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Benthic microalgae serve as the major food resource for porcelain crabs (*Petrolisthes* spp.) in oyster reefs: gut content and pigment evidence[1]

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Abstract

Suspension-feeding porcelain crabs (*Petrolisthes* spp.) are often the most abundant decapod crustaceans in oyster reef habitat. Analysis of water column and subtidal algal biomass from three Texas estuaries suggests that planktonic food resources are insufficient for porcelain crab growth. Pigment composition of porcelain crab muscle and digestive track contents included the diatom pigment fucoxanthin and cyanobacterial pigment canthaxanthin with digestive track samples containing attached (adnate) benthic diatoms as well as benthic cyanobacteria not found in the water column. Feeding appendages on porcelain crabs include numerous cirri with serrated edges as well as fewer more brush-like longer units. Benthic food resources are in sufficient supply to support porcelain crab biomass.

Keywords

benthic diatoms; filamentous cyanobacteria; pigments; porcelain crab; oyster reef; trophic coupling

1. Introduction

The socioeconomic importance of oyster reefs is well-established, as oysters provide ecosystem services as a keystone species (Paine 1966) and as ecosystem engineers (Jones et al. 1994). Porcelain crabs (*Petrolisthes galathinus* Bosc) are suspension feeding decapods that are found, often in great abundance, in oyster reef habitat throughout the Gulf of Mexico. Felder et al. (2009) list 21 species of porcelain crabs, including 8 in the genus *Petrolisthes.* While *Petrolisthes armatus* and *P. galathinus* range throughout the Gulf of Mexico whereas the remainder of the species are generally restricted to the more tropical areas of the southern Gulf. These crabs are eaten by consumers such as crested gobies (*Lophogobius cyprinoides*) and are thought to represent an additional trophic pathway because they seem to have a diet that differs from the bivalves (e.g., eastern oyster

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Crassostrea virginica) that are the foundation of the reef (Yeager and Layman 2011). Johnson and Freeman (2005) assessed digestive capacity and gut contents in six crab species, with porcelain crabs (*Petrolisthes elongatus*) exhibiting herbivorous enzyme activity, as previously suggested from gut content analyses (Kropp 1981). Caine (1975) reported porcelain crabs scraping oyster shell using the ventral margin of their chilipeds to loosen and resuspend attached algae algae/detritus and maxillipeds for suspension feeding. Achituv and Pedrotti (1999) determined that active feeding on phytoplankton under differing flow conditions enhanced energy acquired by porcelain crabs. Interpretation of feeding selectivity is difficult in laboratory studies, since animals are limited to food provided in terms of type, quality, and quantity (McGlaun and Withers 2012). While Johnson and Freeman (2005) suggest that *P. elongatus* has too little chitinase available to digest zooplankters, *P. galathinus* ate *Artemia* spp. nauplii enthusiastically in laboratory experiments (McGlaun and Withers 2012). Crabs fed an animal-only diet exhibited metabolic rates that were orders of magnitude higher than crabs fed phytoplankton or mixed microalgae. Despite their enthusiasm for the animal diet, the ratio of zooplankton biomass to phytoplankton biomass in natural systems is very low (e.g., Havens et al. 2009), thus the availability of zooplankters for ingestion is likely rare, or at best, episodic. Porcelain crabs are almost exclusively fed *A. salina* in laboratory studies (Hartman and Hartman 1977, Whitman et al. 2001), perhaps because of the difficulty maintaining algal cultures in exponential phase for optimal animal health.

Plant resources available for use by higher trophic levels include storage molecules, such as lipids/fatty acids, as well as photo-protective compounds such as carotenoids and mycosporine-like amino acids (Bandaranayake 1998). Algal pigments can provide a unique tracer for monitoring food preferences of organisms, particularly carotenoid markers specific to algal classes (Jeffrey et al. 2001). Carotenoid accumulation in fishes is well documented (Li et al. 2007, Grether et al. 1999) with retention of carotenoids for weeks to months (Li et al. 2011), potentially providing antioxidant/immuno-protective ability (Kolluru et al. 2006). These tracers are similar to other chemical methods (stable isotopes for example) in integrating long-term food sources within consumer biomass.

Numerous methods have been used to elucidate food web relationships including single and multiple stable isotopes (Bouillon et al. 2014, Johnson and Freeman 2005, Cocheret de la Morinière et al. 2003, Sullivan and Moncreiff 1990), gut content analysis (Ranvestel et al. 2004, Cocheret de la Morinière et al. 2003, Schmid-Araya and Schmid 2000), lipid/fatty acid or other biomarkers (Thurber 2015, Li et al. 2007, Grether et al. 1999), or immunological approaches (Feller et al. 1979). Often the result of these single analysis methods can be difficult to interpret when confounding issues co-occur such as shifting source material quality and quantity, omnivory, and age-dependent food selection changes (Thurber 2015, Matthews and Mazumder 2004, Riera et al. 1999). Because many of these methods rely on a single sampling event, it is critical that variation is established for food resources to differentiate trophic dietary variation versus trophic level variation (Mathews and Mazumder 2004, Bolnick et al. 2003) or that multiple approaches are used to confirm interpretation. Additionally, the method of analyses, such as examining gut contents with stereo microscopes (~60× magnification) or using a single producer sample for isotopic signature, can bias interpretation.

Considering the typical density of phytoplankton in meso-eutrophic coastal systems (Table 1), there often may be insufficient food available for efficient porcelain crab grazing on planktonic algae in microtidal systems. Typical phytoplankton mean chlorophyll *a* concentrations are <50 mg m^{-2} in water columns of 1–15 m deep (Fulford et al. 2007), whereas sediment pigment concentrations are up to 50 times higher and consolidated in a layer less than 1 cm thick. Assuming modest success with maxillipeds sweeping planktonic organisms, the amount of food successfully consumed from planktonic harvesting must be extremely low and could account for the inability of the larvae of *Pagurus longicarpus* Say, another anomuran crab, to metamorphose (Roberts 1971).

Food sources of porcelain crab collected from three different south Texas estuaries were evaluated using digestive track content analysis and pigment profiles of muscle. Available food resources were evaluated using phytoplankton net tows, sampling attached algae, crab gut contents, and crab muscle tissue pigment content. We hypothesized that benthic forms such as diatoms and cyanobacteria were a major portion of porcelain crab diet and that combined taxonomic and chemical analyses would provide insights about food preferences.

2. Methods

Field sampling for porcelain crabs occurred during October-November 2015. Sterile, aged oyster shells were placed in Copano Bay, TX (28° 06′ 57.89″N, 97° 02′ 55.31″W) for 14 d to recruit porcelain crabs from nearby commercially harvested oyster reefs, and transported in ambient water back to the laboratory. Field samples from remnant oyster reefs were obtained from Nueces (27° 52′ 09.45″N, 97° 29′ 58.99″W) and Aransas Bays (28° 7′ 32.63″N, 96° 58′51.26″W). Phytoplankton and sediment samples were preserved with Lugols iodine (Throndsen 1978).

In the laboratory, plankton samples were examined using the Utermöhl sedimentation method and inverted microscopy (Hasle 1978). Water samples were examined at 400× magnification using ≥10 random fields and a minimum count of 200 cells, with a 100× scan of the settling chamber for rarer large forms and zooplankton (Zimba et al. 2002). Algal biomass was estimated using the Utermöhl sedimentation method as described by Venrick (1978). Conversion of cell numbers to biovolume was used to normalize for the 2 orders of magnitude difference in cell size (Hildebrand et al. 1999).

Benthic algae were brushed from oyster shells into 0.2 um filtered seawater and subsamples were preserved for taxonomic analysis and HPLC algal pigment analyses. Benthic material was examined using inverted microscopy as described for water samples. One porcelain crab was preserved from each site in 10% formalin to qualitatively evaluate all algae in the digestive track. The remaining porcelain crabs were rinsed with fresh water and immediately frozen at −80 °C. Crabs were thawed, and the digestive track was dissected from muscle tissue. The digestive track and muscle tissue were then freeze dried.

Pigment composition of crab muscle and digestive track was determined after acetone extraction, as previously described by Li et al. (2007). Briefly, crabs were partially thawed and digestive track and muscle samples were dissected, sonicated after acetone addition,

then extracted in the dark for 4 hrs, clarified, and the supernatant ampulated in HPLC vials. Samples were analyzed on a HP1100 high performance HPLC equipped with DAD detector; authentic standards were used for identification and quantitation (Zimba et al. 1999).

Digestive track samples extracted for HPLC analyses were prepared for diatom identification by boiling material in nitric acid, rinsing sedimented frustules with deionized water until neutral pH was obtained, and examined using SEM and light microscopy. Additional frozen material was examined for identification of non-diatom taxa. Data from cell counts were normalized to biovolume equivalents (Strathmann 1967, Hillebrand et al. 1999) to compare historic pigment concentrations to cell biovolume/carbon equivalents. Historic data was retrieved from the TCEQ database (http://www80.tceq.texas.gov/SwqmisWeb/public/crpweb.faces#).

Porcelain crabs were collected during Spring 2016 from Copano Bay and preserved in 10% isopropanol. Maxillipeds and outer mouthparts were removed, dehydrated in ethanol, sputter-coated using gold-palladium, and viewed using a Joel JCM-500 scanning electron microscope. Distance between cirri was measured to evaluate capture efficiency.

3. Results

3.1. Copano Bay

Pigment content of crab digestive track samples and muscle tissue (n=20) contained large concentrations of fucoxanthin, a carotenoid biomarker of brown plant line algae, particularly diatoms (Figure 1). Other ubiquitous pigments included chlorophyll *a* and *beta*-carotene. Over 90% of diatom frustules identified in porcelain crab digestive track samples were either fresh-brackish water *Planothidium delicatulum* (Kűtzing) Round and Bukhtiyarova or the brackish-water taxa *Cocconeis disculus* (Schuman) Cl. No recognizable centric diatoms (e.g., spines from *Chaetoceros*, or valves/girdle bands) were identified in digestive track samples.

Phytoplankton samples in Copano Bay were dominated by centric diatoms, particularly *Chaetoceros* spp. (notably *C. compressus* Lauder, and *C. socialis* Lauder) and *Aulucoseira mobilensis (*Bailey) Grunow, the dinoflagellates *Prorocentrum compressum* (Bailey) Abé ex Dodge and *Pyrodinium bahamense* Plate (Figure 2). Sediment algae were exclusively dominated by pennate diatoms, including *Navicula phyllepta* Kützing, *Planothidium delicatulum* (Kűtzing) Round and Bukhtiyarova, *N. sydowii* Cholnoky, *Nitzschia amphibia* Grunow, *Gyrosigma* spp., *Cocconeis disculus* (Schuman) Cl., *Achnanthes hauckiana* Kűtzing) Round and Bukhtiyarova, and *Amphora* spp. (including *A. wisei* [Salah] Simonsen). Both motile (*Navicula, Nitzschia*) and adnate taxa (*Amphora, Cocconeis, Achnanthes*) were only found in sediment samples. Cyanobacteria in the water column (filamentous forms specifically) were different genera from those found in the sediments.

3.2. Aransas Bay

Pigment content of digestive track samples (n=8) contained large concentrations of canthaxanthin (exclusive to cyanobacteria) and fucoxanthin (brown plant line pigment–primarily diatoms). Concentrations of fucoxanthin in muscle tissue were larger than

concentrations in the digestive track whereas concentrations of the cyanobacterial pigment canthaxanthin were larger in the digestive tract (Figure 2).

Phytoplankton samples in Aransas Bay were dominated by centric diatoms, particularly *Chaetoceros* spp. (notably *C. compressus* Lauder) and *Cyclotella* spp., with large amounts of spherical ultraphytoplankton <1.0 μm in diameter. Sediment algae were dominated by pennate diatoms and the filamentous cyanobacterium *Phormidium sp.* Benthic diatoms included *Navicula phyllepta* Kützing, *N. sydowii* Cholnoky, *Nitzschia amphibia* Grunow, *Gyrosigma* spp., *Cocconeis disculus* (Schuman) Cl., *Planothidium delicatulum*, and *Amphora* spp. (including *A. wisei* [Salah] Simonsen) and two larger taxa). Both motile (*Navicula, Nitzschia*) and adnate taxa (*Amphora, Cocconeis, Achnanthes*) were only found in sediment samples. In Aransas Bay, digestive track samples contained cyanobacteria (predominately *Phormidium* sp.) and multiple adnate diatom taxa dominated by *Fallacia pgymae* (Kűtz.) Stickle & Mann and *Navicymbula pusilla* Krammer.

3.3. Nueces Bay

Crab digestive track samples (n=6) contained large amounts of fucoxanthin and the cyanobacterial carotenoid canthaxanthin. Muscle tissue contained slightly greater concentrations of fucoxanthin than in the digestive track, whereas canthaxanthin concentrations were slightly less in the muscle tissue.

Water column samples in Nueces Bay contained large amounts of organic debris which confounded identification. Large abundances of flagellates, spherical cyanobacteria, and smaller amounts of centric diatoms were identified in water column samples. Benthic samples were dominated by a diverse diatom flora and the cyanobacteria *Phormidium* sp. The benthic cyanobacterium *Phormidium* sp. and a lineolate *Navicula* were most abundant in Nueces Bay porcelain crab digestive tracks.

3.4. Copano Bay Crab SEM

Structure of the outer (3rd) maxilliped (Figure 3), which is used to sweep the water during suspension feeding, includes a dense aggregation of both frond-like (upper right) and more abundant shorter serrated-forms of cirri (lower left). Distance between cirri averaged 17 μm in the longer frond and 5 μm in the shorter serrated cirri. The inner mouth (2nd maxilliped) has smooth cirri (Figure 3a). Overall length of the serrated cirri averaged 1.4 mm and 1.9 mm for frond-like cirri.

4. Discussion

Oyster reefs have two diverse functionalities: one based on the oyster as the terminal end member of the food web, and the other involving trophic passage from crabs to fish (Yeager and Layman 2011). Because porcelain and other crabs use crevices in the reef as refugia, competition for planktonic food could limit prey access. Pseudofeces from oyster feeding could provide additional food resources for benthic animals.

Simultaneous analysis of planktonic and benthic algae, coupled with muscle and digestive track analyses, identified benthis algae as the major food resource for porcelain crabs.

Centric diatoms in planktonic microalgae were not found in digestive samples, whereas benthic forms were. Porcelain crab populations are unlikely to be sustained by phytoplankton in any of the three Texas bay systems surveyed because: 1) plankton algal community composition is dominated by cyanobacteria of low nutritional value; and 2) algal cell sizes tended to be small; and the specific algae identified by pigment and taxonomic analyses with the digestive and muscles of the crabs are rare or nonexistent in the water column. Although slight differences in cell count and pigment data were evident (particularly dinoflagellate abundance/peridinen pigment absence in Copano Bay), overall both methods provided complementary data. Pigment profiles and digestive track analyses both corroborated the use of non-planktonic food resources by porcelain crabs in the bays we sampled. Only slightly motile/adnate benthic diatoms were found in porcelain crab digestive tracks from all bays and no planktonic diatom species were present. Cyanobacteria, when present, were also benthic filamentous forms. This is in contrast with Johnston and Freeman (2005) who found only brown and green algae in the stomachs of *Petrolisthes elongatus*.

Available phytoplankton chlorophyll concentrations for two annual cycles from Texas CEQ samples within the three bays averaged <10 μg C L^{-1}. Converting cell count data to carbon equivalents (Strathmann et al. 1967) and assuming a carbon:chlorophyll ratio of 45, sediment carbon equaled over 1 gcm-^{2} whereas water column concentrations of carbon from phytoplankton equaled <10 mg C L^{-1}, similar to other estuaries (see Table 1). Assuming zooplankton densities in these three Texas estuaries are similar to densities summarized from the literature by Rios-Jara (1988) and Buskey (1993), typical copepod densities are ~20–8100 individuals L^{-1}. The feeding area of a 1 cm porcelain crab would occupy is <2.54 cm^{3}, requiring 155 animals to clear one liter of water (assuming 100% efficiency of mixing the water column and particle capture), providing < 0.14–52 zooplankters per crab. Average density of porcelain crabs in nearby St Charles Bay Texas averaged 288 porcelain crabs m^{-2} (George et al. 2015) suggesting that if these animals were feeding from a well-mixed water column they could clear 3.204–6.5 L/day individually or 923–1850 L/day assuming active feeding from 12–24 hrs daily. For these reasons there is insufficient plankton to sustain porcelain crabs populations from these resources.

Techniques for evaluating food webs can be considered short, medium, or long-term—this depends on the sampling frequency relative to the organism's lifetime. For instance, phytoplankton with a doubling rate of ~1/day can be characterized with a single daily sample (short), whereas copepods with a 14 day egg-adult cycle might be considered medium term, and porcelain crabs, with a two-year life expectancy, might be considered long term. The collection of single food source samples (as is done for stable isotope analyses for example) may not provide an accurate longer-term perspective of food sources unless you consider the lifespan of the organisms at each trophic level. The use of carotenoid biomarkers derived from specific classes of algae/cyanobacteria can provide insights with regard to food preferences (Grether et al. 1999) and also provides normalization on medium to long time scales. Cyanobacterial biomarkers such as aphanaxanthin and myxoxanthin can be used to subset filamentous versus coccoid cyanobacteria (Zimba and Grimm 2003), whereas canthaxanthin is formed from β-carotene through echinenone by ketolasis (Takaichi 2011) and in our experience is found in late exponential phase cyanobacterial populations.

Pigment survival through gut/digestive track passage is well documented in fish species (Grether et al. 1999). Li et al. (2011) reported retention of the carotenoids zeaxanthin and lutein from catfish fed a pigmented diet of 8–12 weeks. Increased use of carotenoid pigments in consumer muscle tissue may provide an additional tool to average food resource utilization.

Recognition of specific algal assemblages in field and digestive track samples, coupled with monitoring pigment assimilation, provides several lines of evidence to evaluate importance of phytoplankton or benthic attached diatoms as a food resource for porcelain crabs. Analysis of maxilliped cirral spacing in porcelain crabs (*Petrolisthes* spp.) collected from Texas suggests that particles between 5–15 micrometers would be retained by the cirri (Figure 3) and that actual ingestion rates would depend on efficiency of transfer from the longer cirri to the shorter forms and passage into the mouth. The relatively length of these cirri (< 1.4 mm) as well as the rapidity of sweeping would also limit the rate at which particles could be captured and removed from the water column. Scraping and resuspending benthic microalgae/cyanobacteria using these structures may be much more efficient in terms of energetic expenditures vs energy concentration and capture. Nicol's (1932) description of both feeding structures and behaviors of *Porcellana* (=*Pisidia*) *longicornis* is similar to descriptions of other porcellanids such as *Petrolisthes armatus* (Caine 1975), *P. cinctipes* (Wicksten 1973), *P. cabrilloi* (Kropp 1981), *P. alobatus* (Laurie 1926), or *Polyonyx gibbesi* (Caine 1975).

These somewhat conflicting observations suggest that porcelain crab diets may vary in time and space, and may depend greatly on the availability of algal food resources. It does seem clear however, that the porcelain crabs we sampled are not using plankton as the major food resource and, like *Petrolisthes armatus* in subtropical oyster reefs, are unlikely to compete for food resources with oysters from plankton. In the porcelain crabs we sampled, fucoxanthin was abundant in their muscle tissue, providing evidence of long-term use of non-planktonic food resources. Benthic diatom densities in hard bottom, three-dimensional habitat are very large compared to densities of benthic diatoms in the water column (Figure 1). It is likely that porcelain crabs disrupt sediment diatom communities, and consume this food resource as previously suggested by Caines (1975). The use of multiple indices of diet seems to provide greater insight than single measurement methods and is recommended to investigate food webs.

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Highlights

- Porcelain crab digestive and muscle pigment content suggests that benthic algae serve as a major food resource.
- Digestive tract content consists of benthic algae not phytoplankton.

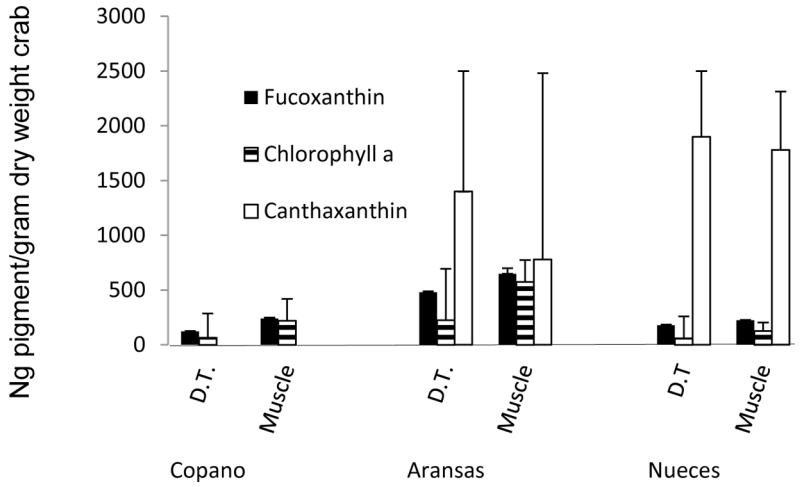

Figure 1.

Digestive track (D.T.) and muscle content of lipophilic pigments in porcelain crabs from Copano Bay (n=20), Aransas Bay (n=8), and Nueces Bay (n=6), Texas, USA. Error bars are standard deviations.

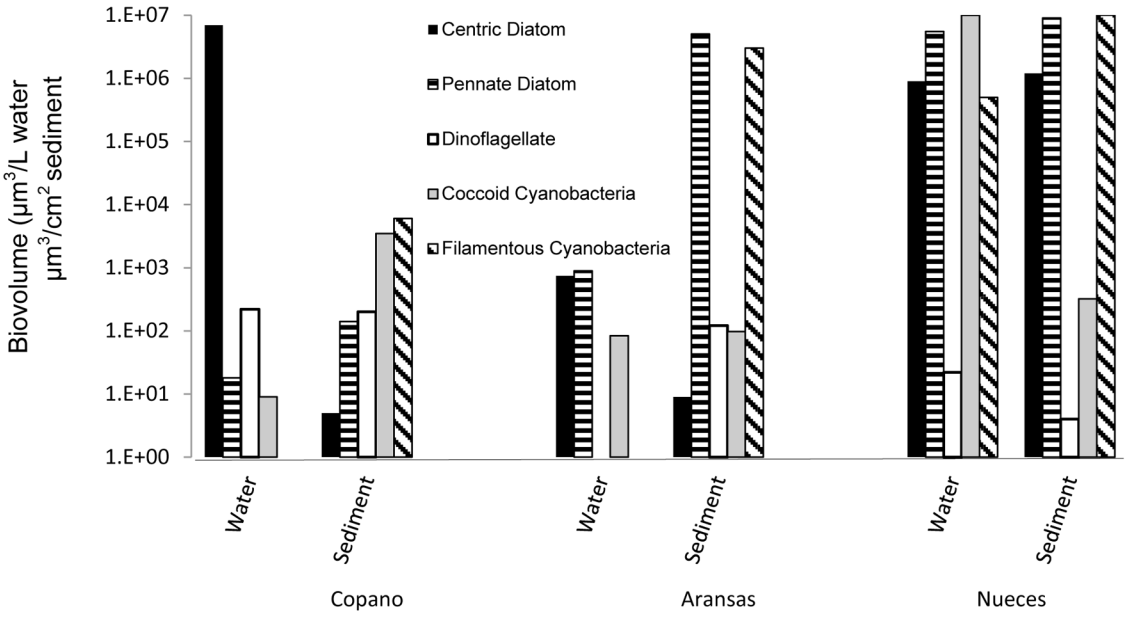

Figure 2.

Biovolume equivalents of water column and subtidal sediment sample algae collected concurrently with porcelain crab harvests in Aransas, Copano, and Nueces bays, Texas, USA. Cell number of algae were converted to biovolume using appropriate formula for water column and algae on the sediment surface.

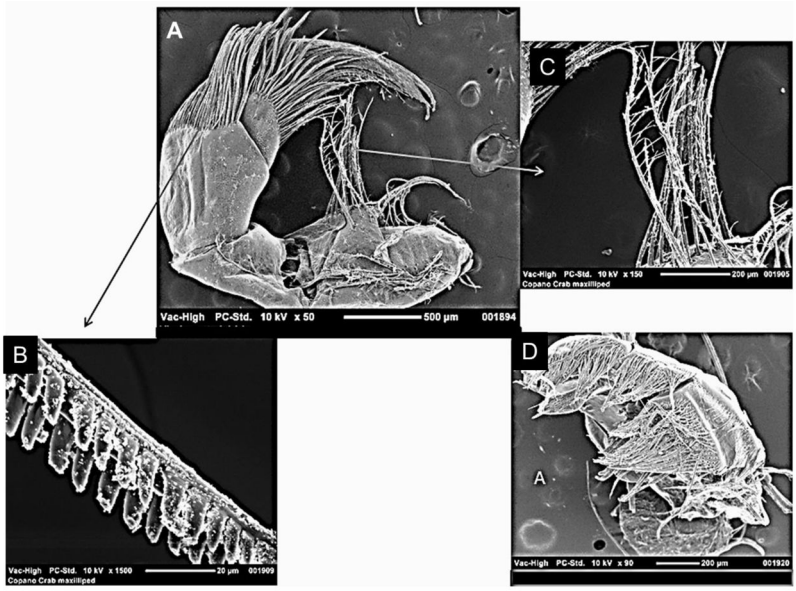

Figure 3.

Porcelain crab feeding structures associated with third maxilliped. A: Entire third maxilliped from porcelain crab. B: Double-edged shorter cirri located on the external side of A. C: Bristle-like longer cirri the the internal side of A. D: Internal mouth section (second maxilliped) from porcelain crab with smooth cirri.

Table 1

Comparative standing stock biomass (as chlorophyll *a*) of water column and subtidal microalgae in estuarine habitats. Units are mg m^{-2} for water column and mg m^{-2} for sediments.

Location	Phytoplankton	Subtidal Algae	Reference
Flax Pond, NY	6.5	—	Moll 1977
Buzzards Bay, MA	25	50	Roman and Tenore 1978
Chesapeake Bay, MD	55	245–389	Malone 1985
Apalachicola Bay, FL	12.5	—	Mortazavi et al. 2000
Fort Matanzas, FL	4.7	—	Dix et al. 2013
Moreton Bay, Australia	5.5–9.0	—	Quigg et al. 2010