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Cover image - Patch reef near the wall off Grotto Beach (photo by Lee Florea).

Spatial variation in the diet of *Octopus vulgaris* at San Salvador, The Bahamas

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1. Abstract

We characterized the diet of the *Octopus vulgaris*, common octopus, population at four nearshore locations around San Salvador Island, The Bahamas, using the contents of middens, piles of prey remains left outside octopus dens. Similar to other populations, the diet of *O. vulgaris* at San Salvador is broad, including at least 52 prey types, but concentrated on a few common types, with three prey types accounting for 45% of prey items. Octopus diet varied significantly among locations around San Salvador, both in diversity (number of prey types) and composition (what species). We hypothesize that diet differences are caused by habitat-related variation in prey availability.

2. Introduction

Shallow-water octopuses are mobile, versatile predators of benthic and demersal animals. To support the high metabolic and growth rates necessary for an active lifestyle and short lifespan, larger species are voracious feeders and often considered important predators in near-shore communities (Ambrose and Nelson 1983; Ambrose 1986; Rodhouse and Nigmatullin 1996). Because octopuses feed on a wide range of species and can influence prey distribution and abundance, knowledge of their feeding ecology will contribute to an understanding of benthic community structure.

Although the taxonomy of *Octopus vulgaris* Cuvier, 1797, the common octopus, has recently come under scrutiny, current evidence indicates that it has a circumglobal distribution in tropical to temperate waters (De Luca et al. 2014). The diet of *O. vulgaris* has been studied in several locations throughout its range; *O. vulgaris* feeds primarily on benthic molluscs and crustaceans, although the breadth and specific composition of its diet varies geographically (Smale and Buchan 1981; Ambrose and Nelson 1983; Mather 1991; Smith 2003; Anderson et al. 2008). Given its wide range, geographic variation in diet, and potential role in benthic community structure, characterizing the diet of *O. vulgaris* from a variety of locations is necessary for a complete understanding of its biology and ecological role.

The diets of shallow-water octopods are frequently studied using the contents of middens, piles of prey remains left outside the den (Dodge and Scheel 1999). This method can easily identify prey with hard body parts that are not completely consumed (e.g., molluscs and crustaceans), and provide a picture of the diet integrated over time. However, remains of small or mainly soft-bodied prey are usually not deposited in middens; in addition, the composition of a midden can change over time because physical forces, such as waves, currents, or gravity, and other organisms may remove items at non-random rates (Ambrose 1983; Mather 1991; Smith 2003). To reduce bias from the non-random removal of remains, some studies have used frequent (e.g. daily or semi-daily), repeated collections of midden contents from individual dens (Anderson et al. 2008; Leite et al. 2009; Kuhlmann and McCabe 2014). As with other diet estimation methods (e.g., for octopods: direct observation, stomach contents), results must be interpreted in the context of these limitations.

We used frequent, repeated collections of midden contents to study the diet of *O. vulgaris* in the coastal waters of San Salvador Island in The Bahamas. Here, we address the following questions: 1) What is the diet of *O. vulgaris* in the population at San Salvador? and 2) Does diet vary among site locations around San Salvador?

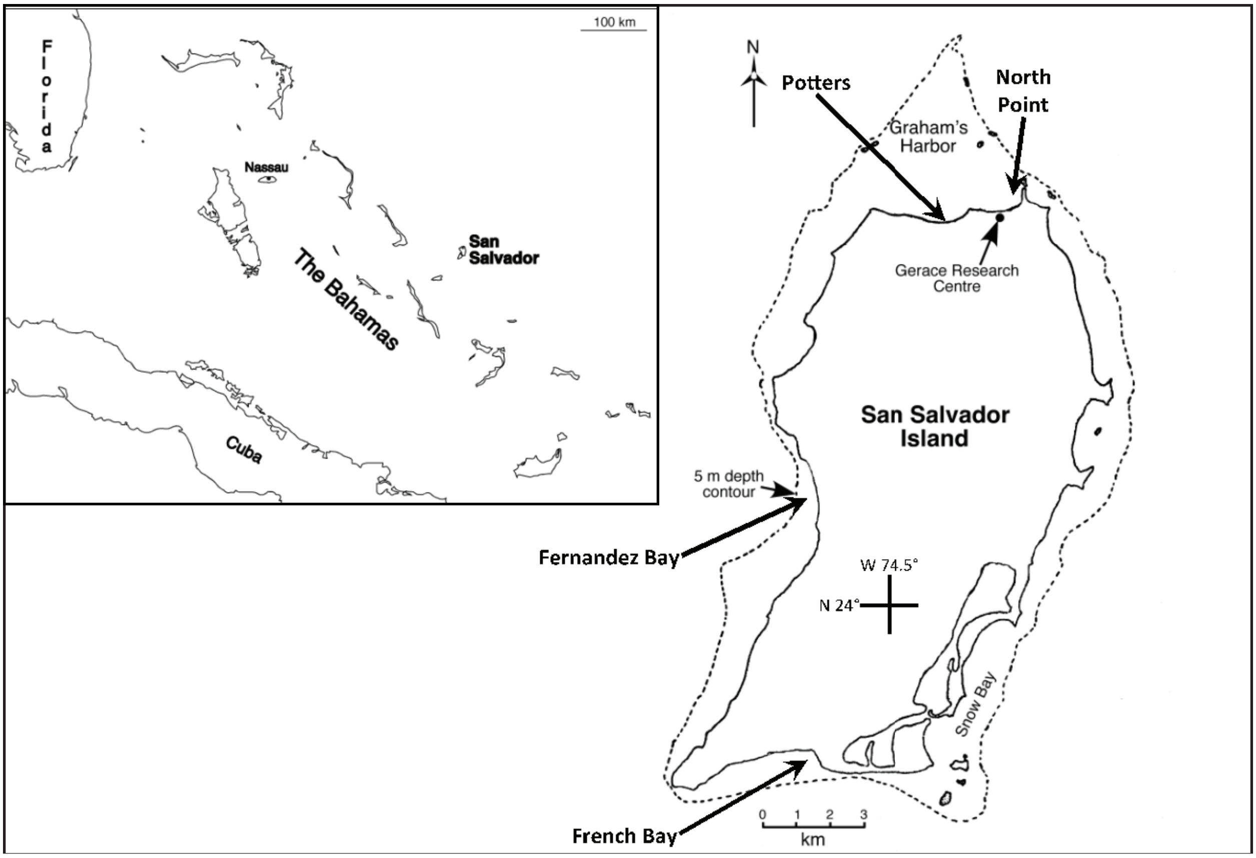

Figure 1. Map of San Salvador Island, The Bahamas (R) showing the 4 study locations. Inset (L) shows the location of San Salvador in The Bahamas (modified from http://histgeo.ac-aix-marseille.fr).

3. Methods

We observed octopuses at four near-shore (water depth ≤ 3 m) locations around San Salvador with different benthic habitat types (Figure 1). The North Point site is dominated by sea grass beds composed of *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* (Smith et al. 1990). The sea grass grades into hard substrate at the lower edge of the intertidal zone. At Potters, sea grass is interspersed with patches of exposed bedrock with scattered solution holes and associated hardbottom benthic community (small coral heads, sponges, and soft corals). The Fernandez Bay substrate is exposed bedrock with numerous ledges, solution holes, and associated hardbottom community. At the French Bay site, most observations were in a rocky area at the very lower edge of the intertidal zone; the adjacent subtidal habitat consists of patches of sea grass (*T. testudinum* and *S. filiforme*) (Smith et al. 1990) separated by channels of sand and coral rubble.

We collected midden contents from octopus dens in June 2011, January 2013, and March 2014. We located dens by systematically searching a location while snorkeling. We identified presumptive dens by the presence of characteristic prey remains (mollusc shells and crustacean exoskeletons) outside a crevice or the presence of an octopus in a crevice; octopuses were not seen at all presumptive dens (see Table 1). When possible, we visually (in the field or photographically) confirmed the species identity of the octopus. All individuals that could be identified were *O. vulgaris*, so we assume that our entire sample was this species.

For all collections, we recorded shelter type, habitat type, and the presence of an octopus then collected all prey remains in a numbered mesh bag. On the first visit, the den was marked with a numbered flag and a surface float to aid relocation. We then returned to the

Table 1. Characteristics of *Octopus vulgaris* midden content collections at San Salvador Island. Prey characteristics are calculated excluding items collected on the first visit to the den. We tested for differences among locations with analysis of variance (ANOVA) when data met parametric assumptions and nonparametric Kruskal-Wallis (K-W) tests when they did not. Data in the form of frequencies were compared among locations using likelihood-ratio contingency table analyses (G-test).

	N	**Collections** [median (range)]	**Interval** (days) [median (range)]	**Length of observation** (days) [median (range)]	**Dens with octopus present** (%)	**Octopus occupancy** (proportion of visits) [median (range)]	**Total number of prey types**	**Prey types/den** [mean ± SE]	**Prey items/den** [median (range)]
Location									
North Point	26	7 (3 – 10)	2 (1 – 6)	12 (4 – 18)	84.6	0.5 (0 – 1)	40	13.0 ± 1.0	59 (4 – 199)
Potters	7	7 (6 – 8)	2 (1 – 3)	13 (12 13)	100.0	0.7 (0.3 – 1)	28	11.6 ± 1.3	22 (13 – 47)
Fernandez Bay	3	6 (5 – 7)	2 (1 – 6)	12 (12 – 18)	100.0	0.8 (0.3 – 0.8)	18	10.0 ± 2.7	28 (7-30)
French Bay	7	6 (5 – 6)	2 (1 – 4)	12 (10 – 12)	85.7	0.6 (0 – 1)	21	8.3 ± 1.0	72 (12 – 131)
All locations	43	7 (3 – 10)	2 (1 – 6)	12 (4 – 18)	88.4	0.6 (0 – 1)	52	11.8 ± 0.7	47 (4 – 199)
Among locations:									
P		0.08	0.02	0.73	0.42	0.55		0.09	0.03
Test		K-W	K-W	K-W	G-test	K-W		ANOVA	K-W
Test statistic		H = 6.77	H = 9.67	H = 1.30	G = 2.85	H = 2.14		F = 2.36	H = 9.00
df		3	3	3	3	3		3, 39	3

den at intervals of 1 – 6 days, usually (> 90% of collections) 3 days or fewer, for up to 18 days to collect any new prey remains.

In the laboratory, we identified and enumerated the prey remains following Kaplan (1988), Abbott and Morris (1995), and Redfern (2013). When possible, we identified mollusc remains to species. Crustacean remains were frequently partial (e.g., appendages) or fragmented and so not consistently identifiable to species; they were grouped into larger taxomonic categories when possible or listed as "miscellaneous crustacean" when not. We categorized gastropod shells with old damage to the aperture or spire as hermit crabs, since this type of damage is unlikely to be caused by octopus predation on live gastropods. For prey types with multiple potential parts (bivalves and crustaceans), we counted the minimum number of individuals represented by the parts, considering size and symmetry (e.g., right and left chelae).

We assumed that a single octopus deposited all prey remains at a particular den during the duration of our observations, so we summed the prey items from all collections after the first (visits 2+) for each den. In a few cases, several potential shelters (usually queen conch [*Strombus gigas*] shells) with middens occurred in close proximity to one another. If we never saw more than one octopus in this group of shelters on a single collection day, we assumed all prey remains were left by one octopus and combined all collections for the group of shelters.

Because of the large number of prey types in *O. vulgaris's* diet, we used principal component analysis (PCA) to compare diet composition among locations. PCA simplifies multivariate relationships by generating new variables (components) that are combinations of original variables and show common patterns of variation (Gotelli and Ellison 2004). We used proportional occurrence of prey types in middens as the variables in the PCA; prey types that correlate most strongly with the new components are most important in determining observed patterns. To test for differences in diet, we compared values of the first two components among locations using analysis of variance (ANOVA).

4. Results

We collected middens from 43 presumptive octopus dens (Table 1). Dens were visited 3 – 10 times (median = 7) over 4 – 18 days (median = 12) at a median interval of 2 days (range: 1 – 6 days). An octopus was seen at least once in 88% (all but 5) of dens (Table 1); because typical octopus prey items accumulated between visits at the presumptive dens where we never observed an octopus, we assumed these 5 dens were occupied between our visits. At North Point, large queen conch (*S. gigas*) shells were the most common den type; at the other locations, solution holes were most common (Table 2). Den type proportions differed significantly among locations (G-test: $G = 44.81$, $n = 43$, $df = 6$, $P < 0.0005$).

We identified a total of 52 prey types in octopus middens (visits 2+ only) (Table 3). The most common prey items were medium-sized gastropods (long-spined star [*Astrea phoebia*] and knobby turban snails [*Turbo castaneus*]) and spider crabs (*Majidae*); these 3 prey types together made up about 45% of midden contents (Table 3, Figure 2). Over 20% of prey types were represented by a single specimen and about 50% of prey types were represented by 10 individuals or fewer.

Among locations, we did not find significant differences in octopus occupancy patterns or characteristics of our sampling other than the number of dens sampled and the interval between collections (Table 1), but measures of octopus diet did differ among the study locations. The total number of prey types collected was highest at North Point and lowest at French Bay (Table 1). However, this could be caused by differences in sample size (number of prey items), which follows the same pattern. Prey types per den did not differ significantly among locations; however, the number of

Table 2. Number of observed *Octopus vulgaris* dens by den type and location. Coral head complex = living or dead coral heads with various other sessile invertebrates (sponges, soft corals, *etc*.) and algae. Solution hole = a hole or crevice in bedrock.

	Den type		
Location	Queen conch shell	Coral head complex	Solution hole
North Point	25	0	1
Potters	2	2	3
Fernandez Bay	0	1	2
French Bay	0	0	7

prey items per den was significantly different (Table 1). After controlling for the number of prey items, the difference in prey types per den became significant (ANCOVA, log(prey items) as covariate: F = 8.76; df = 3, 38; P < 0.0005), with French Bay having fewer prey types than the other locations.

Diet composition was most similar between North Point and Potters (Figure 2). North Point middens had a higher proportion of knobby turban (*T. castaneus*) and long-spined star snails (*A. phoebia*) than Potters, but the major prey categories were generally similar. Middens at Fernandez Bay had high proportions of several prey types not common at other locations, notably rough lima (*Lima scabra*), Atlantic gray cowrie (*Cypraea cinerea*), and queen conch (*S. gigas*). Middens at French Bay were dominated by gaudy asaphis clams (*Asaphis deflorata*), a species not found at any other location. Fernandez Bay and French Bay were clearly and significantly separated from North Point and Potters along both of the first two PCA axes (Figure 3) (PC 1: ANOVA; F = 77.73; df = 3, 39; P < 0.0005. PC 2: ANOVA; F = 18.22, df = 3, 39; P < 0.0005). The Atlantic gray cowrie (*C. cinerea*), queen conch (*S. gigas*), and xanthid crabs had high positive loadings on principle axis 1; knobby turban (*T. castaneus*), cerith (*Cerithium* spp.), and apple murex (*Phyllonotus pomum*) snails had high negative loadings. Principle axis 2 had high positive loading for smooth tegula snails (*Tegula fasciata*) and negative loadings for gaudy asaphis (*A. deflorata*) and bearded ark (*Barbatia cancellaria*) clams.

5. Discussion

Octopus vulgaris at San Salvador have a broad diet that includes at least 52 species of bivalves, gastropods, and crustaceans. However, the diet is dominated by a few prey types, with many prey types very rare; for example ~50% of prey types occurred less than 10 times out of 2543 total prey items. Populations of *O. vulgaris* in other locations show similar dietary patterns (Smale and Buchan 1981; Ambrose and Nelson 1983; Mather 1991; Smith 2003; Anderson et al. 2008). The number of prey types consumed by San Salvador *O. vulgaris* is among the highest reported for this species. These large-scale geographical differences in *O. vulgaris's* diet breadth are likely attributable to regional differences in prey species richness. Given the broad distribution of *O. vulgaris* (or a complex of very similar species) (De Luca et al. 2014), it is not surprising that this species has foraging behaviors that allow it to exploit a wide variety of prey species.

Even within the San Salvador *O. vulgaris* population, we detected differences in diet breadth and composition among site locations around the island (Figures 2 and 3). A likely explanation is habitat-related differences in prey availability. The two locations that clustered together in the principal component analysis, North Point and Potters, are spatially close, lying within the same large bay (Graham's Harbour, Figure 1), and are most

Table 3. Composition of *Octopus vulgaris* midden contents collected at four locations at San Salvador Island. Values are the percent of midden contents for each prey type, averaged over all dens, excluding items collected on the first visit.

Taxon	Common name	Mean % of midden contents
Bivalves		
Asaphis deflorata	Gaudy asaphis	8.436
Chione sp.	Small venus	5.791
Periglypta listerii	Princess venus	3.560
Codakia orbicularis	Tiger lucine	3.108
Lucina pensylvanica	Pennsylvania lucine	2.574
Tucetona pectinata	Comb bittersweet	2.083
Americardia media	Atlantic strawberry cockle	0.906
	Oyster spp.	0.521
Barbatia cancellaria	Bearded ark	0.515
Pinnidae	Pen shell	0.416
Lima scabra	Rough lima	0.399
Tellina radiata	Sunrise tellin	0.375
Acropagia fausta	Lucky tellin	0.238
Tellina sybaritica	Dwarf tellin	0.233
Modiolus americanus	Tulip mussel	0.198
Tellina alternata	Lined tellin	0.154
Papyridea soleniformes	Spiny paper cockle	0.135
Brachidontes modiolus	Yellow mussel	0.090
Lima sp.	Other lima	0.083
Isognomon radiatus	Lister's tree oyster	0.078
Laevicardium laevigatum	Egg cockle	0.073
Divaricella quadrisulcata	Cross-hatched lucine	0.022
Tellina squamifera	Crenulate tellin	0.021
Aadara notabilis	Eared ark	0.021
Gastropods		
Turbo castaneus	Knobby turban	14.517
Astrea phoebia	Long-spined star snail	11.721
Phyllonotus pomum	Apple murex	5.219
Natica canrena	Colorful moon snail	4.333
Cerithium spp.	Cerith	3.489
Fasciolaria tulipa	Tulip snail	1.963
Bulla striata	Striated bubble	1.567
Cypraea cinerea	Atlantic gray cowrie	1.459
Strombus gigas	Queen conch	1.105
Tegula fasciata	Smooth tegula	1.086
Tonna maculosa	Partridge snail	0.757
Conus spp.	Cone snail	0.256
Olivella sp.	Dwarf olive	0.246
Cymatium cribbaenum	Dog-head triton	0.155
Pyramidella dolabrata	Giant Atlantic pyram	0.145
Nerita spp.	Nerite	0.133
Fissurellidae	Keyhole limpet	0.102
Charonia variegata	Atlantic triton	0.083
Cassis spp.	Helmet	0.029
Cymatium nicobarium	Gold-mouthed triton	0.026
Cittarium pica	WI top snail	0.018
Crustaceans		
Majidae	Spider crab	10.717
Calappa spp.	Shame-faced crab	3.632
Xanthidae	Xanthid crab	3.274
Crustacea	Misc. crustacean	1.490
Portunidae	Swimming crab	1.249
Anomura	Hermit crab	1.085
Alpheid	Snapping shrimp	0.111

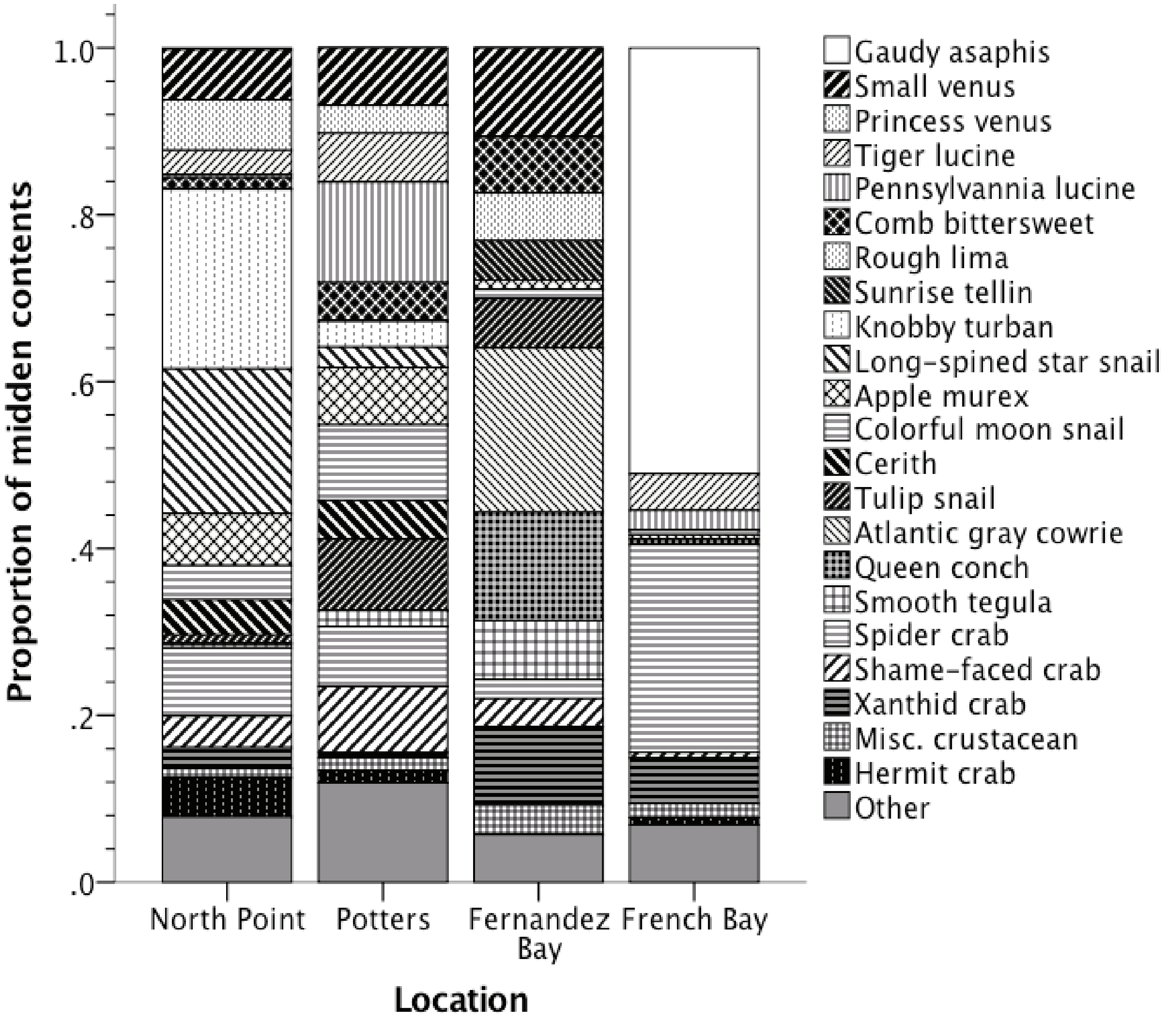

Figure 2. Mean proportion of *Octopus vulgaris* midden contents collected on visits 2+ from dens at four locations at San Salvador Island. "Other" includes all prey types with an overall mean proportion < 0.01. See Table 3 for scientific names of prey species.

similar in habitat among the locations we sampled. The benthic habitat at Fernandez Bay is exposed bedrock, lacking sea grass entirely, while French Bay is a much higher-energy sea grass environment than the Graham's Harbour locations. Since it is likely that the benthic invertebrate communities differ among these habitats, we hypothesize that octopus diet differences reflect, at least in part, habitat-related differences in available prey.

In addition to geographical variation in breadth and composition of *O. vulgaris's* diet at multiple spatial scales, individuals' diets may also vary significantly within a population; several populations of *O. vulgaris*, including San Salvador's, include individuals with specialized diets (i.e., diets significantly narrower than the average) (Mather 1991; Anderson et al. 2008; Kuhlmann and McCabe 2014). This suggests that inter-individual differences among octopuses may also significantly influence diet, although the factors that are involved in octopus diet specialization remain to be determined.

Although our study did not directly measure octopus abundance or density, based on the number found per time and area searched, *O. vulgaris* appear to be more abundant and more dense at North Point than other locations, especially Fernandez Bay and Potters. This

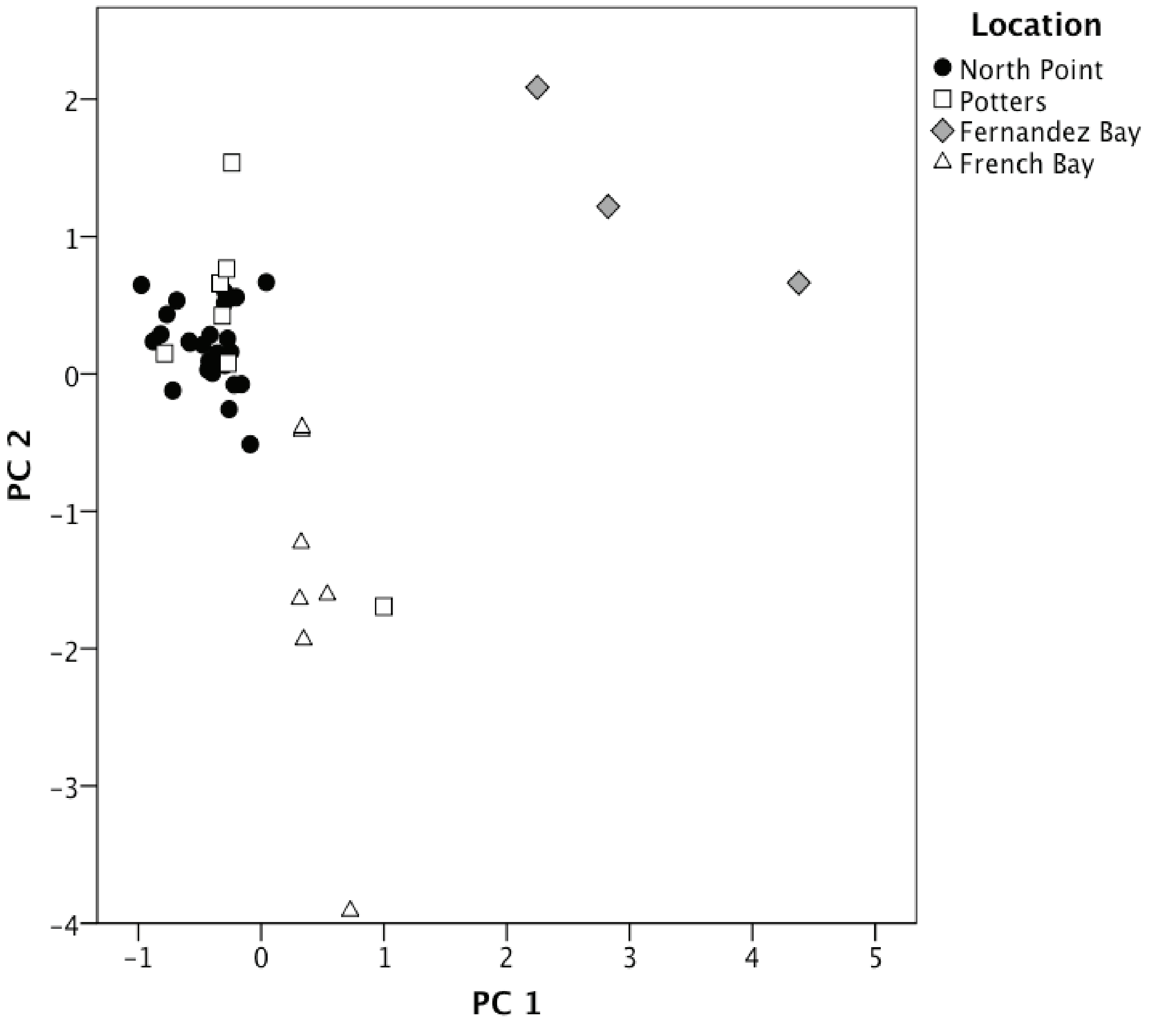

Figure 3. Scatter plot of Principal Component 1 (PC 1) and Principal Component 2 (PC 2) for collections of midden contents of *Octopus vulgaris* dens (n = 43) at four locations at San Salvador Island. PC 1 and PC 2 are the result of a principal component analysis conducted on proportions of midden contents of 52 prey types (See Table 3).

pattern is interesting because nearly all the octopuses at North Point were living in artificial shelters: shells discarded into the water by the queen conch fishery (Table 1). The substrate at North Point has very little exposed rock, so crevices and other hard shelters apart from discarded shells are extremely rare. At this location, shelter may be the limiting resource for *O. vulgaris*, as has been suggested for other octopus populations living in soft-sediment habitats (Mather 1982; Iribarne 1990; Anderson et al. 1999; Katsanevakis and Verriopoulos 2004). In contrast, Potters and Fernandez Bay have much more exposed rock and an apparent abundance of natural shelters (ledges, solution holes, and crevices in coral heads) but fewer octopuses, suggesting that food, not shelter, may be limiting at those locations. It is possible that the artificial shelters resulting from the local queen conch fishery are allowing *O. vulgaris* to exploit a food-rich habitat at North Point that would otherwise be unused because of a lack of shelters, another example of facilitation causing an expansion of a species' realized niche (Bruno et al. 2003).

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