WHY IS OCTOPUS CYANEA GRAY IN HAWAII SPECIALIZING IN CRABS AS PREY?

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INTRODUCTION

Foraging strategies and prey choice are vital parts of each species’ survival strategy (Stephens & Krebs 1986), and Curio (1976) has suggested that searching predators expend so much energy on this activity that they are likely to take nearly all the prey that they encounter. Octopuses fit into this category, coming out from their protective den and exploring likely areas by chemotactile search (Yarnall 1969, Mather 1991, Forsythe & Hanlon 1997, Leite, Haimovici & Mather 2009), although the search is saltatory (O’Brien, Evans & Browman 1989), and focuses on areas likely to contain crab and molluscan prey. The result of such a search is usually remains of a wide variety of prey species discarded in the middens outside octopus homes (Hartwick et al. 1978, Ambrose 1984, Mather 1991, Vincent et al. 1998), although a large percentage of remains is from a few species. Yet not all octopus species in all situations take a wide variety of prey, and such selectivity is interesting to evaluate.

Several pressures might dictate a pattern of wide prey choice by octopuses, who are often described as specializing generalists (Mather 1991, Vincent et al. 1998, Anderson et al. 2009). If octopuses lived in varying habitats, they might depend on local prey availability. For instance, Octopus vulgaris in South Africa living near a mussel reef had a high percentage of these bivalves in their diet (Smale & Buchan 1981) and Enteroctopus dofleini on Vancouver Island, presumably near a bed of Clinocardium cockles, took a large proportion of these animals (Hartwick et al. 1978). In contrast, those in Prince William Sound, Alaska, took almost none (Vincent et al. 1998, Scheel et al. 2007). The prediction that diet would track prey abundance is not always followed, however, as O. bimaculatus on Bird Rock, California did not take the very plentiful gastropod Tegula eiseni (Ambrose 1984), and E. dofleini in Alaska chose very few Hapalostoma gaster crabs (Vincent et al. 1998). Tracing the influences on selectivity might be easier if one followed a species that took only a narrow range of prey.

Even in octopuses that take a variety of prey species, individuals often specialize on a few (Hartwick et al. 1978, Vincent et al. 1998, Anderson et al. 2009) and even those in the same location in subsequent years may specialize differently (Mather 1991). Still, the selected prey species are taken from a wide variety of gastropod and bivalve molluscs as well as decapod crustaceans. One exception to this variety is O. rubescens sheltering in discarded beer bottles on sand/mud substrate in Puget Sound, Washington (Anderson et al. 1999). Their prey was predominantly the gastropod Olivella baeatica, but this might have been the result of the unusual occupancy of a depauperate habitat due to artificial shelter (discarded beer bottles) availability. O. tehuelchus, a small species off the coast of Argentina, is reported to take predominantly crab prey (Iribarne et al. 1991) but only lab studies of preference were reported.

Fragmentary data on prey consumption of O. cyanea in Hawaii (Van Heuken 1966, Yarnall 1978) suggest that this species in this location represents an exception to the generalist rule. O. cyanea in Hawaii nearly always chose crabs as prey, although the same species in the Tuamoto archipelago apparently took a wider variety of prey species (Forsythe & Hanlon 1997). What influences would move a species or a population from a specializing generalist to a true specialist? Wells (1978) comments on O. vulgaris’ preference for crabs in the lab and Iribarne et al.’s (1991) studies in the same situation showed a decided preference for this group. Yet lab preference is not always matched by field availability (Ambrose 1984, Vincent et al. 1998, Scheel et al. 2007). Just because most octopuses prefer crabs when a selection of prey species is offered to them doesn’t mean they will find and consume only them in the field—and most species and populations do not.
This study will evaluate the foraging and prey choice of *O. cyanea* on the reef in Hawaii and in captivity in an outdoor pond, to see whether there are any special influences that predict a preference of this species for crabs.

**PROCEDURES**

*Subjects:* Subjects for the first phase were twenty adult and subadult *O. cyanea*, estimated at 1-3 kg weight, never captured but located on the coral reef. In the second phase, four octopuses of a similar size range were kept in captivity two at a time for two weeks each. Although there are no ethical guidelines in the United States for care of invertebrates and the Canadian Council of Animal Care guidelines had not extended to cephalopods in 1993-5, when this work was done, care of animals followed suitable procedures nevertheless.

*Method:* 1) Field observations: Octopuses were located in their dens on the reef platform of Coconut Island, Kaneohe Bay, Hawaii. They were in 1-2 m deep water, either close to the edge of the reef or within landmarks between the fringing reef and the island itself. Remains of prey were collected daily from all dens. Dens were checked for octopus presence until two days after they were no longer occupied, and the empty dens were checked for prey remains for a week. Size of crab remains were measured by carapace width. If an octopus stayed in a den for at least four days after the initial collection, daily collections of remains were used to estimate intake. Daytime activity of octopuses was checked two ways. First, an hourly check of six dens was made from 0600 until 1900. Second, long-term observation of one octopus was carried on from 0600 to 1900, for 54 hours during five days.

2) Observations in captivity: Two pairs of octopuses, one at a time, were placed in an enclosed pond on the island. It had a trapezoidal shape, with long axis approximately 14 m and short one 11 m, and averaged 1 m deep (see Yarnall 1969). Drainage through a sluice gate at one end meant that the normal tidal flow was maintained, and this opening was blocked with wire mesh. While the pond contained many small crabs already, it was stocked with approximately 200 crabs, mostly Xanthids and Portunids, collected from the shores of the island; crabs were thus present in abundance. A 5 m observation tower was used by observers; it allowed a good view of and maintenance of distance from the octopuses. Each pair of octopuses was observed from 0630 to 1930 each day for eight days, and duration of hunting calculated. Remains of prey were collected each day at noon (when the octopuses were most likely to be inactive), measured by carapace width and the intake calculated.

*Results:* 1) Field observations: Nineteen species were represented in the remains of 1028 prey individuals collected outside octopus dens, but 95% of these were of five crab genera – *Thalamita, Leptodiad, Phymodius, Calappa* and *Platypodia*.

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**Table I.** – Daily intake of crab prey by *Octopus cyanea* at ten dens, measured by carapaces left in the midden outside or within the den.

<table>
<thead>
<tr>
<th>Octopus (named for landmark or location)</th>
<th>Days tallied</th>
<th>Prey items in midden</th>
<th>Items per day</th>
<th>Crab carapace width in mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>5</td>
<td>32</td>
<td>6.4</td>
<td>24</td>
</tr>
<tr>
<td>Big</td>
<td>15</td>
<td>145</td>
<td>9.7</td>
<td>2</td>
</tr>
<tr>
<td>Canal</td>
<td>9</td>
<td>58</td>
<td>6.4</td>
<td>29</td>
</tr>
<tr>
<td>Pipeline</td>
<td>18</td>
<td>119</td>
<td>6.6</td>
<td>29</td>
</tr>
<tr>
<td>Rebar</td>
<td>10</td>
<td>95</td>
<td>9.5</td>
<td>33</td>
</tr>
<tr>
<td>Beach</td>
<td>4</td>
<td>28</td>
<td>7.0</td>
<td>24</td>
</tr>
<tr>
<td>Conehead</td>
<td>7</td>
<td>52</td>
<td>7.4</td>
<td>26</td>
</tr>
<tr>
<td>Ledge</td>
<td>7</td>
<td>66</td>
<td>9.4</td>
<td>30</td>
</tr>
<tr>
<td>Cliff</td>
<td>4</td>
<td>24</td>
<td>6.0</td>
<td>27</td>
</tr>
<tr>
<td>Black Rox</td>
<td>7</td>
<td>40</td>
<td>5.7</td>
<td>28</td>
</tr>
</tbody>
</table>

Mean: 9, 76, 7.6, 29
Of the remaining fourteen species, eight were other small crabs and six were small bivalve molluscs. The octopuses consumed an average of six prey species, and most prey were very small; see Fig. 1 for the size distribution of common prey. Ten octopus dens were occupied long enough (mean = nine days) to give daily intake estimates, with the number of prey per day averaging 7.6 crabs with a mean carapace width of 29 mm (Table I), which was designated a Standard Crab. If one extrapolates the flow chart of Mather (1991) detailing the fate of prey remains after an octopus has eaten it, 1/4 of crustacean remains would be lost from the midden in the first 24 hours. As well, her octopuses consumed 1/3 of prey outside their dens, and the losses added to the prey remains found suggest a mean intake by these octopuses of 15 crabs per day. There was no significant correlation between the estimated octopus size and the number of crab prey remains found (r = 0.25, n.s.), nor did an informal correlation between the exposure of the octopus den to currents and waves and the number of remains result in a significant relationship.

For the single octopus den visited long-term, 14/54 daytime observations (25 %) resulted in octopus absence. During the 368 hourly visits to dens of the six octopuses followed for an average of six days, they were absent in 90, or 25 %. Their activity followed the crepuscular rhythm that Yarnall (1969) also recorded. Again extrapolating from Mather (1991), who found that octopuses spent 62 % of their time away from dens exploring for food, these Octopus cyanea would have been foraging for 0.62 x 180 or 112 minutes, thus capturing a crab on average every seven minutes.

2) Observations in captivity: Octopuses in the ponds consumed the same crab diet as those on the reef, overwhelmingly the three most common in the field. Crab size varied and thus had to be standardized against the size of those taken in the field. To do this, the cube of the carapace width was calculated as a proportion of the cube of the carapace width of the Standard Crab and the intake adjusted accordingly. Mean intake of all octopuses averaged 20 Standard Crabs in the first day of the study and fell to 4.5 crabs by day eight (Fig. 2A). Continuous observation resulted in much finer assessment of foraging time; the octopuses averaged 62 minutes hunting per day in the first day and this rose steadily with prey depletion to 110 minutes per day, almost exactly the same as in the field, by the end of the trial (Fig. 2B).

DISCUSSION

This study is one of the few that assesses not only prey choice but also intake and effort of an octopus in the field and in captivity. Clearly, Octopus cyanea in Hawaii have a narrow prey preference for crabs, strikingly different from that of Octopus vulgaris (Smale & Buchan 1981, Ambrose & Nelson 1983, Mather 1991) and E. dofleini (Hartwick et al. 1978, Vincent et al. 1998). Yet they were taking predominantly small crabs and many of them, an estimated 15 per octopus per day on the reef. The observations in captivity suggest that there was an abundance of crab prey in the natural environment as even with an excess of crab prey, the octopuses did not take many more than in the field. In addition, their hunting time of 62 minutes rising to 110 with depletion was not much more than was estimated for those in the field. Clearly the reefs of Kaneohe Bay had a surplus of small crabs.

Yet the apparently dense population of crabs on the reefs is not necessarily a predictive factor for such a diet specialization in an octopus species. For one thing, Forsythe & Hanlon (1979) informally report a much more varied diet for the same species in the Tuamotu islands. Why would different populations of the same species, in similar habitat, have such different prey selection? For another, though human settlement has changed the ecology of Kaneohe Bay, decreasing the abundance of near-shore animals, earlier though less systematic observations of Octopus cyanea prey choice (van Heukelem 1966, Yarnall 1969) showed the same selectivity for crabs. A third piece of evidence that argues against a depauperate environment causing a narrow prey selectivity is that the fauna of Kaneohe Bay, while perhaps lacking large crabs that might have been taken by humans, is rich and varied. In particular, snails of the genus Tegula, some of which were common prey for Octopus bimaculatus in California

Fig. 2 – A: Mean hunting time of four Octopus cyanea (n = 4), observed from 0630-1930 daily for eight days, at Coconut Island in August 1994. B: Mean intake as number of standard crab units of Octopus cyanea (n = 4) at Coconut Island over eight consecutive days in August 1994.
(Ambrose 1984), were extremely abundant on the reefs.

If neither habitat homogeneity nor relative abundance of the prey taken could predict the diet of O. cyanea in Hawaii, what pressures might restrict their input to crabs? Perhaps this is an offshoot of the octopod preference for crabs, found in the lab for O. vulgaris by Wells and his colleagues (1978) and in the field in Bermuda (Mather 1991), and also for O. bimaculatus (Ambrose 1984), O. insularis (Leite et al. 2009), and O. tehuelchus (Iribarne et al. 1991). It may be that an abundance of crab prey interacts with a general selectivity to allow the O. cyanea to act on a preference that most other octopuses do not have the opportunity for. High density of crab prey may have allowed this population to simply express this octopod tendency, and thus turned a generalist into a specialist.

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REFERENCES


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