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DIET AND FECUNDITY OF COLUMBUS CRABS, *PLANES MINUTUS*, ASSOCIATED WITH OCEANIC-STAGE LOGGERHEAD SEA TURTLES, *CARETTA CARETTA*, AND INANIMATE FLOTSAM

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ABSTRACT

The digestive tract contents of 85 Columbus crabs, *Planes minutus*, are presented. Crabs were collected from oceanic-stage loggerhead turtles, *Carettta caretta*, and inanimate flotsam near the Azores. The numbers of eggs carried by ovigerous crabs ($n = 28$) are also presented. Numbers of eggs between turtle crabs and flotsam crabs were similar. Dietary analysis yielded 11 food types from *P. minutus*. Crabs from turtles contained a higher diversity of food items than crabs from inanimate flotsam. The diet of *P. minutus* was composed primarily of neustonic invertebrates and algae—similar to prey items found from oceanic-stage loggerhead turtles in past studies. The types of food consumed by *P. minutus* suggest that crabs may obtain food by consuming other epibionts, by hunting neuston from their substrate, or by capturing food particles expelled by host turtles.

Grapsid crabs of the genus *Planes* are colloquially known as Columbus crabs, apparently due to the discovery of a crab, likely a *Planes*, from "floating weed" during Christopher Columbus' voyage to the New World. Like other members of its genus, *Planes minutus* (Linnaeus, 1758) is a relatively small pelagic species that is dependent upon flotsam for survival (Chace, 1951), occupying a variety of flotsam types as clinging substratum, including oceanic-stage loggerhead sea turtles, *Caretta caretta* (Linnaeus, 1758), from the eastern North Atlantic (Dellinger *et al.*, 1997; Frick *et al.*, 2003).

Several studies have investigated the association between *P. minutus* and young loggerhead turtles (see Frick *et al.*, 2000). However, little is known of the foraging ecology and fecundity of Columbus crabs, and there are no studies that quantify the diet and number of eggs of *P. minutus*. We identify and quantify the food items consumed by 71 *P. minutus* from loggerhead turtles captured near the Azores. We also report dietary data from 14 *P. minutus* collected from inanimate flotsam near the Azores. The size and number of eggs of *P. minutus* were determined and compared between crabs collected from loggerhead turtles and those collected from flotsam.

MATERIALS AND METHODS

Turtles were captured using dipnets near the Azores from 1986 through 1994 during the months March–November. Curved carapace length (± 0.1 cm) of each turtle was measured from the anterior point at midline (nuchal scute) to the posterior notch at midline between the supracaudals with a flexible fiberglass tape measure. Turtles were released soon after capture.

Crabs ($n = 71$) were removed from turtles and preserved in either 70% ethyl alcohol or 10% Formalin, depending upon preservative availability. Crabs ($n = 14$) were also removed from inanimate flotsam during the same period. Crabs were assigned to gender and maturity following Dellinger *et al.* (1997). Maximum carapace length and width were recorded from crabs in millimeters (mm) using Vernier calipers. Species determination was made by comparing the combined lengths of the three distal segments of the second walking leg with the carapace length (see Chace, 1951; Spivak and Bas, 1999).

Digesta strings, from the intestinal and abdominal regions, and the contents of the cardiac and pyloric chambers (stomach) were removed from each crab and viewed under light microscopy (up to 1000×). Stomach contents and digesta strings were then identified to the lowest taxon possible. The composition of the diet for each crab was recorded using a points system developed by Hynes (1950) and Hartnoll (1963) in which 20 points are assigned to a full stomach, 10 to a half full stomach, etc. These points are then allocated among the diet items in the digestive tract according to their volume. The points allocated to each type of food are summed for all crabs and expressed as a percentage of the total number of points, giving the composition of the diet as percent of volume.

Eggs from each ovigerous *P. minutus* ($n = 20$ from turtles and 8 from flotsam) were staged following Hartnoll (1963) and counted to determine fecundity. Pleopods bearing eggs were cut from the female's abdomen with a scalpel, placed in a sodium solution and shaken until the eggs separated from the pleopods. Egg counts were made under light microscopy (magnification up to 30×). Masses of the spherical eggs were spread one layer thick over a 7.5 cm × 5 cm glass microscope slide that was sectioned into a grid of 140—5 mm × 5 mm squares. The number of eggs within a single 5 mm × 5 mm square was counted and multiplied by the number of squares containing eggs. The diameters of 10 randomly chosen eggs per ovigerous crab were recorded in microns using a computer interfaced digital stereomicroscope/micrometer.

RESULTS

A total of 71 *P. minutus* was collected from oceanic-stage loggerhead turtles near the Azores, usually in the space above the tail and beneath the carapace (upper shell) of the host turtle. However, two *P. minutus* were found among barnacles (*Lepas* sp.) on the host's carapace. Fifty-six crabs were collected from 38 individual turtles. These turtles hosted crabs as singletons ($n = 23$ turtles; 57%), heterosexual adult pairs ($n = 12$ turtles; 21%) and trios ($n = 3$ turtles; 7%). In addition, 15 crabs were collected from an unknown number of turtles with no supporting host data. Of the crabs collected, 65 were adults (35 females and 30 males) and 6 were juveniles (4 males and 2 females). Juvenile crabs always occurred in association with adult crabs; no turtle hosted only juvenile crabs.

Host turtle size ranged 13.6–59.6 cm curved carapace length (mean = 34.5 cm). Adult female crabs (11–22 mm carapace width; mean = 16.47 mm; $n = 35$) were significantly larger than adult males (10–19 mm; mean = 15.03 mm; $n = 30$) (t test, $t = -2.4121$, $df = 63$, $P = 0.0188$). Similarly, juvenile female crabs were larger than juvenile males, 9.25–13.5 mm (mean = 11.34) and 6–8.5 mm (mean = 6.63 mm), respectively. The juvenile-crab sample size was too small to determine whether any significant differences in size exist between juvenile male and female *P. minutus*.

Twenty adult female *P. minutus* collected from *C. caretta* were ovigerous. Ovigerous crabs were significantly larger (11–22 mm; mean = 17.32) than non-ovigerous adult female crabs (13.5–18.5 mm; mean = 15.35; $n = 15$) (t test, $t = 2.4417$; $df = 33$; $P = 0.02$). Ovigerous females collected from turtles carried an average of 8934 eggs (range: 400–22,248 eggs/female) ranging in size from 258.8–393.3 (mean = 319.5) microns in diameter. Stage 1 eggs, which are eggs of uniform color and even yolk distribution, represented 50% ($n = 10$ clutches) of the eggs measured from crabs taken from turtles. Stage 2 eggs, eggs containing a clear area devoid of yolk, and stage 3 eggs, eggs containing pigmented eyespots, represented 40% ($n = 8$ clutches) and 10% ($n = 2$ clutches) of the eggs measured from crabs taken from turtles, respectively. Stage 4 eggs (hatching) and stage 5 eggs (hatched or empty eggs) were not observed from this group of crabs. The diameters of the *P. minutus* eggs varied according to embryonic stage; stage 1 eggs were smaller (mean = 261.2 microns) than stage 2 (mean = 324.3 microns) and stage 3 eggs (mean = 382.6 microns).

Fourteen *P. minutus* were collected from two items of inanimate flotsam (a small buoy covered in *Lepas* barnacles and a small (10 × 15 cm) piece of wood). Of these crabs, 4 were adult males and 10 were adult females. A single heterosexual pair was collected from wood flotsam, and the remainder of the sample of crabs from flotsam was taken from the buoy. The mean carapace widths of adult male and female *P. minutus* from inanimate flotsam were 15.8 mm (range = 15–17 mm) and 16.2 (range = 13.75–17.5 mm), respectively.

Eight female crabs from flotsam were ovigerous. The mean carapace width of ovigerous crabs from flotsam was greater (16.7 mm; range = 15.75–17.75 mm) than that of nonovigerous females (13.9 mm; range = 13.75–14 mm). The sample size of crabs from flotsam was too small to determine whether any significant size differences exist between male and female *P. minutus* and between ovigerous and nonovigerous crabs from inanimate flotsam. Ovigerous females collected from flotsam carried an average of 8907 eggs (range: 3200–20,394 eggs/female) ranging in size 248.6–373.6 (mean = 301.4) microns in diameter. Stage 1, 2, and 3 eggs represented 50% ($n = 4$ clutches), 25% ($n = 2$ clutches) and 25% ($n = 2$ clutches) of the eggs measured from crabs taken from the buoy, respectively. Stage 4 and 5 eggs were also absent from ovigerous females inhabiting flotsam. Stage 1 eggs from crabs taken from flotsam were smaller in diameter (mean = 254.9 microns) than stage 2 (mean = 313.4 microns) and stage 3 eggs (mean = 371.0 microns).

There was no significant difference in size between *P. minutus* from *C. caretta* and those collected from flotsam for both males (t test, $t = -0.6771$; $df = 32$; $P = 0.5$) and females (t test, $t = 0.3892$; $df = 43$; $P = 0.7$).

Dietary analysis yielded 11 food types from *P. minutus* hosted by loggerhead turtles (Table

Table 1. Diet composition for *P. minutus* collected from loggerhead turtles. Data are number of points totaled for each food type present with percent composition in parentheses. See text for generic or specific designation of selected (*) food types.

Diet	All crabs	All adult females	Nonovigerous females	Ovigerous females	Adult males	Juvenile females	Juvenile males
Number of crabs	71	35	15	20	30	2	4
Total points	944	485	264	221	416	12	31
Diatoms	115 (12)	63 (13)	34 (13)	29 (13)	52 (13)	–	–
Other algae	118 (13)	40 (8)	16 (6)	24 (10)	47 (11)	12 (100)	19 (61)
Hydroid	72 (7)	39 (8)	22 (8)	17 (8)	33 (8)	–	–
Euphausid	82 (9)	40 (8)	30 (11)	10 (5)	42 (10)	–	–
Amphipod*	33 (3)	13 (3)	–	13 (6)	20 (5)	–	–
Pycnogonid*	36 (4)	14 (3)	12 (5)	2 (1)	22 (5)	–	–
Conspecific	53 (6)	32 (7)	10 (4)	22 (10)	21 (5)	–	–
Cirriped*	33 (3)	21 (4)	16 (6)	5 (2)	5 (1)	–	7 (23)
Gastropod*	45 (5)	20 (4)	20 (8)	–	25 (6)	–	–
Unidentified animal material	300 (32)	170 (35)	91 (34)	79 (36)	125 (30)	–	5 (16)
Unidentified plant material	57 (6)	33 (7)	13 (5)	20 (9)	24 (6)	–	–

1). Most food items were highly comminuted, and identification as to genus or species was only possible for four food types listed in Table 1. Three crabs containing amphipods contained identifiable anterior portions and gnathopods of *Caprella* sp. and *Podocerus chelonophilus* (Chevreux and de Guerne, 1888). Two crabs containing pycnogonid material contained the remains of *Endeis spinosa* (Montagu, 1808) and *Callipallene phantoma* (Dohrn, 1881). Four crabs containing cirriped material had consumed the cirri from *Lepas* sp. barnacles and *Lepas* sp. cyprids. Two adult male crabs carried single specimens of the pedunculate barnacle *Conchoderma virgatum* (Spengler, 1789) with the chelipeds or walking legs. These crabs had full stomachs that contained lepadomorph cirri. Female crabs from the same host turtles as the males contained the same barnacle cirri. Five crabs containing gastropod material had consumed purple shell fragments and eggs capsules of *Janthina* sp. snails. The remainder of the material from crabs containing amphipod, pycnogonid, cirriped, and gastropod food items were unidentifiable as to genus or species.

Adult crabs consumed similar types and amounts (total points; Table 1) of food regardless of sex, reproductive condition (ovigerous or nonovigerous), or mean carapace width (which varied significantly between some crab groups). Of the material that could be identified, diatoms composed the highest percentage (13%), which was consistent across the three groups of adults. Juvenile crab diets were composed of more algae than those of adult crabs, and juvenile male crabs consumed more animal material than did juvenile females. The cirriped material from juvenile male crabs was represented solely by *Lepas* sp. cyprids.

The diets of crabs that occurred on the same host turtles as heterosexual pairs are compared in Table 2. Overall, there appears to be no marked gender-based resource partitioning occurring between adults that, theoretically, have access to the same food resources on a shared host.

Crabs from flotsam consumed fewer types of food than crabs from turtles (Table 3). Unidentified algae represented the bulk of the diets observed from those crabs. Male crabs from flotsam contained only algae. Conspecifics and cirriped material were only found in female crabs. The cirriped material from female crabs from flotsam was represented solely by *Lepas* sp. cyprids.

DISCUSSION

Laboratory studies by Davenport (1992) represent the only information on prey capture and food handling in adult *P. minutus*. The crabs observed by Davenport (1992) obtained some food items via grazing flotsam that was placed into tanks, but crabs would also lunge or swim into the water column to obtain prey items (salps, postlarval flying fish, juvenile puffer fish, pilot fish, euphausids, isopods, or small squid). Some crabs would carry surplus prey using the dactyl spines of the walking legs for up to 24 hours before the item was consumed.

Many of the food items, particularly sessile forms, presented in Table 1 could have been obtained by crabs via browsing. Wild crabs may have captured euphausids in a swimming fashion as described by Davenport (1992). In addition, we found crabs storing or carrying food

Table 2. Diet composition for *P. minutus* heterosexual pairs occurring on *Caretta*.

Diet	Adult males	Adult females
Number of crabs	15	15
Total points	236	249
Diatoms	36 (15)	37 (15)
Other algae	14 (6)	12 (5)
Hydroid	11 (5)	19 (8)
Euphausid	30 (13)	20 (8)
Amphipod	6 (2)	7 (3)
Pycnogonid	13 (6)	8 (3)
Conspecific	22 (9)	22 (9)
Cirriped	3 (1)	6 (2)
Gastropod	12 (5)	10 (4)
Unid. animal material	72 (31)	80 (32)
Unid. plant material	17 (7)	28 (11)

items as described by Davenport (1992). Geiselman (1983) noted that Columbus crabs living within *Sargassum* weed are predominately carnivorous (prey not stated) but also eat *Sargassum* and tar balls. A single ovigerous female *P. minutus* from a juvenile loggerhead captured near Madeira contained euphausids, *Lepas* barnacle cyprids, amphipods, and other *P. minutus* (Davenport, 1994). The latter three species are also commonly observed as loggerhead epibionts, suggesting a cleaning association between crabs and turtles (Davenport, 1994; Frick *et al.*, 2000). Data from the current study supports a cleaning association between *C. caretta* and *P. minutus* because many of the food items we found from *P. minutus* are the same or similar to the species reported as epibiota from loggerhead turtles captured near the Azores, with the exception of gastropods and euphausids (see Frick *et al.*, 2003). However, the extent to which the foraging behavior of *P. minutus* might benefit host turtles is still unknown.

Adult crabs confined to the same turtle fed on similar prey types and quantities of each type (Table 2). There are no studies that investigate the foraging behavior of *P. minutus* when sharing a substrate with conspecifics. The presence of competitors may alter the observed foraging behavior of *P. minutus* (Davenport 1992). Crabs may lose portions of captured prey in disputes with other crabs sharing the same substrate, which could contribute to the similarity in diets between adult crab pairs. Laboratory studies would help to determine the foraging behavior of multiple *P. minutus* when sharing the same substrate.

Agonistic behavior in *P. minutus* is suggested by the presence of conspecifics within stomach contents. The size of the conspecific fragments encountered suggests that large juvenile crabs, similar in size to those reported from this study, were consumed by *P. minutus*. Conspecifics were only consumed by adult crabs collected from turtles also hosting juvenile specimens. Moulted crab exuvia could be a possible source of conspecific fragments.

Although few juvenile crabs were available for stomach contents analysis, it is apparent that algae are important in the diet of immature crabs. The presence of animal material in the diets of juvenile male crabs ($n = 4$) and its absence from juvenile female crabs ($n = 2$) could be an artifact of sample size. The lower diversity of prey items consumed by juvenile *P. minutus* compared with adults may be real or an artifact of the small sample size. Perhaps juvenile *P. minutus* lack the ability to capture motile or floating prey, or adults may steal high quality prey captured by juveniles. Additional studies on the diets of juvenile *P. minutus* are needed to evaluate differences in diet selection between juvenile males and females and between juveniles and adults.

Gastropods (*Janthina* sp.) were represented in the diet of *P. minutus* as minute shell fragments and egg capsules. *Janthina* sp. are pelagic snails that create bubble rafts of air trapped in mucus to remain afloat and on which they lay their eggs. Columbus crabs would undoubtedly be capable of capturing *Janthina* and associated eggs while hunting from *C. caretta*. However, *Janthina* is a reported food item of young loggerheads from the Azores (Van Nierop and Den Hartog, 1984), so *P. minutus* may consume fragments of prey items initially captured and crushed for consumption by host turtles. During the initial stages of food consumption, scraps of food often drift out of and away from the mouth the turtle. *Planes minutus* may retrieve food particles released by their host turtles, possibly accounting for similarities between the diets of Columbus crabs and oceanic-stage loggerhead turtles.

The unidentified plant and animal material presented in Table 1 is probably highly masticated or digested remnants of the identifiable food items presented in Table 1. However, in several cases we encountered gelatinous animal material from crab guts. Initially we assumed this material to be cnidarian, but no nematocysts were encountered. The gelatinous material may represent apical or gonadal cnidarian tissue devoid of nematocysts or salps, another item recorded from the diet of oceanic loggerheads and also readily taken by captive Columbus

Table 3. Diet composition of *P. minutus* collected from inanimate flotsam (buoy and wood). Cirriped material (*) was represented solely by *Lepas* sp. cyprids.

Diet	All crabs	Ovigerous females	Nonovigerous adult females	All adult females	Adult males
Number of crabs	14	8	2	10	4
Total points	71	42	12	54	17
Algae	45 (63)	16 (38)	12 (100)	28 (52)	17 (100)
Conspecific	17 (24)	17 (41)	–	17 (31)	–
Cirriped*	9 (13)	9 (21)	–	9 (17)	–

crabs. Moreover, captive *P. minutus* only ate the top or "nucleus" of the salp and discarded the rest (Davenport, 1992). The nucleus contains the stomach, potentially the most nutritious portion of a salp. Salp stomachs contain compacted phytoplankton, detritus, and zooplankton (Kashkina, 1986), possibly an additional source of unidentified material in our study. Crabs on turtles may also feed upon the shedding skin and feces of host turtles (Crane, 1937), accounting for more of the reported unidentified material.

Planes minutus is omnivorous when symbiotic with oceanic-stage loggerhead sea turtles. The diet of *P. minutus* presented here probably represents a combination of epibionts of host turtles, pelagic and neustonic organisms captured near turtles, and food particles seized by crabs while turtles are feeding. Ours is the first in-depth analysis of the diet of *P. minutus* when symbiotic with *C. caretta*. Studies are needed that quantify prey items of Columbus crabs from other animate flotsam (e.g., pelagic snails, colonial cnidarians). The foraging ecology and other aspects of the life history of *P. minutus* may well vary with respect to substrate type.

The diets of *P. minutus* collected from inanimate flotsam suggest that these specimens may have obtained much of their food—conspecifics, algae, and barnacle cyprids—via grazing and through agonistic interactions with other Columbus crabs. Although the sample size of 14 crabs from flotsam is relatively small, the dietary data presented in Table 3 suggest that *P. minutus* are exposed to a wider variety of potential prey or food items when symbiotic with *C. caretta* than when living upon inanimate flotsam. Whether the behavior (feeding and diving) of host turtles is responsible for the diversity of food types consumed by crabs or whether crabs are exposed to a wider variety of epibionts (potential prey items) on turtles than on inanimate flotsam is unknown.

The mean adult sizes of crabs from turtles and crabs from flotsam were not significantly different, and ovigerous crabs from flotsam carried similar amounts and sizes of eggs. Therefore, type of substrate does not appear to be related to egg production. However, Columbus crabs may benefit by association with loggerhead turtles because agonistic interactions with other *P. minutus* seem to be more uncommon on turtles than on inanimate flotsam. Conspecifics were more common in the diets of crabs on flotsam than in crabs on turtles, 24% and 6%, respectively (Tables 1, 3). Additionally, Dellinger *et al.* (1997) reported that agonistic interactions were more common in crabs inhabiting inanimate flotsam than those found on turtles. Increased agonistic interactions between *P. minutus* would decrease survival probabilities and reproductive output as energy is diverted from reproduction to repair injuries. Larger sample sizes of crabs from a variety of substrate types are necessary for evaluation of effects of substrate on the demography of Columbus crabs.

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