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The Diet of *Octopus bimaculoides* in Mission Bay, California (Mollusca: Cephalopoda)

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ABSTRACT A year-long survey of *Octopus bimaculoides* Pickford & McConnaughey (1949) dens in three different subtidal habitats was conducted in Mission Bay, California. Habitat complexity and stability were positively associated with prey species richness, species abundance, and den availability. Collectively, 38 species of bivalves and 22 species of gastropods were recorded from octopi debris fields. Two species of bivalve at each site comprised approximately 60% or greater of the bivalves in the debris fields. Bivalves species represented 85% of the take, the remainder being gastropods. With the exception of the bubble snail, most gastropods were drilled, while most bivalves were not. Crustacean remains were infrequently found in debris fields. Prey species in other phyla may have been consumed, but their remains were not found in the debris fields.

KEY WORDS Diet, habitat complexity, habitat stability, prey species, *Octopus bimaculoides*

INTRODUCTION

Although *Octopus bimaculoides* can be a common inshore species, details regarding the natural diet of this species are lacking. This paper reports *in situ* findings in three varied habitats of Mission Bay, San Diego, California. The goals of this study were to: (1) determine the prey species found in debris fields of octopi dens in different subtidal habitats, (2) evaluate the contribution of the various prey species to the diet of *O. bimaculoides*, (3) identify which mollusks are pulled open vs. drilled, (4) compare and contrast habitat complexity, stability, and diet in these different subtidal environments, and (5) a review of literature relevant to the life history of *O. bimaculoides*. The findings reported may not be inclusive of all potential prey species, but rather those species who's remains were found in the debris fields of the octopi dens.

Two similar appearing species of octopi occur in southern California, *Octopus bimaculoides* Pickford & McConnaughey 1949 and *Octopus bimaculatus* Verrill, 1883. They were believed to be one species until differences in their reproductive biology were noted. *Octopus bimaculoides* (Figure 1) produces larger eggs

Figure 1. *Octopus bimaculoides* in Mission Bay.

(9-17 mm) and upon hatching the small octopi take up residence in the benthic community, while the eggs of *O. bimaculatus* are small (2-4 mm) and upon hatching the larvae enter the planktonic community (Pickford & McConnaughey 1949, Forsythe & Hanlon 1988a, Ambrose 1988).

Dominguez-Contreras *et. al*. (2018) evaluated the distribution and genetic structure of three species of *Octopus* in the northern Gulf of California and the Pacific side of northwestern Baja California, Mexico. Two species had planktonic larvae *O. bimaculatus* and *O. hubbsorum* Berry 1953 and one species *O. bimaculoides* had direct development. They found that populations of *O. bimaculoides* had low genetic diversity and higher levels of kinship, compared to the two species with planktonic larvae. In essence, *O. bimaculoides* puts all of its eggs in one basket, while the other two species spread their genetic material far and wide. The difference in reproductive strategies has many ecological and evolutionary implications.

Based on both field observations and laboratory studies Forsythe & Hanlon (1988a & 1988b), published details regarding growth, reproduction, effects of temperature on development, and skin display patterns. *Octopus bimaculoides* has a life span of approximately 1-1.5 years and reproduces only once. Depending upon the location, peak reproduction is between October and May. Lang (1986) reported female *O. bimaculoides in situ* were brooding eggs on a year-round basis, but did not identify a peak period. Growth rate is temperature dependent especially for developing embryos and juveniles. Females lay clusters of eggs on hard surfaces in protected rocky dens, and during that time, they often do not feed, and die shortly after their eggs hatch. I have observed *O. bimaculoides* as it goes through senescence, it becomes less efficient in its actions, skin may begin to sluff, the animal coloration is dull, and often seen fully exposed during the day. The first time I observed post reproductive individuals in decline was alarming.

Walderon *et. al.* (2011) demonstrated chemoreceptors associated with the tentacles of *O. bimaculoides* have a role in detecting food, and the presence and even the sex of a nearby conspecific member of the population. Ramirez & Oakley (2015) removed patches of skin from *O. bimaculoides*, and found that, photo sensitive proteins activated chromatophores resulting in color change without interaction of the eyes or brain. The biological importance may be that it allows portions of the animal, such as a tentacle that may exit the den before the mantle, to quickly adapt to the surroundings. Derby *et. al*. (2007) suggested the ink of mollusks such as cephalopods protect these organisms with a collection of chemicals that cause sensory disruption to the predator, combined with other compounds associated with decaying matter. In the case of the octopus, such disruption, even if momentary, may allow the octopus to escape.

The moderate size, ease of laboratory culture and behavioral traits have made the genus *Octopus* the subject of many studies, which are mentioned only for awareness and include: social behavior, learning, problem solving, senescence, digestive enzymes, pigmentation, chemo-receptors, toxins, muscle function, sucker dynamics, regeneration of limbs, reproduction, anatomy, brain and nervous system function, parasites and laboratory culture.

Under natural conditions *O. bimaculoides* is a corpuscular/nocturnal predator. Upon capturing prey, the octopus returns to the safety of the den to consume the meal. Afterwards, the shell is discarded at the entrance, while others may be

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incorporated into the den opening, especially if the den is at the rock/sand interface. The debris field outside the dens has been termed a midden, implying a large collection of shells. How many shells constitute a midden is not universally defined. Ambrose (1983) in detailed studies of *O. bimaculatus*, suggested that 20 shells constitute a midden and therefore concluded middens were not formed by that species. I use the term debris field, as it accounts for variable numbers of shells associated with each den. In this study, debris field of *O. bimaculoides* contained 5 to over 30 shells.

Wodinsky (1969) described four steps in the process of an octopus capturing and consuming its prey: (1) prey recognition/selection (2) pull open or drill the prey (3) inject toxins yes/no (4) consume prey and discard. Between steps one and two I would add; (1.1) attack and subdue and (1.2) move to less exposed location to process prey (usually the den). Wodinsky (1969) conducted experiments related to prey selection and drilling, and provides a generic review of literature associated with each of the four steps.

Abbreviations.
MB = Mainer's Basin
MP = Mainer's Point
UW = Underwater
VC = Ventura Cove

METHODS

A Nikon Cool pic underwater camera was used to document observations and habitat. All sites were surveyed bi-monthly for one year. Each site was surveyed using SCUBA and dead shells and crustaceans associated with the dens were placed in prelabeled sample bags. Intact dead gastropods associated with the dens were collected. Only bivalves with both valves still attached were collected and scored. Intact bivalves could confirm if they had been drilled or not and suggested they were recently preyed upon by octopi. Bivalves that were separated or broken were not collected or scored. Shells were lightly washed, dried, identified, measured, and returned to the bay, but not in the area of the study sites. In addition to the scheduled sampling, numerous monthly visits to the sites were made to make general observations.

The wet weight of notable prey species was determined as follows. Bivalves and gastropods that contributed significantly to the diet were collected alive and frozen briefly. The following day shells were measured and allowed to thaw. Bivalves were removed from their shell by cutting the abductor muscle and the animal was placed on a paper towel to absorb surface moisture. Any portion of the abductor left in the shell was removed and added to the material on the paper. Gastropods were treated in a similar fashion, but removed entirely by either fragmenting the shell, or removing it intact with forceps. Animals that were damaged during this process were discarded. Any bits of shell attached to the animal were removed, as was external mucus and the operculum. Once the appearance of the extracted animal was matte rather than wet, they were removed from the paper and weighed on a CCT series scale and the weight rounded to the nearest 0.1 gram. The data was recorded and the pan of the scale cleaned and the scale zeroed in preparation for the next sample.

Study Sites - Southwest Mission Bay.
(see Figure 2)

Mariner's Point MP (Figure 3) has extensive rocky rip-rap that lines the shore to a depth of 4-5 m and terminates on the clean sand bottom with occasional patches of eel grass (*Zostera marina* Linnaeus, 1753). The rocky habitat supports various marine algae, and in turn

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herbivorous gastropods. Tidal currents are present.

Mariner's Basin MB (Figure 4) is located on the west side of Mariner's Point. The area is characterized as sand with little sediment, there are few scattered rocks and eel grass is dominant and present year-round. Currents are minimal and the depth on the shelf is 2-3 meters. The dredged portion of the basin is typically 6-7 meters, and was not part of the study area.
Ventura Cove VC (Figure 5). The study area was north of the designated swimming area and west of the main Channel. The habitat is sparse, with silty-sand, and patchy eel grass during the summer, that is absent or greatly reduced during the winter. No rocks are present and daily tidal currents are present. The survey depth was 4-5 meters.

RESULTS

Table 1 provides a summary of each study site and includes habitat assessment, relative abundance of octopi, total number of shelled mollusk species collected in debris fields, and percent of bivalves and gastropods recovered from each of three habitats.

Bivalves. Table 2 summarizes the data collected for each of three sites, and lists the author of each species, and the page in Coan *et. al*. (2000), where photos, distribution and descriptions for each species can be found. A total of 3,102 bivalves were collected, representing 38 species associated with octopi dens. The most commonly consumed bivalves were the California Jackknife Clam *Tagelus subteres* which accounted for 46% to 53% of bivalves taken at all three sites. Bivalves such as *Chione undatella*, *Gari californica*, *Protothaca staminea*, *Saxadomus nuttalli*, *Trachycardium quadragenarium*, and *Tresus nuttallii* from Mariner's Basin were slightly smaller than the same species found in debris fields at Mariner's Point. The size of *Tagelus subteres* and *Tagelus californianus* at both of those locations did not differ significantly.

Gastropods. Table 3 summarizes the data for each of three sites and lists the author for each gastropod species. The gastropods are illustrated in Berschauer & Clark 2019. Collectively 528 shells, representing 22 species of gastropods were associated with octopi dens. The bubble snail *Bulla gouldiana* was the only gastropod commonly consumed in all three habitats. At Mariner's Basin, the dietary preference of two octopi made the small purple olive *Callianax biplicata* (formally *Olivella*) the most frequently taken gastropod at that site. Another octopus targeted various species of moon snails.

Figure 8 provides estimates of biomass vs. size for various mollusks commonly consumed at the study sites. When looking at prey species of vastly different sizes, it may be important to also evaluate biomass when considering the overall contribution of a specific prey species to the diet of the predator.

DISCUSSION

Anderson (2006) published a key to the west coast octopi species, which works well for animals that have been captured. Unfortunately, working *in situ*, with animals in their dens or den entrance, characters such as the configuration of the false-eyespot (ocelli), or the ratio of arm length to mantle size, are not visible. While diving and observing octopi in their dens, it was impossible to determine that only *O. bimaculoides* inhabited every den. When visible, they typically have a tentacle wrapped around their body just below their eyes (Figure 6). Any intrusive method to capture octopi would be destructive to both the habitat and den, and potentially injurious to the animal. A cross section of octopi were captured for identification upon completion of this study and only *O. bimaculoides* were found.

In Mission Bay, *O. bimaculoides* is an opportunistic corpuscular/nocturnal hunter feeding primarily on bivalves, gastropods, and occasionally crustaceans. Only seven crab carapaces were found during the study, all but one was from Mariner's Point; they include four Yellow Crabs, *Cancer anthonyi* Rathbun, 1897 and three Red Rock crabs *Cancer productus* Randall, 1839. Based on frequent monthly observations, the crabs were uncommon at these sites. Other species of soft bodied invertebrates and fish may have been consumed but their remains were not found associated with the dens.

Other Predators of Mollusks. *Octopus bimaculoides* is one of many predators of mollusks in Mission Bay. Although only shells in the debris fields were evaluated, it was still necessary to identify shells that may have been preyed upon by other predators from those taken by the octopus.

In the area of the study sites, subtidal vertebrate predators that focus on mollusks included the Horn Shark *Heterodontus francisci* Girard, 1855, with a strong preference for the Speckled Scallop *Argopecten ventricosus,* and rays including the large Bat Ray *Myllobatis californica* T.H. Gill, 1865. I have observed bat rays working in the sand for bivalves, and taking Wavy Top Turban *Megastraea undosa* off rocks and over sand. Both of these predators crush the shells, and the remains are discarded, but shell fragments appear in their waste. Various species of crabs and the Spiny Lobster *Panulirus interruptus* J.W. Randall, 1840, also consume mollusks, but again, they break the shell to gain access. The spiny lobster, horn shark and bat rays were observed at all three study sites.

Other predators of mollusks in the bay include the Giant Star Fish *Pisaster giganteus* Stimpson, 1857, but not observed at the three sites during this study, and numerous gastropods, especially *Forreria belcheri* Jousseaume 1850, *Pteropurpura festiva*, and three species of Naticidae. These species drill the shell or in the case of *F. belcheri* abrade the lip of the bivalve. Fortunately, the patterns are distinctive and easily distinguished from the drilling caused by this octopus. For these reasons, only intact bivalves that were still hinged and found in the debris field were scored.

Habitat Complexity and Mollusks Consumed. Habitat complexity and stability are critical factors that influence both octopi abundance and prey diversity. Mariner's Basin (MB) and Mariner's Point (MP) scored high, as no observable change to the habitat or food availability were observed during the survey period of one-year Table 1. Ventura Cove (VC) was scored low for stability, as virtually all of the eel grass cover is lost in the winter leaving a near barren sand habitat, and secondarily, the transient nature of the swimming *Argopecten ventricosus*. Figure 2 is a map of the southwestern portion of Mission Bay indicating the location of each study site. Figures 3-5 are underwater photos of the typical habitat associated with each of the three study sites.

In this study, instability of cover, lack of den sites and prey was reflected by the general absence of mature octopi in VC. The loss of eel grass in VC is an annual fall-winter event but, by late spring eel grass beds may reappear. The same pattern for eel grass loss and regrowth occurs in nearby Santa Barbara Cove. Results for MB may have been similar to those of VC, but the year-round persistence of dense eel grass and occurrence of the occasion rock provide cover, den sites, and support additional prey species.

The extensive rocky habitat of Mariner's Point, supports a wide variety of algae, which in turn supports herbivorous gastropods and provides shelter and resources for other invertebrates and vertebrates. The rocky habitat is greatly reduced in MB and absent from VC. Surprisingly, only 19 species of bivalves were consumed by octopi in VC, while at both MB and MP 32 species were consumed at each. The nature of instability at VC does not explain why there were 40% fewer bivalve species found in the debris fields. The substrate in VC may be less suitable for a variety of clams than MP or MB. Tables 2 and 3 summarizes the species and numbers of bivalves and gastropods found in debris fields at each location. The number and types of mollusks species consumed is an indirect measure of habitat complexity. Those numbers also reflect both prey abundance (opportunity) and dietary preference (desirability). As habitat complexity decreased so did prey diversity and the relative abundance of octopi (Table 1).

Mariner's Point MP (Table 1, Figure 3) (54 species and 1,951 individuals). The habitat is dominated by rocky rip-rap debris. Octopus dens were located among the rocks or at the rock-sand interface. Thirty-two species of bivalves were consumed, representing 1,523 individuals collected in the debris fields (Table 2). The California Jackknife Clam *Tagelus subteres* represented 53% of all bivalves taken, followed by *Saxidomus nuttalli* 10.1% and *Gari californica* at 6.8% (Table 2). Bivalves collected in the debris fields represented 78% of the shells, gastropods the remainder.

Twenty-two species of gastropods (428 individuals) were collected at this site. The Bubble Snail, *Bulla gouldiana* (21%) and olive *Callianax biplicata* (35%) accounted for 56% of the total number of gastropods taken (Table 3). The majority of the olives were consumed by only two octopi.

Mariner's Basin MB (Table 1, Figure 4) (40 species & 1,082 individuals). The habitat is sand dominated by eel grass year-round. Octopi dens were located among the roots of eel grass and under or between the occasional rock. Mariner's Basin had 32 species of bivalves, representing 1,020 individuals. *Tagelus subteres* accounted for 46.6% of the bivalves taken, followed by *Laevicardium substriatum* 11.6% and *Chione undatella* 10.1% (Table 2). No mature specimens of the larger bivalve species such as *Saxidomus* and *Semele*, were found in the debris fields, only juveniles which were typically opened without drilling. Although both MB and MP each had 32 species of bivalves in the debris field, only 21 of those species occurred in both locations.

Eight species of gastropods (62 individuals) were found associated with octopi dens. The primary gastropod taken was *Bulla gouldiana* 51.6%, followed by *Megastraea undosa* (16.1%) and *Tegula eiseni* (12.9%).

Ventura Cove VC (Table 1, Figure 5) (24 species & 597 individuals). The study area is dominated by silty-sand with transitory eel grass that is present during the summer but greatly reduced or absent during fall and winter. No rocks are present. The habitat has both low diversity and low stability.

Adequate den sites of reproductively active octopi are absent, as eggs must be attached to a hard surface. As a result, smaller octopi that use unique den opportunities (*e.g.* among eel grass roots, the occasional soda can, bottle, empty *Megastraea undosa* shells, hinged bivalves, potato chip bag partly buried, sponge and sand depression (Figure 6) were the norm. The

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bivalves used for these mobile dens included *Anadara multicostata*, and large specimens of *Argopecten ventricosus,* and halves of *A. ventricosus* are used to shield the otherwise exposed portions of the octopus (Figure 7). Dens made in the sand appeared to be supported, at least around the openings, with shell debris, and were often partially covered with dead strands of eel grass buried in the sand. The dead buried eel grass was covered by shifting sand and provided a supportive matrix and probably the reason those sites were selected (Figure 6). Due to the lack of suitable den sites, mature octopi do not typically reside in this habitat.

A total of 559 bivalve shells were collected, representing 19 species. The prominent bivalves taken at this location are *Tagelus subteres* 49.2%, *Laevicardium substriatum* 17.2%, and *Argopecten ventricosus* 17.4%.

Although juvenile octopi are always present, larger adult animals were only observed when the speckled scallops were abundant in June. Speckled Scallop *A. ventricosus* is exceedingly mobile and a strong swimmer. The species is transient, but when present, 3-12 scallops/m^2 was typical. The scallops are not an easy target as they have a strong flight response, but at high densities not everyone moves fast enough. When scallops are present the number of octopi in VC increases and decreases sharply when the scallops move on. The scallops ranged in size from 13 to 65 mm in diameter, the average was 36 mm with a median of 45 mm. All scallops were opened by pulling, they were not drilled. A study by Lang (1986) of *O. bimaculoides* at Agua Hedionda Lagoon in Carlsbad, California found *A. ventricosus* to be the major prey item, and they were both drilled and pulled open. Although not stated, the scallop population must have been persistent, rather than transient as in VC.

Only five species of gastropods, representing 38 individuals were found associated with octopi dens. *Bulla gouldiana* represented 81.6% of the gastropods associated with dens (Table 3).

Pull or Drill – Diet. Bivalves are often pulled open; when that is unsuccessful, the shell may be drilled. Shelled gastropods are more likely to be drilled than bivalves but in either case this leaves the shells intact. There is no agreement as to how the genus *Octopus* drills. Octopi use their radula to bore through the shell; a process that may be augmented with chemicals secreted by the octopus (Wodinsky 1969, Steer & Semmens 2003, Anderson & Mather 2007). After the shell is penetrated, toxins from the posterior salivary gland are introduced, through the small opening, which induces paralysis, allowing the prey to be removed and consumed (Ghiretti 1960, Nixon *et. al.* 1980, Steer & Semmens 2003). The drilling activity had been assumed to be performed by the radula of the octopus, but in the case of *O. vulgaris*, Cuvier, 1797, Nixon *et. al.* (1980) removed the beak and radula and found that the octopus drilled the shell with a structure on the salivary gland. When the radula was left in-tact and the structure on the salivary gland removed, the octopus was unable to drill. The author is not aware of similar experiments with *O. bimaculoides* or *O. bimaculatus*, but it brings into question the drilling mechanism commonly attributed to these two species. It may be that various species have different methods for accomplishing the task of drilling prey.

The external diameter of the hole drilled appears related to the thickness of the shell under attack. To penetrate the 3.5 mm thick base of a wavy top snail, the bore width on the surface of the shell was 3.5 mm; the bore hole diameter for *Tegula eiseni* with shell thickness of 0.7 to 1.4 mm ranged from 1.05 mm to 1.5 mm in diameter. Regardless of shell thickness, the final diameter of the hole, that opens into the cavity of the prey, is approximately 0.3 mm. In their study of *O. vulgaris,* Nixon & Maconnachie (1988) reported the shape of the cavity drilled was influenced by characteristics of the shell, not the size of the octopus, which is consistent with current observations for *O. bimaculoides.*

Targeting bivalve or gastropod that do not require the octopus to expend time and energy to drill the shell would seem ideal. In the current study, the bivalve *Tagelus subteres* and the gastropod *Bulla gouldiana* are not drilled and accounted for the majority of bivalves and gastropods taken at each location. Anderson & Mather (2007) found that in laboratory conditions that *Entreocotopus dofleini* (Wulker, 1910) preferentially consumed bivalves that could be opened by pulling over those that had to be drilled. Dodge & Scheel (1999) working on the same species noted that crustaceans were routinely drilled, but bivalves were not; they also noted the composition of prey species differed based on the habitat.

Gastropods. With the exception of the *Bulla gouldiana*, all gastropod species in the debris were drilled to varying degrees. The four most commonly consumed gastropods were *Megastraea undosa*, *Callianax biplicata*, *Tegula eiseni* and *B. gouldiana.* and collectively these four species accounted for 81.3% of the 525 gastropod shells collected in debris fields.

Tegula eiseni was drilled 94.5% of the time. The body whorl was targeted 55.5% of the time, penultimate whorl 36%, base 5.5%. The olive *Callianax biplicata* is a small species, and although it lacks an operculum it can withdraw deep into the shell. Ninety-one percent of the olives in the debris fields had been drilled. Drilling occurred only on the penultimate and ultimate whorl, on the aperture side of the shell.

Wavy top turbans *Megastraea undosa* were not found in the debris field if they were smaller than 32 mm or greater than 101 mm (base diameter). Shells were drilled only on the aperture surface (73%) near the point of attachment for the muscular foot to the columella, the remaining 27% showed no physical damage.

Bivalves. Among the bivalves only six of the 38 species associated with the dens were periodically drilled, the majority were pulled open. *Protothaca staminea*, *P. laciniata*, *Semele decisa*, and *Leporimetis obesa* were infrequently drilled. Approximately 21% of the *Chione undatella* were drilled, typically near the lip, and drilling location was unrelated to the clam size.

The sixth species drilled was *Saxidomus nuttalli,* the juveniles were not drilled, larger individuals between 60-80 mm were drilled approximately 12% of the time while larger specimens 81-101 mm were drilled 71% of the time. Anderson *et al*. 2008 used five zones to describe the location where octopi drilled bivalves (umbo, posterior adductor, central, anterior adductor, and ventral). Based on these regions, successful drilling events on mature *S. nuttalli* occurred in the area of the unbo (75%), upper anterior adductor (7%), central (14.5%). posterior adductor zone (3.5%), ventral (none).

Bivalves such as *Argopecten*, *Chione*, *Laevicardium*, *Limaria*, *Donax*, *Trachycardium*, *Musculista*, and *Americardia* may be found on the surface of the sand, or in the case of *Chione*, *Protothace* and *Donax* they may also be buried just below the surface. The California Jackknife clam *Tagelus subteres,* which is a significant component of the diet, is deeply buried in the sand except when feeding, as are *Saxidomus nuttalli* and *Tresus nuttallii.* Mature *Tresus nuttalli* can exceed 200 mm in length, but only

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juveniles under 60 mm were associated with dens. How they capture these three species was not apparent. Having pursued those species with a shovel at other locations during low tide, I have only had success with *Tagelus*. The success of the octopi especially with *Saxidomus* and *Tresus* is impressive. The Rock Scallop *Crassadoma gigantea* that were consumed were juveniles prior to attaching to rocks.

Dietary Preferences and Avoidance. Individual octopi are biased regarding prey selection, as they collect prey of a size that allows successful manipulation and subsequent consumption. For example, even though present, Wavy turbans smaller than 32 mm or larger than 105 mm were not found in the debris fields.

Three *O. bimaculoides* at MP exhibited strong preferences for specific gastropods. One octopus accounted for the majority of the moon snails consumed. Moon snails smaller than approximately 2.5 cm were not drilled, while larger individuals were consistently drilled on the ventral surface or the upper portion of the body whorls.

The vast majority of the olives were consumed by two octopi at MP. Considering the number of prey species available, targeting the smallest resource which had to be drilled, may represent individual dietary preference. The two dens accounted for approximately 76% of the 150 olive *Callianax biplicata* in debris fields at MP. Neither octopus fed exclusively on *C. biplicata* but the numbers taken were disproportional compared to their cohorts. Approximately 92% of the olives were drilled. Drilling occurred on both the lower half of the penultimate whorl and body whorl adjacent to the suture. In the other two habitats with more sand and olives, only 5 olives were recorded in debris fields (Table 3).

The two most commonly consumed gastropods were the Olive (155) and the Bubble Snail (153). In this situation, I question the value of using only capture data as a measure of dietary significance. On the surface, the data suggest that olives are an important food source, but only two octopi consumed 76% of the olives. This observation lead to an evaluation of prey biomass for various species that contributed notably to the octopi diet (see Numbers vs. Biomass).

Species seemingly under-utilized. Under-utilized prey species are defined here as species that were frequently observed in the habitat but seldomly found in the debris fields. The large Key Hole limpet *Megathura crenulata* is a common species, and the animal too large to with-draw under its shell. As such, it is potentially exposed directly to the bite of an octopus, yet the number taken indicates they are infrequently eaten. It is speculation, but all of the mollusks that are drilled or pulled open by the octopi have soft or relatively soft body tissue. The exposed foot of *M. crenulata* is very dense and tough, perhaps making it less palatable to octopi.

Evans (1980) reported finding thousands of dead Chestnut Cowries, *Neobernaya spadicea*, over the course of a few months off Laguna Beach, southern California. He collected 208 dead shells on one dive and reported that 89.4% had been drilled on the posterior inner lip, and believed that the remainder had also been eaten by octopi without drilling the shell.

At MP, live cowries were observed during nearly every dive, yet only one specimen was found in debris fields. Other common predatory gastropods such as *Pteopurpura trialata*, *Pteropurpura festiva* and *Kelletia kelletii* although common, were absent or nearly so in the debris fields. The murex *Pteropurpura* *festiva*, was often observed singly or in groups feeding with impunity on remains of meat on the muscle scar of large bivalves discarded near the den entrances by the octopus. Ambrose (1984) also noted under-utilization of certain prey species by *O. bimaculatus* and provided a list of prey species consumed in the field and laboratory.

Numbers vs. Biomass. Do numbers alone adequately represent the importance of a given prey species? To address this question, a follow-up study of prey biomass was undertaken. Approximately thirty live individuals of varying size were collected for each of eight species. The animals were removed from the shell and evaluated as described in the methods. The results are present in Figure 8. Some species such as *Saxidomus nuttalli*, and *Laevicardium substriatum*, which were notable food sources could not be live collected in sufficient numbers to generate meaningful information. Numerically, the small olive appears to be an important gastropod in the diet of the octopi. But, only two octopi accounted for 114 of the 150 olives taken at Mariner's Point. Considering the availability of prey, these two individuals demonstrated a strong personal dietary preference. Even if the 150 olives had been consumed randomly by the population at large, would the olive have been an important food source?

For discussion purposes, I am assuming that the food value of soft bodied mollusks is somewhat similar regardless of the species. Plotting wet weight of animal tissue against shell size provides an approximate relationship between biomass and prey size. Based on average size range of species collected in the debris fields, a rough estimate of biomass per prey species consumed can be generated. Figure 8 provides such data for eight species that were collected in sufficient number. The orange dot on each graph indicates the average size of the prey species found in the debris field of the octopi dens at MP. The average sized olive had a biomass of 0.37 gr, the average Jackknife clam *Tagelus subteres,* had a biomass of approximately 2.2 gr or nearly six times greater than the olive. Based on casual observation, filter feeding clams, the Bubble snail and olive probably have lower body weight to gut content than large algae feeding gastropods, such as *Megastraea undosa*. This disparity could be partially addressed by removing undigested gut contents and possible other non-consumable tissue, and then weighting and plotting the more edible protein source against shell size. I realize the limitations and the time involved in this approach, but it may better reflect the food value of a given species to the octopi.

SUMMARY

Ambrose (1983, 1984) studied the diet and biology of *O. bimaculatus* off Santa Catalina Island in Southern California and evaluated midden formation, he reported that only 3% of the dens were associated with 5 or more shells in their debris field and he concluded that *O. bimaculatus* does not produce midden. There was no indication the octopi purposely removed the shells, and Ambrose attributed their disappearance to environmental factors and hermit crabs.

Octopus bimaculoides in the rocky habitat of outer Mission Bay do produce a debris field sufficiently large to be termed a midden. If all shells in the debris fields had been collected (regardless of condition) the count would have been much higher. It is only speculation, but large debris fields advertise the presence of the octopus, which may encourage conspecifics to look elsewhere for their next den, thereby preventing confrontations. Some octopi at MP had dens located 6-7 m from the nearest sand, but the exterior of those dens was littered with bivalves, indicating they returned to their den with prey, prior to consumption. Based on the laboratory observations by Cigliano (1993) regarding den competition in *O. bimaculoides*, it may be that the most mature/dominant individual had dens in close proximity to the bivalve resource, and those much farther away, but still utilizing that resource, were less dominant. Large debris fields may come at a cost, if predators of the octopus selectively look for dens in the area of shell debris.

The composition of the debris field reflects the local environment, combined with prey availability and preference of the octopus. As such, dietary information from the study of debris fields in varied habitats continues to provide insight into the plasticity of the behavior, which allows the secretive octopus to be a successful predator of a wide array of prey species. I would not speculate that the diet of *O. bimaculatus* reported by Ambrose (1984) and the diet of *O. bimaculoides* reported here, reflects species differences, it is just as likely to reflect the dietary opportunity presented in different environments.

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Study Site	Habitat* Components	Habitat Stability/ Complexity	Relative Octopi Density	Bivalve Species Consumed	Number Bivalve Found	Gastropod Species Consumed	Number Gastropod Found
Mariner's Point	Rock / algae / sand / eel grass	High High	High	32	1,523 78%	22	428 22%
Mariner's Basin	Eel grass / sand / rock / algae	High Moderate	Moderate	32	1,020 94.3%	8	62 5.7%
Ventura Cove	Sand / eel grass transient	Low Low	Low	19	559 94.1%	5	38 5.9%

Table 1. Summary of habitat diversity and stability, relative octopi abundance, and number of mollusk species associated with dens at each of three study sites. *Habitat differs between sites and important components are ranked in order of dominance.

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Fig. 2. Location of study sites in Mission Bay, (1) Mariner's Point, (2) Mariner's Basin, (3) Ventura Cove.

Fig. 3. Mariner's Point UW habitat. Location 1.

Fig. 4. Mariner's Basin UW habitat. Location 2.

Fig. 5. Ventura Cove UW habitat. Location 3.

Fig. 6. *O. bimaculoides* at entry of sand/eel grass den. Ventura Cove.

Fig. 7. *Anadara multicostata* as mobile den *Argopecten ventricosus* as shield. Ventura Cove.

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Table 2. Bivalve Summary		**Mariner's Point**		**Mariner's Basin**		**Ventura Cove**		
Species Coan *et al.*, 2000	Page Coan	Total	% of total	Total	% of total	Total	% of total	Sum
Americardia biangulata (Brod. & Sowerby 1829)	359	1	0.07	4	0.39	2	0.36	7
Anadara multicostata (Sowerby, 1833)	134			1	0.10	4	0.72	5
Argopecten ventricosus (Carpenter, 1864)	235			10	0.98	97	17.35	107
Chione californiensis (Broderip, 1835)	369			5	0.20	1	0.18	6
Chione undatella (Sowerby, 1835)	369	26	1.71	103	10.13	28	5.01	157
Clinocardium nuttalli (Conrad, 1837*)*	351			1	0.10			1
Crassadoma gigantea (Gray, 1825)	238	3	0.20					3
Cryptomya californica (Conrad, 1837)	474	29	1.90	2	0.20			31
Cumingia californica (Conrad, 1837)	437	6	0.39	5	0.48			11
Cyathodonta pedroana Dall, 1915	536	3	0.20	1	0.10	2	0.36	6
Diplodonta orbella (Gould, 1851)	270	19	1.25	2	0.20			21
Donax californicus (Conrad, 1837)	422			1	0.10			1
Donax gouldi Dall, 1921	423	3	0.20	1	0.10			4
Gari californica (Conrad, 1849)	426	104	6.83	37	3.64	1	0.18	142
Heterodonax pacificus (Conrad, 1837)	428	1	0.07					1
Laevicardium substriatum (Conrad, 1837)	360	48	3.15	118	11.60	96	17.17	262
Leporimetis obesa (Deshayes, 1855)	420	17	1.12	7	0.69			24
Limaria hemphilli Hertlein & Strong, 1946	205	18	1.18	6	0.59	1	0.18	24
Lucinisca nuttalli (Conrad, 1837)	263			1	0.10			1
Macoma nasuta (Conrad, 1837)	420	11	0.72	12	1.18	2	0.36	25
Macoma secta (Conrad, 1837)	417	10	0.66	4	0.39			14
Mactrotoma californica (Conrad, 1837)	457	42	2.76	15	1.47	5	0.89	62
Mactrotoma nasuta (Gould, 1851)	456	2	0.13					2
Mactromeris hemphillii (Dall, 1894)	454	3	0.20					3
Musculista senhousia (Ben. in Cantor 1842)	167	14	0.92	6	0.59	3	0.54	23
Nuttallia nuttallii (Conrad, 1837)	429	2	0.13			4	0.72	6
Periploma planiusculum (Sowerby, 1834)	540	2	0.13	1	0.10			3
Pitar newcombianus (Gabb, 1865)	380	1	0.07					1
Protothaca laciniata (Carpenter, 1864)	374	38	2.50	45	4.42	1	0.18	84
Protothaca staminea (Conrad, 1837)	374	8	0.53	11	1.08	3	0.54	22
Saxidomus nuttalli (Conrad, 1837)	386	154	10.11	47	4.62	6	1.07	207
Semele decisa (Conrad, 1837)	432	52	3.42	24	2.36			76
Solen rostriformis Dunker, 1867	444	3	0.20	2	0.20			5
Tagelus californianus (Conrad, 1837)	441	25	1.64	34	3.34	15	2.68	74
Tagelus subteres (Conrad, 1837)	442	807	52.99	475	46.71	275	49.19	1557
Trachycardium quadragenarium (Conrad,1837)	362	54	3.55	29	2.85	12	2.15	95
Tresus nuttallii (Conrad, 1837)	463	16	1.05	3	0.29			19
Venerupis philippinarum (Adams & Reeve, 1850)	387	1	0.07	7	0.69	1	0.18	9
Total		1,523	100%	1,020	100%	559	100%	3102

Table 2. Summary of bivalves recovered from debris fields in three distinctly different habitats.

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Table 3. Gastropod Summary	**Mariner's Point**			**Mariner's Basin**			**Ventura Cove**	
Species Berschauer & Clark, 2019	Total	% of total		Total	% of total		Total	% of total
Bulla gouldiana Pilsbry, 1893	90	21.0		32	51.6		31	81.6
Californiconus californicus Reeves, 1844	13	3.0		2	3.2		3	7.9
Callianax biplicata (Sowerby, 1825)	150	35.0		3	4.8		2	5.3
Haliotis fulgens Philippi, 1845	2	0.5						
Kelletia kelletii (Forbes, 1852)	4	0.9						
Maxwellia gemma (Sowerby, 1879)	3	0.7						
Megathura crenulata (Sowerby, 1825)	15	3.5						
Megastraea undosa (Wood, 1829)	50	11.7		10	16.1			
Nassarius fossatus (Gould, 1849)	1	0.2					1	1.4
Neobernaya spadicea (Swainson, 1832)	1	0.2						
Neverita alata (Pilsbry, 1929)	2	0.5						
Neverita lewisii (Gould, 1847)	1	0.2						
Neverita reclusiana (Deshayes, 1839)	9	2.1		2	3.2			
Norrisia norrisi (Sowerby, 1838)	12	2.8		4	6.5		1	2.6
Pteropurpura festiva (Hinds, 1844)	4	0.9						
Roperia poulsoni (Carpenter, 1864)	3	0.7						
Sinum scopulosum (Conrad, 1849)	3	0.7						
Tegula aureotincta (Forbes, 1852)	8	1.9		1	1.6			
Tegula eiseni Jordan, 1936	52	12.1		8	12.9			
Tegula funebralis (A. Adams, 1855)	2	0.5						
Tegula regina (Stearns, 1892)	1	0.2						
Trivia solandri (Sowerby, 1832)	2	0.5						
Gastropod total	428	100%		62	100%		38	100%

Table 3. Summary of gastropods recovered from debris fields in three distinctly different habitats.

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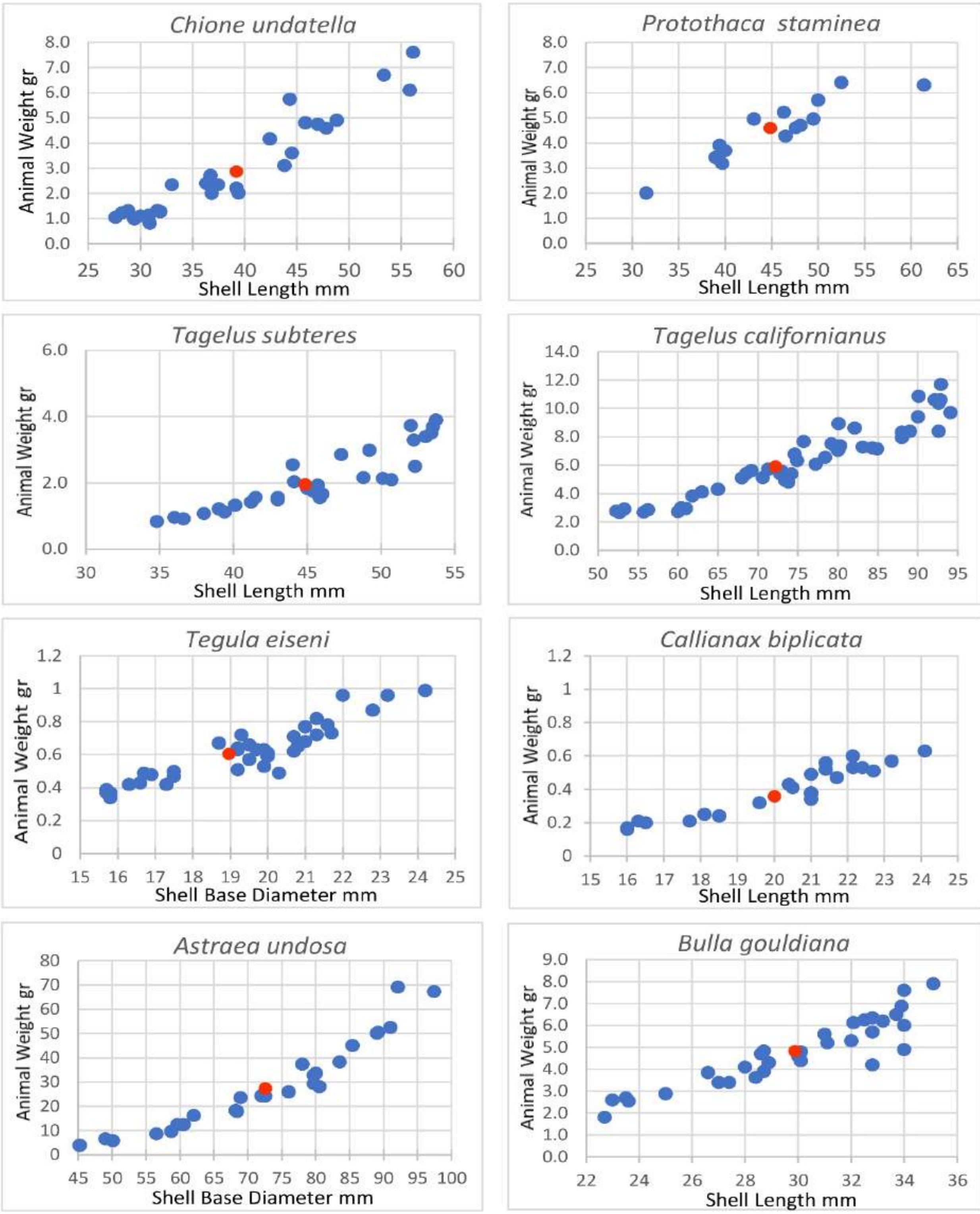

Figure 8. Wet-weigh biomass vs. shell size of eight prey species commonly consumed by *Octopus bimaculoides* at Mariner's Point, Mission Bay. The red dot represents the average size of the prey species found in the debris fields.