

Use of Multiple Chemical Tracers to Define Habitat Use of Indo-Pacific Mangrove Crab, *Scylla Serrata* (Decapoda: Portunidae)

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Abstract The mangrove or mud crab, *Scylla serrata*, is an important component of mangrove fisheries throughout the Indo-Pacific. Understanding crab diets and habitat use should assist in managing these fisheries and could provide

additional justification for conservation of the mangrove ecosystem itself. We used multiple chemical tracers to test whether crab movements were restricted to local mangrove forests, or extended to include adjacent seagrass beds and reef flats. We sampled three mangrove forests on the island of Kosrae in the Federated States of Micronesia at Lelu Harbor, Okat River, and Utwe tidal channel. Samples of *S. serrata* and likely food sources were analyzed for stable carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) isotopes. *Scylla serrata* tissues also were analyzed for phosphorus (P), cations (K, Ca, Mg, Na), and trace elements (Mn, Fe, Cu, Zn, and B). Discriminant analysis indicated that at least 87% of the crabs remain in each site as distinct populations. Crab stable isotope values indicated potential differences in habitat use within estuaries. Values for $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ in crabs from Okat and Utwe were low and similar to values expected from animals feeding within mangrove forests, e.g., feeding on infauna that had average $\delta^{13}\text{C}$ values near -26.5‰ . In contrast, crabs from Lelu had higher $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values, with average values of -21.8 and 7.8‰ , respectively. These higher isotope values are consistent with increased crab foraging on reef flats and seagrasses. Given that *S. serrata* have been observed feeding on adjacent reef and seagrass environments on Kosrae, it is likely that they move in and out of the mangroves for feeding. Isotope mixing model results support these conclusions, with the greatest mangrove ecosystem contribution to *S. serrata* diet occurring in the largest mangrove forests. Conserving larger island mangrove forests (> 1 km deep) appears to support crab foraging activities.

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Introduction

Scylla serrata, of the family Portunidae, is commonly known as mangrove or mud crab. *Scylla serrata* is one of the largest and most commercially important species of crabs found in mangrove forests and adjacent saltwater estuaries in the Indo-west Pacific. Because of their large size, high meat yield, and delicate flavor, these crabs are a valued source of food and income throughout their native range (Robertson and Kruger 1994; Trino et al. 1999). For example, on the western Pacific island of Kosrae, Federated States of Micronesia (5°19'N, 163°00'E), *S. serrata* provide 55% of the ~\$1 million in goods harvested annually from mangrove forests (Naylor and Drew 1998), and sustainable crab yields may become an important goal of mangrove forest management. Understanding how *S. serrata* use contiguous ecosystems, e.g., mangrove forests and adjacent seagrass beds and reef flats, may assist with conservation and wise use not only of crabs but coastal habitats as well.

Scylla serrata movement patterns and foraging behavior are not well known. Adult *S. serrata* life history and feeding patterns are generally believed to be characterized by small-scale movement around relatively permanent burrows in areas of sufficient food availability, free-range foraging within a 1–2 km area, and a spawning migration by females up to 95 km offshore (Hill 1978; Perrine 1978; Hyland et al. 1984; Akil and Jiddawi 1999; Walton et al. 2006). Gut content analysis, direct observation, and initial stable isotope work suggest that *S. serrata* are opportunistic scavengers and omnivores (Arriola 1940; Thimdee et al. 2001, 2004). Seagrass and seagrass-epiphytes may be important components in the diets of mangrove crabs, in addition to items found in the mangrove forest itself (Benstead et al. 2006).

Taxonomic revisions over the last several years have recognized as few as one and as many as four different species of mangrove crabs across the Indo-Pacific; four are now recognized (Keenan et al. 1998). Whereas some earlier information may have applied to all four species, some probably did not. Because only one species (*S. serrata*) is found in Kosrae (Shelley 2001), this island is useful for establishing baseline data for that species.

In recent years, Kosraeans have perceived that the local *S. serrata* population is decreasing (Naylor et al. 2002), possibly a result of overharvesting or habitat loss because of mangrove forest site conversion. Despite the importance of *S. serrata* to the Kosraean economy, habitat and dietary requirements and the impact of harvesting on crab population dynamics remain unknown. Without such information, it is difficult to assess the long-term sustainability of *S. serrata* populations on Kosrae and the Indo-Pacific. To study crab movements without the intrusive impacts of tagging, we used natural chemical markers (stable isotopes,

phosphorus, and trace metals) to characterize the habitat use and residency of mangrove crabs.

If *S. serrata* movements are indeed local, combinations of markers could distinguish among individuals collected in different areas, but if crabs freely move among reef flats, seagrass beds, and mangrove forests, little chemical distinction would be expected. In addition, if *S. serrata* feed exclusively in mangrove forests, with little movement among habitats, they should have stable isotope compositions similar to those of mangrove forest “residents,” those animals that spend their adult life stages in mangrove forests and restrict their movement over small spatial scales. This study used multiple chemical tracers to test whether crab movements were restricted to local mangrove forests or included adjacent seagrass beds and reef flats. In addition, by measuring chemical tracers in primary producers and infauna as well as crabs, we indirectly examined the biogeochemical environment of three different mangrove forests, under the premise that crab tissue chemistry differences may reflect the environmental biogeochemical differences among forests.

Materials and Methods

Study Site Description

This study was conducted in June 2002 on the small (112 km²) high island of Kosrae, Federated States of Micronesia. Mangrove forests account for ~15% of the area of the island and occupy 2/3 of the island's shoreline, consisting of a belt of vegetation up to 1,500 m deep. Fringing reefs are located a short distance offshore from the mangrove forests, ranging from 50 to 500 m wide on the windward and leeward coasts, respectively. Seagrass beds are found on reef tops. Annual mean air temperature is 27°C, and annual rainfall is non-seasonal and high, ranging from 5,000–6,000 mm (Merlin et al. 1993). Study sites were located in non-contiguous mangrove stands and are known locally as the Utwe Tidal Channel (Utwe, 5°16'48"N, 162°57'40"E), Lelu Harbor (Lelu, 5°19'22"N, 163°00'56"E), and Okat River (Okat, 5°20'37"N, 162°58'02"E). These sites were located about 10 km apart around the perimeter of the island, and previous tagging studies showed that crab population densities there were high (21 crabs per hectare). Estuarine waters sampled at these sites had comparable water temperatures (28.7–31.8°C), salinities (26.8–30.1‰), and dissolved oxygen concentrations (3.9–5.4 mg L⁻¹). Utwe is in a remote part of the island; it is a lagoon protected from open marine exchange and has little anthropogenic disturbance. Lelu is also well protected but is in one of the most populated parts of the island. It is a shallow bay with a causeway restricting water flow along

one side. Okat is remote from urban development but adjacent to a commercial airport and harbor. Kosrae has eleven mangrove species, and three are dominant: *Rhizophora apiculata*, *Bruguiera gymnorhiza*, and *Sonneratia alba* (Ewel et al. 1998). Three species of seagrasses are found on Kosrae: *Enhalus acoroides*, *Thalassia hemprichii*, and *Cymodocea rotundata* (Green and Short 2003).

Sample Collection and Preparation

We collected several types of samples for a food-web study based on stable isotope analysis. For primary producers, the following collections were made at three replicate sites in each estuary. Both green and brown leaves were collected to evaluate potential differences in fresh and detrital leaf stable isotope values. Pooled samples of green leaves containing a mixture of mangrove species ($n=20$ leaves) were collected randomly at 1–2 m heights from separate trees in the mangrove understory from each of the three replicate sites. Brown mangrove leaves representing a mixture of mangroves species were collected at random from the sediment surface and pooled ($n=20$ leaves). In addition, suspended particulate organic matter (POM) was collected within mangrove forests by filtering 300 ml of seawater adjacent to the sampling stations onto pre-combusted GFF filters (Fry et al. 1991). Surface sediments (0–1 cm deep) were collected and processed for benthic microalgae (BMA) pigment content as follows. Approximately 1 cm³ of surface sediment was extracted in 5 ml of acetone for 24 hr in the dark. Acetone-extracted pigments were filtered to remove particulate material, then adsorbed and dried on pre-combusted GFF filters. This technique reduced the chance of sediment contamination, because the extract was free of fine sediment and detritus. However, acetone can co-extract several compounds other than pigments and degraded plant pigments (e.g., phaeophytin, Wright et al. 1997), possibly confounding stable isotope values. While imperfect, acetone extracts represent samples enriched in BMA pigments versus ambient surface mud samples. Whole algal samples were collected from sediments and mangrove roots by scraping surface algae with sediments and rinsing off as much sediment as possible using deionized water. The rinsed algal material, which did include some sediment contribution, was analyzed for comparison with the acetone extracts. Sediments were soaked in 10% HCl to remove carbonates and dried prior to isotope analysis.

Sediments for infaunal samples were collected from several mangrove and adjacent habitats (reef flats and seagrass beds) within each estuary (3–4 replicate cores per habitat per estuary; cores were 33 cm² × 5 cm deep). These samples were processed as follows. Sediments were preserved in 10% formalin prior to sieving. Sediments were sieved on 45 and 300 μm sieves to collect nematodes

and larger macrofauna, respectively. In the laboratory, infauna were sorted, pooled to species level when possible, and transferred to tin capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. Gut contents were not removed from these small organisms prior to analysis. The dominant infaunal taxa present in the mangrove forest and reef-flat sediments were determined based on previously collected core samples (Demopoulos, unpublished data). For smaller species, 5–50 animals were pooled per sample to meet required minimum aliquots of 5 μg C and 10 μg N per sample for stable isotope analysis (Carman and Fry 2002). Small crabs (non-*S. serrata*, e.g., grapsids and ocypodids) were collected by hand from mangrove sediments and tree roots. Gastropods and bivalves were collected within the mangrove forest, including on mangrove roots, and their soft tissues were dissected, rinsed with distilled water, and frozen until further analysis.

Scylla serrata were caught in estuaries and tidal creeks in mangrove forests using baited traps that were separated by distances of at least 100 m. Six traps were left overnight for a total of four consecutive trapping nights per estuary. Traps were checked daily, and sex, carapace width, and weight were recorded for each crab caught. Reef-associated crabs, e.g., *Thalamita crenata*, were also collected from the baited traps and from adjacent reef-flats by hand. *Scylla serrata* cheliped muscles and samples of soft tissue from gastropods and barnacles were dissected and rinsed with distilled water for isotope and chemistry determinations. For other crabs (e.g., Grapsidae and *T. crenata*), and some test samples of *S. serrata*, whole chitinous chelipeds from five individuals of each species were combined and homogenized for isotope analysis. In addition, stomach contents from grapsid crabs collected inside mangrove forests were analyzed to evaluate isotope variability in different crab sample types. Stable isotope values from stomach contents represent recently ingested diet items, whereas muscle and chitinous claw isotope values reflect the longer-term integrated diet. Whenever possible, a minimum of three replicate samples was analyzed for each species per site. All samples were dried at 60°C and, with the exception of infauna and filter samples, ground to a fine powder and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. All chitin-containing samples were acid-treated to remove carbonates prior to isotope analysis. Whole filter and infaunal samples were placed in tin cups and analyzed. Stable isotope analyses of *S. serrata* were made on individual organisms.

Isotope Analysis

Samples were analyzed for C, N, and S isotope compositions referenced to Vienna PeeDee Belemnite (VPDB), atmospheric N₂, and Vienna Canyon Diablo Troilite (VCDT), respectively (Peterson and Fry 1987). Analyses were performed using an elemental analyzer interfaced to a

Table 1 Stable isotope values and C/N for chitin and muscle tissue samples from *Scylla serrata*

	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N
Muscle	-21.8±0.6	7.8±0.3	3.8±0.1
Claw chitin + muscle	-22.2±1.2	6.7±0.6	3.9±0.1
Claw chitin only	-23.6±1.4	3.2±0.8	4.7±0.1

Data are mean values (n=9, ±95% confidence limits).

Finnegan MAT Delta-S or Delta-Plus stable isotope ratio mass spectrometer via a Finnegan MAT ConFlo II interface. Reproducibility was monitored using several organic reference standards (Fry 2007). Following isotope analysis, preserved infaunal samples were corrected for formalin preservation by adding 1‰ to $\delta^{13}\text{C}$ values of preserved sample (Sarakinis et al. 2002; Demopoulos et al. 2007). The corrected values are reported here.

Tissue Type Comparisons

Whole chelipeds (combined muscle and chitin) and muscle tissue from *S. serrata* were analyzed separately for stable isotopes to quantify possible isotope differences from different crab tissue types. The average $\delta^{13}\text{C}$ values of muscle and muscle plus chitin samples were statistically identical (Table 1, paired *t* test, $p>0.05$), so no correction was used for stable carbon isotope values from non-*Scylla* crab values prior to mixing model calculations.

Crab Tissue Cation Analysis

Scylla serrata cheliped muscle tissue was analyzed for phosphorus, trace metal, and cation concentrations (K, Ca, Mg, Na, Mn, Fe, Cu, Zn, and B) using inductively coupled plasma-atomic emission spectroscopy (ICP-AES). Individual samples were first digested in acid and then run with standards according to Kalra (1998).

Statistical Analyses

Initially, the stable isotope, trace metal, cation, and phosphorus data were examined separately. For example, stable isotope values at different sites were compared using Pearson's product moment correlation and univariate ANOVA tests.

Discriminant analysis of tissue chemistry data was used to separate the three estuary sites (McLachlan 1992). Crab samples were grouped based on the untransformed tissue data analyzed for the following components: P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn, B, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$. All the variables were used in the initial discriminant analysis. A stepwise subtraction removed correlated variables; the final model represented only uncorrelated ($r<0.65$), significant variables. The 0.65 value was used following the general

recommendation of McGarigal et al. (2000) and because this value provided a natural cut-off value for our data. Correlation of variables used in the discriminant analysis model was examined using the tolerance statistic, ranging from 0 to 1. A small value indicates that the variable is strongly correlated with one or more of the other variables. For example, a tolerance estimate of zero indicates that 100% of the variance of that variable can be explained by the other variables used in the discriminant analysis. Relative importance of individual variables in discriminating sites was evaluated using the *F-to-remove* statistic (estimated during discriminant analysis procedure). Variables with large *F-to-remove* values are most useful in discriminating sites (e.g., Okat vs. Utwe). Multivariate analysis of variance (MANOVA) was used to identify differences among tracers by sites. All statistical analyses were performed using SPSS statistical software. Errors associated with mean values are 95% CL unless otherwise stated.

Isotope Mixing Models and Habitat Contribution Estimates

We averaged stable carbon isotope values for animals residing exclusively in mangrove forests or reef flats/seagrass beds, including adult sediment infauna (polychaetes, oligochaetes, nematodes, and clams) and small crabs (*Metapograpus latifrons*, *Parasesarma plicatum*, and unidentified tree crabs and fiddler crabs), to provide endmembers for both habitat types. In order to determine which species were habitat residents, infaunal species compositions from mangrove forests and from adjacent reef flats and seagrasses were compared. Adult infauna with small dispersal capabilities (mm to a few cm) exclusively found in these respective habitat types were defined as

Table 2 Mean (±95% CL) *Scylla serrata* weights, carapace widths, and muscle tissue stable isotopes, cations, trace metals, and phosphorus concentrations from each watershed

	Utwe (n=13)	Okat (n=26)	Lelu (n=22)
Wet weight (g)	834±110	739±100	524±96
Width (mm)	170±6	151±5	141±7
$\delta^{13}\text{C}$ ‰	-26.2±0.7	-24.7±0.4	-21.7±0.7
$\delta^{34}\text{S}$ ‰	-3.8±2.4	0.5±1.5	6.1±1.1
$\delta^{15}\text{N}$ ‰	5.7±0.5	7.1±0.2	7.8±0.3
P mmol kg ⁻¹	322±22	287±9	292±13
K mmol kg ⁻¹	404±54	290±44	430±26
Ca mmol kg ⁻¹	75±32	172±40	154±20
Mg mmol kg ⁻¹	85±10	110±8	106±8
Na mmol kg ⁻¹	604±65	755±86	733±91
Mn mmol kg ⁻¹	0.05±0.02	0.06±0.02	0.08±0.02
Fe mmol kg ⁻¹	0.85±0.21	1.14±0.22	1.41±0.28
Cu mmol kg ⁻¹	0.76±0.16	0.28±0.06	0.42±0.12
Zn mmol kg ⁻¹	5.13±0.35	4.68±0.36	4.38±0.38
B mmol kg ⁻¹	0.62±0.24	1.84±0.95	1.33±0.49

habitat residents (Demopoulos 2004). IsoError 1.04, an isotope modeling program (Phillips and Gregg 2001), was used to estimate the percent contribution of habitat type to *S. serrata* isotope values. This method accounts for the variability in the $\delta^{13}\text{C}$ values of the mixture (consumer) and the two sources (reef/seagrass versus mangrove forest endmembers) using means and standard deviations of $\delta^{13}\text{C}$ values for *S. serrata* and endmembers from each site. In this model, foods are aggregated by habitat rather than considered individually so that the mixing model assesses the overall dietary importance of the mangrove habitat, not the importance of mangrove leaf detritus in crab diets.

To evaluate how the size of a mangrove stand may relate to habitat use by the crabs, land-to-sea extent of mangrove forests

(referred to here as “depth”) was calculated using recent maps of mangrove forest area (Hauff et al. 2006). Transects at each of the three sites ($n=5-16$) were delineated on the map running perpendicular to the coastline, each separated by 0.5 km. Depth of mangrove forest in kilometers was measured on each transect, then averaged for each of the three estuary sites.

Results

Patterns in Chemistry of *Scylla serrata* Among Sites

Average isotope values of *S. serrata* muscle tissues were distinct among sites, with Lelu more enriched in ^{13}C , ^{34}S , and

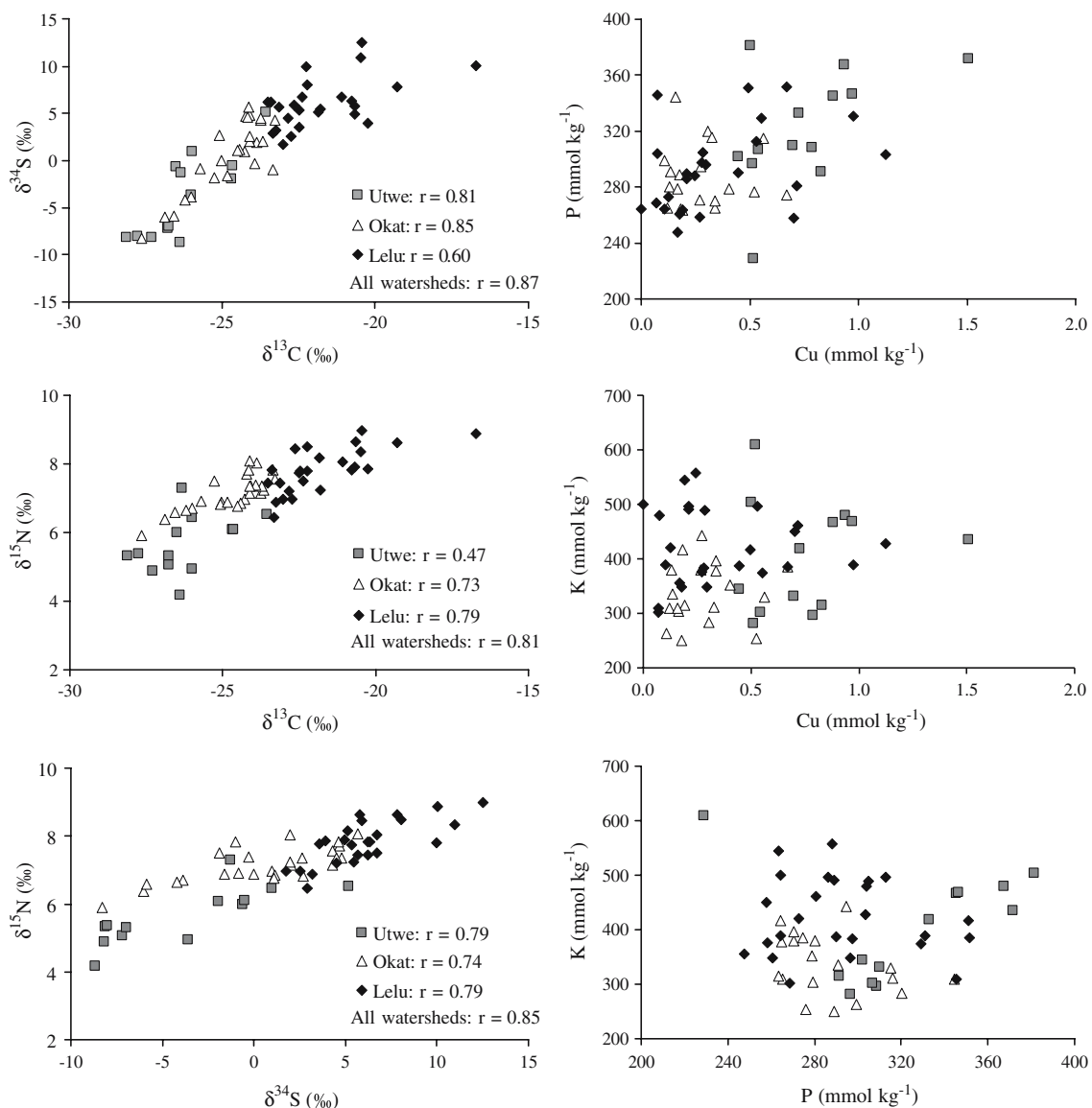


Fig. 1 Correlations between $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$, and between $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ for *S. serrata* muscle tissue from all crabs analyzed in each estuary. The r values are significant at $p < 0.001$ and an

examination of the significant differences is discussed in the text. Correlations between Cu and P and K and between P and K for *S. serrata* muscle tissue from all crabs analyzed in each estuary

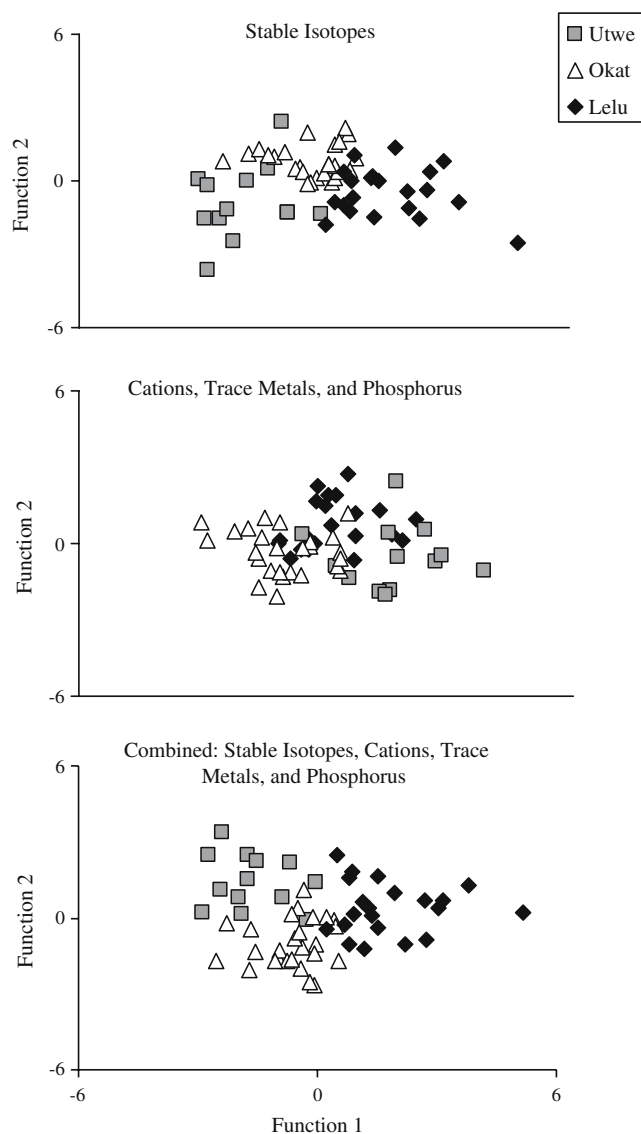


Fig. 2 Results from the discriminant analysis of crab muscle tissue analysis for (1) stable isotopes only, (2) cations, trace metals, and phosphorus only, and (3) stable isotopes, cations, trace metals, and phosphorus

^{15}N than Utwe, while Okat had intermediate values (Table 2, Fig. 1). Mean isotope values of crab muscle tissue from each site were significantly different ($\delta^{15}\text{N}$: $F_{2,66}=20.902$, $p<0.001$; $\delta^{34}\text{S}$: $F=32.85$, $p<0.001$; and $\delta^{13}\text{C}$: $F=52.204$, $p<0.001$).

Some trace metals and cations as well as P concentrations differed in crab tissues among sites. In particular, Utwe *S. serrata* had significantly higher concentrations of Cu and P than Lelu and Okat crabs (Table 2, Fig. 1; MANOVA, $p<0.001$ for Cu and $p=0.021$ and 0.002 for P at Lelu and Okat, respectively). Utwe crabs also had lower concentrations of Ca and Mg than Okat crabs (Table 2; MANOVA, $p=0.002$). Lelu crabs had higher concentrations of Ca, Mg, and Fe than Utwe crabs (MANOVA, $p=0.016$, 0.015 , and 0.033 , respectively) and higher K ($p=0.002$) and Cu ($p=0.019$) concentrations than Okat crabs (Table 2, Fig. 1).

To distinguish patterns due to diet alone among *S. serrata* from different sites, discriminant analysis (DA) was run for stable isotopes separately from trace metals, cations and phosphorus. Only seven samples (12%) were not classified correctly (i.e., designated from correct site, Fig. 2). After running the DA for cations, trace metals, and phosphorus, 20 samples (33%) were not classified correctly (Fig. 2). An overall DA yielded distinct separations of crab muscle tissue data among the three sites using $\delta^{13}\text{C}$, P, K, Na, Fe, Cu, Zn, and B data (Fig. 2) based on cross validated or jackknifed classification (group assignment excluded case being classified). Several variables were not included in the final analysis (Fig. 2) because they were correlated with other variables (e.g., $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ were not included because they correlated with $\delta^{13}\text{C}$, Fig. 1). Variables for which $r\geq 0.65$ were not used in the analysis (McGarigal et al. 2000). Almost all the samples (87%) were correctly classified into each separate estuary. Two significant canonical discriminant functions were returned by the analysis: function 1 separated Lelu from Okat and Utwe estuaries and function 2 separated Okat from Utwe. *F-to-remove* values of all variables used in the final analysis were high and the tolerance >0.9 , indicating that there was no problem with collinearity.

An examination of the standardized canonical discriminant function coefficients helped identify variables that discriminated among the three sites. Higher $\delta^{13}\text{C}$ and K values were positively correlated with function 1 (Table 3), whereas negative coefficients were obtained for B concentrations. Copper was strongly associated with function 2. Thus, variables related to food (e.g., $\delta^{13}\text{C}$) and geochemical environment (e.g. K, Cu) were all important in distinguishing crab origins.

Isotope Patterns in Primary Source Pools

Green leaf $\delta^{13}\text{C}$ values ranged from -37.3‰ to -34.1‰ and $\delta^{15}\text{N}$ from 1.3‰ to 3.6‰ (Table 4). Brown leaf $\delta^{15}\text{N}$ values were similar to green leaves and sediments, ranging from 1.9‰ to 2.9‰ , but average $\delta^{13}\text{C}$ values ($-33.1\pm 0.6\text{‰}$)

Table 3 Correlation coefficient of each predicted variable with discriminant function for crab data shown in Fig. 2

Variable	Function 1 (66.5 %)	Function 2 (33.5 %)
$\delta^{13}\text{C}$	0.932	-0.061
K	0.214	0.383
B	-0.240	-0.122
Cu	-0.081	0.864
P	0.025	0.298
Na	0.027	0.080
Fe	-0.031	-0.024

Numbers in parentheses represent the % variance explained for each of the two functions.

Table 4 Stable isotope values for primary producers and sediment collected from mangroves in Okat, Utwe, and Lelu

	Utwe		Okat		Lelu	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Mangrove Leaves						
Green (4)	-34.1±1.0	1.3±0.5	-35.6±1.3	3.6±0.8	-37.3±0.2	2.9±1.4
Brown (4)	-32.1±0.5	2.9±0.0	-34.1±0.6	2.1±0.8	-33.1±0.7	1.9±0.7
Particulate Organic Matter (1–3)	-30.0±0.6		-23.3±0.9		-23.5	
Benthic microalgae-acetone extracts (12)						
interior-sunny			-30.4±0.1			
interior-shade	-30.7±0.3		-30.1±0.5		-30.5±0.2	
bank	-30.4±0.6	2.7±1.6			-30.0±0.1	
Root epiphytes-whole (4)	-30.5±0.3	1.7±0.7				
Root epiphytes-acetone extract (4)	-29.9±1.8					
<i>Rhizophora</i> epiflora-whole (1)			-27.4	1.3		
<i>Rhizophora</i> epiflora-acetone extract (1)			-29.0			
<i>Sonneratia</i> epiflora-whole (1)			-27.0			
<i>Sonneratia</i> epiflora-acetone extract (1)			-27.1	2.2		
Sediments						
interior (4–5)	-27.9±0.2	1.9±0.5	-28.3±0.1	2.4±0.1	-28.1±0.4	1.6±0.2
bank (4–5)	-28.0±0.1	2.2±0.5			-27.9±0.1	1.9±0.4

Data are mean δ values ($\pm 95\%$ confidence limits). Benthic microalgae samples were collected from sun exposed mangrove creekbed sediments (sunny) and in the interior shade. Numbers in parentheses refer to sample size. Epiphyte/epiflora data reflect either acetone extracted samples or whole samples.

were enriched in ^{13}C relative to the green leaves ($-35.7 \pm 1.0\%$) and depleted in ^{13}C relative to surface sediments ($-28.0 \pm 0.2\%$). There were no significant differences in $\delta^{13}\text{C}$ values of benthic microalgae (BMA) among estuaries. Average $\delta^{13}\text{C}$ values from acetone extracts ($-30.2 \pm 0.2\%$) and whole algae material ($-29.3 \pm 1.5\%$) were similar (paired t test, $p=0.513$); thus, it was concluded that the extracted material was representative of BMA $\delta^{13}\text{C}$ values. BMA acetone extracts provided insufficient N for $\delta^{15}\text{N}$ analysis.

Sediment Macrofaunal and Meiofaunal Isotope Composition

Invertebrates collected at each of the mangrove forests included crabs, molluscs, nematodes, and polychaete and oligochaete annelids (Table 5). Crabs found in mangrove forests included grapsid (*Metapograpsus latifrons*), sesarmid (*Parasesarma plicatum* and 1 unidentified species), and an unidentified species of Ocypodidae. For all three mangrove forests, *Metapograpsus latifrons* had the largest range in crab $\delta^{13}\text{C}$ values (-26.1 to -21.4%). Mangrove molluscs had the greatest range in $\delta^{13}\text{C}$ values; oysters had the highest and the bivalve, *Anodontia edentula*, the lowest values ($-20.3 \pm 0.1\%$ and $-34.4 \pm 0.3\%$, respectively). Sediment infauna (oligochaetes, polychaetes, and nematodes) had very similar $\delta^{13}\text{C}$ values. However, nematodes had the highest $\delta^{15}\text{N}$ values (5.5 to 6.9‰) for all the sediment infauna from the mangrove forests. In contrast, sediment infauna found on

adjacent reef flats and seagrass beds were enriched in $\delta^{13}\text{C}$ relative to their mangrove forest counterparts (Table 5).

Estimated Mangrove Ecosystem Source Contributions

Mangrove-forest $\delta^{13}\text{C}$ endmembers from each estuary, calculated by averaging isotope values for sediment infauna (e.g., sabellids, syllids, nematodes), molluscs, and grapsid, sesarmid, and ocypodid crabs (e.g., *Metapograpsus latifrons*, *Parasesarma plicatum*, see Table 5), were mangrove_{Utwe} $\pm 1\text{SD} = -26.6 \pm 3.1\%$ (N=13), mangrove_{Okat} = $-25.2 \pm 2.1\%$ (N=12), and mangrove_{Lelu} = $-27.1 \pm 1.9\%$ (N=9). Adjacent reef-flat/seagrass $\delta^{13}\text{C}$ endmembers were also calculated from sediment reef-flat/seagrass infauna and reef crabs (*Thalamita crenata*): reef-flat_{Utwe} = $-21.7 \pm 1.3\%$ (N=7), reef-flat_{Okat} = $-14.9 \pm 1.7\%$ (N=6), and reef-flat_{Lelu} = $-14.9 \pm 1.0\%$ (N=5). This method aggregated multiple sources from a bottom-up trophic perspective, from sediment fauna to *S. serrata*, resulting in two habitat endmembers: reef-flat including seagrass versus mangrove ecosystem. Using these endmembers and *Scylla serrata* stable $\delta^{13}\text{C}$ values (Table 2), IsoError mixing model results estimated the average percent contribution of mangrove forests to mangrove crabs as $92 \pm 17\%$ (range=55–100%) for Utwe, $95 \pm 6\%$ (range=82–100%) for Okat, and $57 \pm 4\%$ (range=48–65%) for Lelu; ranges represent the lower and upper 95% confidence interval. When mangrove forest depth was plotted against percent mangrove contribution, the highest contributions corresponded to the deepest mangrove forests

Table 5 Stable isotope values for fauna collected from mangroves and reef flats in Okat, Utwe, and Lelu

	Utwe		Okat		Lelu	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
MANGROVE FAUNA						
Molluscs						
<i>Anodontia edentula</i> (gill) (8)	-34.4±0.3	2.1±0.3				
<i>Anodontia edentula</i> (mantle) (5)	-32.8±0.4	4.1±0.5				
Oysters (2)			-20.3±0.1	5.3±0.2		
Other Bivalves (1)	-25.0	3.5	-26.6	2.3	-27.4	3.4
Whelks (1)			-23.0	4.0		
Crustaceans						
<i>Metapograpsus latifrons</i> (3)	-23.6±2.2	2.6±0.9	-26.2±0.1	3.7±0.5	-24.5±0.9	3.9±0.8
<i>Metapograpsus latifrons</i> -sc (2-3)	-27.4±1.7	2.0±0.7	-28.7±0.5	4.0±0.5	-28.7±1.0	2.2±0.7
Other tree crabs (2)	-19.7±2.2	3.7±0.4				
Other tree crabs-sc (2)	-24.2±0.1	2.5±1.2				
<i>Parasesarma plicatum</i> (2–5)	-25.0±0.5	1.9±0.1	-26.0±0.3	3.8±0.4	-23.9±0.4	3.7±0.7
<i>Parasesarma plicatum</i> -sc (2–5)	-29.1±0.2	1.4±0.6	-30.1±1.6	3.3±0.3	-29.2±0.2	2.4±0.6
Fiddler Crab (1)			-22.3	3.3		
Sediment infauna						
Nematodes (3–4)	-28.3±1.7	5.8±0.5	-26.5±0.8	6.4±0.3	-29.6±0.4	5.7±0.3
Oligochaetes						
sp. 1 (2–3)	-27.4±0.1	1.3±0.5	-26.7±0.3	1.4±0.7		
sp. 2 (3)	-27.5±0.3	1.3±0.3	-26.4±0.8	2.7±0.4	-27.4±1.2	1.2±0.9
Community (1–2)	-27.1	-2.5	-26.1±0.4	1.4±0.2	-28.6	-0.6
Capitellids (3)	-27.1±0.4	0.4±0.2	-26.5±0.5	2.4±0.5	-28.6±0.9	0.1±0.7
Sabellids (2–4)	-27.3±0.2	2.1±0.9	-25.3±0.2	2.5±0.8	-27.0±0.3	2.4±0.2
Syllids						
sp. 2 (2)	-27.5±0.6	2.1±0.9			-26.6±0.9	3.1±0.6
Community (1)	-27.2	2.5				
REEF-FLAT FAUNA						
Crustaceans						
<i>Thalamita crenata</i> (4)	-22.8±0.9	3.8±0.5			-16.4±1.2	6.9±0.8
Sediment infauna						
Nematodes (3)	-21.0±0.9	4.9±1.4	-14.8±1.0	4.0±0.2	-14.4±1.8	3.5±0.2
Oligochaetes						
sp. 2 (2)	-22.4±1.3	3.8±0.7				
Capitellids	-22.2±0.2	4.8±0.3	-15.7±1.9	3.7±1.2		
Syllids						
sp. 1 (2–4)	-23.1±0.4	6.2±0.3	-12.6±1.6	2.5±2.0	-14.6±0.6	5.9±0.4
sp. 2 (2–3)	-20.8±1.0	4.9±0.9	-14.8±0.6	3.0±0.8	-15.4±0.7	3.1±2.1
sp. 3 (3)			-13.9±1.3	2.5±0.6		
Community (1–3)	-19.5	5.2			-13.7±0.2	2.8±0.6
Sabellids (4)			-17.6±1.4	1.7±0.8		

Data are mean δ values ($\pm 95\%$ confidence limits). Confidence limits refer to among-core variability. Numbers in parentheses indicate sample size. Values in bold were used to calculate endmember sources for mixing models. Sc=stomach contents.

(Fig. 3). A curve was fitted to data from three estuaries and an extrapolated point at (0, 0) representing no mangrove contribution at zero mangrove area.

Discussion

Crabs from each site in Kosrae had a distinctive combination of chemical markers. These results, together with

previous reports of restricted ranges for adult *S. serrata* (Hill et al. 1982), support the premise that populations of these crabs restrict their movements in Kosrae to distinct mangrove forests. Our results with free-ranging crabs support the finding of limited movement documented for crabs that were extensively handled during previous tag-release studies and seemed to move no more than 1 km within a single molt cycle (Bonine et al. 2008). One implication of limited movement is that stocks of adults in

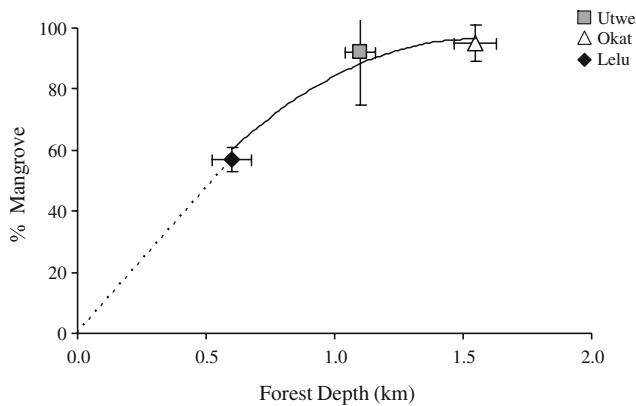


Fig. 3 Effect of mangrove forest depth (km) on percent mangrove contribution to *S. serrata* from Utwe, Okat, and Lelu. Error bars represent ± 1 SE. Equation of the curve: $y = -41.0x^2 + 126.2x - 0.9$, $r^2 = 0.996$. Curve was fitted to data from three estuaries (solid line) plus an extrapolated point (dashed line) at (0, 0) representing no mangrove contribution at zero mangrove area

an area depend primarily on the number of local crabs reaching maturity (cf., Hyland et al. 1984), so that populations of crabs should be managed on a localized basis. This study therefore validates the results of a recent trapping study on Kosrae that supports local management (Ewel 2008).

Using a combination of tracers (isotopes, trace metals, cations, and phosphorus) enhanced our understanding of the chemical environment of these crabs. For example, different tissue concentrations of trace metals, cations, and phosphorus in crab muscle tissue may be a function of bioavailability (Reinfeldt and Fisher 1994; Rainbow and Black 2002), which may reflect the composition of source materials and their chemical reactivity in the mangrove environment. For example, Cu tissue concentration strongly separated Utwe crabs from the other two sites, possibly because Utwe crabs had the highest Cu concentration in their watershed. Cu is abundant in volcanic sediments (e.g., 2.3–3.9 $\mu\text{mol g}^{-1}$, Meijer and Buurman 2003), and can become bioavailable via direct uptake from the surrounding environment and through diet, e.g., enzymatic digestion of sediments and/or sediment-associated organisms including infauna. Using chemical variables in combination with food-related stable isotope metrics yielded a more complete picture of crab movements and origins. This overall combination of variables probably represents uptake from both water (you are what you swim in) and diet (“you are what you eat less what you excrete”, Fry 2006).

Differences among sites also may reflect landscape patterns. Mangrove forests in Okat and Utwe are among the most extensive on Kosrae, whereas mangrove forests at Lelu are narrow and cover less area (Fig. 3). Seagrass beds, on the other hand, are more extensive at Lelu and less so at Okat, both of them reduced by development and pollution over the last several decades (Green and Short 2003).

Although seagrasses were scattered around the area where we trapped in the Utwe-Walung tidal channel, there were no discrete seagrass beds; a bed can be found more than 1 km to the west (U.S. Army Corps of Engineers 1987). Smaller/narrower mangrove forests apparently correspond to smaller mangrove ecosystem source contributions (Fig. 3). In a previous food-web study on Kosrae using stable isotopes, Benstead et al. (2006) found that the lowest relative contribution of mangrove sources to animal diets corresponded to reef-flat areas with a narrow mangrove belt (such as our site at Lelu). Okat’s scattered seagrass meadows and substantial mangrove forests may have been responsible for the intermediate mangrove ecosystem and marine contributions in that study. *Scylla serrata* isotope values from Benstead et al. (2006) (collected September–December 2000, 2–3 crabs per site) were similar to values measured in this study, suggesting stability in crab isotope values through time, enhanced by our more extensive sample replication (2–3 crabs per site for Benstead et al. vs 13–26 crabs for our study), our examination of two sites not included in their study, and our ability to characterize variability. Moreover, the isotope values they measured for seagrasses agree with values obtained from our seagrass samples. By quantifying the depth of mangrove forests to explain mangrove ecosystem contribution to and habitat use by *S. serrata* (viz. Fig. 3), we clarify the picture that Benstead et al. (2006) sketched.

The invertebrate taxa collected in mangrove environments from this study are similar to those found in other mangrove ecosystems (Sheridan 1997; Bouillon et al. 2004b; Demopoulos et al. 2007; Kon et al. 2007). However, few stable isotope data exist for mangrove invertebrates, in particular for sediment infauna (e.g. polychaetes, oligochaetes, and nematodes, Table 5). Our results for *Parasesarma plicatum* are consistent with isotope data for congeners collected in mangroves in India and Australia (Bouillon et al. 2004b; Guest et al. 2004). In addition, sediment infaunal isotope data are comparable to isotope values of fauna from mangroves in Puerto Rico and Yap, Federated States of Micronesia (Demopoulos 2004; Demopoulos et al. 2007; Demopoulos, unpublished data).

If we had relied on traditional, plant-based isotope mixing models, mangrove ecosystem contributions would have appeared small. For example, small resident crabs such as *Metapograpsus latifrons* and also crab stomach contents all were enriched in ^{13}C relative to mangrove leaf values (Table 5), suggesting less mangrove ecosystem subsidy than expected for a mangrove-forest resident. However, after using the two-source mixing model based on habitat rather than on mangrove leaf material, mangrove importance was high; it appears that mangrove habitat utilization is typically underestimated in the stable isotope literature (Fry and Smith 2002; see review by Fry and Ewel

2003; Bouillon et al. 2004a). The key to calculating overall mangrove habitat use was the selection of resident fauna as endmembers in mixing models, rather than selection of mangrove plant leaf material as an endmember.

The multi-elemental tracer technique used in this study allowed us to examine the natural geochemical environment from the top down; the crab sampled and recorded the environmental chemistry in its tissues. It is a variation on the elemental fingerprinting technique which uses natural tags derived from the physical and chemical environment (Becker et al. 2005). This work is part of an emerging approach using multiple chemical markers to study ecological niches and habitat issues. It was surprising that there were clear site differences in the stable isotopes and elemental chemistry of crab muscle tissue and that both isotopes and individual elements were equally strong in significantly separating the crab populations by estuary. Future studies will have to pinpoint the origins of the chemical differences we measured in our top-down approach. The chemical differences in the crabs could have arisen in any of these three areas: (1) watershed and water chemistry that differ across sites because of geological or human settlement reasons, (2) biogeochemical cycling in sediments that differ in their oxidation/reduction status across our sites, and (3) the food web itself if different prey items are uniquely labeled and if the crabs eat a different mixture of these food items in each of the watersheds. Future studies using the elemental fingerprinting technique may best use a top-down approach initially to survey and identify chemical differences followed by a bottom-up approach (e.g., measuring site specific samples for sediment and water chemistry) to explore possible causes for these differences.

In conclusion, chemical markers and discriminant analysis showed that adult crabs residing in three different mangrove forests belonged to distinct populations, probably moving over small spatial scales and between mangrove forest and adjacent reef-flats and seagrasses. This study represents the first species-specific study of habitat use and residency of *S. serrata*, an unstudied yet important fishery. Because the Kosrae *S. serrata* fishery appears to depend on isolated populations residing in different sites, crab harvest in each local mangrove forest may best be managed independently from the others. Smaller mangrove habitat size apparently was sufficient to encourage crab feeding from reef flats and seagrasses as well as mangrove forests (Fig. 3). Conservation of larger mangrove forest units may be important for preserving optimal conditions for crab feeding and production.

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