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Interspecies differences in food sources for the tropical callichirid shrimp *Neocallichirus* spp. on San Salvador Island, Bahamas

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ABSTRACT: At least 4 species of callichirid shrimp coexist in the shallow marine settings of San Salvador Island, an isolated, small platform of the all-carbonates Bahama Archipelago, implying that interspecific competition or trophic niche segregation occurs between these shrimp species. Carbon and nitrogen stable isotope analyses were conducted on soft tissues of 3 callichirid species, *Neocallichirus cacahuate*, *N. grandimana*, and *N. maryae*, to determine the food sources for each species. These analyses revealed that the isotopic trophic niches for these 3 species do not overlap. The most important food source for all 3 species was manatee grass *Syringodium filiforme*. The second most important food source for *N. cacahuate* and *N. grandimana* was drifting seaweed *Sargassum* sp., whereas that for *N. maryae* was turtle grass *Thalassia testudium*. These food-source adaptations likely contribute to the high species diversity of callichirid shrimp in tropical settings such as those found on San Salvador Island.

KEY WORDS: Axiidea · Callichiridae · *Neocallichirus* · Food sources · Stable isotopes · Bahamas

1. INTRODUCTION

Callichirid shrimp (Decapoda: Axiidea, sensu Poore et al. 2019) are common deep burrowers and powerful bioturbators in intertidal to shallow subtidal sandy substrates in temperate and tropical zones (Dworschak 2004, Dworschak et al. 2012). The burrowing activities of these shrimp are particularly important in seafloor ecosystems because they influence nutrient cycling in seabed sediments (Ziebis et al. 1996, Kristensen et al. 2012). Callichirids are common in the shallow marine settings of the numerous islands of the all-carbonate platforms of the Bahama Archipelago. Four species of callichirids, *Neocallichirus cacahuate*, *N. grandimana*, *N. maryae*, and *Glypturus acanthochirus*, have been identified dur-

ing previous fieldwork on San Salvador Island (Curran & Seike 2017), a small island located atop an isolated platform on the east-central edge of the Bahama Archipelago. Thus, this island could be a 'hot spot' of callichirid diversity, with offshore and deeper settings remaining to be explored.

The co-occurrence of at least 4 callichirid species in the shallow marine environments around San Salvador Island suggests that interspecific competition or trophic niche segregation may occur among these species. In general, resource partitioning is important for species coexistence because niche overlap of co-occurring species reflects intense competition (Geange et al. 2011), indicating that the callichirid shrimp around San Salvador Island have species-specific trophic strategies. Previous research using carbon

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and nitrogen stable isotope analyses has revealed trophic niche partitioning among co-occurring benthic invertebrates in intertidal to shallow subtidal sandy substrates in temperate and tropical zones (Boon et al. 1997, Abed-Navandi & Dworschak 2005, Abed-Navandi et al. 2005, Seike & Goto 2020, Yunda-Guarin et al. 2022).

Several recent carbon and nitrogen stable isotope studies have documented the dietary preferences of axiidean and gebiidean shrimp, including callichirid species in shallow marine settings (Boon et al. 1997, Abed-Navandi & Dworschak 2005, Abed-Navandi et al. 2005, Leduc et al. 2006, Umezawa et al. 2018). Stable isotope analysis may provide information about the trophic niches of the co-occurring callichirid shrimp of the shallow marine ecosystems of San Salvador Island and reveal whether resource partitioning occurs among the shrimp or not. Although previous studies investigated the major food sources of *Neocallichirus* species based on their stable isotope analyses (Murphy & Kremer 1992, Abed-Navandi & Dworschak 2005), a robust isotopic result was not obtained.

This study tested the hypothesis that the co-occurring callichirid species show trophic niche partitioning to avoid interspecific competitive exclusion. We investigated this hypothesis by using multiple complementary approaches and by determining the isotope trophic niche and food source contributions for each shrimp species. We also discuss burrow morphology of these species, as reported by Curran & Seike (2017), because these morphologies reflect the different feeding strategies of the species (Nickell & Atkinson 1995).

2. MATERIALS AND METHODS

2.1. Study sites

Fieldwork for this study was conducted in January 2015 at 2 primary sites on San Salvador Island: Graham's Harbour (Fig. 1A) and Pigeon Creek (Fig. 1B). Located at the north end of the island, Graham's Harbour is a high-energy, windward lagoon that is rimmed to the northeast by North Point, to the north by a bank-barrier coral reef and offshore cays, and is largely open to the west. The Holocene depositional evolution of Graham's Harbour was the subject of a comprehensive study by Colby & Boardman (1989). A detailed sediment facies analysis conducted on the eastern edge of the lagoon identified 3 distinct ecologic zones (Randazzo & Baisley 1995: their Figs. 1 & 2).

The nearshore margin of the *Thalassia* zone is mostly devoid of vegetation, and callichirid burrows are abundant in a sandy band of about 30 m running from the beach of the Gerace Research Centre campus east to the Government dock area (Fig. 1C); further details are given in Curran & Seike (2017). Thick seagrass beds of *Thalassia testudinum* (turtle grass) and *Syringodium filiforme* (manatee grass), with *Halodule wrightii* (shoalweed) as a minor component, lie in slightly deeper water offshore from this sandy margin (Fig. 1D).

Located at the southeastern corner of San Salvador (Fig. 1B), Pigeon Creek is a slightly hypersaline lagoon without freshwater flow. The sedimentology of Pigeon Creek has been described in detail by Mitchell (1987) and expanded by Cummins et al. (1995), including an analysis of its molluscan taphonomy. Our site in Pigeon Creek for this study was a small, intertidal sand flat on the south arm of Pigeon Creek (Fig. 1E), very close to the inlet to the open Atlantic Ocean (Curran & Seike 2017). Here, narrow burrow openings (~1 cm diameter) with small sediment cones formed by *Neocallichirus grandimana* are common. A thick fringe of red mangroves *Rhizophora mangle* borders both arms of Pigeon Creek, and seagrass (*T. testudinum* and *S. filiforme*) beds are widespread but discontinuous offshore. Shallow subtidal sandy areas with mounds and funnels generated by *N. maryae* and bordered by seagrass beds lie close to the *N. grandimana* site.

2.2. Callichirids and their burrows on San Salvador

2.2.1. *Neocallichirus cacahuate*

N. cacahuate Felder & Manning, 1995 (Fig. 2A) was originally reported as a minor component of the thalassinidean community of an intertidal flat on Peanut Island, located just inside the Lake Worth Inlet in Palm Beach County on the Atlantic coast of southern Florida (Felder & Manning 1995). The geographic range of *N. cacahuate* was significantly extended with its identification from sandy, shallow subtidal habitats in Graham's Harbour and Long Bay on San Salvador Island (Curran & Seike 2017), where it appears to be at least fairly common, and from northeastern Brazil (Pachelle et al. 2017). Our concerted attempts to make burrow casts for *N. cacahuate* were unsuccessful. The burrow morphology is unknown, but hand excavations indicate that individuals likely form deep and substantial burrow systems.

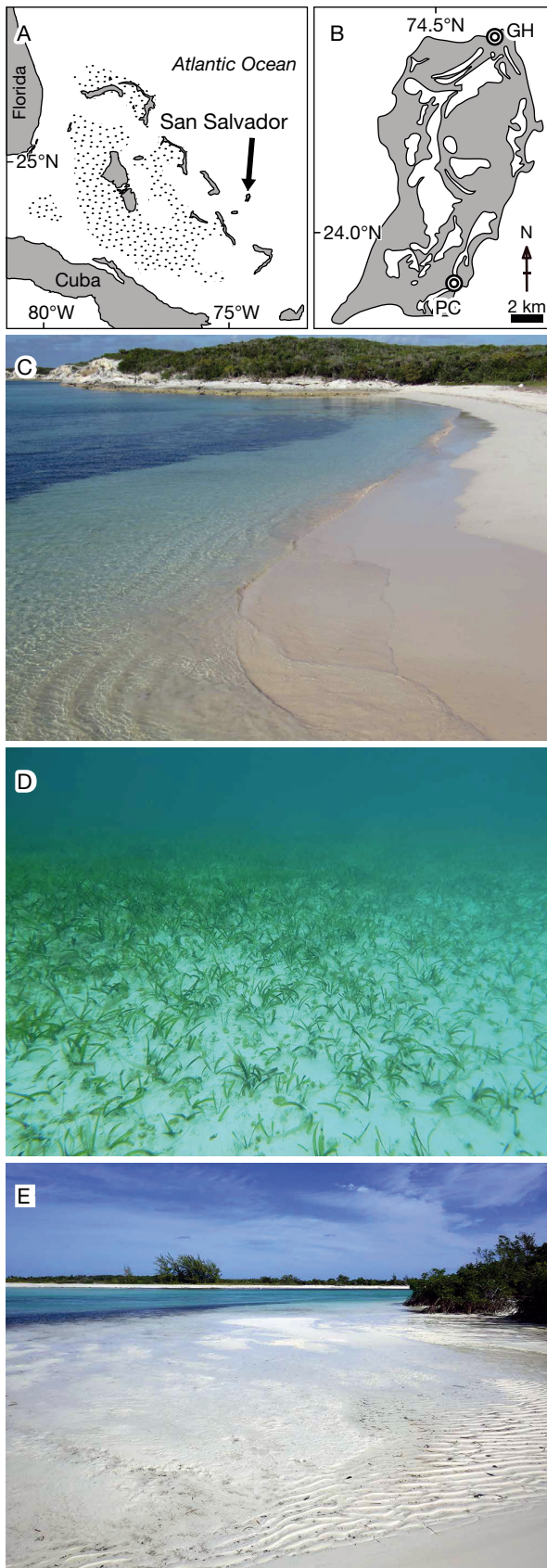


Fig. 1. Location and environmental characteristics of the study sites. (A) Location of San Salvador Island within the Bahama Archipelago. (B) Study sites on San Salvador. GH: Grahams Harbour, PC: Pigeon Creek. (C) Coastline of Grahams Harbour site. (D) Seafloor of Grahams Harbour site in February 2011; seagrass is dominant, including abundant *Thalassia testudium* and less abundant *Syringodium filiforme*. Burrows of callichirids *Neocallichirus maryae* and *N. cacahuate* are common, particularly in more open areas (Curran & Seike 2017). (E) Intertidal flat of the Pigeon Creek site in January 2015; *N. grandimana* burrows are common here. Nearby, shallow subtidal sandy areas near seagrass beds commonly exhibit mounds and funnels created by *N. maryae*

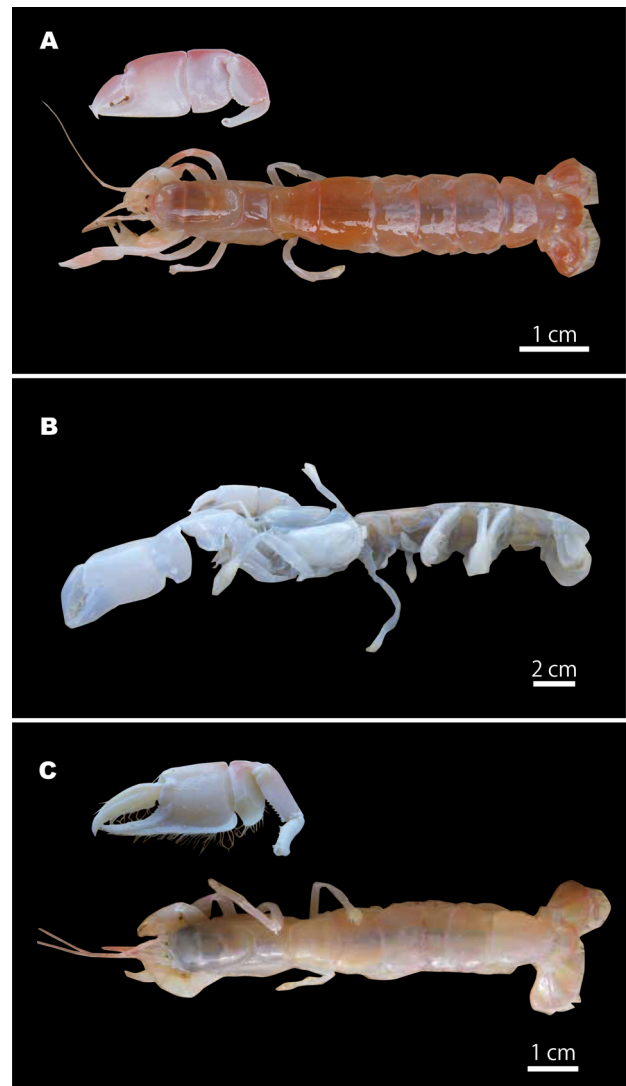


Fig. 2. *Neocallichirus* species analyzed in this study. (A) *N. cacahuate*. (B) *N. grandimana*. (C) *N. maryae*

2.2.2. *Neocallichirus grandimana*

N. grandimana (Gibbes, 1850) (Fig. 2B); junior synonym is *Glypterus branneri* Rathbun, 1900; is one of the most common intertidal and shallow subtidal callichirids of the western Atlantic. This species has wide geographic distribution, including southern Florida (Felder & Manning 1995), the Bahamas (Curran & Seike 2017), the Caribbean (Dworschak & Ott 1993), and, most recently, south of Brazil (Pachelle & Tavares 2020). In addition, *N. grandimana* has been reported from the Pacific coast of Columbia (Lemaitre & Ramos 1992), giving this species an ampho-American distribution range.

At our intertidal study site on San Salvador, burrow openings were typically about 1 cm in diameter

(Fig. 3B). Although Dworschak & Ott (1993) reported simple, shallow, and mainly horizontal burrows for this species in Belize, the burrow cast made by Curran & Seike (2017) revealed a robust and more complex burrow form that extended to at least 0.5 m depth and probably deeper (Fig. 3A). Short tunnels that branched off from major tunnels had knob-like termini or chamber structures that were commonly stuffed with vegetative matter (Fig. 3C). An X-ray CT image from the cast of a burrow tunnel segment contained a major cheliped which confirmed the identity of the burrow maker (Fig. 3D).

The deep and rectangularly branched structure (layered lattice) of these burrows has been interpreted as resulting from subsurface sediment mining (deposit-feeding) by these shrimp (Nickell & Atkin-

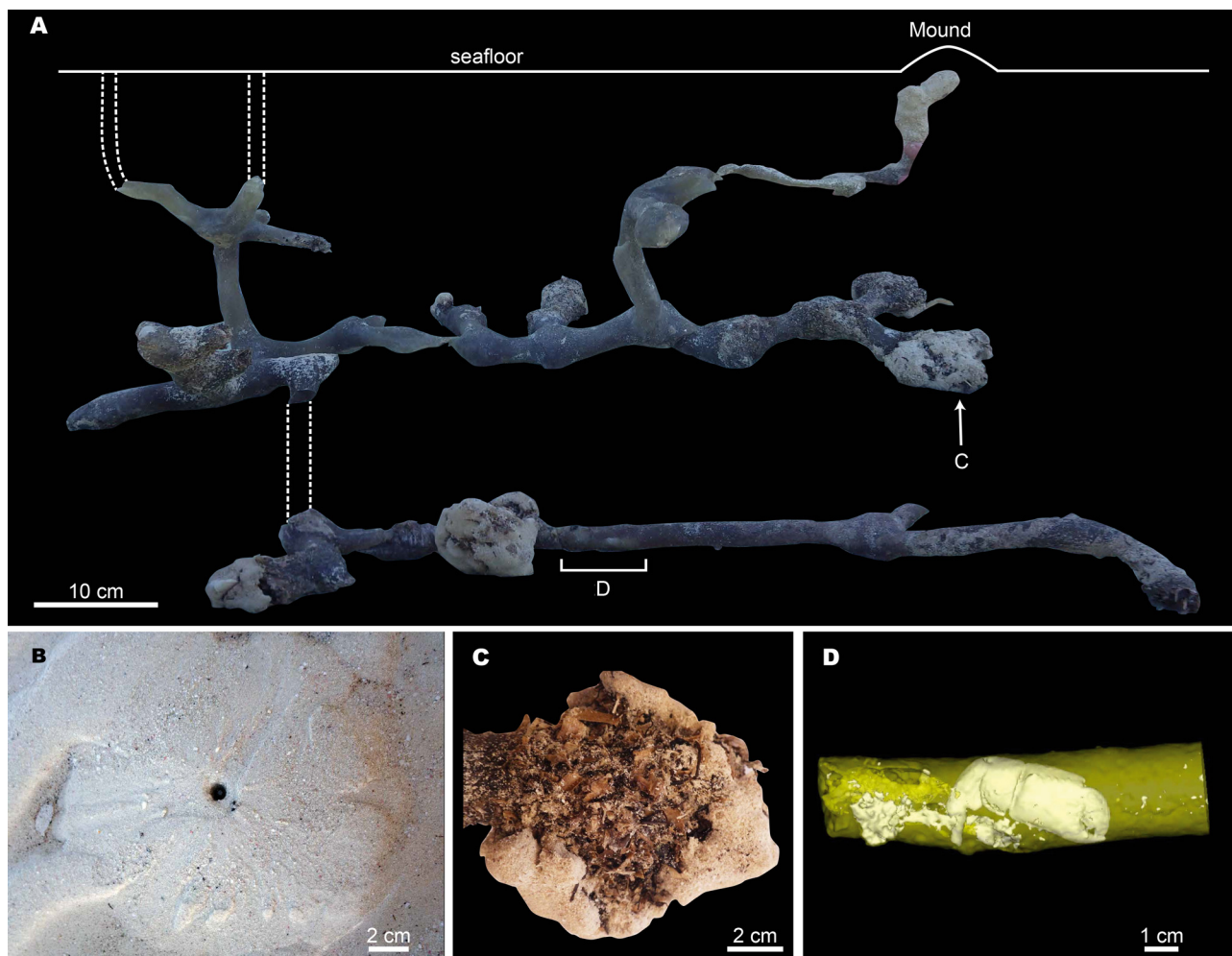


Fig. 3. Burrow characteristics of *Neocallichirus grandimana* at the Pigeon Creek site. (A) Cast of *N. grandimana* burrow, expanded and modified from Curran & Seike (2017; their Fig. 7) with addition of the lower-level burrow cast. (B) Aperture of *N. grandimana* burrow on the tidal flat surface. (C) Close-up view of the lower surface of a chamber of the *N. grandimana* burrow. Note aggregation of plant detritus at the base of the chamber. (D) X-ray CT image of part of the burrow cast. Green and white colors represent burrow cast (polyester resin) and hard structure (major cheliped) of the shrimp, respectively

son 1995). The knob-like terminus (chamber) structures stuffed with vegetative matter imply that the food source for these shrimp is plant debris. This indicates that *N. grandimana* mines subsurface sediment for plant debris and stores it in the burrow chambers for later use.

2.2.3. *Neocallichirus maryae*

N. maryae Karasawa, 2004 (Fig. 2C); formerly *Callianassa rathbunae* Schmitt, 1935, and preoccupied by the fossil *C. rathbunae* Glaessner, 1929; also has a wide distribution throughout the subtropical and tropical western North Atlantic. It has been reported from Bermuda (Abed-Navandi 2000), southern Florida and the Bahamas (Curran & Seike 2017), south of the Caribbean, and beyond to northeastern Brazil (Pachelle et al. 2017).

This callichirid can be common in shallow subtidal, sandy-bottom settings and will generate well-defined mound and funnel structures under fair-weather conditions (Fig. 4A). Individuals of *N. maryae* are known to form complex burrows (Fig. 4C–E; Suchanek 1985, Griffis & Suchanek 1991, Curran & Seike 2017); the entire burrow morphology is U-shaped, but it has numerous small chambers. An X-ray CT image of a part of one of our burrow casts revealed major and minor shrimp chelipeds preserved within, thus permitting confirmation of the species that makes this burrow form (Fig. 4F).

In the field, individuals that looked like *N. maryae* were commonly situated at the entrance of their burrows (Fig. 4B), although it is possible that at least some might have been individuals of a different species. The goal of this behavior appears to be to catch floating seagrass leaves as they are moved close to the burrow opening by wave-generated currents. When a diver extends a seagrass leaf near a shrimp poised at the burrow opening, the individual will gladly take it from the hand. Once within the burrow, such plant detritus is stored within the chambers (Fig. 4C). These 3 *Neocallichirus* species are thought to be closely related based on their molecular phylogenetic analyses (Robles et al. 2020).

2.3. Collection and sample preparation of shrimp and their food sources

The field survey was conducted in January 2015. Using a yabby pump, we collected *Neocallichirus* shrimp for the stable isotope analysis from seagrass

meadows in Grahams Harbour and from tidal flats bordering Pigeon Creek (Fig. 1A,B). We attempted to obtain >10 individuals, but this was extremely difficult for *N. maryae*. The complex burrow morphology of *N. maryae* made the suctioning upward of individual shrimp difficult. We collected samples of *N. cacahuete* (n = 21) and *N. maryae* (n = 2) from the Grahams Harbour site, and samples of *N. grandimana* (n = 12) and *N. maryae* (n = 1) from the Pigeon Creek site. Immediately after collection, muscle tissue samples were dissected from abdominal muscles and claws of the shrimp and dried at 60°C in an oven in the Gerace Research Centre sample preparation laboratory for later stable isotope analysis. Samples of potential food sources for the shrimp, including seafloor litter of *S. filiforme*, *T. testudium*, and *R. mangle*, and samples of drifting *Sargassum* sp., were collected from the Pigeon Creek site. Plant and algal debris is particularly abundant along protected coastal areas of San Salvador and also within burrows of the callichirid shrimp, suggesting that this is the food source for these shrimp. Soon after collection, the plant materials were washed in clean water to remove epibionts and then dried at 60°C. Subsequently, the dried samples were packaged and transported to Japan for stable isotope analysis in the laboratories of the Atmosphere and Ocean Research Institute, The University of Tokyo.

2.4. Stable isotope analyses and food-source modeling

To remove inorganic carbon, all samples were acidified with 1 N HCl and dried again at 60°C. Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were measured with an isotope-ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific) coupled with an elemental analyzer (Flash2000, Thermo Fisher Scientific). Stable isotope ratios are expressed in δ notation as deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta^{13}\text{C}, \delta^{15}\text{N} = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 10^3 \quad (1)$$

where R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Vienna Pee Dee Belemnite and atmospheric nitrogen were used as isotope standards for carbon and nitrogen, respectively. Analytical precision of the Delta V Advantage mass spectrometer system, based on standard deviation of the internal reference replicates, was <0.15‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

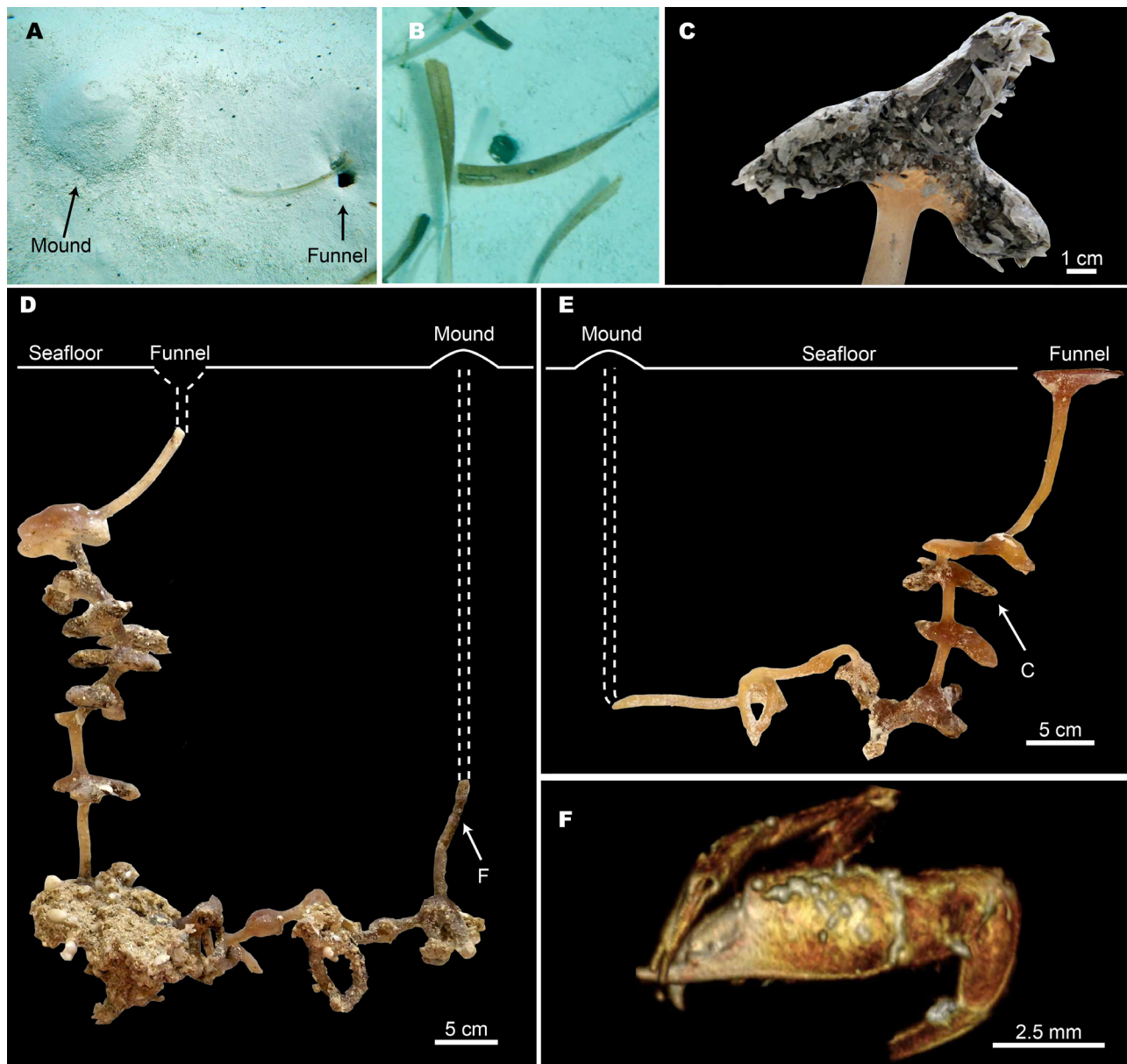


Fig. 4. Burrow characteristics of *Neocallichirus maryae* in Grahams Harbour. (A) Mound and funnel of *N. maryae* burrow system. (B) A shrimp, likely *N. maryae*, at the entrance of its burrow in Grahams Harbour. This appears to be behavior for catching seagrass leaves drifting by the burrow opening. (C) Close-up view of the lower surface of a chamber from the *N. maryae* burrow cast shown in (E). Note aggregation of plant detritus within this chamber. (D) Largely complete resin casts of *N. maryae* burrows, modified from Curran & Seike (2017; their Fig. 5A). (E) Another *N. maryae* burrow cast, modified from Curran & Seike (2017; their Fig. 5B). (F) X-ray CT image of segment of the burrow cast shown in (D). Major and minor shrimp chelipeds were preserved in resin, thus confirming *N. maryae* as the burrow producer

ANOVA was used to examine the effect of shrimp species on isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, $\alpha = 0.05$). A post hoc Tukey's test was performed when significant differences were found ($\alpha = 0.05$). We used the Stable Isotope Bayesian Ellipses in R (SIBER) package version 2.1.6 (Jackson et al. 2011) to characterize the isotopic trophic niche for the 3 *Neocallichirus*

species. Isotopic trophic niche was estimated and compared using the following variables: Layman metric of convex hull area (TA), standard ellipse areas (SEA), and standard ellipse areas corrected for small sample sizes (SEAc, an ellipse that contains 40% of the data regardless of sample size). We also calculated the magnitude of the isotopic overlap

between the 3 *Neocallichirus* species based on the SEAc calculation.

The Stable Isotope Mixing Models in R (SIMMR) package version 0.4.5 (Parnell 2021) was used to partition the proportional contributions of potential food sources for the 3 shrimp species based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures. The SIMMR model works by determining the probability distributions of sources that contribute to the observed mixed signal, while accounting for uncertainty in signatures of the sources and isotopic fractionation. We defined 4 sources (*Sargassum* sp., *S. filiforme*, *T. testudium*, and *R. mangle*) as end members for the isotopic mixing model. The trophic enrichment factors for muscle tissue of the calianassid shrimp *Nihonotrypaea harmandi* (2.0‰ for carbon and 3.9‰ for nitrogen; Yokoyama et al. 2005a) was used. In addition, widely accepted values for the trophic enrichment factors ($0.4 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $3.4 \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ per trophic step; Post 2002) were also used. All statistical analyses were conducted using R version 4.1.2 (R Core Team 2021).

3. RESULTS

3.1. Isotopic niche of *Neocallichirus*

The isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the food sources are shown in Fig. 5. Food sources most depleted in $\delta^{13}\text{C}$ were *Rhizophora mangle* (-26.1‰), followed by *Sargassum* sp. (-17.6‰), *Thalassia testudium* (-10.4‰), and *Syringodium filiforme*, which was least depleted (-8.5‰). For $\delta^{15}\text{N}$ values, *S. filiforme* was the most depleted (-1.8‰) in $\delta^{15}\text{N}$, with *Sargassum* sp. (-0.6‰), *R. mangle* (0.3‰), and *T. testudium* (1.1‰) being more enriched.

The detailed isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for the *Neocallichirus* species are also shown in Fig. 5. Values of $\delta^{13}\text{C}$ varied by species (ANOVA, $F_{2,33} = 12.008$, $p < 0.001$). The species most depleted in $\delta^{13}\text{C}$ was *N. grandimana* (mean: -13.9‰), followed by *N. cacahuete* (mean: -12.7‰), and *N. maryae*, which was least depleted (mean: -10.1‰). All pairwise comparisons between the species were significant (Tukey's test, $p < 0.05$). Values of $\delta^{15}\text{N}$ also varied by species (ANOVA, $F_{2,33} = 16.388$, $p < 0.001$). *N. cacahuete* was most depleted (mean: 0.8‰), with *N. maryae* (mean: 0.9‰) and *N. grandimana* (mean: 2.1‰) being more enriched. The value for *N. grandimana* differed significantly from those of the other species (Tukey's test, $p < 0.05$), although *N. maryae* was not significantly different from *N. cacahuete* (Tukey's test, $p > 0.05$).

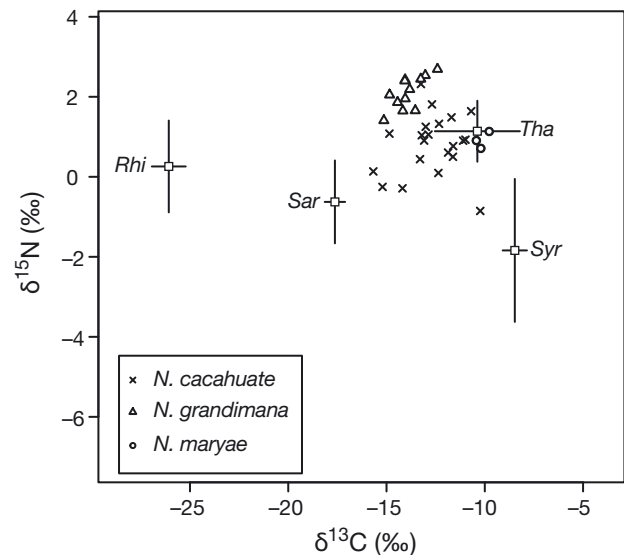


Fig. 5. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the 3 *Neocallichirus* species. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of potential food sources, including *Sargassum* sp. (Sar), *Syringodium filiforme* (Syr), *Thalassia testudium* (Tha), and *Rhizophora mangle* (Rhi), and with 2 σ error bars. Stable isotope values for the 3 *Neocallichirus* species are not corrected for isotopic discrimination

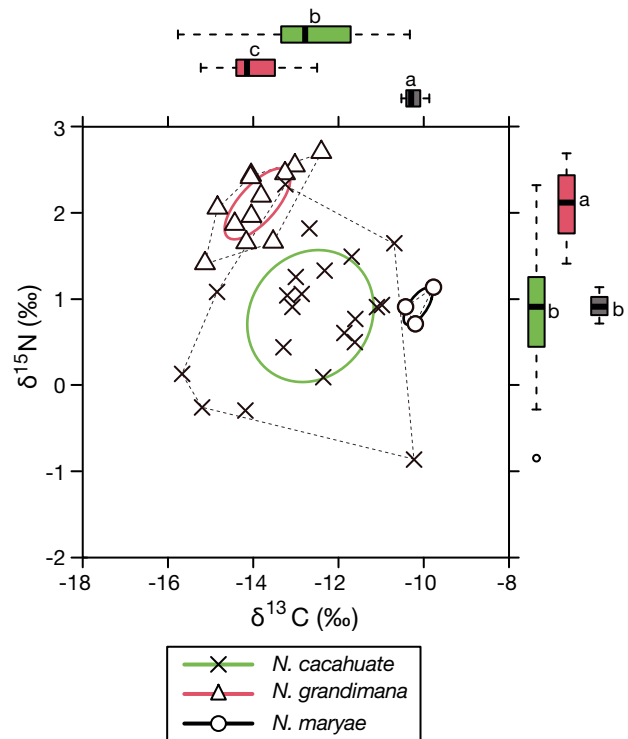


Fig. 6. Overlap of Bayesian standard ellipse at 40% confidence (SEAc) for the 3 *Neocallichirus* species. Convex full areas (dotted line) are also depicted. Boxplot shows $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the 3 *Neocallichirus* species. Bold lines: medians; boxes: 25th and 75th percentiles; whiskers: 1.5 \times interquartile range; dots: outliers. Different letters indicate significant differences in mean values ($p < 0.05$; Tukey's test)

We used the SIBER models of isotope signatures to infer the isotopic niche of each *Neocallichirus* species (Fig. 6). For *N. cacahuate*, the TA, SEA, and SEAc values were 11.3, 3.5, and 3.6, respectively. For *N. grandimana*, the equivalent values were 1.6, 0.7, and 0.8, respectively, and for *N. maryae*, they were 0.1, 0.2, and 0.3, respectively. The SEAc of the 3 *Neocallichirus* species did not overlap (Fig. 6).

3.2. Mixing model

We used the SIMMR models of isotope signatures to infer food sources for the *Neocallichirus* species. These models are based on the trophic enrichment factors of previous researchers (trophic enrichment factors for muscle tissue of callinassid shrimp from Yokoyama et al. 2005a, and the widely accepted factors of Post 2002), and both showed similar patterns.

Results based on the taxon-specific values for the trophic enrichment factor (Fig. 7) were as follows: *N. cacahuate*, the median percentage contributions and 95% CI for *Sargassum* sp., *T. testudium*, *S. filiforme*, and *R. mangle* were 25.5% (3.0–61.2%), 5.3% (0.9–20.7%), 46.8% (26.3–62.7%), and 20.3% (2.8–33.1%), respectively. For *N. grandimana*, the equivalent values were 32.7% (3.1–75.2%), 4.9% (0.9–17.7%), 36.9% (14.0–53.8%), and 24.2% (2.4–40.2%), respectively, and for *N. maryae*, they were 15.5% (2.1–39.4%), 13.2% (1.9–63.1%), 57.8% (10.2–76.0%), and 10.5% (1.9–22.9%), respectively.

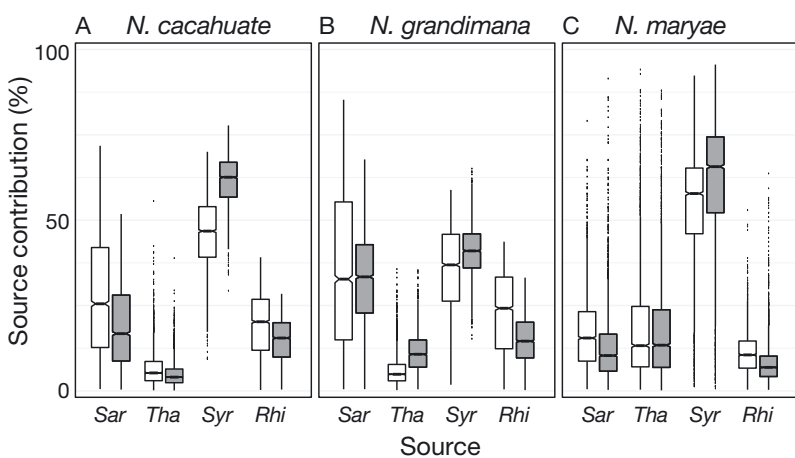


Fig. 7. Percentage contributions of food sources including *Sargassum* sp. (*Sar*), *Thalassia testudium* (*Tha*), *Syringodium filiforme* (*Syr*), and *Rhizophora mangle* (*Rhi*) to the diet of the 3 *Neocallichirus* species. Results are based on taxon-specific trophic enrichment factors (open boxes) and widely accepted trophic enrichment factors (gray boxes). Bold lines: medians; boxes: 25th and 75th percentiles; whiskers: 1.5× interquartile range; dots: outliers

Results based on the widely accepted values for the trophic enrichment factor (Fig. 7) were as follows: For *N. cacahuate*, the median percentage contributions and 95% CI for *Sargassum* sp., *T. testudium*, *S. filiforme*, and *R. mangle* were 15.8% (2.0–42.8%), 3.8% (0.8–13.3%), 63.1% (47.8–72.9%), and 16.0% (2.7–25.2%), respectively. For *N. grandimana*, the equivalent values were 33.3% (7.6–56.4%), 10.9% (2.2–23.8%), 40.8% (26.4–55.8%), and 14.5% (2.8–28.2%), respectively, and for *N. maryae*, they were 10.1% (1.7–42.2%), 13.0% (1.6–64.1%), 66.9% (11.4–86.3%), and 6.8% (1.3–25.5%), respectively.

4. DISCUSSION

4.1. Interspecies differences in food sources among the *Neocallichirus* species

The SIBER model revealed that the 3 co-occurring *Neocallichirus* species exhibit trophic niche partitioning. These 3 shrimp species inhabiting the same geographic area differ not only regarding feeding mode (burrow morphology), but also isotopic trophic niche (Fig. 6), although the precise feeding mode (burrow morphology) of *N. cacahuate* remains unknown.

The SIMMR model also showed that food sources of the 3 *Neocallichirus* species partially differ (Fig. 7). Even though we used the SIMMR model based on 2 different trophic enrichment factors, the distribution of food source contributions was almost the same for these 3 species. This suggests that results based on the model are valid and robust. The most important food source for all 3 species was *Syringodium filiforme*. Although *Thalassia testudium* is the most prominent seagrass vegetation in the study sites (Fig. 1), this is not the most important food source for the *Neocallichirus* shrimp, implying that food choice is not a result of the nearest vegetation but originates from active selection by the shrimp. The shrimp store seagrass leaves in their burrow chambers and then consume the leaves after some decay. Decayed leaves are known to contain abundant microorganisms such as bacteria, which is the major source of essential nutrients for detritivores. Microbial biomass on decayed *S. filiforme* leaves

is known to be much greater than on decayed *Thalassia* and mangrove leaves (Blum et al. 1988). This may well be the reason why *S. filiforme* is the most common food source for these *Neocallichirus* species. Conversely, the second most important food source differed between the species.

In addition, the SIMMR model showed that *N. maryae* feeds mainly on drifting seagrass leaves (*S. filiforme* and *T. testudium*), with the combined contribution to the shrimp diet being >70% (Fig. 7). Plant detritus aggregated within the chambers of the burrow (Fig. 4C) also suggests that *N. maryae* consumes seagrass leaves. In contrast, the model also showed that this species does not utilize *Sargassum* sp. and *Rhizophora mangle* (Fig. 7).

In contrast to the present study, previous studies have postulated that *N. maryae* is a deposit feeder, feeding on benthic microalgae. Suchanek (1983) concluded that *N. maryae* is a deposit feeder because the burrow morphology of this shrimp is multi-branched. Murphy & Kremer (1992) reported $\delta^{13}\text{C}$ values for shrimp collected from the British Virgin Islands in the summer season. Although it was not stated which shrimp body part was used for isotope analysis, the $\delta^{13}\text{C}$ value was 19.17‰, which corresponded to that of benthic microalgae in the habitat of this shrimp. Given the above observation, these shrimp appear to have derived approximately 100% of their nutritional requirements from benthic microalgae.

The mean $\delta^{13}\text{C}$ value for *N. maryae* in the present study was 10.1‰, which is 9‰ higher than that reported by Murphy & Kremer (1992). This large difference cannot be explained by a difference in sampling season or the sampled shrimp body parts alone. The variations in $\delta^{13}\text{C}$ values for callichirid body parts and sampling season are <0.6‰ (Yokoyama et al. 2005a) and <0.5‰ (Shimoda et al. 2007), respectively. The sizable difference in $\delta^{13}\text{C}$ values for *N. maryae* (as *Callianassa rathbunae*) reported by Murphy & Kremer (1992) and measured in the present study suggests that this difference resulted from bodies of different callichirid species being analyzed, rather than from plasticity of feeding preference in *N. maryae*. New species of *Neocallichirus* are continuing to be discovered (Felder & Manning 1995, Karasawa 2004, Hernáez et al. 2020), suggesting that misidentification was certainly possible; and Murphy & Kremer (1992) alluded to the fact that their specimens were difficult to identify to species level.

Suchanek (1983) interpreted *N. maryae* as a deposit feeder based on burrow morphology. However, the burrow cast obtained by Suchanek (1983) represents only the upper part of the burrow system, con-

sidering the burrow casting results of Curran & Seike (2017; see our Fig. 4D,E, modified and expanded from their Fig. 5A,B). Knowledge of whole burrow morphology enhances the interpretation of callichirid feeding behavior, and, in this case, we were fortunate to have been able to obtain a near-complete burrow cast from the field plus measure stable isotope ratios. We also observed the behavior of shrimp waiting near their burrow entrances to capture passing seagrass leaves (Fig. 4B), which is a typical behavior for seagrass-eating shrimp (Dworschak et al. 2006, Seike & Goto, 2017). In addition, our cast captured aggregated plant debris in the burrow chamber (Fig. 4C). Carbonate sediments in tropical, shallow marine settings are known to have low organic content (Miyajima et al. 1998), further implying that *N. maryae* is not a deposit feeder. The absence of multibranched structure in *N. maryae* burrow also suggests that the shrimp do not gather seagrass leaves by subsurface sediment mining but by catching leaves drifting just above the seafloor surface.

Although Abed-Navandi & Dworschak (2005) concluded that the major food source of *N. grandimana* is seagrass leaves based on their stable isotope analyses, a robust isotopic result was not obtained. The *N. grandimana* burrow cast of Dworschak & Ott (1993) was incomplete considering the casting results of Curran & Seike (2017; their Fig. 7). For the above reasons, the feeding strategy of this species was unresolved by the previous studies.

Our burrow casts from the Pigeon Creek site revealed the near-complete burrow morphology of *N. grandimana*, including features of the burrow aperture. Along with the stable isotope ratio analyses of the shrimp and plant material contained in the burrows, we can accurately determine the feeding ecology of this species. The narrow burrow aperture suggests that this shrimp cannot normally emerge from the subsurface, and thus exploits food from subsurface sediment, rather than from the overlying waters. The deep and multi-branched burrow also suggests subsurface feeding by this species. As stated earlier, the carbonate sediments of tropical islands typically have low organic content (Miyajima et al. 1998). However, this case is an exception. The Pigeon Creek tidal channel is narrow, lined with red mangroves, and has strong diurnal tidal-current exchange with the open Atlantic Ocean, providing a continuous supply of *Sargassum*. Vegetative material can easily become buried in the shifting sediments of the channel margins. The branched structures (layered lattice) of the burrows of *N. grandimana* indi-

cate subsurface deposit feeding by this shrimp (Nickell & Atkinson 1995). The presence of the knob-like termini (chamber) structures stuffed with vegetative matter clearly indicates that the food source for this shrimp is buried plant debris, mined from subsurface sediment and stored in its burrow chambers for later consumption.

The SIMMR model revealed that *N. grandimana* mainly consumes *S. filiforme* and also *Sargassum* sp. (Fig. 7). In addition, the food source contribution of *R. mangle* was >10% for both trophic enrichment factors. Thus *N. grandimana* shrimp have a relatively varied diet. In contrast to *N. maryae*, the dietary contribution of *T. testudium* was relatively low (Fig. 7). As discussed above, *N. grandimana* mines the detrital (decayed) seagrass leaves from subsurface sediment. Although the decay process of *T. testudium* leaves is slower than that of *S. filiforme*, the detrital *T. testudium* leaves have much less microbial biomass than those of *S. filiforme* (Blum et al. 1988), indicating that decayed leaves of *T. testudium* contain less food available for detritivores than those of *S. filiforme*. This could be the reason why *T. testudium* leaves are not readily available for later consumption by *N. grandimana*.

The result of the SIMMR model for *N. cacahuete* is similar to that of *N. grandimana* (Fig. 7), indicating that *N. cacahuete* utilizes plant material buried in the sediment for its food. However, the complete feeding strategy of *N. cacahuete* remains unconfirmed due to our inability to make representative burrow casts for this species. Hopefully these difficulties can be overcome in the future.

4.2. Trophic strategies of the *Neocallichirus* shrimp

Carbon and nitrogen stable isotope analyses reported in previous studies have revealed that callichirid and upogebiid shrimp living in temperate zone shallow marine settings feed mainly on benthic microalgae and marine phytoplankton (e.g. Yokoyama et al. 2005b, Leduc et al. 2006, Shimoda et al. 2007, Seike & Goto 2020, Seike et al. 2020), while terrestrial and riverine plant materials are only minor food source constituents for these shrimp in these settings.

In tropical settings, microalgae such as benthic diatoms and bacterial mat matter are also important food sources for callichirid and upogebiid shrimp (Murphy & Kremer 1992). Abed-Navandi & Dworschak (2005) reported that the major food source for *Glypturus acanthochirus* is cyanobacterial mat mat-

ter. On the intertidal sand flats of Pigeon Creek, the small-sized *Upogebia vasquezi* shrimp create a complex U-shaped burrow (Curran & Martin 2003), indicating that they are filter feeders and consume microalgae suspended in overlying waters (Nickell & Atkinson 1995, Lindahl & Baden 1997, Seike et al. 2020).

In addition to microalgae on the substrate and in overlying waters, studies employing stable isotope analysis methods have revealed that seagrass leaves are important food sources for callichirid shrimps such as *Corallianassa longiventris* and *C. coutierei*, the axiid shrimp *Axiopsis serratifrons*, and the strahlaxiid shrimp *Neaxius acanthus* (Abed-Navandi & Dworschak 2005, Kneer et al. 2008). Also, a field survey and aquarium experiments revealed that the major food source for 2 species, *C. longiventris* and *Pestarella tyrrhena*, is seagrass debris (Dworschak et al. 2006).

The results of the present study showed that drifting seaweed (*Sargassum* sp.) and quasi-terrestrial plant leaves (*R. mangle*) are also important food sources for *N. grandimana*. Because seafloor carbonate substrates in the tropical zone are typically low in organic content, callichirids are normally not deposit feeders, as they can utilize several plant materials found in seawater as their food sources. However, our study showed that *N. grandimana* can have a highly diverse diet with up to at least 24% *R. mangle* leaf material, thereby exhibiting high diversity in feeding ecology. This ecological adaptation likely contributes considerably to the high species diversity of callichirid shrimp documented from the shallow-marine settings around San Salvador Island.

Data availability. All data is publicly available online in the figshare data repository; <https://doi.org/10.6084/m9.figshare.21960512.v1>.

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