

Chapter 20

Habitat Ecology of *Enteroctopus dofleini* from Middens and Live Prey Surveys in Prince William Sound, Alaska

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1 Introduction

The population ecology of mobile predators is often regulated by a complex mix of factors. Understanding the mechanisms that regulate the abundance and distribution of organisms remains a central goal of marine ecology (Estes and Peterson, 1998). Recent studies have emphasized the success of using multiple mechanisms to understand control of population dynamics, particularly in marine species (National Science Foundation, 1998; Connolly and Roughgarden, 1998; Karlson, 2002). At a fundamental level, population change may be represented as births (recruitment) minus deaths plus immigration minus emigration. The latter two may be combined as habitat selection. In this paper, we focus on habitat selection in the giant Pacific Octopus *Enteroctopus dofleini* (Wülker, 1910), whether habitat selection can be

linked to diet and prey availability, and the potential role of habitat selection in local population fluctuations.

The dynamics of habitat association in octopus, including *Enteroctopus dofleini*, are complex and likely important to fisheries and marine communities (e.g., Garstang, 1900; Griffiths and Hockey, 1987; Smith and Herrnkind, 1992; Mather, 1993). However, habitat selection by octopuses has received little rigorous attention (Anderson, 1997). Limited research on octopus distribution suggests that many coastal benthic species are characterized by substantial density fluctuations at a particular site (Garstang, 1900; Rees and Lumby, 1954; Mather, 1982), and that this is also the case for *E. dofleini* (see Hartwick and Thorarinsson, 1978; Hartwick et al., 1984a). While both ontogenetic and migratory mechanisms are suggested to account for this, the emphasis for *E. dofleini* has been on migration (Hartwick, 1983; Hochberg, 1998). Octopuses may exercise substantial choice in matters of diet and shelter (Iribarne, 1990; Laidig et al., 1995; Anderson, 1997) and often modify shelters to their satisfaction (Legac, 1969; Mather, 1994; D. Scheel, personal observation, 1998).

A number of physical habitat characteristics may influence octopus density and distribution (Anderson, 1997; Scheel, 2002). The availability of shelters influences octopus distribution and may limit abundance (Aronson, 1986), although not always in obvious ways (Frazer and Lindberg, 1994) nor for populations in rocky or reef habitats (Ambrose, 1988; Anderson, 1997). Dens do not appear to be limiting for *Enteroctopus dofleini* in the eastern North Pacific (Hartwick, 1983; Hartwick et al., 1984b), although this may not be the case in the western North Pacific where a successful commercial lair-pot fishery for this species suggests that dens are in demand (Hartwick, 1983), at least during the migratory movements.

Physical habitat characteristics may have a large influence on *Enteroctopus dofleini* ecology, as suggested by differences between eastern and western North Pacific movement patterns (for review of fisheries biology, see Hartwick and Barriga, 1997; Gillespie et al., 1998). In waters off Vancouver Island (eastern North Pacific), Mather et al., (1985) found that *E. dofleini* had relatively small home ranges over a 15-day period; and Hartwick et al., (1984b) found that 59% of tagged individuals occupied a single den for over a month. Hartwick et al., (1988) used lair-pot sampling at adjacent onshore and offshore sites to capture, tag, and release 191 individuals. On recapture of 81, none had moved between the two sites. This site fidelity in rocky habitats contrasts with data from Japan, where tagged *E. dofleini* were recovered in a commercial fishery by lair-pot trap-lining on soft substrate fishing grounds (Mottet, 1975; Nagasawa et al., 1993). Thirty-two percent of recovered octopuses (85 of 264 tags) made relatively long-distance movements of 5–50 km over periods of 6–18 months (Sato, 1994, 1996); the remainder moved less than 5 km. No evidence from the eastern Pacific indicates this scale of movement, despite at least a handful of studies that had the potential to detect it. Rigby (2003, 2004) found that the timing of movements in Japanese waters corresponded to onshore temperatures exceeding the bounds of optimal physiological functioning of

E. dofleini (7°C–9.5°C). This suggests that differences in seasonal temperature fluctuations between the eastern and western Pacific may account for differences in behavior, and underscores the importance of habitat selection to octopus ecology and fisheries. However, further data are required to warrant this conclusion.

In the eastern Pacific, neither den availability nor seasonal temperature changes appear to drive the distribution of *Enteroctopus dofleini*; and it is reasonable to consider whether biological factors such as the distribution of prey, predators, or vegetative cover may drive patterns of distribution and abundance. Few studies have obtained quantitative data about predation on octopuses, although several studies documented the presence of potential predators (including fish and marine mammal predators) or indirect evidence of partial predation (i.e., scars or partial arm loss). Hartwick et al. (1988) report a higher incidence of such scars on *Enteroctopus dofleini* from deeper habitats (37–110m), as well as the occurrence of octopuses in the stomachs of fish predators (Lingcod *Ophiodon elongatus* and Spiny dogfish *Squalus acanthias*) from those depths. Octopuses feed on a diverse array of prey species and are often considered to be generalist predators. Field studies have found that octopus diets, including those of *E. dofleini*, may be influenced by both food preferences and prey availability (Hartwick et al., 1981; Ambrose, 1984). Thus, prey availability is also likely to influence octopus distribution (Anderson, 1997).

In the eastern north Pacific, juvenile *Enteroctopus dofleini* (to approximately 15 kg) found in shallow water occupy dens under boulders and in rock crevices, and feed on a variety of benthic prey, including primarily crabs and bivalves (Hartwick et al., 1981; Vincent et al., 1998). During this life stage, they appear to be central-place foragers (*sensu* Curio, 1976) occupying home ranges of less than 250 m² and switching dens frequently (Hartwick et al., 1984b; Mather et al., 1985). Prey are often brought back to the den and consumed there; the remains of hard-shelled prey accumulate at the mouth of the den as a midden. Diet as characterized by midden piles collected from dens has been a principle avenue of inquiry (Hartwick et al., 1981; Mather et al., 1985; Cosgrove, 1987; Anderson, 1994; Vincent et al., 1998; Dodge and Scheel, 1999), although very little work has been done to examine what portion of diet is represented in midden piles or to understand the foraging ecology of juvenile *E. dofleini* (for exceptions, see Mather et al., 1985; Vincent et al., 1998). In this part of their range, *E. dofleini* appear to be dependent on rocky habitat for denning, although they apparently forage in other habitats such as eel grass beds and sand flats as well as in rocky areas (Hartwick et al., 1981).

In intertidal habitats in Prince William Sound, Alaska, Scheel (2002) found *Enteroctopus dofleini* on soft substrates (mud, sand, or gravel) rather than hard (bedrock, rock outcrops, large cobble fields) and where boulders were present rather than absent. Octopus numbers increased fivefold in areas adjacent to dense kelp versus those adjacent to areas with sparse kelp (Scheel, 2002). Diet composition appeared to be variable with small changes in depth or location (Vincent et al., 1998), possibly because of concomitant changes in prey populations. In a small sample of intertidal prey abundance, octopus counts were higher on those transects where live crabs were more abundant, suggesting that selection of habitats within the intertidal may be influenced by prey abundance (Vincent et al., 1998).

This paper examines prey availability and quality (energy value, handling time) as aspects of habitat quality associated with local variation in counts of *Enteroctopus dofleini* in Prince William Sound, Alaska, and describes efforts to address the role of habitat selection and foraging behavior in octopus ecology.

2 Methods

2.1 Study Sites and Population Trends

Observations were made along the south-central Alaskan coast during May, June, and July from 1995–1996, 1998, and 2001–2004. Most work was conducted in Prince William Sound, AK. The majority of sites around Prince William Sound were visited once in 1995, 1996, or 1998. In addition, several sites were visited repeatedly: most notably Gibbon's Anchorage on Green Island (60°16'N, 147°27'W) plus a nearby cove, and Ellamar near the village of Tatitlek (60°53'N, 146°42'W), a site at which octopuses are harvested, plus a site on nearby Busby Island where no known harvest occurs. A description of habitats surveyed and octopus counts for the years 1995, 1996, and 1998 was previously published (Scheel, 2002).

Population data are based on beach walk transects conducted at these sites. See Scheel (2002) for detailed methods. Transect data for 2001–2004 were collected at the Green Island, Ellamar, and Busby Island sites mentioned above. Differences in octopus density (count per 1,000 m² surveyed area) between years and among sites were analyzed with nonparametric median tests and Kruskal–Wallace one-way analyses of variance by ranks (SPSS 12.0 2003), as counts and densities were nonnormal (zero was the most frequent value).

2.2 Prey: Middens, Live Surveys, and Energetics

In conjunction with transect sampling, remains of recent prey items (estimated to be <7 days old based on algae growth on inner surfaces and signs of weathering) were collected from all middens found on each transect, identified to species, measured, and counted (minimum number of individuals represented). Octopus bite or drill marks were recorded for each prey item (Dodge and Scheel, 1999; Vincent et al., 1998). Surveys of live prey were also conducted. Live prey surveys consisted of 0.5 × 0.5 m quadrats in 1996 and 1.0 × 1.0 m quadrats in 2001–2004, located on beach walk transects, at the start and at 1–9 randomly chosen distances from the start along the transect length. Within each quadrat, rocks, and kelp were moved and all epibenthic mobile individuals of potential prey were identified to species and counted. Rocks were replaced to their original orientation and position to minimize disruption to the habitat; rocks too large to replace precisely were sampled

to the best of our ability without moving. Carapace size or shell width were recorded for bivalves, gastropods, chitons, and crabs. Specimens were collected, frozen, and held at -40°C for subsequent analysis of energy content. Analyzed samples were thawed, dissected, the soft tissue dried in a drying oven, and pelletized. Pellets were combusted using a Parr Microbomb calorimeter to determine energy content. Analyses in this paper focus on the crabs *Cancer oregonensis*, *Telmessus cheiragonus*, *Lophopanopeus bellus*, and *Pugettia gracilis* (major hard-bodied prey, Vincent et al., 1998), as well as *Cancer productus* and the bivalve *Protothaca staminea*, the next most frequent hard-bodied prey that commonly occurred in octopus middens in Prince William Sound intertidal habitats. These six taxa are hereafter referred to as “major hard-bodied prey species.” Two additional crab species, *Hapalogaster mertensii* and *Cryptolithodes sitchensis*, were also included in some analyses to contrast species comprising a minor portion of prey remains but commonly occurring in live prey surveys.

2.3 Relocation Experiment

Three octopuses in 1996 and four in 2003 were captured, tagged, and released; and their subsequent selection of habitats monitored. All tagged and released octopuses were obtained within the intertidal zone during beach walk surveys. Sonic-tagged animals were given unique identifiers (names) for record-keeping. The 1996 animals were released where captured (control for handling artifacts, *sensu* Chapman, 1986); those in 2003 were relocated away from the preferred octopus habitat and released either in shallow water (relocation control) or deep water (experimental treatment). Octopuses caught were weighed, sexed, and measured (interocular and mantle length). Midden piles were collected from the dens of these animals for analysis of diet. Octopus 4kg or larger were transferred to a research vessel for anesthesia and tagging and were placed in holding tanks with flow-through seawater. Cold-water anesthesia was used (Anderson, 1996; Andrews and Tansey, 1981). Octopus and seawater were gradually chilled to 3°C , at which temperature they became nonresponsive, and held at $2-3^{\circ}\text{C}$ during tag implantation. Tags were either attached through arm muscle on cable-tie loops (1996) or implanted through a small incision in the dermal layer only, above the web, on the third left arm of the octopus (2003). The implant wound was blotted dry, pinched closed, and sealed with Nexaband, a veterinary adhesive. Respiration rates, color, and posture returned to preanesthesia condition shortly after the water and octopus were rewarmed to ambient temperature. It should be noted here that all implanted tags (2003) were lost within 24h of release of the octopus (see Results). Loss of a tag (regardless of attachment method) was suspected after a period of at least 24h without any tag movement; in several cases (2 of 3 in 1996; 1 of 4 in 2003), tags were confirmed lost by recovering of the tag from a recently occupied octopus den. Due to loss of tags in 2003 within 24h of implant, subcutaneous implantation by the method described here cannot be recommended for future studies.

Capture, release, and relocation habitats were surveyed via SCUBA surveys for all sites, except one below 40 m depth. That site was surveyed by camcorder lowered to the site. In each case a 1 m² plot was sampled. Variables collected were depth, slope, substrate, kelp and *Zostera* cover, available prey, and presence or absence of boulders (Scheel, 2002). A habitat quality index (HQI) was calculated as the sum of a depth index (shallow, <10 m = 1; deeper = 0), substrate (soft, silt to gravel = 1, or hard, cobble to bedrock = 0), boulders (present = 1, absent = 0), kelp cover (by percent cover 0, 0.25, 0.5, etc.), and presence of major hard-bodied prey species (Vincent et al., 1998; 0.2 per species constrained to a maximum prey score of 1.0). Two versions of this index were calculated, one including all five habitat characters (HQI₅, which thus varies from one to five) and one without prey data (HQI₄, which varies from one to four). Only HQI₄ were calculated for 1996 surveys, as prey data were not collected at that time. For either index, increasing scores indicate habitat characteristics associated with greater octopus counts (Vincent et al., 1998; Scheel, 2002).

We calculated HQI₄s for all transects (1995–2004). Transects with missing data were omitted. The distribution of HQI₄ scores was examined to confirm whether HQIs actually correlate with octopus count at a site.

3 Results

Population trends are based on 82 beach walk transect surveys described in Scheel (2002, only transects in Prince William Sound included) plus an additional 25 beach walk transects conducted in the period 2001–2004 using the same methods. On these transects, we recorded 90 octopuses in a total of 333,000 m² area surveyed. Prey of octopuses are described here from a total of 249 middens (containing 2,731 items) and 88 live prey quadrats (containing 1,098 items). All samples were collected during beach walk transects in Prince William Sound and Kachemak Bay in 1996, 1998, and 2001–2004.

3.1 Population Trends

Octopus densities were lowest in 1995 and 2004, while density rose in the intervening years (Fig. 20.1; nonparametric medians test: $N = 107$, chi-square = 15.537, $df = 5$, asymptotic sig. = 0.008; Kruskal–Wallace ANOVA: $N = 107$, chi-square = 11.284, $df = 5$, asymptotic sig. = 0.046). Overall beach walk densities in 2002 ($N = 7$, average density = 0.85 per 1,000 m²) were nearly four times those found in 1995 ($N = 30$, average density = 0.22 per 1,000 m²), and have declined since (Fig. 20.1). An apparent low at the start of the study in 1995, and a subsequent rise and then fall again by 2004 can be found in all Green Island sites taken together (Kruskal–Wallace ANOVA: $N = 37$, chi-square = 1.897, $df = 5$, not significant), in

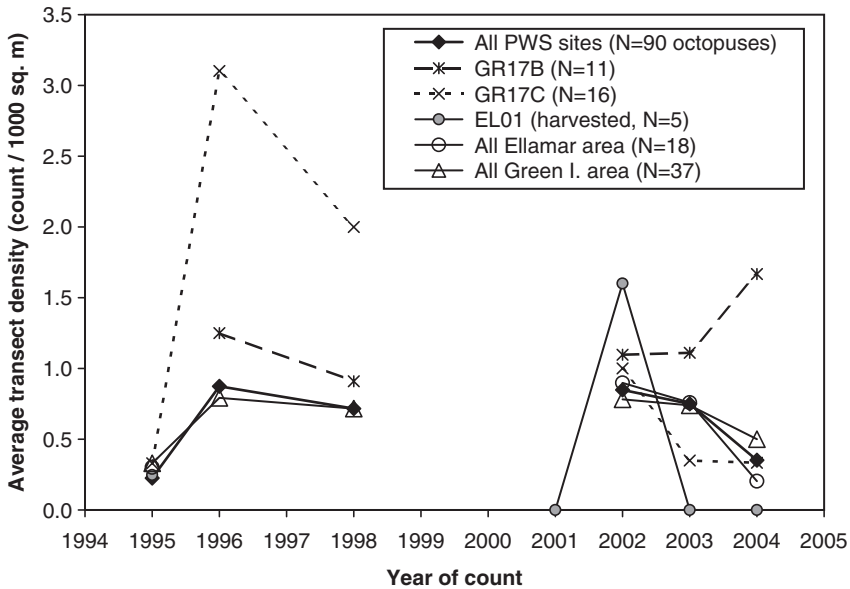


Fig. 20.1 Octopus counts over all sites (heavy line) and select individual sites. PWS- Prince William Sound; GR17B, GR17C -Green Island sites; EL01 -harvested Ellamar site. Sampling effort was not equal at each site.

the most frequently sampled Green Island sites taken individually (Fig. 20.1; GR17C and in contrast GR17B), and in all Ellamar areas sites (including Busby Island) taken together (Kruskal–Wallace ANOVA: $N = 37$, chi-square = 4.152, $df = 5$, not significant; see Fig. 20.1). Year to year differences at each location did not approach significance due to the lower sample size when the data were subdivided. One site showing a contrasting pattern is the harvested EL01 site (Ellamar), which although low in 1995 shows an apparent decline to near-zero octopus densities in the period 2001–2004. Only one octopus was found (in 2002) on beach walk transects during this period. However, this site is regularly harvested by local residents, who are reported to harvest the beach in the days or months preceding our beach walk transects. Exact harvest rates are not known, but human residency at Ellamar has increased over the decade of this study.

3.2 Prey: Middens, Live Surveys, and Energetics

A sample of 26 prey items representing eight species of common crabs and bivalves collected during beach walk transects were analyzed for energy content. Energy density of prey varied from 3,000 to 5,800 cal/g dry weight. However, variation was not a function of prey species (Fig. 20.2, top; ANOVA: $N = 26$, $df = 25$, $f = 0.250$, $p = 0.95$).

Table 20.1 Sizes (carapace or valve width) of prey species commonly represented in both live prey surveys and octopus middens.

Species	N_M (N_L) ¹	Mean width (cm)		HSD ²
		Middens	Live	
<i>Hapalogaster mertensii</i>	1 (126)	1.4	1.3	a
<i>Pugettia gracilis</i>	107 (121)	2.0	1.6	ab
<i>Lophopanopeus bellus</i>	63 (122)	2.2	1.5	ab
<i>Cancer oregonensis</i>	219 (121)	2.3	1.6	bc
<i>Chlamys</i> sp.	61 (0)	2.3	–	c
<i>Protothaca staminea</i>	110 (0)	2.8	–	d
<i>Cryptolithodes</i> sp.	17 (8)	4.1	4.5	e
<i>Telmessus cheiragonus</i>	224 (41)	4.6	2.9	e
<i>Cancer productus</i>	102 (4)	5.8	3.5	f

¹ N_M = number of prey items from middens (N_L = number from live prey surveys).

²Tukey HSD homogeneous subsets on midden and live prey samples combined. Species marked with different letters were significantly different in size distribution.

Species were, therefore, lumped for analysis of energy density by size. No correlation existed between energy density and either dry weight of whole body soft tissue (meat per prey item) or prey size (carapace or valve width; see Fig. 20.2, top; ANOVA: $N = 26$, $df = 25$, $f = 0.150$, $p = 0.861$). However, the amount of meat per prey item increased exponentially with prey size (Fig. 20.2, bottom; exponential curve fitting: *Cryptolithodes sitchensis* omitted, $N = 23$, adjusted R square = 0.784, $df = 22$, $F = 80.88$, $p < 0.00001$). This was not true, however, of *C. sitchensis* (Fig. 20.2, bottom), a crab species with an unusually wide and flat carapace that covers both the body and legs of the crab. Whole-body energy content per prey item may be expressed as cal/g dry-weight (Fig. 20.2, top) times g dry-weight per item (Fig. 20.2, bottom) and, thus, rises rapidly with prey size. With the exception of *C. sitchensis*, whole body energy of prey items is not correlated with species of prey except as prey species vary in maximum body size.

A total of 249 middens containing 2,731 items were recorded, of which 2,260 items (83%) were major hard-body prey (see methods; Vincent et al., 1998), *Cryptolithodes* sp. or *Hapalogaster mertensii*. The sample of live individuals of potential prey consisted of $N = 88$ quadrats in which were recorded 1,098 items; of these, 26 quadrats (30%) contained at least one major hard-body prey, *Cryptolithodes* sp. or *H. mertensii* individual, and a total of 566 individuals of these species were recorded in quadrats.

The prey representation from the middens (Table 20.1, $N = 904$ items) was shifted toward larger sizes, relative to that measured during live prey quadrats ($N = 543$, Fig. 20.3 top). Average carapace sizes differed among species (Table 20.1; ANOVA: $F = 76.8$, $df = 8$, $p < 0.001$). The largest crabs were *Cancer productus* and *Telmessus cheiragonus* (*Cryptolithodes* sp. also had a large carapace but contains very little meat for its size, see above); while the smallest were *Hapalogaster mertensii* (a species avoided by octopuses, Vincent et al., 1998), *Pugettia gracilis*, and *Lophopanopeus bellus* (Table 20.1). For species represented

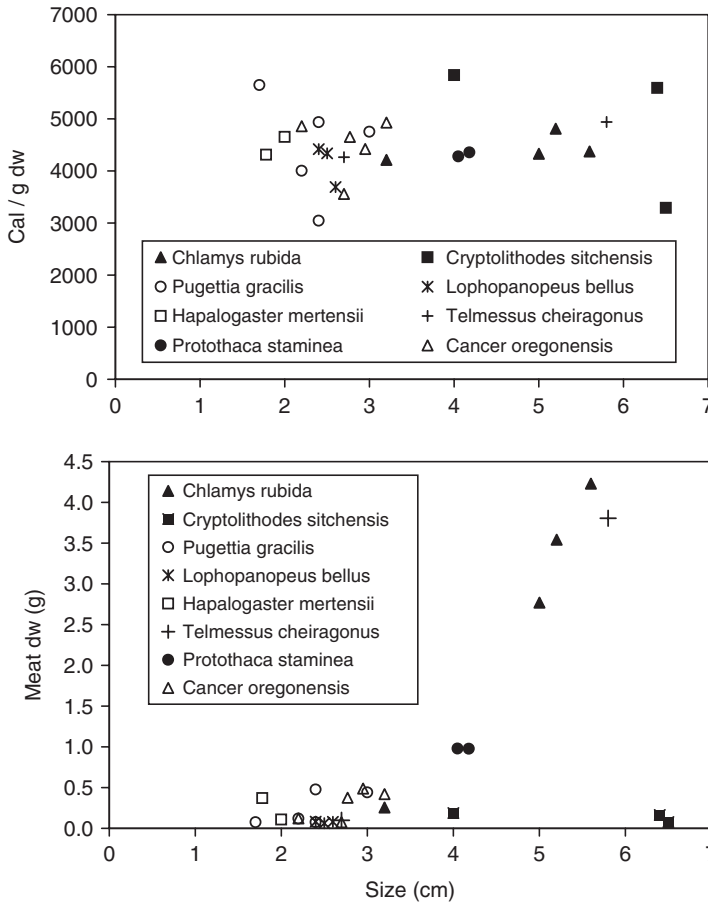


Fig. 20.2 Energy density (per gram, top panel) and whole-body energy (bottom) of select species of octopus prey.

in both middens and live prey samples, mean size in middens was larger than mean size in live prey samples (Table 20.1, ANOVA, $N = 1,447$ prey items of seven taxa; difference by species, between live prey and middens: $F = 7.978$, $df = 6$, $p < 0.001$). For three of four crab species represented by more than 40 individuals in both live prey and midden samples (Table 20.1), the size of remains from middens increased over the study period while the average size in live prey quadrats decreased (Fig. 20.3, middle panel and *Cancer oregonensis* in bottom panel). Size differences among years for *P. gracilis* did not show this pattern; and those of other species were not considered due to only minor representation either in the middens or in the live prey surveys.

Methods by which octopus open prey may leave marks on hard remains of prey. The size of carapace or valve remains of the most common species in

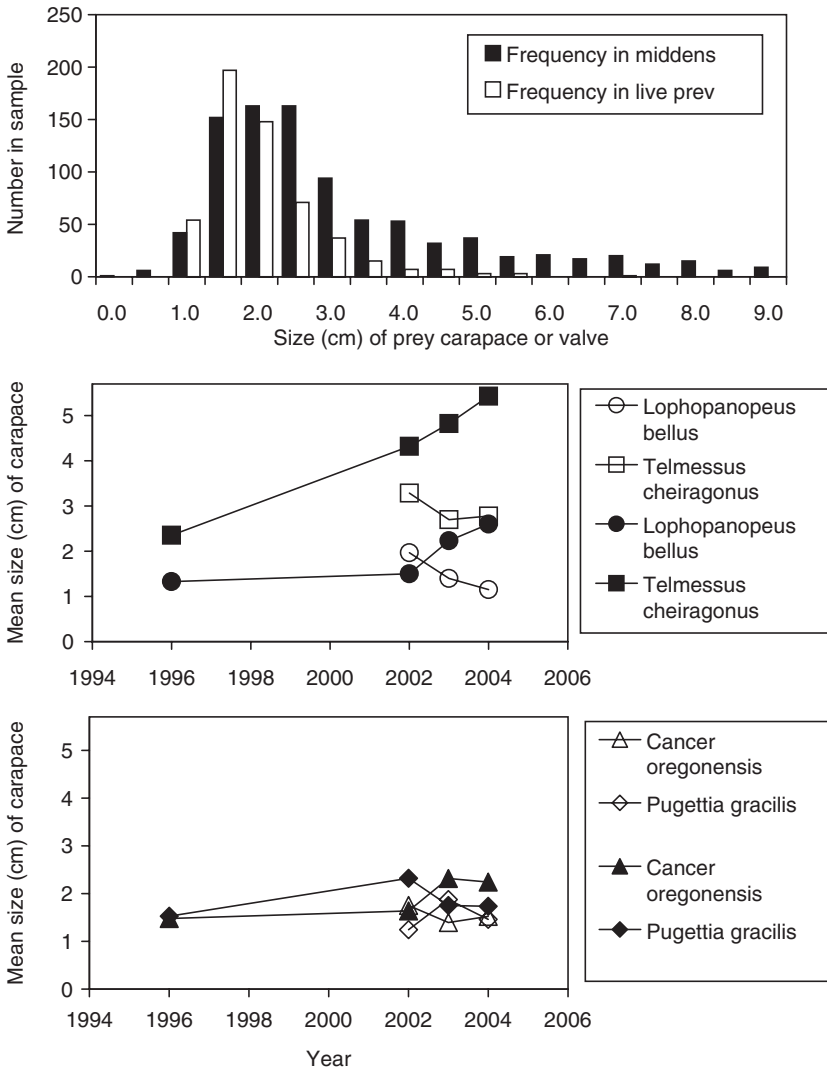


Fig. 20.3 Number of prey by size (top), and mean size of prey (middle and bottom) in middens (solid symbols) and live prey surveys (open symbols).

middens varied among prey species and by type of mark found (Table 20.2; N = 824 prey items from middens [615 unmarked, 183 drilled, and 26 bitten] of six species; there was a significant interaction effect between species and method of opening prey; see Table 20.2 for results for individual species.). *Telmessus* crabs were bitten or drilled on the carapace least often (these crabs were often bitten on the legs, however) and two species of *Cancer* crabs and the clam *Protothaca staminea* were drilled or bitten most often (Table 20.2). Furthermore, for *Cancer*

Table 20.2 Proportion of carapaces and bivalve shells in middens bearing drill or bite marks for select species (top), and for *P. staminea* fed to named captive octopuses (bottom). Drilled remains were significantly larger than unmarked remains of *P. staminea* in both middens and prey fed to captive octopuses^a, and for *C. productus* carapaces in middens.

Species	N	Drilled	Number (Proportion)			P
			Unmarked	Bite	F ^b	
<i>Telmessus cheiragonus</i>	224	5 (2%)	213 (95%)	6 (3%) ^c	1.283	0.279
<i>Pugettia gracilis</i>	107	23 (21%)	84 (79%)	0 (-)	0.036	0.850
<i>Lophopanopeus bellus</i>	63	14 (22%)	49 (78%)	0 (-)	0.371	0.545
<i>Protothaca staminea</i>	110	32 (29%)	69 (63%)	9 (8%)	7.531	0.001 ^d
<i>Cancer productus</i>	101	30 (30%)	67 (66%)	4 (4%)	4.158	0.018 ^c
<i>Cancer oregonensis</i>	219	79 (36%)	133 (61%)	7 (3%)	0.882	0.415
Ellamar	57	37 (65%)	6 (11%)	14 (25%)		
Wesley Sands	28	12 (43%)	14 (50%)	2 (7%)		
Inky Waters	44	21 (48%)	21 (48%)	2 (5%)		
Ocho	130	79 (61%)	40 (31%)	11 (8%)		

^aTukey HSD comparisons, drill-bite, mean difference = 0.03 cm, $p = 0.975$; drill-unmarked, mean difference = 0.3 cm, $p = 0.005$; bite-unmarked, mean difference = 0.2 cm, $p = 0.162$.

^bdf = 2 except where no bites were recorded, in which cases, df = 1.

^cAlthough *T. cheiragonus* remains seldom bear bite marks on the carapace, 35 of 148 legs (25%) of this species found in middens in 1996–2004 bore bite marks (Dodge and Scheel, 1999). Because only one leg may need to be bitten to subdue each crab, this may reflect the percentage of individual *Telmessus* that are opened by biting. *Cancer productus* and possibly other crabs may also be bitten on the leg, apparently with less frequency (Dodge and Scheel, 1999).

^dDrilled valves (mean size = 3.3 cm) larger than unmarked (mean size = 2.6 cm) and bitten valves (2.5 cm). Tukey HSD comparisons, drill-bite, mean difference = 0.8 cm, $p = 0.049$; drill-unmarked, mean difference = 0.7 cm, $p = 0.001$; bite-unmarked, mean difference = 0.08, $p = 0.960$.

^eDrilled carapaces (mean size = 6.6 cm) larger than unmarked (5.3 cm); while bitten (6.0 cm) were not significantly different from either drilled or unmarked. Tukey HSD comparisons, drill-bite, mean difference = 0.5 cm, $p = 0.882$; drill-unmarked, mean difference = 1.3 cm, $p = 0.014$; bite-unmarked, mean difference = 0.7 cm, $p = 0.748$.

productus and *P. staminea*, drilled individuals were significantly larger than those unmarked; and for *P. staminea*, drilled individuals were also significantly larger than bitten. These differences were not seen for the other species. Remains of *P. staminea* prey of four captive octopuses were analyzed in the same way (Table 20.2), and showed similar trends although octopuses were fed food of slightly different average sizes.

Midden compositions were examined for the years 1996, 1998, and 2002–2004 for dens (N = 102 middens) in the Green Island and Ellamar areas only (where octopus count transects were repeated most often). Midden contents were analyzed as summed prey size (an index of the energy content represented by each midden), and count and species diversity of items per midden. Summed prey sizes but neither number of items nor species diversity (Shannon index) per midden were significantly lower in 1996 and 1998 than in other years (Kruskal–Wallace ANOVA by years, Table 20.3). There were no significant differences

Table 20.3 *Kruskal Wallis Test for differences in midden content, with Year and Region as grouping variables: (a) Midden content differed between years in the size of prey (sum of prey length), but not in number of items per midden nor diversity (Shannon Index, SI). (b) Mean value of summed prey size and number of items [and items of major hard-bodied prey (MHB) only] per midden by year. Size of prey items was lower in 1996 and 1998 than in later years.*

(a)	Years		Asymp. Sig.	Regions		Asymp Sig.
	Chi-Square	df		Chi-Square	df	
Sum prey length	16.096	4	0.003	1.068	1	0.301
Items per midden	8.372	4	0.079	0.110	1	0.741
SI	7.263	4	0.123	1.461	1	0.227

(b)	Year	Sum of prey size	Number of items	Number of MHB items
	1996	16.8	6.4	3.7
	1998	7.1	4.7	3.6
	2002	21.6	5.6	4.3
	2003	19.8	6.7	4.9
	2004	19.8	5.2	3.9
	Total	17.9	5.9	4.2

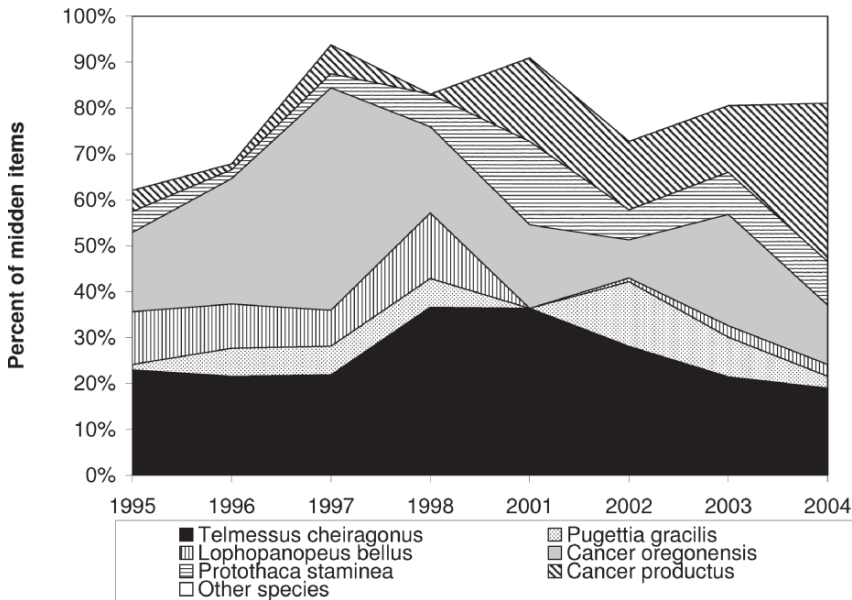


Fig. 20.4 *Over-all species composition of remains found in the midden.*

between the Green Island and Ellamar areas. At Green Island sites, the low summed size of midden items in 1996 and 1998 appears to be due to the scarcity (absence in 1998) of the large crab *Cancer productus* (mean carapace width = 5.8 cm, N = 102) in that year (see Table 20.1, Fig. 20.4). This crab increased to

18% of midden items in 2001 and reached a high of 34% of all midden items in 2004. In contrast, the other large crab found in middens, *Telmessus cheiragonus* (Table 20.1, Fig. 20.4), gradually declined in abundance in middens from a high of 37% in 1998 to a low of 19% in 2004; and *Cancer oregonensis*, a small crab, also declined in representation in the middens since 1997 (Fig. 20.4). Over the same period and on the same beaches, the overall abundance of five species of crabs in live prey samples increased (Fig. 20.5; MANOVA: $F = 6.176$, $df = 20$, $p < 0.001$; differences by sampling region were not significant: $F = 0.535$, $df = 10$, $p < 0.864$). These increases were due to increased counts of *C. oregonensis* (between subject effects, $F = 12.563$, $df = 4$, $p < 0.001$), *Pugettia gracilis* ($F = 12.360$, $df = 4$, $p < 0.001$), and included the first occurrences of *C. productus* in these samples in 2004. Significant variation in *Lophopanopeus bellus* counts ($F = 4.214$, $df = 4$, $p = 0.003$) offset some of these increases in 2003, which was nevertheless the year in which crabs were at their greatest abundance. Counts of *T. cheiragonus* did not change significantly over these years.

3.3 Relocation Experiment

Tag retention, determined as the time postrelease before the tag stopped moving for all subsequent relocations, was 17–51 days in 1996, but less than 24 h in 2003 due to different attachment methods. Thus, results in 2003 reflect very short-term movements, and do not necessarily indicate final choice of habitat. Immediately on release, octopuses either readily reoccupied their previous dens (1996, released where captured), sought nearby shelter under kelp if it was available (2003, shallow releases), or fled (2003, deep releases, no cover in vicinity). Two octopuses, possibly seeking shelter, approached divers immediately on release.

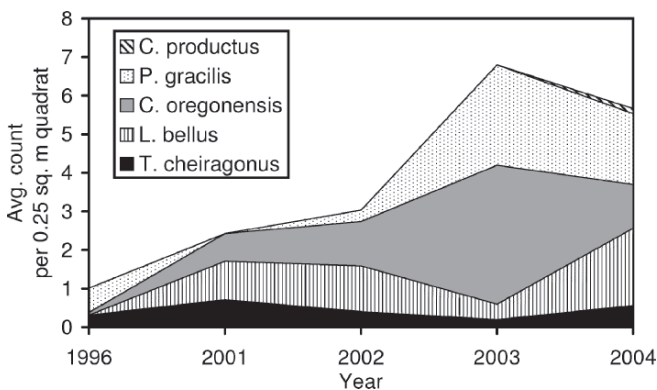


Fig. 20.5 Individuals per quadrat of select crab species in live prey surveys, demonstrating the increase in prey availability over the course of this study.

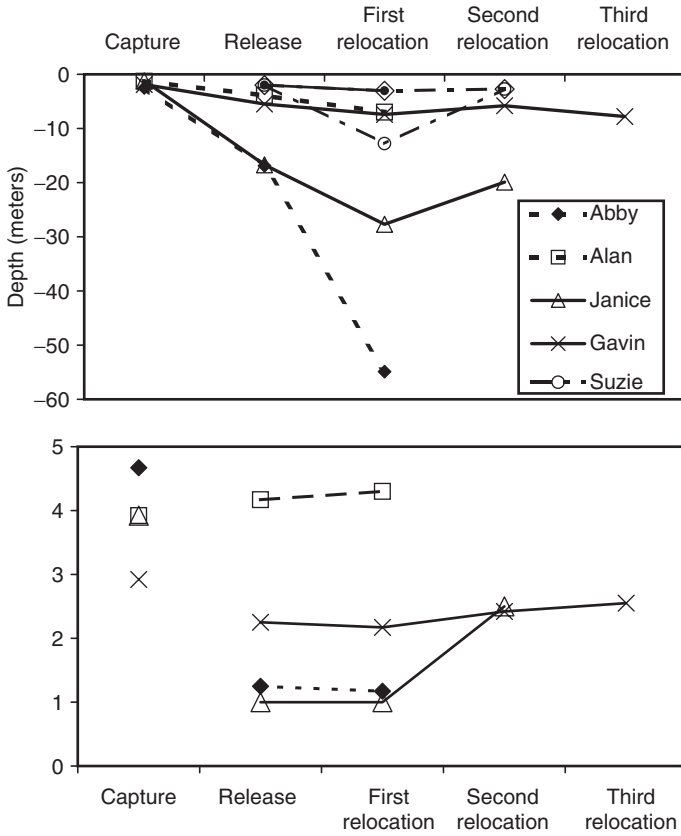


Fig. 20.6 Captured and released octopuses moved deeper and selected higher quality habitats during relocation.

All octopuses moved deeper by 2–40 m following release (Table 20.4), although not all remained deeper at their final relocation. The 1996 controls (released where captured) moved 3–13 m deeper, and subsequently returned to shallow water (<3 m). Two moved within hours of release; the third (Petunia) remained in her release location for three days before briefly moving deeper and then returning to her intertidal capture location. Habitat quality indices (without prey, HQI_{4s}) for the 1996 releases did not increase above capture/release sites as the octopuses moved (Table 20.4). The 2003 controls (relocated shallow) each moved deeper by <4 m; while the 2003 treatment (relocated deep) each moved deeper by >10 m (Fig. 20.6, top). However, Gavin (relocated shallow) was released in a location where substantially deeper water was not directly accessible. While the distance that the octopuses moved was not correlated with the time postrelease until tag loss, Alan (relocated shallow) moved least and was released into the highest HQI , suggesting a link between movement and

Table 20.4 *Octopuses in the relocation experiment. Depths relative to mean lower low water.*

Octopus	Weight (kg)	Sex	Capture depth (m)	Release depth (m)	Final relocation depth (m)	Capture HQI ₄	Release HQI ₄	Final Relocation HQI ₄	Lowest relocation HQI ₄
Petunia ¹	6.3	F	+0.1	+0.1	-0.3	3.5	=capture	3.5	
Beth ¹	7.1	F	-1.0	-1.0	-2.7	3.5	=capture	3.0	
Suzi ¹	7.4	F	-1.0	-1.0	-2.7	3.5	=capture	3.0	
Alan ²	4.0	M	-1.3	-3.9	-7.0	3.8	4.0	4.0	=final ³
Gavin ²	5.3	M	-1.9	-5.5	-7.8	2.3	2.3	2.5	2.0
Abby ²	7.6	F	-2.5	-16.9	-54.9	4.0	1.3	1.0	=final ³
Janice ²	5.1	F	-1.2	-16.7	-19.9	3.8	1.0	2.0	1.0

¹1996 octopus, released at capture site (control for handling artifacts). Lowest HQIs at relocation sites not available as only release and final relocation sites were surveyed.

²2003 octopus, relocated and released either shallow (<6 m, relocation control) or deep (>10 m, treatment). Total distance moved within the first 24 h postrelease was 22 m for Alan, and 297, 344, and 563 m respectively for Gavin, Abby, and Janice.

³Alan and Abby were only tracked to a single relocation site, that was thus the lowest, highest, and final relocation HQI.

habitat quality. Indeed, Alan was the only octopus to be released in an area with HQIs greater than his capture location.

For relocated (2003) octopuses, mean postrelease change in habitat quality index was 0.64, with only one value (for Abby) being negative (Fig. 20.6, bottom). Due to small sample size, habitat quality was not significantly different between capture and release sites; between release and relocation sites; nor between release and final relocation sites (HQI₅ paired sample t-test, release to capture: $t = 1.919$, $df = 3$, $p = 0.076$, $n = 4$; release to first relocation: $t = 0.151$, $df = 3$, $p = 0.445$, $n = 4$; release to final relocation: $t = -1.305$, $df = 3$, $p = 0.142$, $n = 4$).

Across all 128 transects conducted 1995–2004, those in habitats with HQI₄ greater than or equal to 2.75 had significantly greater octopus density than those in habitats with lower HQI₄s (Independent samples t-test: $HQI \geq 2.75$, $N = 85$, avg density = 1.0 octopus per 1,000 sq. m surveyed; $HQI < 2.75$, $N = 41$, avg density = 0.4 octopus/1,000 sq. m, $t = 2.823$, $df = 121$, $p = 0.006$, $N = 2$ transects dropped due to missing data; equal variances not assumed). Thus, there were significantly more octopuses on transects with higher habitat quality. HQI₄ did not, however, correlate with midden contents, which as indicators of octopus foraging success might also be expected to indicate habitat quality. No relationships were apparent between HQI₄ or octopus density and either a Shannon Index (SI) of prey diversity in midden piles, the number of items in a midden, or summed size of all items in a midden. While surprising, this lack of correlation would be consistent with time- or risk-minimizing, if risk-adverse octopuses invested more foraging effort in poor habitats and spent more time in shelter where habitats were richer.

4 Discussion

Because foraging is so clearly related to an animal's fitness, natural selection should result in the evolution of animals that are effective foragers. It may or may not follow that animal population fluctuations are influenced by foraging success and food availability. A wide body of work explores these two relationships, including consumer–resource competition, foraging, and habitat selection theories for the relationship of feeding to fitness, and trophic theory for the relation of resource (prey) availability to population size.

Foragers may show functional (Holling, 1959), aggregative (relating numbers of foragers to the abundance of their food, e.g., Piatt, 1990) and population responses to food availability. Functional responses determine the diet of individual predators, while aggregative and population responses together determine local populations of foragers. Foraging theory and habitat selection theory together have been used to address whether foragers maximize foraging functions of fitness by aggregating in particular habitats (Vincent et al., 1996). Here we examine whether considerations of classical foraging theory (Schoener, 1971; Pulliam, 1974; Curio, 1976; Stephens and Krebs, 1986), including energetic value of prey, prey handling time, and prey abundance can explain patterns of variation in octopus counts.

Because population density is determined by recruitment, habitat selection, and mortality, it is very difficult to tease apart historical reasons for density changes without data on all three of these aspects of octopus ecology. We had available data on population counts, habitat characteristics, and trends in prey availability only; and thus were restricted to a correlative retrospective that should be more useful in framing specific hypotheses about octopus habitat selection than in explicitly testing them. Within these limitations, however, we found that octopuses have diets reflecting rate-maximizing foraging strategies, but that population trends did not reflect prey availability.

4.1 Population Trends

Within the sample years surveyed in this study, average octopus densities have varied nearly fourfold from lows of 0.22–0.33 octopus/1,000 m² in 1995 and 2004 to a high of 0.72–0.85 octopus/1,000 m² in 1998 and 2002 (Fig. 20.1). There was considerably more variation among sites (Fig. 20.1).

Can the sources of variation in a population be assigned? The Ellamar study site (EL01, Fig. 20.1) was near a village, while other sites were not near human population centers. Reports from residents at Ellamar were that harvest from this site occurred every year and had increased over the course of the study (although no records were kept); and octopuses were recorded at Ellamar in our samples only in 1995 and 2002. No known harvest occurs at our other study sites which are remote from human residences. In general, it is very difficult to accumulate data that

directly measure recruitment or harvest and other mortality. However, at widely separated sites in the Sound (Fig. 20.1, All Ellamar area vs. All Green I. Area) population trends were similar, indicating that the sources of variation driving the trends were regional rather than local. Local sources might include recovery of sea otter populations from the 1989 *Exxon Valdez* oil spill or from hunting by Native Alaskans in the vicinity of the Ellamar study area. Regional sources might include climatic and oceanographic drivers, or human harvests that drive changes in predators or prey of octopuses over the scale of the entire Sound.

Our analyses in this paper were, therefore, focused on determining whether population fluctuations could be accounted for by changes in habitat characteristics that influence habitat selection. In this study, higher octopus densities were found at sites with higher habitat quality indices (HQI₄; included measures for depth, substrate, boulders, kelp cover, but not presence of prey). During this study, depth, substrate type, and boulders at sites have not changed, and therefore cannot account for fluctuations in octopus counts. However, kelp cover may change, or may correlate with other biological parameters such as prey availability.

Using foraging and habitat selection theory, the effect of prey availability on octopus counts can be considered in at least three ways. With or without an aggregative response, if octopuses acted as foraging time- or risk-minimizers (Schoener, 1971), where fitness was maximized when foraging time spent to obtain a given energy requirement was minimized, then no relationship between prey availability and octopus counts would be expected (other than at a threshold point). In this case, midden content, however, would be stable in the face of varying prey abundance as octopuses expended more effort foraging in habitats with low foraging success but minimized effort in habitats with higher success rates. Alternatively, if octopuses acted as rate maximizing foragers and habitat selectors, population counts as well as midden contents would parallel prey availability (Schoener, 1971). If octopuses were rate maximizing foragers, but population counts were limited by differential recruitment or mortality rather than resource abundance, then, once again, no relationship between prey availability and octopus count would be found. However, in this case, midden content, although not octopus counts, would be expected to mirror differences in prey availability. (Note that this list of alternatives is not exhaustive.) Finally, foraging theory makes predictions about how prey selectivity, handling time, and encounter rates are related to foraging success, and our data on octopus diet can be considered in light of these three parameters.

4.2 Prey: Middens, Live Surveys, and Energetics

What then can be discerned regarding these predictions from our analyses of prey and middens? First, although octopuses have been referred to as generalist (unselective) predators (Mather, 1993; Smith, 2003; but see Ambrose, 1984), our data indicate that they were selective of certain prey species and prey sizes, possibly in a manner consistent with foraging theory for rate-maximizing foragers. Octopus

middens lacked certain prey species and contained excesses of others, relative to live prey surveys (compare relative abundance in middens and live surveys, Table 20.1), indicating either octopus selection of preferred prey or differential susceptibility of prey to octopus predation. Availability of *Cancer oregonensis*, *Pugettia gracilis*, and possibly *Cancer productus* increased over the course of the study (Fig. 20.5). In the middens, however, *P. gracilis* did not increase in representation while *C. oregonensis* declined, and *C. productus* increased out of proportion to its occurrence in live prey surveys (Fig. 20.4). These patterns indicate selective predation rather than differential susceptibility of prey. Second, octopuses selected larger individuals of all prey species (Table 1) and for several did so increasingly over the duration of the study (Fig. 20.3). Because prey species are equivalent in energetic content (Fig. 20.2, upper panel) and larger prey have greater energy content (Fig. 20.2, lower panel), this resulted in greater foraging success (higher summed prey size in middens) in later years of the study (Table 20.3). Higher foraging success was the result of choosing larger individuals in later years (Fig. 20.3, lower panels) as well as greater availability and use of larger species (Figs. 20.4, 5) and not catching more individuals (Table 20.3). Third, octopus methods for opening prey (drill, bite, or pull, Hartwick et al., 1978; Steer and Semmens, 2003, with pull generally represented by unmarked shells although, for details, see Mather and Nixon, 1995; Grisley et al., 1996; Dodge and Scheel, 1999) depended on the size and species of prey (Table 20.2), with larger prey more likely to be drilled or bitten. Drilling and biting take considerably longer than pulling to open prey (Steer and Semmens, 2003).

As gain rate is a complex function of prey availability (encounter rate), handling time, and energetic content, it is not possible to determine whether these patterns represent rate-maximization foraging without further data. Predictions for time- or risk-minimizing are that foragers should minimize variance in gain rates in productive habitats but maximize it in unproductive ones; while for rate-maximizing foragers predictions are that diet breadth should be narrower in productive habitats and greater in unproductive ones. In this study, early years were less productive than later years (Fig. 5). The increase in use of larger species as their abundance increased, and the selection of larger prey items, represented a narrowing of diet breadth, and was therefore consistent with rate-maximizing foraging.

4.3 Relocation Experiment

Tagging has been a challenge in octopus studies. Mather et al. (1985) tagged four *Enteroctopus dofleini*; their attachment method, using metal hooks, allowed 4–15 days of observation. Mather et al. (1985) documented that octopuses make frequent short foraging trips and establish home ranges of 250 m²; however, they did not provide habitat data. Octopuses have sensitive skin, and have been witnessed to tear out tags (G. Ivey, personal communication to AL, 2004); Ivey implanted tags dermally and had an average retention of 27 h. She has had tag retention as long as 14 days using tags attached by cable tie through the septum (G. Ivey, personal communication to DS, 2004), a method

similar to that reported in this study for the 1996 releases. Attachment through the mantle (Rigby, 2004) has resulted in tag retention exceeding 21 days. The tags attempted in this study were quite large; use of smaller tags implanted inside the mantle (Rigby, 2004; G. Ivey, personal communication to DS, 2004; in squid, Webber and O'Dor, 1986; O'Dor et al., 1988) appears to be the method of choice for active instrumentation of cephalopods.

All instrumented octopuses in this study, regardless of treatment, moved deeper on release. Do these data support any interpretation other than that octopuses increase movement rates (at random with respect to habitat quality) or move to deeper water on handling? As we released five of seven octopuses in shallow water (<6 m depth, Table 20.4) one could argue that by chance alone they would move to deeper water. However, the data do not entirely support this. Petunia (released where captured) remained three days at her release site prior to moving, while Alan (relocated shallow) was released into higher quality habitat than his capture site and moved little at all (his tag was found in an unoccupied den with a midden, indicating he denned and foraged in the area). Furthermore, the greatest increase in depth came from the two treatment octopuses, which by this argument had the most opportunity to move shallow, but did not.

Alternatively, perhaps handled octopuses prefer deeper water as a response to stress (i.e., to avoid visual predators), the opposite pattern to that predicted by the hypothesis of active habitat selection for high-HQI sites. This explains the greater depth attained by octopuses relocated to deep water, and the fact that all 1996 octopuses (released where captured) initially moved at least slightly deeper. However, the 1996 and 2003 controls released in high HQI habitat showed little movement or depth change (Beth, Petunia, Alan, Table 20.4), while Suzi returned from deeper water to a site with a higher HQI. While this suggests that initial movement to deep water may be a result of handling, it also seems that relocated octopuses do not remain in deeper habitats for long.

Finally, it appears that octopuses show more movement when released into low HQI habitat. Indeed, for the 2003 octopuses, release HQIs are inversely related to the total distance moved by each octopus (Table 20.4, footnote 2) and not correlated with tag retention time. Due to short tag retention times on all 2003 releases, this study was unable to determine whether octopuses stayed for long at any relocation site. However, these results, albeit preliminary, indicate that the postrelease movements were affected by habitat quality [as reflected in release depth, Scheel (2002) and in HQI] at least as much or more than by chance or by handling artifacts. Octopuses seem more likely to leave a low-HQI site than to leave a high-HQI site. Further tracking and habitat data are needed to confirm this conclusion.

4.4 Habitat Selection and Foraging Models – Status and Need

The above sections led us to suggest that, first, octopus middens are consistent with octopuses acting as rate-maximizing foragers; and second, octopus response to relocation depends on habitat quality. With these initial conclusions in hand, can we

now correlate prey availability and the abundance of octopuses as a rate-maximizing predator showing aggregative response to prey?

This straightforward prospect does not hold up to scrutiny. While HQI_4 and octopus density were correlated with each other, neither showed significant correlation with any aspect of midden content, including diversity of items or measures of foraging success (number of items, summed length of items). Characters used in calculating HQI may be related to cover for octopuses (boulders and substrate), food availability (prey presence or absence), or both (kelp, depth, substrate), but other interpretations are possible. For example, kelp may serve as cover, as a food resource aggregating prey populations, or cover to potential prey, or may alter octopus and prey larval recruitment (Gaines and Roughgarden, 1987). While the correlation of these characters with octopus counts has previously been established (Scheel, 2002), little data exist to test mechanisms causing the correlation.

Nor did octopus population trends mirror prey population trends as measured in live prey surveys over the course of this study. Octopus densities increased and then declined over time (Fig. 20.1), while major prey densities increased throughout the study (Fig. 20.5). Furthermore, of the three predictions formulated above, the data allow us to reject both rate-maximizing forager alternatives: midden data was stable in the face of changing prey availability. Nor did octopus count parallel habitat productivity as reflected in live prey abundance. We are thus left with the alternative of octopuses as risk- or time-minimizing foragers. This behavior is consistent with the importance of shelter in octopus ecology. However, a more sophisticated approach to formulating hypotheses about foraging and habitat selection is needed.

Patch (habitat) selection models include the trade-off of foraging gain rate against (1) metabolic, (2) predation, and (3) missed-opportunity costs of foraging (Charnov, 1976; Brown, 1988). While foraging, octopuses may select prey as rate-maximizing foragers (as suggested by their selectivity for larger prey items and species). Metabolic costs are unlikely to vary among habitats. However, movement among foraging patches (Charnov, 1976) may be minimized due to high predation risk while in poor HQI_4 patches, which are characterized by low shelter and greater depth. Octopus life history reflects specialization on risk-minimization strategies (Hanlon and Messenger, 1996). Octopuses display diverse cryptic, deimatic, and protean escape behaviors¹. Other risk-minimizing strategies include use of dens for shelter, and transport of captured prey to the den for handling and consumption. Few data are available to examine perceived predation risk among octopuses, but within- and between-patch travel rates while foraging in habitats with varying cover could be used to examine active management of risk by octopuses. Missed opportunities costs potentially include those for reproductive activities, social activities, grooming and physiological maintenance, and den construction or maintenance. Octopuses increasingly forego foraging at the onset of maturity and reproductive activities, so that trade-off is managed by life history and unlikely to affect the sub-mature juvenile octopuses in this study. Octopuses are solitary, and, hence, social

¹Deimatic displays function to threaten, startle or frighten, from Deimos, Greek god of terror; while protean behaviors involve changing shape, from Proteus, a shape-changing sea-god.

activities are not important. Finally, grooming and den maintenance are both performed at the den and seem to occupy relatively little time, although the role of sleep in octopus is still uncertain. These trade-offs are promising avenues for further research, but at this time seem likely to be of minor importance to octopuses relative to foraging success and risk from predators.

Patch selection by octopuses should be modeled as a function of trade-off between foraging success within depletable patches (gain rate) and predation risk. The need for this type of model is emphasized by the following considerations. First, the lack of correlation between octopus counts or HQI_4 , and any aspect of midden content suggests that prey abundance be excluded as a determinant of habitat selection. Second, if so, of the habitat characteristics measured (depth, substrate, boulders, kelp cover), only kelp cover varies from year-to-year. Third, we do not have data to exclude the hypothesis that kelp cover may directly affect predation rates upon octopuses; however, kelp effects on prey densities or perception of predation risk were not suggested by our analyses (i.e., measured prey density did not significantly correlate with octopus counts; nor did foraging success rate measured from midden contents, which is expected to correlate with foraging effort).

Testing of this proposed model would require detailed data on within- and between-patch movement rates, and characteristics of habitat through which octopuses forage, as well as perceived predation risk estimated as proportion of time spent in and associated with a den; prey encounter rate, measured as counts



Fig. 20.7 *Shadow* during field testing in Prince William Sound. *Shadow* is a prototype submersible vehicle designed to remotely videotape a sonic-tagged benthic marine animal.

of representative prey encountered per minute foraging; average energetic rate of gain, measured as energetic content of captured prey per minute foraging over the full duration of each foraging bout; and giving-up harvest rate (also a measure of perceived risk), measured as energetic content of captured prey per minute foraging at the end of each foraging bout. Giving-up harvest rate corresponds to a rate that just balances metabolic costs, predation costs, and missed-opportunity costs of foraging in a patch (Charnov, 1976; Brown, 1988).

Such data have been hard to collect in foraging studies, even for terrestrial organisms, and new techniques are required to obtain such data for mobile benthic marine organisms such as octopuses. Shallow, tropical water videography has shown some promise for octopuses (Forsythe and Hanlon, 1997). One approach under development by the authors for cold or deep water is the use of acoustic-positioning telemetry, already adapted for cephalopod studies (e.g., O'Dor et al., 1988; Rigby, 2004), to simultaneously track both a target animal and a submersible vehicle for collection of behavioral and habitat data as the target animal forages and seeks shelter (Shadow, Fig. 20.7). Telemetry has been successfully used for positioning information in cephalopod studies, and the addition of underwater data would substantially increase the utility of such studies in interpreting movement data.

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