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Remains of the Prey—Recognizing the Midden Piles of *Octopus dofleini* (Wülker)

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Abstract. We described the contents and the field signs of 52 midden piles found outside occupied dens of *Octopus dofleini* (Wülker, 1910) in Prince William Sound and Cook Inlet, Alaska. The contents of midden piles are important data for describing octopus diets; yet the field signs for distinguishing octopus midden piles from remains left by other processes can be subtle. Remains of four crab species, *Telmessus cheiragonus* (Telesius, 1815), *Cancer oregonensis* (Dana, 1852), *Pugettia gracilis* Dana, 1851, and *Lophopanopeus bellus* (Stimpson, 1860), composed 74% of the prey individuals represented in intertidal middens in Prince William Sound. However, the same species were not typical of other locations: *Chlamys hastata* (Sowerby, 1843) and *C. rubida* (Hinds, 1845) were the most common species represented in subtidal middens, while the crab *P. gracilis* Dana, 1851, and the mussel *Mytilus trossulus* Gould, 1850, were among the most common in intertidal middens found in Cook Inlet. Drills were found on the hard remains of six species of crabs (75% of eight Crustacea species, 27% of 22 total species). Fifty-six percent of drill marks on crab species were located toward the carapace posterior. Of the crab species sampled in Prince William Sound that were drilled at all, *C. oregonensis* was the species most often drilled (36%), whereas *T. cheiragonus* was drilled least often (6%). Drills of *O. dofleini* on crabs were oblong (2–6 × 1–2.5 mm), and came to a point at one or both ends. Drill marks tapered toward the inside of the shell, and when the final perforation of the inner surface was made, the drill was no more than a pinpoint. A previously undescribed mark in prey remains, the bite mark, occurred on the leg of *T. cheiragonus*. Bites on weathered prey remains were about 1.2 cm long × 0.5 cm wide, occurring on the inside and outside of the leg.

INTRODUCTION

Animal "signs," including tracks, scat, wallows, nests or dens, and bones, feathers, or other remains of prey, have been important data in studies of many different species, and have been used to indicate presence or absence, to estimate population size, breeding activity, and foraging ranges, and to examine diet. A great many marine organisms also leave "sign," particularly the remains of hard-shelled prey. For example, in the northeastern Pacific, sea otters feed on clams and discard the shells (Kvitek et al., 1992). *Pycnopodia helianthoides* (Brandt, 1835), the sunflower star, also hunts clams, sometimes in the holes dug by sea otters. Sea stars push the sediment out of the way leaving behind a berm of sand or gravel and the empty shells of their bivalve prey (Kvitek et al., 1992). Octopuses feed on many different bivalves and clams, including *Saxidomus giganteus* Deshayes, 1839, which is also a prey of otters (Riedman & Estes, 1988), and discard the remains in midden piles (Hartwick et al., 1981; Hartwick & Thorarinsson, 1978; Mather, 1991, 1994; Mather & O'Dor, 1991). Distinguishing whether a clam has been opened by a sea otter, a sea star, or an octopus is useful for determining impacts of predators on invertebrate communities, requires specialized knowledge, and can limit research in some studies (e.g., Fotheringham, 1974; Kvitek et al., 1992).

Determining how animal remains arrived at their present location on a beach or on the sea floor requires paying attention to sometimes subtle clues (e.g., Fotheringham, 1974). Even so, identifying the source of animal remains can be an important research tool. Descriptions of prey middens have been a primary method of describing octopus diets; for example, in a sample of 12 papers investigating the diet of octopuses (Table 1) midden analysis was used in eight. Octopuses are often mobile and leave midden piles behind, so that the absence of an octopus at a midden pile does not necessarily imply that the remains were left by some other predator. Despite this, few descriptions of the "signs" left by octopuses have been published (but see Hartwick et al., 1978; Ambrose, 1983) to assist the beginning octopus researcher or to be used by someone working on species other than octopuses, but interested in attributing marine invertebrate remains to the animals that killed them. In this paper, we report field signs indicative of the presence of *Octopus dofleini* on beaches in Prince William Sound and Cook Inlet, Alaska, and describe the methods by which middens left by *O. dofleini* may be recognized.

From captive studies, octopuses, including *O. dofleini*, are known to use three different techniques to gain entry to hard-shelled prey: they may pull it apart, "drill" through the shell (Nixon, 1979; Hartwick, 1981), or bite it open (Anderson, 1994). The latter two methods leave

Table 1

Methods used to determine diet in a sample of octopus studies.

Species studied	Method of determining diet	Location	Source
Octopus dofleini	stomach contents	Japan, review article	Mottet, 1975
O. dofleini	midden counts	British Columbia	Hartwick et al., 1981
O. dofleini	midden counts	British Columbia	Mather et al., 1985
O. dofleini	midden counts	British Columbia	Cosgrove, 1987
O. dofleini	observation	Washington, captive study	Anderson, 1991
O. dofleini	midden counts	Washington	Anderson, 1994
O. dofleini	midden counts	Alaska	Vincent et al., 1998
O. rubescens	midden counts	California	Laidig et al., 1995
O. vulgaris	midden counts	South Africa	Smale & Buchan, 1981
O. vulgaris	midden counts	Bermuda	Mather & O'Dor, 1991
O. vulgaris	midden counts	Bermuda	Mather, 1991
O. vulgaris	stomach contents	Spanish Mediterranean	Sanchez & Obarti, 1993

marks on the prey that may be used to identify remains left by octopuses. The drill mark has frequently been mentioned in the literature (e.g., for *O. dofleini,* Hartwick et al., 1978, 1981; Hartwick, 1983), but described for *O. dofleini* only on *Saxidomus giganteus,* a bivalve (Ambrose et al., 1988). In this paper, we provide the first published descriptions of *O. dofleini* drills on crab species.

METHODS

Three study sites, Port Graham in Cook Inlet (59°21′N, 151°49′W) and Green (60°14′N, 147°14′W) and Montague (60°16′N, 147°26′W) Islands in Prince William Sound were surveyed for *Octopus dofleini.* The surveys consisted of intertidal beach walks and SCUBA dives, to depths of 33 m below mean lower low water (MLLW). Dens were identified by the presence of an octopus. If den litter was present at an occupied den, all bits were collected for later measurement and identification (following Foster 1991 for bivalves and Kozloff 1987 for all other taxa). Remains were judged to be either fresh (without algae growth on inner surfaces and unweathered) or old (either with algal growth or weathered). Old remains were not counted and measured as part of the octopus midden, as these remains may have been buried in the sediment until excavated by the octopus when making its den. All specimens collected were inspected for octopus drills or other signs of handling by octopus, and the locations of such marks were noted. Measurements of the lengths and widths were taken of bivalves, crab carapaces, and crab legs.

RESULTS

Prey remains were collected from 52 intertidal and subtidal sites located outside occupied dens and attributed to *Octopus dofleini* on the basis of the octopus in attendance. Middens characteristically contained crab remains: for example, of the 42 middens found at intertidal dens in Prince William Sound, 40 contained at least one item from a crab. The most common species in these intertidal middens were *Telmessus cheiragonus, Cancer oregonensis, Pugettia gracilis,* and *Lophopanopeus bellus,* which together composed 74% of the sample of prey (estimated minimum individuals represented by midden items, Table 2). However, middens in other locations often had a different composition. Subtidal middens, collected from the same areas in the Sound but from depths between −5 and −33 m MLLW, were dominated by remains of scallops and other bivalves, rather than of crabs (Table 3); while four intertidal middens from Port Graham (in Cook Inlet, Alaska) contained a mixture of crabs and bivalves, but the most abundant species there were not the same as in the Sound (Table 4).

Inspection of midden remains sometimes revealed marks left by the octopus: we found both "drill" and "bite" marks (Figure 1). The drill mark of *O. dofleini* on carapaces of *Cancer oregonensis* and *Lophopanopeus bellus* (Figure 1a) was oblong, about 1.5–3.0 millimeters long and 0.25–2.0 millimeters wide, and usually came to a point at one or both ends. The drill gradually tapered from the outside of the shell toward the inside. The final perforation of the inner surface may be no more than a pinpoint. The only other drill marks that we found on shells in this area (not in octopus middens) were moon snail drill marks that were larger and almost perfectly round, and were readily distinguishable by size and shape from the marks of *Octopus dofleini.* Drills were found on the carapace or chelipeds of six species of prey (27% of 22 species found in middens, Tables 2–5).

Drill marks were more frequently encountered on some species than others. Of the crab remains found in intertidal middens in the Sound (Table 2), the carapaces of *Cancer oregonensis* and of *Pugettia gracilis* were most often drilled, while those of *Telmessus cheiragonus* were

Table 2

Prey remains found in 42 intertidal midden piles left by *Octopus dofleini* on Green and Montague Islands, Prince William Sound, AK.

Taxon	Species	Count found[1] (prop. of sample in parentheses)	No. drilled	Avg. size[2] (sample size)
Decapoda	*Telmessus cheiragonus* (Telesius, 1815)	70 (0.30)	4 (0.06)	3.55 (70)
Decapoda	*Cancer oregonensis* (Dana, 1852)	58 (0.25)	21 (0.36)	1.99 (55)
Decapoda	*Pugettia gracilis* Dana, 1851	23 (0.10)	6 (0.26)	2.77 (21)
Decapoda	*Lophopanopeus bellus* (Stimpson, 1860)	20 (0.09)	2 (0.10)	1.57 (18)
Bivalvia	*Macoma inquinata* (Deshayes, 1855)	17 (0.07)	0	2.75 (15)
Bivalvia	*Protothaca staminea* (Conrad, 1837)	17 (0.07)	0	2.16 (16)
Bivalvia	*Saxidomus giganteus* Deshayes, 1839	8 (0.03)	0	2.63 (8)
Gastropoda	*Littorina sitkana* Philippi, 1845	4 (0.02)	0	
Bivalvia	*Chlamys hastata* (Sowerby, 1843)	3 (0.013)	0	3.83 (3)
Bivalvia	*Pododesmus macroschisma* (Deshayes, 1839)	3 (0.01)	0	6.40 (3)
Polyplacophora	*Tonicella lineata* (Wood, 1815)	2 (0.01)	0	1.20 (1)
Bivalvia	*Mytilus trossulus* Gould, 1850	2 (0.01)	0	1.95 (2)
Decapoda	*Cancer productus* Randall, 1839	2 (0.01)	0	6.00 (1)
Decapoda	*Cryptolithodes sitchensis* Brandt, 1853	2 (0.01)	0	
Bivalvia	*Chlamys rubida* (Hinds, 1845)	1 (0.004)	0	
Decapoda	*Hapalogaster mertensii* Brandt, 1850	1 (0.004)	0	
Decapoda	*Phyllolithodes papillosus* Brandt, 1849	1 (0.004)	0	5.0 (1)
Gastropoda	*Trichotropis cancellata* Hinds, 1849	1 (0.004)	0	10.5 (1)

[1] For crabs, only the number of carapaces is given, indicating the minimum number of individuals represented in the litter; for bivalves, each count indicates either the left valve, right valve, or both when still attached.

[2] The mean of the carapace length (cm) for crabs and of valve length for bivalves. Sample size is indicated in parentheses (in some cases, remains were broken and could not be measured, although the fragments could be identified to species).

only infrequently drilled. In contrast to crabs, most bivalves were not drilled (Tables 2–4). *Chlamys* sp. valves found at both intertidal and subtidal dens were never drilled (n = 19), nor were any other bivalves collected in the Sound (Tables 2 & 3). However, drills were recorded on four bivalves from middens in front of unoccupied dens in Port Graham (Figure 1b).

We also examined the locations of drill marks on crab remains, using a sample of 50 drilled carapaces and 21 drilled chelipeds (of all species) collected from midden piles at both occupied and unoccupied dens in Prince William Sound (including remains in Tables 2, 3, 5, and additional remains not listed). Each item was drilled only once. On carapaces, 38% of the drills (n = 19 of 50) were placed over the posterior midline (Figure 2a). Additional drills were placed immediately to the right (n = 6) or to the left (n = 3) of the posterior midline, so that 56% (n = 28) of the drills were located in the posterior medial portion of the carapaces. The next most common position drilled was over the medial central portion of carapaces (n = 18 or 36%), including drills on the central midline (n = 9) and immediately to the right (n = 4) or left (n = 5) of midline. The remaining 8% of the drills (n = 4) were located in the left posterior section of the

Table 3

Prey remains found in six subtidal midden piles left by *Octopus dofleini* near Green and Montague Islands, Prince William Sound, AK.

Taxon	Species	No. found[1]	No. drilled	Avg. size[1]
Bivalvia	*Chlamys hastata* (Sowerby, 1843)	9 (0.24)	0	2.46 (9)
Bivalvia	*Chlamys rubida* (Hinds, 1845)	6 (0.16)	0	2.23 (6)
Bivalvia	*Macoma inquinata* (Deshayes, 1855)	5 (0.14)	0	3.58 (5)
Decapoda	*Cancer oregonensis* (Dana, 1852)	5 (0.14)	4 (0.80)	1.68 (5)
Decapoda	*Pugettia gracilis* Dana, 1851	4 (0.11)	0	2.70 (3)
Decapoda	*Lophopanopeus bellus* (Stimpson, 1860)	4 (0.11)	0	1.68 (4)
Gastropoda	*Acmaea* sp.	3 (0.08)	0	1.73 (3)
Bivalvia	*Pododesmus macroschisma* (Deshayes, 1839)	1 (0.03)	0	2.60 (1)

[1] Details as in Table 2.

Table 4

Prey remains found in four intertidal midden piles left by *Octopus dofleini* Port Graham, Cook Inlet, AK.

Taxon	Species	No. found[1]	No. drilled	Avg. size[1]
Decapoda	*Pugettia gracilis* Dana, 1851	7 (0.35)	0	2.63 (7)
Bivalvia	*Mytilus trossulus* Gould, 1850	4 (0.20)	0	2.98 (4)
Decapoda	*Cancer oregonensis* (Dana, 1852)	3 (0.15)	2 (0.67)	2.17 (3)
Bivalvia	*Protothaca staminea* (Conrad, 1857)	2 (0.10)	0	1.95 (2)
Bivalvia	*Macoma nasuta* (Conrad, 1837)	1 (0.05)	0	1.80 (1)
Gastropoda	*Nucella emarginata* (Deshayes, 1839)	1 (0.05)	0	2.70 (1)
Gastropoda	*Nucella lima* (Gmelin, 1791)	1 (0.05)	0	2.60 (1)
Bivalvia	*Saxidomus giganteus* Deshayes, 1839	1 (0.05)	0	2.60 (1)

[13] Details as in Table 2.

carapaces. Chelipeds were drilled on both inner (67%) and outer surfaces (33%) (Figure 2b, c), most commonly over the cheliped midline, but occasionally dorsal or ventral of the midline. We observed only one drill that was beyond the cheliped joint, but still on the leg of the crab. The Port Graham bivalves (n = 4) were drilled toward the posterior of the umbo (Figure 1b).

A previously undescribed mark, which we term the "bite mark" (Figure 1c), was found exclusively on the penultimate segment of the 1st (cheliped) leg of *Telmessus cheiragonus.* As implied by the name, we believe the bite mark is made when the octopus uses its beak to bite through the leg of this prey species. Bite marks were oval in shape and greatly varied in size depending on the amount of weathering of the remains. In the freshest specimens, bite marks were about 1.2 cm long × 0.5 cm wide, located on the inside of the leg, and extending the entire length of the segment. The bite mark is apparently placed at a weak point in the leg exoskeleton and has a tendency to expand as prey remains break down. Bite marks were not found on the legs of other prey species; however, only five legs from species other than *T. cheiragonus* were examined. Of the 1st legs examined (n = 112) from Prince William Sound 29% (32) had bite marks. No bite marks were recorded from Port Graham, although only four *T. cheiragonus* 1st legs were found in that area.

DISCUSSION

We describe remains found in 52 middens found outside the dens of *Octopus dofleini* in order to assist beginning octopus researchers (or those expert on species other than octopuses) in recognizing an octopus midden. The composition of the midden may be helpful, as most middens consisted primarily of crab and bivalve remains. Most middens in the intertidal in Prince William Sound contained one or more of four crab species (Table 2), so that this species composition was characteristic of middens. However, the characteristic species were different at different depths and geographic locations (compare with Tables 3, 4). The local distinctiveness of octopus midden piles has been noted in several papers detailing that octopuses in different areas eat different species or handle prey differently (References in Table 1), but may also result from factors influencing the residence time of prey remains in middens under different conditions (Ambrose, 1983; Mather, 1991). Closer inspection of prey remains from middens revealed that octopuses left marks on some of their prey during the process of killing and consuming them. However, some species of prey were more likely to be marked than others, and most items in middens were not marked by the octopus. In our sample, three species of crabs were likely to be drilled on the carapace (Tables 2–4) or a cheliped (Table 5), and a "bite" mark was often found on the leg of the crab *Telmessus cheiragonus.* However, most items of any species, and almost all bivalve remains examined, bore no mark of being handled by *O. dofleini.*

Octopuses typically drill many of their hard-shelled prey. The behavior has been reported for a number of octopus species (*Octopus dofleini*: Hartwick et al., 1978; Ambrose et al., 1988; *O. bimaculatus* Verrill and *O. bimaculoides* Pickford & McConnaughey: Pilson & Taylor 1961; *O. mimus* Gould, 1852: Cortez et al., 1998; *Eledone cirrhosa* (Lamarck): Boyle & Knobloch, 1981; Grisely et al., 1996) and studied in detail in *O. vulgaris* Cuvier, 1797 (discussed in Nixon & Maconnachie, 1988). The average dimensions of holes drilled by *O. dofleini* in the butter clam were 1.03 mm on the outer surface of the shell and 0.56 mm on the inner surface of the shell (Ambrose et al., 1988), while drill holes made by *O. vulgaris* on *Mytilus* sp. were round with average dimensions of 1.1 mm on the outer surface and only 0.2 mm on the inner surface. In the latter species, drill holes were made primarily with the salivary papilla (Nixon, 1980), the secretions of which dissolve the shell (Nixon & Maconnachie, 1988). Multiple drill holes were common on an individual prey item of *O. vulgaris* (Nixon, 1979). On bivalves, *O. vulgaris* usually placed holes over the adductor muscle (Nixon & Maconnachie, 1988); and salivary toxins were secreted through the hole to paralyze, kill, or partially digest the prey.

Some octopuses drill crustaceans as well as bivalves

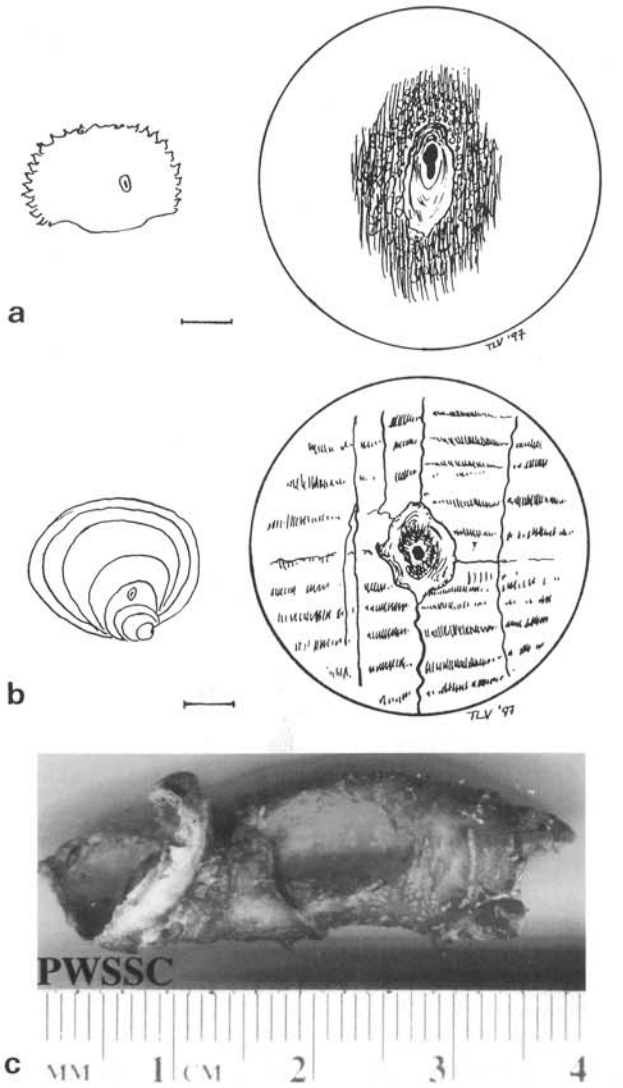

Figure 1

Illustrations of the marks found in the prey remains of *Octopus dofleini*: typical drill mark on (a) the carapace of the Oregon *Cancer* crab, *Cancer oregonensis,* and (b) the umbo of the bivalve, *Protothaca staminea* (the circle shows the view through a microscope; the scale bar shows one millimeter); and (c) typical bite mark on the leg of the helmet crab, *Telmessus cheiragonus.* At the time of publication, images of these and other prey remains from octopus middens are available at www.pwssc.gen.ak.us/~dls/octopus/specimens/ on the world-wide web. Now at http://marine.alaskapacific.edu/octopus/EXPEDITION Middens.php

(*Octopus vulgaris,* Guerra & Nixon, 1987; *Eledone cirrhosa,* Boyle & Knobloch, 1981; Grisley et al., 1996). Although drilling as a predatory behavior against mollusks has been described in detail (e.g., Pilson & Taylor, 1961; Nixon, 1979; Ambrose et al., 1988; Nixon & Maconnachie, 1988), work with crustaceans has focused on the toxicity of saliva to this taxa (e.g., Ghiretti, 1959, 1960; Pilson & Taylor, 1961, but for exceptions see Guerra & Nixon, 1987; Boyle & Knobloch, 1981; Mather & Nixon, 1995; Grisley et al., 1996). Drilling of crustacean prey has been noted for *O. dofleini* (Hartwick et al., 1981) although not described in detail. We found that *Cancer oregonensis, Pugettia gracilis,* and *Lophopanopeus bellus* remains were often drilled (10–41% of carapaces, Tables 2–4), whereas bivalve prey and some crabs (e.g., *Telmessus cheiragonus*) were most often not. We found only a single drill mark per prey item regardless of species, in

Table 5

Crab chelipeds found in 42 intertidal midden piles left by *Octopus dofleini* on Green and Montague Islands, Prince William Sound, AK.

Species	Count found[1]	No. drilled	Avg. size[2]
Cancer oregonensis (Dana, 1852)	115 (0.54)	4 (0.03)	1.59 (114)
Lophopanopeus bellus (Stimpson, 1860)	51 (0.24)	4 (0.08)	1.67 (51)
Telmessus cheiragonus (Telesius, 1815)	35 (0.16)	4 (0.11)	2.83 (32)
Pugettia gracilis Dana, 1851	9 (0.04)	2 (0.22)	1.67 (9)
Hapalogaster mertensii Brandt, 1850	3 (0.01)	2 (0.67)	2.57 (3)
Cancer productus Randall, 1839	1 (0.005)	1 (1.00)	4.00 (1)

[1] The number of crab chelipeds found. This does not indicate the minimum number of prey individuals represented in the litter as both left and right chelipeds were usually found in the same midden. Details as in Table 2.

[2] Size is the mean of cheliped lengths (cm). Details as in Table 2.

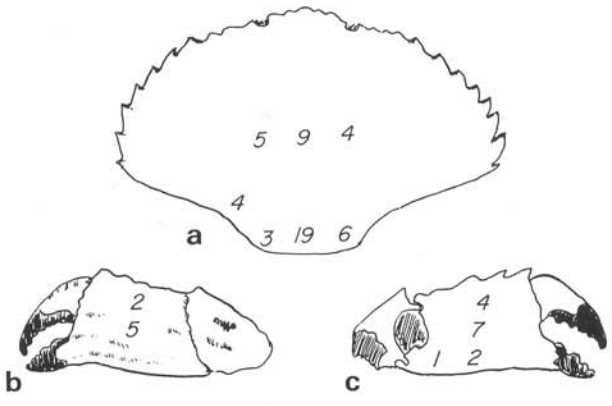

Figure 2

Illustrations of the position and number of *O. dofleini* drills (a) on carapaces of the five most abundant crab species in middens (Table 2), (b) on the outer surface, and (c) inner surface of chelipeds of the same species, plus *Hapalogaster mertensii* (species in Table 5).

contrast to Nixon's (1979) study of *Octopus vulgaris* which found that some species were drilled only once while others were drilled multiple times. Whether this difference is characteristic of the difference in prey (mostly crabs in this study versus gastropods in Nixon, 1979) or of the octopus species remains to be determined. Drilling was not employed preferentially to open the largest prey: *Telmessus cheiragonus* were typically larger than the other crab species, yet were least frequently drilled. The exoskeleton of *T. cheiragonus* is thinner and softer than that of the crabs that were more often drilled (personal observation), and this species probably is easier for the octopuses to pull apart or bite open, techniques that may be attempted in preference to drilling (Hartwick et al., 1981).

Bite marks were previously undescribed and little is known about how octopuses utilize their beaks when capturing prey. *Octopus dofleini* are known to "chip the edges of the (bivalve) shell or break it with their beaks" (Anderson, 1994). We observed bite marks on the largest segment of the leg on a soft-shelled crab species *Telmessus cheiragonus.* The marks were 0.3 to 3.0 cm in length. We could find no data on the size of gape in an octopus. However, using Robinson & Hartwick (1983) we estimated the beak dimensions of a 2.6 kg octopus (the average size of the octopuses that left the middens described in this study). The pigment upper-lateral-wall length (PULWL) was estimated to be 18.8 mm while the total upper-crest length was 30.3 mm. Assuming an octopus' gape would be at most half the PULWL, *O. dofleini* may be able to make bites as large as 9.4 mm and therefore were probably capable of inflicting the marks we describe. In addition, we fed a captive octopus a live *T. cheiragonus* crab and collected the crab remains immediately after feeding. A fresh mark, similar to worn marks found on remains in middens, was found on the penultimate segment of one leg (Figure 1c), confirming that *Octopus dofleini* does make this mark when feeding on *T. cheiragonus.* A captive octopus also left a bite mark on the remains of a *Cancer productus* crab, the first such mark we have seen on remains of any crab other than *T. cheiragonus.*

Descriptions of prey middens have been a primary method of describing octopus diets (Table 1). Despite this reliance, published information on recognizing when remains are left by octopuses is scarce. The composition of midden piles varies from place to place and depends on local habitat as well as other factors (Hartwick et al., 1981; Ambrose, 1984; Vincent et al., 1998), which means that the species that are characteristic of octopus middens must be learned locally. It is not possible to ascribe any single prey remain to a particular cause or process when the remain was found in the absence of an obvious predator and was not marked by the cause of mortality. However, drill marks on one or more items within a midden provide a conclusive indication that the midden contents were left by a foraging octopus. This definite mark of handling left by octopuses allows the beginning researcher to attribute at least some middens to octopuses and learn what prey are characteristic in a locality. Using a suite of factors, including the association of unmarked items with octopuses in their dens or with items marked by drill holes or bites in the same midden, the researcher can become familiar with prey species that, while locally common in octopus middens, are handled in such a way as to leave no physical marks (e.g., *Chlamys rubida* and *C. hastata* in this study). While some ambiguity will always remain when middens consist only of unmarked items, this local knowledge of how octopuses typically handle each prey species is the only way that the source of such remains can be inferred.

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LITERATURE CITED

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

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

AMBROSE, R. F., B. J. LEIGHTON & E. B. HARTWICK. 1988. Characterization of boreholes by *Octopus dofleini* in the bivalve *Saxidomus giganteus.* Journal of Zoology, London 214:491–503.

ANDERSON, R. C. 1991. The fish-catching ability of *Octopus dofleini.* Journal of Cephalopod Biology 2(1):75–76.

ANDERSON, R. C. 1994. Octopus bites calm. The Festivus 26(5): 58–59.

BOYLE, P. R. & D. KNOBLOCH. 1981. Hole boring of crustacean prey by the octopus *Eledone cirrhosa* (Mollusca, Cephalopoda). Journal of Zoology London 193:1–10.

CORTEZ, T., B. G. CASTRO & A. GUERRA. 1998. Drilling behaviour of Octopus mimus Gould. Journal of Experimental Marine Biology and Ecology 224:193–203.

COSGROVE, J. A. 1987. Aspects of the natural history of *Octopus dofleini,* the giant Pacific octopus. M. Sc. Thesis, University of Victoria.

FOSTER, N. R. 1991. Intertidal Bivalves: A Guide to the Common Marine Bivalves of Alaska. University of Alaska Press: Fairbanks. 152 pp.

FOTHERINGHAM, N. 1974. Trophic complexity in a littoral boulderfield. Limnology and Oceanography 19(1):84–91.

GHIRETTI, F. 1959. Cephalotoxin: the crab-paralysing agent of the posterior salivary glands of cephalopods. Nature 4669:1192–1193.

GHIRETTI, F. 1960. Toxicity of octopus saliva against Crustacea. Annals of the New York Academy of Sciences 90:726–741.

GRISLEY, M. S., P. R. BOYLE & L. N. KEY. 1996. Eye puncture as a route of entry for saliva during predation on crabs by the octopus *Eledone cirrhosa* (Lamarck). Journal of Experimental Marine Biology and Ecology 202:225–237.

GUERRA, A. & M. NIXON. 1987. Crab and mollusc shell drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Ria de Bigo (north-west Spain). Journal of Zoology London 211: 515–523.

HARTWICK, E. B. 1983. *Octopus dofleini.* Pp. 277–291 in P. R. Boyle (ed.), Cephalopod Life Cycles. Vol I. Academic Press: London.

HARTWICK, E. B. & G. THORARINSSON. 1978. Den associates of the giant Pacific octopus, *Octopus dofleini* (Wülker). Ophelia 17(1):163–166.

HARTWICK, E. B., G. THORARINSSON & L. TULLOCH. 1978. Methods of attack by Octopus dofleini (Wülker) on captured bivalve and gastropod prey. Marine Behaviour and Physiology 5:193–200.

HARTWICK, E. B., L. TULLOCH & S. MACDONALD. 1981. Feeding and growth of *Octopus dofleini* (Wülker). The Veliger 24(2): 129–138.

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

KVITEK, R. G., J. S. OLIVER, A. R. DEGRANGE & B. S. ANDERSON. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology 73(2):413–428.

LAIDIG, T. E., P. B. ADAMS, C. H. BAXTER & J. L. BUTLER. 1995. Feeding on Euphausiids by *Octopus rubescens.* California Fish and Game. Vol. 81:2.

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

MATHER, J. A. 1994. 'Home' choice and modification by juvenile *Octopus vulgaris* (Mollusca: Cephalopoda): specialized intelligence and tool use? Journal of Zoology, London 233: 359–368.

MATHER, J. A. & M. NIXON. 1995. Octopus vulgaris (Cephalopoda) drills the chelae of crabs in Bermuda. Journal of Molluscan Studies 61:405–406.

MATHER, J. A. & R. K. O'DOR. 1991. Foraging strategies and predation risk shape the natural history of juvenile *Octopus vulgaris.* Bulletin of Marine Science 49(1–2):256–259.

MATHER, J. A., S. RESLER & J. COSGROVE. 1985. Activity and movement patterns of *Octopus dofleini.* Marine Behaviour and Physiology 11:301–314.

MOTTET, M. G. 1975. The fishery biology of *Octopus dofleini* (Wülker). Technical Report No. 16, Management & Research Division, Washington Department of Fisheries.

NIXON, M. 1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. Malacologia 18:431–443.

NIXON, M. 1980. The salivary papilla of Octopus as an accessory radula for drilling shells. Journal of Zoology, London 190: 53–57.

NIXON, M. & E. MACONNACHIE. 1988. Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. Journal of Zoology, London 216:687–716.

PILSON, M. E. Q. & P. E. TAYLOR. 1961. Hole drilling by Octopus. Science 134:1366–1368.

RIEDMAN, M. I. & J. A. ESTES. 1988. A review of the history, distribution, and foraging ecology of sea otters. Pp. 4–21 in G. R. VanBlaricom & J. A. Estes (eds.), Ecological Studies, 65: The Community Ecology of Sea Otters. Springer-Verlag: New York.

ROBINSON, S. M. C. & E. B. HARTWICK. 1983. Relationship between beak morphometrics and live wet weight of the giant Pacific octopus, *Octopus dofleini martini* (Wülker). The Veliger 26(1):26–29.

SANCHEZ, P. & R. OBARTI. 1993. The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. Pp. 477–487 in T. Okutani, R. K. O'Dor & T. Kubodera (eds.), Recent Advances in Cephalopod Fisheries Biology. 1st ed., Vol. I. Tokai University Press: Tokyo.

SMALE, M. J. & P. R. BUCHAN. 1981. Biology of *Octopus vulgaris* off the east coast of South Africa. Marine Biology 65:1–12.

VINCENT, T. L. S., D. SCHEEL & K. HOUGH. 1998. Some aspects of diet and foraging behavior of *Octopus dofleini* in its northernmost range. Marine Ecology 19(1):13–29.