Omnivory in the diet of juvenile dungeness crab, *Cancer magister* Dana

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Abstract

Juvenile Dungeness crab (*Cancer magister* Dana) have always been considered strict carnivores; however, early instars have been observed ingesting filamentous, epiphytic diatoms in the field. To investigate the potential importance of diatoms in the diet of this species, wild-caught megalopae were raised to the third juvenile instar on a variety of dietary treatments. Although the animals that were fed only filamentous diatoms (*Melosira* sp. and *Grammatophora* sp.) had intermolt periods 20–25% longer than those raised on mussel (*Mytilus* sp.) flesh or a mix of diatoms and mussels, there was no difference in molt size increment between the treatments. This ability to utilize such alternative food resources at a lower trophic level may be especially important in years of high settlement into coastal estuaries, when large numbers of juvenile crab are known to cause dramatic reductions in prey densities. © 1998 Elsevier Science B.V.

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1. Introduction

The Dungeness crab, *Cancer magister* Dana, is one of the largest and most important crustaceans commercially on the west coast of the United States. Previous investigations into the diet of this species suggest that it is an opportunistic predator, but there is also evidence of ontogenetic changes in diet. Gotshall (1977) reported 40 different identifiable food items from the stomachs of crabs collected in northern California, with clams, fish, isopods, and amphipods occurring most frequently. Fish were the most frequently noted prey taxon in the smaller crabs (<100 mm carapace width, CW), while clam remains were noted most often in large crabs (>150 mm CW). A similar study
conducted in the Queen Charlotte Islands (BC, Canada) revealed that crabs < 100 mm CW were feeding primarily on small crustaceans, while those > 166 mm CW fed primarily on clams (Butler, 1954).

Using a modified version of the Index of Relative Importance (Pinkas et al., 1971; Stevens et al., 1982) examined the diet of *C. magister* in Grays Harbor (WA, USA). During the first year the dominant prey items were small bivalves and crustaceans (including conspecifics); second year crabs fed primarily on shrimp (*Crangon* spp.) and small fish, while third year crabs ate significantly more fish and fewer shrimp. The stomachs of some of the smallest crabs (15–30 mm CW) examined in this study contained only sand and unidentified organic material (Stevens et al., 1982), and no data are available in the literature for smaller juvenile instars.

Field observations by one of us (GCJ) have revealed first and second instar *C. magister* appearing to graze on eelgrass epiphytes and on filamentous diatoms coating oyster shells. These observations suggest that juvenile Dungeness crab may have more of an omnivorous diet than has been assumed, or have the ability to utilize diatoms or algae as an alternative food source when prey density is reduced. This latter scenario is possible when large numbers of newly-settled *C. magister* deplete populations of small bivalves and other prey organisms. Ruiz (1987) documented dramatic declines in the density of small clams in Bodega Bay (CA, USA); within 2 months of a heavy recruitment by settling *C. magister* the densities of two species of *Transennella* declined from 100–10 000/m$^2$ to < 1/m$^2$. Concurrent predation on tube-dwelling tanaids resulted in changes in sediment grain size and community structure, and were likely responsible for declines in shorebird numbers and significant reductions in the physiological condition of dunlins (Ruiz, 1987; Ruiz et al., 1989). Similar qualitative observations of dramatic reductions in *Transennella* in Coos Bay (OR, USA) have reportedly coincided with Dungeness crab recruitment (Asson-Batres, 1986), and predation by juvenile *C. magister* residing in intertidal shell areas of Grays Harbor virtually eliminates newly settled *Mya* (Palacios, 1994).

We investigated the potential use of filamentous benthic diatoms by juvenile *C. magister* by two methods: (1) rearing crabs on a variety of dietary treatments and monitoring mortality, growth (as measured by the increase in CW at molting), and intermolt period (time between molts), and (2) calculation of the total assimilation efficiency of crabs fed only diatoms.

2. Materials and methods

Thirty *C. magister* megalopae [Puget Sound cohort, sensu Dinnel et al. (1992)] were captured at the water’s surface 17 July 1996 in Anacortes (WA, USA) and transported to Shannon Point Marine Center. They were held in 1 l containers (10–12 per container) supplied with unfiltered seawater; upon molting into the first juvenile instar stage they were measured (maximum CW, including the tenth anterolateral tooth) and placed individually into 11.2 cm diameter finger bowls filled with 250 ml of 5 μm filtered sea water. The bowls were randomly interspersed in a shallow seawater table, bathed with ambient seawater to maintain a temperature of 11–12°C, and aerated with a small pump
several times each day; the water was changed daily and the bowls cleaned with filtered seawater to remove uneaten food and fecal material.

Six instars were assigned to each of five feeding regimes: mussel; “clean” diatom; “raw” diatom; mixed mussel and diatom; and an unfed control. Crabs were fed ad libitum twice daily at 1000 and 1800 hours; amounts were adjusted so that there would not be excessive leftover food that could foul the water. The mussel treatment received fresh *Mytilus* sp. flesh only, typically a piece approximately the length of the crab’s cheliped. For the “clean” diatom treatment, filamentous diatoms (*Melosira* sp. and *Grammatophora* sp.) were collected from the outflow raceway of the laboratory seawater system and individual strands carefully teased out using forceps and a dissecting scope; each crab was given a clump with a diameter approximately equal to the crab’s CW. “Raw” diatoms consisted of the same material without the various nematodes, copepods, ostracods and other associated plant and animal material removed. The mixed diet treatment received mussel flesh at the 1000 feeding and diatoms at the 1800 feeding, while the control group received only filtered sea water.

Duration of instar stages and size increases at molting were compared using one-way analyses of variance (ANOVA), and homogeneous groups detected using the Tukey test. Size increase data (expressed as percentage increase in CW) were arcsin transformed prior to analysis.

To examine the assimilation efficiency of crabs feeding on diatoms, feces were collected over a 5 day period from experimental animals in the “clean” diatom treatment, following their molt to second instar. In order to minimize bacterial degradation the fecal material was collected within 15 min of extrusion, pipetted onto filter paper and rinsed with distilled water to remove salts, and immediately frozen. Due to the small amounts of material involved, the feces from all five crabs were pooled. “Clean” diatom samples were similarly rinsed and frozen.

Feces and diatom samples were dried to constant weight at 80°C and weighed to the nearest 0.0001 g on tared aluminum dishes (previously ashed for 1 h at 550°C to remove possible contaminants). The samples were then ashed at 550°C for 4 h, reweighed, and total assimilation efficiency calculated using the following equation, modified from Montgomery and Gerking (1980):

\[
\left[ 1.0 - \frac{\text{% ash in diatom sample}}{\text{% ash in crab feces}} \right] \times 100\%
\]

3. Results

The 30 megalopae all molted to first instar within a 9 day period. All crabs in the unfed control group died before molting to the second juvenile instar, as did one in the “clean” diatom treatment; the remaining “clean” diatom treatment crabs and those on “raw” diatom, mixed, and mussel diets all molted successfully to second and third instars.

Crabs fed only mussel or a mixture of mussel and diatoms molted from first to second instars significantly earlier than those provided with “raw” or “clean” diatoms, who
molted an average of 5 days later (Fig. 1A; Table 1A, one-way ANOVA $p=0.0001$). This same pattern held for the molt from second to third instar (Fig. 1B; Table 1B, $p=0.0001$).

Of the crabs that molted to second instar, there were no significant differences in molt increment in the various diet treatments (Fig. 1C; Table 1C, $p=0.9148$), nor were there significant differences in the molt increment between second and third instars (Fig. 1D; Table 1D, $p=0.437$).

The total assimilation efficiency calculated for second instar *C. magister* provided with “clean” diatoms was 31.7%.

### 4. Discussion

The discovery that juvenile *C. magister* can survive and grow on a diet of filamentous
Table 1
Results of one-way ANOVAs comparing juvenile *C. magister* growth and instar durations in fed treatments; crabs fed diets containing mussels had significantly shorter intermolt periods than those in the diatom treatments

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Duration of first instar stage</td>
<td>Treatment</td>
<td>3</td>
<td>152.112</td>
<td>50.704</td>
<td>24.47</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>19</td>
<td>39.367</td>
<td>2.072</td>
<td></td>
</tr>
<tr>
<td>(B) Duration of second instar stage</td>
<td>Treatment</td>
<td>3</td>
<td>145.938</td>
<td>48.646</td>
<td>12.60</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>19</td>
<td>73.367</td>
<td>3.861</td>
<td></td>
</tr>
<tr>
<td>(C) Increase in size at molt from first to second instar</td>
<td>Treatment</td>
<td>3</td>
<td>0.003</td>
<td>0.001</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>19</td>
<td>0.110</td>
<td>0.006</td>
<td></td>
</tr>
<tr>
<td>(D) Increase in size at molt from second to third instar</td>
<td>Treatment</td>
<td>3</td>
<td>0.005</td>
<td>0.002</td>
<td>0.950</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>19</td>
<td>0.033</td>
<td>0.002</td>
<td></td>
</tr>
</tbody>
</table>

diatoms carries important implications for the early life history of this species. This ability to utilize such an abundant additional food resource is an important, yet previously overlooked, factor in the calculation of energy budgets and measures of prey biomass, and clearly needs to be taken into consideration when assessing the ecological effects of heavy crab recruitment and its impact on benthic communities. Heavy *C. magister* recruitment can decimate local populations of small clams and other prey (Ruiz, 1987), but the ability to feed at a lower trophic level may allow juveniles to maintain much higher densities than can be supported by stocks of more conventional food items alone. In addition, such a switch in feeding methods may reduce cannibalism.

Recruitment of juvenile Dungeness crab coincides with the period of greatest primary production; in Padilla Bay (WA, USA), the early summer production and biomass of epiphytes attached to eelgrass can exceed that of the eelgrass itself (Thom, 1990). Juvenile *C. magister* have been observed up to 0.5 m above bottom, clinging to eelgrass with mouthparts appressed to the broad side of the blade and appearing to ingest the epiphytic diatoms and other material adhering to the surface (GCJ, pers. obs.). When crabs feed in this manner they undoubtedly ingest some small organisms along with the diatoms, but the contribution of this relative to the other material may not be significant.

The copepods, flatworms, ostracods, tanaids and other animals present in “raw” diatoms had no measurable effect on growth relative to those receiving only “clean” diatoms, indicating that the crabs in this treatment were gaining nutrition primarily from the plant material. Such nutrition is not limited to cellular contents since diatoms have attached bacteria and extracellular substances that can also be utilized; some copepod nauplii subsist by scraping mucous and bacteria off the surfaces of diatoms without breaking the frustules (Decho and Fleeger, 1988) and newly-settled abalone also utilize these extracellular components until they become large enough to break into the diatoms (Kawamura and Takami, 1995). Our examination of the feces of experimental crabs revealed some intact chloroplasts, but with the exception of occasional very small,
pennate diatoms in feces from “raw” diatom treatment crabs, no unbroken frustules were ever found. Within minutes of ingesting diatom clumps the anterior regions of a crab’s carapace would become visibly darker, as the greenish cell contents apparently began entering the hepatopancreas. Considering how well the crabs grew on the diatom diet, it appears that they effectively utilized these cellular components; however, the importance of proteins from the associated bacteria is not known and it remains to be seen whether axenic diatom culture would support growth. This ability to assimilate diatoms may have been carried over from the zoeal stages, since diatoms appear in the stomach contents of C. magister larvae and the zoeae of this species have been raised through several stages in captivity on a diet of diatoms alone (Hartman and Letterman, 1978).

The 31.7% assimilation efficiency reported here for crabs eating “clean” diatoms must be considered very preliminary and used with caution, since it is only a single measure from a pooled sample. There are few studies of assimilation efficiency for Crustacea in the literature, and both the definition of it and the method of determination vary a great deal. Conover (1966) reported assimilation efficiencies ranging from 18.8–87.9% for copepods feeding on six species of planktonic diatoms, while values of 42.2–80.1% have been reported for Euphausia superba feeding on phytoplankton (Schnack, 1985). The two genera of filamentous diatoms used in this study occur in areas frequented by juvenile Dungeness crabs and where they have been observed feeding on diatoms. Melosira spp. were common colonizers of experimental clay cylinders placed on an intertidal mud flat and were preferentially ingested by gastropods (Nicotri, 1977), while Grammatophora occurs as an epiphyte on eelgrass (Phillips, 1972).

Another potential food source that should not be overlooked is the abundant microalgae occurring in the upper layers of the sediment. Such material accounts for 10.8% of the primary production of Grays Harbor estuary (Thom, 1984), and the high proportion of sand reported in the stomachs of small crab from this area (Stevens et al., 1982) may reflect a utilization of this resource. Haefner (1990) warned against the common tendency to dismiss sand in crab stomachs, which is usually assumed to have been ingested unintentionally with prey.

Based on available size-at-instar data for “Puget Sound” cohort juveniles, it appears that molt increments for the crabs used in this experiment were equal to those of wild juveniles (MacKay and Weymouth, 1935; Dinnel et al., 1992); however, equivalent data for comparison of growth rates are not available. Intermolt periods are very difficult to measure in nature (Hartnoll, 1982), and there is evidence both from field sampling (Armstrong and Gunderson, 1985) and laboratory experiments (Kondzela, 1986) that growth rates in C. magister are strongly affected by temperature. The average intermolt period for second instar crabs receiving only mussel (18.0 days) was similar to that measured for second instar “oceanic” cohort crabs fed clam meat (18.2 days; Orensanz and Gallucci, 1988), but in the laboratory seawater systems the crabs in both experiments almost certainly experienced colder average temperatures than those living in the intertidal zone.

The early postlarval life history of many decapods is poorly known, but there has been some previous evidence of predatory species showing similar ontogenetic shifts in diet.
Newly-settled lobster, *Homarus americanus*, can survive and grow by feeding on phytoplankton that they filter from the water while remaining in the shelter of their burrows (Barshaw, 1989; Lavalli, 1991). Detritus and plant material are far more prevalent in stomach samples of juvenile *Callinectes sapidus* than in adults (Laughlin, 1982), and similar dietary shifts have been reported for other portunids (Paul, 1981; Ropes, 1989; Stoner and Buchanan, 1990). Feder et al. (1980) reported a high frequency of occurrence of diatoms, including *Melosira*, in the stomachs of recently-settled king crab *Paralithodes camtschaticus*, and during the present study several *Cancer oregonensis* captured and maintained in the same manner as the *C. magister* grew well on a diet of “raw” diatoms only. Benthic diatoms may prove to be an important nutritional source for newly-settled crabs who, because of their small size and vulnerability to a wide suite of predators, may be limited in their ability to range widely in search of food.

Acknowledgements

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