Diet specialization in *Octopus vulgaris* at San Salvador, Bahamas

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ABSTRACT: Populations of resource generalists are often made up of individuals specializing on a narrower range of resources; such individual specialization can have important ecological and evolutionary significance. We quantified individual diet variation in *Octopus vulgaris*, the common octopus, at 3 locations around San Salvador, Bahamas, using repeated collections of midden contents. We quantified the degree of individual specialization using the proportional similarity index and individual diet breadth using the Berger-Parker index of dominance and the number of prey types per den. As in other populations, the San Salvador *O. vulgaris* population has a broad diet, consuming at least 49 prey types; however, most individuals (59%) had significantly specialized diets. The amount of specialization varied significantly among locations. At one location, all octopuses were generalists and consumed relatively uniform proportions of prey types (lower dominance) compared to the other 2 locations, where about 70% of individuals were specialists with diets dominated by 1 or a few prey types. Individual specialization has been documented in numerous species but mostly vertebrates; this is only the second quantified example from the cephalopods.

KEY WORDS: Octopus · Diet · Individual specialization · Bahamas

INTRODUCTION

Many populations of resource generalists are actually made up of individuals that specialize on a narrower subset of resources (Bolnick et al. 2003). This individual variation has been documented in many species, nearly 200 in a review by Araújo et al. (2011), from a broad range of taxa, but the majority of examples are vertebrates. A thorough understanding of individual variation requires examples from a more representative range of taxa.

Knowledge of individual variation is important because it can have significant ecological and evolutionary effects. At the population level, individual specialization may help stabilize population dynamics in the face of competition and predation, change the effects of frequency-dependent intraspecific competition, and influence a population's ability for diversification or speciation; within communities, it can

change the form of selection on prey populations and alter interspecific interactions (Bolnick et al. 2003). For example, individual variation in habitat use in the Eurasian perch *Perca fluviatilis* affects trophic linking of spatially separated food chains (Quevedo et al. 2009), and manipulating the proportions of 2 behavioral types in colonies of the spider *Anelosimus studiosus* changed the nature of its interspecific interactions with web associates from amensalism to commensalism or mutualism (Pruitt & Ferrari 2011).

Octopus vulgaris, the common octopus, has a circumglobal distribution in tropical to temperate waters (Warnke et al. 2004, Guerra et al. 2010). *O. vulgaris* is considered to be a generalist predator of benthic molluscs and crustaceans, although the breadth and specific composition of its diet vary geographically (Smale & Buchan 1981, Ambrose & Nelson 1983, Mather 1991, Smith 2003, Anderson et al. 2008, Kuhlmann & McCabe unpubl. data). The diets of *O. vul-*

garis and other shallow-water octopods are frequently studied using the contents of middens, piles of prey remains left outside the den (Fig. 1) (Dodge & Scheel 1999). This method can easily identify shelled prey
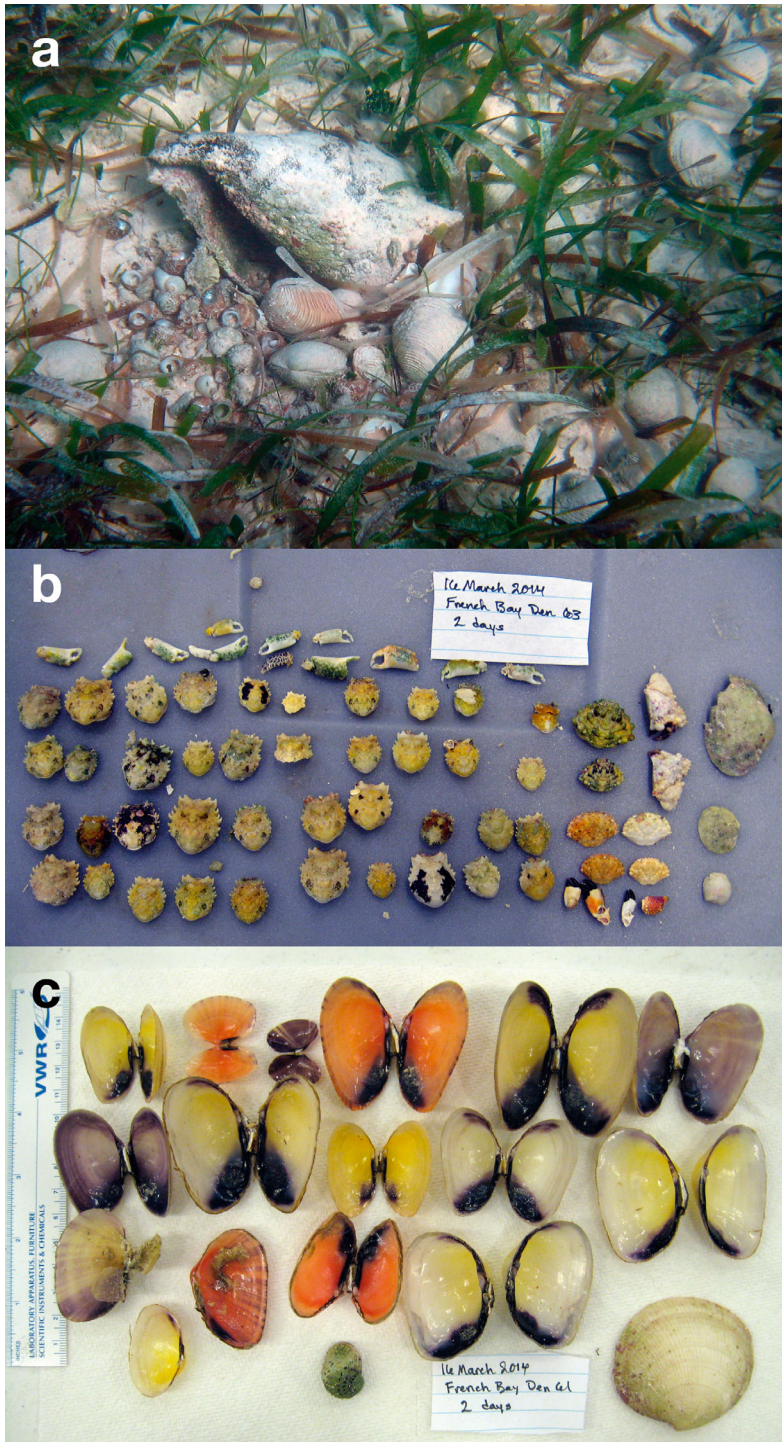

Fig. 1. (a) Octopus den (queen conch *Strombus gigas* shell) and midden. (b,c) Examples of octopus midden contents collected on the same day from 2 dens <70 m apart at French Bay (San Salvador Island, Bahamas)

that are not completely consumed, such as large molluscs or crustaceans, and provides a picture of the diet integrated over time; however, it may miss small and softer-bodied prey that are consumed completely and prey consumed away from the den (Smith 2003). In addition, the composition of a midden changes over time because physical forces and other organisms remove items at non-random rates (Ambrose 1983, Mather 1991). As with other diet estimation methods (e.g. for octopods, direct observation, stomach contents), results must be interpreted in the context of these limitations (Smith 2003).

Shallow-water octopods are versatile, intelligent predators that are capable of learning foraging behaviors (Fiorito et al. 1990, Boal et al. 2000) and are known to exhibit persistent behavioral types, or personalities (Mather & Anderson 1993, Jordan 2010). These traits make them excellent candidates to exhibit individual variation in foraging characteristics, e.g. diet. The giant Pacific octopus *Enteroctopus dofleini* exhibits individual diet specialization, and geographic variation in specialization has been quantified across its range in the North Pacific (Scheel & Anderson 2012). Individual diet specialization has been suggested for populations of *O. vulgaris*, *O. cyanea*, and *O. maorum* (Mather 1991, Grubert et al. 1999, Anderson et al. 2008, Mather et al. 2012) but has not been rigorously quantified in those species (e.g. by the methods suggested by Bolnick et al. 2002). Quantifying individual-level resource specialization, rather than just determining its presence or absence, is necessary for comparison to other studies and to test hypotheses about its origins or effects (Bolnick et al. 2002).

We used the midden contents of *O. vulgaris* from the coastal waters of San Salvador Island in the Bahamas to investigate the following questions: (1) Do some individual octopuses in the population have specialized diets? (2) Does the amount or degree of diet specialization vary geographically around San Salvador?

MATERIALS AND METHODS

San Salvador is a small island (~11 × 19 km) atop a small, isolated platform at the edge of the continental shelf (Shaklee 2008) (Fig. 2). The shallow-water shelf (≤15 m) surrounding the island is narrow, with a sharp shelf-break to deep water usually <1 km from shore and in some places <0.25 km (Diehl et al. 1988).

We observed octopuses at 3 nearshore (water depth ≤3 m) locations around San Salvador with different benthic habitat types (Fig. 2). The North Point site is dominated by seagrass beds composed of *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* (Smith et al. 1990). The seagrass grades into hard substrate at the lower edge of the intertidal zone. At Potters, seagrass is interspersed with patches of exposed bedrock with scattered solution holes and associated hard-bottom benthic community (small coral heads, sponges, and soft corals). 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 seagrass (*T. testudinum* and *S. filiforme*) (Smith et al. 1990) separated by channels of sand and coral rubble.

We collected octopus midden contents in January and 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 (Fig. 1a); an octopus was not seen at all presumptive dens (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 *Octopus vulgaris*, so we assume that our entire sample was this species. For each new den, we recorded shelter type, habitat type, and the presence of an octopus and then collected all prey remains in a numbered mesh bag. The den was marked with a numbered flag and a surface float to aid relocation. We then returned to the den to collect any new prey remains at intervals of 1 to 5 d, usually (>90% of collections) 3 d or fewer.

In the laboratory, we identified, enumerated, and usually measured (for molluscs, shell height; for crustaceans, carapace width) the prey remains following the methods of Kaplan (1988), Abbott & Morris (1995), and Redfern (2013). When possible, we identified mollusc remains to species. Crustacean remains were frequently not identifiable to species and so were grouped into larger taxonomic categories
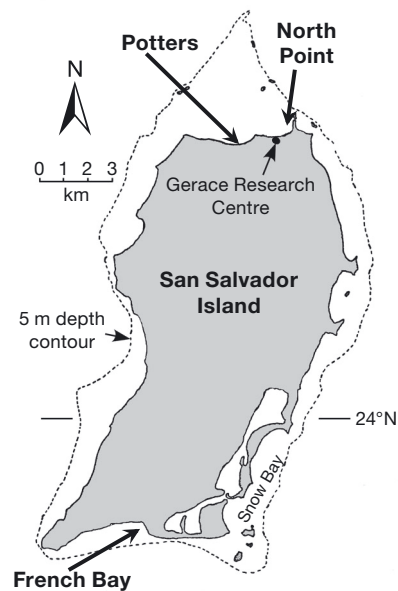

Fig. 2. San Salvador Island, Bahamas (bottom), showing the 3 study locations; above is the location of San Salvador in the Bahamas (modified from http://histgeo.ac-aix-marseille.fr)

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).

Because physical forces and other species (e.g. hermit crabs) selectively remove prey remains once deposited, large clams become over-represented and lighter remains, like crustacean parts, become under-represented in middens as they age (Ambrose 1983, Mather 1991, Kuhlmann & McCabe unpubl. data). To more accurately estimate octopus diets, we

Table 1. Characteristics of sampled *Octopus vulgaris* dens at 3 locations around San Salvador Island (upper table), Bahamas, and statistical comparison among locations (lower table). Den type: coral head complex = living or dead coral heads with various other sessile invertebrates (e.g. sponges, soft corals) and algae; solution hole = a hole or crevice in bedrock. *Locations differ significantly at p < 0.05

Location	No. of dens	Den type Queen conch shell	Den type Coral head complex	Den type Solution hole	Dens with octopus present (%)	Octopus occupancy (median proportion of visits [range])	Length of observation (median days [range])	No. of collections (median [range])	Interval (median days [range])
North Point	27	26	0	1	85.2	0.50 [0–1]	12 [4–18]	7 [2–10]	1.9 [1–5]
Potters	7	2	2	3	100.0	0.71 [0.33–1]	13 [12–13]	7 [6–8]	2.2 [1.9–2.4]
French Bay	7	0	0	7	85.7	0.60 [0–1]	12 [10–12]	6 [5–6]	2.4 [2.4–2.5]
All locations	41	28	2	11	87.8	0.57 [0–1]	12 [4–18]	7 [2–10]	2.4 [1–5]
Among locations									
p					0.37	0.33	0.66	0.025*	0.54
Test					*G*-test	Kruskal-Wallis	Kruskal-Wallis	Kruskal-Wallis	Kruskal-Wallis
Test statistic					$G = 2.01$	$H = 2.25$	$H = 0.83$	$H = 7.39$	$H = 1.22$
df					2	2	2	2	2

did not include the midden contents from the first collection in our analysis. 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 for each den. In a few cases, several potential shelters (usually queen conch shells) with middens occurred close to one another. If we never saw more than 1 octopus in this group of shelters on a single collection day, we assumed that all prey remains were left by 1 octopus and combined all collections for the group of shelters. At one den at North Point, we only collected 1 prey item after the first observation; we excluded this den from the analyses presented here. Including that den did not qualitatively change the results.

We examined individual diet specialization using the proportional similarity index, PS_i (Bolnick et al. 2002). This index estimates individual specialization by comparing the diet overlap of each individual to the sample population. For an individual that consumes prey in the same proportion as the overall population, a generalist, $PS_i = 1$; a value closer to zero indicates a diet less similar to the population average or more specialized. We used the computer program IndSpec1 (Bolnick 2002) to calculate PS_i. Because octopus diet varies among locations at San Salvador (Kuhlmann & McCabe unpubl. data), we calculated PS_i separately for each location; thus, individuals are compared to the average diet for their location, not the San Salvador sample as a whole. For each indi-

vidual, IndSpec1 also generated Monte Carlo null distributions for PS_i by creating 5000 randomly drawn diets with the same number of prey items; the proportion of these pseudoreplicate null diets with smaller PS_i values than the observed diet was used as a p-value to test the null hypothesis that an individual is a generalist. Because of the large number of hypothesis tests, we applied the Bonferroni correction to significance levels; thus, $p \leq 0.05/n$ = a specialist and $p > (0.05/n)$ = a generalist, where n is the number of dens observed at a particular location.

In addition, we measured individual diet breadth with the Berger-Parker index of dominance, *d*, and the number of prey types per den. Berger-Parker *d* is simply the maximum proportion of all the prey types in an individual's diet and is considered a robust measure of dominance (Southwood & Henderson 2000).

We compared characteristics of collections among locations or foraging types using ANOVA when data met parametric assumptions and nonparametric Kruskal-Wallis or Mann-Whitney *U*-tests when they did not. Because the number of prey types in a collection is strongly correlated to the size of the collection (number of prey items), we also compared the number of prey types among locations and forager types using ANCOVA with the number of prey items ($\log_{10}$ transformed to improve linearity) as the covariate. Data in the form of frequencies (octopus sightings and den types) were compared among locations using likelihood-ratio contingency table analyses (*G*-test).

RESULTS

We collected prey from 41 presumptive octopus dens (Table 1). At North Point, large queen conch *Strombus gigas* shells were the most common den type; at the other locations, solution holes were most common (Table 1); den type proportion varied significantly among locations (*G*-test: $G = 38.72$, df = 4, $p < 0.0005$). An octopus was seen at least once in all but 6 dens (88%) (Table 1); because typical octopus prey items accumulated between collection visits at the presumptive dens where we never observed an octopus, we assumed that these 6 dens were occupied between our visits. Neither the occurrence of an octopus in dens nor sampling characteristics varied significantly among locations, with the exception of the number of collections, where there was a much greater range of values at North Point than at the other locations (Table 1).

We identified 49 prey types in middens. The most common prey items were 2 medium-sized gastropods, *Turbo castaneus* (knobby turban snails) and *Astrea phoebia* (long-spined star snail), and spider crabs (Majidae) (Table 2). Over 20% of prey types occurred only once, while the 4 most common types of prey accounted for >55% of all midden items.

Of the 41 octopuses, 24 (59%) had diets that were significantly less similar to their location's average diet (lower PS_i) than expected by chance; that is, they were specialists (Table 3). Specialists consumed significantly more prey types than generalists (Fig. 3) (ANOVA: $F = 4.25$, df = 1, 39, $p = 0.037$); however, prey types per den was strongly correlated to the number of prey items (Spearman's r = 0.64, $p < 0.001$), and we collected more prey items per den from specialists than from generalists (Mann-Whitney *U*-test: $Z = 4.45$, n = 41, $p < 0.0005$). After controlling for the number of prey items, prey types per den did not significantly differ among forager types (ANCOVA with $\log_{10}$ [number of prey items] as covariate: $F = 4.64$, df = 1, 38, $p = 0.11$). Dominance was significantly higher for specialists than for generalists (Fig. 4) (Mann-Whitney *U*-test: $Z = 2.00$, n = 41, $p =$

Table 2. Percent of items of different prey types collected from *Octopus vulgaris* middens at 3 locations around San Salvador, Bahamas, excluding the first collection. n = 2483 total prey items. Percent is calculated as the mean of all individuals' percents

Taxon	Common name	Mean % of midden contents
Bivalves		
Asaphis deflorata	Gaudy asaphis	8.847
Chione spp.	Small venus	5.290
Periglypta listerii	Princess venus	4.710
Codakia orbicularis	Tiger lucine	3.748
Lucina pensylvanica	Pennsylvania lucine	2.700
Tucetona pectinata	Comb bittersweet	1.697
Americardia media	Atlantic strawberry cockle	0.950
Other oyster	Oyster	0.547
Barbatia cancellaria	Bearded ark	0.540
Pinnidae	Pen shell	0.436
Acropagia fausta	Lucky tellin	0.250
Tellina sybaritica	Dwarf tellin	0.244
Tellina alternata	Lined tellin	0.162
Papyridea soleniformes	Spiny paper cockle	0.142
Brachidontes modiolus	Yellow mussel	0.095
Isognomon radiatus	Lister's tree oyster	0.082
Laevicardium laevigatum	Egg cockle	0.077
Modiolus americanus	Tulip mussel	0.045
Tellina radiata	Sunrise tellin	0.045
Divaricella quadrisulcata	Cross-hatched lucine	0.023
Tellina squamifera	Crenulate tellin	0.022
Aadara notabilis	Eared ark	0.022
Gastropods		
Turbo castaneus	Knobby turban	15.225
Astrea phoebia	Long-spined star snail	12.293
Phyllonotus pomum	Apple murex	5.393
Natica canrena	Colorful moon snail	4.464
Cerithium spp.	Cerith	3.659
Fasciolaria tulipa	Tulip snail	2.117
Bulla striata	Striated bubble	1.644
Tonna maculosa	Partridge snail	0.794
Tegula fasciata	Smooth tegula	0.622
Olivella sp.	Dwarf olive	0.258
Strombus gigas	Queen conch	0.206
Conus spp.	Cone snail	0.188
Cymatium cribbaenum	Dog-head triton	0.163
Pyramidella dolabrata	Giant Atlantic pyram	0.152
Nerita spp.	Nerite	0.139
Fissurellidae	Keyhole limpet	0.107
Cypraea cinerea	Atlantic gray cowrie	0.090
Cassis	Helmet	0.030
Cymatium nicobarium	Gold-mouthed triton	0.028
Cittarium pica	WI top snail	0.019
Crustaceans		
Majidae	Spider crab	11.072
Calappa spp.	Shame-faced crab	4.053
Xanthidae	Xanthid crab	2.743
Portunidae	Swimming crab	1.310
Crustacea	Misc. crustacean	1.307
Anomura	Hermit crab	1.138
Alpheid	Snapping shrimp	0.116

Table 3. Summary of diet characteristics for *Octopus vulgaris* at 3 locations around San Salvador, Bahamas (upper table), and statistical comparison among locations (lower table). IS = index of similarity, the mean of PS$_i$ values. **Locations differ significantly at p < 0.01

| Location	n	Total no. of prey types	No. of prey types den^{-1} (mean ± SE)	No. of prey items den^{-1} (median [range])	IS	% specialists
North Point	27	41	12.70 ± 0.98	58 (4–199)	0.55	70.4
Potters	7	28	11.57 ± 1.34	22 (13–47)	0.53	0.0
French Bay	7	21	8.29 ± 0.97	72 (12–131)	0.59	71.4
All locations	41	49	11.76 ± 0.74	54 (4–199)		58.5
Among locations						
p			0.086	0.053	0.58	0.001**
Test			ANOVA	Kruskal-Wallis	Kruskal-Wallis	*G*-test
Test statistic			*F* = 2.62	*H* = 5.89	*H* = 1.11	*G* = 14.45
df			2,38	2	2	2
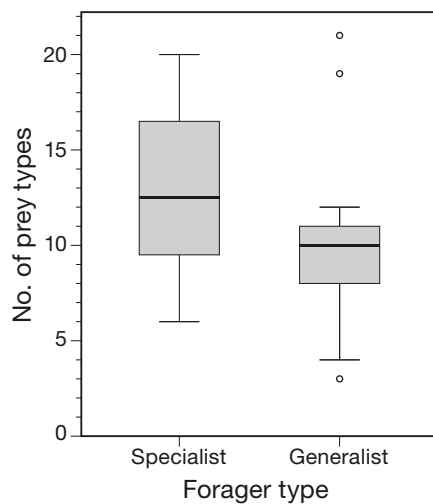
Fig. 3. Number of prey types per octopus den for specialist (n = 24) and generalist (n = 17) foragers. Box plots show median (bold horizontal line), interquartile range (IQR, boxes), and range (bars) up to 1.5 × IQR past the quartile. Outliers (data points >1.5 × IQR past the quartile) are shown as open circles
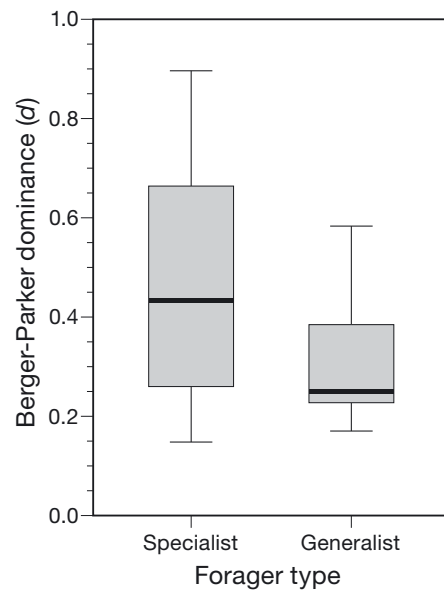

Fig. 4. Berger-Parker dominance, *d*, of proportional midden contents for specialist (n = 24) and generalist (n = 17) foraging octopuses. Box plots show median (bold horizontal line), interquartile range (boxes), and range (bars)

0.046). Specialists tended to have a high proportion of at least 1 common prey type compared to the location average: knobby turban snails *T. castaneus* or long-spined star snails *A. phoebia* at North Point and gaudy asaphis *Asaphis deflorata* or spider crabs (Majidae) at French Bay (Fig. 5). Generalists, especially at Potters, tended to have a more uniform distribution of prey type proportions.

The number of prey types per den was not significantly different among locations (Table 3). However, the difference in prey items per den among locations was nearly statistically significant (Table 3), and after controlling for the number of prey items, prey types per den differed significantly among locations

(ANCOVA with log$_{10}$ [number of prey items] as covariate: *F* = 12.80, df = 2,37, p < 0.0001), with Potters having the highest adjusted mean and French Bay the lowest. Mean similarity (IS) did not differ among locations, but the proportion of specialists did (Table 3); most individuals were specialists at North Point and French Bay, while all were generalists at Potters. Dominance differed significantly among locations (Kruskal-Wallis test: *H* = 18.07, df = 2, p < 0.0005). Median dominance was higher at French Bay compared to the other sites, and dominance values at North Point showed a greater range of values than those at Potters (Fig. 6).
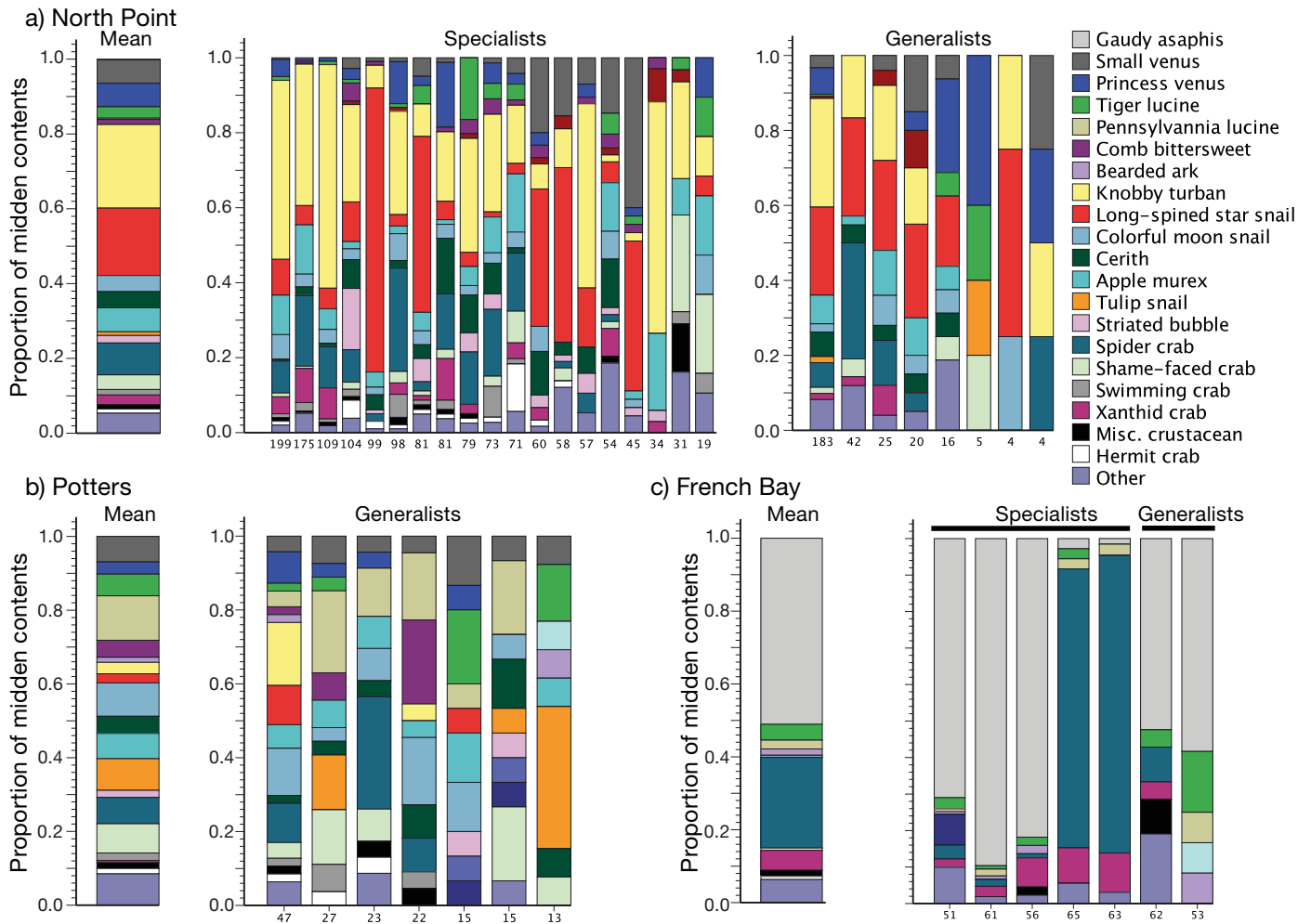
Fig. 5. Proportion of *Octopus vulgaris* midden contents from multiday collections, excluding collection 1, at 3 locations (North Point, Potters, French Bay) at San Salvador Island, Bahamas. For graphical clarity, prey types with an overall mean proportion <0.01 are grouped as 'Other'. 'Mean' is the overall average for the location; other bars show collections from individual dens. Values below the bars are the number of prey items collected from that den
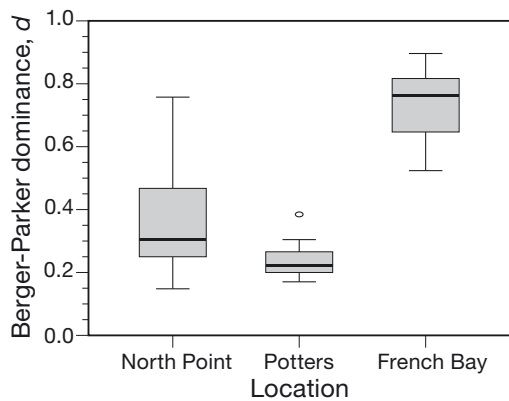

Fig. 6. Berger-Parker dominance, *d*, of midden contents for octopuses at 3 locations around San Salvador, The Bahamas. Box plots show median (bold horizontal line), interquartile range (IQR, boxes), and range (bars) up to 1.5 × IQR past the quartile. Outliers (data points > 1.5 × IQR past the quartile) are shown as open circles. Sample sizes: North Point, n = 27; Potters, n = 7; French Bay, n = 7)

DISCUSSION

The diet of *Octopus vulgaris* at San Salvador Island is broad, encompassing at least 49 prey types; similar to other populations of this species, *O. vulgaris* at San Salvador is a generalist predator at the population level (Smale & Buchan 1981, Ambrose & Nelson 1983, Mather 1991, Smith 2003, Anderson et al. 2008). However, most individuals in our study had a narrower diet than the average for their location; that is, they were specialists. Therefore, the population's niche width is wide, but individual niches are much narrower and variable: a generalist population made up of specialists. Based on less quantitative measures, other studies have concluded the same about other populations of *O. vulgaris* (Mather 1991, Anderson et al. 2008), so individual diet variation may be widespread in this species. Although individ-

ual specialization has been documented in numerous species (Bolnick et al. 2003, Araújo et al. 2011), to our knowledge it has only been quantified so far in 1 other cephalopod, *Enteroctopus dofleini* (Scheel & Anderson 2012).

At 2 locations, North Point and French Bay, octopuses exhibited strong between-individual differences in diet. At both locations, some individuals had generalist diets while some were specialists, and the dominant prey species tended to vary among the specialists (Figs. 1b,c & 5). It is unlikely that these differences in diet were entirely caused by differences in prey availability, since many dens were close enough for the home ranges of the occupants to overlap (Mather 1991), and there was no apparent spatial pattern of specialists and generalists within locations. It is possible that some between-individual variation is a result of age- or sex-related differences in foraging. For example, the diet and rate of food intake varies by sex and age or size in both *O. vulgaris* and *O. mimis* (Smale & Buchan 1981, Cortez et al. 1995). In addition, several octopus species are known to exhibit consistent behavioral types, or personalities (Mather & Anderson 1993, Jordan 2010), which could result in individuals using different diet optimization criteria. For example, some individuals may be risk-averse ('shy') and minimize exposure to predation while others are not ('bold') and maximize rate of energy intake, resulting in differences in diet (Araújo et al. 2011). Factors leading to diet specialization in the San Salvador *O. vulgaris* population remain to be investigated.

We found geographical variation in the amount of individual specialization, with most octopuses specialists at North Point and French Bay and none at Potters (Table 3). Octopus diets at Potters also tended to be broader and have more uniform proportions of prey types (lower dominance) than those at the other locations (Figs. 5 & 6). The reasons for these differences remain to be explored. A variety of ecological factors that are likely to vary spatially can affect individual specialization, including competition, predation risk, and the diversity or distribution of prey (Araújo et al. 2011). Although we did not directly measure octopus density, in 2014 we spent approximately equal effort (search time) at North Point and Potters, yet we found nearly twice as many octopuses at North Point in spite of an abundance of potential dens (e.g. solution holes) at Potters. Although search time was much less at French Bay than at the other locations, all the octopuses at French Bay were located along an ~150 m stretch of shore, in some cases only a few meters apart. In contrast, the octopuses at Potters were widely separated and spread over a much larger area. These observations suggest that octopus density may be much lower at Potters than at the other 2 locations, possibly an indication of lower prey abundances (higher competition). Foraging theory predicts that higher intraspecific competition can either increase or decrease individual specialization (Svanbäck & Bolnick 2005), although empirical evidence consistently finds that individual specialization increases with competition (Araújo et al. 2011). If the lack of specialization in octopuses at Potters is a result of higher competition for prey, it would be an interesting exception to empirical trends but consistent with the predictions of foraging theory.

One way to investigate the effect of resource availability on individual specialization by octopuses is to use repeated midden collections to measure provisioning rate ('meal size') on a daily or semi-daily basis. We would expect meal size to be positively correlated to prey availability, so examining patterns of individual specialization in relation to provisioning rate would be revealing. A challenge of this method is that it requires size estimates of individual prey items. For octopods, the shells of most mollusc prey are discarded whole and can be easily measured, but other prey types are more difficult; for example, crustacean remains tend to be partial (e.g. appendages) or fragmented. Because of these difficulties, we did not record size measurements for a large and non-random subset of the prey items we collected in this study, so we could not apply this method to these data. This line of inquiry into the factors influencing diet specialization would be profitable to explore in the future.

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