# Variability in the Diet Specialization of *Enteroctopus dofleini* (Cephalopoda: Octopodidae) in the Eastern Pacific Examined from Midden Contents

Author(s): David Scheel and Roland Anderson
Source: American Malacological Bulletin, 30(2):267-279. 2012.
Published By: American Malacological Society
DOI: http://dx.doi.org/10.4003/006.030.0206
URL: http://www.bioone.org/doi/full/10.4003/006.030.0206

*Amer. Malac. Bull.* **30**(2): 267–279 (2012)

# Variability in the diet specialization of *Enteroctopus dofleini* (Cephalopoda: Octopodidae) in the eastern Pacific examined from midden contents

**David Scheel[1] and Roland Anderson[2]**

[1]Alaska Pacific University, 4101 University Dr. Anchorage, Alaska 99508, U.S.A.

[2]Seattle Aquarium, 1486 Alaskan Way, Seattle, Washington 98101, U.S.A.

Correspondence, David Scheel: dscheel@alaskapacific.edu

**Abstract.** We examined variation in dietary specialization of *Enteroctopus dofleini* (Wülker, 1910), the giant Pacific octopus, from Puget Sound to the Aleutian Islands, as represented in midden remains. Dietary specialization was measured from midden contents as: species richness (R) and Cardona's niche breadth (regional indices), and proportional similarity of a midden to the regional sample (an individual index). We found an influence of items per midden and prey species maximum size on these indices. In Puget Sound, middens and common prey species were large, richness, R = 21 species, and individuals specialized more often than in other areas, typically on large prey species. In Saanich Inlet, British Columbia, middens were smaller, R = 9 species, and the large crab *Cancer productus* was common in nearly all middens, such that the population specialized rather than the individual. In Prince William Sound, Alaska, middens contained fewer individuals of smaller prey species, R = 52 species, and diet was generalized at both the population and the individual levels. Cardona's niche breadth ranged from .11 to .14 except in the Aleutian Islands, Alaska where it was higher (.30). Most individual *E. dofleini* were generalists, and dietary species richness was very high (R = 69 species overall). Specialists within a generalist population were common only where middens and dominant prey were both large.

**Key words:** geographic variation; individual specialization; proportional similarity; prey choice

The diets of some octopuses are well described from midden data, however, prey choice by octopuses is poorly understood. At the same time, individual variation in octopus diets is poorly described, although known to exist (*Octopus vulgaris* (Cuvier, 1797): Anderson *et al.* 2008; Mather *et al.* in press; *O. insularis* (Leite *et al.*, 2008): Leite *et al.* 2009).

Many marine animals exhibit such individual variation in diet composition and this is often attributable to the influence of learning on foraging choices (West 1986). For example, for grazing herbivorous sea slugs individual preference was related to grazing history (Jensen 1989) and the high learning costs associated with switching prey (Jensen 1989; Trowbridge 1991). Sea otters also exhibit long-lived, individual variation in diet based on learning (Estes *et al.* 2003) as do seabirds (Woo *et al.* 2008).

Octopuses exhibit problem-solving intelligence (Fiorito 1990; Mather 1995) and spatial memory (Mather 1991b), are capable of short-distance navigation (Alves *et al.* 2008) and of learning both spatial (Boal *et al.* 2000) and foraging tasks (Anderson and Mather 2010). *Octopus cyanea* (Gray, 1849) are speculative tactile foragers (Yarnall 1969; Forsythe and Hanlon 1997). Similar foraging behavior has been documented for other octopuses although typically in less detail (e.g. *Enteroctopus dofleini* (Wülker, 1910): Johnson 1942; Cosgrove 2002; *O. ornatus* (Gould, 1852): Roper and Hochberg 1988; *O. maorum* (Hutton, 1880): Vafiadis 1998; for an exception for *O. vulgaris*: Mather 1991a; Mather and O'Dor 1991) and often primarily through examination of middens (e.g. *E. dofleini*: Hartwick *et al.* 1981; Vincent *et al.* 1998). At the same time, octopuses appear to be time minimizers rather than rate-maximizing foragers (McQuaid 1994; Scheel *et al.* 2007; Leite *et al.* 2009). Curio (1976) suggested that searching predators are unselective of prey because they expend so much energy on search that they will take what results from each search effort. For example, *E. dofleini* learned to forage on a fishing net and used dens nearby (Rigby and Sakurai 2005); but were stationary or hiding > 90% of the time (Scheel and Bisson 2012). For some octopuses, prey selection is also known to vary in relation to octopus body-size (Smith 2003) and among geographic regions (Vincent *et al.* 1998; Ibáñez and Chong 2008).

Octopuses have been variously described as generalists (based on diverse marine benthic taxa appearing in their diet e.g., Bouth *et al.* 2011), and as specialists (because only a few species dominate octopus diet, Mather 1991a; Mather and O'Dor 1991; Vincent *et al.* 1998; Anderson *et al.* 2008). However, increasingly these diets are being described as those of a specializing predator, due to the dietary dominance of few taxa (e.g. *Octopus insularis*: Leite *et al.* 2009; Bouth *et al.* 2011; *O. cyanea*: Mather 2011); because octopuses are individually specialized while generalizing at the population level (*O. vulgaris*: Anderson *et al.* 2008), or because they are known

to exhibit size and species selectivity (*Enteroctopus dofleini*: Scheel *et al.* 2007) in their diet. Digestibility and nutritional needs may also lead to individual specializing because although bivalve prey provided higher energy gain rates, *O. rubescens* (Berry, 1953) lipid absorption efficiency was higher on crustacean prey (Onthank and Cowles 2011), *E. dofleini* growth rate was higher on mixed than monotypic diets (Rigby and Sakurai 2004), and cephalopod growth efficiency may be finely tuned to nutrient ratios (Lee 1994).

In this paper, we present new data on the predatory behavior (as represented by diet determined from midden piles) of *Enteroctopus dofleini* and examine the variation in diet and individual specialization at locations from Puget Sound to the Aleutian Islands. The sensitivity of *E. dofleini* behavior to temperature fluctuations is well established (Prescott 1962; Rigby and Sakurai 2004), although geographic variation in this response remains to be worked out. Harley (2011) emphasized the role of marine benthic predator-prey dynamics varying along a geographic gradient in mediating the response of communities to climate change. In this paper we survey *E. dofleini* diet across a wide portion of its geographic range, which data continue to build a foundation for a better understanding of octopus predatory behavior and benthic food-web dynamics.

## METHODS

We assessed diet of the giant Pacific octopus, *Enteroctopus dofleini*, from remains of prey individuals found in middens outside octopus dens. Middens were recognized by the presence of an octopus, a den excavated in a characteristic fashion, and/or the presence of distinct marks (drills, bites) indicative of octopus predation on prey remains (Dodge and Scheel 1999). Middens were surveyed by divers (Puget Sound, WA at depths to 10 m; Saanich Inlet, BC at depths to greater than 7 m, Cosgrove 2003–2006; Amchitka and Adak, Aleutian Islands, Alaska at depths to 16 m. Fig. 1), and by beach-walks during low tide series between May and September (Prince William Sound, and Kachemak Bay in Cook Inlet, Alaska. Scheel 2002; Scheel *et al.* 2007). At each den we recorded by species the number of individuals represented in the prey remains. Only the Prince William Sound and Saanich Inlet data were used to examine diet variability over years because (with minor exception) the annual span of data from other regions was two years or less (Table 1). Remains present at a den were only scored as prey if they were fresh, judged by the lack of erosion and encrusting growth (diatoms, algae, spat) on interior surfaces kept clean in life. Thus, midden records represent recent foraging because remains are epiphyte-free for only a few days.

### Individual specialization

We examined individual specialization of diet from two measures: the proportional similarity of each midden to the population diet recorded from all middens for each geographic region (which compares the niche breadth of each midden *i* to the niche breadth of the population, Feinsinger *et al.* 1981; Bolnick *et al.* 2002); and Cardona's (1991) niche breadth (B'), which were calculated from occurrence frequency of each prey species $j = 1....R$ in middens:

Proportional similarity, $PS_i = \sum^{j} \min(p_{ij}, q_j)$

Cardona's niche breadth, $B' = (\sum^{j} f_j - \sigma) / (100\ R)$, where $f_j = (100\ N_j/N)$

where $p_{ij}$ is the proportion of prey individuals of species *j* within midden *i*, $q_j$ = proportion of that species across all middens from a sampling region (notation following Bolnick *et al.* 2002), $N_j$ = number of middens containing species *j*, *N* = number of middens, $\sigma$ = standard deviation of $f_j$, R = the number of prey species used by the population (notation modified from Cardona 1991). $PS_i$ takes on a minimum value of $q_j$ for individuals specializing entirely on species *j*, and the value 1.0 for individuals leaving prey remains in proportion to the population as a whole. The average of $PS_i$ over a population of middens is a measure of individual specialization within a population. B' has lower values when individuals specialize, and approaches one as all members of a

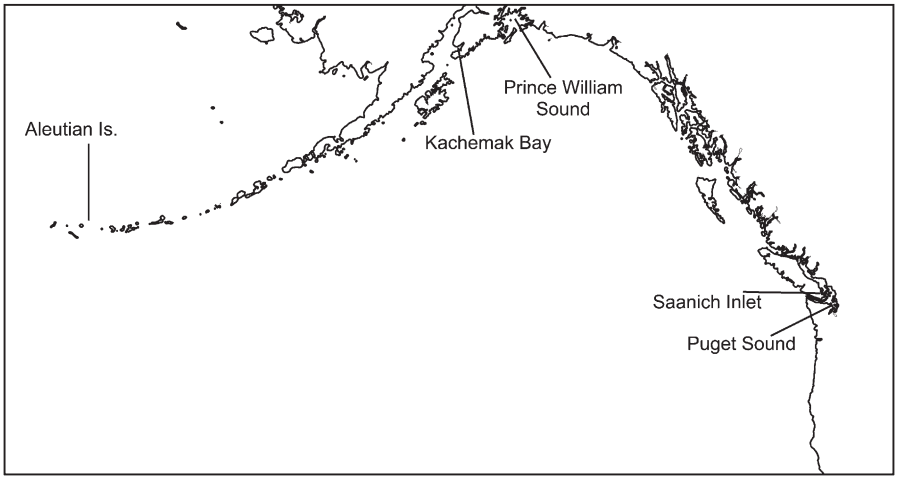


**Figure 1.** Sampling locations in the north Pacific. 'Aleutian Islands' indicates the approximate location within the chain where sampling was conducted at Amchitka and Adak Islands.

**Table 1.** Minimum number of prey individuals, *N*, represented in middens (proportion of total prey items) (percent of middens where present) at dens of giant Pacific octopuses by geographic region (see text for details). Bold indicates dietary dominance (= $N_i/\sum N_j$, $N_j$ ranked s.t. j = 1 for the most common species, see Methods for details). Cardona's (1991) niche breadth is calculated for each region from proportions of middens containing each species.

| Taxonomic name | Puget Sound | Saanich Inlet | Prince William Sound | Cook Inlet | Amchitka & Adak | Total |
|---|---|---|---|---|---|---|
| CRUSTACEA: *Cancer productus* J.W. Randall, 1840 | **389 (.45)** (81) | **476 (.81)** (99) | 617 (.20) (60) | 2 (.01) (5) | | 1484 (.30) |
| CRUSTACEA: *Cancer oregonensis* (Dana, 1852) | 1 (.00) (2) | | **766 (.25)** (65) | 148 (.42) (70) | 2 (.03) (20) | 917 (.19) |
| CRUSTACEA: *Telmessus cheiragonus (*Tilesius, 1812) | 3 (.00) (4) | 16 (.03) (13) | 528 (.17) (51) | **156 (.44)** (91) | | 703 (.14) |
| CRUSTACEA: *Pugettia gracilis* Dana, 1851 | 2 (.00) (2) | | 373 (.12) (37) | 21 (.06) (25) | 5 (.08) (40) | 401 (.08) |
| BIVALVIA: *Pododesmus macrochisma* (Deshayes, 1839) | 137 (.16) (19) | | 80 (.03) (11) | 1 (.00) (2) | **20 (.32)** (70) | 238 (.05) |
| CRUSTACEA: *Lophopanopeus bellus* (Stimpson, 1860) | | | 207 (.07) (30) | 2 (.01) (5) | | 209 (.04) |
| BIVALVIA: *Clinocardium nuttallii* (Conrad, 1837) | 107 (.12) (42) | | 53 (.02) (6) | 1 (.00) (2) | | 161 (.03) |
| BIVALVIA: *Saxidomus gigantea* (Deshayes, 1839) | 76 (.09) (35) | | 54 (.02) (9) | 3 (.01) (5) | | 133 (.03) |
| CRUSTACEA: *Pugettia producta* (J.W. Randall, 1840) | 10 (.01) (15) | 79 (.14) (28) | 1 (.00) () | | | 90 (.02) |
| BIVALVIA*: Protothaca staminea* (Conrad, 1837) | 10 (.01) (12) | | 74 (.02) (11) | 5 (.01) (5) | | 89 (.02) |
| BIVALVIA: *Macoma* sp.[a] Leach, 1819 | | 2 (.00) (1) | 59 (.02) (8) | 4 (.01) (5) | | 65 (.01) |
| BIVALVIA: *Chlamys hastata* (Sowerby, 1842) | 38 (.04) (4) | | 5 (.00) (1) | | | 43 (.01) |
| CRUSTACEA: *Cancer magister* Dana, 1852 | 37 (.04) (25) | | 2 (.00) () | | | 39 (.01) |
| CRUSTACEA: *Hapalogaster mertensii* Brandt, 1850 | | | 31 (.01) (6) | 4 (.01) (9) | | 35 (.01) |
| GASTROPODA: *Euspira lewisii* (Gould, 1847) | 7 (.01) (10) | 2 (.00) (1) | 20 (.01) (4) | 1 (.00) (2) | | 30 (.01) |
| CRUSTACEA: *Cancer gracilis* Dana, 1852 | 25 (.03) (17) | | | | | 25 (.01) |
| CRUSTACEA: *Cryptolithodes sitchensis* Brandt, 1853 | | | 24 (.01) (3) | | | 24 (.00) |
| BIVALVIA: *Modiolus modiolus* (Linnaeus, 1758) | | | 2 (.00) () | | 20 (.32) (40) | 22 (.00) |
| BIVALVIA: Unidentified | | | 20 (.01) (3) | | | 20 (.00) |
| BIVALVIA: *Humilaria kennerleyi* (Reeve, 1863) | 17 (.02) (10) | | 2 (.00) () | | | 19 (.00) |
| POLYPLACOPHORA: *Tonicella lineata* (W. Wood, 1815) | | | 17 (.01) (4) | | | 17 (.00) |
| BIVALVIA: *Mytilus* sp.[b] Linnaeus, 1758 | 3 (.00) (4) | | 11 (.00) (2) | 1 (.00) (2) | | 15 (.00) |
| BIVALVIA: *Gari californica* (Conrad, 1849) | 1 (.00) (2) | | 14 (.00) (3) | | | 15 (.00) |
| ECHINOIDEA: *Strongylocentrotus droebachiensis* (O.F. Müller, 1776) | | | 14 (.00) (3) | | | 14 (.00) |
| CRUSTACEA: *Hemigrapsus* sp.[c] Dana, 1851 | | 4 (.01) (2) | 7 (.00) () | 1 (.00) (2) | | 12 (.00) |
| BIVALVIA: *Tresus capax* (Gould, 1850) | 1 (.00) (2) | | 3 (.00) (1) | 2 (.01) (2) | | 6 (.00) |
| TELEOSTEI: various | | 2 (.00) (2) | 2 (.00) () | | | 4 (.00) |
| GASTROPODA: *Nucella lima* (Gmelin, 1791) | | | | | 4 (.06) (10) | 4 (.00) |
| GASTROPODA: *Nucella lamellosa* (Gmelin, 1791) | 1 (.00) (2) | | 3 (.00) (1) | | | 4 (.00) |
| CRUSTACEA: *Scyra acutifrons* Dana, 1851 | | 3 (.01) | | | | 3 (.00) |
| BIVALVIA: *Serripes groenlandicus* (Mohr, 1786) | | | | | 3 (.05) (10) | 3 (.00) |
| CRUSTACEA: unidentified lithoid crab | | 1 (.00) | 1 (.00) () | | | 2 (.00) |
| BIVALVIA: *Clinocardium ciliatum* (Fabricius, 1780) | | | | | 2 (.03) (20) | 2 (.00) |
| BIVALVIA: *Crassostrea gigas* (Thunberg, 1793) | 1 (.00) (2) | | | | | 1 (.00) |
| BIVALVIA: *Entodesma saxicola* (Baird, 1863) | 1 (.00) (2) | | | | | 1 (.00) |
| POLYPLACOPHORA: *Cryptochiton stelleri* (Middendorff, 1847) | 1 (.00) (2) | | | | | 1 (.00) |
| Individuals of other taxa[d] | | (3) | 47 (.02) (11) | | 6 (.10) (50) | 53 (.01) |

**Table 1.** (Continued)

| Taxonomic name | Puget Sound | Saanich Inlet | Prince William Sound | Cook Inlet | Amchitka & Adak | Total |
|---|---|---|---|---|---|---|
| Total prey items represented | 868 | 585 | 3037 | 352 | 62 | 4904 |
| [d]Number of other taxa found | - | - | 24 | - | 5 | 30 |
| Total taxa found (species richness) | 21 | 9 | 52 | 15 | 12 | 69 |
| Average Proportional Similarity, PS | 0.45 | 0.77 | 0.40 | 0.48 | 0.34 | |
| Cardona's niche breadth (B') | (.13) | (.14) | (.11) | (.14) | (.30) | |
| Total number of den visits | 52 | 87 | 440 | 44 | 10 | 633 |
| Years of sample | 1996 (n = 1) | 2002–2006 | 1997–1998 | 2010 | 2011 | |
| | 2005 (n = 1) | | 2001–2011 | | | |
| | 2009–2010 | | | | | |

[a] *Macoma* was identified as *M.* sp. in Puget Sound and as *M. inquinata* (Deshayes, 1855) in PWS.

[b] *Mytilus* sp. was identified as *M. trossulus* Gould, 1850 in Puget Sound, and as *M. edulis* Linnaeus, 1758 in PWS.

[c] *Hemigrapsus* was recorded as *H.* sp. in Puget Sound and as *H. oregonensis* (Dana, 1851) or *H.* sp. in PWS.

population have identical diets. Finally, we used R (species richness) and the Berger-Parker diversity index (indicating dominance, $d$ = maximum of $q_j$, Magurran 1988) as additional measures of regional octopus dietary breadth.

We tested whether each midden represented a random sample from the regional population of all prey represented in middens using the likelihood ratio,

$$\lambda_i = \Pi_j \, (q_j / p_{ij})^{\, n_{ij}}$$

where $\Pi_j$ denotes the serial product over species $j$, and $n_{ij}$ is the number of prey items of species $j$ in midden $i$. The quantity -2 ln ($\lambda_i$) has an approximately chi-square distribution with (R-1) degrees of freedom (Bolnick et al. 2002). As this test was run for each of the 633 middens (Table 1), we used a more conservative $p < 0.001$ to identify significantly specialized middens.

## RESULTS

Diets were compared from a sample of middens collected in the years 1996–2011 at octopus dens in intertidal and sub-tidal sites (Table 1; prey items per midden: mode = 4, range $n_i$ = 1 to 58). Over all areas (Fig. 1), octopus middens contained remains of 69 taxa, but 80% of all prey came from just five crab species and the bivalve *Pododesmus macrochisma* (Deshayes, 1839). Another 10% of all prey came from an additional three bivalve species and the crab *Pugettia producta*, so that across all areas 90% of prey items came from only ten species.

### Regional diets

Diet as represented by middens differed among sampled regions (Table 1, Fig. 1). In Saanich Inlet, where dietary species richness was low (R = 9 species) and dietary dominance high ($d$ = 81% of prey items from one species), *Cancer productus* was the most common prey in the middens. *Cancer productus* similarly dominated middens in Puget Sound, however, richness and dominance were both moderately high. In south-central Alaska, five crab species, including both *C. productus* and *C. oregonensis* were common in middens in Prince William Sound (PWS), where the highest richness and lowest dominance were found (Table 1). Three of these crabs were also prevalent in Cook Inlet middens, although richness and dominance were moderate. *Telmessus cheiragonus* and *C. oregonensis* were abundant in middens in both these south-central regions, where middens were predominantly of intertidal dens. Both richness and dominance were low in middens from Amchitka and Adak Islands because these middens were dominated by two bivalve species, and relatively few other species were represented.

Further, middens in Puget Sound were larger than in the other regions (Puget Sound, $\bar{x}$ = 16.6 prey/midden; other regions, $\bar{x}$ = 6.9. Chi-squared test, $df = 16$, $\chi^2 = 59.6$, $p < .001$). The dominant species in Puget Sound and Saanich Inlet (*Cancer productus*, to carapace width 20 cm) is a larger crab than the crab species that replace it in Alaska middens (*Telmessus cheiragonus* to 10 cm, *C. oregonensis* to 4.3 cm, *Pugettia gracilis* to 3.2 cm). The other common prey in Puget Sound middens were large bivalve species (*Pododesmus macrochisma*, *Clinocardium nuttallii* (Conrad, 1837), and *Saxidomus gigantea* (Deshayes, 1839)) which comprised smaller portions of the diet in most other areas (Table 1), such that middens in Puget Sound especially represent more food than those found in British Columbia (fewer prey) or in south-central Alaska (fewer prey and smaller species of prey).

The size, richness and composition of middens varied across the years 2002–2006. A typical midden early during this period contained more prey individuals and had higher species richness than middens later, in both PWS and BC, although the timing of the decline was not the same in both locations (Fig. 2). Smaller middens thus became more frequent. Composition of the diet also changed across years. In both Prince William Sound and Saanich Inlet, the proportion of the population diet comprised of *Cancer productus* increased in the period 2003 to 2005 from the 2002 level; while those of *Pugettia gracilis* and *Telmessus cheiragonus* decreased in the same period (Fig. 3). In the Prince William Sound sample, the midden representation of other small crabs such as *Cancer oregonensis* also varied across years. *Cancer oregonensis* was more abundant in the middens of Prince William Sound octopuses in 2003 and 2005 relative to

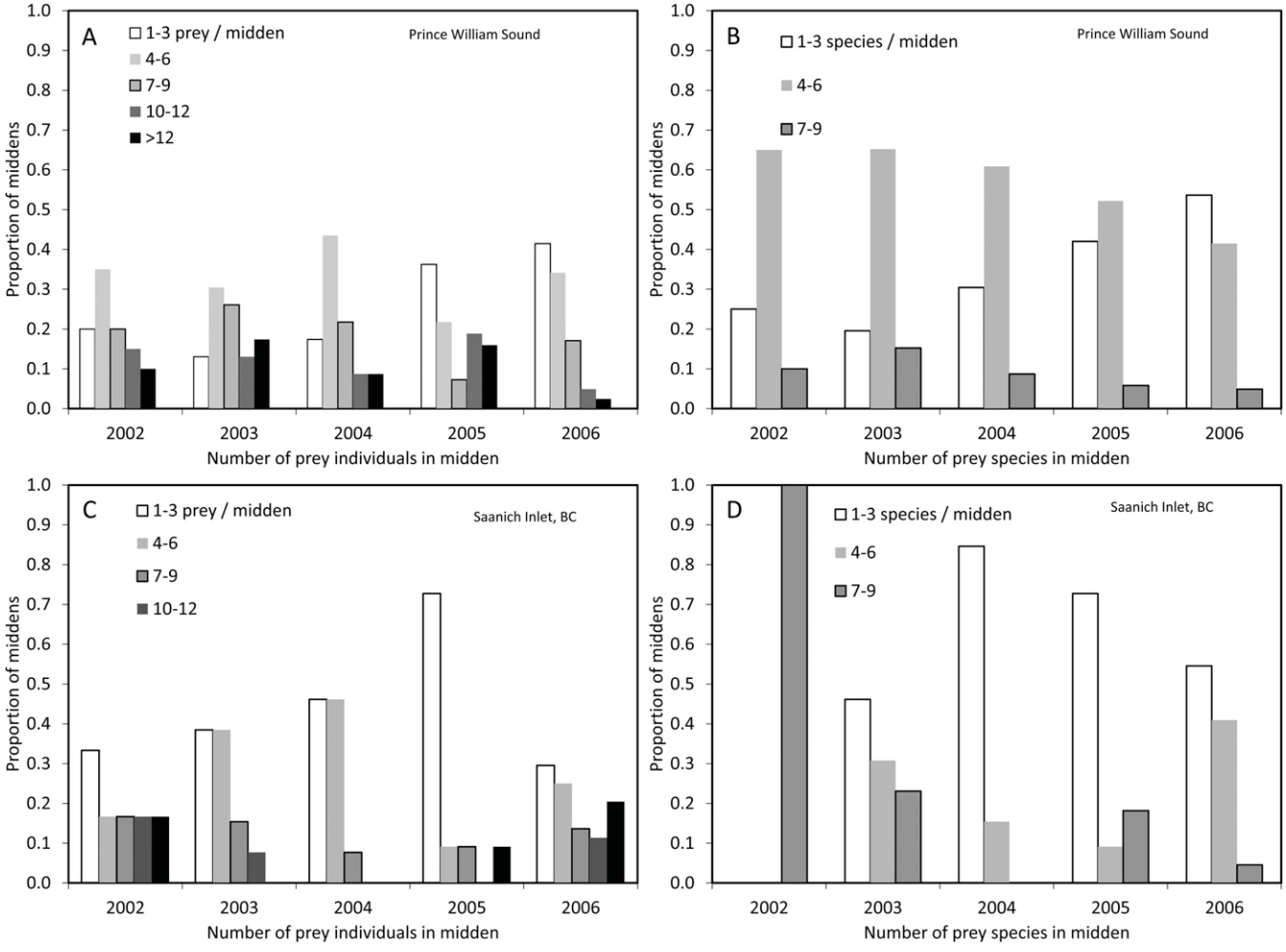


**Figure 2.** Midden size (proportion of middens by number of prey individuals, **A**, **C**) and richness (proportion of middens by number of species, **B**, **D**) left by giant Pacific octopuses in Prince William Sound and Saanich Inlet, BC, by year of sampling.

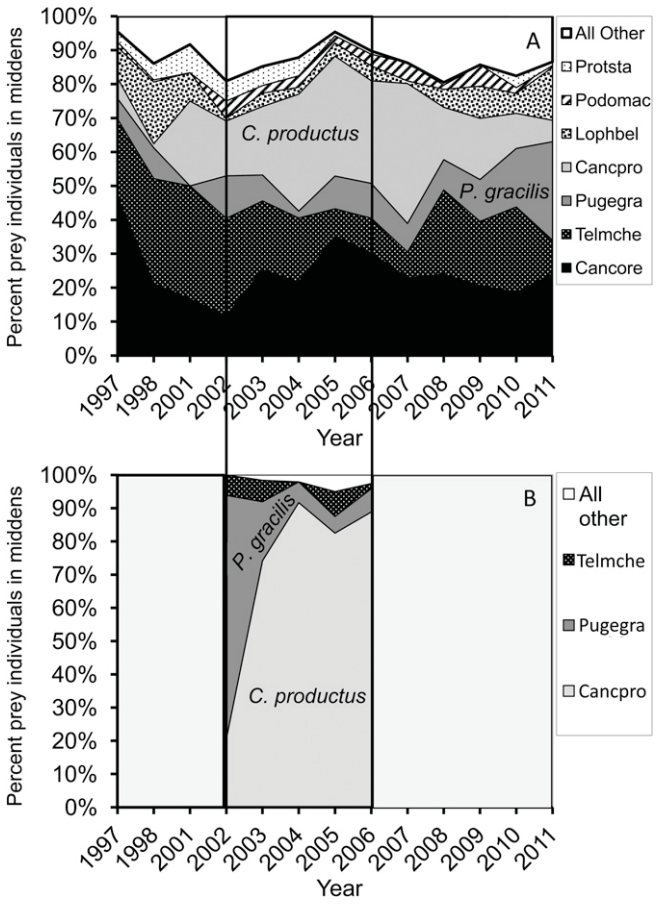


**Figure 3.** Species composition of prey individuals found in middens left by giant Pacific octopuses in Prince William Sound (**A**, remains of 3037 prey individuals represented in 440 middens) and Saanich Inlet, BC (**B**, remains of 585 prey individuals represented in 90 middens) by year of sampling. Species abbreviations consist of the first four letters of the genus name and first three letters of the specific name (i.e. *Prototheca staminea* becomes Protsta, see Table 1 for full species names). Data were unavailable for Saanich Inlet except for years shown.

2002. Because prey species differ in size, fewer individuals in the midden may not represent lower caloric intake, as a larger species (*C. productus*) was substituted for smaller (*Pugettia gracilis*).

**Individual diets**

Most individual octopus middens did not significantly differ from the regional population of midden items over all years (Figs. 4–5, Puget Sound $N = 10$ of 52 middens differed: df = 21, $\lambda_i > \chi^2_{21,\, p < .0001} = 46.8$; Saanich Inlet $N = 2$ of 87 middens: df = 9, $\lambda_i > \chi^2_{9,\, p < .0001} = 27.9$; PWS NS $N = 440$ middens: df = 54, $\lambda_i < \chi^2_{54,\, p < .0001} = 86.7$; Cook Inlet NS $N = 44$: df = 15, $\lambda_i < \chi^2_{15,\, p < .0001} = 37.7$; Aleutians NS $N = 10$: df = 12, $\lambda_i < \chi^2_{12,\, p < .0001} = 32.9$). Overall the frequency distribution of midden proportional similarities varied little by regions (Fig. 4), except for Saanich Inlet, BC, where the mode was .81 to .9. Midden richness was low and dietary dominance high in Saanich Inlet (Table 1); but these middens differed little from the population sample. The population prey was dominated by a single species (Table 1, *Cancer productus*), most middens contained only that prey species (50 of $N = 87$ middens), and nearly all middens (99%) contained at least one *C. productus*. The only two instances of specialization in Saanich Inlet were on the crab *Pugettia producta*. In contrast, for Puget Sound, 10 of 52 middens (19%) differed significantly, and individuals specialized on the bivalves *Clinocardium nuttallii*, *Pododesmus macrochisma*, *Saxidomus gigantea* ($N = 2$ each), *Humilaria kennerleyi* (Reeve, 1863), *Chlamys hastata* (G. B. Sowerby II, 1842) ($N = 1$ each) or on the crabs *Cancer magister* or *Cancer productus* ($N = 1$ each). In all cases of significant specialization, the midden contained remains of at least 12 prey items, typically over twenty (Fig. 5).

Patterns of specialization with items per midden varied across regions. In Puget Sound (and also Cook Inlet) proportional similarities averaged about 0.5 (Table 1) but there was no relationship to items per midden (Fig. 5). This was different in Saanich Inlet, where proportional similarities averaged nearly 0.8, although there was still no relationship to items per midden. However, in Prince William Sound and in the Aleutians, proportional similarities on average were only slightly lower than in Puget Sound, but increased with items per midden.

## DISCUSSION

Human Aleut hunter gatherers subsisting on intertidal marine resources in the Aleutian Islands, Alaska have been characterized as super-generalists, consuming > 25% of available species, more than any other animal foraging in the intertidal (Travis 2012). That study, based on data from middens left by humans over a 5000-year period, found that Aleuts ate 50 different species. In this report, we document comparable species richness in the diet of *Enteroctopus dofleini* from samples spanning just 17 years, including 52 intertidal species where diet was most diverse (Prince William Sound) and 69 species over all regions (Table 1). Thus, *E. dofleini* appears under certain conditions also to act as a super-generalist forager. *E. dofleini* were specialists within a generalist population only where middens and dominant prey were both large (Puget Sound), while the population specialized only where large prey species dominated in middens of smaller modal size (Saanich Inlet). In contrast,

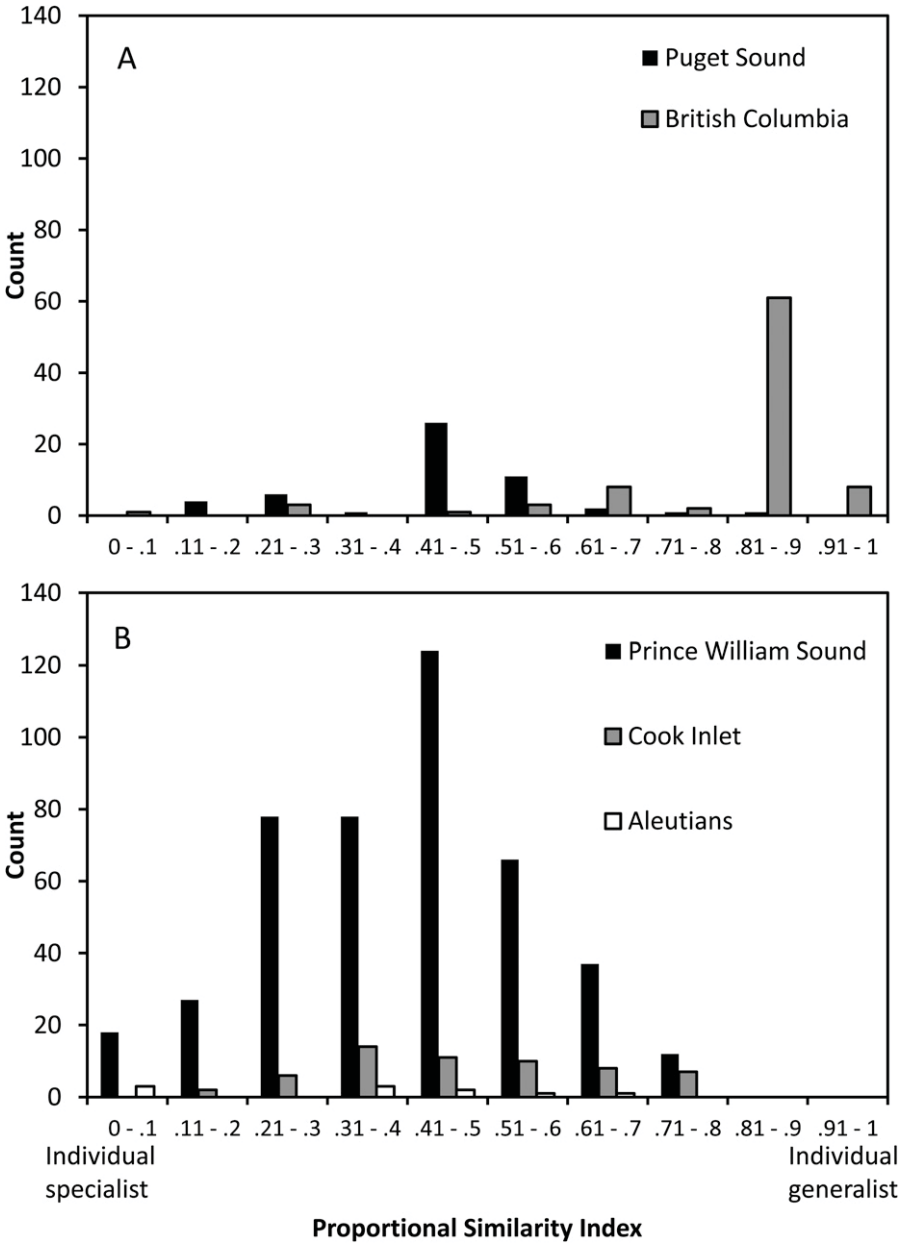


**Figure 4.** Frequency distribution of proportional similarity of middens left by giant Pacific octopuses to the population midden sample for Puget Sound and Saanich Inlet (**A**) and three areas in Alaska (**B**).

*E. dofleini* were generalists when middens and prey were both smallest (Prince William Sound).

Several factors may contribute to these regional differences in dietary specialization, but they can be considered as factors that affect how well middens represent diet (Mather 1991a), and factors affecting octopus foraging (including differences in prey availability). First, middens are dynamic (Ambrose 1983, Mather 1991a) as midden remains are removed by both biotic agents (e.g. hermit crabs) and erosion of items from the midden by burying or by currents. Hermit crabs affect the residence-time of snail shells in middens (Ambrose 1983), but gastropods were only a minor component of middens in our study. Exposure of middens to waves and currents also does not appear to explain differences in midden richness, composition and specialization. For example, the relative abundance of bivalves (less likely to bury or be swept away) to crustacean exoskeletons (more likely to be removed, Mather 1991a) was highest in the Aleutians and Puget Sound, and lowest in Kachemak Bay and Saanich Inlet (Table 1). Current exposure may be high in the Aleutians but summer wave exposure was not (because the samples were collected at depth); Kachemak Bay has high wave exposure (long fetch and intertidal sampling); while Saanich Inlet and Puget Sound are both highly protected waters. Thus any hypothesis of differential erosion of the middens as a function of local wave energy appears unable to explain the differences we observed.

Are differences in midden composition and specialization consistent with explanations of octopus behavior other than changes in diet selection behavior? For example, octopus den residency time may have differed among regions. The accumulation of midden items over longer periods (or alternatively by multiple individual octopuses each using the den for shorter periods) could result in more items and greater species richness per midden relative to a midden left by one octopus over a short time period. However, we included only fresh prey remains (see methods) in our sample, and thus limited the variation across regions in midden age. *Enteroctopus dofleini* forages near its den (Mather et al. 1985, Scheel unpublished data) every two to three days or more frequently (Scheel and Bisson 2012), and thus, fresh prey remains from middens generally will include only remains from the one or two most recent foraging bouts (plus any prey recently taken near the den). Variation in den residency time or foraging frequency thus

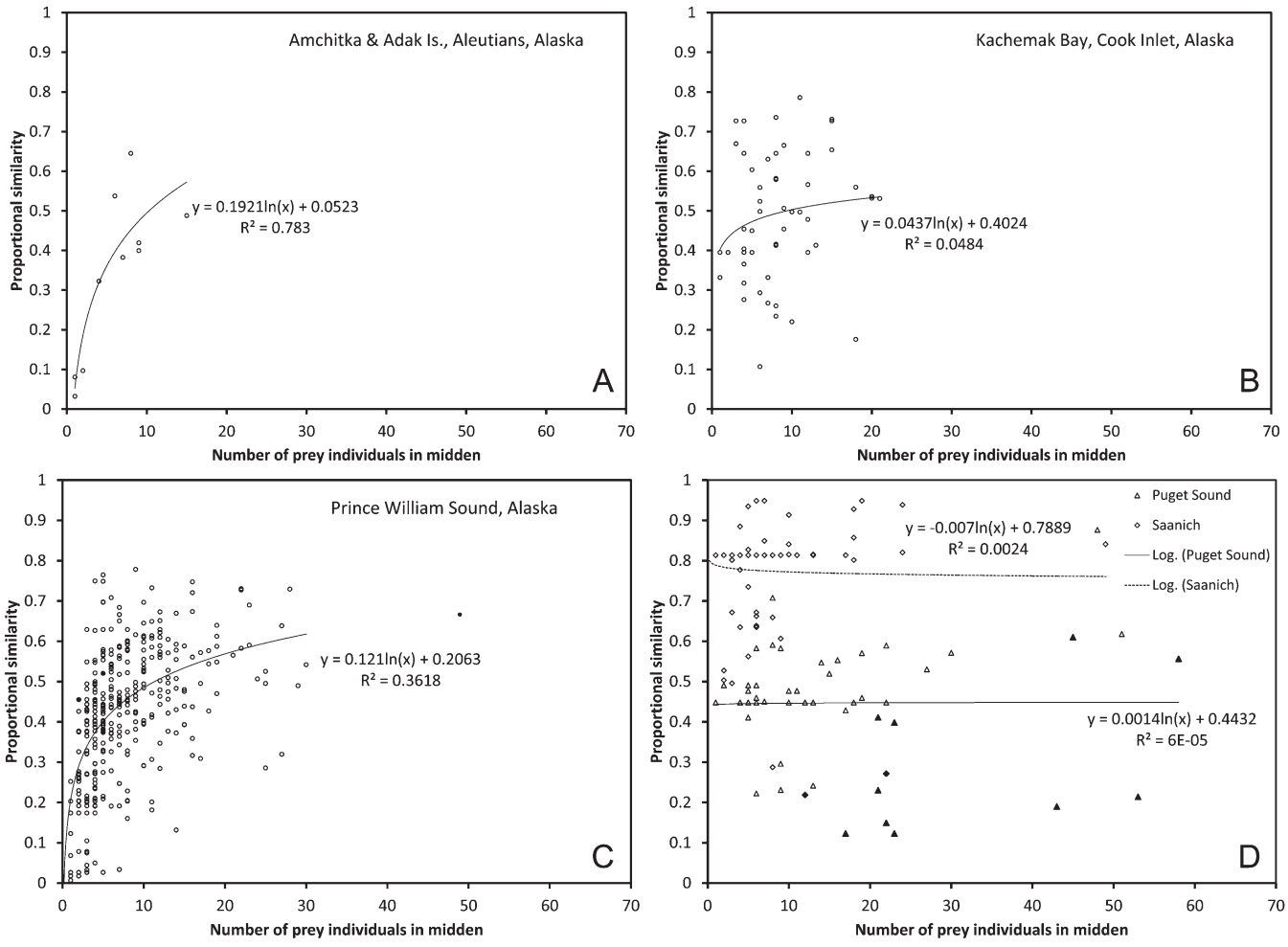


**Figure 5.** The proportional similarity of middens (each point represents one midden) left by giant Pacific octopuses to the population midden sample by items per midden in each sampling area. Large filled symbols (**D**, Puget Sound, Saanich Inlet) indicate midden contents representing statistically significant specialization in diet (see methods). Lines (and equations) indicate natural logarithmic fit to data.

appears unable to explain regional variation in the specialization of midden contents.

In contrast, our results are consistent with the hypothesis that octopus diet selection behavior was different among sampling regions: when large preferred prey were abundant in middens, foraging *Enteroctopus dofleini* all specialized in the same way (perhaps as rate-maximizing foragers). When large preferred prey were not abundant in middens, individuals appeared to take prey as encountered, leading to a relationship between $PS_i$ and the number of items per midden (Alaska, Fig. 5). Thus, we observed that specialization and food content per midden both were reduced from Puget Sound north and west across the range. The distinction between specialization (proportion of individual diet comprised of one species) and similarity (of one diet to the population, $PS_i$) is important (see Mather *et al*. in press). In Saanich Inlet where *C. productus* occurred in 99% of middens, average $PS_i$ was high but in another sense nearly every midden was specialized on this single species.

Is it possible to say that midden contents reflect octopus foraging responses to habitat quality or habitat richness? Intertidal species richness is high in south central Alaska and peaks just below the depth where intertidal octopus dens are most abundant (Konar *et al*. 2009, 2010, Pohle *et al*. 2010). Scheel *et al.* (2007) found no *Enteroctopus dofleini* population response to densities of live prey in the habitat, but did find that individual midden contents reflected changes in prey abundance. *Enteroctopus dofleini* foraging outcomes also responded to changing prey populations, as average

crab size available in the environment declined for some species during a time in which average prey size in the middens increased, indicating increased selectivity by octopuses (Scheel *et al*. 2007). Similarly, Ambrose (1984) found that midden contents of *Octopus bimaculatus* reflected aspects of both prey preference and prey availability. Further, different octopus species behave differently and the relationship of these differences to prey availability is poorly known. *Octopus rubescens* fed predominantly on the most widely available prey in its habitat (Anderson *et al*. 1999), but *O. cyanea* selectively chose just a few crab species despite wide availability of alternate prey (Mather 2011). *Octopus tehuelchus* (D'Orbigny, 1834) in intertidal habitats exhibited considerable prey selectivity possibly connected to chemical deterrents in the prey (Iribarne *et al*. 1991). *Enteroctopus dofleini* also exhibits species selectivity in prey choice (Vincent *et al*. 1998). Thus, midden contents are unlikely to mirror prey availability exactly, but instead will be influenced by availability, octopus prey preferences (e.g. for larger prey, Scheel *et al*. 2007), and variation in foraging effort (foraging habitat selection, Scheel and Bisson 2012; foraging time, etc.). Clearly dietary specialization may occur where octopuses forage most successfully both at the population level (Table 1, R varies from 9 to 52) and the individual level (Fig. 5: 10% of Puget Sound middens were specialized).

In both Saanich Inlet, BC and Prince William Sound, AK during the years 2002 to 2006, *Cancer productus* comprised an increasing proportion of octopus diet (Fig. 3), and the proportion of middens containing only a few prey individuals increased, as did that of middens containing only a few species (Fig. 2). *Cancer productus* is a large crab, and the proportion of middens containing a smaller species, *Pugettia gracilis*, was less in both areas when *C. productus* dominated middens. Because *C. productus* first appeared on live prey surveys at Prince William Sound sites in 2004 (Scheel *et al.* 2007), and their abundance increased in this time period (Scheel, unpublished data), this suggests three things. First, *C. productus* is a preferred prey whose representation in the diet scales with abundance. Second because *C. productus* increased in the diet in both areas, a coastal-wide *C. productus* recruitment event may have preceded these years. Third, an abundance of larger prey may shelter smaller prey such as *P. gracilis* from octopus predation, a conclusion consistent with selectivity of octopuses for larger individuals (Scheel *et al*. 2007); and with predictions of optimal foraging theory that a greater range of prey types will be eaten the lower the overall abundance of food (Schoener 1971).

The specialization in Puget Sound of 10% of middens notwithstanding, the dominant pattern is not one of individual specialization within a generalist population. Similarly, Mather *et al*. (in press) found populations of mixed specialists and generalists across five populations of three octopus species (*Octopus vulgaris*, *O. cyanea*, *Enteroctopus dofleini*). Octopus growth rate may be higher on mixed species diets (Rigby and Sakurai 2004) and most octopuses appeared not to specialize (Fig. 5), even where middens indicated the most food consumed (Puget Sound). At the same time, *E. dofleini* diet may be highly dominated by a single prey or be extraordinarily diverse (Table 1) but in each case individuals in the population all behaved similarly: a specialized population in Saanich Inlet; and a generalized population without specializing individuals in Alaska. This pattern is apparent in the relation of items per midden (sample drawn from the prey population) to midden proportional similarity: in a generalizing population, individual generalization increased towards an asymptote as items per midden increased (Fig. 5, Alaska). In a specialized population, there was no relationship, as the population diet was dominated by a single species and again all individuals resemble the population as a whole (Saanich Inlet). Thus diet specialization, while variable, appears to be a function of foraging success as indicated by prey species' maximum size and number of consumed individuals.

In contrast, Cardona's index of niche breadth (B', Table 1) revealed little of differences between regions in specialization as it did not differentiate clearly between Alaska samples (generalists) and those further south (population or some individual specialization), except in the case of the Aleutian octopuses. The Aleutian B' was more than twice that of other populations and diet in these samples was evenly dominated by just two species; one of which occurred in 70% of all middens. These two species were both large bivalves and this is the only sample dominated by bivalves rather than crustaceans. Onthank and Cowles (2011) found that *Octopus rubescens* have lower lipid absorption efficiencies on bivalve than crustacean prey. It is notable in this context that these bivalves were both large and abundant at the Aleutian sampling sites compared to other Alaska sites (Scheel pers. observation). The hypothesis that Aleutian octopuses rely on bivalves because this prey is sufficiently superabundant to offset lower digestive efficiency could not be assessed in this study.

Prey availability affects many aspects of predator ecology, but especially diet and foraging behavior. Adaptive foragers may select diet to maximize gain rates (MacArthur and Pianka 1966), minimize risk (Stephens and Charnov 1982), or to reduce missed-opportunity-costs (Schoener 1971; Brown 1988) as well as possibly due to nutrient or processing constraints (e.g. Onthank and Cowles 2011). Our results indicate that where middens contained fewer, smaller prey items, *Enteroctopus dofleini* was more generalized in diet, presumably a result of including smaller prey

(Scheel *et al*. 2007; as predicted by rate-maximization theory, Stephens and Krebs 1986) and spending more time foraging, each of which alter the predator's functional response to prey (Holling 1959). It has also been suggested that octopuses follow a win-switch strategy (Mather 2008) in which localized prey depletion favors selection of new habitat, perhaps by changing movement strategies (Scheel and Bisson 2012). Finally, octopus growth rates, and thus time to maturation, vary with food supply (Hartwick *et al*. 1981; Robinson and Hartwick 1986), so that population response to changes in prey availability may occur, although these may not be detectable against a background of variable recruitment (Garstang 1900; Rees and Lumby 1954; Scheel *et al*. 2007).

Biological trait variation, including variation in diet selection, occurs between species and may even drive speciation among eco-types (e.g. killer whales, Baird *et al*. 1992; Pilot *et al*. 2010). Such variation also occurs among individuals as a result of individual developmental and learning histories (Darwin 1859; Baldwin 1896) and contributes to personality differences (Mather and Anderson 1993; Sinn *et al*. 2010). In these analyses we can see variation among individuals within and also among populations. For example, African lions exhibit variation in specialization of hunting roles, which occurs in some populations (Stander 1992) but not others (Scheel and Packer 1991); and individual lions may exhibit specialization of diet even within a cooperatively hunting group (Yeakel *et al*. 2009). Like these examples, variation in individual specialization of diet among northeastern Pacific populations of *Enteroctopus dofleini* lies between that of the species and the individual, and may be related to local environments and individuals' learned differences. Unfortunately, few data about prey abundances and micro-habitats, or data about octopus growth rates, were available for these populations and we were unable to examine the role of environmental differences in accounting for population differences. Data on individual histories of foraging octopuses will be even more difficult to obtain.

Declines in prey abundance have led to a higher reliance on small prey and greater dietary species richness among Chugach Alutiiq natives in south central Alaska foraging on the same prey types and in the same habitats as these octopuses (Salomon *et al.* 2007). Similarly, Caddy and Rodhouse (1998) and Piatkowski *et al.* (2001) suggest that cephalopods are increasing in the world oceans because of depletion of their predators and competitors; and a rise in generalist species has been reported in many other contexts (Clavel *et al.* 2010). The flexible response of octopuses to be either specialists or generalists indicates that ecosystems may also lose specialists if foraging success declines as habitat quality or richness declines. Clavel *et al.* (2010) categorize species as specialists primarily according to morphological parameters, and by this measure, coleoid cephalopods may be the ultimate generalists using suckers, beak, radula, and venom to capture and consume a wide variety of prey whenever a generalist diet maximizes aspects of fitness.

## ACKNOWLEDGMENTS

We thank J. Cosgrove (Saanich Inlet), G. Becken, S. Blazina, J. Christiansen, G. Jensen, J. Kocsis, S. Larson, D. Linzee, and C. Lorenz (Puget Sound) for sharing midden data, and J. Mather and anonymous reviewers for discussion of some of the ideas presented here. D. S. thanks Dr. Stephen Jewett, Institute of Marine Science, University of Alaska Fairbanks and the crew of the R/V Norseman; and Captain N. Oppen of the R/V Tempest for their professionalism, hard work, and good humor in the field; and fellow researchers C. Lyons, T. L. S. Vincent, students of the 2008–2009 and 2011 Fall Marine Field Work classes at Alaska Pacific University (APU), Thomas L. and P. J. Vincent, J. P. and L. H. Scheel, and many others for collaboration in aspects of these studies. Some records analyzed in this paper were collected in partial fulfillment of requirements for the Bachelor of Science in Marine Biology (by D. Frohbeiter, A. Kjellgren, J. Smith, B. Robinson) or the Master's of Science in Environmental Science (by C. Lyons, D. Pulgretova) at APU. Long-term financial support for this study was provided to D. S. through APU from donations by the Pollock Conservation Consortium (2001–2011); with additional support from the National Science Foundation (Grant #0115882 2001-2003), Exxon Valdez Oil Spill Trustee Council (1995–1997), West Coast and Polar Regions Underseas Research Center (University of Alaska Fairbanks National Undersea Research Program, NOAA 1998, 2010), Alaska Space Grant Program NASA (2008–2010), and Alaska Fisheries Development Foundation (2006) to D. S. and T. L. S. Vincent. Findings and conclusions presented by the authors are their own and do not necessarily reflect the views or positions of the supporting organizations.

The research was conducted under Alaska Department of Fish & Game Fish Resource permits to D. S. This research complies with the current laws of the United States and Canada. The authors declare that they have no conflict of interest.

## LITERATURE CITED

Alves, C., J. G. Boal, and L. Dickel. 2008. Short-distance navigation in cephalopods: A review and synthesis. *Cognitive Processes* **9:** 239–247.

Ambrose, R. F. 1983. Midden formation by octopuses: The role of biotic and abiotic factors. *Marine Behaviour and Physiology* **10:** 137–144.

Ambrose, R. F. 1984. Food preferences, prey availability, and the diet of *Octopus bimaculatus* Verrill. *Journal of Experimental Marine Biology and Ecology* **77:** 29–44.

Anderson, R. C., P. D. Hughes, J. A. Mather, and C. W. Steele. 1999. Determination of the diet of *Octopus rubescens* Berry, 1953 (Cephalopoda: Octopodidae), through examination of its beer bottle dens in Puget Sound. *Malacologia* **41:** 455–460.

Anderson, R. C. and J. A. Mather. 2010. It's all in the cues: Octopuses (*Enteroctopus dofleini*) learn to open jars. *Ferrantia* **59:** 8–13.

Anderson, R. C., J. B. Wood, and J. A. Mather. 2008. *Octopus vulgaris* in the Caribbean is a specializing generalist. *Marine Ecology Progress Series* **371:** 199–202.

Baird, R. W., P. A. Abrams, and L. M. Dill. 1992. Possible indirect interactions between transient and resident killer whales: Implications for the evolution of foraging specializations in the genus *Orcinus*. *Oecologia* **89:** 125–132.

Baldwin, J. M. 1896. A new factor in evolution. *American Naturalist* **30:** 441–451.

Boal, J. G., A. W. Dunham, K. T. William, and R. T. Hanlon. 2000. Experimental evidence for spatial learning in octopuses (*Octopus bimaculoides*). *Journal of Comparative Psychology* **114:** 246–252.

Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. *Ecology* **83:** 2936–2941.

Bouth, H. F., T. S. Leite, F. D. d. Lima, and J. E. L. Oliveira. 2011. Atol das Rocas: An oasis for *Octopus insularis* juveniles (Cephalopoda: Octopodidae). *Zoologia* (Curitiba, Impresso) **28:** 45–52.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* **22:** 37–47.

Caddy, J. F. and P. G. Rodhouse. 1998. Cephalopod and groundfish landings: Evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries* **8:** 431–444.

Cardona, L. 1991. Measurement of trophic niche breadth using occurrence frequencies. *Journal of Fish Biology* **39:** 901–903.

Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9:** 222–228.

Cosgrove, J. A. 2002. An *in situ* observation of webover hunting by *Enteroctopus dofleini* (Wülker, 1910). *The Canadian Field-Naturalist* **117:** 117–118.

Cosgrove J. A. 2003–2006. *A Report on Underwater Research Activities Conducted in the Gowlland Tod Provincial Park (November 1–October 31)*. Report for Gowlland Tod Park.

Curio E. 1976. *The Ethology of Predation*. Springer-Verlag, New York.

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

Dodge, R. and D. Scheel. 1999. Remains of the prey-recognizing the midden piles of *Octopus dofleini* (Wülker). *The Veliger* **42:** 260–266.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: Patterns, causes and implications. *Journal of Animal Ecology* **72:** 144–155.

Feinsinger, P., E. E. Spears, and R. W. Poole. 1981. A simple measure of niche breadth. *Ecology* **62:** 27–32.

Fiorito, G., C. Von Planta, and P. Scotto. 1990. Problem solving ability of *Octopus vulgaris* Lamarck (Mollusca, Cephalopoda). *Behavioral and Neural Biology* **53:** 217–230.

Forsythe, J. W. and R. T. Hanlon. 1997. Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. *Journal of Experimental Marine Biology and Ecology* **209:** 15–31.

Garstang, W. 1900. The plague of octopus on the south coast, and its effect on the crab and lobster fisheries. *Journal of the Marine Biological Association of the United Kingdom* **6:** 260–273.

Harley, C. D. G. 2011. Climate Change, Keystone Predation, and Biodiversity Loss. *Science* **334:** 1124–1127.

Hartwick, B., L. Tulloch, and S. MacDonald. 1981. Feeding and growth of *Octopus dofleini* (Wülker). *The Veliger* **24:** 129–138.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* **91:** 385–398.

Ibáñez, C. M. and J. V. Chong. 2008. Feeding ecology of *Enteroctopus megalocyathus* at three localities of southern Chile. *Journal of the Marine Biological Association of the United Kingdom* **88:** 793–798.

Iribarne, O. O., M. E. Fernandez, and H. Zucchini. 1991. Prey selection by the small Patagonian octopus *Octopus tehuelchus* d'Orbigny. *Journal of Experimental Marine Biology and Ecology* **148:** 271–281.

Jensen, K. 1989. Learning as a factor in diet selection by *Elysia viridis* (Montagu) (Opisthobranchia). *Journal of Molluscan Studies* **55:** 79–88.

Johnson, M. W. 1942. Some observations on the feeding habits of the octopus. *Science* **95:** 478–479.

Konar, B., K. Iken, J. J. Cruz-Motta, L. Benedetti-Cecchi, A. Knowlton, G. Pohle, P. Miloslavich, M. Edwards, T. Trott, E. Kimani, R. Riosmena-Rodriguez, M. Wong, S. Jenkins, A. Silva, I. S. Pinto, and Y. Shirayama. 2010. Current patterns of macroalgal diversity and biomass in northern hemisphere rocky shores. *PloS One* **5:** e13195.

Konar, B., K. Iken, and M. Edwards. 2009. Depth-stratified community zonation patterns on Gulf of Alaska rocky shores. *Marine Ecology* **30:** 63–73.

Lee, P. 1994. Nutrition of cephalopods: Fueling the system. *Marine and Freshwater Behaviour and Physiology* **25:** 35–51.

Leite, T. S., M. Haimovici, and J. Mather. 2009. *Octopus insularis* (Octopodidae), evidences of a specialized predator and a time-minimizing hunter. *Marine Biology* **156:** 2355–2367.

Leite, T. S., M. Haimovici, W. Molina, and K. Warnke. 2008. Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *Journal of Molluscan Studies* **74:** 63–74.

MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* **100:** 603–609.

Magurran, A. E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton.

Mather, J. A. 1991a. Foraging, feeding and prey remains in middens of juvenile *Octopus vulgaris* (Mollusca: Cephalopoda). *Journal of Zoology, London* **224:** 27–39.

Mather, J. A. 1991b. Navigation by spatial memory and use of visual landmarks in octopuses. *Journal of Comparative Physiology A* **168:** 491–497.

Mather, J. A. 1995. Cognition in cephalopods. *Advances in the Study of Behavior* **24:** 317–353.

Mather, J. A. 2008. Cephalopod consciousness: Behavioural evidence. *Consciousness and Cognition* **17:** 37–48.

Mather, J. A. 2011. Why are *Octopus cyanea* Gray in Hawaii specializing in crabs as prey? *Vie et Milieu* **61:** 181–184.

Mather, J. A. and R. C. Anderson. 1993. Personalities of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology* **107:** 336–340.

Mather, J. A., T. S. Leite, and A. T. Batista. In press. Individual prey choices of octopuses: Why are they generalist or specialist? *Current Zoology*.

Mather, J. A. and R. K. O'Dor. 1991. Foraging strategies and predation risk shape the natural history of juvenile *Octopus vulgaris*. Bulletin of Marine Science **49:** 256–269.

Mather, J. A., S. Resler, and J. Cosgrove. 1985. Activity and movement patterns of *Octopus dofleini*. *Marine Behaviour and Physiology* **11:** 301–314.

McQuaid, C. D. 1994. Feeding behaviour and selection of bivalve prey by *Octopus vulgaris* Cuvier. *Journal of Experimental Marine Biology and Ecology* **177:** 187–202.

Onthank, K. L. and D. L. Cowles. 2011. Prey selection in *Octopus rubescens*: Possible roles of energy budgeting and prey nutritional composition. *Marine Biology* **158:** 2795–2804.

Piatkowski, U., G. Pierce, and M. Morais de Cunha. 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: An overview. *Fisheries Research* **52:** 5–10.

Pilot, M., M. E. Dahlheim, and A. R. Hoelzel. 2010. Social cohesion among kin, gene flow without dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*). *Journal of Evolutionary Biology* **23:** 20–31.

Pohle, G., K. Iken, K. R. Clarke, T. Trott, B. Konar, J. J. Cruz-Motta, M. Wong, L. Benedetti-Cecchi, A. Mead, P. Miloslavich, N. Mieszkowska, R. Milne, L. Tamburello, A. Knowlton, E. Kimani, and Y. Shirayama. 2011. Aspects of benthic Decapod diversity and distribution from rocky nearshore habitat at geographically widely dispersed sites. *PloS One* **6:** e18606.

Prescott, J. H. 1962. Octopus, alive. *Drum and Croaker*: 5–8.

Rees, W. J. and J. R. Lumby. 1954. The abundance of octopus in the English channel. *Journal of the Marine Biological Association of the United Kingdom* **33:** 515–536.

Rigby, R. P. and Y. Sakurai. 2004. Temperature and feeding related to growth efficiency of immature octopuses *Enteroctopus dofleini*. *Suisanzoshoku* **52:** 29–36.

Rigby, P. R. and Y. Sakurai. 2005. Multidimensional tracking of Giant Pacific Octopus in northern Japan reveals unexpected foraging behavior. *Marine Technology Society Journal* **39:** 64–67.

Robinson, S. and E. Hartwick. 1986. Analysis of growth based on tag-recapture of the giant Pacific octopus *Octopus dofleini martini*. *Journal of Zoology. Series A* **209:** 559–572.

Roper, C. F. E. and F. G. Hochberg. 1988. Behavior and systematics of cephalopods from Lizard Island, Australia, based on color and body patterns. *Malacologia* **29:** 153–193.

Salomon, A. K., N. M. Tanape Sr., and H. P. Huntington. 2007. Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecological Applications* **17:** 1752–1770.

Scheel, D. 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. *Marine Ecology* **23:** 185–206.

Scheel, D. and L. Bisson. 2012. Movement patterns of giant Pacific octopuses, *Enteroctopus dofleini* (Wülker, 1910). *Journal of Experimental Marine Biology and Ecology* **416–417:** 21–31.

Scheel, D., A. Lauster, and T. L. S. Vincent. 2007. Habitat ecology of *Enteroctopus dofleini* from middens and live prey surveys in Prince William Sound, AK. *In*: N. H. Landman, ed., *Cephalopods Present and Past: New Insights and Fresh Perspectives*. Springer. Pp. 434–458.

Scheel, D. and C. Packer. 1991. Group hunting behavior of lions: A search for cooperation. *Animal Behaviour* **41:** 697–709.

Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2:** 369–404.

Sinn, D. L., N. A. Moltschaniwskyj, E. Wapstra, and S. R. X. Dall. 2010. Are behavioral syndromes invariant? Spatiotemporal variation in shy/bold behavior in squid. *Behavioral Ecology and Sociobiology* **64:** 693–702.

Smith, C. D. 2003. Diet of *Octopus vulgaris* in False Bay, South Africa. *Marine Biology* **143:** 1127–1133.

Stander, P. E. 1992. Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology* **29:** 445–454.

Stephens, D. and E. Charnov. 1982. Optimal Foraging: Some simple stochastic models. *Behavioral Ecology and Sociobiology* **10:** 251–263.

Stephens, D. and J. Krebs. 1986. *Foraging theory*. Monographs in behavior and ecology. Princeton Academic Press, Princeton.

Travis, J. 2012. No omnivore's dilemma for Alaskan hunter-gatherers. *Science* **335:** 898.

Trowbridge, C. D. 1991. Diet specialization limits herbivorous sea slug's capacity to switch among food species. *Ecology* **72:** 1880–1888.

Vafiadis, P. 1998. Intertidal sighting and behaviour of *Octopus maorum* Hutton 1880. *The Victorian Naturalist* **115:** 100–104.

West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (= *Thais*) *emarginata*. *Ecology* **67:** 798–809.

Vincent, T. L. S., D. Scheel, and K. R. Hough. 1998. Some aspects of diet and foraging behavior of *Octopus dofleini* (Wulker, 1910) in its northernmost range. *Marine Ecology* **19:** 13–29.

Woo, K. J., K. H. Elliott, M. Davidson, A. J. Gaston, and G. K. Davoren. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology* **77:** 1082–1091.

Yarnall, J. L. 1969. Aspects of the behaviour of *Octopus cyanea* Gray. *Animal Behaviour* **17:** 747–754.

Yeakel, J. D., B. D. Patterson, K. Fox-Dobbs, M. M. Okumura, T. E. Cerling, J. W. Moore, P. L. Koch, and N. J. Dominy. 2009. Cooperation and individuality among man-eating lions. *Proceedings of the National Academy of Sciences* **106:** 19040–19043.

**Submitted:** January 13, 2012; **accepted:** April 9, 2012;
**final revisions received:** 24 May 2012