Errata: Hapalogaster mertensii was incorrectly identified as Acantholithodes hispidus in this paper. In addition, in Fig. 5 caption reference should be to Fig. 4 not Fig. 3.

P.S.Z.N.: Marine Ecology, 19 (1): 13–29 (1998)
© 1998 Blackwell Wissenschafts-Verlag, Berlin
ISSN 0173-9565

Accepted: October 9, 1997

Some Aspects of Diet and Foraging Behavior of *Octopus dofleini* (Wülker, 1910) in its Northernmost Range

T. L. S. Vincent*, D. Scheel & K. R. Hough

Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574, USA.

With 7 figures and 2 tables

Key words: *Octopus dofleini*, cephalopod, diet, foraging behavior, Alaska.

Abstract. Diet and foraging behavior of *Octopus dofleini* in Prince William Sound and Port Graham, Alaska, were studied from collections of den litter, measurements of octopuses and estimates of live prey abundance. Based on 193 den collections from depths of −31 to +1.3 m, a diet of hard-bodied prey could be identified. The five most common litter species made up 80% of the litter remains, with nearly 30 species of various taxa making up the rest. The proportions of major hard-bodied prey species in each litter pile significantly differed with depth of den, associated substrata, presence of cobble and geographical location but not with the presence of boulders or outcrop, the density of kelp or season of litter collection. Octopus weight was not significantly correlated with the size of prey remains although *O. dofleini* may take a wide range of prey sizes once it reaches 2.5 kg. *O. dofleini* was more likely to be found at sites with crabs, although no litter species was significantly preferred over its estimated abundance, and one species was significantly avoided. These results suggest that *O. dofleini* includes suitable bivalve and crab species in its diet in relation to live abundance, while at the same time exercising an element of selectivity, as some species were actively avoided. Comparison of litter remains from the northern-most range of *O. dofleini* with those published for British Columbia show that diet breadth was similar, but the identity of major hard-bodied prey species was very different for Alaskan octopuses.

Problem

Octopus dofleini resides in Pacific coastal waters from southern California, north along the coastline of the Pacific Northwestern Americas, across the Aleutians and south to Japan (Hartwick, 1983). The diet and foraging behavior of this octopus have been sporadically documented in English language literature. A review of Japanese literature from the 1960s has given some stomach content information from octopuses collected in fishing pots (Mottet, 1975). Field studies conducted on Vancouver Island, British Columbia, in the late 1970s – early 1980s (Hartwick *et al.*, 1981; Mather *et al.*, 1985; Robinson & Hartwick, 1986; Cosgrove, 1987)

*Address for correspondence: Biology Department, St. Lawrence University, Canton, NY 13617, USA. E mail: tvin@music.stlawu.edu

U. S. Copyright Clearance Center Code Statement: 0173-9565/98/1901-0013$14.00/0

have also addressed diet (based on litter piles) and, to a lesser extent, foraging behavior (based on sonar and tagging studies). However, the diet and foraging behavior of this octopus have not been studied in other areas of its range. The northern-most extreme for *O. dofleini* (Gulf of Alaska) is of special interest for several reasons. First, diet may change if the availability of prey species changes (c.f., HARTWICK *et al.*, 1981 and COSGROVE, 1987). Second, colder water temperatures and differences in day-length may change feeding rates and feeding behavior, which, in turn, may influence the growth rates of octopuses (ROBINSON & HARTWICK, 1986; SANCHEZ & OBARTI 1993) and, perhaps, their impact as a near-shore predator.

A review of Japanese literature from the 1960s has documented *O. dofleini* stomach contents composed of fish, shrimp and crab, including occasional sea cucumber, tunicate, sea star, squid and octopus (MOTTET, 1975). Vancouver Island studies have shown that *O. dofleini* feeds primarily on bivalves and crabs, although the prominence of soft-bodied prey in the diet could not be assessed. As in the Japanese studies, *O. dofleini* was occasionally found to take a wide variety of other species including echinoderms, limpets, octopuses and even a sea gull (HARTWICK *et al.*, 1981; COSGROVE, 1987). Based on these studies, diet breadth appears wide and indicates that *O. dofleini* takes items opportunistically. However, it is unclear whether *O. dofleini* forages primarily on abundant prey and moves when food supply becomes low (MATHER *et al.*, 1985) or whether it actively seeks preferred prey (HARTWICK *et al.*, 1981). This question has not been addressed directly, because no study has systematically recorded the availability of live prey species near octopus dens. Resolving the generality of *O. dofleini*'s diet will provide a first step to understanding the nature and importance of *O. dofleini* as a predator in near-shore communities (MURDOCH, 1969).

We present data on diet and some aspects of foraging behavior based on litter remains of *O. dofleini* in a previously undocumented area of Prince William Sound and Lower Cook Inlet, Alaska. This study addresses breadth of diet, changes in diet, prey preference, consumption rates and growth of *O. dofleini* in the northern-most part of its range.

Material and Methods

1. Study sites and sampling

Surveys for *O. dofleini* in Cook Inlet (59°21′N, 151°49′W) and Prince William Sound [Green Is. (60°14′N, 147°14′W), Montague Is. (60°16′N, 147°26′W), Windy Bay (60°34′N, 145°59′W), and west PWS (60°05′N, 148° ± 10′W)] were conducted on 32 near-shore dives and 51 intertidal transects between May 31 and December 11, 1996. Near-shore SCUBA diving and intertidal beach surveys were conducted on the same dates during low tide series below −0.6 m mean lower low water (MLLW; May/June, June/July, July/August, September, December). Some intertidal sites at Green and Montague Islands were visited repeatedly over this period. Extreme tidal heights in Prince William Sound were 4.5 m above MLLW to −1.1 m, for a tide range of 5.6 m. Tide fluctuations were more extreme in Cook Inlet; at Port Graham, the tidal extremes were from 6.5 m MLLW to −1.7 m MLLW, a range of 8.2 m. Distances between survey transects varied between 10 m and 3° longitude/latitude.

Intertidal beach and near-shore SCUBA surveys were conducted in measured linear transects designed to be 100 m long and 10 m wide, but actual length and width varied depending on natural features at each site. Two (intertidal) or three (diving) observers moving abreast of one another searched each transect for octopus dens. In the intertidal, we followed the zero depth contour (usually for 100 m) and searched the area (usually about 10 m wide) between the upper *Fucus* zone (about +1.2 m MLLW) to the low water line (between −0.66 and −1.1 m MLLW). On dives, we followed a particular depth contour, and the width of the transect was determined by water visibility (using a SECCHI disk). We recorded substrata, percent kelp cover, presence or absence of boulders, outcrop and cobble on each transect. Substratum was defined by the dominant underlying matrix and was recorded as 'soft' if gravel (mm-cm) or sand, and 'hard' if broken rubble (jagged rocks cm-m), cobble (rounded rocks cm-m), bedrock (unbroken rock) or outcrop (rock projection). Suspected dens were investigated by sight and using a flexible probe (green alder branch or a hose). If the den was suspected to be occupied, we extracted the octopus by injecting a small amount of dilute bleach, a mild irritant. Octopuses were weighed, measured and examined to determine their sex and checked for scars. Intertidal den depths were estimated from tide heights and time; depths of subtidal dens were recorded using a submersible pressure gauge. Occupied dens were marked to aid relocation. If den litter was present, all items were collected and identity of each species was recorded. We also identified the 'minimum number of individuals' that made up each litter pile. For example, a litter pile with three *Cancer oregonensis* carapaces, two left chelipeds of *C. oregonensis* and five right chelipeds of *C. oregonensis* would indicate that at least 5 individuals of *C. oregonensis* were consumed. Measurements of carapace or valve length and width were recorded for 33 litter collections of crab and bivalve species at dens where octopuses were extracted and weighed.

Octopus prey species were sampled by two different methods. In the first case, on intertidal searches only, sampling for octopus prey species was conducted concurrently with octopus den searches along 100 m transects at eight intertidal sites between 30 June and 1 August 1996. Transects were laid out on a meter tape lying parallel to shore near zero MLLW. Five 0.25 m^2 plots were located inland at 20 m intervals and five 0.25 m^2 plots were located towards the water at 20 m intervals. Each plot was located a random distance from the centre of the transect within a 10 m band. Each plot was carefully examined (i.e., moveable rocks were overturned, ground surface probed) and all epifaunal species were recorded.

In the second case, on both intertidal and subtidal searches, we visually estimated the densities of prey species as we searched for octopuses along transects where we also collected habitat data (see above). Results are given for 6 subtidal sites (between −35 m and −4.5 m depths) and 12 intertidal sites (above −1.5 m depth) where octopus dens were found. Live densities were recorded as abundant (at least 11 individuals per 100 m transect), occasional (at least 2 individuals per 100 m transect) and rare (at least 1 individual per 100 m transect). We estimated live prey categorically rather than numerically as a matter of efficiency; given time of air supply (on dives) and the rising tides (in the intertidal), it was not possible to provide more detail on prey abundance while simultaneously searching a transect for octopuses.

2. Statistical analyses

A Poisson regression (Statistix 3.1) was used to determine linear relationships between the number of litter individuals at a den versus six depth categories. Depth categories were determined by examining the distribution of dens by depth and looking for obvious groupings. These categories were (1) dens at $\leqslant -1000$ cm MLLW; (2) −999 to −450 cm MLLW; (3) −449 to −55 cm MLLW; (4) −54 to 0 cm MLLW; (5) +1 to +50 cm MLLW; and (6) > +50 cm MLLW. Dens in depth categories 3–5 (intertidal) had less distinctive groupings and divisions were made at a more arbitrary level. Normal regressions (REG procedure of SAS 6.03) were used to determine linear relationships between octopus wet weight and length, width, or length × width of prey remains.

The proportion of each species in a litter pile (y) was calculated for each den. This statistic was transformed as $z = \arcsin(y)^{0.5}$ to stabilize variance. A regression (REG procedure of SAS 6.03) of the "z's" of the five most common species was calculated versus depth of den (continuous variable). In addition, the effects of seven habitat variables on the "z's" of the five most common species were examined in multivariate analyses of co-variance (GLM procedure of SAS 6.03), with depth of den as a continuous co-variate. The seven variables were substratum type (soft, hard), percent cover of kelp (>50%, <50%), boulders (present, absent), outcrop (present, absent), cobble (present, absent), geography (Port Graham, west Prince William Sound, Green Is., Montague Is., Windy Bay) and season of litter collection (spring: March 21–June 21, summer: June 22–December 21). Overall significance of each variable was determined using WILKS' Lambda. Least square means were calculated from univariate analyses of variance. Significant differences between LS means were determined from t-values (GLM procedure of SAS 6.03). All relationships were deemed significant if $P < 0.05$.

Comparisons of litter and live prey abundances were used to determine preference or avoidance of species found at a particular site. The number of individuals of each litter species was summed over all transects at a site. Abundance categories were used to estimate live species densities on each transect. Our estimates of prey preference were kept conservative (less likely to reject the null hypothesis of no preference or avoidance). If a density estimate was not available for a particular litter species collected at a site, this species was excluded from analysis. This strategy eliminated possible sources of error from overlooking rare species in our searches, but also omitted possible cases of strong selection by octopuses. To convert recorded density categories to a numerical form for analysis, densities for each species were calculated by taking the minimum number per transect (11, 2 or 1). Numerical estimates were summed over all transects at a site. For each species, the difference between its proportion of all litter at a site and its proportion of all live prey at a site was calculated. WILCOXON signed ranks tests at $\alpha = 0.05$ were used to test whether calculated differences between the proportions were significantly more negative or more positive than zero (1-sided test for each species, depending on direction of difference). Significant differences suggest preference (positive difference) or avoidance (negative difference) of particular species.

Results

1. Litter remains

Based on 193 den middens from depths of −31 to +1.3 m at Port Graham and Prince William Sound, *Octopus dofleini* consumed mostly crabs (77% of remains; n = 1059 items), with bivalves a distant second choice (19% of remains). Table 1 shows that the top five species, *Cancer oregonensis*, *Telmessus cheiragonus*, *Lophopanopeus bellus*, *Pugettia gracilis* and *Chlamys* spp. (scallops *C. hastata* and *C. rubida*), made up 80% of the total number of individuals found in the litter. The rest of the remains consisted of a large assortment of other crabs, bivales, chitons, limpets, barnacles, gastropods and sea urchins and each contributed less than 5% to the total. Fresh shrimp and octopus parts were also discovered, though remains of such soft-bodied prey were unlikely to be found by searches of den litter. Thus, the importance of soft-bodied prey in the diet is likely under-represented by this sample.

Only 6 of 193 den middens (4 of 168 intertidal, 2 of 25 subtidal) did not contain at least one individual of the top 5 prey species listed in Table 1, and 123 of these collections (107 of 168 intertidal and 16 of 25 subtidal) contained no other species but these. For these reasons, and because of limitations in sample numbers for the other prey species, the following analyses are restricted to the top five species in Table 1. These 5 taxa are hereafter referred to as the 'major hard-bodied prey species'.

Figure 1 shows the number of individuals of each major hard-bodied prey species as a proportion of all individuals collected in a particular depth category, allowing comparisons of midden composition across depth categories by eliminating den midden sampling bias. This figure illustrates a change in midden composition with depth of den (n = 1048 individuals from 191 midden collections; 2 den midden depths not available). Note that a higher proportion of minor prey species were included at shallower depths. In addition, shallower depth categories had significantly fewer individuals per den midden (Fig. 2; Poisson regression: df = 189,

Table 1. The diet of *Octopus dofleini* based on collection of litter at dens. The number and percent of the total minimum number of individuals (1059) found in 193 litter collections are shown for each prey species. Taxonomic names are taken from FOSTER (1991; bivalves) and KOZLOFF (1987).

taxon	species	number	% total
Decapoda	*Cancer oregonensis* (DANA, 1852)	295	27.86
Decapoda	*Telmessus cheiragonus* (TELESIUS, 1815)	214	20.21
Decapoda	*Lophopanopeus bellus* (STIMPSON, 1860)	137	12.94
Decapoda	*Pugettia gracilis* DANA, 1851	110	10.39
Bivalvia	*Chlamys* spp. (*C. hastata*, *C. rubida* combined)	87	8.22
Bivalvia	*Protothaca staminea* (CONRAD, 1837)	36	3.49
Bivalvia	*Pododesmus macroschisma* (DESHAYES, 1839)	31	2.93
Bivalvia	*Macoma inquinata* (DESHAYES, 1855)	27	2.55
Decapoda	*Cancer productus* RANDALL, 1839	22	2.08
Decapoda	*Acantholithodes hispidus* (STIMPSON, 1860)	10	0.94
Bivalvia	*Saxidomus giganteus* DESHAYES, 1839	10	0.94
Polyplacophora	*Tonicella lineata* (WOOD, 1815)	10	0.94
Decapoda	*Cryptolithodes sitchensis* BRANDT, 1853	7	0.66
Decapoda	*Cancer magister* DANA, 1852	6	0.57
Bivalvia	*Mytilus edulis* LINNAEUS, 1758	6	0.57
Polyplacophora	unknown chiton	6	0.57
Gastropoda	*Acmaea* sp.	5	0.47
Gastropoda	*Littorina sitkana* PHILIPPI, 1845	5	0.47
Cirripedia	*Semibalanus cariosus* (PALLAS, 1788)	5	0.47
Decapoda	unknown crab	5	0.47
Bivalvia	unknown	3	0.28
Echinoidea	unknown urchin	3	0.28
Decapoda	*Cancer gracilis* DANA, 1852	2	0.19
Bivalvia	*Humilaria kennerleyi* (REEVE, 1863)	2	0.19
Bivalvia	*Macoma nasuta* (CONRAD, 1837)	2	0.19
Decapoda	*Phyllolithodes papillosus* BRANDT, 1849	2	0.19
Gastropoda	unknown	2	0.19
Decapoda	unknown shrimp	2	0.19
Decapoda	*Hyas lyratus* DANA, 1851	1	0.09
Cephalopoda	*Octopus dofleini* (WÜLKER, 1910)	1	0.09
Decapoda	*Oregonia gracilis* DANA, 1851	1	0.09
Echinoidea	*Strongylocentrotus droebachiensis* (MÜLLER 1776)	1	0.09
Bivalvia	*Tellina carpenteri* DALL, 1900	1	0.09
Gastropoda	*Trichotropis cancellata* HINDS, 1849	1	0.09

$t = -3.00$, $P < 0.0031$). Regressions of the number of individuals of each major hard-bodied prey species as a proportion of all individuals collected at a particular den versus actual depth of den were statistically significant for some species ($n = 191$ den collections). *Cancer oregonensis* and *Telmessus cheiragonus* made up a greater proportion of a litter pile at shallower depths (respectively, $df = 1$, $F = 5.16$, $P < 0.02$, $r^2 = 0.03$ and $df = 1$, $F = 4.51$, $P < 0.04$, $r^2 = 0.02$). *Chlamys* spp. made up a greater proportion at deeper depths ($df = 1$, $F = 186.91$, $P < 0.0001$, $r^2 = 0.50$). There were no significant relationships with depth for *Lophopanopeus bellus* ($df = 1$, $F = 1.59$) and *Pugettia gracilis* ($df = 1$, $F = 0.78$).

To look for changes in diet with den habitat, geographical location and season of litter collection we analyzed the number of individuals of each major hard-

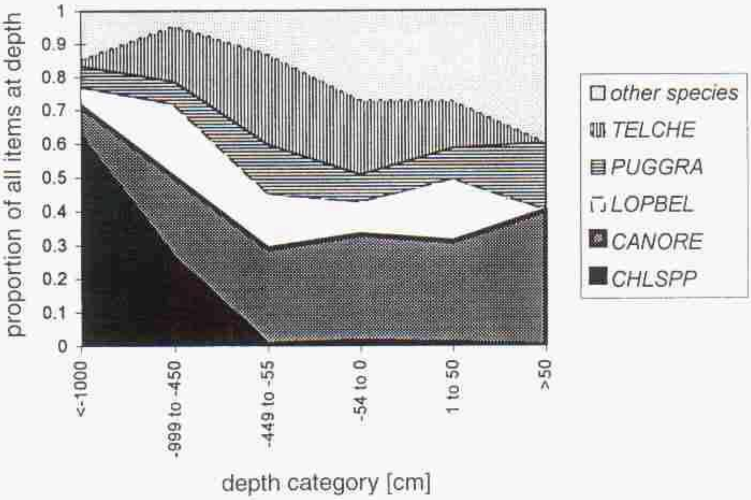


Fig. 1. Proportions of the five most common midden species in a particular depth category are shown versus depth. Proportions were calculated from the sum of all individuals found in the litter piles at dens within each depth category (see Fig. 2 for number of den collections per depth category). The five most common species over all litter piles were *Cancer oregonensis* (CANORE), *Telmessus cheiragonus* (TELCHE), *Lophopanopeus bellus* (LOPBEL), *Pugettia gracilis* (PUGGRA) and *Chlamys* spp. (CHLSPP) (Table 1). There were $n = 108$ litter items for dens at $\leqslant -1000$ cm MLLW, $n = 42$ for -999 to -450 cm MLLW, $n = 352$ for -449 to -55 cm MLLW, $n = 420$ for -54 to 0 cm MLLW, $n = 116$ for 1 to $+50$ cm MLLW, and $n = 10$ for $> +50$ cm MLLW. Note: two litter collections had no depth data and were not included in this figure ($n = 11$ items).

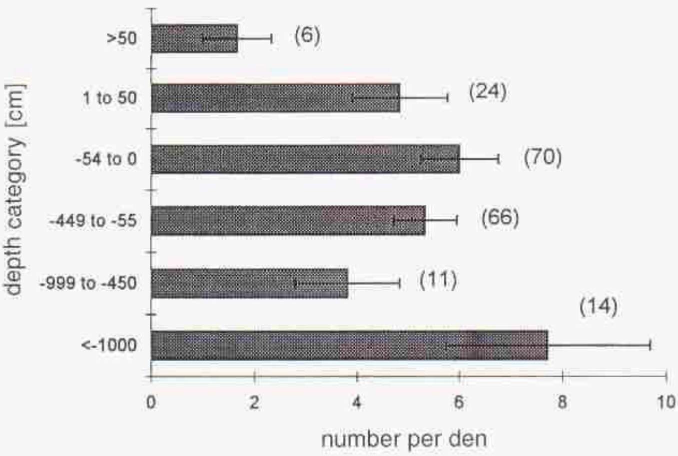


Fig. 2. The mean minimum number of individuals in the litter per den are shown for each depth category. The number of den-litter collections for each depth are shown in parentheses and standard errors (± 1) are given for the mean number of items per den collection. Note: two litter collections had no depth data and were not included in this figure.

bodied prey species in proportion to all individuals collected at a particular den versus all measured characteristics (Table 2; $n = 186$ den middens; some data were missing for 7 midden samples and these were not included). Overall, there were significant effects of den depth, substratum, presence of cobble and geography but

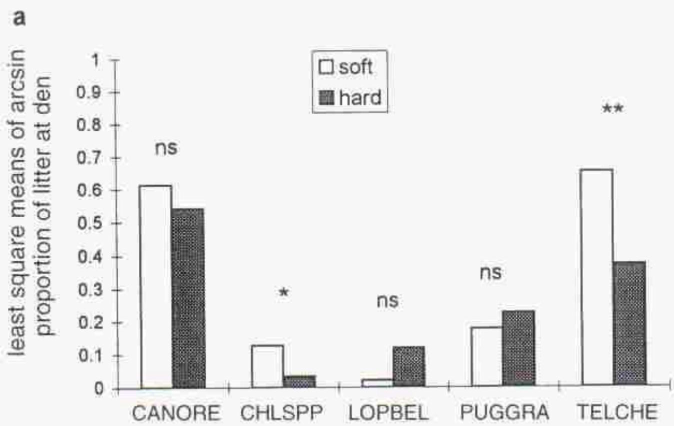
Table 2. The arcsin of the number of individuals of each major hard-bodied prey species in proportion to all individuals collected at a particular den was analyzed with respect to habitat characteristics associated with that den (n = 186 litter collections). Multivariate analyses of co-variance for all five major hard-bodied prey species are presented, followed by unvariate analyses of each species.

analysis	source	df	F	P<	significance
MANCOVA	substratum	5,170	4.48	0.0007***	
	boulders	5,170	1.51	0.1896	
	outcrop	5,170	1.16	0.3299	
	cobble	5,170	2.49	0.0331*	
	kelp	5,170	1.75	0.1257	
	geography	20,565	3.33	0.0001***	
	season	5,170	1.78	0.1201	
	depth	5,170	17.99	0.0001***	
Cancer oregonensis	model	11	3.03	0.0010**	$r^2 = 0.16$
	substratum	1	0.51	0.4781	
	boulders	1	2.64	0.1060	
	outcrop	1	0.14	0.7086	
	cobble	1	5.59	0.0192*	
	kelp	1	2.17	0.1425	
	geography	4	3.42	0.0101*	
	season	1	2.10	0.1487	
	depth	1	5.24	0.0233*	
Chlamys spp.	model	11	17.16	0.0001***	$r^2 = 0.52$
	substratum	1	5.03	0.0261*	
	boulders	1	0.20	0.6574	
	outcrop	1	0.58	0.4459	
	cobble	1	1.81	0.1797	
	kelp	1	0.34	0.5632	
	geography	4	0.50	0.7342	
	season	1	0.37	0.5451	
	depth	1	88.65	0.0001***	
Lophopanopeus bellus	model	11	3.68	0.0001***	$r^2 = 0.19$
	substratum	1	2.17	0.1425	
	boulders	1	5.72	0.0178*	
	outcrop	1	0.78	0.3785	
	cobble	1	2.80	0.0960	
	kelp	1	5.84	0.0167*	
	geography	4	5.43	0.0004***	
	season	1	1.62	0.2048	
	depth	1	2.48	0.1168	
Pugettia gracilis	model	11	2.39	0.0089**	$r^2 = 0.13$
	substratum	1	0.47	0.4928	
	boulders	1	0.54	0.4622	
	outcrop	1	1.69	0.1950	
	cobble	1	0.67	0.4154	
	kelp	1	0.21	0.6458	
	geography	4	4.78	0.0011**	
	season	1	0.04	0.8405	
	depth	1	0.05	0.8294	
Telmessus cheiragonus	model	11	5.88	0.0001***	$r^2 = 0.27$
	substratum	1	9.13	0.0029**	
	boulders	1	0.57	0.4503	
	outcrop	1	0.27	0.6030	
	cobble	1	0.36	0.5468	
	kelp	1	1.29	0.2575	
	geography	4	4.73	0.0012**	
	season	1	7.34	0.0074**	
	depth	1	1.19	0.2762	

not presence of boulders or outcrop, density of kelp, or season of litter collection (Table 2, MANCOVA). Dens at sites with soft substrata (n = 103 out of 186 den middens) had significantly greater proportions of *Chlamys* spp. and *Telmessus cheiragonus* (Table 2, univariate analyses for these two species; see also Fig. 3). Dens near cobble (n = 115) had more *Cancer oregonensis* (Table 2; Fig. 3). Geographical location had a significant effect on litter proportions of all species but *Chlamys* spp. (Table 2).

2. Indications of foraging behavior

Sampling for live octopus prey species was conducted along 100 m transects at eight intertidal sites between 30 June and 1 August 1996 (n = 80 0.25 m^2 plots).



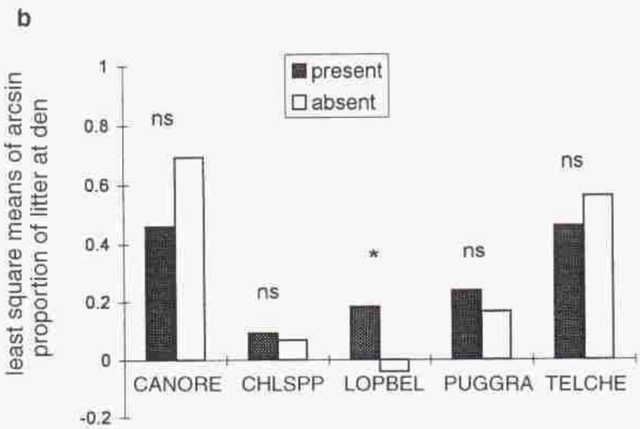
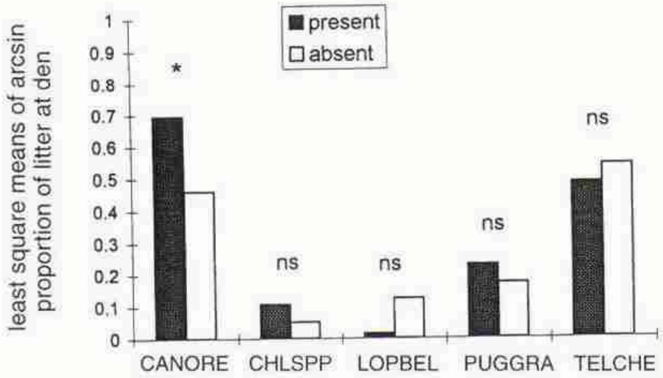
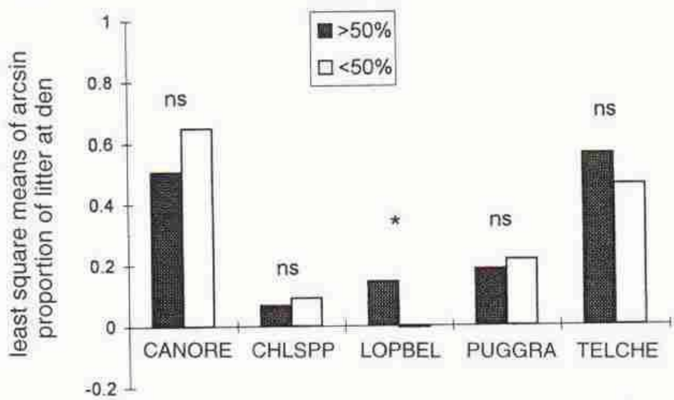


Fig. 3. Least square means for (a) substratum, (b) boulders, (c) cobble, (d) kelp and (e) season are shown for *Cancer oregonensis* (CANORE), *Chlamys* spp. (CHLSPP), *Lophopanopeus bellus* (LOPBEL), *Pugettia gracilis* (PUGGRA) and *Telmessus cheiragonus* (TELCHE). Least square means are derived from univariate analyses in Table 2 and significant differences are shown for P < 0.05 (*) and P < 0.01 (**).

c



d



e

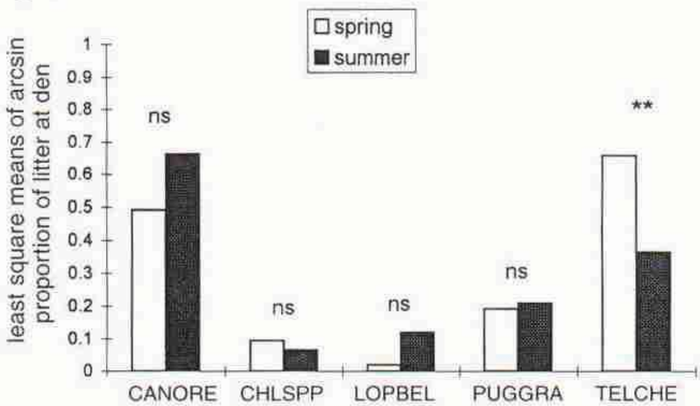


Fig. 3. continued.

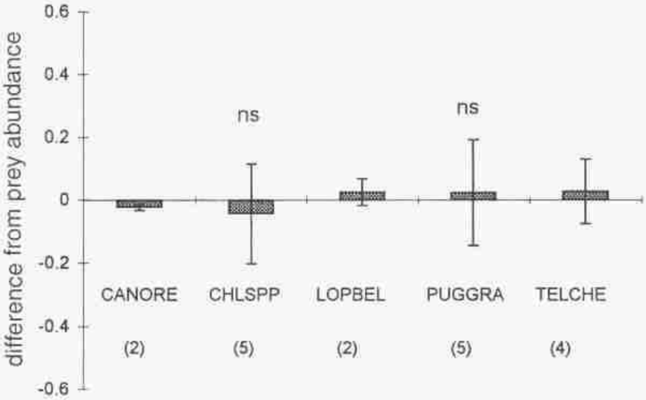


Fig. 4. Subtidal prey preference. At 6 subtidal sites with octopus dens, the number of individuals of each species was recorded for all litter collections and live densities of litter species were estimated for each site (repeat visits to sites not included). Overall, only five species were considered: *Cancer oregonensis* (CANORE), *Telmessus cheiragonus* (TELCHE), *Lophopanopeus bellus* (LOPBEL), *Pugettia gracilis* (PUGGRA) and *Chlamys* spp. (CHLSPP). The proportions of these five species were calculated for each site. For each species, the difference between its proportion of all litter at a site and its proportion of all prey species at a site was calculated. The average and standard error of this difference are shown for each species and the number of sites where this species was present (live) is shown in parentheses.

Major hard-bodied prey species were present at only four of these sites. A chi-square goodness of fit test for presence of live crabs at a site versus number of octopus dens at a site was significant ($\chi^2 = 11.84$, df = 1, $P < 0.001$). When all samples were considered, potential prey taxa (c.f., Table 1) were ranked in abundance as follows: 30 chitons, 22 crabs, 3 limpets, 3 gastropods, 3 sea urchins, 3 shrimp. Considering crabs only, a total of 10 *Pugettia gracilis*, 5 *Acantholithodes hispidus*, 5 *Telmessus cheiragonus* and 1 *Cancer oregonensis* were found.

Live hard-body prey densities were also estimated at 6 subtidal and 12 intertidal sites with octopus dens. Weighted percentages of the prey community were calculated for each prey species at a site and compared with the percentage of prey represented by all den litter at a site (see Methods). Figure 4 indicates the difference between representation in litter and representation as live prey for subtidal-sites. Based on WILCOXON signed ranks tests at $\alpha = 0.05$, there were no significant differences between *Chlamys* spp. or *Pugettia gracilis* live and litter percentages. There were not enough site replicates for other species to test for significance. Figure 5 indicates the difference between representation in litter and representation as live prey for intertidal sites. Based on WILCOXON signed ranks tests at $\alpha = 0.05$, *Acantholithodes hispidus* was significantly avoided by octopuses. There were no significant differences between *Pugettia gracilis* or *Telmessus cheiragonus* live and litter percentages. There were not enough site replicates for other species to test for significance.

We were able to look for a relationship between octopus wet weight and prey size from nineteen den collections. Data were available for both octopus weight and average carapace width of *Telmessus cheiragonus* remains per den (there were too few remains for analyses of other species where octopus weight was known). Figure 6 shows the relationship between octopus wet weight and average carapace

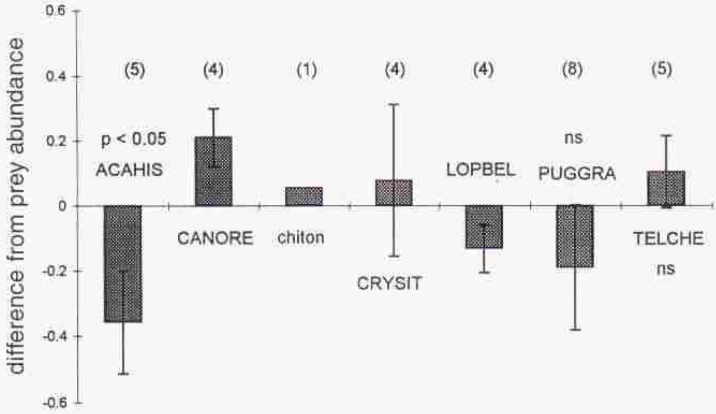


Fig. 5. Intertidal prey preference. At 12 intertidal sites with octopus dens, the number of individuals of each species was recorded for all litter collections and live densities of litter species were estimated for each site (repeat visits to sites not included). Live densities were recorded as in Fig. 3. If a density estimate was not available for a particular litter species collected at a site, this species was excluded from analysis. Overall, only seven species were considered: *Acantholithodes hispidus* (ACAHIS), *Cancer oregonensis* (CANORE), undetermined chiton, *Cryptolithodes sitchensis* (CRYSIT), *Telmessus cheiragonus* (TELCHE), *Lophopanopeus bellus* (LOPBEL) and *Pugettia gracilis* (PUGGRA). The average standard error of the difference between proportions of live and litter are shown for each species and the number of sites where this species was present (live) is shown in parentheses.

Fig. 4

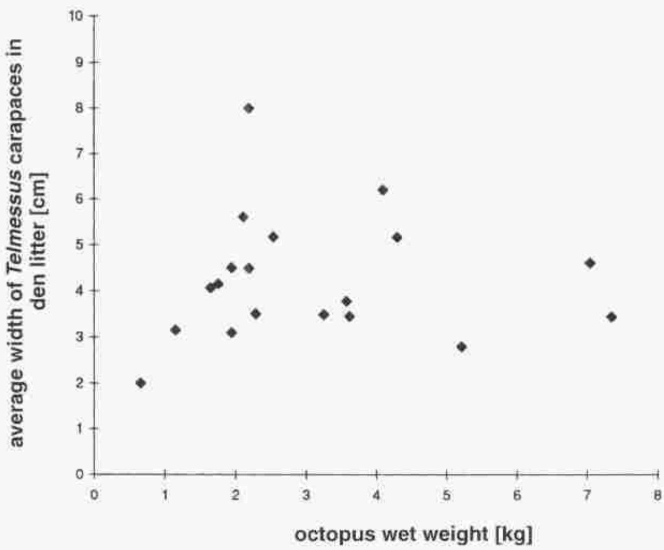


Fig. 6. Octopus weight versus prey size. The wet weights of 19 *O. dofleini* are shown versus the average carapace width of *Telmessus cheiragonus* crabs found in the midden pile of that particular octopus.

width of *T. cheiragonus* found at a den. There was no significant relationship between octopus weight and carapace width (df = 1, F = 0.02; Fig. 6).

Data from eleven intertidal dens were available where all litter had been removed within the previous 3 days. Fifteen recollections allowed us to calculate daily consumption rates of hard-bodied prey at the dens of intertidal octopuses. On average, an intertidal octopus consumed 3.1 prey individuals per day, with a range

Fig. 7. Number of individual prey consumed at a den per day. The average and standard error of the number of prey items found in the litter per day at eleven intertidal dens are shown. Data represent fifteen recollections where litter had been removed within the previous three days.

of 0.5 to 8.5 individuals. Figure 7 shows the average number of items consumed daily in broad prey classifications. Note that soft-bodied prey items and prey consumed away from the den could not be recorded; thus, daily consumption rates are minimum estimates. In addition, we assumed that all of these items were equally likely to remain in the litter pile between den visits (2 1-day intervals, 9 2-day intervals, 4 3-day intervals). MATHER (1991) found that the lifespan of prey items in the litter piles of *Octopus vulgaris* could vary depending on prey type. Crab parts were more likely to disappear in 2–3 days, bivalves and chitons were more likely to disappear in 8 days, and gastropods could disappear in 2–6 days (MATHER, 1991). Because crab parts are more likely to disappear first, Fig. 7 likely underestimates the importance of crabs in the diet versus bivalves, chitons and gastropods.

We obtained only one usable datum for calculating growth rates of *O. dofleini* from tagged-recaptured individuals. A tagged female octopus from Green Island weighed 2.12 kg on 1 August 1996 and was weighed again at 5.70 kg on 9 December 1996, a change of 3.58 kg in 130 days. ROBINSON & HARTWICK (1986) found that British Columbian *O. dofleini* growth rates fit a model of slow growth between January and June and a fast growth model between July and December. Based on their slow growth model, the Green Island octopus was calculated to be 4.24 kg by 9 December 1996 (actual weight 1.46 kg more than expected). Based on the fast growth model, the weight was calculated to be 8.98 kg (actual weight 3.28 kg less than expected). However, the daily growth rate expressed as a fraction of the mean weight during the observation period, 0.7 percent, was within the range of high growth calculated by HARTWICK *et al.* (1981; 0.5–1.8 percent).

Discussion

We were able to identify hard-bodied prey items consumed at the dens of *Octopus dofleini* in the northern-most part of its range. Although rates of litter retention at octopus dens may differ for hard-bodied prey species, and some prey items can be consumed away from the den (MATHER, 1991), a comparison of *O. dofleini* diet can be made with other studies that used similar techniques to ours. We found that nearly 70% of the litter remains of *O. dofleini* was composed of the crabs *Cancer oregonensis*, *Telmessus cheiragonus*, *Lophopanopeus bellus* and *Pugettia gracilis* (Table 1). The most common bivalves, *Chlamys* spp., made up 8% of the remains. The composition of this diet was strikingly different from that published for *O. dofleini* at Vancouver Island, British Columbia. HARTWICK *et al.* (1981) found 29% of the litter remains were composed of *Clinocardium nuttallii* (not found in Alaskan litter), 27% *Cancer* spp. (mostly *C. productus*; c.f. 2% in Alaskan litter) and 16% *Protothaca staminea* (c.f. 3%). COSGROVE (1987) reported 86% of the litter remains were composed of *Cancer productus* (c.f. 2%). *Telmessus cheiragonus*, which made up 20% of Alaskan litter, occurred as 0.24% of the remains in British Columbia. Dietary diversity (H′; MAGURRAN, 1988), which reflects breadth and evenness, can be calculated from diet lists in HARTWICK *et al.* (1981) and COSGROVE (1987). The diversity of the Alaskan diet ($H' = 2.23$; from Table 1) is similar to that in HARTWICK *et al.* (1981; $H' = 2.02$) but both of these are much greater than that in COSGROVE (1987; $H' = 0.69$). According to optimal foraging theory (HUGHES, 1980), diet breadth should reflect both environmental and competitive constraints. Not much is known about productivity and competition among these three sites since comparable measurements of prey and competitor abundance are lacking. However, it appears that although diet breadth is malleable, it probably does not change with general differences in productivity in relation to latitude between Vancouver Is. (49°) and south-central Alaskan (59–60°) sites. In addition, the growth of one octopus at Green Is., Prince William Sound, shows that growth rates between octopuses in Alaska and British Columbia may be similar (reflecting no latitude effect) or slightly less (reflecting some latitude effect), though this cannot be resolved with the data available.

Dietary differences between dens in different habitats within Prince William Sound and Port Graham (Table 2) reflected the general disparity in diets both between Alaska and British Columbia and within Vancouver Island itself (HARTWICK *et al.*, 1981 vs COSGROVE, 1987). We found differences in the composition of den litter depending on den depth, the softness of substratum near the den, the presence of cobble near the den, and whether the den was located at Port Graham, west Prince William Sound, Green Is., Montague Is., or Windy Bay. Deeper dens had more *Chlamys* spp. and less *Cancer oregonensis*. Dens at sites with soft substrata tended to have a greater proportion of *Chlamys* spp. and *Telmessus cheiragonus*. Dens near cobble tended to have more *Cancer oregonensis*. Geographical location had a significant effect on litter proportions of all species by *Chlamys* spp.

HARTWICK *et al.* (1981) ran a multiple regression of percent crabs in the litter versus den site, depth and date of litter collection. As with our results, den site proved to be a significant factor; in contrast to our results, however, depth was not. While the range of depths is not given for HARTWICK *et al.*'s (1981) analysis, that study was part of several done around Vancouver Island from 1977–1987 (HARTWICK, 1983 reviewed early work; also HARTWICK *et al.*, 1984 a,b; MATHER *et al.*, 1985; ROBINSON & HARTWICK, 1986; COSGROVE, 1987; HARTWICK *et al.*, 1988). This work primarily found dens at depths deeper than ours, which may explain why there were no depth effects. Analyses of prey vs substratum and other den habitat characteristics have not been conducted in previous studies of *O. dofleini*, although HARTWICK *et al.* (1981) inferred from the dominance of clams in the feeding litter that this octopus prefers to forage on soft substrata. However, there was no attempt to determine whether this was because of the proximity and abundance of clams versus crabs.

We found proportions of species in den litter collections at a site to be very similar to proportions of these species available at a site in both subtidal (Fig. 4) and intertidal (Fig. 5) areas. Live *Chlamys* spp., which were most abundant in den litter at greater depths, also occurred more abundantly at subtidal sites. Likewise, live *Cancer oregonensis*, more abundant in den litter at lesser depths, also occurred more abundantly at intertidal sites. The prominence of certain species in the litter in dens near soft substrata or cobble may also reflect the availability of prey species in those habitats. *Chlamys rubida* is associated with soft bottoms (although *Chlamys hastata* is not; BOURNE, 1987), and *Cancer oregonensis* is associated with structurally complex substrata (ORENSANZ & GALLUCCI, 1988).

These results indicate that *O. dofleini* is a generalist predator that varies its diet depending on prey abundance. In theory, generalist 'switching' predators, that switch to the most abundant prey, are likely to increase prey diversity (MURDOCH, 1969), reflecting a possible important role for *O. dofleini* in near-shore habitats. However, several factors, given below, may complicate this picture.

First, although *O. dofleini* may primarily consume abundant species, it does appear to exercise some discrimination between prey. Intertidal octopus dens were more likely to be found in habitats containing crabs. In addition, although both chitons and crabs were highly abundant across sites, crabs made up most of the litter, while chitons were rarely represented. HARTWICK *et al.* (1981) reported that octopuses fed *ad libitum* in almost all cases preferred fish over crabs, followed by soft-shelled clam and then other prey items. Based on foraging theory, we would expect this preference to be related to energy gain versus handling time (PULLIAM, 1974). HARTWICK *et al.* (1981) found two handling strategies of hard-bodied prey – pull open or drill – and that drilling was resorted to only after pulling was attempted. MCQUAID (1994) also reported two handling strategies in *O. vulgaris* – pull open or drill. Drilling was found to have a longer handling time and was energetically worthwhile only when prey held a larger energy content. We observed that *O. dofleini* tends to drill *Cancer oregonensis*, *Lophopanopeus bellus* and *Pugettia gracilis* far more than *Telmessus cheiragonus*, a much larger crab species with a thinner shell (DODGE & SCHEEL, unpublished). Thus, if energy content per gram is similar among crabs, *Telmessus* should be preferred over other crabs since it is both a larger species and is apparently opened without use of drilling (the more time-consuming technique). However, we could find no evidence of this in our study. Likewise, there was no reason to suspect that *Acantholithodes hispidus*, a soft-shelled crab (pers. obs.), should have been avoided by *O. dofleini* (Fig. 5) based on its size or presumed handling time. Yet, our data show strong avoidance of this crab that was widely available to intertidal octopuses, suggesting other factors may be important.

Second, size selectivity (as size reflects energy content per prey item) is predicted for optimally foraging predators, resulting in a positive relationship between predator and prey size within a species (HUGHES, 1980). We found no relationship between octopus wet weight and the width of *Telmessus* carapace remains, although Fig. 6 shows that a wide range of prey sizes can be taken once an octopus reaches 2.5 kg. HARTWICK *et al.* (1981), on the other hand, found a positive relationship between octopus weight and prey size. Octopus weights ranged from less than 1 kg to 27 kg. Octopuses in our study ranged from less than 1 kg to 9 kg. The HARTWICK *et al.* (1981, fig. 3) data appear to have a great deal of variance and the relationship would probably be obscured for octopuses under 9 kg.

Third, if absolute prey abundance is important (as abundance relates to encounter rates), predators should forage in productive habitats to maximize rate of gain (CHARNOV, 1976). Based on sonar-tracking, MATHER *et al.* (1985) reported that *O. dofleini* makes frequent short foraging trips. We also conducted a sonar-tracking study at our Alaskan sites (SCHEEL, unpublished) and found that octopuses stayed within a 150 m radius over 44 days, clearly foraging within this circumference. Telemetered octopuses moved between intertidal and subtidal sites easily, yet most octopuses from our study occurred in the intertidal (SCHEEL, unpublished). The prominence of octopuses at shallower depths is probably not related to increased food supply in the intertidal, since deeper dens had as many or more items of den litter (Fig. 2). However some caution should be applied to this interpretation, as no information is available on relative loss rates of various species from a litter pile (*Chlamys* spp. made up more of the litter at deeper dens) or on the potential variation of loss rates with depth. Mean consumption rates of 3 items per day were measured for intertidal dens but subtidal rates were not measured.

Fourth, *O. dofleini* may also exhibit selective tendencies based on external factors such as predation risk and interspecific competition. The ecology of one predator/competitor in particular may be important to *O. dofleini*. The historical distribution of the sea otter (*Enhydra lutris*) overlaps the range of *O. dofleini* in its entirety (RIEDMAN & ESTES, 1988). Sea otters prefer abalones (*Haliotis* spp.), rock crabs (*Cancer* spp.) and sea urchins (*Strongylocentrotus* spp.), which have higher caloric value, followed by *Pugettia* spp., clams, mussels, octopuses, barnacles, scallops, sea stars and chitons (reference in RIEDMAN & ESTES, 1988). Otters in Prince William Sound feed on *Cancer magister*, *Telmessus cheiragonus*, *Mytilus edulis*, *Macoma inquinata* and *Protothaca staminea* (KVITEK & OLIVER, 1988), as well as on *O. dofleini* (pers. obs.). Clearly, there is diet overlap between sea otters and *O. dofleini*. Is competition with and/or predation by sea otters important? On both rocky and soft substrata, sea otters cause population declines in epifaunal prey, but on rocky substrata, small prey can escape sea otters in crevices (KVITEK & OLIVER, 1988). Since octopuses can capture prey from crevices (MATHER, 1991), one could hypothesize scenarios of both predation risk and habitat selection for octopuses, sea otters, and their epifaunal prey involving tradeoffs between foraging on soft or rocky substrata (as in BROWN, 1988; LIMA & DILL, 1990).

The diet and foraging behavior of *O. dofleini* is not easily scrutable based on the simple assumption that it is a generalist 'switching' predator nor on optimal foraging assumptions regarding handling time, prey size or encounter rates. Though it appears to forage on the most abundant crabs and bivalves available near its den, it does significantly avoid some abundant species. Aspects of its behavior from this and other studies point to energetic considerations as well as interactions between competitors and predators as important modifiers in the diet and foraging behavior of this octopus.

Conclusions

Analyses of diet and some aspects of foraging behavior of *Octopus dofleini* in Prince William Sound and Port Graham, Alaska, were made from collections of den litter, measurements of octopus and estimates of live prey abundance. Overall, comparisons of litter remains from the northern-most range of *O. dofleini* with those published for British Columbia show that diet breadth was similar, but the identity of major hard-bodied prey species was very different, suggesting that this octopus interacts with different prey communities across its range. The proportions of major hard-bodied prey species in Alaskan litter piles significantly differed with depth of den, associated substratum, presence of cobble and geographical locations, and seemed to reflect general prey availability. There was no significant preference or avoidance of many prey species relative to their abundance. However, *O. dofleini* was more likely to be found at sites with crabs and although no litter species was significantly preferred over its estimated abundance, one species was significantly avoided. These results suggest that while *O. dofleini* may behave as a generalist predator, aspects of its behavior based on this and other studies point to energetic considerations as well as interactions between competitors and predators that may be important modifiers in the diet and foraging behavior. These factors may, in turn, influence the impact of *O. dofleini* as a predator in near-shore communities.

Acknowledgements

This study would not have been possible without the knowledge, assistance and goodwill of people in Chenega Bay, Port Graham, Tatitlek and Cordova. In particular, MIKE ELESHANSKY, DOUG BRUCK, SIMEON KVASHNIKOFF Jr. and JERRY TOTEMOFF provided knowledge and assistance in the field; and MARTHA VLASOFF, WALTER MEGANIK Jr., JODY SEITZ and the fishermen of Cordova shared their knowledge and encouragement. We thank SCOTT WILBOR, KATHLEEN POLLET, BECCA DODGE, ROGER TRANI and Cordova Water Sports, MICHAEL KYTE, DAN LOGAN, NEAL OPPEN, BETH HALEY and TOM KLINE for assistance with field work; NORA FOSTER for assistance with museum specimens; and a special thanks to Cap'n NEAL-DAWG OPPEN and RENEE ERNSTER of the F/V Tempest and PAT the pilot of Cordova Air for their support and interest in this project. We thank reviewers of the Exxon Valdez Oil Spill Restoration Office for comments on the design and analysis of this research, and the Exxon Valdez Oil Spill Trustee Council and Project AWARE for financial support.

References

BOURNE, N. F., 1987: Scallops. In: R. M. HARBO & G. S. JAMIESON (Eds.), Status of Invertebrate Fisheries off the Pacific coast of Canada (1985/86). Can. Tech. Rep. Fish. Aquat. Sci., **1576:** 107–112.

BROWN, J. S., 1988: Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol., **22:** 37–47.

CHARNOV, E. L., 1976: Optimal foraging: the marginal value theorem. Theor. Popul. Biol., **9:** 129–136.

COSGROVE, J. A., 1987: Aspects of the natural history of *Octopus dofleini*, the Giant Pacific Octopus. M.Sc. Thesis, University of Victoria; 100 pp.

FOSTER, N. R., 1991: Intertidal bivalves: a guide to the common marine bivalves of Alaska. University of Alaska Press, Fairbanks; 152 pp.

HARTWICK, E. B., 1983: *Octopus dofleini*. In: P. R. BOYLE (Ed.), Cephalopod life cycles. Volume I. Academic Press, London: 277–291.

——, R. F. AMBROSE & S. M. C. ROBINSON, 1984a: Dynamics of shallow-water populations of *Octopus dofleini*. Mar. Biol., **82:** 65–72.

——, R. F. AMBROSE & S. M. C. ROBINSON, 1984b: Den utilization and the movements of tagged *Octopus dofleini*. Mar. Behav. Physiol., **11:** 95–110.

——, S. M. C. ROBINSON, R. F. AMBROSE, D. TROTTER & M. WALSH, 1988: Inshore-offshore comparison of *Octopus dofleini* with special reference to abundance, growth and physical condition during winter. Malacologia, **29:** 57–68.

——, L. TULLOCH & S. MACDONALD, 1981: Feeding and growth of *Octopus dofleini*. Veliger, **24:** 129–138.

HUGHES, R. N., 1980: Optimal foraging theory in the marine context. Oceanogr. Mar. Biol. Annu. Rev., **18:** 423–481.

KOZLOFF, E. N., 1987: Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle; 511 pp.

KVITEK, R. G. & J. S. OLIVER, 1988: Sea otter foraging habits and effects on prey populations and communities in soft-bottom environments. In: G. R. VANBLARICOM & J. A. ESTES (Eds.), The Community Ecology of Sea Otters. Springer-Verlag, New York: 22–47.

LIMA, S. L. & L. M. DILL, 1990: Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool., **68:** 619–640.

MAGURRAN, A. E., 1988: Ecological diversity and its measurement. Princeton University Press, Princeton; 179 pp.

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

——, S. RESLER & J. COSGROVE, 1985: Activity and movement patterns of *Octopus dofleini*. Mar. Behav. Physiol., **11:** 301–314.

MCQUAID, C. D., 1994: Feeding behaviour and selection of bivalve prey by *Octopus vulgaris*. J. Exp. Mar. Biol. Ecol., **177:** 187–202.

MOTTET, M. G., 1975: The fishery biology of *Octopus dofleini* (WÜLKER). Technical Report No. 16. Management and Research Division, Washington Department of Fisheries; 37 pp.

MURDOCH, W. W., 1969: Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr., **39:** 335–354.

ORENSANZ, J. M. & V. F. GALLUCCI, 1988: Comparative study of postlarval life-history schedules in four sympatric species of *Cancer*. J. Crust. Biol., **8:** 187–220.

PULLIAM, H. R., 1974: On the theory of optimal diets. Am. Nat., **108:** 59–75.

RIEDMAN, M. I. & J. A. ESTES, 1988: A review of the history, distribution, and foraging ecology of sea otters. In: G. R. VANBLARICOM & J. A. ESTES (Eds.), The Community Ecology of Sea Otters. Springer-Verlag, New York: 4–21.

ROBINSON, S. M. C. & E. B. HARTWICK, 1986: Analysis of growth based on tag-recapture of Giant Pacific octopus *Octopus dofleini martini*. J. Zool., London, **209:** 559–572.

SANCHEZ, P. & R. OBARTI, 1993: The biology and fishery of *O. vulgaris* caught with clay pots on the Spanish Mediterranean coast. In: T. OKUTANI, R. K. O'DOR & T. KUBODERA (Eds.), Recent Advances in Cephalopod Fisheries Biology, 1st Edition. Volume 1. Tokai University Press, Tokyo: 477–487.