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Characteristics of Habitats Used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska

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With 6 figures and 6 tables

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Abstract. Habitat characteristics associated with the giant Pacific octopus, *Enteroctopus dofleini* (Wülker 1910), were studied in Prince William Sound and Port Graham, Alaska, from beach walk, SCUBA and submersible surveys at depths of 0 to 197 m. Octopus counts on beach walk transects were positively correlated with soft substrates (sand, gravel or broken rubble), the presence of boulders, and dense kelp cover immediately offshore of the transect; and negatively correlated with depth on SCUBA transects. No significant habitat correlations were found with counts on submersible transects. On beach walks, octopus counts were reduced on hard substrates to 38 % of the counts on soft substrates. Counts increased five-fold in the presence of boulders over counts in their absence, and increased fifteen-fold adjacent to dense (> 75 %) kelp cover over counts adjacent to sparse (< 25 %) kelp cover. On SCUBA transects, the average density at less than 5 m depth was over five times that below 5 m. No trends in octopus size or sex ratio were detected with depth. Den use was inversely correlated with depth although there was no indication that den availability declined with depth. Octopuses were found at densities from 0 to 2.5 per 1000 m^2. These densities were only 1 to 50 % of densities of the same species recorded in British Columbia in the late 1970s and early 1980s. Few data are available to test recruitment, mortality, and habitat selection hypotheses that would account for differences between habitats. However, the presence of the highest octopus densities in intertidal and very shallow subtidal areas indicates the likely importance of near-shore, shallow-water habitats, and highlights the vulnerability of octopus populations to changes in these habitats.

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Problem

The habitat in which an organism lives sets the stage for every aspect of its life, from meeting day-to-day energy requirements to species coexistence, evolutionary adaptations, and speciation. Habitat selection and use are thus important areas of study. Like all organisms, octopuses must obtain food, remain safe from predators or conspecifics, and maintain physiological homeostasis (at least within normal ranges) in the habitats they use. Although octopuses feed on many organisms (*e.g.,* Mather, 1991; Hanlon & Messenger, 1996) they also have prey preferences, indicating that prey availability influences habitat use (Mather & O'Dor, 1991). Physiological requirements (temperature, salinity, and oxygen) have not been examined closely for their influence on octopus habitat use. Temperature is known to affect egg maturation (Hartwick, 1983), abundance, and reproduction (Rees & Lumby, 1954), while salinity affects survival in juveniles (Hartwick, 1983) and local abundance (Hartwick *et al.*, 1984a). Octopuses maintain homeostasis for oxygen in low oxygen environments behaviorally by regulating respiration and skin circulation (Wells & Wells, 1983; Madan & Wells, 1996). Protection from predators and dominant conspecifics (Cigliano, 1993) has probably restricted some benthic octopuses to areas with suitable dens, although Aronson (1986) found that shelter use can directly limit octopus numbers even in the absence of predators, and a number of benthic species appear to live without dens on sand or mud flats and rely on crypsis and escape responses to avoid predation (Norman, 2000).

In general, however, the specifics of octopus habitat use remain poorly known. While growth and injury rates (Hartwick *et al.*, 1988; Smale & Buchan, 1981; Voight, 1992), physiological adaptations (Seibel *et al.*, 1997; Childress & Seibel, 1998), and local densities (Aronson, 1986; Iribarne, 1990; T. Anderson, 1997) are known to differ between habitats, few authors have examined characteristics of habitat, aside from dens, that may account for these differences. Beyond den availability (Aronson, 1986; Mather, 1982; Iribarne, 1990), a preference for edge habitats (reef edge) in *Octopus tetricus* (T. Anderson, 1997) or a preference for backreef over reeftop and forereef habitat in *O. cyanea* (Forsythe & Hanlon, 1997) influence habitat use.

The range of *Enteroctopus dofleini*, the Giant Pacific octopus, – previously *Octopus dofleini* Wülker 1910 (see Hochberg, 1998) – extends from Baja California in Mexico northward to Alaska and the Aleutian Islands in the eastern north Pacific and to Japan in the western north Pacific ocean. Diet, growth, and movement have been studied for this species in waters off Vancouver Island, British Columbia, Canada and in Japan; and aspects of the habitat ecology (*i. e.* dens, prey types) have been described from shallow subtidal waters (0 to 30 m) off Canada. In the eastern Pacific, Hartwick (1983) and Hartwick & Barriga (1997) reviewed early work, but see also Hartwick *et al.* (1984a, 1984b, 1988), Mather *et al.* (1985), Robinson & Hartwick (1986), Cosgrove (1987, 1993), Anderson (1996, 1997b) and Vincent *et al.* (1998). In the western Pacific, see *e.g.,* Mottet (1975) and Sato (1994, 1996). The studies in both areas were primarily related to fisheries biology. Information on habitat use of *E. dofleini* in Alaska and the northeastern Pacific ocean is important because this large octopus species is harvested by several different fisheries (diving, personal use and subsistence, trap, and trawl; Hartwick & Barriga, 1997). Moreover, commercial interest in this species is growing as increasing demand and declining supply overseas may provide a market incentive to develop an Alaska fishery (*e.g.,* Hartwick & Barriga, 1997). Subsistence harvest of intertidal juvenile animals suggests that populations may depend on nursery habitats in shallow coastal areas (*e.g.,* intertidal habitats, kelp beds, very shallow subtidal areas), typically considered at high risk of human disturbance including oil spills (*e.g.,* the 1989 'Exxon Valdez' oil spill in Prince William Sound), other pollutants and fertilizers, commercial fishing gear, and recreational use. Understanding habitat use can reveal ecological processes regulating growth rates, recruitment, survival and population dynamics, and is thus critical to management of important habitats.

Despite this need, a general description of habitat characteristics associated with the presence of *Enteroctopus dofleini* is lacking. It is unclear whether, and the extent to which, *E. dofleini* chooses habitat during recruitment (*i. e.* at settlement), actively as a benthic juvenile (subadult, *sensu* Young & Harman, 1988), or not at all, although recruitment is known to be variable within a single location for many species (*e.g., E. dofleini*, Hartwick *et al.*, 1984a; Hartwick & Barriga, 1997; *Octopus bimaculatus*, Ambrose, 1988; *O. vulgaris*, Rees & Lumby, 1954). The depth limits (especially the lower limit) of suitable habitats for this species are poorly known and the factors influencing differential recruitment into, mortality within, or selection among available habitats remain unknown. This paper is an initial step towards elucidating these issues by systematically examining the distribution and habitat use of *E. dofleini* in Prince William Sound and Cook Inlet, Alaska. Extensive use of intertidal habitats by this species in Alaska provided an opportunity to sample habitat use without the limitations or expense of underwater sampling. I present these data alongside comparable but more limited data collected by subtidal SCUBA and submersible diving in the same areas. I test three hypotheses that examine the role of topology, vegetation, and depth in determining octopus distributions: (1) physical habitat characteristics (substrate, boulders and others) can predict counts of octopus; (2) biological habitat characteristics (kelp or *Zostera* eel grass beds) can predict counts of octopus; and (3) the size distribution of octopus is not uniform, with larger individuals more common in deeper waters. This size-depth distribution may be expected if shallow water or large size provide a refuge from predators, or if larger individuals move off shore preparatory to the onset of mating and reproductive behaviors (see Hartwick *et al.*, 1988; Hochberg, 1997b).

Material and Methods

1. Study sites

Observations were made along the south-central coast of Alaska during June and July 1995, March to December 1996, and May and June 1998. Most work was conducted in Prince William Sound, AK (Fig. 1) during June and July. The Sound is a large, deep (to 870 m), tidal-influenced system. Extreme tidal heights were 5 m above mean lower low water (MLLW) to –1 m MLLW. Most sites around Prince William Sound were visited once or twice in 1995 and/or once in 1996. In addition, three sites were visited repeatedly in 1996 (Fig. 1): Windy Bay on Hawkins Island (60°34′ N, 145°59′ W), Gibbon's Anchorage on Green Island (60°16′ N, 147°27′ W), and an unnamed bay south of Stockdale Harbor on Montague Island (60°18′ N, 147°13′ W). Surveys also were made in March and July 1996 in Port Graham (59°21′ N, 151°49′ W, Fig. 1), a small protected fjord of Cook Inlet. The shoreline in Port Graham was generally not as steep or rocky as Prince William Sound. Tidal extremes at Port Graham were from 7 to –2 m MLLW. Surveys in 1998 were made at previously visited beaches on Green Island and by submersible along the western shelf of Green Island (60°16–18′ N, 147°25–32′ W), which consisted of a series of ridges, probably comprised of tilted turbidite layers (Lethcoe, 1990), descending from intertidal areas to below 250 m. The steeper scarp faces of these ridges faced downslope (northwest) and often accumulated loose material and boulders at their bases whereas the more gentle

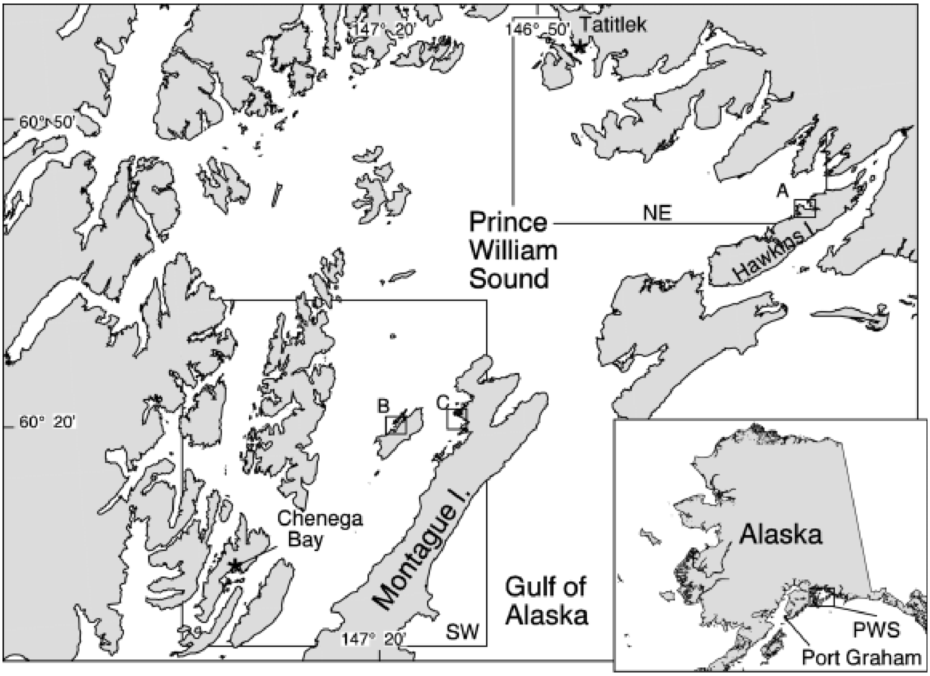

Fig. 1. Sampling regions in northeast (NE) and southwest (SW) Prince William Sound. SCUBA dive and beach walk sampling locations were spread throughout the two regions. Letters indicate locations that were sampled repeatedly: A: Windy Bay, Hawkins Island; B: Gibbon's Anchorage, Green Island; C: unnamed bay south of Port Chalmers, Montague Island. Inset shows study locations in Prince William Sound (PWS) and Port Graham, Alaska; asterisks the locations of the villages of Tatitlek and Chenega Bay.

dip slopes were landward (southeast). The Green Island ridge series enabled a natural experiment consisting of "replicate" rock ridge habitats at different depths. This series of ridges was mapped for this study in 1997 and 1998 using commercial echo-sounder sonar (typically used as a depth sounder or 'fish finder') and GPS to provide a two-dimensional profile along the ship's track of the depth and location of individual ridges (Schlee *et al.*, 1995).

2. Transect surveys

A research team (see Acknowledgements) and I conducted transect surveys in intertidal, shallow subtidal, and deeper subtidal areas (Table 1), using essentially the same technique at each depth. Transect surveys at all depths involved observers visually searching for juvenile or adult octopus (typically 500 g or larger, but individuals as small as about 10 g were recorded during deeper subtidal surveys), or their signs (middens at dens) along linear transects while also recording habitat information. In all cases, the area searched was estimated as the length of the transect times an estimate of transect width (based on distance from the centerline at which an octopus, den or signs could be spotted. This distance was a function of water clarity and observer search behavior such as zig-zagging). The recorded habitat characteristics included depth relative to mean lower low water (MLLW), substrate, presence or absence of boulders, and extent of other available cover (*e.g.,* broad-leaf kelp).

Substrate was defined by the dominant underlying matrix and was recorded as "soft" if mud, sand, gravel, or broken rubble (to 10 cm maximum particle size) and "hard" if cobble (10 cm to 1 m), bedrock (unbroken rock), or outcrop (rock projection). This division corresponded to substrates that octopuses could dig into

Table 1. Sampling design described in this paper for three transect techniques used to survey octopus densities at various depths.

technique	depth*	purpose	design	limitations
beach walk	+ 2 to – 1.5	Hypothesis: octopus associated with physical (substrate, boulders) & biological (vegetation) habitat characteristics. Depth was not a factor because all data collected from intertidal areas.	partial factorial	
SCUBA	– 0.5 to – 23.5	Hypothesis: octopus are associated with kelp. Depth categories: above –5; –5 to –10; –10 to –15; and below –15 m (see Fig. 6).	shallow vs. deep transects in dense vs. sparse kelp cover	depth & kelp cover correlated (see Results)
submersible	– 9.2 to – 197	(1) Hypothesis: octopus size distribution skewed toward larger animals at depth; (2) describe characteristics of habitats used by octopus below –30 m depth. Depth categories: –9 to –40 m (overlaps SCUBA surveys); –50 to –80; –85 to –120; and –150 to –200 m.	parallel transects along depth contours	small sample size (n = 21 transects and 18 octopus)

* Depth range [m] relative to mean lower low water (MLLW) of recorded transect samples.

(soft) versus those they could not (hard). Clearly, such distinctions are subjective and reflect a continuum of sizes: flat particles (broken rubble) are lighter relative to their linear size (and thus easier to move) than round ones (gravel or cobble), and larger octopuses are capable of moving increasingly large particles while excavating a den. Habitat features (depth, substrate, boulders and other cover) were evaluated as independent predictors of octopus counts using Poisson (discrete) regression.

Suspected octopus dens were identified by any one or more of the following signs: excavation under a boulder or rock; presence of a berm of gravel at the base of a boulder or rock; or a pile (midden) of crustacean, mollusc, and/or brachiopod shells representing typical octopus prey. Suspected dens were investigated by sight and using a flexible probe. Occupants were extracted by injecting a small amount of dilute sodium hypochlorite, a mild irritant. Use of a den was confirmed if characteristic marks (drills, bites) were found on shells in the midden (Dodge & Scheel, 1999) or if an octopus was seen at the den (not all dens have middens). If no octopus was seen or extracted the den was considered unoccupied (even if marked items in the midden confirmed prior use). Only occupied dens were used in all analyses. Dens were classified as either boulder (octopus sheltered under a large rock resting on top of any underlying substrate) or crevice (octopus sheltered in a crack or crevice in a more extensive hard substrate such as an outcrop, vertical wall, or bedrock). Above water during low tides, octopus were encountered in dens where they retreated as the tide fell (dens typically retain a small pool of water). When submerged, however, octopus were encountered either in a den, outside of a den but associated with it, or not associated with any obvious den nearby.

Beach walk transects were conducted in intertidal areas on foot during tides below –0.6 m MLLW. Ninety percent of the area sampled by beach walk transects (and over 95 % of the area sampled by SCUBA transects) was surveyed during June and July 1995 and 1996. Survey sites were chosen to sample habitats with different combinations of substrate, boulders, slope, and kelp cover at different depths. In 1995, individual sites were selected based on visual inspection from a small boat. In 1996, aerial surveys were flown during the early May low-tide series to select intertidal shoreline segments that fell into the following four habitat types: (1) steep without boulders or heavy kelp cover; (2) shallow-sloped without boulders or heavy kelp cover; (3) shallow-sloped with boulders but without heavy kelp; and (4) shallow-sloped with boulders and heavy kelp. Transects were linear surveys designed to be 100 m long and 10 m wide. Actual length and width varied depending on natural features at each site. Length and width were measured using a Leitz optical rangefinder, accurate to within 10 % for distances up to 1000 m, or with a 100 m measuring tape.

Two observers moving abreast of one another searched each transect for octopus dens. Observers 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 m MLLW) to the low water line (between –0.6 and –2 m MLLW). On beach walk transects, kelp cover on the transect and kelp cover adjacent to the transect (in the area just below the water line at the lower edge of intertidal transects) were recorded as percent cover (visually estimated as < 25 %, 25–50 %, 50–75 % or >75 % of Order Laminariales broad-leaf kelps, *e.g., Alaria marginata, Laminaria saccharina, Costaria costata*). In addition to kelp cover and the other three characteristics mentioned above, beach slope (estimated as one of four categories: flat, with a rise-to-run ratio less than 1:8; low, from 1:8–1:6; medium, from 1:5–1:3; and steep, > 1:3), and percent cover of *Zostera* eel grass in or adjacent to the transect were recorded. I also included two other variables in analyses of beach walk transects: sampling region (Fig. 1: northeast or southwest Prince William Sound, Port Graham) to look for regional differences; and because large amounts of oil were deposited in intertidal areas following the 1989 'Exxon Valdez' oil spill, I noted records of the presence of oil from the Alaska Department of Environmental Conservation (1989). Sites with heavy or moderate oil pollution in 1989 are classified as 'oiled' and those with none to light oil exposure in 1989 as 'un-oiled' or reference (Sundberg *et al.*, 1996). Captured octopus were weighed with a spring scale and subsequently released back into the den where captured. The irritant appeared to disperse quickly, as octopus frequently reentered the den where captured.

SCUBA transects followed the same procedures as beach walk transects, with the following differences. SCUBA sites were chosen at the down-slope base of submerged rock ridges, based on the bottom profile as shown by commercial echo-sounder sonar. In addition, paired dive sites, one shallow (2.0 to 11.6 m) and one deep (9.2 to 19.1 m), were located offshore of intertidal transects and at several sites in eastern Prince William Sound (Fig 1). SCUBA dives were considered paired only if the two dives were conducted on the same cruise (within seven days of each other) and at the same location, and differed in depth by at least 5 m. Transects were conducted by two or three SCUBA divers following a particular depth contour. Maximum, minimum, and contour depth of each transect were determined using submersible pressure gauges. SCUBA transects were typically 3–9 m wide and had a difference of 5 m or less between maximum and minimum depth. Analyses were based on the contour at the depth on which sampling was centered, recorded in one of four depth categories (5 m or shallower, 5–10 m, 10–15 m, and below 15 m). Transect lengths were measured underwater using a 100 m tape or on the surface from buoys deployed at the start and end of each transect. Visibility underwater was measured by Secchi disk and the width of each transect estimated by each diver based on visibility, kelp cover, and local terrain. Due to limited visibility, only kelp cover within each transect (and not kelp cover adjacent to the transect) was recorded. Octopuses were weighed and measured at the surface and released at the surface above their capture location. Due to the intent to test the association of octopus with kelp cover, the analyses of SCUBA transect data were limited to search area and kelp cover (Table 1; other habitat characteristics, cf. beach walk transects, were omitted).

Submersible transects also followed the same procedures as beach walk transects, with the following differences. All sampling was conducted from the two-man research submersible 'Delta' by one observer (either the author or T. L. S. Vincent) and one submersible pilot during May 1998. Transects were situated on the Green Island ridge series described above, within one of four depth categories (9–40 m, 50–80 m, 85–120 m, or 150–200 m). Analyses were based on the depth category for each dive. Exact dive sites were chosen as for SCUBA surveys, with the addition of side-scan sonar to aid in locating sub-surface features. Continuous data collectors recorded salinity, percent oxygen saturation, temperature, depth, and the location of the submersible (using Trackpoint II and differential GPS, accurate to within 5 m) throughout each dive. The surveyed transect also was video-taped continuously during each dive, and tapes were reviewed on the surface to record details of substrate and cover. Submersible transects were designed to be 1000 m long, but actual length varied depending on natural features at each site. Visibility was estimated by the pilot at the start of each dive, and transect width was calculated as length (measured from the tracking system) times visibility. Data recorded included area, depth, substrate, and cover. Boulders and kelp cover were subsumed under the latter variable (see below); slope was not analyzed due to the lack of an effect in the intertidal analyses (see Results); region and oiling history were not relevant because the depths on the Green Island shelf (single region) were below those where oil was deposited on the substrate.

3. Survey design and statistics

The various surveys had several different but overlapping intents (Table 1). Beach walk transects were intended to test the hypothesis that both physical and biological habitat characteristics are useful in predicting octopus counts. SCUBA surveys were designed to test the hypothesized association of octopus with dense Laminariales (brown algae) kelp cover. Submersible surveys were designed to test the hypothesis that larger animals were more prevalent at depth and to describe octopus habitats below SCUBA depths (*i. e.* below 30 m). The SCUBA surveys slightly overlapped the beach walk and submersible surveys in depth range. Data from this overlap were too sparse for statistical analysis, but did allow a qualitative comparison of densities (see Results). Individual survey sites were not systematically re-sampled at the same dates and times as would be necessary to rigorously compare survey techniques. All data sets contributed to an over-all description of octopus habitat.

For each beach walk transect, the beach segment was selected for homogeneous slope, substrate, and kelp cover. Sampling was discontinued before 100 m if a major habitat-type change (*e.g.,* from bedrock to gravel) was encountered. In SCUBA and submersible, the locations of major habitat changes along the transect were recorded. In such cases, the benthic area searched was calculated separately for each habitat. For SCUBA transects where the variable of interest was kelp cover, and where survey distances were short (< 100 m, less than the home range diameter of an octopus; Mather *et al.*, 1985; and author, unpublished data), kelp cover was analyzed as a weighted average over the area surveyed. Submersible transects were close to 1000 m long (more than three times home range diameter) and habitat characteristics and cover varied dramatically within a single transect. Individual submersible transects were therefore subdivided for analyses into 'sections' of uniform substrate and cover. Sections were greater than 10 m long (if < 10 m, data were added to most similar adjacent section). Thus 21 transect dives yielded 263 sections. To adjust for pseudo-independence of these sections and the increased "sample" size, a transect number was included as a block effect in the analysis.

Counts of octopus numbers on each transect were analyzed using Poisson (discrete) regression models, and each transect was treated as an independent sample (except submersible transects, where each section was treated as an independent sample, see above). Poisson regression is the standard model used when the dependent variable is count data (McCullagh & Nelder, 1983; Cameron & Trivedi, 1998). An assumption of Poisson

Table 2. Numbers of transects conducted by survey type, year, and sampling region. Numbers of *Enteroctopus* found on transect surveys are indicated in parentheses. Sampling regions for SCUBA transects were not tabulated by depth.

survey type	beach walks	SCUBA transects		SCUBA transects by depth (includes paired transects)				submersible transects
year & sample region		total	paired	< 5 m	5–10 m	10–15 m	> 15 m	depths from 10–200 m
Port Graham (1996 only)	18 (16)	–	–	–	–	–	–	–
Prince William Sound (1995–98 total)	72 (57)	56 (19)[e]	18 (8)	6 (5)	10 (3)	23 (6)	17 (5)	21 (18)
1995	30 (27)	23 (8)	–	0	1 (0)	8 (3)	14 (5)	–
1996	42 (30)	33 (11)	18 (8)[f]	6 (5)	9 (3)	15 (3)	3 (0)	–
1998	–	–	not tabulated					21 (18)[g]
Green Island [a]	16 (17)	13 (5)						–
N Montague Island [b]	13 (9)	12 (6)						–
other SW PWS [c]	32 (23)	12 (1)						–
NE PWS [d]	11 (8)	19 (7)						–

[a] At Green Island, one beach walk transect (6 octopus found) and two SCUBA transects (2 octopus) were conducted in 1995; the remainder were conducted in 1996.

[b] At N Montague Island, all beach walk and SCUBA transects were conducted in 1996.

[c] At other southwest Prince William Sound sites, survey effort was roughly split between 1995 (18 beach walk transects, 13 octopus; 8 SCUBA transects, 1 octopus) and 1996 (14 beach walk transects, 10 octopus; 4 SCUBA transects, 0 octopus).

[d] At northeast Prince William Sound sites, all beach walk transects were conducted in 1995. SCUBA transects were conducted in both 1995 (13 transects, 5 octopus) and 1996 (6 transects, 2 octopus).

[e] Of 56 SCUBA transects and 19 octopus, three transects including 1 octopus were dropped from Poisson regression analysis due to missing data.

[f] See Table 5.

[g] Submersible transects were all conducted in 1998 along the western shelf of Green Island.

Table 3. The count of *Enteroctopus* encountered on each transect was analyzed with respect to habitat characteristics associated with that transect. Multi-variate Poisson regression results are presented for each of the three transect types.

analysis	n var./mean	source	coefficient	size of effect[a]	drop-in-deviance	df	P = significance[d]
beach walk	87[b]	area (forced)	0.00011	1.000	10.9	1	<0.001***
	1.992	substrate	–0.9526	0.386	8.7	1	0.004**
		boulders	1.7481	5.744	10.7	1	0.001***
		adjacent kelp cover	0.3309	1.392	9.8	1	0.002**
		kelp cover in transect	–0.1316	0.877	1.2	1	0.273
		Zostera cover (in & adjacent)	0.0023	1.002	0	1	1.000
		slope	–0.302	0.739	2.78	1	0.095
		region	0.344	1.411	2.0	2	0.368
		oiling history	0.993	2.699	2.13	1	0.144
SCUBA	53[b]	area (forced)	0.0002	1.000	1.99	1	0.158
	0.99	depth [cm]	0.0009	1.001	3.86	1	0.049*
		kelp cover	0.0312	1.032	0.27	1	0.603
submersible	263[c]	area (forced)	0.0009	1.001	5.93	1	0.015*
	1.05	dive (forced)	0.0074	1.007	0.06	1	0.806
		depth [m]	0.1990	1.220	0.72	1	0.396
		substrate	0.7120	2.038	1.44	1	0.230
		cover	–0.5485	0.578	0.89	1	0.345

[a] 'Size of effect' = exp(coefficient). A value of 1.05 indicates that a 1-unit increase in the independent variable increases the dependent variable by five percent when all other variables are held constant. Values of less than one indicate that octopus are associated with a soft rather than hard substrate (beach walks), and with the absence rather than the presence of cover (submersible). Depth in this regression (SCUBA) is measured in centimeters and values deeper than mean lower low water (MLLW) are negative (for ease of applying tide table corrections). Therefore the measured effect of 1.001 (0.1 % per centimeter) converts to 10 % increase in octopus counts per meter change in depth, as water becomes shallower (*i. e.* counts are highest in shallow water; see Fig. 6 and discussion in text).

[b] Some sets with missing data were dropped from these analyses.

[c] n = 263 sections from 21 transect dives. See text for explanation.

[d] * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

regression is that the (conditional) variance and mean are equal (equidispersion; Cameron & Trivedi, 1998). This assumption was tested by comparing the mean and variance of the count variable. If the variance is more than twice the sample mean, then the assumption of equidispersion should be rejected (data are overdispersed; Cameron & Trivedi, 1998: 77). Regressions were run in a reverse step-wise fashion using a p-value of 0.1 to drop a variable, with the area of the transect included (forced) in each run. A maximum-likelihood method, in which the drop-in-deviance has an asymptotic chi-square distribution, was used to assess each variable in the over-all model (Ramsey & Schafer, 1997).

Sample sizes ranged from n = 18 to n = 57 octopus counted on n = 21 to n = 87 transects (Tables 2 and 3). I assumed that the chi-squared distribution applied to the models of these data. I considered results for the beach walk transects significant at $P = 0.01$ rather than 0.05 to reduce the experiment-wide error rate due to the large number of drop-in-deviance tests used in the analyses. Statistical procedures for the SCUBA transects were identical, except that I considered only two variables, namely, vegetation within the SCUBA transect and depth. SCUBA surveys were specifically designed to test the effect of these two variables, and no other variables were considered here. Results were considered significant at $P < 0.05$ because fewer tests were required. Statistical procedures for the submersible data included analysis of depth, substrate, and cover only, and the results were also considered significant at $P < 0.05$. Another assumption of Poisson regression is that there is no excessive collinearity between independent variables. This does not appear to be a problem for the beach walk or submersible transects, although percent kelp cover and depth were correlated on SCUBA transects (see Results). However, because kelp cover was dropped during reverse step-wise regression, collinearity does not affect my conclusions regarding the effect of depth on octopus. Prey availability and diet also may influence octopus habitat use. These factors were too complex to permit inclusion here, but data from this study were presented in Vincent *et al.* (1998) and I consider these in the Discussion.

4. *Octopus* measurements

When an octopus could be captured and handled (beach walk and SCUBA sampling), the following measurements were recorded: wet weight, interocular distance, mantle length (tip of mantle to between the eyes), and sex (in males, the right third arm is hectocotylized and modified at the tip by the presence of the ligula in individuals 300 g or larger. Smaller individuals were recorded as female in six cases where the right third arm was inspected and lacking a ligula; as sex unknown otherwise). In the submersible sampling, octopuses were video taped for the duration of the encounter and sex was only recorded if the tip of the right third arm could be closely inspected in the field. Scale was indicated in each frame of the video by a pair of red dots from parallel lasers spaced 20 cm apart. Interocular distance and mantle length were estimated from the video using the laser scale, and weight estimates were made by the observer in the submersible at the time of the encounter and by linear regression. The regression using interocular distance (IO, $n = 106$, $r^2 = 0.85$) was:

$$\ln(\text{weight estimate}) = 2.8233 \cdot \ln(\text{IO}) + 2.347$$

and that using mantle length (ML, $n = 117$, $r^2 = 0.66$) was:

$$\ln(\text{weight estimate}) = 2.1976 \cdot \ln(\text{ML}) + 1.8025$$

Regression equations were determined from a sample in this study of 117 captured octopus for which weight and one or both length measurements were available. Finally weights were recorded either as measured (if available) or as estimated weight, the latter based on the interocular distance regression (if available) or on the mantle length regression. In one case, no measurement was available from videotape, and the observer's estimate was used.

Results

1. Sample effort, octopus, and water chemistry

I completed a total of 176 survey transects (90 by beach walk, 56 by SCUBA, 21 from submersible). SCUBA transects comprised 61.9 diver hours. The distribution of surveys by method, year, geographic location (for beach walk transects), and depth (for SCUBA transects) is given in Table 2. A total of 116 octopus were found during these surveys (Table 2), at depths ranging from 0 m above MLLW to 183 m below. Of these, 19 were found by SCUBA, or one every 3.3 diver hours. An additional 62 octopus were observed incidentally (not on a survey transect) during the study yielding a total of 178 animals. Of these, weights or weight estimates are available for 176 and sex was recorded for 117. Weight and depth were not correlated (Fig. 2). Only 9 octopus found below 10 m depth (6 females and 3 males) were sexed so no analysis of sex versus depth was possible. For individuals found shallower than 10 m, the average mass of females ($n = 76$) was 2600 g (range 4 to 7530 g), of males ($n = 32$) 2800 g (range 300 to 9000 g).

Profiles of water chemistry (temperature, oxygen saturation, and salinity) recorded from the submersible 'Delta' are typical of Spring water profiles in Prince William Sound (Fig. 3). Temperature ranged over 0.7 °C, declining from a maximum at the surface to a minimum at about 100 m depth. Below 100 m to 200 m, temperature slowly rose again. Oxygen was saturated at the surface and declined to about 70 % saturation at 200 m. Salinity varied over 1.5; the water was freshest at the surface (32) and salinity increased with depth.

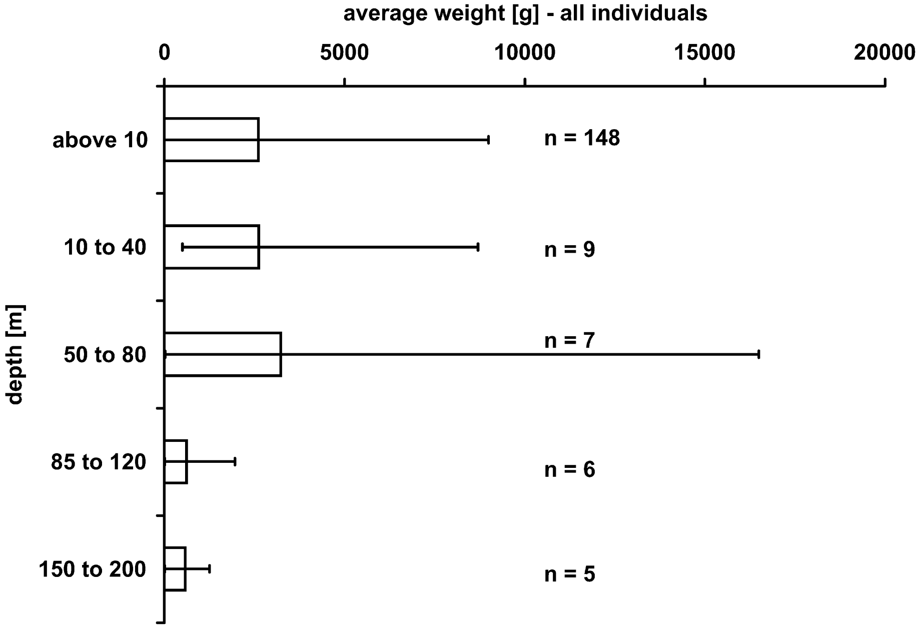

Fig. 2. Average weight, in grams, of *Enteroctopus* recorded from various depths (sample size indicated beside each bar) including animals measured during beach walk, SCUBA, and submersible transects as well as those captured incidentally. Values from submersible transects were estimated by linear regression from measurements of body size (see text for details). Bars indicate **range** of the data, not error.

2. Habitat associations

The beach walks were best able to detect habitat associations of octopus (more surveys, more octopus; Tables 2–3). The assumption of equidispersion (ratio of variance to mean not greater than 2.0) for Poisson regressions was tested and met for each of the three samples analyzed using this test (Table 3).

The largest areas surveyed on beach walk transects were comprised of boulders on soft substrate, either adjacent or not adjacent to kelp beds (Figs. 4 and 5), although hard beaches with boulders adjacent to kelp beds were also well represented in the sample. This occurred for three reasons. First, there is a correlation between the area surveyed and beach slope (on steep beaches, relatively little shoreline is exposed by the retreating tide); and in Prince William Sound, flat or gently sloped beaches tend to occur at the base of rocky ridges, to be comprised of soft sediments, and to include boulders sloughed off the rocky ridge. (Flat, soft sediment beaches also occurred away from rocky ridges, *e.g.,* mud flats, but these beaches characteristically lacked boulders.) Second, rocky ridges above sediment, gravel or rubble slopes are common intertidal and subtidal habitats in Prince William Sound, regardless of aerial extent of the habitat exposed at low tide. Third, these beaches fit a preliminary model of good octopus habitat and hence were sampled more frequently than beaches identified as poor habitat and where octopus were seldom if ever found. The latter beach types as well as mud flats

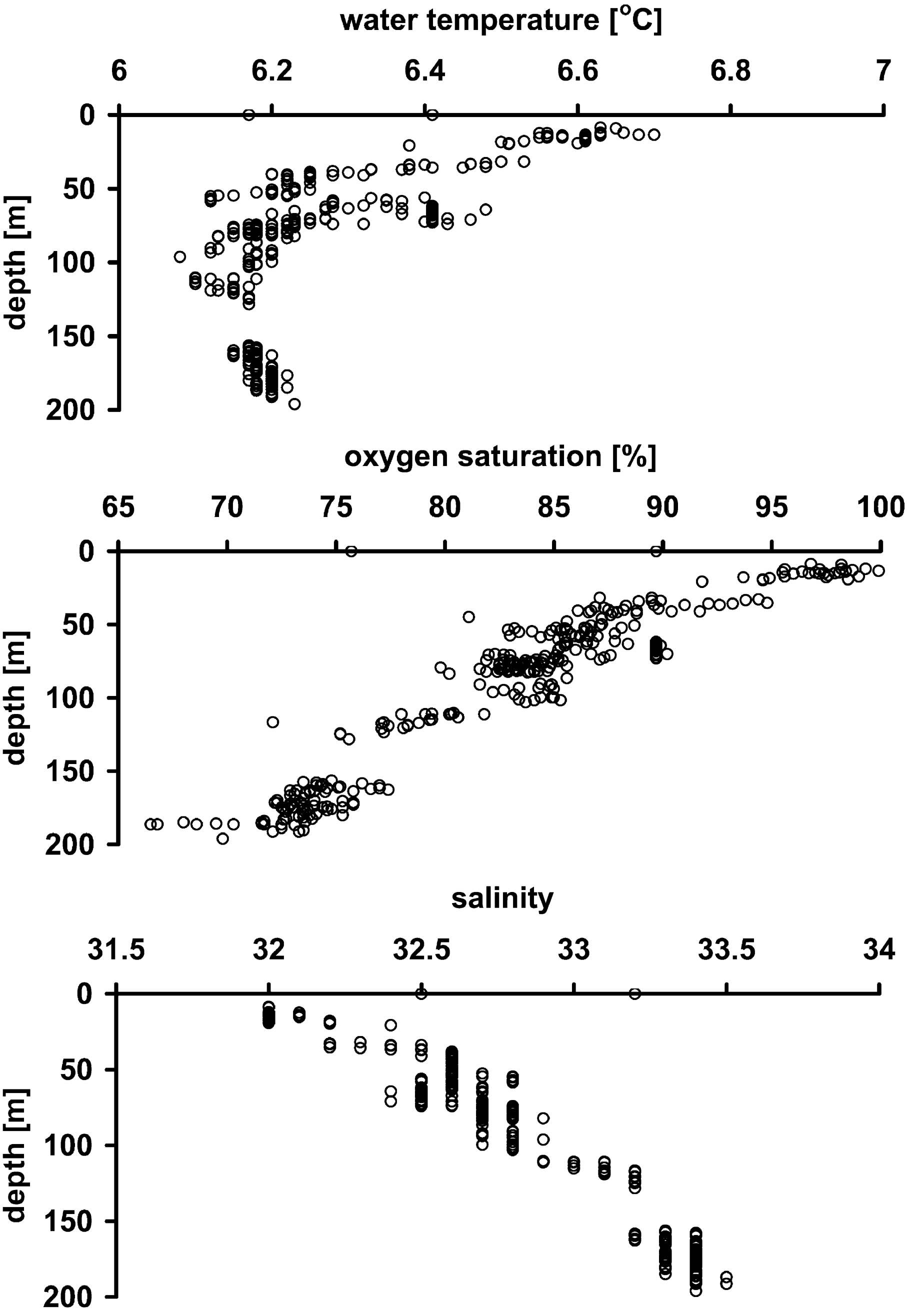

Fig. 3. Physical parameters of water sampled during all May 1998 dives from the submersible 'Delta' near Green Island in Prince William Sound.

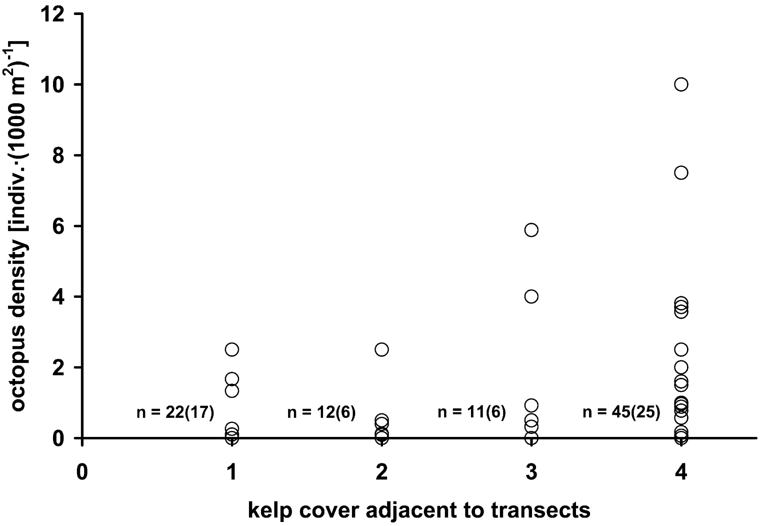

Fig. 4. Octopus density and adjacent kelp cover recorded from beach walk transects. Adjacent kelp cover was recorded from the area just below the water line at the lower edge of intertidal transects as percent cover (visually estimated as 1 = < 25 %; 2 = 25–50 %; 3 = 50–75 %; or 4 = > 75 %) of Order Laminariales broad-leaf kelps. Each data point represents one transect approximately 100 m long by 10 m wide. Number of transects are indicated, with the number of coincident points of density = 0 in parentheses. See text for details.

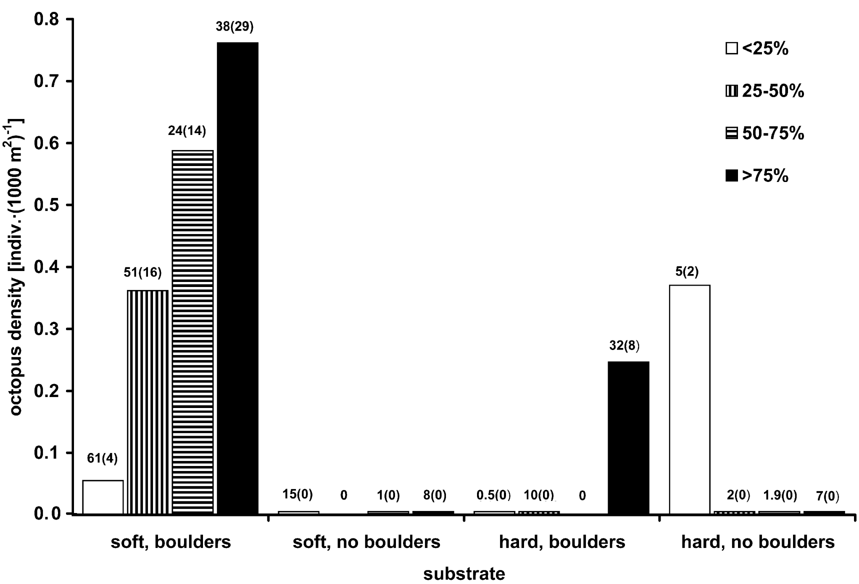

Fig. 5. Octopus density in different intertidal habitat types. Percent cover of broad-leaf kelp adjacent to each transect is shown in the key. The area searched (in 1000 m^2), with the number of octopus found in parentheses, is indicated above each column. Substrate characteristics were: soft (mud, sand, gravel, or broken rubble) versus hard (bedrock, rock outcrops, or cobble fields), and boulders present versus boulders absent. These form four substrate categories as indicated.

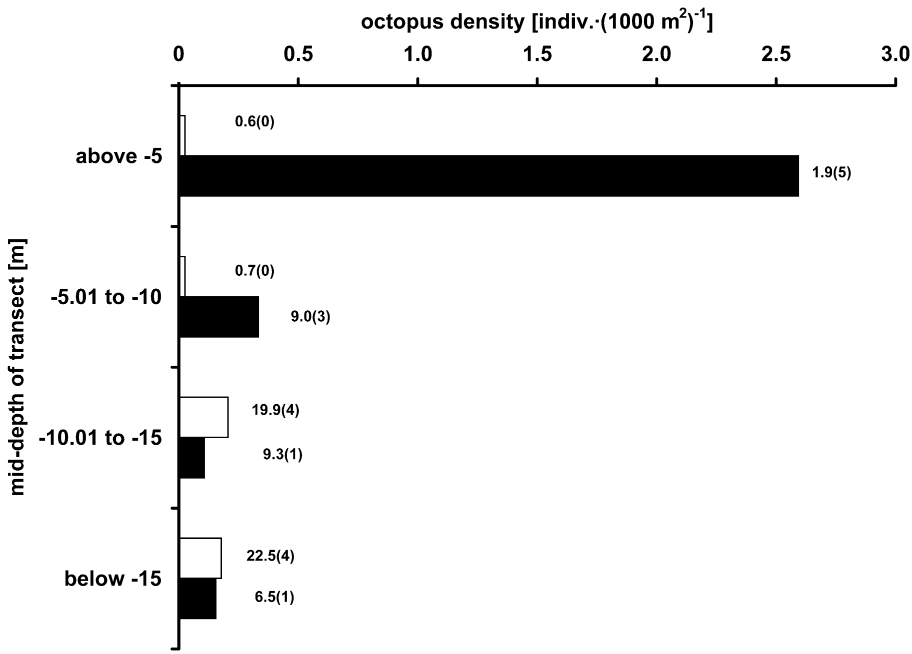

Fig. 6. Octopus density at different depths on SCUBA dive transects. Sample sizes indicated beside each column are as in Fig. 5. Open bars indicate in-transect broad-leaf kelp cover of < 50 %; dark bars, kelp cover of > 50 %.

were sampled sufficiently to establish the relative absence of octopus there (Table 3, Fig. 5).

In beach walk transects, octopus counts were significantly associated with the total area searched and with increasing kelp cover adjacent to the transect (Table 3, Figs. 4 and 5). Octopus counts also were higher on soft substrates with boulders compared to soft substrates without boulders or to hard substrates with or without boulders (Fig. 5). No significant associations were found with kelp cover on the transect, *Zostera* (eel grass) cover on and adjacent to the transect, slope, geographic region, or oiling history (Table 3). Average densities in different habitat types on beach walks ranged from 0 to 0.78 octopus per 1000 m^2 searched (Figs. 4 and 5).

SCUBA transects were conducted in habitats similar to most beach walk transects, that is, on gentle slopes comprised of soft sediments and boulders at the base of submarine rocky ridges. This habitat was explicitly chosen (see Methods) over other habitats such as steep, hard, submarine cliffs, although some cobble fields (hard) were also surveyed. Thus the primary environmental variables on SCUBA transects were available kelp cover and depth (Fig. 6).

On SCUBA transects, no significant associations were found with search area or with kelp cover (Table 1), but higher octopus counts were significantly associated with shallower transect depth (Table 3, Fig. 6). However, kelp cover and depth were significantly correlated. (On SCUBA transects in 1996, greater kelp cover was significantly correlated with shallower transect depth: linear regression, n = 33, $r^2 = 0.30$, $P < 0.001$.

Table 4. Characteristics of habitat searched by SCUBA diving.

depth [m]	SCUBA transects	dense kelp[a]	boulders on soft substrate[b]
0 to –5	6	76 (5)	57 (3)
–5 to –10	10	93 (7)	70 (6)
–10 to –15	21[c]	33 (6)	74 (13)
below –15	16[c]	22 (6)	34 (7)

[a] The percent of search area covered by transects (and number of dives in parentheses) on which dense kelp (> 50 % cover) was recorded.
[b] Percent of search area covered by transects (and number of dives in parentheses) on which boulders on soft substrates were recorded.
[c] Number of transects does not match Table 2 because 3 dives with missing data were not included in this tabulation.

See also Table 4). Only 9 sets of paired SCUBA transects were completed (Table 5). Low sample size and the large number of pairs with zero counts (n = 5) preclude meaningful statistical analyses as paired data. Within these pairs, 6 of the 8 octopus found were on the shallower transect.

More octopus were found in dense kelp cover, even though the algae typically obscured the bottom. This was particularly true where kelp was anchored to larger material (*e. g.,* boulders or large rubble) deposited on soft sediment. Suitable substrate was also required, however, rather than kelp alone. Octopus densities in kelp beds anchored in cobble fields (a hard substrate, where round cobble typically > 0.5 m diameter rested on a pile of similar rocks) were only 16 % of those in kelp beds anchored to boulders resting on gravel or broken rubble (soft sediment; densities in cobble fields: 1 octopus in 1934 m^2 searched; in boulders on gravel or broken rubble: 5 octopus in 1583 m^2 searched. These ranged from 2 to 13 m depth). Average densities in shallow water kelp beds surveyed by SCUBA ranged from 0 to 2.5 octopus per 1000 m^2 searched (Fig. 6).

Table 5. Octopus counts on 9 sets of paired SCUBA surveys, where the depth difference between the shallow and deep dive was at least 5 m. All dives in this table were included in regression analyses (Table 3).

	deep dives				shallow dives			
general location in PWS	depth [m]	kelp cover	area*	count	depth [m]	kelp cover	area*	count
Hawkins Island								
Windy Bay	17.5	< 25 %	510	0	8.3	< 25 %	200	0
Montague Island								
Stockdale Harbor	11.0	< 25 %	200	0	2.8	25–50 %	100	0
Port Chalmers	12.8	< 25 %	600	1	2.0	25–50 %	750	2
north island	13.2	< 25 %	750	0	6.1	25–50 %	1200	1
northwest island	9.2	25–50 %	428	0	2.3	25–50 %	258	1
Chicken Island	19.1	< 25 %	800	0	11.6	< 25 %	900	0
Green Island								
Putnam Pt.	13.4	< 25 %	457	1	6.0	25–50 %	800	2
west island	14.8	25–50 %	600	0	9.4	25–50 %	900	0
Gibbon’s Anchorage	10.2	25–50 %	212	0	2.5	25–50 %	620	0

* Area searched, in m^2.

The availability of habitat with boulders on soft substrate did not decline with depth, except perhaps below 15 m (Table 4).

Sites for submersible transects also were chosen to sample the same habitat (gentle slopes comprised of soft sediment and boulders at the base of rock ridges). Most transect sections were soft sediment, although about 50 % of the sections were steep rather than gently sloping, and about 60 % were not immediately within sight of a rock ridge. Boulders and other cover were about equally prevalent on steep and gentle slopes. These discrepancies reflect the difficulties locating and running a transect at the base of a rock ridge: transect lengths were often longer than ridge segments; underwater ridges often sat on steep rather than shallow slopes; visibility was often only a few meters, making it difficult to maintain visual contact with a ridge segment.

The submersible enabled habitat associations to be described in deeper water (Table 1). Higher octopus counts were significantly associated with greater area searched. No significant associations were found within dives, with depth, substrate, or available cover (Table 3). Octopus were more likely to be encountered here in the absence of rock ridges, boulders, or other cover than on SCUBA transects in the absence of similar cover (see below). A similar comparison to beach walk transects was not appropriate because octopus on beaches were restricted to shallow-water pools (typically inside dens) during the low tide survey periods. Average densities in each depth category were 0.16 octopus $\cdot$ $(1000\ m^2)^{-1}$ (9–40 m), 0.20 $\cdot$ $(1000\ m^2)^{-1}$ (50–80 m), 0.17 $\cdot$ $(1000\ m^2)^{-1}$ (85–120 m) and 0.38 $\cdot$ $(1000\ m^2)^{-1}$ (150–200 m).

3. Den use

Den descriptions were available for 158 octopus (data was not recorded or inadequate for 20 animals), of which 105 were associated with a boulder den (average octopus weight 2.5 kg; average den depth 6.0 m), 41 with a crevice den (avg. weight 2.25 kg, avg. depth 6.8 m), and 12 found out in the open not obviously associated with any nearby den (avg. weight 0.62 kg, avg. depth 82.5 m). Animals not associated with a den were clearly smaller than those in dens and were found in submerged habitat, rather than in habitat exposed by low tides (8 were found by submersible, 3 by SCUBA, 1 during a beach walk swimming along the water line).

Table 6. Counts of octopus detected inside a den or out in the open during SCUBA and submersible surveys.

	SCUBA (shallow)	submersible (deep)	average depth[1] [m]	average estimated weight[1] [g]
inside den	18	4	48 (4)	1067
out in the open	4	13	129 (13)	511
Fisher exact test[2]	n = 39, P (2-tailed) < 0.001			
Mann-Whitney U test[3]			$R_{out}/n_{out} = 10.8$, $R_{in}/n_{in} = 3.00$, $U = 50.0$, $P < 0.001$	
			$R_{out}/n_{out} = 7.88$, $R_{in}/n_{in} = 12.6$, $U = 40.5$, $P < 0.131$	

[1] For octopus detected by submersible (n indicated in parentheses).
[2] Comparison is between the frequency of 'in' vs. 'out' on SCUBA vs. submersible samples.
[3] The first comparison is between depths of octopus found in dens versus those found out of dens; the second comparison is between estimated weights of the same animals.

Octopus were more likely to be out of their dens when detected by submersible (deep) than when detected by SCUBA (shallow) (Table 6; Fisher exact test). Perhaps octopuses in their dens are more difficult to spot by submersible versus by SCUBA. However, for submersible data only, the average depth of octopus out of their dens was deeper than of those in their dens, which suggests that the difference in the two surveys reflects a change in octopus behavior, rather than in observer ability. The average body size of the two groups on submersible surveys only were not significantly different (Table 6; Mann-Whitney U tests).

Discussion

Characteristics of habitats used by the Giant Pacific Octopus, *Enteroctopus dofleini*, were identified using three similar methods for progressively deeper surveys (Table 1). The null hypotheses that physical and biological habitat characteristics do not influence octopus distributions were rejected. However, the null hypothesis of no difference in octopus size distribution across depth could not be rejected. Despite slight differences in survey methods by depth, the results nevertheless indicated that depth is an important component of habitat. *E. dofleini* were more abundant in intertidal and subtidal areas at less than 5 m depth than in deeper areas. This was apparent from data using a single method (SCUBA; Fig. 6). The effect was large (average density at less than 5 m depth was over five times that measured on deeper SCUBA surveys; Table 3, Fig. 6). This also holds true across data sets (shallow versus deep SCUBA, Fig. 6, and submersible). While the highest average densities from beach walk surveys (boulders on soft substrate adjacent to dense kelp; Fig. 5) were not as high as on < 5 m depth SCUBA surveys, they were higher than on all deeper SCUBA or submersible surveys. Paired dives also support this pattern: 6 of 8 octopus were found on the shallower dive of a pair (Table 5), although small sample size precluded statistical analysis.

Is it reasonable to compare results across survey methods? On one hand, search efficiency probably declined with increasing depth. Visibility decreased from beach walks to SCUBA to submersible. On the other hand, shallow SCUBA surveys (–0.5 to –5 m) recorded an average octopus density in dense kelp greater than the highest average beach walk values (+2 to –1.5 m; Figs. 5 and 6). Thus, although these two results differed by a factor of three at similar depth, both indicate the highest average densities shallower than 5 m and that these values were greater than those below that depth. The average octopus densities at –9 to –40 m were similar, whether recorded by SCUBA or submersible (SCUBA from –10 to –23.5 m, 0.1 to 0.2 per 1000 m^2, see Fig. 6; submersible from –9 to –40 m, 0.14 per 1000 m^2, see Results). Thus, results from these methods are roughly comparable.

Depth probably does not directly influence octopus ecology, but many physical and biological factors that co-vary with depth may play a role. Octopuses may tend to occur within specific boundaries of salinity, temperature, or oxygen. Hartwick and co-workers (1984a) and Hartwick & Barriga (1997) discuss a positive correlation of octopus abundance with salinity in the range of 19–27. Death may result at salinities below 17 ppt (Hartwick, 1983). A similar positive correlation between salinity above 34 and abundance was found for several species of *Loligo* squid in the North Sea (Waluda & Pierce, 1998). The salinity range in Prince William Sound in May 1998 (Fig. 3) was

32–34, more saline than the waters in which Hartwick reports decreased octopus abundance. The 1998 values are slightly higher than in previous years (1994 to 1997) in May at a nearby station (29 to 32.5, S. Vaughan unpublished data). Salinity was lowest at the surface, where octopus counts in 1995–1996 were high. Octopuses are not known to avoid high (33–35) salinities. Thus salinity does not appear to explain the depth variation in octopus densities. Both the temperature and oxygen saturation were highest at the surface and declined with depth (reflecting octopus densities). However, neither variable showed an abrupt change in shallow water; nor were the changes very large. Temperature varied by 0.6 °C between the surface and 100 m depth during May in 1998 (Fig. 3). May values from 1994 to1997 in nearby waters were slightly cooler (5.3 to 6.5 °C at the surface, 4.8–5.2 °C at 100 m; S. Vaughan, unpublished data). The May 1998 temperatures were at the low end of those typical of the species' presence in waters off Canada and Washington (7–15 °C, Hartwick & Barriga, 1997; 6–13 °C, Anderson, 1997a), although previous northeastern Pacific studies were located further south in warmer waters. Such temperature changes are within the known tolerances of this species (Anderson, 1997a). Oxygen saturation declined from near 100 % (~ 9.6 mg $\cdot$ l^{-1}, Spotte, 1992, p. 152) to less than 80 % (~ 7.7 mg $\cdot$ l^{-1}) over the same depth range (Fig. 3). *Enteroctopus dofleini* has been successfully maintained in captivity at dissolved oxygen levels of 8.8 ppm (Anderson, 1997a). Octopuses can regulate their oxygen intake through increased respiration to saturations of 50 % or less (*Octopus vulgaris*, Wells & Wells, 1983). Therefore, physical and chemical parameters of water do not account for the effect of water depth on octopus density.

The incirrate octopuses include specialists in different habitats, including several families of oceanic (epi- and meso-pelagic) species (Norman, 2000). The family Octopodidae includes benthic forms. While many octopuses live on rocky or coral reefs, others are known to inhabit kelp holdfasts, sand, or mud habitats (*e.g., Octopus californicus*, see Hochberg, 1997a; *O. bimaculoides*, see Lang, 1997; *O. bimaculatus*, see Ambrose, 1988). Some species reach their highest densities in intertidal and shallow subtidal areas (*Octopus tehuelchus*, see Iribarne, 1990) or forage intertidally during low tides (Mather, 1991; Norman, 2000). *Enteroctopus dofleini* primarily occurs near rocky reefs and boulder areas with sand-shell hash bottoms but are also known from sand or silt flats (Hartwick & Barriga, 1997).

The relatively large data set from beach walk transects (Table 2) revealed that octopus counts were higher when (1) boulders were present in the habitat, (2) the substrate was soft, and (3) there was dense kelp cover adjacent to the transect (Table 3, Figs. 4 and 5). These results match general habitat descriptions from Japan and British Columbia (Mottet, 1975; Hartwick, 1983; Hartwick & Barriga, 1997). The smaller submersible data set yielded different results (SCUBA data were intended for different purpose; Table 1). Each of these effects were substantial (Table 3; Figs. 4 and 5): (1) hard substrates reduced octopus counts to 38 % of the values on soft substrates; (2) the presence of boulders increased counts five-fold over counts in their absence; and (3) an increase of 25 % in adjacent kelp cover increased counts by 39 %. Cumulatively, these three variables explained a significant portion of the variance in the intertidal data, whereas the remaining variables did not (kelp cover in transect, *Zostera* cover, slope, region, and oiling history; Table 3).

What is responsible for these correlations? Substrate may affect settlement rates. For example, juvenile cod, silver hake and cunner recruitment to the substrate varies by sea floor habitat (see Lindholm *et al.*, 2001, and references therein). Substrate also may affect mortality rates (by providing shelter), and habitat selection, in turn affecting density. Correlations between density and boulders suggest that this substrate plays a critical role as shelter, but does not indicate the extent to which shelter influences recruitment, mortality, and habitat selection. Shelter quality is known to influence productivity in at least one octopus species (Iribarne, 1990), and shelter abundance influences local density for many small octopuses (*Octopus joubini*; Mather, 1982; *O. tehuelchus*; Iribarne, 1990; *O. tetricus*; T. Anderson, 1997). In this study, *Enteroctopus* individuals were more likely to be out in the open (not associated with a den) in deeper water, and also were more likely to be found sitting outside rather than inside their dens when detected by submersible (deeper) versus SCUBA (shallow; Table 6). In deeper habitats, the animals may rely less on the available shelter (independent of differences in size with depth; or fewer boulders below –5 m, see Table 4; or different survey techniques). These behavioral observations suggest that octopus density is not limited by the absence of desirable cover as depth increases. Paust (1988; 1997) suggested that the abundance of natural dens in north Gulf of Alaska waters may account for the poor success of lair-pot fishing for octopus here; this further indicates that availability of desirable dens is not limiting.

The correlation of density with adjacent kelp cover may involve several mechanisms. Kelp may provide cover, enhance recruitment, or afford rich foraging opportunities. No data on predation risk to octopus in various habitats is available, so the influence of predation on local density cannot be addressed. To the extent that cover and predation are correlated, however, predation apparently does not limit density at depth (see above). *Enteroctopus dofleini* settle out of the plankton at a weight of 2.5 to 5 g, and I have found them at this size under rocks, in tide pools in intertidal areas, and in subtidal kelp beds (unpublished data). Lower current flow through kelp beds may enhance recruitment directly (Stachowicz, 2001), or kelp may serve as attachment substrate for juveniles (juvenile *Octopus bimaculatus* in kelp holdfasts, Ambrose, 1988; *Octopus* paralarvae on floating substrate, Nixon & Mangold, 1996). However, factors influencing recruitment to different habitats remain unknown.

Factors affecting habitat selection in this species are also unknown. In this study, midden content, reflecting dietary content, varied with depth, substrate (soft or hard, and presence of cobble), and geographic region of sampling, but not with the presence of boulders, outcrops, kelp cover in the transect, or season (Vincent *et al.,* 1998). Subtidal dens had more items in middens than intertidal dens. Middens from soft substrate habitats had a greater proportion of the molluscs *Chlamys* spp. and the crab *Telmessus cheiragonus,* while middens from habitats with cobble had a greater proportion of the crab *Cancer oregonensis*. These results may suggest habitat preferences of the respective prey species or the persistance of prey remains in the midden (Ambrose, 1983; Mather, 1991), more than habitat selection by octopus. At present, prey availability and post-settlement habitat selection cannot be correlated. Major, hard-bodied prey of *Enteroctopus dofleini* in Alaska (Vincent *et al.*, 1998) do not support commercial fisheries, and hence their distributions with depth and substrate are not well reported. The results presented here, however, suggest that further studies of recruitment, diet, and prey selection may shed light on variation in octopus densities among local habitats.

The highest average densities recorded in this study were 0.8 octopus per 1000 m^2 on beach walk surveys (Fig. 5) and 2.5 per 1000 m^2 on shallow subtidal surveys (Fig. 6). These contrast with average values from British Columbia (Vancouver Island) of 4.9 to 13.3 individuals per 1000 m^2 on SCUBA surveys (Hartwick *et al.*, 1978, 1984a), or

10–70 kg per diver hour (Hartwick & Barriga, 1997: p. 53). In Alaska the rates were 0.31 animals (< 1 kg) per diver hour. This is less than 50 % and perhaps as low as 1 % of densities recorded in Canada in the late 1970s and early 1980s. The preceding discussion therefore applies to habitats where these animals are relatively scarce.

The reasons for this scarcity are outside the scope of this study. However, the results suggest that (1) Prince William Sound, at the northern extreme of this species' range, may be marginal habitat; (2) prey suitability may limit populations here (diet, as reflected by midden content, consists primarily of clams and the crab *Cancer productus* in Canada (Hartwick *et al.*, 1981; Cosgrove, 1987) and of other smaller crabs in this study (Vincent *et al.*, 1998); (3) sea otters (both competitor and predator of octopus) were abundant in Prince William Sound in the late 1990s and scarce around Vancouver Island in the late 1970s and early 1980s; or (4) recruitment was low prior to the study period. Alternatively, I may have been studying a depressed population following the 'Exxon Valdez' oil spill, although the effect of the spill would be regional rather than local because I found no correlation between the oiling history of a beach and the octopus density (Table 3). Regional effects of oil on octopus may arise from impacts to epibenthic habitat or food (*e.g.,* Highsmith *et al.*, 1996; Poggiale & Dauvin, 2001).

Finally, the depth range of this species in the southern part of its range is reported as intertidal to 1500 m versus intertidal to only 100 m in the northern part of the range (Hochberg, 1998). Paust (1997), however, noted this species in Alaska to depths of 120 fathoms (219 m). In this study, we confirmed the occurrence of *Enteroctopus dofleini* in its northern range to at least 182 m. This depth range extension is documented by video and still photography in which characteristic features of this species are visible (Anderson, 1995, unpublished key; Hochberg, 1998; Scheel, 1999).

Conclusions

Analyses of habitat characteristics associated with *Enteroctopus dofleini* and some aspects of den use behavior at various depths were made from data collected by beach walk, SCUBA, and submersible transect surveys from intertidal areas to 197 m depth in Prince William Sound and Port Graham, Alaska. Overall, octopus counts were higher in habitats with soft substrate, where boulders were present, adjacent to dense kelp cover, and in water depths less than 5 m. These habitat characteristics were similar to those previously described for the species off Canada (British Columbia) and Japan, although the influence of depth and vegetation were not emphasized by other authors. The physical and chemical properties of the sea water at or adjacent to study sites in Alaska do not explain variation by depth. Data on available substrate suggest that den availability is not limiting to octopus in deeper habitats. This is supported by the observation that use of available dens and association with dens both decline with depth, whereas den availability remains relatively constant. More octopus adjacent to kelp beds and in shallow water may reflect greater recruitment to these habitats, reduced mortality due to cover, or active habitat selection for areas that provide greater access to prey or to non-den cover (such as kelp beds). These hypotheses remain to be tested. Further studies of recruitment, diet, and prey selection may be useful in understanding what regulates local octopus density. These data point to the likely importance of near-shore, very shallow-water habitats for octopus populations, and highlight the vulnerability of octopus populations to changes in these habitats.

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