

Ontogenetic changes in diet and related morphological adaptations in *Ocypode gaudichaudii*

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Abstract. There are conflicting reports as to whether *Ocypode gaudichaudii* individuals switch from carnivory as juveniles to deposit-feeding primarily on diatoms as adults, or whether they expand diet range and become omnivorous with maturity. At the onset of deposit-feeding, crabs develop specialized claws with truncated ends that they use to shovel sediment during foraging. Eighty-eight crabs were collected from Culebra Island (Republic of Panama) to study how the diet of this crab shifts with changes in claw shape, mouthpart proportions, and setation, as well as gastric mill width. Forty-four crabs had identifiable material in their foreguts: 30 had animal material, 12 had diatoms, and two had a mix of both. There were no differences between the gastric mill, mandibles, and the proximal endites of the first maxillipeds of predators and deposit-feeders, but extra rows of plumose setae were present on the second maxilliped of deposit-feeding crabs with carapace length (CL) >10.6 mm. All individuals with CL <12.3 mm and non-truncated claws ate animals, but those with larger CL and truncated claws had animal, diatom, or mixed diets; hence, claw truncation does not restrict the crab's diet to diatoms but, instead, broadens the diet to include both animals and diatoms. Perhaps this is a strategy to balance the economics of foraging on animals and diatoms on medium to low-energy beaches that lack the larger invertebrates that adults of other species of ghost crabs eat. More generally, our study shows that specialized feeding structures need not imply a narrow or specialist diet.

Additional key words: claw morphology, ontogeny, diet shift, niche breadth, ghost crab

Organisms often change their resource requirements and their nutrient and habitat preferences as they grow (Werner & Gilliam 1984). Changes in resource utilization can affect species interactions and the ecological roles of organisms in communities and ecosystems at different life stages (Bolker et al. 2003). Fish, amphibians, reptiles, and many invertebrate taxa exhibit varying degrees of ontogenetic changes (Werner & Gilliam 1984). While the shift in resource use in some invertebrate taxa is subtle (e.g., bivalves, polychaetes), discrete changes are evident in those that metamorphose or change habitats during development, as is typical of holometabolous insects (Wilbur 1980; Hentschel 1998; Rossi et al. 2004). Despite the ubiquitous occurrence of ontogenetic niche shifts, stage-structured populations are often perceived to consist of identical

individuals with similar traits as the changing types and intensities of interactions during ontogenetic development are complex to study.

There are currently few empirical studies of the effects of dietary shifts in benthic invertebrates. A gradual diet shift from microphytobenthos to a mixture of microphytobenthos and microphytoplankton in *Macoma balthica* (LINNAEUS 1758) can alter the trophic interactions in benthic food webs as tellinid clams are an important intermediate trophic link between primary producers (microalgae) and top predators such as crabs (Hentschel 1998; Rossi et al. 2004). Decapods have complex life cycles and change their diets at different life stages (Sainte-Marie & Chabot 2002; Antonio et al. 2011). The most extreme diet shifts occur when land crabs transition from the marine environment they inhabit as planktonic larvae to the terrestrial environment when they become juveniles (Haywood & Kenyon 2009). Claw morphology and foraging habits of deca-

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pod crustaceans are closely related (Lee & Seed 1992; Wilcox & Rochette 2015) and some crabs change their diets as their claws grow larger and stronger (Freire et al. 1996). Although the decapod chela is a simple structure consisting of a movable dactyl and a fixed propodus, many variations in claw shape and size exist. Molluscivorous crabs have claws with large chela height and short dactyls for crushing. By contrast, crabs that prey on soft-bodied moving invertebrates have longer and thinner dactyls with smaller chela height for catching, holding, and shredding (Yamada & Boulding 1998; Wilcox & Rochette 2015).

Ontogenetic diet shifts in brachyurans occur when their foraging strategies change in concert with morphological changes to the chelae and feeding structures (Perez & Bellwood 1988). Chelae in the sandy shore crab *Matuta lunaris* (FORSKÅL 1775) change from the “tearing” and “cutting” form at small sizes to the “crushing” form at larger sizes as individuals’ diets shift from soft crustaceans to hard-shelled prey (Perez 1986). Edgell & Rochette (2009) demonstrated that ontogenetic changes in the predatory crusher claw in European green crabs, *Carcinus maenas* (LINNAEUS 1758), can be induced by a diet of littorinid snails with different shell thickness. Most of the *C. maenas* individuals that fed on thin-shelled littorinid snails adopted a shell-crushing feeding strategy and developed larger crusher claws after two molts, while crabs that fed on thick-shelled snails by probing their apertures had smaller claws. Among the crabs that predominantly crushed shells, those that fed on snails with thicker shells had bigger crusher claws. Diet and behavior did not affect the growth of the smaller cutter claws of the individuals that developed larger crusher claws.

Ghost crabs from the genus *Ocypode* are the most common semi-terrestrial brachyurans on sand beaches around the world. They are opportunistic feeders and are known for their varied modes of feeding, including predation, scavenging, and deposit-feeding (in *O. ceratophthalmus* (PALLAS 1772) of all ages, and in adult *O. quadrata* (FABRICIUS 1787); Jones 1972; Wolcott 1978; Robertson & Pfeiffer 1982). As top benthic predators of sand beaches, the varied feeding modes of ghost crabs can have profound cascading trophic effects on intertidal communities (Koepcke & Koepcke 1952). Unlike other species of ghost crabs, *Ocypode gaudichaudii* H. MILNE EDWARDS & LUCAS 1834 individuals are specialized deposit-feeders when adult, and they are the only *Ocypode* species that exhibits a marked change in claw morphology during ontogeny. At about 10 mm carapace length, the inner surfaces of the dactyl and pollex

of both claws become slightly concave and the tips broaden or become truncated (Crane 1941).

The morphology of other structures used in feeding by ocypodid crabs has also been linked to diet. Increased development in size and setation of proximal endites of the first maxillipeds and plumose setae on the inner margin of the second maxillipeds may be adaptations for deposit-feeding in *Ocypode* crabs (Crane 1941; Tweedie 1950; Jones 1972). Mandibles are used to cut up food items into smaller pieces before ingestion (Jones 1972). Larger gut volume indicates a greater extent of herbivory in fiddler crabs (Griffen & Mosblack 2011).

According to laboratory and field studies by Crane (1941), individuals of *O. gaudichaudii* show a change in diet as their claws truncate during development—juvenile crabs prey on small arthropods but adults are deposit-feeders, using their truncated claws to shovel sediment with diatoms into their mouthparts. However, two subsequent field studies by Koepcke & Koepcke (1953) and Trott (1988) reported that adults of *O. gaudichaudii* are not only deposit-feeders but also predators or scavengers. These studies suggest that the diet of individual *O. gaudichaudii* broadens with ontogeny and the development of truncated claws. This contradicts Crane’s (1941) deductions about the diet shift in *O. gaudichaudii* and challenges the widely held general belief that specialized feeding structures result in specialized and narrow diets. The lack of close association between diet and trophic morphology, known as Liem’s paradox, was first observed in African cichlids in which fishes with dentition highly specialized for scraping algae were found to feed on a wide range of prey (Liem 1980). This type of paradox has not been documented in brachyuran crabs.

In semi-terrestrial brachyurans, there are to date no studies on feeding ecology that combine analysis of diet and morphology of feeding structures at different developmental stages. The objective of this study is to determine whether diet in *O. gaudichaudii* is related to the ontogenetic morphological changes in its claws, mouthparts, mandibles, and gastric mill.

Methods

All specimens of *Ocypode gaudichaudii* were collected from the sheltered intertidal sandy shore on Culebra Island, Panama (8°54’45”N, 79°31’48”W) on 21 and 22 August, 2010. Eighty-eight individuals comprising juveniles with carapace length ≤ 10.6 mm and adult crabs (male and female crabs) with carapace length ≥ 12.3 mm, were excavated from their burrows in the intertidal zone when the tide receded

during the day. Mean air temperature during sampling of the crabs on the 2 d was 28°C. All crabs were frozen at -10°C within 3 h of capture to minimize enzymatic digestion and reduce the chance that crabs evacuated their guts (about 3.5 h after feeding; A.Y.P. Yong, unpubl. data). Following freezing, crabs were preserved in 70% ethanol and were shipped to the laboratory in the National Institute of Education, Nanyang Technological University, Singapore, for morphometric measurements and diet analysis. Morphometric measurements were made on 82 crabs with both chelipeds intact, and diet analysis was carried out for all 88 crabs. Carapace length (CL), from the posterior edge of the carapace to the tip of the front of each crab, was measured with a pair of digital Vernier calipers (Mitutoyo) to the nearest 0.1 mm. We measured CL instead of the more conventional carapace width for comparison with Crane's (1941) observations that in *O. gaudichaudii* claw truncation and deposit-feeding were present at carapace length 9–10 mm. The sex of each individual was determined by the presence of gonopods in males or pleopods in females. Smaller crabs without visible gonopods or pleopods were considered to be juveniles of undetermined sex. The range of CL in males and females was compared with a box-and-whisker plot. A two-sample *t*-test was used to test for the difference in CL between males and females, after testing for equal variance (Levene's test statistic=2.37, *p*=0.13) with the level of significance set at $\alpha=0.05$.

Both the major and minor chelae of each crab were removed for morphometric measurements. Each chela was held in a fixed position with black adhesive putty (Bostik, Black Tack) before the lateral surface was photographed using an image processing system that comprised a Zeiss Stemi SV11 stereomicroscope, a Canon digital camera EOS 450D, and Canon Utility image capturing software.

Lengths of the truncated parts at the tips of the dactyl (Dt) and pollex (Pt) of the major and minor chelae (Fig. 1) were measured from the 1200 dpi digital photographs in the image processing software ImageJ (Schneider et al. 2012). We judged that the tips of the dactyl and pollex exhibited truncation when they turned toward the midline of the claw at an angle exceeding 10° (Fig. 1). Claws that did not exhibit truncation were assigned a length value of zero.

Data analysis

Relationships between CL and the truncated lengths at the dactyl (Dt) and pollex tips (Pt) of the chelae were estimated by linear regression. The data were adjusted to the allometric equation $y=ax^b$ with CL as the independent variable, the length of truncation at the claw tips as dependent variables, and the values of *a* and *b* as growth constants. Logarithmic transformation was applied to linearize the power function for each relationship. A slope of $b>1$ indicated positive allometric growth, $b<1$ indicated negative allometric growth, and $b=1$ indicated isometric growth. We judged the relationships to be linear if the coefficient of determination (R^2) of the regression using untransformed variables was greater than the regression using log-transformed variables.

To compare patterns of truncation between sexes, we used ANCOVA with "Length of truncation at the dactyl tip" or "Length of truncation at the pollex tip" as the response variable, "Sex" as the factor, and "Carapace length" as the covariate. All data were tested for homogeneity of variance with Levene's test before an ANCOVA was carried out. The ANCOVAs for length of truncation at the dactyl and pollex tips in males and females were performed to determine whether the sexes differ in the pattern of truncation with increasing size. If slopes



Fig. 1. Length of the truncated part at the dactyl (Dt) and pollex tips (Pt) of the left major chela of *Ocypode gaudichaudii* at the juvenile, young adult, and adult stages. Scale bar=1 mm.

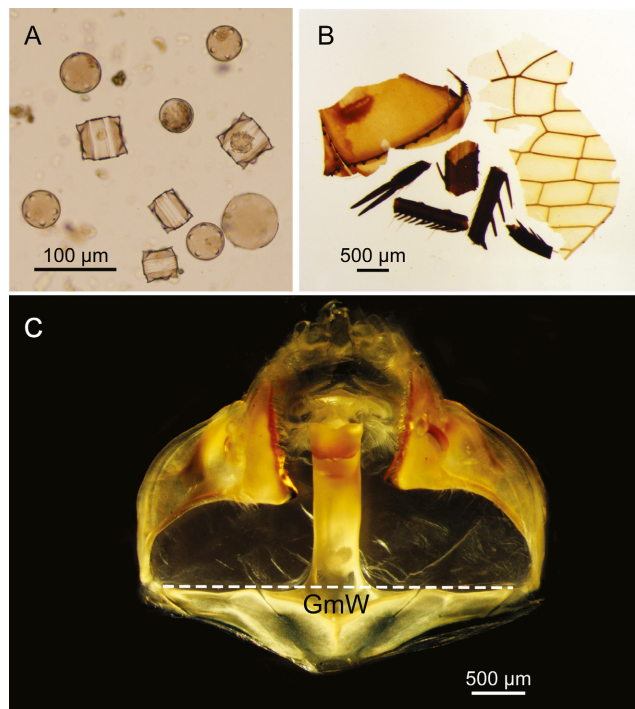


Fig. 2. Foregut contents and gastric mill of *Ocypode gaudichaudii*. **A.** Diatoms. **B.** Animal parts. **C.** Width of the gastric mill (GmW). Scale bars A=100 µm; B, C=500 µm.

did not differ significantly, a test of intercepts was carried out. All statistical analyses were done using MINTAB software (MINITAB, Inc., Release 14, 2003) with the level of significance set at $\alpha=0.05$.

Diet composition of the crabs was determined by examining gut contents. All foreguts were removed and non-empty ones were dissected. The contents of each foregut were flushed into a Petri dish with distilled water and examined under a stereomicroscope (Zeiss Stemi SV11). All items in the gut were identified to lowest taxon possible and sorted into either diatoms (Fig. 2A) or animal parts (Fig. 2B). When both categories were present in a single gut, their relative abundances were estimated by separating the two types of food, measuring volume of each in a Sedgewick Rafter counting cell, and then calculating the proportions of the total volume of gut material in each category. The gastric mill of each dissected foregut was photographed at 20x magnification. The width of each gastric mill (Fig. 2C) was measured from the 1200 dpi digital image with ImageJ. The relationship between gastric mill width and CL was estimated by linear regression.

The proximal endite of the left first maxilliped, the left second maxilliped, and the mandibles of each crab were removed and examined under a

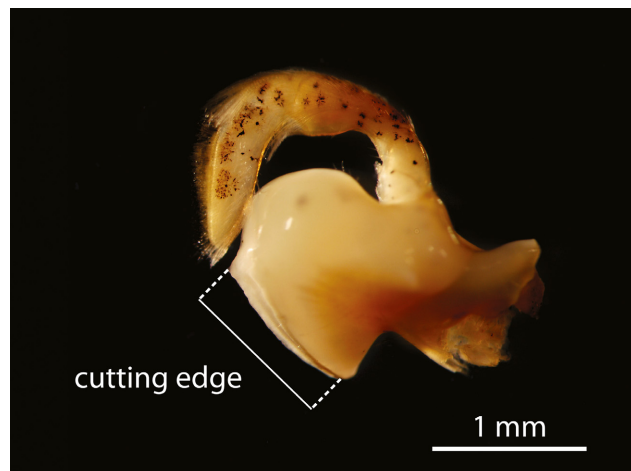


Fig. 3. Cutting-edge length of left mandible of *Ocypode gaudichaudii*. Scale bar=1 mm.

stereomicroscope. Plumose setae on the inner margin of the merus of maxilliped 2 were enumerated under a stereomicroscope. We used regression analysis to determine the relationship between number of plumose setae on inner margin of second maxilliped and carapace length. For maxilliped setation, an ANCOVA was performed using a GLM with “Number of plumose setae” as the response variable, “diet” as the factor, and “Carapace length” as the covariate for the crabs with different types of diet. The ANCOVA was applied to test for the difference in slopes of the regression lines between the types of diet after testing for homogeneity of variance with Levene’s test. If the slopes did not differ significantly, a test of intercepts was carried out. The outer surface of the mandible was photographed and length of the mandible cutting edge (Fig. 3) was measured from the 1200 dpi digital images in ImageJ. “Length of the mandible cutting edge” was regressed against “Carapace length” CL to determine the relationship between the variables by linear regression.

Results

The 82 crabs with intact chelipeds consisted of 27 females, 29 males, and 26 juveniles. Seventy (85%) of them were left-handed. Carapace length of males ranged 12.3–21.1 mm but females ranged 13.4–21.9 mm CL (Fig. 4). There was no significant difference between the mean CL of male and female crabs (t -test: $t=0.61$, $df=54$, $p=0.54$; CL male= 16.3 ± 0.4 mm, CL female= 15.9 ± 0.5 mm). Mean CL of the juvenile crabs was 6.2 ± 0.2 mm. Truncation at the dactyl and pollex tips in the major chelae began when the crabs

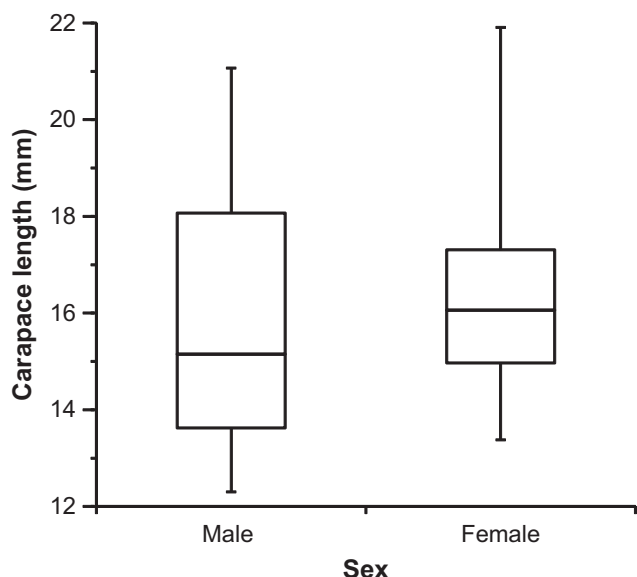


Fig. 4. Box-and-whisker plot of median carapace length and interquartile range of male ($n=29$) and female ($n=27$) *Ocypode gaudichaudii*.

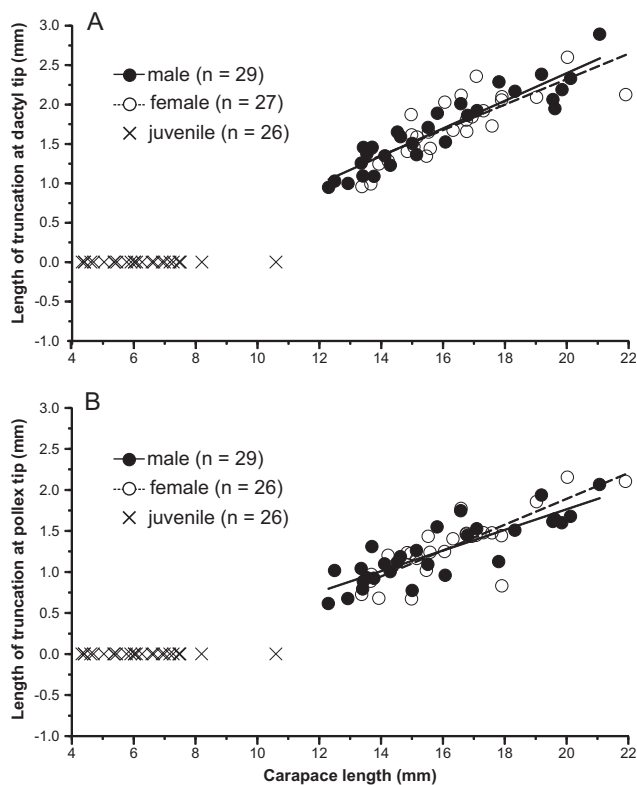


Fig. 5. Scatterplot and fitted regression lines of the truncated length at the **A.** dactyl and **B.** pollex tips of the major claw of juvenile, female and male *Ocypode gaudichaudii* against carapace length. Claw tips that did not exhibit truncation were assigned length=0.

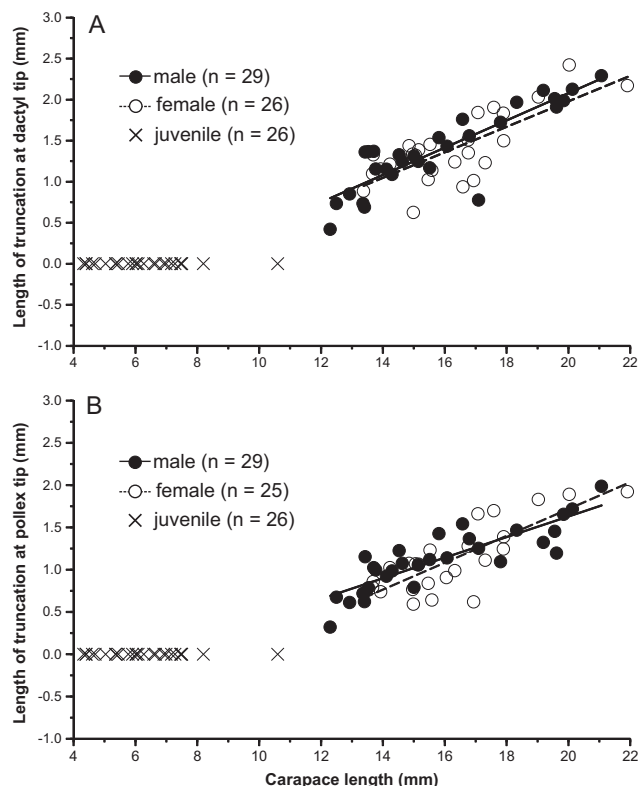


Fig. 6. Scatterplot and fitted regression lines of the truncated length at the **A.** dactyl and **B.** pollex tips of the minor claw of juvenile female and male *Ocypode gaudichaudii* against carapace length.

were 10.6–12.3 mm CL (Fig. 5A,B). A similar trend was observed in the minor chelae (Fig. 6A,B).

Allometric growth of the truncated lengths at the claw tips (dactyl and pollex) occurs with increasing CL when the truncated lengths at the claw tips of all the crabs (juvenile and adults) were considered (Figs. 5A,B, 6A,B). However, when the R^2 values of the regression lines of both the transformed and non-transformed data of the adult crabs were compared, R^2 values of the transformed data were similar to or less than those of the non-transformed data (Table 1). The results suggest that a simple linear relationship adequately explains how truncated length at the claw tip scales with body size. ANCOVA results for the major chelae showed that there was no significant difference ($p>0.05$) between the slopes or between the intercepts of regression lines of males and females for the truncated length on the dactyl and pollex in relation to body length (Table 2): the lengths of the truncated claw tips are not sexually dimorphic. Similar results were obtained for the truncated lengths on the minor claw tips. The truncated lengths of the dactyl and pollex tips of males and females were combined. Although there was no

Table 1. Results of regression analyses testing for relationships between length of truncation at claw tips of the major and minor claws, and carapace length in male and female *Ocypode gaudichaudii*.

Claw	Truncation	Sex	Regression equation	R^2	df ₁ , df ₂	F	p
Major	Dactyl tip	Male	$y = -1.1 + 0.2x$	0.87	1, 27	173.06	<0.05
		Female	$y = -0.9 + 0.2x$	0.66	1, 25	49.20	<0.05
	Pollex tip	Male	$y = -0.8 + 0.1x$	0.73	1, 27	72.93	<0.05
		Female	$y = -1.3 + 0.2x$	0.67	1, 24	47.72	<0.05
Minor	Dactyl tip	Male	$y = -1.2 + 0.2x$	0.77	1, 27	88.02	<0.05
		Female	$y = -1.1 + 0.2x$	0.57	1, 24	32.32	<0.05
	Pollex tip	Male	$y = -0.8 + 0.1x$	0.72	1, 27	70.97	<0.05
		Female	$y = -1.5 + 0.2x$	0.66	1, 23	43.86	<0.05
Log ₁₀ -transformed							
Major	Dactyl tip	Male	$\log_{10}y = -1.8 + 1.7 \log_{10}x$	0.86	1, 27	164.38	<0.05
		Female	$\log_{10}y = -1.8 + 1.7 \log_{10}x$	0.68	1, 25	54.15	<0.05
	Pollex tip	Male	$\log_{10}y = -1.9 + 1.7 \log_{10}x$	0.70	1, 27	62.83	<0.05
		Female	$\log_{10}y = -2.3 + 2.0 \log_{10}x$	0.59	1, 24	33.99	<0.05
Minor	Dactyl tip	Male	$\log_{10}y = -2.3 + 2.1 \log_{10}x$	0.65	1, 27	51.03	<0.05
		Female	$\log_{10}y = -1.9 + 1.7 \log_{10}x$	0.46	1, 24	20.60	<0.05
	Pollex tip	Male	$\log_{10}y = -2.3 + 1.9 \log_{10}x$	0.66	1, 27	51.84	<0.05
		Female	$\log_{10}y = -2.6 + 2.1 \log_{10}x$	0.56	1, 23	29.47	<0.05

significant difference ($p > 0.05$) between the slopes or between the intercepts of the regression lines for truncated lengths at the dactyl and pollex of the major and minor claws (Table 2), the length of the truncated tip of the dactyl of each claw was consistently greater than that at the pollex. Mean Dt and Pt for the major claw were 1.16 ± 0.10 mm and 0.87 ± 0.08 mm, respectively. For the minor claw, mean Dt and Pt were 0.95 ± 0.08 mm and 0.76 ± 0.07 mm, respectively.

Only 44 (50%) of the crabs examined had food in their foreguts, and overall, more crabs (68%) ingested animal prey than diatoms (Table 3). The most frequent animal remains observed were rove beetle (Staphylinidae) parts. Animal parts were present in the foreguts of all juvenile crabs with non-truncated claws (Table 3). The remaining 24 adult crabs with truncated claws ingested either animal parts, diatoms, or both. Remnants of isopods and an unidentified beetle were observed in two adult crabs. Only diatoms of the *Aulacodiscus* genus were found in the gut of adult crabs. A similar number of adult crabs fed on either animal prey or diatoms only. In two adult crabs, a mixture of both diatoms and animal parts was found (Table 3), with mean relative abundances of 84% (CL=15.0 mm) and 16% (CL=21.9 mm), respectively. Mean carapace length of the crabs that fed on animal parts (16.5 ± 0.9 mm) was less than that of the crabs that fed on diatoms (17.5 ± 0.6 mm) or had a mixed diet (18.5 ± 3.5 mm) (Fig. 7). There were no differences in the gastric mill width and length of the mandible

cutting edge between the animal predators and deposit-feeders (see Appendix S1 for adult morphological measurements.). Similarly, no obvious ontogenetic differences were observed in the setation of the proximal endites (Fig. 8A,B). However, extra rows of plumose setae were observed on maxilliped 2 of the larger crabs (Fig. 8C,D). Setation on the inner margin of the second maxilliped was increased in crabs with longer CL ($R^2 = 0.89$) (Fig. 9A,B), but neither the slopes nor intercepts of those regressions differed between adult deposit-feeders and adult predators ($p > 0.05$).

Discussion

There was clear evidence that juvenile crabs with non-truncated claws were exclusively predatory and that adult crabs were not specialized feeders. Our findings on the diet of juvenile crabs were consistent with previous field observations and gut content analyses by Crane (1941) and Koepcke & Koepcke (1953). The most striking observations were that (1) there was no distinct diet shift, and (2) diet in *Ocypode gaudichaudii* did not correspond with the development of truncated claws as reported by Crane (1941). Our results indicate that diet in *O. gaudichaudii* with specialized truncated claws was not constrained to diatoms. The presence of a mixture of diatoms and animals in the adult crabs with truncated claws implies that niche breadth in *O. gaudichaudii* expanded during ontogeny. The similar frequency of occurrence of

Table 2. Results of ANCOVAs testing slopes and intercepts of regression equations estimating relationships among morphological variables in *Ocypode gaudichaudii*: (A) truncation at the dactyl and pollex tips on the major claw in males versus females; (B) truncation at the dactyl and pollex tips on the minor claw in males versus females; (C) truncation at the dactyl tip versus pollex tip at the major claw; (D) truncation at the dactyl tip versus pollex tip at the minor claw.

Source	df ₁ , df ₂	F	p		Inference
A. Major claw					
Dactyl tip					
Sex	1, 52	0.22	0.64	n.s.	Intercepts not different
Carapace length	1, 52	172.59	<0.05		
Sex×Carapace length	1, 52	0.28	0.60	n.s.	Slopes not different
Pollex tip					
Sex	1, 51	1.31	0.26	n.s.	Intercepts not different
Carapace length	1, 51	113.87	<0.05		
Sex×Carapace length	1, 51	1.36	0.25	n.s.	Slopes not different
B. Minor claw					
Dactyl tip					
Sex	1, 51	0.05	0.82	n.s.	Intercepts not different
Carapace length	1, 51	102.36	<0.05		
Sex×Carapace length	1, 51	0.12	0.73	n.s.	Slopes not different
Pollex tip					
Sex	1, 50	2.20	0.14	n.s.	Intercepts not different
Carapace length	1, 50	108.32	<0.05		
Sex×Carapace length	1, 50	1.88	0.18	n.s.	Slopes not different
C. Major claw					
Dactyl tip cf pollex tip					
Claw tip	1, 107	0.12	0.73	n.s.	Intercepts not different
Carapace length	1, 107	311.07	<0.05		
Claw tip×Carapace length	1, 107	3.48	0.07	n.s.	Slopes not different
D. Minor claw					
Dactyl tip cf pollex tip					
Claw tip	1, 105	0.26	0.61	n.s.	Intercepts not different
Carapace length	1, 105	221.69	<0.05		
Claw tip×Carapace length	1, 105	1.86	0.18	n.s.	Slopes not different

n.s., not significant.

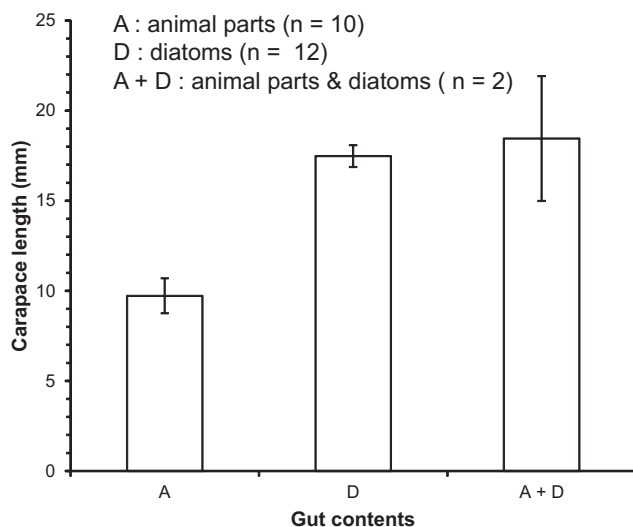
deposit-feeding and predation among adults suggests that adult *O. gaudichaudii* are opportunistic, as are other species of ghost crabs (Tweedie 1950; Wolcott 1978).

Diet expansion in *O. gaudichaudii* could be driven by an ontogenetic change in absorption efficiency, similar to that suggested from studies of diet shift in polychaetes, in which juvenile worms feed on more nutritive food (e.g., benthic diatoms) until reaching a certain size, when they switch to a diet of sediment with lower nutritive value (Jumars et al. 1990). Hentschel (1998) attributed the diet shift to constraints imposed by juveniles' short, small guts in processing sufficient sediment to meet the nutritional demands for growth and metabolism. Perhaps the broadening of diet in *O. gaudichaudii* is the consequence of adult crabs not finding sufficient numbers of whole arthropod prey, such as rove beetles, to

support growth on the mid- to low-energy beaches where this crab lives. To compensate, adult crabs could have shifted to deposit-feeding to meet their energy demands. Unlike other deposit-feeding ocypodids such as fiddler crabs, ghost crabs lack spoon-tipped setae on their second maxillipeds to help remove organic matter from sand grains. Therefore, the rows of plumose setae on the second maxilliped of larger crabs could be an ontogenetic morphological change for deposit-feeding. However, our results showed that there is no significant difference in the number of plumose setae on the inner margin of the second maxilliped in either deposit-feeding or predatory adults, suggesting that there is no adaptation in the number of plumose setae for deposit-feeding. The lack of distinct ontogenetic morphological changes in the other feeding structures examined precludes these structures as predictors of niche breadth.

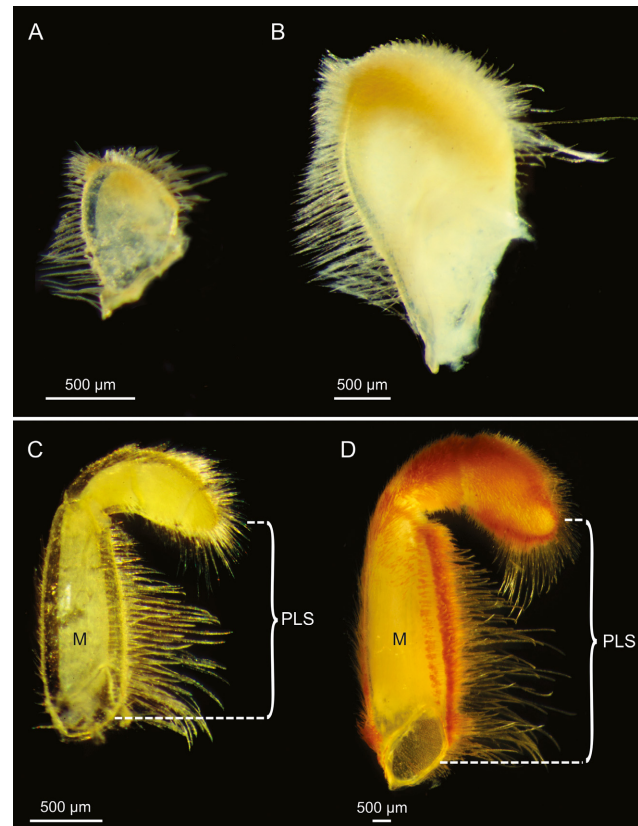
Table 3. Number of foreguts examined containing each diet type, in juveniles or adults of *Ocypode gaudichaudii*.

Diet	Non-truncated claws Juvenile	Truncated claws Adult	Frequency of occurrence
	Animals	20	
Diatoms	0	12	12 (27%)
Animals and diatoms	0	2	2 (5%)
Total	20	24	44

**Fig. 7.** Distribution of carapace length of adult *Ocypode gaudichaudii* with different foregut contents (mean \pm S.E.).

The discordance of specialized claw morphology and a generalist diet in *O. gaudichaudii* concurs with Liem's paradox, the observation that cichlid fishes with specialized morphology have a broad diet (Liem 1980; Robinson & Wilson 1998). For example, individuals of the African cichlid *Astatoreochromis alluaudi*, with pharyngeal jaws for consumption of hard-bodied mollusks, feed on soft-bodied insects as well (Cosandey-Godin et al. 2008). This challenges the paradigm that functional design and niche width are closely correlated.

A few hypotheses were proposed to account for Liem's paradox. Liem (1990) dismissed the importance of competition as the driving factor for phenotypic diversity. He proposed that the evolution of specialized phenotypes is non-adaptive and attributed ecomorphological mismatches to genetic constraints. Robinson & Wilson (1998) criticized the hypothesis for its non-adherence to the conventional competition-based model of optimal foraging and resolved the paradox with a model. The model is based on

**Fig. 8.** Left proximal endites of the first maxillipeds and second maxillipeds of *Ocypode gaudichaudii*. Proximal endite from maxilliped 1 of **A.** juvenile, and **B.** adult. Plumose setae (PLS) on the inner margin of the merus (M) from maxilliped 2 of **C.** juvenile, and **D.** adult. Scale bars A,B,C,D=500 μ m.

optimal foraging theory and assumes asymmetry in the relative reward (e.g., different handling time and energy payoff) when different prey items were consumed. Fluctuations in resource availability can influence the foraging strategies of consumers (Binning et al. 2009). Consumers tend to be opportunistic and feed on the resource they encounter most often when food is abundant. When resources are scarce, phenotypic specialization will be adaptive if it allows consumers to exploit resources that are not accessible to competitors (Robinson & Wilson 1998; Cosandey-Godin et al. 2008; Binning & Chapman 2010). This model can be applied to explain versatility in the cichlid *Perissodus paradoxus* at handling a wide repertoire of food with dentition specialized for scraping algae (Liem & Summers 2000).

The greater occurrence of an animal rather than a diatom diet in *O. gaudichaudii* could reflect preference. The development of a mismatch in trophic morphology and diet may enable larger crabs to cope with the constant fluctuation of food resources

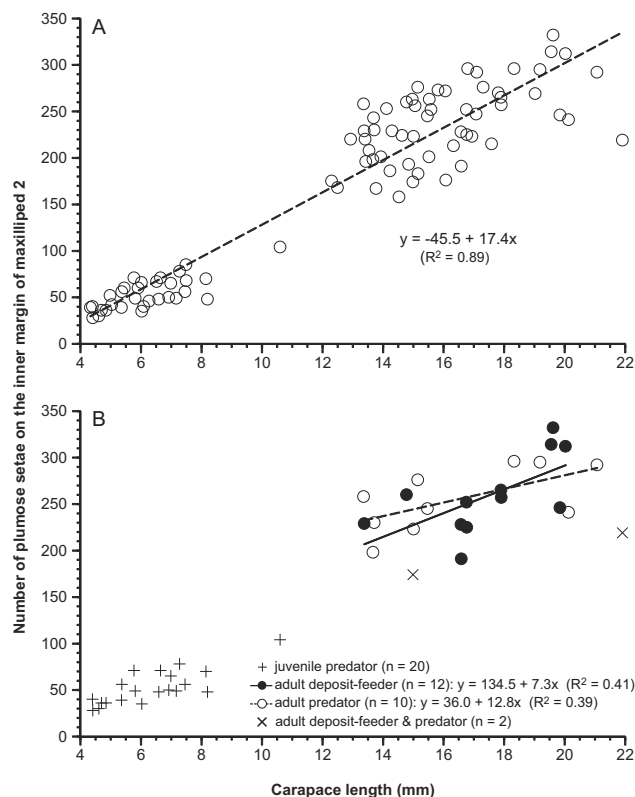


Fig. 9. Scatterplot and fitted regression lines of “Number of plumose setae on the inner margin of second maxilliped” against “Carapace length” of **A.** all *Ocypode gaudichaudii* collected, and **B.** *O. gaudichaudii* with different foregut contents.

at the intertidal shore. When overall food resources are low, *O. gaudichaudii* individuals with specialized claws will be able to obtain greater amounts of food by deposit-feeding rather than preying on scarce mobile animals.

Studies on the functional feeding morphology and diet of organisms at different life stages can provide insights into their trophic ecology (Liem & Summers 2000). While there is a growing body of literature with examples of morphological specialists that are dietary generalists, most of these studies focus on the occurrence of ecomorphological mismatches in fishes (McKaye & Marsh 1983). However, there is only one previous study on invertebrates; in the mantis shrimp *Neogonodactylus bredini*, specialized raptorial appendages are used to shatter the shells of hard-shelled prey, but individuals feed on both soft and hard-shelled prey (deVries 2012). Our study of *O. gaudichaudii* is the first that integrates functional morphology of semi-terrestrial brachyurans with ontogenetic diet shift. Further work is required to study the relationship among resource

abundance, competition, and environmental factors on trophic morphology and foraging strategy in *O. gaudichaudii* to have a better understanding of the trophic dynamics of tropical sandy shores.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Morphological measurements (mean±SE) from adults of *Ocypode gaudichaudii* with different fore-gut contents. All measurements are in mm.