season (December–April). This is consistent with studies of other tropical regions worldwide, which suggest that $\delta^{18}\text{O}_{\text{precip}}$ values fluctuate seasonally in response to changes in precipitation, with higher

oxygen isotope ratios found during drier months (Edirisinghe et al., 2017). The New Caledonia archipelago is also regularly affected by large tropical storm or cyclone events, which are associated with rainwater of low isotopic value $\delta^{18}\text{O}$ (Miller et al., 2006; Sánchez-Murillo et al., 2019). Here we estimated patterns of local monthly $\delta^{18}\text{O}_{\text{precip}}$ using the Online Isotope in Precipitation Calculator (OIPC), which incorporates oxygen and hydrogen isotope data from meteorological stations in a model that also uses latitude, longitude and elevation to predict the isotope composition of precipitation (Bowen et al., 2005). Results of the model indicates that the oxygen isotope ratios of precipitation at both locations in New Caledonia would be positively coupled with temperature and precipitation (Figs 3 and 4), with lower $\delta^{18}\text{O}_{\text{precip}}$ estimated for the cold and dry season (April–November). These results contradict the two-year $\delta^{18}\text{O}_{\text{precip}}$ data collected on Lifou, which had lower $\delta^{18}\text{O}_{\text{precip}}$ during the warm and wet season (December–April).

New Zealand

New Zealand climatology is complex due to its wide latitudinal spread and unique topography that interacts with prevailing westerly winds, giving rise to a myriad of microclimates (Sturman and Tapper, 1996). The nearest meteorological station to Spirits Bay is located in Kaitaia (-35.108°N, 173.258°E), about 100 km south of the location where snail shells were collected (Fig. 2C). Data obtained from this station span 1967 to 1985 and include monthly averages for four variables: MP (Fig. 5A), mean daily maximum air temperature (MMT_{max} ; Fig. 5B), mean daily minimum air temperature (MMT_{min} ; Fig. 5B), and mean 09:00h relative humidity (Fig. 5C). These data indicate a more temperate climate characterised by large diurnal temperature fluctuations that vary between a warm and dry summer season (December–March) and a cool and rainy winter season (June–August). Interannually, precipitation amounts are more consistent than in New Caledonia, and there was no month with an anomalously high precipitation rate. Between 1967 and 1985 MMT_{max} oscillated between 15 and 26°C and MMT_{min} oscillated between 5 and 15°C. Relative humidity is highest between May and August (around 90%) and lowest between October and February (below 80%).

The oxygen isotope composition of rainwater in New Zealand is influenced by the interplay between air masses derived from subtropical regions to the north, and subantarctic regions to the south. In addition, as in New Caledonia, northern New Zealand is sometimes subject to tropical storms in the form of extra-tropical cyclones, which occur with greatest frequency in February and March (Lorrey et al., 2014). While these storm systems occur on average about once per year, they are far less frequent than those that occur in the tropics, but can still bring heavy rainfall relative to normal amounts for the time of year. For the whole of New Zealand,

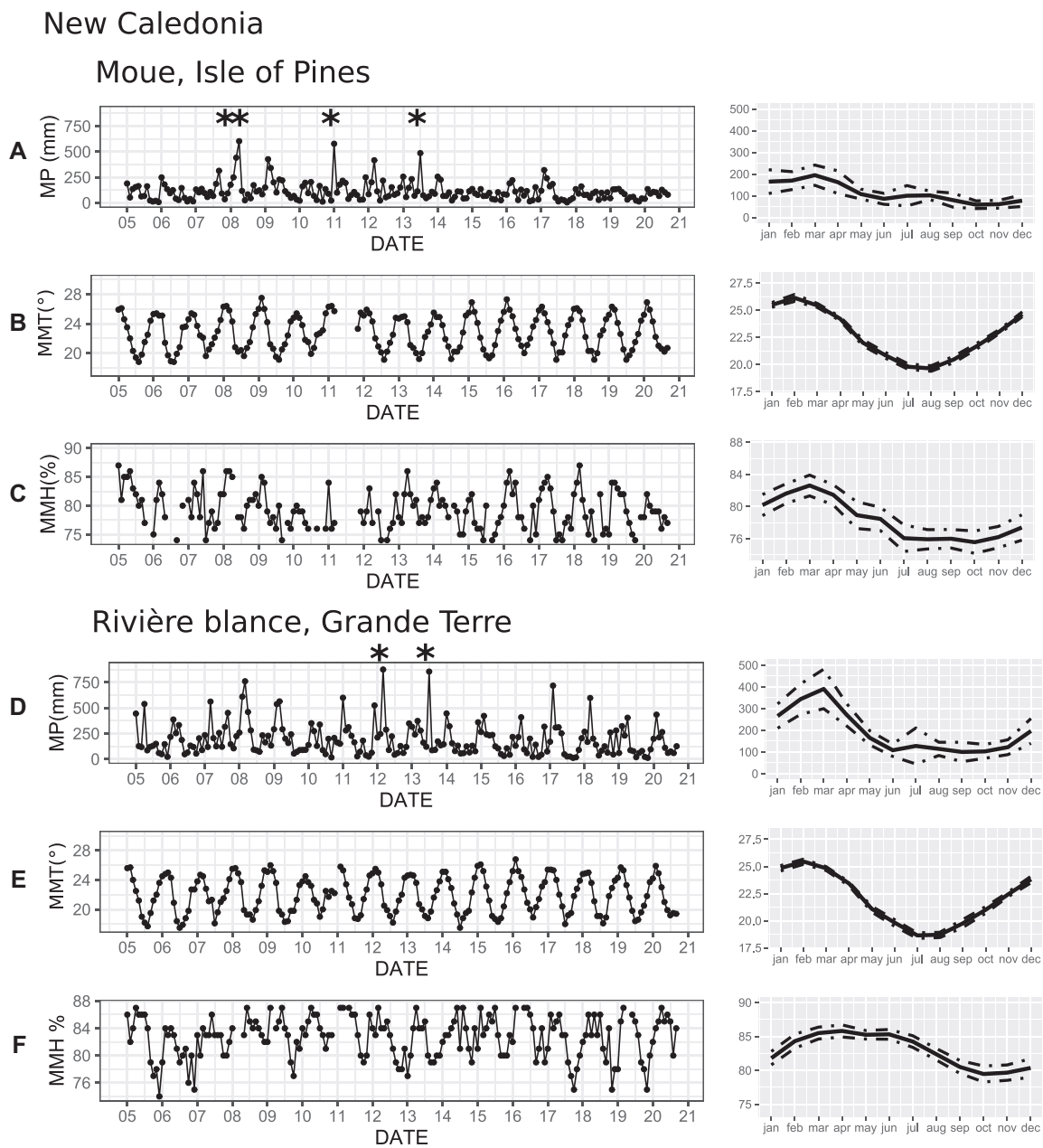


Figure 3. Meteorological (left) and one-year monthly averaged climatology (right) data for three variables of interest (monthly cumulative precipitation (MP), monthly mean temperature (MMT) and monthly mean humidity (MMH)) collected between 2005 and 2021 at meteorological stations close to Gadji (A-C) and Forêt Nord (D-F). Asterisks on top of monthly precipitation data indicate months with anomalously high precipitation rates. Dotted lines surrounding climatology plots indicate 95% confidence intervals for the variable of interest.

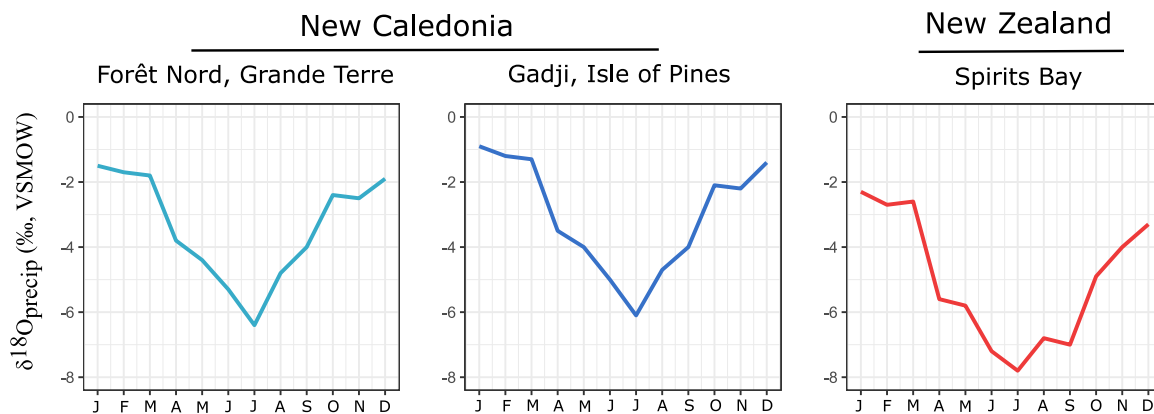


Figure 4. Model-estimated $\delta^{18}\text{O}$ (‰, VSMOW) in precipitation water of the three *Placostylus* sampling sites, as predicted by the OIPC. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

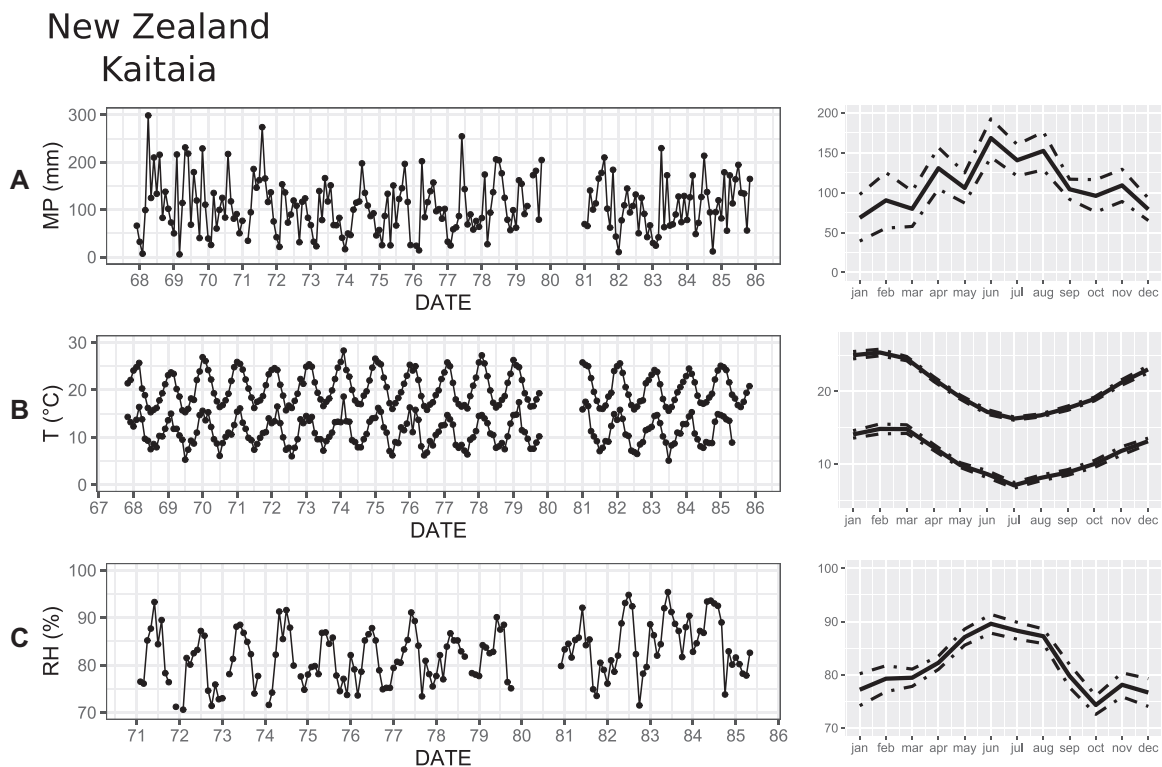


Figure 5. Meteorological (left) and one-year monthly averaged climatology (right) data for four variables of interest (monthly cumulative precipitation (MP), monthly mean of the daily maximum and minimum air temperature (T) and monthly mean 09:00h relative humidity (RH)) collected between 1967 and 1985 at Kaitaia. Dotted lines surrounding climatology plots indicate 95% confidence intervals for the variable of interest.

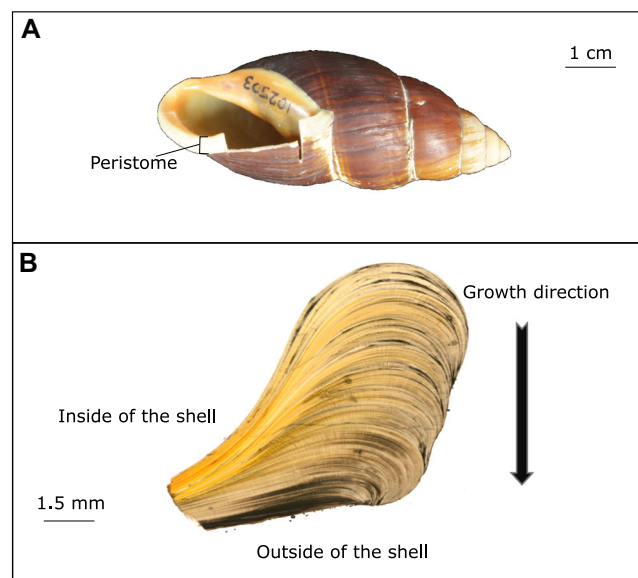


Figure 6. (A) *Placostylus ambagiosus* shell, with part of the peristome detached for isotopic sample analysis. (B) Transversal view of the peristome seen with a transmission light microscope, showing the carbonate growth lines produced as the peristome thickens throughout adulthood. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

only two stations have been incorporated into the Global Network for Isotopes in Precipitation (GNIP), one in Kaitaia and one in Invercargill. Current efforts are focused on improving the geographical coverage of sampling stations for isotopes in precipitation as well as the accuracy of predictive models (Baisden et al., 2016; McComb et al., 2019). Noticeably, the highest $\delta^{18}\text{O}_{\text{precip}}$ are observed at the Kaitaia station, close to where *Placostylus* snails live. Despite shortcomings for spatiotemporal coverage, we used the OIPC to estimate local $\delta^{18}\text{O}_{\text{precip}}$ in Spirits Bay (Bowen et al., 2005). Based on this model, $\delta^{18}\text{O}_{\text{precip}}$ would appear to be positively coupled with

temperature (Figs 4 and 5B) and negatively coupled with precipitation and relative humidity (Figs 4 and 5A, D), with the lowest $\delta^{18}\text{O}_{\text{precip}}$ values occurring during the winter season.

Methods

Shell structure and sampling approach

Placostylus snails produce large conical aragonitic shells ranging from 6 to 15 cm in length, with a dextral orientation (Fig. 6A).

Snails usually reach sexual maturity within three to five years. Once sexual maturity is complete, snail shell growth stops. However, the peristome (outer lip surrounding the aperture of the shell) keeps thickening at a rate roughly estimated to be between 0.1 and 0.4 mm/year for New Caledonian species (Brescia et al., 2008) and between 0 and 0.6 mm/year for New Zealand species (Stringer et al., 2014). Microscopic photography of the peristome region revealed the presence of carbonate growth lines ranging from the outer edge of the lip towards the shell (Fig. 6B). This part of the shell was targeted for sampling carbon and oxygen isotope variability through time, and the outermost layers of carbonate material are considered the most recent. All shells chosen for sampling were determined to be from adult (mature) snails, and sampling was restricted to the growth layers of carbonate material formed during adulthood.

For all specimens, the peristome was detached from whole shells using a circular saw and the cleaned shells were embedded in epoxy resin. Thick (500 μm) and thin (250 μm) sections were sliced from the epoxy mount using a Struer Accutom 50 mechanised thin section machine fitted with a wafer saw at the National Institute of Water and Atmospheric Research (NIWA) in Auckland, New Zealand. Thin sections were used for microscopic photography (Fig. 6B), while the thick sections were used for sampling. Carbonate samples were drilled along lines parallel to the growth lines found in the peristome. All carbonate samples were extracted from thick sections using a New Wave micromill (ESI) with a 250 μm wide drill bit and an even spacing between sampling lines of 200–215 μm . Approximately 150 μg of carbonate powder was collected for each sample using a scalpel blade and put in standard 0.2 ml plastic tubes. Carbonate samples were then weighed, acidified with phosphoric acid at 75°C and the evolved CO_2 subsequently analysed using mass spectrometers to quantify both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Four shells (FN8.1, FN8.5, GA11, GA13) were analysed using a MAT 25 mass spectrometer at the NIWA stable isotope laboratory in Wellington, New Zealand. The other five shells (GA04, GA08, NZ01, NZ02, NZ03) were analysed using Nu Instruments Horizon Continuous Flow IRMS (CF-IRMS) at the Mawson Analytical Spectrometry Services of the University of Adelaide. ResData are reported in delta notation (‰), relative to the Vienna PeeDee Belemnite (VPDB) standards for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Internal precisions were estimated by averaging the standard errors of six repeat measurements on the sample gas against reference gas. Across all samples the maximum value was 0.02. External precisions were estimated per run as the standard deviation of all standards measured alongside the samples, and had a maximum value of 0.07 across all runs. Ten replicates were realised at random across the samples analysed at the University of Adelaide and 19 replicates across the samples analysed at the NIWA stable isotope laboratory. Isolated data points with seemingly low or high values were systematically replicated. When replicated, the isotope values were averaged across replicates.

Statistical analysis

For both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, summary statistics were computed for each individual shell, including the mean, standard deviation, maximum and minimum values. To identify ontogenetic trends within each shell, simple linear regression models were fit, with the isotope ratio of interest as a response variable and the numbered sequential increment used as a numerical predictive variable. Positive linear relationships, as indicated by a positive coefficient of correlation values, signify trends toward higher stable isotope ratios later in the organism's life, while negative values imply lower isotope ratios towards the more recent outer layers.

Linear mixed models were used to compare shell isotope data ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) both between populations from different geographical areas and between species from the same location. The full dataset of nine shells was used to compare average isotope values between New Zealand and New Caledonia. A subset of this dataset containing six shells from New Caledonia was used to compare isotope values between the two locations in New Caledonia (Gadji and Forêt Nord). The four shells collected in Gadji from two different species were used as a dataset to study variations at a species level (*P. fibratus*/*P. porphyrostomus*).

Linear mixed models were computed using the lmer package (Bates et al., 2015) in R 4.0.4 (R Development Core Team, R., R Core Team, 2017) and were built with both $\delta^{18}\text{O}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{shell}}$ as a response variable, the shell ID as a random variable and either the geographical region or the snail species as a fixed parameter. In this context, variations in the slope value of fixed parameters can be interpreted as an average variation in isotope value between the regions or species of interest, while variation between shells is averaged around the intercept value of the model. We used likelihood-ratio tests between nested models to test whether adding geographical area or species of snail significantly improves overall model likelihoods, and generated *p*-values.

The $\delta^{18}\text{O}_{\text{shell}}$ obtained from the nine *Placostylus* whole shells were averaged and compared with climatic and geographic predictors using simple linear regression models in R 4.0.4 (R Development Core Team, R., R Core Team, 2017). Estimation methods of relative humidity and temperature were different between the meteorological stations of New Zealand and New Caledonia, with the temperature station in New Zealand only providing averaged values of maximum and minimum daily temperature estimates, and 09:00h relative humidity. Consequently, only annual precipitation (mm) could be compared with averaged $\delta^{18}\text{O}_{\text{shell}}$ values across the three sampling locations. In addition to this, $\delta^{18}\text{O}_{\text{shell}}$ values were compared with latitudinal position and $\delta^{18}\text{O}_{\text{precip}}$ (‰, Vienna Standard Mean Ocean Water (VSMOW)) as estimated by the OIPC.

Results

Shell $\delta^{18}\text{O}$

Across the entire dataset, $\delta^{18}\text{O}_{\text{shell}}$ values range between -5.3 and 0.39 ‰, with averaged shell values ranging from -3.24 to -0.84 ‰ (Table 2, Fig. 7). Individual oxygen isotope profiles exhibit a cusped pattern, characteristic of interannual growth in accretionary molluscs (Judd et al., 2018). This suggests that each stable isotope profile captures between one and three complete years of growth (Fig. 8). Specimens from New Zealand have, in general, higher $\delta^{18}\text{O}$ values and exhibit lower amplitude intra-shell variability (Figs 7 and 8, Table 2). This observation is corroborated by a geographic linear mixed model, which indicates that the $\delta^{18}\text{O}$ values from New Zealand shells are 1.23 ‰ higher than their counterparts in New Caledonia (*p*-value = 0.003). In New Caledonia, the difference in $\delta^{18}\text{O}_{\text{shell}}$ values between shells from Gadji and Forêt Nord was extremely small ($+0.1$ ‰ for shells from Gadji; *p*-value = 0.83). We observe strong consistency in the mean and standard deviation of $\delta^{18}\text{O}_{\text{shell}}$ values between the two *P. fibratus* at Forêt Nord, as with the two *P. porphyrostomus* specimens from Gadji. However, comparison of $\delta^{18}\text{O}_{\text{shell}}$ values between different species at Gadji reveals higher values in *P. porphyrostomus* ($n = 2$) compared with *P. fibratus* ($n = 2$) ($+1.15$ ‰; *p*-value = 0.01). A linear temporal trend in shell

Table 2. Isotopic summary statistics for nine *Placostylus* shells, comprising statistics on aggregated $\delta^{18}\text{O}$ (‰, VPDB) and $\delta^{13}\text{C}$ (‰, VPDB) values (sd: standard deviation, min: minimum isotopic value, max: maximum isotopic value) and statistics for linear models showing temporal trends in high-resolution isotopic profiles within each shell separately (β : slope parameter of the linear models, R-squared: percentage of variation explained by the linear model, p -value: computed from a t -test on whether β differs from zero). Summary statistics for estimated environmental water $\delta^{18}\text{O}$ (‰, VSMOW) are also presented here and are based on OIPC monthly estimation data for the three sampling locations.

Shell ID	Carbon isotope ratio $\delta^{13}\text{C}$							Oxygen isotope ratio $\delta^{18}\text{O}$						
	mean	sd	min	max	β	R-squared	p -value	mean	sd	min	max	β	R-squared	p -value
FN8.1	-11.74	0.38	-12.38	-10.99	0.00	0.00	0.59	-2.26	1.09	-5.3	-0.54	0.03	0.07	0.075
FN8.5	-9.78	0.88	-11.66	-8.43	-0.05	0.40	1.4E-05	-2.21	0.89	-5.07	-0.49	-0.01	0.03	0.146
GA04	-11.58	0.81	-13.28	-10.20	-0.08	0.71	1.9E-08	-2.36	0.85	-4.18	-0.74	-0.01	0.00	0.682
GA08	-11.82	0.35	-12.33	-11.20	-0.01	0.00	0.633	-3.24	0.61	-4.19	-1.92	0.05	0.03	0.263
GA11	-12.18	0.44	-13.26	-11.41	-0.03	0.16	0.0231	-1.44	1.16	-5.39	0.38	0.07	0.24	0.006
GA13	-11.65	1.00	-13.31	-10.16	-0.09	0.85	8.75E-16	-1.65	1.06	-3.87	0.39	-0.01	0.00	0.709
NZ01	-9.14	0.55	-10.40	-8.49	0.04	0.25	0.008	-0.98	0.54	-1.80	0.30	0.01	0.00	0.684
NZ02	-9.76	0.36	-10.31	-9.11	0.04	0.24	0.023	-0.98	0.49	-1.85	-0.31	-0.03	0.05	0.185
NZ03	-9.83	0.54	-11.03	-8.67	0.06	0.44	7.96E-04	-0.84	0.43	-1.75	-0.26	0.00	0.00	0.847
OIPC Gadjj								-3.03	1.74	-6.10	-0.90			
OIPC Forêt Nord								-3.38	1.63	-6.40	-1.50			
OIPC Cape Reinga								-5.00	1.98	-7.80	-2.30			

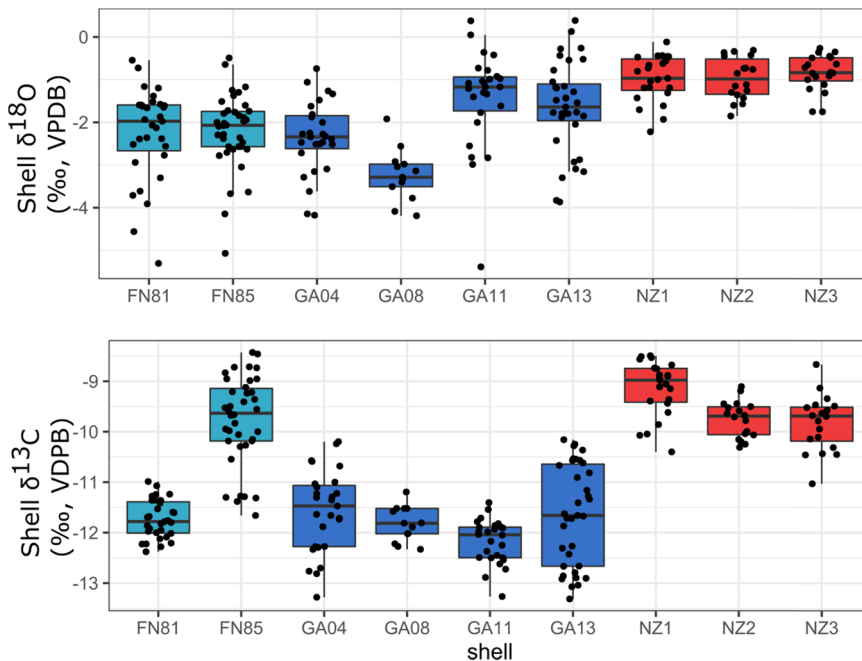


Figure 7. Box and whisker plots of the pooled isotopic values from nine *Placostylus* shells from three different locations in New Zealand and New Caledonia. (A) Distribution of $\delta^{18}\text{O}_{\text{carb}}$. (B) Distribution of $\delta^{13}\text{C}_{\text{carb}}$ values. The horizontal lines of the boxes indicate median, first and third quartiles. Points outside of the range covered by the vertical lines are considered outliers. [Color figure can be viewed at wileyonlinelibrary.com]

high-resolution profile is observed in only one of the nine shells (GA11; Table 2).

The observation that $\delta^{18}\text{O}_{\text{shell}}$ values are higher in New Zealand than in New Caledonia runs counter to the expectation based on predicted $\delta^{18}\text{O}_{\text{precip}}$ values. The OIPC model predicts lower $\delta^{18}\text{O}_{\text{precip}}$ values in New Zealand (annual average of -4.58‰ at the New Zealand location, -2.61 and -2.96‰ for the two New Caledonian locations, Table 2). Further, across all shells and locations, the variability of recovered $\delta^{18}\text{O}_{\text{shell}}$ values is routinely smaller than what is expected in environmental water on an annual timescale (Fig. 4; Table 2).

Due to the high $\delta^{18}\text{O}_{\text{shell}}$ values found in New Zealand, a positive correlation was found when correlating whole-shell averaged $\delta^{18}\text{O}_{\text{shell}}$ values to latitude (expressed in absolute values, $+0.1\text{‰}$ per degree of latitude, $p = 0.02$). Similarly, a negative correlation was found between whole-shell averaged $\delta^{18}\text{O}_{\text{shell}}$ values and $\delta^{18}\text{O}_{\text{precip}}$ as predicted by the OIPC

(-0.7‰ in $\delta^{18}\text{O}_{\text{shell}}$ value per ‰ in $\delta^{18}\text{O}_{\text{precip}}$ value, $p = 0.01$). No tangible correlation was found between whole-shell averaged $\delta^{18}\text{O}_{\text{shell}}$ and annual precipitation ($p = 0.3$).

Shell $\delta^{13}\text{C}$

Across the entire dataset, $\delta^{13}\text{C}_{\text{shell}}$ values range between -13.33 and -8.43‰ , with averaged shell values ranging from -12.18 to -9.14‰ (Table 2, Figs 7 and 8). Though cyclic intra-shell patterns are visible in many profiles, these are often superimposed on longer-term ontogenetic trends. In fact, linear temporal trends are observed in seven of the nine shells and are associated with higher values of dispersion parameters (Table 2). In New Caledonia, $\delta^{13}\text{C}_{\text{shell}}$ profiles display a negative trend, with lower isotopic values towards more recent carbonate increments, while in New Zealand a positive trend is observed with higher isotopic values in more recent layers (Table 2, Fig. 8).

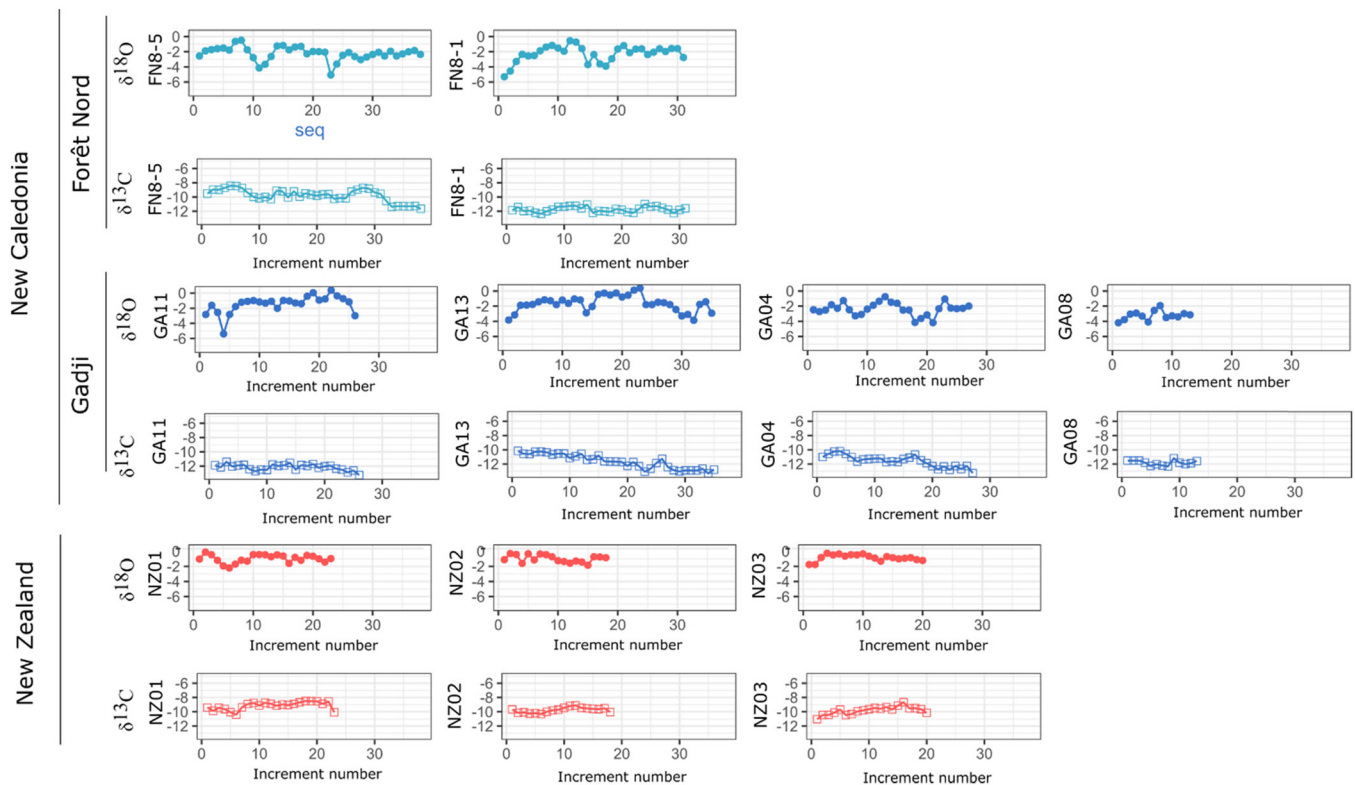


Figure 8. High-resolution isotopic profiles ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) for nine *Placostylus* shells from three different locations and two geographical areas. Filled circles show the $\delta^{18}\text{O}$ (‰, VPDB) and empty squares show $\delta^{13}\text{C}$ (‰, VPDB), with both plotted against the increment sample number (later samples are ontologically more recent). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3536)]

The carbon isotope values from New Zealand are statistically distinct from those in New Caledonia, with linear mixed models indicating higher average $\delta^{13}\text{C}_{\text{shell}}$ values in New Zealand (+1.87‰, p -value = 0.002). Within New Caledonia, shells from Gadji had marginally lower $\delta^{13}\text{C}$ values than shells from Forêt Nord (−1.05‰, p -value = 0.07). Comparison of $\delta^{13}\text{C}_{\text{shell}}$ values between *P. fibratus* and *P. porphyrostomus* specimens at Gadji reveals minor differences in $\delta^{13}\text{C}_{\text{shell}}$ variations (+0.22‰, p -value = 0.34). A strong difference in distribution of $\delta^{13}\text{C}_{\text{shell}}$ values is observed between the specimens in Forêt Nord (Table 2, Fig. 7), which were collected on exactly the same day from the same population.

Discussion

In this study, we present stable isotope profiles of nine specimens of modern *Placostylus* representing: (1) three sampling sites (Forêt Nord, Gadji, and Spirits Bay); (2) two distinct climatological regimes (New Caledonia and New Zealand); and (3) three different species of *Placostylus* (*P. fibratus*, *P. porphyrostomus* and *P. ambagiosus*). The high-resolution sampling approach employed here enables us to explore the variability of stable isotopic values from *Placostylus* shells on both a seasonal and ontogenetic timescale. Furthermore, combining data from multiple locations and taxa with modern climatological data from those same sites facilitates a comprehensive analysis of the environmental parameters controlling the $\delta^{18}\text{O}_{\text{shell}}$ and $\delta^{13}\text{C}_{\text{shell}}$ values.

Environmental controls on average shell $\delta^{18}\text{O}$

Placostylus $\delta^{18}\text{O}_{\text{shell}}$ values were, on average, higher in New Zealand than in New Caledonia (Fig. 7). In contrast, the $\delta^{18}\text{O}_{\text{precip}}$ predicted by the OIPC is, on average, lower in New

Zealand than in New Caledonia (Fig. 4). This disparity can be explained by either: (1) an actual enrichment in ^{18}O in the rainwater at Spirits Bay, New Zealand, that is not predicted by the OIPC model; or (2) a temperature effect via a biological fractionation process. The deficiency of GNIP recording stations for the southwest Pacific region means that OIPC predictions in the region are based on an extrapolation of the relationship between $\delta^{18}\text{O}_{\text{precip}}$ and latitude/altitude variables with no correction based on *in situ* measurements (Bowen and Wilkinson, 2002). Therefore, offsets between actual rainwater isotope values and values predicted by the OIPC model are quite likely. Recent sampling of New Zealand rainwater showed that the highest $\delta^{18}\text{O}_{\text{precip}}$ values were found in the northern part of the country (Baisden et al., 2016). In addition, all sampling locations are found in a relatively maritime setting, with each site located <10 km from the sea. The influence of the oxygen isotope from surrounding seawater on $\delta^{18}\text{O}_{\text{precip}}$ and the local water vapour are not accounted for in the OIPC predictions, and here they could potentially explain parts of the offset between $\delta^{18}\text{O}_{\text{precip}}$ calculated in the OIPC and the actual $\delta^{18}\text{O}_{\text{precip}}$. Additionally, the $\delta^{18}\text{O}_{\text{shell}}$ is influenced by the ambient temperature at the time of carbonate precipitation, with higher values indicative of colder temperatures due to the fractionation of oxygen isotopes into biogenic aragonite (Grossman and Ku, 1986). As a whole, New Zealand experiences a colder climate than New Caledonia, with large diurnal temperature variability (Fig. 5B). Thus, biological fractionation due to colder temperatures, particularly at night when studies suggest that *Placostylus* is most active (Brescia et al., 2008), could, in part, also explain the higher values in New Zealand.

Within New Caledonia, Forêt Nord receives far more precipitation than Gadji, particularly during the summer rainy season (Fig. 3). Despite this, the $\delta^{18}\text{O}_{\text{shell}}$ values were not lower in Forêt Nord, as a negative correlation between precipitation amount and shell $\delta^{18}\text{O}_{\text{shell}}$ would predict (Bao

et al., 2019; A. L. Prendergast, Stevens, Barker, O'Connell 2015; Yanes et al., 2009). However, OIPC predicts similar $\delta^{18}\text{O}_{\text{precip}}$ values at the two locations, which makes sense since their close geographical proximity implies the precipitation water received would mostly be of the same origin. Therefore, it is likely that the similarity in the $\delta^{18}\text{O}_{\text{carb}}$ of the two New Caledonia sites reflects similar $\delta^{18}\text{O}_{\text{precip}}$ values regardless of differences in precipitation amount.

When sampling specimens from the same location, environmental heterogeneity should be limited and therefore differences in $\delta^{18}\text{O}_{\text{shell}}$ values most likely reflect differences in the controls on isotope fractionation (e.g. biological processes). Higher $\delta^{18}\text{O}_{\text{shell}}$ values are usually observed in larger species of snails (Yanes et al., 2017). The four shells from Gadji represent two distinct *Placostylus* species. The two *P. fibratus* shells had, on average, lower $\delta^{18}\text{O}_{\text{shell}}$ values than the two *P. porphyrostomus* shells, but they are from the bigger of the two species we analysed (Dowle et al., 2015; Qenu et al., 2020). With only two samples of each species, the dataset is too small to draw concrete conclusions, but the results are counter to previously reported findings.

Similarly, because our dataset only constituted nine shells, there are severe statistical limitations to the interpretation of whole-shell averaged $\delta^{18}\text{O}_{\text{shell}}$ values in relation to environmental or geographic variables (Fig. 9). It is, however, interesting to note that the positive relationship observed with latitude (in absolute values) is here of opposite trend to the negative correlation observed across a large continental scale in North America (Yanes et al., 2019). For precipitation, the negative correlation between $\delta^{18}\text{O}_{\text{shell}}$ values and annual precipitation is similar to the ones found across Northern Lybia (Prendergast, Stevens, Barker, O'Connell 2015) and in the East Asian monsoon region (Bao et al., 2019), but of an opposite trend to the one found across Northern America (Yanes et al., 2019). These differences in patterns once again highlight the local nature of the relationships between $\delta^{18}\text{O}_{\text{shell}}$ and precipitation amount, and the lack of a universal relationship. In this region, more extensive sampling of *Placostylus* shells from other locations in the southwest Pacific could help to better decipher the relationships between $\delta^{18}\text{O}_{\text{shell}}$ values and environmental controls. From the preliminary results in this study, observations generally drawn from continental settings in the northern hemisphere appear to not necessarily hold true for this region of the southwest Pacific.

Environmental controls on the seasonal variability of shell $\delta^{18}\text{O}$

The specimens from all three locations exhibit smaller intra-shell variability in $\delta^{18}\text{O}_{\text{shell}}$ values than that anticipated by the OIPC predicted seasonal range of $\delta^{18}\text{O}_{\text{precip}}$ at their respective sampling sites (Fig. 4). Furthermore, the shells from New

Zealand exhibit very low $\delta^{18}\text{O}_{\text{shell}}$ variability compared with those in New Caledonia. This disparity could be due to the New Zealand shells growing during (and thus recording) a smaller fraction of the annual cycle. To be active and produce shell material, land snails require a high relative humidity, and relatively high temperatures (Nicolai and Ansart, 2017). While relative humidity stays constantly high throughout the year in all locations (Figs 3C, F and 4C), temperatures can get significantly lower in New Zealand than in New Caledonia, especially during the winter nocturnal periods through which snails are supposedly active (Fig. 5B). Conditions of optimal snail shell growth are therefore more likely to be met throughout the entire year in New Caledonia than in New Zealand, which could explain the lower $\delta^{18}\text{O}_{\text{shell}}$ variability of New Zealand *Placostylus*. In this context, most of the growth of the New Zealand shells would be biased toward the warmer summer months between December and March. Coincidentally, these are also the months with theoretically the highest $\delta^{18}\text{O}_{\text{precip}}$, and a seasonally biased shell growth could therefore also explain the higher $\delta^{18}\text{O}_{\text{shell}}$ values found in New Zealand.

The pattern of intra-shell variation of the New Caledonia shells is characterised by stable periods of relatively high $\delta^{18}\text{O}_{\text{shell}}$ values followed by rapid drops in $\delta^{18}\text{O}_{\text{shell}}$. This pattern was not observed in *Placostylus* shells from New Zealand. Other high-resolution records of tropical land snails have similarly reported short periods of low $\delta^{18}\text{O}_{\text{shell}}$ values, which have been linked to extreme rainfall events during the monsoon season in Indian samples of *Lissachatina fulica* (Ghosh et al., 2017), and to months of higher precipitation in *Cerion* snails from the Bahamas (Baldini et al., 2007). Given the presence of multiple months with very high levels of precipitation in New Caledonia within the sampled timeframe, we hypothesise that the rapid excursions toward lower isotopic values observed in the high-resolution $\delta^{18}\text{O}$ profiles may be related to periods of intense rainfall and lower $\delta^{18}\text{O}_{\text{precip}}$.

Shell $\delta^{13}\text{C}$ and *Placostylus* diet

The signal recorded by snail shell $\delta^{13}\text{C}$ values is thought to mainly reflect diet composition (Bao et al., 2018). Values for $\delta^{13}\text{C}$ were highly variable for the *Placostylus* snails of New Caledonia, and, on average, lower than the values found in New Zealand. Higher $\delta^{13}\text{C}$ values can reflect a higher intake of C4 plants if the diet of the land snail includes a mix of C3 and C4 plants or can be related to variations in the $\delta^{13}\text{C}$ signature of C3 plant in non-mixed diets. *Placostylus* snails are believed to forage and feed mostly on leaves falling in their litter environment (Brescia et al., 2008; Parrish et al., 2014). Therefore, their diet should here mostly be constituted of C3 plants. In this situation the variations in $\delta^{13}\text{C}$ could indicate external

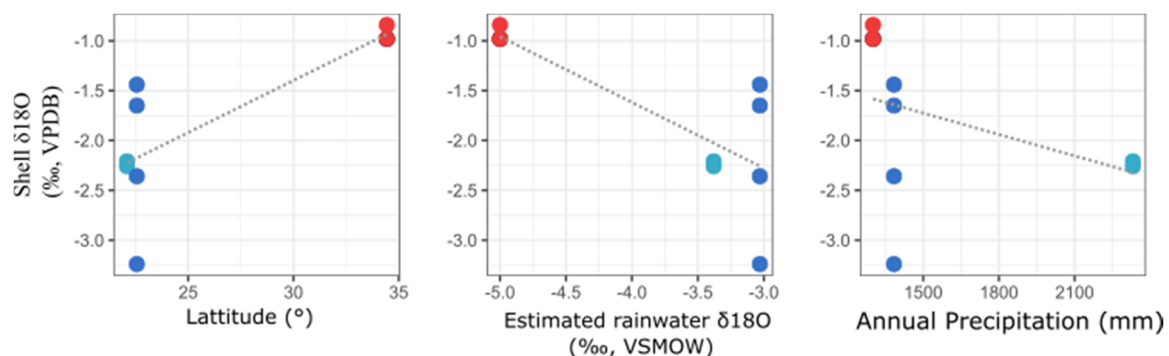


Figure 9. Linear regressions of whole-shell average *Placostylus* $\delta^{18}\text{O}_{\text{shell}}$ values against three predicting variables: latitude (°, absolute value), as estimated by the OIPC and average annual precipitation (mm) of closest meteorological station. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

environmental forcings as leaf carbon isotope signatures of C3 plants are known to vary according to moisture and rainfall levels (Diefendorf et al., 2010; Tibby et al., 2016). These could explain the apparent temporal co-variation of $\delta^{13}\text{C}_{\text{shell}}$ and $\delta^{18}\text{O}_{\text{shell}}$ observed in some *Placostylus* shells (e.g. FN8.5, NZ01; Fig. 8). However, due to the locations of all shells sampled here and their proximity to locations with an abundance of C4 plants it is impossible to completely rule out a mixed diet. The strong variability of $\delta^{13}\text{C}$ signatures in the shells from New Caledonia, sometimes within the same location, suggests a non-specialist diet. Sympatric shells of *P. fibratus* and *P. porphyrostomus* did not demonstrate differences in $\delta^{13}\text{C}$ values, which indicates a similar diet composition for the two species. Intra-shell temporal trends in $\delta^{13}\text{C}$ values were observed in both New Zealand and New Caledonia but in an opposite direction, with an increase in $\delta^{13}\text{C}$ values over time in New Zealand, and a decrease in $\delta^{13}\text{C}$ values over time in New Caledonia (Fig. 8; Table 2). These trends could reflect a change in preferential diet over the lifespan of terrestrial snails.

Implications for palaeoclimate studies using *Placostylus*

We developed a protocol to sample three to five years of accretional carbonate growth from modern *Placostylus* shells, which have an extent and fossil repartition within the southwest Pacific region (Ponder et al., 2003; Quenu et al., 2021). *Placostylus* fossil shells could be sampled using the same method, thereby retrieving snapshots of past isotope and climate variability. As a single proxy, the number of *Placostylus* shells required to establish a continuous chronology of isotopic records would be enormous, but this could be alleviated by using a combination of multiple palaeoclimate proxies with distinct profiles. In northern New Zealand, there are abundant fossil records of intact *Placostylus* shells that cover parts of the late Holocene (Brook, 1999b), a period that is also covered by high-resolution tree ring data (Boswijk et al., 2014; Lorrey et al., 2018). Multiproxy palaeoclimate studies are therefore a possibility in this region, with precisely dated *Placostylus* shells potentially providing useful complementary information to the long-term palaeoclimate trends gathered from tree rings of *Agathis australis*, which also captures hydroclimatic variations in its isotope signatures (Lorrey et al., 2016). In New Caledonia and other isolated islands of the southwest Pacific, fossil *Placostylus* shells could provide pioneer data for a geographical area where Quaternary terrestrial palaeoclimate studies are still scarce (Tajika et al., 2022). In this location, it would be particularly interesting to see whether the $\delta^{18}\text{O}_{\text{carb}}$ patterns observed in modern shells are also observed in the fossil record.

Conclusion

Here, we provided the first stable isotopic data for the land snail *Placostylus* in two regions with contrasting climatic regimes. In addition to differences in whole-shell carbon and oxygen isotope values, the shells from the two regions also exhibited differences in their high-resolution stable isotope profiles. These differences are potentially reflective of the different environmental conditions occurring at shell formation, and are probably influenced by the snails' behaviour. The sampling protocol developed here will enable further work on fossil *Placostylus* shells, which can potentially hold valuable palaeoclimate insights for the southwest Pacific region.

Additional sampling of extant *Placostylus* shells should be realised with a simultaneous sampling of meteoric and surface

waters to ascertain $\delta^{18}\text{O}$ values. One of the main limitations of this study was the reliance on predictive models (OIPC) to compare shell isotope values to rainwater isotope signatures. Establishing $\delta^{18}\text{O}$ values of environmental water during the lifespan of snails would here allow us to have a better understanding of the biological fractionation process and its consequences for $\delta^{18}\text{O}_{\text{snail}}$ values.

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Conflicts of interest—None of the authors has a conflict of interest to disclose.

Data availability statement

The isotopic data used in this study can be publicly accessed at the following address: https://figshare.com/articles/dataset/Placostylus_stable_isotopes/20448702. R scripts used for figure generation and analyses can be found at <https://github.com/MQuenu/Snail-isotope-code>.

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