ORIGINAL PAPER

Trophic niche of the invasive *Cherax quadricarinatus* and extent of competition with native shrimps in insular freshwater food webs

Thomas Baudry [ORCID] · **Juliette Smith-Ravin** · **Alexandre Arqué** · **Jean-Pierre Goût** · **Julien Cucherousset** · **Jean-Marc Paillisson** · **Frédéric Grandjean**

Abstract Quantifying the trophic niche of non-native species is a valuable way to measure both their invasion success and putative impacts on recipient food webs. Theory predicts that successful invasive species display flexible diet depending on environment conditions, have large trophic niche, and can overlap the trophic niche of functionally similar native species. We investigated these predictions using the redclaw crayfish (*Cherax quadricarinatus*) as an invasive species model and omnivorous and detritivorous shrimps as native competitors in recently invaded insular Martinican streams (Caribbean region). Although the redclaw crayfish is globally widespread, little is known about its trophic ecology and potential impacts on other crustaceans in its non-native regions. Using stable isotope analyses to quantify the trophic ecology of redclaw crayfish, we found that it occupied a central position in the food webs, with a primary consumer tendency at the population level. Evidence for ontogenetic shifts was found with different trajectories across streams, highlighting its trophic flexibility to environmental conditions. However, redclaw fed on a limited range of resources (small niche sizes) probably due to the local context, characterised by simplified food webs. Crayfish and shrimps shared partly similar food resources ($20.5 \pm 9.7\%$ of niche overlap with omnivorous shrimps and $14.9 \pm 13.8\%$ with detritivorous shrimps). Finally, a slight shift in trophic niche (without niche constriction) of native crustaceans (mainly omnivorous shrimps) was observed when cooccurring with crayfish. Stable isotope analysis revealed here no

---

Joint Last Authors: Jean-Marc Paillisson and Frédéric Grandjean.

T. Baudry (✉) · F. Grandjean
Laboratoire Ecologie et Biologie des Interactions, Université de Poitiers, UMR CNRS 7267, Equipe Ecologie Evolution Symbiose, Poitiers Cedex, France
e-mail: thmsbaudry@gmail.com

T. Baudry · J. Smith-Ravin
Groupe BIOSPHERES, Université des Antilles, Campus de Schoelcher, Schoelcher, Martinique, France

A. Arqué
Office de l'Eau de Martinique, Fort de France, Martinique, France

J.-P. Goût
Direction de l'Environnement, de l'Aménagement et du Logement de Martinique, Schoelcher, Martinique, France

J. Cucherousset
Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France

J.-M. Paillisson
ECOBIO (Ecosystèmes, Biodiversité, Evolution), CNRS, Université de Rennes, Rennes, France

evidence of striking impact of the newly introduced crayfish on the trophic ecology of native shrimps, but we call for further investigations to assess potential longer-term repercussions on native communities.

Introduction

Freshwater macroinvertebrates are represented by a large number of species, ranging from a few millimeters to several tens of centimeters body size, and belong to different functional groups (Wallace and Webster 1996). They are keystone organisms involved in numerous important ecosystem functions such as nutrient cycling, detritus recycling and energy transfer processes (Wallace and Webster 1996; Nieto et al. 2017; Wissinger et al. 2021). Crayfish are among the most studied group of freshwater macroinvertebrates (Reynolds and Souty-Grosset 2011), since they occur in most aquatic habitats, are generally large-sized organisms dominating benthic biomass, and are omnivore, capable of changing their diet according to life cycle, season, or resource availability (Alcorlo et al. 2004; Olsson et al. 2009; Reynolds et al. 2013). Some crayfish can be qualified as "ecosystem engineers" because they modulate their environment through bioturbation and/or burrowing activities (Momot 1995; Souty-Grosset et al. 2016). All these make crayfish both ecologically important and popular for aquaculture and aquarium trade purposes (i.e. some species presenting extravagant colouring) (Lodge et al. 2012), the downside is that they are commonly recorded that they can be harmful when introduced into new ecosystems (Gherardi et al. 2011; Lodge et al. 2012; Souty-Grosset et al. 2016). Numerous studies have highlighted significant negative impacts of introduced crayfish on native molluscs (Herrmann et al. 2022), other benthic invertebrates (Twardochleb et al. 2013 and references therein; Ercoli et al. 2015) and macrophyte communities (Gherardi and Acquistapace 2007; Souty-Grosset et al. 2016 and references therein).

Introduced species develop new trophic links with native species in recipient ecosystems (predation and competition) while possibly also impacting them by modifying the environment and/or developing antagonistic interactions (Lodge et al. 2012; Ricciardi et al. 2013; McCue et al. 2020). Theory predicts that responses of native species to an invasive competitor (thought to have a competitive advantage; Bollache et al. 2008; Alexander et al. 2014) may occur through changes in trophic niches taking various forms [the use of other food resources, a decrease, or, conversely, an increase in niche breadth, i.e. an ecological displacement sensu David et al. (2017)]. All these processes leading to a decrease in the extent of trophic niche overlap, and ultimately, to favour coexistence with the invasive species. For example, Magoulick and Piercey (2016) empirically observed large diet overlap between native and invasive crayfish, and Veselý et al. (2021) showed that the trophic niches of the spiny-cheek crayfish *Faxonius limosus* and the marbled crayfish *Procambarus virginalis* were narrower when cohabiting with the invasive red swamp crayfish *Procambarus clarkii*. Dietary niche constriction was also observed between competitive decapods, leading to the replacement of a native crab species by the invasive red swamp crayfish (Jackson et al. 2016). Furthermore, the impacts of invasive species can vary according to individual body size and related dietary ontogenetic shifts. Empirical studies using crayfish have indeed demonstrated significant ontogenetic dietary changes (Correia 2003; Alcorlo and Baltanás 2013; Jackson et al. 2017; Veselý et al. 2020). Guan and Wiles (1998) found that adult signal crayfish *Pacifastacus leniusculus* consumed significantly more detritus than juveniles, which preferred macroinvertebrate prey due to specific nutrient requirements for growth and adult crayfish were less able to forage on fast mobile prey.

Impacts of invasive species also depend on the attributes of recipient ecosystems, in other words, environmental conditions and native communities they support (Kestrup and Ricciardi 2009; David et al. 2017). In turn, trophic niches of native and invasive species are constrained by food resource levels in general and more specifically shared resources for competing species (Evangelista et al. 2014). For example, island ecosystems are considered as highly vulnerable to biological invasions owing to typical simplified food webs without top predators and small population sizes (Velmurugan 2008). However, island ecosystems, and especially tropical ones, have been subjected to increased anthropized pressures (such as land artificialization and urbanization, directly

linked to growing human demography) that have led to food web erosion and the arrival of an increasing number of non-native and eventually invasive species (Velmurugan 2008; Barlow et al. 2018; Chong et al. 2021).

Martinique island, in the Caribbean region, is not spared from biological invasions, since several non-native fish and crustacean species have been introduced there (Lim et al. 2002; Dubreuil et al. 2021) including recently, the redclaw crayfish *Cherax quadricarinatus* (four wild established populations were found in 2015; Baudry et al. 2020). This species originates from northeastern Australia and southern Papua New Guinea (Haubrock et al. 2021) and it is considered as a flagship species in aquaculture in the tropics [similarly to the red swamp crayfish in the temperate zone; Oficialdegui et al. (2020)]. The species is present on all continents except Antarctica as reported in a recent monograph conducted by Haubrock et al. (2021). To date, despite its successful worldwide expansion, observational studies on its diet and possible impacts in introduced regions are still limited (see however Marufu et al. 2018; Zengeya et al. 2022). As detailed by Haubrock et al. (2021), its impacts are rather extrapolated from what is documented in other invasive crayfish. Its large body size (> 20 cm in the wild; Kozák et al. 2015), its aggressive behaviour, environmental plasticity (King 1994), growth (up to 100 g in 1 year; Wingfield 2002; Arzola-Gonzalez et al. 2012) and fecundity (sexual maturity at 6 month old, with female able to lay between 200 and 600 eggs, up to 3–5 times a year; de Moor 2002; Tropea et al. 2010), make it a potential perfect invader. In Martinique, the redclaw crayfish has recently become established at many streams over the past few years (Baudry et al. 2021), meaning that it can significantly impact indigenous freshwater fauna, and more particularly functionally similar native shrimp species. As mentioned above, there are only two studies documenting the diet of the redclaw crayfish outside its native range using stable isotope analyses (in the Southern African regions; Marufu et al. 2018; Zengeya et al. 2022). Both studies found that despite its omnivory, diet changes according to crayfish size (i.e. low isotope niche overlap) with small individuals preferring macroinvertebrate prey while larger crayfish extending their diet to macrophytes and detritus. Zengeya et al. (2022) also found variations in the trophic niche of the redclaw crayfish across freshwater ecosystems and variable extent of competition with a native crab species across localities.

In the present study, we investigated the trophic niche of the redclaw crayfish in Martinican streams. First, we quantified the variations in its trophic niche in relation to body size (dietary ontogeny shift hypothesis) and habitats (dietary plasticity hypothesis) using stable isotope analysis. Second, we investigated the extent to which redclaw crayfish compete with native crustaceans (shrimps) belonging to two distinct functional groups (detritivore and omnivore), by quantifying the size and position of their stable isotope niche. Given that redclaw crayfish were found to be omnivore elsewhere, we hypothesized that niche overlap would be higher with the omnivorous shrimp group. In addition, we tested eventual trophic displacement of native shrimps living in sympatry with the redclaw crayfish (outcompeting hypothesis; Elton 1958; David et al. 2017; Haubrock et al. 2021), by comparing niche size and position with streams not invaded by crayfish.

Material and methods

Study area

Martinique is a French volcanic island (1128 km^2) belonging to the Lesser Antilles (14° 39′ 00″ N and 61° 00′ 54″ W, Fig. 1). Its hydrographic network is well developed owing to a rainy tropical climate, including 70 major streams fed by numerous permanent or semi-permanent tributaries, depending on seasons (Baudry et al. 2020). Ten stream stretches (thereafter referred to as stations) were sampled in August–September 2021 (Fig. 1): five stations invaded by redclaw crayfish (I1–I5) and five uninvaded stations (U1–U5), the presence/absence of the species was ascertained thanks to environmental DNA and conventional -trapping and dip-netting- surveys (Baudry et al. 2021). Streams under study were very similar in terms of hydromorphology, environmental features and composition of the native community. They are generally slow flowing, typically composed of alternating pools (especially sandy), flats and inverts, mainly composed of gravel and rocks of varying size, ranging from a few cm to 1 m. Riparian vegetation is dominated by two tree species

Fig. 1 The hydrographical network of Martinique, and location of the five invaded stations by redclaw crayfish (I1 Bassignac, I2 Cacao, I3 Saint-Esprit, I4 Saint-Jacques and I5 Petit Bourg) and the five non-invaded stations studied (U1 Canal, U2 Carbet, U3 Lorrain, U4 Maison Rousse and U5 Nau)
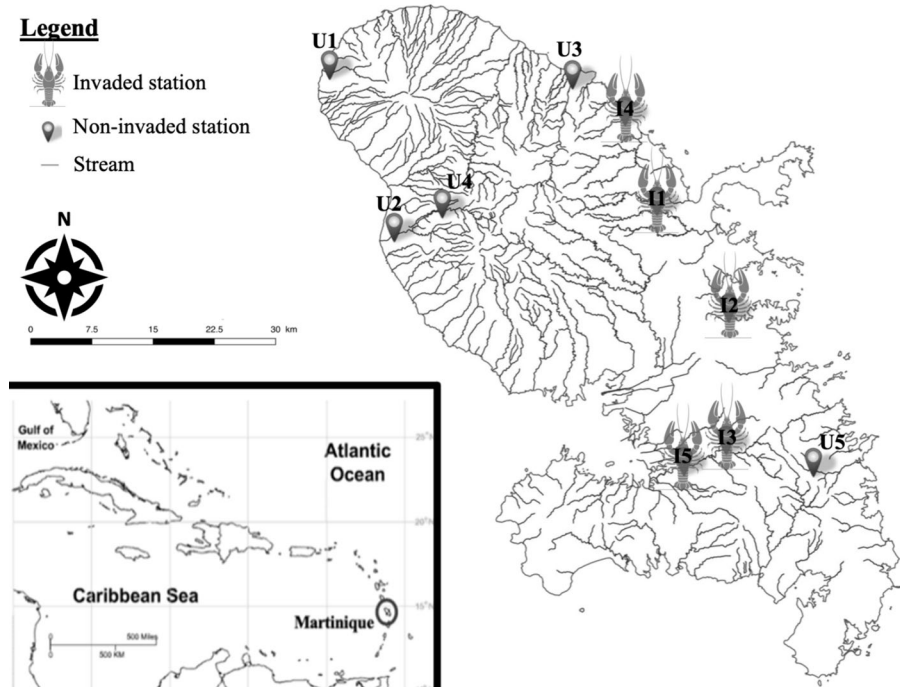
(*Bombacaceae* spp. and *Artocapus altilis*), and an herbaceous plant (*Panicum maximum*). Aquatic vegetation is mostly composed of *Chara* spp. and *Ceratophyllum* spp. (Maddi 2014). Aquatic animal communities are dominated by shrimps (mainly *Atyidae*, *Xiphocarididae* and *Palaemonidae* spp.) and fish (*Gobiidae*, *Eleotridae*, *Poeciliidae* and *Mugilidae* spp.) (Lim et al. 2002). They also include molluscs, the dominant ones being *Neritidae* spp. in flowing stream parts and *Thiaridae* spp. in pools or flat stream parts (Delannoye et al. 2015).

Sample collection

Crayfish and large-sized shrimps were caught using a 12-h trapping session conducted overnight with traps baited with cassava [length × width × height: 80 × 25 × 25 cm, 1-cm mesh size with a single cone-shaped inlet; more details in Baudry et al. (2021)]. Juvenile shrimps were preferably sampled using a kick-net. We repeated sampling, in some cases, with the objective of collecting at least 20 crayfish and 20 shrimps from each of the two distinct trophic groups to seemly capture variation in the stable isotope values at the population/group levels [following recommendations in Jackson et al. (2011)]. Sometimes,

depending on the site, we did not succeed in collecting this number of samples for shrimps (Supplementary Information S1). Based on their feeding habits and their morphology, captured shrimps are commonly classified as mainly detritivore or omnivore. More precisely, *Atyidae* and *Xiphocarididae* spp. are small species (< 35 mm and 50 mm in length, respectively) with cheliped fans (*Atyidae*) (Lim et al. 2002; March and Pringle 2003) or tiny pincers (*Xiphocarididae*) (Pringle et al. 1993; Lim et al. 2002; March and Pringle 2003) used to filter and brush to find fine organic particles or to eat decaying leaf/plant material; they are, hereafter, called detritivorous shrimps. By contrast, *Palaemonidae* (*Macrobrachium* spp.) are large-sized species (for example, > 20 cm in length for *M. carcinus*) with strong claws (sometimes longer than the body) used to feed on plants and animal prey items; they are classed as omnivore in the literature (Lim et al. 2002; Covich et al. 2006; Coat et al. 2009).

In addition, we sampled molluscs and basal resources (biofilm and plants) to standardize stable isotope values between stations (see below). Molluscs (*Thiaridae* and *Neritidae* spp.) were collected by hand. They are documented as presenting a diversified diet, from grazer, detritivore to carnivore (March and Pringle 2003; Coat et al. 2009; Kilham

et al. 2009; Delannoye et al. 2015). Biofilm and algae were collected by scraping the surface of rocks with a scalpel and represented, with aquatic plants, autochthonous vegetal resources whereas leaves of the riparian vegetation constituted the allochthonous plant resources. Basal resources were processed as follow, depending on availability: autochthonous sources were pooled to obtain one/two samples per station (except in U1 where autochthonous sources did not occur, see below) and up to six samples per station were processed for allochthonous sources. Fish specimens were captured together with crustaceans in traps and using a kick-net to provide both a complete overview of Martinican freshwater food webs (poorly documented until now) and a better assessment of the trophic place of the invasive crayfish therein. Common captured fish were either herbivore, with a microphagy tendency [*Gobiidae* and *Sycidium* spp.; Lim et al. (2002); Debrot, (2003)], or predatory [*Eleotridae*, *Poecillidae* and *Mugilidae* spp. (Nordlie 1981; Lim et al. 2002)]. Fish specimens were euthanized using a 250-ppm benzocaine dose. All samples were kept in a cooler box after collection, until return to the laboratory and stored at −20 °C until processing (number of samples processed in Supplementary Information S1).

Sample preparation and stable isotope analysis

To explore the extent of variation in stable isotope values between individuals, crayfish size was measured (from the tip of the rostrum to the end of the telson, to the nearest millimeter) and varied from 20 to 171 mm, with marginal between-station differences (mean value of 98.9 ± 33.64 (s.d.) mm, n = 133; ANOVA test, F = 2.27, p = 0.07). There is no excess in a given crayfish size class among each population which could influence the calculation of niche metrics due to expected ontogenetic dietary changes. Abdominal muscle was sampled for crayfish and shrimps, dorsal muscle for fish and foot for molluscs. All samples, including basal samples were rinsed with distilled water, then oven-dried at 60 °C for 96 h. Samples were ground with a Retsch® Mixer Mill 400 to obtain a fine homogenous powder. Samples were then packed in tin capsules, with 1.01 ± 0.08 mg per sample for crayfish and shrimps, 1.01 ± 0.19 mg per sample for molluscs, 0.97 ± 0.04 mg per sample for fish, and 2.3 ± 1.39 mg per sample for basal samples.

Carbon and nitrogen stable isotope ratios (δ^{13}C as ^{13}C/^{12}C and δ^{15}N as ^{15}N/^{14}N) were measured at the Cornell Isotope Laboratory (Cornell University, Ithaca, NY). Stable isotope ratios were expressed using conventional delta notations δ^{13}C and δ^{15}N relative to international standards, Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. In-house standards were analyzed after every series of ten samples to ensure the analytical accuracy of the measurements; resulting precision values (standard deviation) were 0.10‰ for carbon and 0.13‰ for nitrogen. Two additional in-house standards ('KCRN' corn and 'CBT' trout) were used to perform two-point normalization (linear regression) stable isotope corrections.

Handling of stable isotope data

δ^{13}C and δ^{15}N values of crayfish and shrimps were corrected to allow comparisons between stations (biplots of raw data are available in Supplementary Information S2). Corrected δ^{13}C (δ^{13}Ccor) values were calculated using the following formula:

$$\delta^{13}\text{Ccor} = (\delta^{13}\text{C}i - \delta^{13}\text{C}inv)/\delta^{13}\text{CR}inv$$

where δ^{13}Ci is the carbon isotope ratio of the sample of interest (crayfish or shrimp), and δ^{13}Cinv and δ^{13}CRinv are the mean and range carbon stable isotope ratios of all invertebrates collected in the station considered [molluscs, shrimps and crayfish; see Olsson et al. (2009); Vander Zanden and Rasmussen (1999)].

Likewise, individual trophic positions (TP) were calculated using the following formula (see McCutchan et al. 2003):

$$\text{TP} = 1 + (\delta^{15}\text{N}i - \delta^{15}\text{N}_{P1})/\Delta^{15}\text{N}$$

where δ^{15}N$_i$ is the nitrogen stable isotope ratio of the sample of interest (crayfish or shrimp), δ^{15}N$_{P1}$ is the mean δ^{15}N of primary producers (basal sources) of the station considered (δ^{15}N values of allochthonous and autochthonous sources being before averaged separately), Δ^{15}N is the Trophic Discrimination Factor (set to 2.4 which is commonly used in freshwater tropical environments; Coat et al. 2009), and $\lambda = 1$ is the trophic position attributed to primary producers. TP values of target species were calculated based solely on allochthonous sources in U1 (owing

to the absence of aquatic vegetation and biofilm) but we made sure that it was not responsible for trends in the subsequent analyses by comparing the results with this tributary removed from the dataset (data not shown). Moreover, we did not use molluscs to standardize $\delta^{15}N$ values of crayfish and shrimps because of their potential carnivorous diet as aforementioned that would result in overestimated TP values.

The position of the stable isotope niche of each crayfish population and each shrimp trophic group was calculated as the average $\delta^{13}Ccor$ and TP values in each station. Standard Ellipses Areas corrected for small sample sizes (SEAc) were then calculated (Stable Isotope Bayesian Ellipses—20,000 iterations, 1000 burn-in, 2 chains parameters; Jackson et al. 2011). Lastly, the extent of competition between crustaceans was measured as niche overlap (percentage of SEAc of each trophic shrimp group shared with the second one or with crayfish, depending on stations).

Statistical analyses

Between-station differences in crayfish size was tested using an Analysis of Variance (ANOVA), after data normality and variance homogeneity verification with Shapiro–Wilk and Bartlett tests, respectively. We tested whether $\delta^{13}Ccor$ and TP values of individual crayfish varied according to their size (fixed effect) across the five invaded stations (covariate) using Analysis of Covariance (ANCOVA). Post-hoc pairwise comparisons were performed using Student t-tests (considering Bonferroni-adjusted p values). We also tested whether $\delta^{13}Ccor$ and TP values of each shrimp trophic group were associated with crayfish presence (fixed effect) using separate Generalized linear mixed models integrating a random "station" effect. Lastly, we tested whether SEAc of each shrimp group and SEAc overlap between the two shrimp groups varied between invaded and uninvaded stations using separate Analyses of Variance (ANOVA). All statistical analysis were performed in R v4.2.3 (R Development Core Team 2023) using the SIBER (Jackson et al. 2011), lme4 (Bates et al. 2015) and dplyr (Wickham et al. 2023) packages.

Results

Variations in crayfish stable isotope variables across streams

Redclaw crayfish occupied a relatively central position in the stable isotope space of all invaded stations, with intermediate values across ranges of both stable isotopes (Supplementary Information S2). Mean raw $\delta^{13}C$ values varied slightly between stations (from -23.9 ± 1.06 to $-22.01 \pm 0.9‰$, Supplementary Information S1) and varied more for $\delta^{15}N$ (from 7.76 ± 0.61 to $12.67 \pm 0.89‰$, Supplementary Information S1), leading to a mean $\delta^{13}Ccor$ of $-0.05 \pm 0.08‰$ (range: $-0.12 \pm 0.14‰$ to $0.04 \pm 0.16‰$) and a mean TP of 1.99 ± 0.25 (range: 1.26 ± 0.23 to 2.57 ± 0.37, Table 1). Moreover, SEAc varied by a factor of two depending on stations ($0.85–1.90‰^2$, Table 1).

At the individual level, a significant positive relationship was found between $\delta^{13}Ccorr$ values and crayfish size across all stations (ANCOVA, F = 24.42, $p < 0.001$; Fig. 2A) but higher $\delta^{13}Ccorr$ values were noted in stations I2 and I3 (post-hoc pairwise comparisons, $p < 0.01$). TP values were also significantly correlated to crayfish size but this relationship differed between stations (lower values in I1; ANCOVA, F = 75.67, $p < 0.001$). Specifically, a large increase in TP values with crayfish size was found in I5, a slight increase in I1 and I4, and, conversely, a decrease in TP values with body size in stations I2 and I3 (Fig. 2B, post-hoc pairwise comparisons not shown).

Comparison of shrimp niche variables according to crayfish presence

When co-occurring with crayfish, omnivorous shrimps displayed enriched $\delta^{13}Ccor$ values ($0.1 \pm 0.22‰$ in mean instead of $-0.06 \pm 0.21‰$ in non-invaded stations) whereas no difference were observed in detritivorous shrimps ($-0.06 \pm 0.19‰$ vs. $-0.02 \pm 0.23‰$, respectively; Fig. 3A). A significant decrease in TP values was found for both shrimp groups in presence of crayfish ($2.86 \pm 0.87‰$ vs. $4.12 \pm 0.6‰$ and $2.64 \pm 0.58‰$ vs. $4.00 \pm 0.33‰$; Fig. 3B, see also values in each station in Table 1).

Contrary to our expectation, no differences in shrimp niche size were observed between invaded and uninvaded tributaries (2.72 vs. 3.36‰^{2} for

Table 1 Stable isotope niche position (corrected $\delta^{13}C$—$\delta^{13}C$ corr - and trophic position—TP -, mean±s.d.) and size (corrected Standard Ellipse Area—SEAc) of the invasive crayfish and the two shrimp trophic groups (detritivore and omnivore), and extent of niche overlap between them (expressed as the % of the SEAc of crustacean 1 that is overlapped by the SEAc of crustacean 2, noted crustacean 1 vs. crustacean 2 in the table) in invaded (I1–I5) and unimvaded (U1–U5) stations

Niche variable	Taxa	Station									
		I1	I2	I3	I4	I5	U1	U2	U3	U4	U5
$\delta^{13}C$corr (‰)	Crayfish	−0.12 (±0.13)	0.03 (±0.12)	0.04 (±0.16)	−0.12 (±0.14)	−0.08 (±0.17)	–	–	–	–	–
	Detritivorous shrimps	−0.03 (±0.11)	−0.11 (±0.21)	−0.19 (±0.16)	−0.08 (±0.19)	0.18 (±0.18)	−0.13 (±0.09)	0.05 (±0.31)	−0.13 (±0.17)	0.07 (±0.3)	−0.02 (±0.1)
	Omnivorous shrimps	0.10 (±0.16)	0.18 (±0.14)	0.14 (±0.26)	0.08 (±0.2)	0.02 (±0.26)	−0.05 (±0.17)	−0.09 (±0.26)	−0.12 (±0.28)	0.05 (±0.22)	−0.06 (±0.16)
TP	Crayfish	1.26 (±0.23)	1.86 (±0.17)	2.13 (±0.25)	2.12 (±0.25)	2.57 (±0.37)	–	–	–	–	–
	Detritivorous shrimps	1.70 (±0.18)	3.23 (±0.82)	3.70 (±0.37)	2.59 (±0.2)	3.55 (±0.11)	3.51 (±0.09)	3.72 (±0.43)	4.58 (±0.3)	3.72 (±0.42)	4.49 (±0.59)
	Omnivorous shrimps	2.07 (±0.25)	2.57 (±0.37)	2.85 (±0.47)	2.63 (±0.31)	2.86 (±0.83)	3.89 (±0.16)	3.82 (±0.13)	4.79 (±0.14)	3.75 (±0.39)	4.14 (±0.21)
SEAc (‰^{2})	Crayfish	1.89	0.85	1.25	1.60	1.90	–	–	–	–	–
	Detritivorous shrimps	1.28	7.68	2.06	1.66	0.92	0.36	5.86	4.17	5.49	0.92
	Omnivorous shrimps	2.51	2.07	3.56	2.44	8.19	1.13	1.37	3.48	5.41	8.19
SEAc overlap (%)	Detritivorous shrimps versus crayfish	29.9	10.4	0.001	29.0	5.2	–	–	–	–	–
	Omnivorous shrimps versus crayfish	9.2	14.7	20.8	34.9	23.2	–	–	–	–	–
	Detritivorous versus omnivorous shrimps	29.5	21.0	28.6	51.3	11.3	14.0	22.5	37.9	75.4	34.7

A dash (−) indicates that no data is available

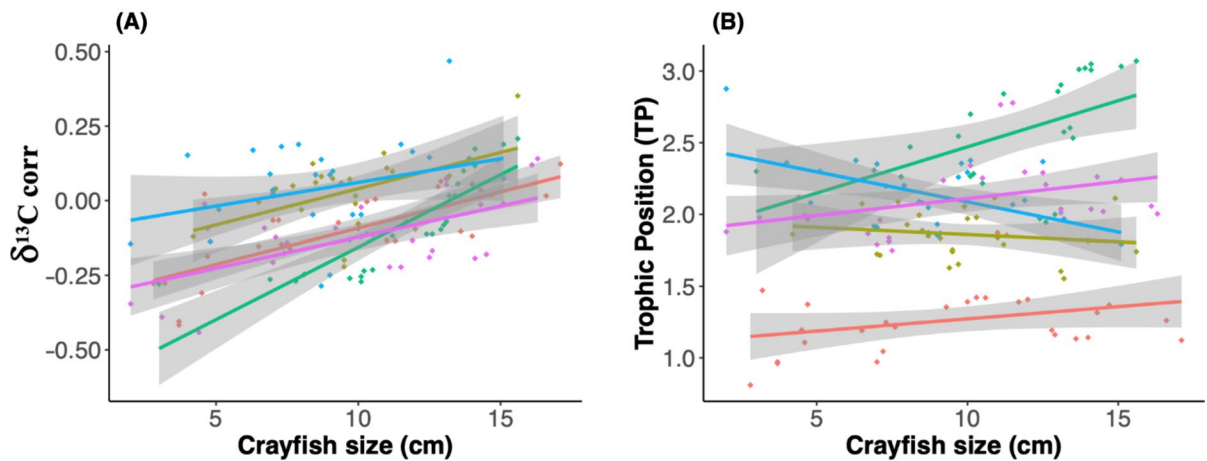**Fig. 2** Variations in **A** individual δ^{13}C corrected (δ^{13}Ccor, in ‰) and **B** trophic position (TP) values according to crayfish size (total length, in cm) in the five invaded stations (I1 to I5, in red, brown, blue, violet, and green, respectively). Grey shade as 95% CI of estimated models
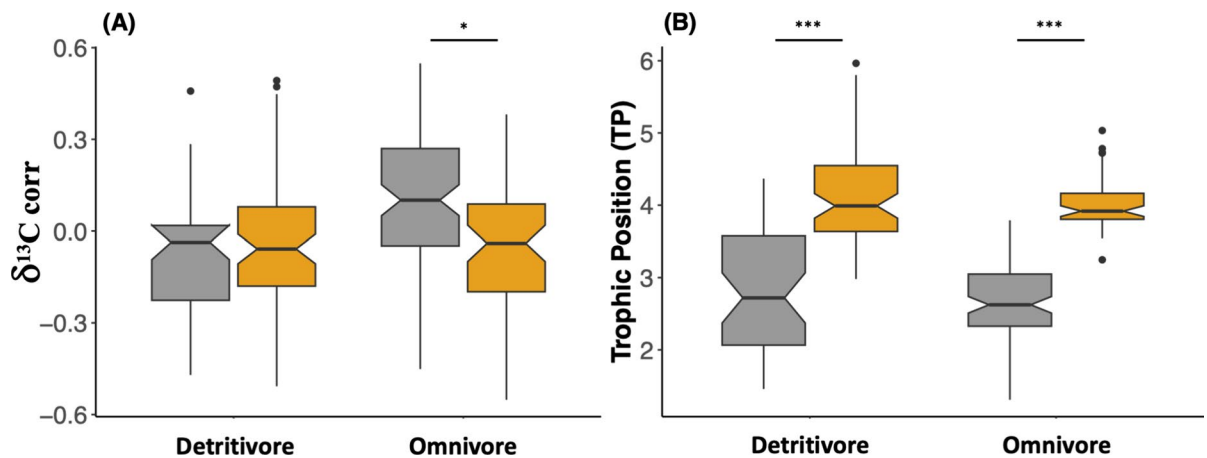

Fig. 3 Comparison of **A** corrected δ^{13}C (δ^{13}Ccor, in ‰) and **B** trophic positions (TP) of the two shrimp trophic groups (detritivore and omnivore) according to crayfish presence in stations (invaded in grey and uninvaded in orange). Boxplots include the minimum, first quartile, median, third quartile and the maximum values excluding outliers which are represented by black dots. *$p = 0.05$, ***$p < 0.001$

detritivorous shrimps; $F = 0.56$, $p = 0.48$; and 3.75 vs. 3.91‰^{2} for omnivorous shrimps; $F = 0.59$, $p = 0.46$); however, large variations occurred within the two sets of stations (Fig. 4, Table 1). Trophic niche was smaller in crayfish than in both shrimp groups (1.50 vs. 2.72‰^{2} for detritivorous shrimps and 3.75‰^{2} for omnivorous shrimps) and, despite large between-station variations, crayfish niche, on average, partially overlapped the niche of detritivorous shrimps (mean value of 14.9 ± 13.8%; range: 0.001–29.9%) and the

one of omnivorous shrimps (20.5 ± 9.7%; range: 9.2–34.9%, Table 1, Fig. 4). In addition, average niche overlap was larger between the two shrimp groups (28.3 ± 14.7%) compared to crayfish (14.9 ± 13.8% and 20.5 ± 9.7% for detritivorous and omnivorous shrimps, respectively). Finally, no significant difference was found in niche overlap between the two shrimp groups when they were, or not, in sympatry with crayfish (28.3 ± 14.7% vs. 36.9 ± 23.6%, respectively; $F = 0.48$, $p = 0.51$).
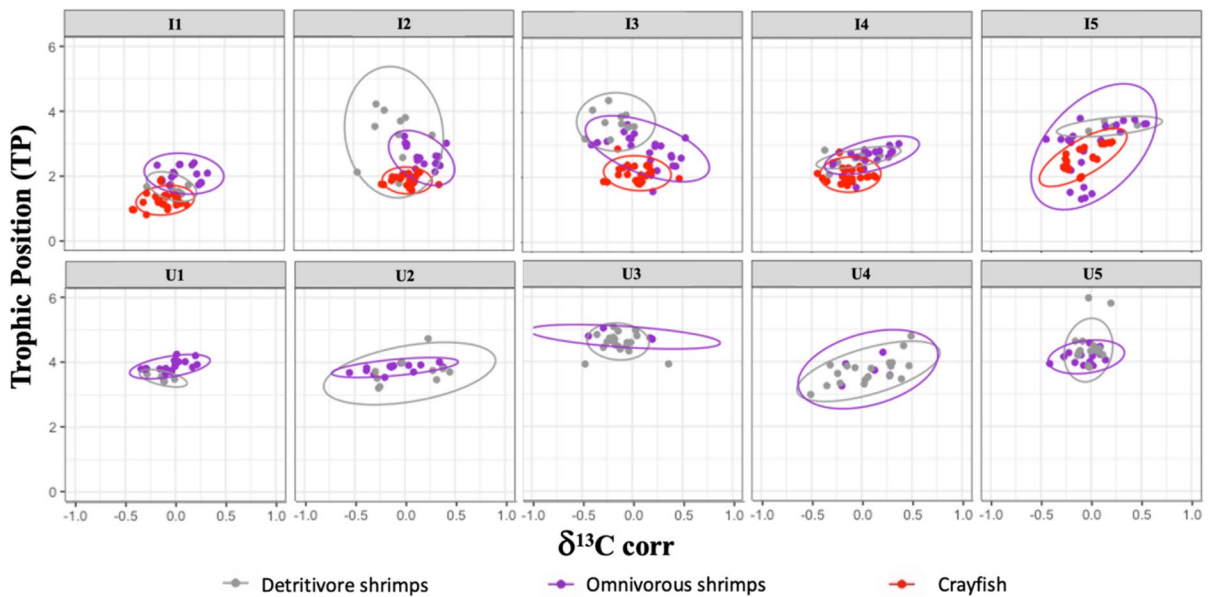
Fig. 4 Stable isotope values (δ^{13}Ccor (in ‰) and trophic positions TP) of individuals of the two shrimp groups (detritivorous and omnivorous shrimps, in grey and violet, respectively) and the invasive redclaw crayfish (in red), with their associated standard ellipses across invaded (I1–I5) and non-invaded (U1–U5) stations. Variable extent of niche overlap is noted between crustaceans

Discussion

Investigating the trophic ecology of invasive species in recipient ecosystems is a valuable way to evaluate its successful invasion ability and possible impacts on native species (McCue et al. 2020). In the present study, we provided unique results on the trophic ecology of the newly established invasive redclaw crayfish (a central position in the food webs with a primary consumer tendency at the population level, and dietary ontogenetic shifts) and low niche overlap with native shrimps in Martinican freshwaters. Below, we discuss these two issues separately, and we conclude by future investigations to progress on these issues and on the potential repercussions on the structure and functioning of invaded ecosystems.

Trophic ecology of the redclaw crayfish

The average TP value of 1.99 of the redclaw crayfish in the freshwater ecosystems of Martinique is broadly lower to what was found in the invaded Southern African region [2.61–2.87 in Marufu et al. (2018), and 2.10–4.10 in Zengeya et al. (2022)]. In turn, our results place the redclaw crayfish mostly at a primary consumer, which aligns with findings in farming conditions (Joyce and Pirozzi 2016). Furthermore, its consistent central position in the Martinican aquatic food webs (TP typical of a primary consumer and δ^{13}Ccor values near zero) suggests that it probably provides a pivotal connection between primary production and detrital matter and higher consumers. This finding is consistent with findings in other invasive crayfish species (see for instance, Alcorlo and Baltanás, 2013; Lipták et al. 2019; Pacioglu et al. 2019; Linzmaier et al. 2020). Finally, the intermediate TP value of crayfish populations can be explained by a diet directed preferentially towards basal resources (plant and detritus material). In the past, it has been documented that, under competitive pressure, newly introduced crayfish rather consume easily accessible materials (plants and detritus) even if they are less nutritious (Gherardi and Acquistapace 2007; Reynolds et al. 2013). Furthermore, the low between-population variations in δ^{13}Ccor and TP values we found, when compared, for instance, to values in Zengeya et al. (2022) probably express the simplified food web architecture in island systems (Vitousek 1988; Myers et al. 2000).

At the individual level, we, however, found within- and between-station variations in TP and δ^{13}Ccor values confirming that the redclaw crayfish was facultative omnivore and, in some extent, flexible in likely food resource use as reported elsewhere in its non-native range (Marufu et al. 2018; Zengeya et al. 2022). More precisely, we found evidence to support both the dietary ontogeny shift and dietary habitat-linked plasticity hypotheses since TP and δ^{13}Ccor varied with crayfish size, with different intensity and, sometimes different trends (the case of δ^{13}Ccor) across stations. Large-sized individuals fed food with lower TP values in some stations (likely in link with food availability), the trend was reversed in other stations, and they had, consistently, enriched δ^{13}Ccor values when compared to small crayfish. Evidence for dietary ontogenetic shifts has been found in other crayfish (to satisfy specific life-stage nutrient requirements; Jones 1990; Momot 1995; Reynolds et al. 2013), but once again with variable extent and some inconsistently across studies (e.g. Guan and Wiles 1998; Alcorlo and Baltanás 2013; Jackson et al. 2017; Veselý et al. 2020). All crayfish species in these specific works were found to be omnivorous and flexible in food resources use, usually moving towards dominant available food sources (see also Ercoli et al. 2014; Zengeya et al. 2022). The two aforementioned hypotheses have also found support in other invasive freshwater crustacean (for instance in the killer shrimp *Dikerogammarus villosus*, Mancini et al. 2021) and taxa, notably in fish (Harms and Turingan 2012; McHugh et al. 2012; Guo et al. 2014), in reptilian (the red-eared slider *Trachemys scripta elegans*, Balzani et al. 2016) and in amphibian (the American bullfrog *Lithobates catesbeianus*, Bissattini et al. 2019).

Extent of competition with native shrimps

The recent expansion of the redclaw crayfish in Martinique suggest that it presumably developed efficient competitive interactions with native ubiquitous crustacean counterparts. The niche position of omnivorous shrimps varied with crayfish presence indicating a trophic displacement (enriched δ^{13}Ccor and lower TP values) without any changes in niche size. Niche overlap of omnivorous shrimps with the invasive crayfish was slightly higher than between detritivorous shrimps and crayfish (c.a. 20 and 15%, respectively, with up to 35% depending on stations for omnivorous shrimps). These findings indicate that crayfish and native omnivorous shrimps share partly the same food resources, and that the invader could mainly impacts shrimps by exploitative competition [see also similar findings with a native omnivorous crab in Zengeya et al. (2022)]. Empirical case studies supporting the competitive superiority hypothesis of introduced crayfish are not rare, but with variable ends: from only partial niche overlap (Olsson et al. 2009; Ercoli et al. 2014; Magoulick and Piercey 2016) to niche constriction leading sometimes to local extirpation of the native competitor (Rabalais and Magoulick 2006; Jackson et al. 2017; Veselý et al. 2021). Competition for shelter and aggressive behaviour are other mechanisms supposed or documented to explain the interactions between invasive crayfish and functionally similar native crustaceans (Banha and Anastácio 2011); but, unfortunately, we did not possess data to explore this issue. A matter that remains unresolved in the present study is whether the observed trophic niche displacement of omnivorous shrimps is sufficient for them to coexist with redclaw crayfish in the future (see below).

Successful invasive species are frequently thought to have a competitive advantage over native species (i.e. a higher efficiency in exploiting available food resources; Bollache et al. 2008; Davidson et al. 2011; Alexander et al. 2014). Consequently, they are expected to feed on a large range of food resources and to have larger trophic niches than functionally similar native species. For instance, Wang et al. (2021) demonstrated that the red swamp crayfish was competitively superior to the native *Macrobrachium nipponense* in the Yangtze (China) thanks to a greater feeding plasticity. Interestingly, in the present study, the niche size of the redclaw crayfish was regularly narrower than the one of both native functional shrimp groups (mean value of 1.50‰^{2} vs. 2.72 and 3.75‰^{2} for detritivorous and omnivorous shrimps). One possible explanation of this result would be that redclaw crayfish do not yet fully use all available food resources since the species recently invaded freshwater food webs in Martinique. An alternative explanation would be that crayfish exploit all available resources indicating that they would not be as harmful as expected and that resource partitioning with native competitors is possible. However, a limitation in our work is to compare crayfish trophic niches with those

of shrimp groups (detritivore and omnivore) and not to a particular shrimp species due to small numbers of specimens usually found in Martinican streams. In such a case, it cannot be excluded that niche size could vary among shrimp species of a group and that the group likely has a wider trophic niche than a single compared species (see similar findings for fish species in Dillon et al. 2021). Further investigations are therefore required to study with more precision the competitive advantage hypothesis of the invasive redclaw crayfish compared to native shrimps. Finally, it is interesting to note that the niche size of shrimps did not vary with redclaw crayfish presence suggesting that the trophic flexibility of the two groups of native crustaceans was not strongly affected in sympatry with the invasive crayfish few years after its introduction. However, additional investigations are needed to examine whether these results would be stable over time (i.e. with increasing invasive crayfish population size).

Conclusive remarks, future prospects and management implications

Our study provides unique findings on the trophic ecology of the invasive redclaw crayfish in insular lotic Caribbean environments few years after its introduction. It occupies a central position in the food webs feeding, however, on a limited range of resources (resulting in small trophic niche sizes compared to that of shrimp groups) probably in line with the simplified food web architecture of insular ecosystems under study. Ontogenetic and habitat-linked changes in the trophic niche of crayfish attest its ability to adapt to changes in food availability which make it a successful invader. Finally, slight changes in the niche position of native competitive crustaceans (mainly in omnivorous shrimps) were observed when living with the invasive crayfish.

It is difficult to claim that the recently introduced redclaw crayfish significantly impact the food web architecture of Martinican freshwaters, even if it is largely documented that insular food webs are highly vulnerable to biological invasions (Velmurugan 2008; Barlow et al. 2018; Chong et al. 2021). We call for additional investigations to elucidate possible long-term effects of redclaw crayfish on native shrimps communities. As a reminder, this species dramatically impacted Southern African recipient ecosystems

15 years after its introduction (Zengeya et al. 2022). Current crayfish abundance in Martinican freshwaters are logically moderate but are expected to increase with time (Baudry et al. 2021). So, we first predict that impacts on native crustaceans would increase with growing redclaw crayfish abundance (the abundance impact hypothesis; Bradley et al. 2019), an issue that has not been tested until now in this species. Second, given that trophic niches vary according to environmental conditions, conducting mesocosm studies under controlled environmental conditions and, for instance, with different crayfish abundance, would be helpful to disentangle the respective effect of both factors. Third, competitive superiority of redclaw crayfish compared to native crustaceans in Martinique remains to be studied using, for instance, functional response experiments. Finally, crayfish and omnivorous shrimps share some similar food resources, this mean that they have partially comparable functional roles. Further studies are thus required to investigate the extent of potential ecological redundancy of redclaw crayfish with native species, and, ultimately, possible implications for the structure and functioning of invaded ecosystems.

As aforementioned, our results may describe a transitory state due to the recent introduction of redclaw crayfish in Martinique. To date, all proposed strategies for managing invasive crayfish species have focused on control measures (see Manfrin et al. 2019). Even though fishing is banned in Martinique (Prefectorial decree no. R02-2017-12-28-003) due to chlordecone contamination in particular, this activity remains a reality, being ancestral and above all lucrative for local fishermen (see Baudry et al. 2022). The effectiveness of such a management method can be limited, even if locally it can significantly reduce crayfish abundance and thus limit new infestations. The challenge in Martinique is to mitigate redclaw crayfish in connected streams. Physical barriers would therefore be required to limit crayfish spreading in parallel to control operations (Reisinger et al. 2024). All those management actions are costly, very time-consuming and cannot be conducted over the long term. Surprisingly, basic information on the demography of invasive species is often lacking while being fundamental for the design of effective management programs. Therefore, monitoring programs should be implemented to track changes in the demography the redclaw crayfish and native shrimp communities and

to identify the causes of change over time and space. More broadly, any management action aimed at maintaining local biodiversity would make freshwater ecosystems more resistant to the invasive crayfish.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Alcorlo P, Baltanás A (2013) The trophic ecology of the red swamp crayfish (*Procambarus clarkii*) in Mediterranean aquatic ecosystems: a stable isotope study. Limnetica 32:121–138. https://doi.org/10.23818/limn.32.12

Alcorlo P, Geiger W, Otero M et al (2004) Feeding preferences and food selection of the red swamp crayfish, *Procambarus clarkii*, in habitats differing in food item diversity. Crustaceana 77:435–453

Alexander ME, Dick JTA, Weyl OLF et al (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biol Lett 10:20130946. https://doi.org/10.1098/rsbl.2013.0946

Arzola-Gonzalez JF, Maya de la Cruz E, Verde Osuna LI et al (2012) Crecimiento, densidad y rentabilidad del cultivo de langosta de agua dulce (Decapoda: *Cherax quadricarinatus*) en Sinaloa, Mexico. Ra Ximhai 8:17–26

Balzani P, Vizzini S, Santini G et al (2016) Stable isotope analysis of trophic niche in two co-occurring native and invasive terrapins, *Emys orbicularis* and *Trachemys scripta elegans*. Biol Invasions 18:3611–3621. https://doi.org/10.1007/s10530-016-1251-x

Banha F, Anastácio PM (2011) Interactions between invasive crayfish and native river shrimp. Knowl Manag Aquat Ecosyst 401:1–12. https://doi.org/10.1051/kmae/2011033

Barlow J, França F, Gardner T et al (2018) The future of hyperdiverse tropical ecosystems. Nature 559:517–526. https://doi.org/10.1038/s41586-018-0301-1

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Baudry T, Becking T, Goût JP et al (2020) Invasion and distribution of the redclaw crayfish, *Cherax quadricarinatus*, in Martinique. Knowl Manag Aquat Ecosyst 421:50. https://doi.org/10.1051/kmae/2020041

Baudry T, Mauvisseau Q, Goût J et al (2021) Mapping a super-invader in a biodiversity hotspot, an eDNA-based success story. Ecol Ind 126:107637. https://doi.org/10.1016/j.ecolind.2021.107637

Baudry T, Gismondi E, Goût J-P et al (2022) The invasive crayfish *Cherax quadricarinatus* facing chlordecone in Martinique: bioaccumulation and depuration study. Chemosphere 286:131926. https://doi.org/10.1016/j.chemosphere.2021.131926

Bissattini A, Buono V, Vignoli L (2019) Disentangling the trophic interactions between American bullfrogs and native anurans: complications resulting from post-metamorphic ontogenetic niche shifts. Aquat Conserv Mar Freshw Ecosyst 29:270–281. https://doi.org/10.1002/aqc.3023

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. Biol Lett 4:166–169. https://doi.org/10.1098/rsbl.2007.0554

Bradley B, Laginhas B, Whitlock R et al (2019) Disentangling the abundance–impact relationship for invasive species. Proc Natl Acad Sci 116:9919–9924. https://doi.org/10.1073/pnas.1818081116

Chong KY, Corlett RT, Nuñez MA et al (2021) Are terrestrial biological invasions different in the tropics? Annu Rev Ecol Evol Syst 52:291–314. https://doi.org/10.1146/annurev-ecolsys-012021-095454

Coat S, Monti D, Bouchon C, Lepoint G (2009) Trophic relationships in a tropical stream food web assessed by stable isotope analysis. Freshw Biol 54:1028–1041. https://doi.org/10.1111/j.1365-2427.2008.02149.x

Correia A (2003) Food choice by the introduced crayfish *Procambarus clarkii*. Ann Zool Fenn 40:517–528

Covich AP, Crowl TA, Heartsill-Scalley T (2006) Effects of drought and hurricane disturbances on headwater distributions of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains. Puerto Rico Freshw Sci 25:99–107. https://doi.org/10.1899/0887-3593(2006)25[99:EODAHD]2.0.CO;2

David P, Thébault E, Anneville O et al (2017) Impacts of invasive species on food webs: a review of empirical data. Adv Ecol Res 56:1–60. https://doi.org/10.1016/bs.aecr.2016.10.001

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. Ecol Lett 14:419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

de Moor I (2002) Potential impacts of alien freshwater crayfish in South Africa. Afr J Aquat Sci 27:125–139. https://doi.org/10.2989/16085914.2002.9626584

Debrot AO (2003) A review of the freshwater fishes of Curaçao, with comments on those of Aruba and Bonaire. Carib J Sci 39:100–108

Delannoye R, Charles L, Pointier J-P, Massemin D (2015) Mollusques continentaux de la Martinique/Non-Marine Molluscs of Martinique, Lesser Antilles, Muséum national d'histoire naturelle

Dillon KS, Fleming CR, Slife C, Leaf RT (2021) Stable isotopic niche variability and overlap across four fish guilds in the North-Central Gulf of Mexico. Mar Coast Fish 13:213–227. https://doi.org/10.1002/mcf2.10148

Dubreuil T, Baudry T, Mauvisseau Q et al (2021) The development of early monitoring tools to detect aquatic invasive species: eDNA assay development and the case of the armored catfish *Hypostomus robinii*. Environ DNA 4:349–362. https://doi.org/10.1002/edn3.260

Elton CS (1958) The ecology of invasions by animals and plants. Springer, New York

Ercoli F, Ruokonen T, Hamalaïnen H (2014) Does the introduced signal crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal lakes? Biol Invasions 16:2025–2036. https://doi.org/10.1034/j.1600-0706.2003.12098.x

Ercoli F, Ruokonen TJ, Koistinen S et al (2015) The introduced signal crayfish and native noble crayfish have different effects on sublittoral macroinvertebrate assemblages in boreal lakes. Freshw Biol 60:1688–1698. https://doi.org/10.1111/fwb.12601

Evangelista C, Boiche A, Lecerf A, Cucherousset J (2014) Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. J Anim Ecol 83:1025–1034. https://doi.org/10.1111/1365-2656.12208

Gherardi F, Acquistapace P (2007) Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake. Freshw Biol 52:1249–1259. https://doi.org/10.1111/j.1365-2427.2007.01760.x

Gherardi F, Aquiloni L, Diéguez-Uribeondo J, Tricarico E (2011) Managing invasive crayfish: Is there a hope? Aquat Sci 73:185–200. https://doi.org/10.1007/s00027-011-0181-z

Guan R, Wiles PR (1998) Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. Aquaculture 169:177–193. https://doi.org/10.1016/S0044-8486(98)00377-9

Guo Z, Liu J, Lek S et al (2014) Trophic niche differences between two congeneric goby species: evidence for ontogenetic diet shift and habitat use. Aquat Biol 20:23–33. https://doi.org/10.3354/ab00530

Harms C, Turingan R (2012) Dietary flexibility despite behavioral stereotypy contributes to successful invasion of the pike killifish, *Belonesox belizanus*, in Florida, USA. Aquat Invasions 7:547–553. https://doi.org/10.3391/ai.2012.7.4.011

Haubrock PJ, Oficialdegui FJ, Zeng Y et al (2021) The redclaw crayfish: a prominent aquaculture species with invasive potential in tropical and subtropical biodiversity hotspots. Rev Aquac 13:1488–1530. https://doi.org/10.1111/raq.12531

Herrmann A, Grabow K, Martens A (2022) The invasive crayfish *Faxonius immunis* causes the collapse of macroinvertebrate communities in Central European ponds. Aquat Ecol 56:741–750. https://doi.org/10.1007/s10452-021-09935-5

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. J Anim Ecol 80:595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson MC, Grey J, Miller K et al (2016) Dietary niche constriction when invaders meet natives: evidence from freshwater decapods. J Anim Ecol 85:1098–1107. https://doi.org/10.1111/1365-2656.12533

Jackson MC, Evangelista C, Zhao T et al (2017) Between-lake variation in the trophic ecology of an invasive crayfish. Freshw Biol 62:1501–1510. https://doi.org/10.1111/fwb.12957

Jones C (1990) The biology and aquaculture potential of the tropical freshwater crayfish, *Cherax quadricarinatus*. Department of Primary Industries Queensland, Brisbane, QLD, Australia

Joyce MK, Pirozzi I (2016) Using stable isotope analysis to determine the contribution of naturally occurring pond biota and supplementary feed to the diet of farmed Australian freshwater crayfish, redclaw (*Cherax quadricarinatus*). Int Aquat Res 8:1–13. https://doi.org/10.1007/s40071-015-0119-5

Kestrup ÅM, Ricciardi A (2009) Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. Biol Invasions 11:2095–2105. https://doi.org/10.1007/s10530-009-9490-8

Kilham SS, Hunte-Brown M, Verburg P et al (2009) Challenges for interpreting stable isotope fractionation of carbon and nitrogen in tropical aquatic ecosystems. SIL Proc 1922–2010(30):749–753. https://doi.org/10.1080/03680770.2009.11902231

King CR (1994) Growth and survival of redclaw crayfish hatchlings (*Cherax quadricarinatus* von Martens) in relation to temperature, with comments on the relative suitability of *Cherax quadricarinatus* and *Cherax destructor* for culture in Queensland. Aquaculture 122:75–80. https://doi.org/10.1016/0044-8486(94)90335-2

Kozák P, Ďuriš Z, Petrusek A et al (2015) Crayfish biology and culture. University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, Vodňany, Czech Republic

Lim P, Meunier FJ, Keith PA, Noël PY (2002) Atlas des poissons et des crustacés d'eau douce de la Martinique. Muséum National d'Histoire Naturelle, Paris. Patrimoines Naturels, 51, 124.

Linzmaier SM, Musseau C, Matern S, Jeschke JM (2020) Trophic ecology of invasive marbled and spiny-cheek crayfish populations. Biol Invasions 22:3339–3356. https://doi.org/10.1007/s10530-020-02328-z

Lipták B, Veselý L, Ercoli F et al (2019) Trophic role of marbled crayfish in a lentic freshwater ecosystem Boris. Aquat Invasions 14:299–309. https://doi.org/10.3391/ai.2019.14.2.09

Lodge DM, Deines A, Gherardi F et al (2012) Global introductions of crayfishes: evaluating the impact of species invasions on ecosystem services. Annu Rev Ecol Evol Syst 43:449–472. https://doi.org/10.1146/annurev-ecolsys-111511-103919

Maddi FA (2014) Contribution à l'inventaire de la flore dulçaquicole de la Martinique: les «espèces exotiques envahissantes». Bilan des prospections

Magoulick DD, Piercey GL (2016) Trophic overlap between native and invasive stream crayfish. Hydrobiologia 766:237–246. https://doi.org/10.1007/s10750-015-2457-0

Mancini F, De Giorgi R, Ludovisi A et al (2021) Ontogenetic shift in the trophic role of the invasive killer shrimp *Dikerogammarus villosus*: a stable isotope study. Biol Invasions 23:1803–1817. https://doi.org/10.1007/s10530-021-02472-0

Manfrin C, Souty-Grosset C, Anastácio PM et al (2019) Detection and control of invasive freshwater crayfish: from traditional to innovative methods. Diversity 11:1–16. https://doi.org/10.3390/d11010005

March JG, Pringle CM (2003) Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. Biotropica 35:84–93. https://doi.org/10.1111/j.1744-7429.2003.tb00265.x

Marufu L, Dalu T, Crispen P et al (2018) The diet of an invasive crayfish, *Cherax quadricarinatus* (Von Martens, 1868), in Lake Kariba, inferred using stomach content and stable isotope analyses. BioInvasions Rec 7:121–132. https://doi.org/10.3391/bir.2018.7.2.03

McCue M, Javal M, Clusella-Trullas S et al (2020) Using stable isotope analysis to answer fundamental questions in invasion ecology: progress and prospects. Methods Ecol Evol 11:196–214. https://doi.org/10.1111/2041-210X.13327

McCutchan JH Jr, Lewis WM Jr, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x

McHugh P, McIntosh A, Howard S, Budy P (2012) Niche flexibility and trout-galaxiid co-occurrence in a hydrologically diverse riverine landscape. Biol Invasions 14:2393–2406. https://doi.org/10.1007/s10530-012-0237-6

Momot WT (1995) Redefining the role of crayfish in aquatic ecosystems. Rev Fish Sci 3:33–63. https://doi.org/10.1080/10641269509388566

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Nieto C, Ovando XMC, Loyola R et al (2017) The role of macroinvertebrates for conservation of freshwater systems. Ecol Evol 7:5502–5513. https://doi.org/10.1002/ece3.3101

Nordlie FG (1981) Feeding and reproductive biology of eleotrid fishes in a tropical estuary. J Fish Biol 18:97–110. https://doi.org/10.1111/j.1095-8649.1981.tb03764.x

Oficialdegui FJ, Sánchez MI, Clavero M (2020) One century away from home: how the red swamp crayfish took over the world. Rev Fish Biol Fish 30:121–135. https://doi.org/10.1007/s11160-020-09594-z

Olsson K, Stenroth P, Nystrom P, Granéli W (2009) Invasions and niche width: Does niche width of an introduced crayfish differ from a native crayfish? Freshw Biol 54:1731–1740. https://doi.org/10.1111/j.1365-2427.2009.02221.x

Pacioglu O, Zubrod JP, Schulz R et al (2019) Two is better than one: combining gut content and stable isotope analyses to infer trophic interactions between native and invasive species. Hydrobiologia 839:25–35. https://doi.org/10.1007/s10750-019-03990-8

Pringle CM, Blake GA, Covich AP et al (1993) Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. Oecologia 93:1–11. https://doi.org/10.1007/BF00321183

R Development Core Team (2023) R: a language and environment for statistical computing. https://www.R-project.org/

Rabalais MR, Magoulick DD (2006) Is competition with the invasive crayfish *Orconectes neglectus chaenodactylus* responsible for the displacement of the native crayfish *Orconectes eupunctus*? Biol Invasions 8:1039–1048. https://doi.org/10.1007/s10530-005-4649-4

Reisinger L, Tripp N, Atchia A et al (2024) Can intensive trapping to reduce the abundance of an invasive crayfish benefit an imperiled congener? Aquat Conserv Mar Freshw Ecosyst 34:e4123. https://doi.org/10.1002/aqc.4123

Reynolds J, Souty-Grosset C (2011) Management of freshwater diodiversity: crayfish as bioindicators. Cambridge University Press, Cambridge

Reynolds J, Souty-Grosset C, Richardson A (2013) Ecological roles of crayfish in freshwater and terrestrial habitats. Freshw Crayfish 19:197–218. https://doi.org/10.5869/fc.2013.v19-2.197

Ricciardi A, Hoopes M, Marchetti M, Lockwood J (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282. https://doi.org/10.1890/13-0183.1

Souty-Grosset C, Anastácio PM, Aquiloni L et al (2016) The red swamp crayfish *Procambarus clarkii* in Europe: impacts on aquatic ecosystems and human well-being. Limnologica 58:78–93. https://doi.org/10.1016/j.limno.2016.03.003

Tropea C, Piazza Y, López LS (2010) Effect of long-term exposure to high temperature on survival, growth and reproductive parameters of the 'redclaw' crayfish *Cherax quadricarinatus*. Aquaculture 302:49–56. https://doi.org/10.1016/j.aquaculture.2010.01.027

Twardochleb LA, Olden JD, Larson ER (2013) A global meta-analysis of the ecological impacts of nonnative crayfish. Freshw Sci 32:1367–1382. https://doi.org/10.1899/12-203.1

Vander Zanden M, Rasmussen J (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80:1395–1404

Velmurugan A (2008) Chapter 1—The nature and characters of tropical islands. In: Sivaperuman C, Velmurugan A, Singh AK, Jaisankar IBT-B, CCA in TI (eds) Biodiversity and climate change adaptation in tropical islands. Academic Press, Cambridge, pp 3–30

Veselý L, Ercoli F, Ruokonen TJ et al (2020) The crayfish distribution, feeding plasticity, seasonal isotopic variation and trophic role across ontogeny and habitat in a canyon-shaped reservoir. Aquat Ecol 54:1169–1183. https://doi.org/10.1007/s10452-020-09801-w

Veselý L, Ruokonen TJ, Weiperth A et al (2021) Trophic niches of three sympatric invasive crayfish of EU concern. Hydrobiologia 848:727–737. https://doi.org/10.1007/s10750-020-04479-5

Vitousek PM (1988) Diversity and biological invasions of oceanic islands. In Wilson EO, Peter FM (eds) Biodiversity. Washington, DC, USA: National Academy Press, pp 181–189

Wallace JB, Webster JR (1996) The role of macroinvertebrates in stream ecosystem function. Annu Rev Entomol 41:115–139. https://doi.org/10.1146/annurev.en.41.010196.000555

Wang Y, Tan W, Li B et al (2021) Habitat alteration facilitates the dominance of invasive species through disrupting niche partitioning in floodplain wetlands. Divers Distrib 27:1861–1871. https://doi.org/10.1111/ddi.13376

Wickham H, François R, Henry L, et al (2023) dplyr: a grammar of data manipulation

Wingfield M (2002) An overview of the Australian freshwater crayfish farming industry. Freshw Crayfish 13:177–184

Wissinger SA, Klemmer AJ, Braccia A et al (2021) Relationships between macroinvertebrates and detritus in freshwater wetlands. Freshw Sci 40:681–698. https://doi.org/10.1086/717487

Zengeya TA, Lombard RJH, Nelwamondo VE et al (2022) Trophic niche of an invasive generalist consumer: Australian redclaw crayfish, *Cherax quadricarinatus*, in the Inkomati River Basin, South Africa. Austral Ecol 47:1480–1494. https://doi.org/10.1111/aec.13230