Title:

Activity space and movement patterns of *Octopus bimaculatus* (Verrill, 1883) around Santa Catalina Island, California

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ABSTRACT

The spatial movement and ecology of highly mobile marine predators can strongly influence, and be influenced by, a variety of ecological factors. Octopuses are voracious predators, and their predatory behavior can have significant impacts on the abundance and diversity of their prey communities. Nine *Octopus bimaculatus* (Verrill, 1883) were tagged and tracked during August 2014 using active tracking techniques. Octopus GPS position was recorded daily over the course of 12.9 ± 5.6 days (mean $\pm$ SD) and continuous movement was tracked for 20.8 ± 5.0 hours (mean $\pm$ SD) for each animal. *O. bimaculatus* occupied an activity space of approximately 6000 ± 3000 km² (mean $\pm$ SD). Larger animals moved over larger areas, but activity space size was not correlated with octopus sex, habitat location, or time of day. Movement distances and diurnal movement patterns were highly variable for this species, both within and between individual octopuses. *O. bimaculatus* were highly mobile compared to other octopuses of similar size tracked in a similar way. These results are contradictory to previous estimates of movement and den fidelity for this species in this area, suggesting either a previous underestimate of *O. bimaculatus* movement, or a change in the way this species moves through its environment. This study pioneered the application of acoustic telemetry to octopuses in California ecosystems, and provides insight into the heterogeneity of octopus behavior and the potential impacts this heterogeneity may have on octopus prey and predator communities.

Key words: Octopus, Acoustic telemetry, Passive tracking, Activity space, Kernel Utilization Distribution, VEMCO

1. Introduction

Understanding the ecological and behavioral drivers of predator movement is critical to understanding their impact on prey communities and the ecosystem as a whole (Barbosa and Castellanos, 2005; Boyd et al., 2006). The spatial movement of highly mobile predators is influenced by a number of factors, including prey availability and distribution, predation risk, habitat availability, and energetic tradeoffs (Swingland and Greenwood, 1983). Because all of these components interact reciprocally, an integrative and comprehensive knowledge of a predator's life history, physiology, foraging ecology, and behavior is needed to understand the drivers and patterns of small and large-scale movement in the field. However, the synthesis of these facets is challenging, especially for behaviorally flexible and complex marine predators (Mather et al., 2014).

Octopuses are one of the most ubiquitous and important predators in benthic coastal ecosystems. They are voracious generalist predators, and their foraging behaviors have significant effects on the abundance of small invertebrates (Ambrose, 1986; Rodhouse and Nigmatullin, 1996; Schmitt, 1987). It is thought that resource distribution strongly dictates octopus spatial movement, but that the patterns and timing of movement are influenced primarily by predation risk (Mather and O'Dor, 1991). The cognitive abilities of octopuses in a lab setting have been well established, but very few researchers have explored these behaviors in a natural setting (Hanlon and Messenger, 1996; Mather, 1995). It is realistic to expect that these animals are utilizing these abilities to navigate through their environment and perform tasks such as foraging and avoiding predation. Like other highly motile marine predators, octopuses may learn to

incorporate new food items into their diet based on encounter rates, and to adopt the most efficient feeding strategy in varying environments (Guttridge et al., 2009; Kieffer and Colgan, 1992). Because octopuses are cryptic and often nocturnal, our understanding of octopus movement is based upon observed patterns of shelter use. Three things are critical to understanding octopus movement: 1) den fidelity, 2) foraging behavior, and 3) home range. For a summary of relevant literature, see Table 1.

Octopuses inhabit dens, but the duration of stay in a single den can vary greatly within a species or a population, and can range from a few days to a few months (*Octopus cyanea*: Forsythe and Hanlon, 1997; Ivey, 2007; Yarnall, 1969; *Enteroctopus dofleini*: Hartwick et al., 1984; Mather et al., 1985; *Octopus vulgaris*: Boyle, 1980; Mather, 1991b; Mather and O'Dor, 1991). Den availability can also influence den fidelity and between-den movement. In areas where dens are limited, den availability and distribution can affect octopus spatial distribution and abundance, and the addition or removal of dens can influence movement (Hartwick et al., 1978; Iribarne, 1990; Mather, 1982; Voight, 1992). In habitats where dens are not limiting, other factors such as predation risk likely dictate movement to another shelter (Ambrose, 1982; Forsythe and Hanlon, 1997; Hartwick et al., 1984).

Octopuses leave their dens primarily to forage. Like den fidelity, the duration of foraging bouts also varies, and may be correlated with foraging success, although Mather and O'Dor (1991) suggest predation risk is also a strong factor. Many studies suggest that octopuses are central place foragers and can return to their den by taking a different route or by swimming in a straight line, suggesting advanced navigation and memory of the surrounding area (Forsythe and Hanlon, 1997; Mather 1991a, 1991b;

Mather and O'Dor, 1991). They are visual and chemotactile hunters that forage opportunistically and speculatively (Hanlon and Messenger, 1996). There is some evidence of prey specialization, which could alter the length of their foraging bouts (Forsythe and Hanlon, 1997; Ivey, 2007; Leite et al., 2009; Yarnall, 1969).

Home range is difficult to measure in octopuses. Home range can only be defined when an animal exhibits site fidelity to that range and the number of recorded locations is adequately large to encompass the entirety of that range (Bolden, 2001; Odum and Kuenzler, 1955). They are not territorial, and thus do not maintain even spacing; neither do they aggregate in response to conspecifics unless mating (Forsythe and Hanlon, 1997; Huffard, 2007; Mather, 1982), although they may aggregate around resources (e.g. Scheel et al. 2016, Caldwell et al. 2016). Their highly mobile nature makes it difficult to discern if they are occupying temporary home ranges before moving on, or switching between dens within a larger permanent home range. Additionally, limitations inherent in current methods and technology do not allow for long term monitoring of octopus movement over the entire area that could be occupied. Current estimates range from 250 m² to 50,000 m² for *Enteroctopus dofleini* (Mather et al., 1985; Scheel and Bisson, 2012), 100 m² to 2000 m² for *O. cyanea* (Forsythe and Hanlon, 1997; Ivey, 2007; Yarnall, 1969), and 100 m² for *O. vulgaris* (Mather and O'Dor, 1991). With the exception of the few studies that used long-term acoustic tracking, these areas are likely underestimates, and do not measure true home range, but rather activity space or area use.

Very recent improvements in tagging technology have allowed for the remote tracking of octopuses. This methodology was previously unfeasible in octopuses due to

large and cumbersome tag size, lack of a hard structure on an octopus to attach a tag, and the flexibility of octopus arms, which allows them to reach inside their mantle cavity and remove a tag. However, improvements in tag design and tagging technique now make this type a research a possibility. Few studies have used acoustic tags to characterize octopus movements, but results from these studies have revealed exciting new details about octopus movement, including evidence of pronounced vertical movement (Rigby and Sakurai, 2005) and the use of depth contours to navigate (Scheel and Bisson, 2012). Thus, use of acoustic tags provides a promising means for further exploring how individual movements and habitat use contribute to the role of octopuses as top marine predators. This study aimed to test the feasibility of existing tagging and tracking techniques on octopuses in complex habitats, and to gather preliminary data on the activity space, displacement distances, activity patterns, and demographic correlates of the California two-spot octopus, *Octopus bimaculatus* (Verrill, 1883).

2. Methods

2.1. Study Area. This study was conducted on Santa Catalina Island, located approximately 20 miles west of Los Angeles, CA. The study area was approximately 4 km² and was established on the leeward side of the island near the USC Wrigley Institute for Environmental Studies (WIES) and the town of Two Harbors, CA (33° 26' N, 118° 29' W). Habitat types in this area include rocky reef, kelp beds, and sandy bottom, but also include man-made habitats such as docks, moorings, and abandoned research structures. Octopuses were collected both inside and outside the Catalina Marine Science Center State Marine Reserve (CMSCSMR), which is part of the larger Blue Cavern State Marine Conservation Area (BCSMCA), hereafter referred to as the MPA

area. Outside the BCSMCA, hereafter referred to as the nonMPA area, recreational and commercial fishing of finfish and shellfish are allowed.

2.2. Study Species. *Octopus bimaculatus* is a common octopus species found subtidally from Point Conception, CA to Baja California, Mexico. Mating occurs year round but peaks in mid-summer (Ambrose, 1988). *O. bimaculatus* consumes a wide variety of invertebrate prey items including bivalves, gastropods, crustaceans, small fish, and other octopods, and can affect the abundance and diversity of prey species (Ambrose, 1984; Ambrose, 1986). Dens do not seem to limit the populations of *O. bimaculatus* as in other species (Ambrose, 1982). Previous research has determined that *O. bimaculatus* individuals can occupy dens for 1 to 5 months (Ambrose, 1982; Ambrose, 1983).

2.3. Acoustic Tagging. SCUBA divers caught octopuses by hand at various depths within the coastal rocky reef habitat around the study area (Table 2). Immediately following capture, den location was marked with a buoy. Individuals were brought to the surface and held in coolers filled with ambient seawater. Octopuses were transported back to the WIES dock to be weighed, measured, and sexed (Table 2). Animals were tagged with a small acoustic transmitter (Model V9-2L, 9 mm diam. x 21 mm, Vemco) following the protocol of Scheel and Bisson (2012). Acoustic tags were epoxied to a modified Peterson Disk (Floy Tag and Mfg., Inc.) fitted with two sharpened nylon posts (Figure 1). The nylon posts were covered with sterile piercing needles, and the tag apparatus was inserted into the mantle cavity and the needles were pushed outward through the mantle. The needles were removed and the tag was held in place with a Floy Disk (Floy Tag and Mfg., Inc.) and nylon nuts. The total weight of the tag apparatus

did not exceed 5 g, which was less than 1% of the weight of any octopus tagged (Table 2). Animals were not anesthetized, as that has been demonstrated to increase stress and recovery time (Scheel and Bisson, 2012). Octopuses were placed in a dark cooler filled with ambient sea water for recovery, then were placed in a mesh bag and released into the den where they had been captured. Total time from capture to release was 76 ± 49 minutes (mean $\pm$ SD, $N = 9$ animals). This tagging method resulted in minimal changes to mobility and is not expected to significantly alter behavior of the animal (Ivey, 2007).

2.4. Acoustic Tracking. Transmitters had frequencies of 63 to 84 kHz and a nominal battery life of 14 days. An initial GPS location was recorded for each tagged octopus upon release, and then the animal was allowed to recover for a minimum of 24 hours before tracking commenced. Thereafter, the position of each octopus was detected once daily using a Vemco VR100 (software v. 2.002) receiver with a gunwale-mounted directional hydrophone (Vemco VH110) and recorded using a hand-held GPS unit (Garmin 72H). The mean ($\pm$ SD) accuracy of the Garmin GPS fixes was 4.91 ± 0.76 m. In addition to these daily position recordings, each octopus was tracked continuously for 24 hours. Continuous tracking within this study is defined as recording the GPS position of the octopus every 10 to 30 minutes for the duration of the tracking period. For 5 octopuses, this sampling effort was divided into two non-contiguous 12-hour tracks that were completed from 12 PM to 12 AM and 12 AM to 12 PM (hereafter referred to as a 12-to-12 Track). For 3 additional octopuses tracking was completed continuously for 24 hours, from 8 PM to 8 PM (hereafter referred to as an 8-to-8 Track) (Table 2). Since the primary goal of this study was to test methodology and gather preliminary data, this

change in tracking schedule was an attempt to adjust and optimize tracking strategies. Due to weather conditions and animal location, daily locations were recorded for a 9th individual but the animal was not tracked continuously.

2.5. Data Analysis. Octopus positional fixes were plotted on a geo-referenced map and analyzed using the statistical packages `adehabitatHR` and `adehabitatTL` in R (v. 12.15.3, R Core Team, 2015; Calenge, 2011) and the GIS program ArcMAP (Version 10.2.2). The area used by an animal, or activity space, was defined by a 95% kernel utilization distribution using the Brownian bridge kernel method (bbKUD). The Brownian bridge kernel method accounts for the time dependence between locations and represents the area that an animal can be expected to be found 95% of the time. Due to the short duration of this study, true home range could not be reliably estimated; therefore, the activity space was estimated for each animal. This activity space was calculated in four ways. Area was first calculated using both the continuous tracking locations and the daily position locations. This measure provided an overall total of area that an individual octopus was found during the study.

Second, area was calculated using only the continuous tracking locations. This measure allowed for a more detailed examination of octopus movement within the tracking period, and is the traditional method by which actively tracked animals are analyzed. For animals tracked with the 12-to-12 method (N=5), area was calculated for each 12-hour tracking period separately. This was done to avoid any inaccurate interpretation by artificially grouping two non-contiguous time periods together. Area for animals tracked using the 8-to-8 method (N=3) was calculated using the full 24-hour set

of location positions. This unavoidable inconsistency was due to logistical difficulties of tracking.

Third, to allow for comparisons across individuals given that not every octopus was tracked in the same way, tracking of each octopus was divided into six 4-hour blocks: 1200-1600, 1600-2000, 2000-2400, 2400-0400, 0400-0800, and 0800-1200. A 95% bbKUD was calculated for each 4-hour time block and was compared between animals. In addition to activity space, track lengths in meters were calculated for each 4-hour time block. It should be noted that given the resolution of recorded positions, these lengths only represent the distances between points and do not capture the likely non-linear path taken by the octopus.

Fourth, differences in activity space were assessed for localities recorded during different times of the day to test the commonly held hypothesis that octopuses are more active at night. Continuous tracks were broken up into day, crepuscular, and night temporal blocks, to account for the many reports of crepuscular behavior (refer to Table 1). Crepuscular was defined as the time between one hour before and one hour after sunrise and sunset. Then 95% bbKUDs were calculated for each animal during each temporal block, and areas of activity were examined for temporal differences in area with ANOVA.

The daily displacements of each animal were also calculated using only the daily position locations to assess den fidelity. In this study, den fidelity was defined as an individual octopus staying in the same location from one day to the next. Therefore, if an animal were to be found in a different location between selected time points, it would be interpreted as a den switch. One 1200 and 2400 point was selected from the continuous

tracks to be included in the displacement calculation. The overall lengths of the displacements were calculated and the maximum displacement was identified.

Finally, to examine potential phenotypic correlates of activity space, relationships among area of the total activity space (using both daily and continuous points) and octopus weight, mantle length, and sex, were analyzed using linear regression, and differences in area between habitat category (MPA versus nonMPA) was analyzed with a two-tailed unpaired t-test.

3. Results

3.1. Tag Retention. A total of nine *O. bimaculatus* were tagged between August 5 and September 5, 2014 (Table 2). Of those, two tags were not retained, one tag was retained for five days, two tags were retained for the duration of each tag's battery life, and four tags were retained and still active when the study ended (Table 3). The three tags that were dislodged from the animals were recovered using a Vemco VUR 96 handheld pinger locator. It is undetermined whether the tags fell off passively, or if the octopuses pulled the tags out, but each tag apparatus was somehow broken upon recovery.

Because it was not immediately apparent that tags had fallen off of two animals soon after deployment, these individuals were tracked for 24 hours before determining that the tags had been lost (i.e, had not moved during that period). Consequently, data from these tags were used to estimate position error and tracking precision for the daily displacement estimations (see section 3.2). The third tag fell off after five days and before the commencement of the second 12-hour track, and thus only the first 12-hour track was used in analysis of activity space. The second 12-hour track where the tag

was off the animal was not used in the estimation of position error. Two animals that retained their tags throughout the study were located using a Vemco VUR96 handheld pinger locator to verify tag attachment approximately one week after deployment, because the detected signal strengths were very low. One was found under a very large boulder with the tag still attached; the other had moved 10 m deeper than its release location and was found under approximately 0.5 m of fallen kelp and a large rock with its tag still attached. These locations accounted for the low signal strengths detected for these octopuses. Collectively, these observations suggest that the primary shortcoming of this tagging procedure was tag retention. However, some tag loss is expected with any telemetry study, and this rate of retention is still higher than all other studies using this method (Ivey, 2007; Scheel and Bisson, 2012).

3.2. Position Error. Because continuous 24-hour tracks were completed for two animals prior to the determination that the tags were no longer attached to the animal, these tracks were used to calculate the accuracy of the positional data. This estimated error was only used to determining the daily net displacement of animals. The tags were recovered less than 0.3 m from the buoy marking the initial capture and release location, implying that the tag was separated from the octopus almost immediately. Error was estimated by calculating the distance between each recorded location and the known starting location of the octopus, and thus the position of the unattached tag. The mean distance ($\pm$ SD) was 13 m ($\pm$ 7.6), and thus any daily octopus displacement greater than 13 m was interpreted to indicate a den switch.

3.3. Activity Space. Each of the 7 octopuses that retained their tags was continuously tracked for up to 25 hours for a total of 125 tracking hours (Table 2). The mean ($\pm$ SD)

activity space for all octopuses using both continuous and daily locations was $6143.4 \pm 3165.5 \text{ m}^2$ (Table 3, Figure 2). Total activity space was not correlated with hours (linear regression, $r^2 = 0.00015$, $df = 5$, $p = 0.9817$) or days (linear regression, $r^2 = 0.0075$, $df = 5$, $p = 0.85$) tracked, indicating that longer tracking duration did not result in larger measured areas and all octopus activity space are comparable regardless of tracking duration. The overall mean ($\pm$ SD) activity space inhabited by octopuses for all 4-hour blocks of time was $1688.2 \pm 440.8 \text{ m}^2$. For a breakdown of activity space sizes per 4-hour time block, see Table 4. Activity space area during any 4-hour block was highly variable, ranging from 428-5871 m^2 . There were no significant differences in activity space between time period (ANOVA, $F = 0.59$, $df = 5$, $p = 0.71$) or between animals (ANOVA, $F = 2.37$, $df = 5$, $p = 0.070$).

The overall mean ($\pm$ SD) track length for each 4-hour block of time was $184.0 \pm 113.0 \text{ m}$. For a breakdown of activity space sizes per 4-hour time block, see Table 5. There were no significant differences in tracking lengths between time period (ANOVA, $F = 1.13$, $df = 5$, $p = 0.37$) or between animals (ANOVA, $F = 1.50$, $df = 5$, $p = 0.24$). Tracking lengths during any 4-hour block was also highly variable, ranging from 55.8-558.5 m.

Total activity space was not significantly correlated with octopus weight (linear regression, $r^2 = 0.0088$, $df = 5$, $p = 0.84$) or mantle length (linear regression, $r^2 = 0.00025$, $df = 5$, $p = 0.97$), and there were no differences between sex (t-test_{two-tailed}, $t = 0.56$, $df = 5$, $p = 0.60$). Octopuses within the MPA occupied a significantly higher activity space than octopuses outside the MPA (t-test_{two-tailed}, $t = 2.60$, $df = 5$, $p = 0.048$). There was a significant positive relationship between 4-hour activity space area and octopus

weight (linear regression, $r^2 = 0.9$, $df = 5$, $p = 0.0038$) and mantle length (linear regression, $r^2 = 0.89$, $df = 5$, $p = 0.005$).

3.4. Activity Patterns. Mean ($\pm$ SD) activity spaces for day, crepuscular, and night temporal blocks were $1423.8 \pm 778.4 \text{ m}^2$, $2131.4 \pm 1738.4 \text{ m}^2$, and $1807.8 \pm 1233.3 \text{ m}^2$, respectively. Activity space sizes within each time period were highly variable. Day activity space ranged from $256\text{-}2890 \text{ m}^2$, crepuscular activity space ranged from $420\text{-}3684 \text{ m}^2$, and night activity space ranged from $889\text{-}6268 \text{ m}^2$. The maximum space values for each time period belonged to the same octopus, which was also the largest octopus tagged. There were no significant differences between activity spaces inhabited during day, night, or crepuscular time periods (ANOVA, $t = 0.64$, $df = 2$, $p = 0.53$).

3.5. Daily Displacement. As indicated by the analyses of the accuracy of positional data, displacement distance was calculated only for successive positions that were located $> 13 \text{ m}$ apart. 45 of 87 (51.7%) were greater than 13 m and were thus interpreted as a den switch. The mean ($\pm$ SD) total length of displacement calculated from the daily positions of each octopus was $232.1 \pm 115.9 \text{ m}$ ($N = 45$). The mean ($\pm$ SD) maximum displacement was $59.5 \pm 45.0 \text{ m}$.

4. Discussion

This study demonstrated a successful application of current tagging methods to *O. bimaculatus* and provided important preliminary data on the movement of this species. These results provide insight into the broad-scale movements of *O. bimaculatus* and do not account for fine-scale movements and habitat use. Our results suggest that *O. bimaculatus* is a very mobile octopus species that exhibits high inter- and intra-individual variability in movement patterns and activity space size. There were no

overall relationships between the metrics of activity space, track length, or displacement with any phenotypic traits of the octopuses, with the exception that larger animals inhabited larger activity spaces. The traits included sex, and time of day (day, crepuscular, night). Octopuses within the MPA occupied a larger activity space than octopuses found outside the MPA. Since only one 24-hour track was completed for each octopus, it is not possible to determine if the differences are due to true differences in individual octopus activity patterns, or due to different conditions experienced by each octopus during the track. Finally, it is interesting to note that there was no significant correlation with octopus size (weight or mantle length) and overall mean activity space utilized by octopuses in this study. There was, however, a very strong significant positive correlation with octopus size and activity space when treating the 4-hour time blocks as separate units. This blocking method isolates periods of time when individual octopuses were most active, and thus each individual's active times become comparable, even if these did not occur during the same time block. The positive relationship between octopus size and activity area has also been found with *E. dofleini* (Scheel and Bisson, 2012). This high variability emphasizes the need for long-term continuous tracking of octopuses to quantify accurate activity space areas and home range sizes, and for methods of decreasing position error.

There are many possible explanations to account for the high variability and overall heterogeneity in *O. bimaculatus* movement patterns. Octopuses are well known to be flexible in their behaviors, and this, combined with their ability to learn and remember certain features of their surrounding environment, create the possibility for variation between individuals and between time periods. For example, it is hypothesized

that octopuses can adjust their diurnal or nocturnal activity levels based on the predators in their area (Meisel et al., 2013). While the densities and species of predators within the activity spaces of the individuals tracked in this study is unknown, it is possible that something similar could be occurring here. *O. bimaculatus* is exposed to a wide variety of predators, including diurnal ones such as the California sheephead (*Semicossyphus pulcher*) and the kelp bass (*Paralabrax clathratus*), as well as nocturnal ones such as the California moray eel (*Gymnothorax mordax*) (Hofmeister, 2015). Since there was a significant difference in the between the activity patterns of octopuses found inside versus outside the MPA, the local environment may be primarily dictating behavioral responses to predator activity on a much smaller scale. Assessing the influence of predator presence on octopus behavior and movement can be improved when information on the predatory composition within an octopus's home range is available.

The activity spaces of *O. bimaculatus* tracked during the study are considerably higher than other octopus species previously reported in the literature using much less conservative estimates of area. Previous measurements of octopus home range or activity space have been calculated over the course of days or weeks, but the estimated activity space for octopuses in the current study during a 4-hour block was higher than a 2-week estimate of home range in other studies. Mather et al. (1985) continuously monitored tagged *Enteroctopus dofleini* and found that after ten days the octopuses' home ranges had reached an asymptote of 250 m². The calculated activity space or home range of *Octopus cyanea* varied from 1320 - 2016 m² over five days (Forsythe and Hanlon, 1997) to 2151 m² over eight days (Ivey, 2007). Scheel and Bisson (2012)

is the only existing study that calculated areas close to those found for *O. bimaculatus*. These authors found that *E. dofleini* of equivalent size to *O. bimaculatus* inhabited a mean area of 4,300 m² over approximately 10 days, compared to the mean area of 6,143 m² over 12.9 days inhabited by *O. bimaculatus* found in the present study. It is likely that the estimated areas for all these studies are artificially small considering the relatively short period of time over which data were collected. However, it is unlikely that these great differences in estimated area are due to methodology, since these other studies estimated area by calculating minimum convex polygons (MCPs), a much less conservative method than bbKUD, and still found relatively small areas. The most likely scenario is that *O. bimaculatus* is highly mobile and uses a relatively large area for foraging and sheltering.

O. bimaculatus is typically considered nocturnal (Hochberg and Fields, 1980), but these results do not support this hypothesis. Variability in diurnal and nocturnal movement has been found for other octopus species, although the variation was not as pronounced. *E. dofleini* has primarily been reported as being nocturnal (Mather et al., 1985; Scheel and Bisson, 2012), but can modify their behavior based on foraging opportunities (Rigby and Sakurai, 2005). *O. cyanea* is mainly crepuscular, and this has been found in Hawaii and French Polynesia (Forsythe and Hanlon, 1997; Ivey, 2007; Yarnall, 1969). *O. vulgaris* has been reported separately as crepuscular (Mather and O'Dor, 1991), primarily nocturnal with short diurnal foraging excursions (Kayes, 1974), and primarily diurnal (Mather, 1988). There is even some evidence that octopuses can switch their activity based on the activity of nearby predators (Meisel et al., 2013) although this has only been tested in the lab. It is likely that the activity patterns of

octopuses are influenced by many complex and interrelated factors such as predator activity and density, prey availability, searching for mates, and shelter availability, and octopuses cannot be placed into traditional activity classifications.

In the present study, octopuses moved to a new location 51.7% of the time, or about once every two days. This frequency is in contrast to values previously reported for this species in this area. Ambrose (1982) estimated that *O. bimaculatus* on Catalina Island remained in the same den for 1 to 5 months, although it should be noted that he was unable to keep track of individual octopuses. The higher mobility of *O. bimaculatus* in the current study could be a result of changes in distribution and density of octopus prey, or of changes in the frequency or intensity of octopus predation (Hofmeister, 2015). If the availability of high value or preferred prey has changed, it can be hypothesized that octopuses would have to increase foraging time and distance traveled to find these prey items. This could result in frequent den switching, especially if octopuses find patches of prey that then become depleted very quickly (Mather et al., 2014). However, data from the current study are not extensive enough to conclusively determine the potential drivers of octopus den switching.

These preliminary estimations of activity space are likely an underestimate for several reasons. First, since octopuses are speculative and exploratory foragers, they rarely move in a straight or directed line (Forsythe and Hanlon, 1997). Second, this tracking method only captured the movement of individual octopuses over a very small time frame (one to two weeks). Each tag had to be less than five percent of the mass of a relatively small octopus, and given current technology the battery life was only expected to persist for approximately fourteen days. Since these octopuses live one to

two years, it is likely that the total home range inhabited by an octopus is much larger than what was observed during this time period. Third, the rocky reef kelp forest environment is challenging for acoustic work as the highly rugose substrate warps the acoustic signal from the tag. Altered acoustics potentially increase inaccuracies in measured animal positions, or result in weak signal strengths of transmitters, which would have decreased the confidence in animal location. In addition to this underestimation of activity space, it was not possible to visually determine the difference between an octopus at rest and an octopus moving in the field due to deep or turbid water, kelp forest density, or visibility at night. Therefore, the values presented here represent movement from an unknown number of foraging bouts. While quantifying daily displacement is a useful metric for determining larger-scale octopus movement, knowledge about individual foraging bouts can provide insight into the decision-making process, time-activity budgets, and habitat choice of octopuses. Future comprehensive studies should combine these large and small-scale measurements of octopus movement.

4.1. Conclusions. This study reports the successful acoustic tagging and active tracking of the smallest octopus species to date, and opens the possibility of gathering movement data for many octopus species around the world. A high tag retention rate, and a finding of substantial movement using conservative methods, shows promise for future telemetry studies. Movement data are crucial to understanding what environmental factors influence octopus spatial ecology, how their behavior will respond to changing environmental conditions, and the impact these changes will have on the community as a whole.

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Figure 1. Photo of a tagged *Octopus bimaculatus*. The modified Peterson disk with attached acoustic transmitter is inside the mantle of the octopus, while the Floy disk backplate and closures (indicated by the arrow) are on the outside of the animal.

COLOR VERSION FOR ONLINE PUBLICATION

Figure 1. Photo of a tagged *Octopus bimaculatus*. The modified Peterson disk with attached acoustic transmitter is inside the mantle of the octopus, while the Floy disk backplate and closures (indicated by the arrow) are on the outside of the animal.

BLACK AND WHITE VERSION FOR PRINT PUBLICATION

Figure 2. Map of the activity spaces of the seven successfully tagged and tracked octopuses. Each letter represents an octopus and indicates the associated activity space. The star indicates the location of the University of California Wrigley Institute for Environmental Studies (USC WIES). The outer circle of each octopus's activity space represents the 95% Brownian Bridge Kernel Utilization Distribution (bbKUD), or the area an octopus can be expected to be found 95% of the time. The middle and innermost lines outline the 65% and 35% bbKUD, respectively.

Table 1. Summary of select octopus movement literature, organized by species. Active tracking involves following acoustically-tagged individual animals from a surface vessel with a hydrophone. Passive tracking involves the semi-permanent placement of receivers *in situ* and utilizing this receiver arrangement to calculate the location of acoustically-tagged animals. Time of day is the time period (nocturnal, diurnal, crepuscular) where the octopuses were observed to be the most active.

Reference	Species	Location	Method	Study Duration	Time of Day	Home Range/ Activity Space Area	Foraging Trips	Den Occupancy
Mather et al. 1985	<i>Enteroctopus dofleini</i>	<i>In situ</i>	Direct observation, active tracking	15 days	Slightly nocturnal	250 m ²	Many short trips a day	Occupied multiple dens over 14 days
Rigby and Sakurai 2005	<i>E. dofleini</i>	<i>In situ</i>	Direct observation, passive tracking	3 months	Correlated with gill net placement	---	Vertical foraging up gill nets	---
Scheel and Bisson 2012	<i>E. dofleini</i>	<i>In situ</i>	Passive and active tracking	7 years passive, 6 months active	Active throughout the day but mostly from midnight to 5 am	4,300-50,000 m ² , larger animals moved more	---	---
Hartwick et al. 1984	<i>E. dofleini</i> , <i>Octopus bimaculatus</i>	<i>In situ</i>	Direct observation	1 year	---	---	---	Average 1 month, probability of <i>O. bimaculatus</i> leaving shelter = 0.461, of <i>E. dofleini</i> = 0.544
Ambrose 1982	<i>O. bimaculatus</i>	<i>In situ</i>	Direct observation	3 - 4 years	Nocturnal	---	---	Less than 1 week to 5 months
Yarnall 1969	<i>Octopus cyanea</i>	Artificial pools	Direct observation	2 months	Crepuscular	109.5 m ²	Mean distance of 27 m for 17 min	At least 1 month
Forsythe and Hanlon 1997	<i>O. cyanea</i>	<i>In situ</i>	Direct observation	5 days	Mainly crepuscular	2,016 m ² and 1,320 m ²	Mean distance of 81 m for 118 min	Up to 6 days

Ivey 2007	<i>O. cyanea</i>	<i>In situ</i>	Active tracking	20 days	Likely crepuscular	87 m ²		Mean distance 57 m for 1.9 hours	No sequential use of dens observed
Mather 1982	<i>Octopus joubini</i>	<i>In situ</i>	Direct observation	Less than 1 month	Nocturnal	---	---	---	Mean occupancy 3.7 days, correlation between number of dens and density
Iribarne 1990	<i>Octopus teheulchus</i>	<i>In situ</i>	Direct observation	1 year	---	---	---	---	Correlation between number of dens and density
Mather and O'Dor 1991	<i>Octopus vulgaris</i>	<i>In situ</i>	Direct observation	2 - 32 days	Crepuscular	117 m ²	9-17% of time spent foraging		Mean occupancy 4.5 - 12.4 depending on year, ranged from 1 day to 3 years
Boyle 1980	<i>O. vulgaris</i>	Lab	Direct observation	25 days	---	---	---		Larger animal occupied preferred den more often
Kayes 1974	<i>O. vulgaris</i>	<i>In situ</i>	Direct observation	11 days	Nocturnal	---	Long trips at night, short trips during the day		---
Mather 1991	<i>O. vulgaris</i>	<i>In situ</i>	Direct observation	Summer of 1985, 1988, 1989	---	---	113 trips among 4 octopuses, 12% of time spent foraging		Mean occupancy 7 days
Mather 1988	<i>O. vulgaris</i>	<i>In situ</i>	Direct observation	5 weeks	Early morning	---	11% of time spent hunting, 13% of time spent eating		---
Meisel et al. 2013	<i>O. vulgaris</i>	Lab	Direct observation	13 days	Inversely correlated with some predator activity times	---	---	---	---

Table 2. Summary of tagged octopuses. ID is the letter code used for each individual octopus. Depth is the depth at which the octopus was caught. Sex is indicated by M (male) or F (female). ML is mantle length, or the distance from the eyes to the tip of the mantle. Location is defined as whether octopuses were caught and tracked inside the marine protected area (MPA) or outside the marine protected area (nonMPA). Where applicable, means are presented with $\pm$ standard deviation (SD). Days with an asterisk (*) indicate individuals whose tag retention was truncated not by transmitter battery life or removal of tag but by the termination of the study. Mean number of days tagged does not include the two control animals. “12-to-12” tracks were tracks divided into two non-contiguous 12-hour tracks that were completed from 12 PM to 12 AM and 12 AM to 12 PM. “8-to-8” tracks were tracks completed continuously for 24 hours, from 8 PM to 8 PM.

ID	Depth (m)	Sex	Weight (g)	ML (cm)	Location	# Days Tagged	Track Type	Track Hours
A	7.9	M	650	10	-	0 (Control)	12-to-12	-
B	5.9	F	510	9	-	0 (Control)	12-to-12	-
C	2.3	M	650	10	MPA	5	12-to-12	12
D	5.4	F	730	10	MPA	19	12-to-12	25
E	7.9	M	600	9	nonMPA	19	12-to-12	22
F	4.1	F	700	9	MPA	15	8-to-8	24
G	6.5	F	550	8	nonMPA	15	8-to-8	18
H	14.3	M	620	11	MPA	10*	NA	-
I	14.9	M	1300	13	nonMPA	7*	8-to-8	24
Mean	7.7	5 M:4 F	701	9.9		12.9		20.8
($\pm$SD)	($\pm$4.3)		($\pm$235)	($\pm$1.4)		($\pm$5.6)		($\pm$5.0)

Table 3. Activity space sizes in m². Activity space calculated using “All” points including locations from the continuous tracks as well as the daily location. Octo ID is the letter assigned to each tracked octopus. The number of fixes indicate the total number of GPS locations acquired for each octopus.

Octo ID	12 Hour Track 1	12 Hour Track 2	24 Hour Track	All	# Fixes
C	2284.80	-	-	9060.85	88
D	4204.39	1258.38	-	11616.68	183
E	2128.09	2579.18	-	4273.65	134
F	-	-	2874.46	6534.48	120
G	-	-	1840.71	2745.38	91
H	-	-	-	4763.32	17
I	-	-	5037.39	4009.15	102
Mean	2872. 43	1918.78	3250.85	6143.36	105
(±SD)	(±1156.17)	(±933.95)	(±1631.24)	(±3165.53)	(±50.64)

Table 4. Activity space sizes in m² for each 4-hour time block for each octopus. Octo ID is the letter assigned to each tracked octopus. The mean $\pm$ standard deviation (SD) activity space size in m² is presented for each octopus across all 4-hour time blocks, and within each time block across all octopuses.

Octo ID	1200-1600	1600-2000	2000-2400	2400-0400	0400-0800	0800-1200	Mean ($\pm$SD)
C	1020.67	819.06	2309.53	-	-	-	1383.09 ($\pm$808.63)
D	1359.84	3746.41	1743.88	884.22	667.39	774.68	1529.40 ($\pm$1159.21)
E	-	1823.87	922.79	1149.40	2458.11	1984.71	1667.78 ($\pm$627.13)
F	655.37	1270.91	1417.20	968.26	2356.58	928.84	1266.19 ($\pm$597.90)
G	-	-	1565.13	428.36	1178.15	789.34	990.24 ($\pm$490.54)
I	1576.10	2282.16	2550.99	5871.08	4428.72	1313.43	3003.75 ($\pm$1781.75)
Mean ($\pm$SD)	1152.99 ($\pm$402.88)	1988.48 ($\pm$1127.62)	1751.59 ($\pm$597.31)	1860.26 ($\pm$2257.80)	2217.79 ($\pm$1453.43)	1158.20 ($\pm$510.63)	

Table 5. Track lengths in meters for each 4-hour time block for each octopus. Octo ID is the letter assigned to each tracked octopus. The mean $\pm$ standard deviation (SD) track length in meters is presented for each octopus across all 4-hour time blocks, and within each time block across all octopuses.

Octo ID	1200-1600	1600-2000	2000-2400	2400-0400	0400-0800	0800-1200	Mean ($\pm$ SD)
C	113.44	149.20	278.09	-	-	-	180.24 ($\pm$86.60)
D	172.42	378.19	275.36	129.60	93.72	116.41	194.28 ($\pm$110.67)
E	-	244.58	125.87	204.94	260.51	209.79	209.14 ($\pm$52.07)
F	78.40	103.18	157.18	139.15	208.21	74.76	126.81 ($\pm$51.60)
G	-	-	164.63	79.08	177.99	55.59	119.32 ($\pm$61.04)
I	97.54	129.02	287.62	391.41	558.46	66.17	255.04 ($\pm$193.95)
Mean ($\pm$SD)	115.45 ($\pm$40.59)	200.83 ($\pm$112.61)	214.79 ($\pm$73.10)	188.84 ($\pm$121.78)	259.78 ($\pm$177.58)	104.55 ($\pm$63.19)	