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Movement, Abundance Patterns, and Foraging Ecology of the California Two Spot Octopus, *Octopus bimaculatus*

by

Jennifer Krista Kaulalani Hofmeister

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:
Professor Roy L. Caldwell, Chair
Professor Eileen Lacey
Professor David Lindberg
Professor Steve Beissinger

Fall 2015

Abstract

Movement, Abundance Patterns, and Foraging Ecology of the California Two Spot Octopus, *Octopus bimaculatus*

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Jennifer Krista Kaulalani Hofmeister

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Roy L. Caldwell, Chair

Understanding the reciprocal interactions between animal behavior and other inter-related systems such as physiology, morphology, ecology, and evolution has been called a "Grand Challenge" for organismal biology. Behavior offers two unique contributions to our understanding of organism response to environmental change: 1) behavior is a rapid and reversible response, and 2) organisms can directly influence their surrounding environment, and thus the stimuli their physiological and morphological systems are exposed to, by "choosing" their environment.

My dissertation utilizes the temperate octopus *Octopus bimaculatus* to understand the reciprocal interactions between behavior and ecology in a human-altered landscape. I use a combination of animal population surveys, dietary analysis, mathematical models, and acoustic telemetry to understand the feedback loops been behavior and ecology. Octopuses play a key predatory role in shaping communities that is unmatched by any other invertebrate. Additionally, their "live fast, die young" life history strategy means their populations respond quickly and dramatically to changes in the environment, which suggests they could be an indicator of ecosystem change. Specifically, I addressed three fundamental questions about octopus behavior and ecology on Santa Catalina Island, CA: 1) What are key environmental variables influence octopus environmental choice?; 2) Where and when do octopuses move?; and 3) Does octopus diet reflect differences in predatory behavior within a human-altered habitat?

The first question addressed a key gap in current knowledge of the environmental variables that influence octopus abundance and distribution in a rocky reef ecosystem by combining intensive population surveys with imperfect detection modeling. Binomial mixture modeling is used when the likelihood of false non-detection is high, and is ideal for studying highly cryptic species like octopuses. Abundance and detection probability was modeled with site and survey-level covariates such as abiotic variables, octopus predator and prey abundances, and habitat structural characteristics. No single abundance covariate explained the data for either year, but detection in 2013 was best modeled with Julian date. Model-averaged estimates of abundance had high ranges of possibility, and all correlations with estimated octopus abundance and environmental variables had weak support. These results highlight the high variability in patterns of octopus abundance and the necessity for integration of multiple environmental factors to elucidate drivers of octopus abundance and small-scale distribution.

The second question quantified movement and habitat use of individual octopuses. This study pioneered acoustic telemetry research on small octopus species and was the first of its kind in the

continental United States. I collected and tagged *O. bimaculatus* and recorded their position over the course of approximately 2 weeks and measured movement continuously over one day for each animal. I found that *O. bimaculatus* is highly mobile and, combined with my survey data, concluded that they do not stay in a single den for more than a few days. Additionally, movement distances and diurnal movement patterns are highly variable, suggesting a behavioral response to avoid predation.

The third question aimed to identify the diet of *O. bimaculatus* using Stable Isotope Analysis (SIA) and assess if octopus diet differed between marine protected area (MPA) sites and non-protected sites. SIA allows for the indirect assessment of diet because the isotopic composition of prey is incorporated with reliable fidelity into the predators' tissues. I analyzed the carbon and nitrogen stable isotope ratios in octopuses and their prey collected inside and outside an MPA. I found that octopus diet differs between MPA and non-MPA sites and octopuses located within the MPA have a more varied diet than those located outside. This difference indicates a change in the predator-prey relationships with the establishment of the MPA and suggests larger changes in the community structure.

Together, these findings yield novel insights into what influences the populations and behavior of octopuses in a rocky reef environment, and lay the groundwork for directly testing how octopuses will respond to and influence the changes in their surrounding community.

Dedicated to my incredible husband,
David Rogers,
who gives me the strength to accomplish more than I ever thought possible.

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CHAPTER 1

Review of *Octopus bimaculatus* (Verrill, 1883) life history

Understanding the reciprocal interactions between animal behavior and other inter-related systems such as physiology, morphology, ecology, and evolution has been called a "Grand Challenge" for organismal biology (Sih et al. 2010). Behavior offers two unique contributions to our understanding of organism response to environmental change: 1) behavior is a rapid and reversible response, and 2) organisms can directly influence their surrounding environment, and thus the stimuli their physiological and morphological systems are exposed to, by "choosing" their environment. My dissertation utilizes the temperate octopus *Octopus bimaculatus* to understand the reciprocal interactions between behavior and ecology in a human-altered landscape.

The California two-spot octopus, *Octopus bimaculatus*, is typically described as occurring from Central California to the tip of Baja California and into the Gulf of Mexico (Hochberg and Fields 1980). However, juveniles and adults have been reported along the entire west cost of Mexico and as far south as Columbia (Nesis 1978, del Carmen Alejo-Plata et al. 2012, del Carmen Alejo-Plata et al. 2014). *O. bimaculatus* looks very similar to its sister species, *Octopus bimaculoides*, but differs in several key ways. Both are characterized by the presence of black and blue ocelli below the eyes and near the base of arms 2 and 3 (Hochberg and Fields 1980). However, the blue pattern within the ocelli in *O. bimaculatus* looks the spokes on a wheel, whereas the pattern in the ocelli of *O. bimaculoides* looks like a chain link (Lang 1989). This difference was the primary mode of species identification in this dissertation. Additionally, *O. bimaculatus* lays smaller eggs, has planktonic rather than benthic hatchlings, is relatively larger in size, has longer arms (4 to 5 times the length of the mantle), and has a relatively shorter hectocotylus, and has a different suite of parasites than *O. bimaculoides* (Pickford and McConnaughey 1949, Hochberg and Fields 1980). These two species are recently diverged and are part of a clade also containing the California red octopus, *Octopus rubescens*, and are in a clade distinct from the giant Pacific octopus, *Enteroctopus dofleini* (de Los Angeles Barriga Sosa et al. 1995).

O. bimaculatus is an archetypal small-egged octopus species. Mating occurs year round, but there is a distinct peak in May and June (Ambrose 1988). Males maintain a distance from the female during mating, and mating time is variable. In the lab, males can mate with a single female multiple times (Fox 1938). The ratio of sperm reservoir to spermatophore length is distinguishable enough in *O. bimaculatus* to use as an additional mode of species differentiation from *O. bimaculoides* (Voight 2001). *O. bimaculatus* lays small eggs, typically 2.5 to 4 mm long, in clutches averaging 20,000 eggs (Ambrose 1981). Eggs are laid year round, but most are laid from April to August. Octopuses that laid eggs earlier in the year were less likely to be reproductively successful (Ambrose 1988). Females lay eggs over several days, attaching egg strands to a hard substrate, then caring for the eggs until hatching. Females typically stop eating once the eggs are laid and she dies soon after the eggs hatch (Fox 1938, Ambrose 1981). As with most cephalopods, *O. bimaculatus* development time is inversely correlated with water temperature (Ambrose 1981). At 19° C, eggs take 50 days on average to develop (Ambrose 1981). The digestive system begins forming at 33 days post-laying, and paralarvae have fully developed digestive tracts upon hatching (Lopez-Peraza et al. 2014). Paralarvae spend 1-3 months as plankton before settling (Ambrose 1981). Mortality is highest during this planktonic phase (Ambrose 1988). Once they settle, juveniles live in kelp holdfasts until they reach a

mantle length of about 5 cm. Settlement occurs year round, and because if the semelparous nature of *O. bimaculatus*, a poor recruitment event is evident once that cohort reached adulthood. Ambrose (1988) observed two patterns of *O. bimaculatus* on Santa Catalina Island. In low recruitment years, there was a drop in octopus abundance in the fall, and in high recruitment years, there was no change in adult abundance. In this same area, adult abundance ranged from 0.5 to 3.0 individuals per 100 m^2 (Ambrose 1988).

O. bimaculatus is found in in rocky reef habitats (Hochberg and Fields 1980), but in many areas are ubiquitous predators found in both high and low relief areas (Schmitt 1982). Typically, *O. bimaculatus* is found in rocky habitats and *O. bimaculoides* are found in sand and mud flats (Pickford and McConnaughey 1949, Hochberg and Fields 1980). Dens are an important resource for *O. bimaculatus*, but unlike many other octopus species, populations in most areas do not appear to be den limited (Ambrose 1982). However, in lab experiments where dens were limiting, individuals were observed to fight over available shelter (Taylor and Chen 1969). On Santa Catalina Island, individuals from half the population remained in the same den for over a month, and of those a few remained in the same den for more than 5 months. About one quarter of the population stayed in the same den for less than a week, and some individuals moved to a new den every day. All observed individuals stayed in the same area and were assumed to be non-transient (Ambrose 1982).

The role of *O. bimaculatus* as a predator has been the primary area of study for this species. They are generalist predators and consume a variety of gastropods, bivalves, crustaceans, and even small fish (Pilson and Taylor 1961, Taylor and Chen 1969, Fotheringham 1974, Ambrose 1984, 1986). On Santa Catalina Island, *O. bimaculatus* consumed more than 55 different prey species from 3 phyla (Ambrose 1984), and in Bahia de los Angeles, Mexico, they consumed 76 different prey species from 8 phyla (Villegas et al. 2014). In this latter population, there is seasonal variation in diet, as well as variation by sex and reproductive status (Villegas et al. 2014). In the lab, *O. bimaculatus* shows high preference for crabs, yet snails dominate their diet in the field. Crabs are relatively rare and snails are very common, suggesting their diet is determined be a balance of preference and prey availability (Ambrose 1984). Octopuses can bring these prey items back to their den, or consume them elsewhere. On Santa Catalina Island about 20% of occupied octopus dens had middens, but the formation of middens were affected by water movement and hermit crabs taking empty shells (Ambrose 1983). The significant impact of *O. bimaculatus* predation on invertebrates has been demonstrated in several communities. In La Jolla, CA, this species was responsible for approximately 50% of snail mortality. Individuals were not selective of prey size, but did seem to avoid non-motile prey like barnacles, muscles, and boring clams (Fotheringham 1974). In two separate studies on Santa Catalina Island, an inverse relationship between octopus abundance and invertebrate prey abundance was observed (Schmitt 1982, Ambrose 1986). In experimental areas with artificially increased prey densities, *O. bimaculatus* aggregated around higher densities of prey, and high densities of one prey species resulted in a decline in density of the other species because of this locally increased octopus predation. This was the first known demonstration of "apparent competition" (Schmitt 1987). It is currently unknown whether octopuses themselves compete directly for prey, but an early study observed that octopuses in a shared tank began fighting once a small scorpionfish (a known prey item) was added to the tank, indicating the potential for octopuses to fight over prey (Taylor and Chen 1969).

The role of *O. bimaculatus* as a prey item is less understood. Moray eels, scorpionfish, sharks, larger fish, and pinnipeds are all predators of *O. bimaculatus*, though the relative contribution and

importance of this octopus to their diets is not known (Hochberg and Fields 1980, del Carmen Alejo-Plata et al. 2014). It is likely that many other species eat *O. bimaculatus*, but have not been reported. While there is no active *O. bimaculatus* fishery in the United States, there is a small but important coastal fishery in Mexico. This fishery is currently unregulated, so it is unknown the quantity of individuals taken or the sustainability of the fishery (Alberto Lopez-Rocha et al. 2012).

This strong foundation of knowledge about the life history of *O. bimaculatus* combined with the clear ecological importance of this species provides an exceptional opportunity to investigate complex research questions about octopus behavioral ecology and the ecosystem at large. Since octopuses serve as both an important predator and prey item, elucidating the drivers of their behavior, population dynamics, and community interactions can provide insight into many other aspects of the tropic web. This dissertation builds off of this foundation and begins to integrate multiple complex aspects of *O. bimaculatus* in order to further understand the complexities and flexibility of octopus behavioral ecology. I used a combination of animal population surveys, dietary analysis, mathematical models, and acoustic telemetry to understand the feedback loops been behavior and ecology. Specifically, I addressed three fundamental questions about octopus behavior and ecology on Santa Catalina Island, CA: 1) What key environmental variables influence octopus abundance and small-scale distribution?; 2) Where and when do octopuses move?; and 3) Does octopus diet reflect differences in predatory behavior within a human-altered habitat?

In order understand and identify which biotic variables could contribute to octopus abundance and small-scale distribution in a complex environment, Chapter 2 presents abundance estimates of *O. bimaculatus* in the field. A binomial mixture model, which allows for the simultaneous estimation of detection probabilities and abundance in an unmarked population, is applied in a novel way in order to identify environmental correlates of octopus abundance. Challenges in the application of this model are presented and discussed.

Octopus patterns of movement could be dependent on a number of factors including, demographic variables, predation risk, intraspecific competition, and prey availability. In Chapter 3, individual *O. bimaculatus* were tagged and tracked using acoustic telemetry in order to begin to identify the variables influencing octopus movement in the wild. The successful application of this technique to a relatively small octopus lays the groundwork for more thorough investigations on octopus habitat choice and the impacts octopus movement can have on prey communities.

Heterogeneity in marine habitat is often driven by anthropogenic pressure, such as alterations in competitor or predator populations. Comparing the behavior of animals in areas of high anthropogenic alteration (non-marine protected areas) with areas of low anthropogenic alteration (marine protected areas) can elucidate the effects, either direct or indirect, that these environmental changes can have on octopus populations. Chapter 4 discusses variation in diet in *O. bimaculatus* between marine protected and non-marine protected areas using stable isotope analysis. Diet is quantified using ^{13}C and ^{15}N stable isotope analysis, and compared across years. A Bayesian mixing model is used to estimate percent contribution of prey species and groups to octopus diet.

Finally, in Chapter 5, I attempt to synthesize these three facets of octopus behavior and ecology and identify potential causes of the observed high variability and heterogeneity in octopus behavior and foraging ecology. Taken together, these three questions address critical gaps in our knowledge of behaviorally complex organisms, and provide insight into the ecological, and potentially evolutionary, drivers, of flexible predatory behavior in a marine environment.

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CHAPTER 2

Estimating the abundance of *Octopus bimaculatus* on Santa Catalina Island, CA: an application and assessment of the binomial mixture model in a marine system

ABSTRACT

Identifying the environmental processes that drive patterns of animal populations is a cornerstone in ecology. However, measurements of abundance can be biased by heterogeneity in detection probability. In order to estimate abundance reliably, binomial mixture models (BMMs) can be applied to provide detectability-corrected abundance estimates of unmarked individuals. Octopuses are ubiquitous and significant predators in coastal marine ecosystems, but population estimates are inherently challenging due to their behavioral and morphological adaptations for predator avoidance. The abundance of *Octopus bimaculatus* around Santa Catalina Island, CA was modeled within a BMM framework. On SCUBA, 24 sites were surveyed for octopuses 3 times in two separate years, 2013 and 2014, for a total of 144 surveys. Predatory fish, moray eel, lobster, and gastropod abundance, as well as percent algae cover and rugosity were measured and used as site and survey-level covariates. Abundance and detection probability was modeled with site and survey-level covariates. No single abundance covariate explained the data for either year, but detection in 2013 was best modeled with Julian date. Model-averaged estimates of abundance had high ranges of possibility, and all correlations with estimated octopus abundance and environmental variables had weak support. These results highlight the high variability in patterns of octopus abundance and the necessity for integration of multiple environmental factors to elucidate drivers of octopus abundance and small-scale distribution.

INTRODUCTION

Measuring the abundance of animals, identifying the key processes that limit populations, and assessing how these populations change over time are cornerstones of ecology (Krebs 2009). For ecologists to derive accurate and meaningful interpretations from abundance patterns in space and time, measurements of abundance from survey methods must be reliable (Lancia et al. 1994). There are two main potential sources of bias involved in the estimation of organism abundance. First, researchers must assume sample locations are representative of the whole area, and extrapolate overall abundance. Since this is a common issue in spatial sampling, methods permitting these inferences are well established (Cochran 1977, Thompson 1992). Second, detection of organisms is imperfect; that is, it is unlikely that an observer is able to find and count all individuals present in a defined area. To account for this source of bias, survey methods collect data in a manner that permits the estimation of a probability of detection (Lancia et al. 1994). Methods used to estimate detection probability include capture-recapture, distance sampling, and multiple observer sampling, which may be time consuming or logistically difficult (Royle and Nichols 2003).

Adequately incorporating detection probabilities into measures of abundance has important implications for our understanding of community interactions and the management of populations and natural resources. Recently, a suite of models called N-mixture or binomial mixture models (BMMs) have been developed to address issues of detection and its relationship with abundance estimates (Royle and Nichols 2003, Royle 2004b, Denes et al. 2015). These models use temporally and spatially replicated counts to simultaneously estimate detection probability and abundance

(Dodd and Dorazio 2004, Royle 2004b, Kery et al. 2005). BMMs work off of two assumptions: first, that the sites are closed to immigration, emigration, birth, and death between visits, and second, that the species in question is either present or absent at the sample location and able to be detected when the sample is taken. BMMs are typically cost and time effective, and they have had wide implications for large-scale studies (Kery et al. 2005, Jakob et al. 2014, Flowers and Hightower 2015). They have been widely applied to populations of birds (Royle 2004a, Kery et al. 2005, Warren et al. 2013, Peron et al. 2014), reptiles (Doré et al. 2011, Buckland et al. 2014), and amphibians (Dodd and Dorazio 2004, Royle et al. 2005, MacNeil and Williams 2014, Otto et al. 2014) with large success in estimating reliable abundance values and correlating these values with environmental and population parameters. Additionally, BMMs have been modified and extended to accommodate a variety of ecological situations such as zero-inflation (Joseph et al. 2009), seasonal dependence (MacNeil and Williams 2014), and correlated behavior (Dorazio et al. 2013).

The application of these types of models in marine environmental monitoring is very limited compared to terrestrial ecosystem, despite the fundamental and unique challenges influencing detectability in the ocean (Monk 2014). A few studies have begun applying BMMs and addressing these complexities inherent in the marine ecosystem and the animals that live there (Hvingel et al. 2012, Dorazio et al. 2013, Wen et al. 2013, Buckland et al. 2014, Zhou et al. 2014, Conn et al. 2015). Octopuses are one of the most difficult species to determine abundance. Their extreme camouflage and ability to fit into and through small spaces makes them very difficult to locate reliably using visual census methods. The majority of the limited information available about octopus abundance comes from fisheries data (Boyle and Boletzky 1996, Balguerias et al. 2002, Leite et al. 2009a, Thiaw et al. 2011). Additionally, octopus abundance has been primarily correlated with abiotic variables. Habitat, particularly habitat containing adequate dens and hard substrate, seem to be the most important abiotic characteristic correlated with octopus abundance (Ambrose 1982, Mather 1982, Aronson 1986, Aronson 1991, Hanlon and Messenger 1996, Anderson 1997, Forsythe and Hanlon 1997, Scheel 2002, Leite et al. 2009a). Depth can also be an important factor and most species have very clear vertical distributions (Guerra 1981, Scheel 2002, Katsanevakis and Verriopoulos 2004, Leite et al. 2009b). Season strongly affects octopus abundance, which is often correlated with sea surface temperature (Rees and Lumby 1954, Guerra 1981, Hartwick et al. 1984, Iribarne 1990, Wurtz et al. 1992, Boyle and Boletzky 1996, Balguerias et al. 2002, Katsanevakis and Verriopoulos 2004, Leite et al. 2009b, Thiaw et al. 2011, Scheel 2015).

There is much higher variability and less clear relationships between octopus abundance and biotic variables. Octopuses are widely considered to be generalist predators (Hanlon and Messenger 1996, Rodhouse and Nigmatullin 1996, but see Anderson et al. 2008 and Leite et al. 2009a), and all available evidence suggests that their populations are not limited by prey availability (Mather 1982, Scheel et al. 2007). A few studies have suggested that predators play a crucial role in limiting populations and driving abundance patterns (Aronson 1986, Ambrose 1988, Mather and O'Dor 1991). Furthermore, competitive and predatory paleontological interactions between teleost fishes and cephalopods have driven the evolution of most of the morphological and behavioral characteristics of modern octopods (Aronson 1991). This further implies that predators and the associated anti-predatory behaviors and adaptations of octopuses play a fundamental role in dictating octopus abundance and density patterns in the wild.

Identifying the biotic and abiotic factors influencing octopus populations have been challenging because a consistent component of octopus populations is interannual variability. Most

exhibit life cycle characteristics including semelparity, low overlap of generations, fast growth, and a short life span, which results in high interannual variation and susceptibility to changes in environmental conditions (Hartwick et al. 1984, Boyle and Boletzky 1996). Because of these traits, it has been challenging to overcome the difficulty in detecting and determining the abundance of octopus populations with confidence. Octopuses play critical ecological roles, both as prey for higher trophic level species (Croxall and Prince 1996, Klages 1996, Smale 1996), and as predators on benthic invertebrates, where they can significantly impact prey abundance and diversity (Ambrose 1986). Understanding the factors limiting their populations and controlling patterns of abundance is crucial for identifying the response of communities to environmental change.

The binomial mixture models (BMM) (Royle 2004b) can incorporate the cryptic ability of octopods into estimates of abundance and allow for the more accurate investigation of environmental covariates that influence octopus abundances. This study applied binomial mixture modeling to a population of the octopus *Octopus bimaculatus* on Santa Catalina Island in southern California in order to estimate detection and abundance of this population and identify the biotic variables influencing octopus abundance and small-scale distribution in this area. Sites were placed both inside and outside a marine protected area (MPA) to take advantage of the heterogeneity in octopus predator densities created by recreational fishing activity outside of the MPA. This study sought to answer the following 4 questions: 1) Do BMMs provide estimates of abundance that are different from octopus count data? 2) What are the sources of detection and abundance heterogeneity in octopus monitoring? 3) Does the current sampling design meet the assumptions of the BMM framework? And 4) What challenges still need to be addressed in order to confidently apply BMMs to the monitoring of octopus populations?

METHODS

Study Site: This study was conducted on Santa Catalina Island, which is located approximately 20 miles west of Los Angeles, CA (Figure 2.1). All sites were 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. Sites were located 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. These areas were selected to take advantage of pre-existing heterogeneity in octopus predator and competitor densities.

Field Surveys: Surveys were completed between June and August in 2013 and May and July in 2014. Twenty-four 100 m^2 (20 m by 5 m) permanent transects were established in the subtidal rocky reef kelp forest environment running perpendicular to shore. Twelve transects, or "sites", were located inside the MPA and twelve were located outside (Figure 2.1). Transect location was determined based on depth and available habitat, and as a result transects were placed in 6 area clusters: Cherry Cove (CH), 4th of July Cove (FJ), Isthmus Cove (IC), South Wall (SW), Intake Pipes (IP), and Pumpernickel (PM) (Figure 2.2). All transects were placed at least 30 m apart and were located within a rocky reef kelp forest habitat and did not extend into the sand bottom areas in order to minimize the abiotic variables, such as den availability, contributing to octopus abundance.

All surveys were done during the day between the hours of 0700 and 1700 since previous successful surveys of this species were conducted during the day (Ambrose 1984). Additionally, a pilot study completed in 2011 determined that octopuses were more reliably detected during the day when they were in their dens, rather than at night when they were foraging. Depth of each transect varied from 15 m at the deepest to 3.5 m at the shallowest. The deepest part of each transect was permanently marked, and at the start of each survey a diver ran a transect tape perpendicular to shore for 20 meters at a pre-established compass heading. During the surveys, divers thoroughly searched the area 2.5 m to either side of the transect tape, using a light to illuminate darker areas.

Each 100 m^2 transect was surveyed by two SCUBA divers of varying octopus-searching experience using a timed band-with survey method for 30 minutes. Algae were moved to get a better look at a potential octopus hiding spaces but rocks were not moved. For each octopus found, the depth, estimated size (mantle length), distance from transect line, and meter mark along the transect line were recorded, and the den was marked with colored flagging tape. Each visit to the transect was given its own unique color of flagging tape so divers could determine if a den had been occupied on a previous survey. At the same time, the numbers of moray eels (*Gymnothorax mordax*), an octopus predator, and California spiny lobsters (*Panulirus interruptus*), a potential octopus competitor and prey item, within the defined area were recorded. Date, time, ocean temperature, transect starting depth, and transect ending depth were also recorded. Temperature and depth were measured with a Suunto Vyper dive computer. A survey was completed at each transect three times throughout the season, and surveys were conducted on average 28.0 ± 9.2 (mean ± SD) days apart in 2013 and 26.9 ± 13.5 (mean ± SD) days apart in 2014 (Figure 2.2).

During the placement of the full transect line at the beginning of each survey, predatory fishes were counted using a swimming band-width method. Fishes were counted as the transect tape was laid out to avoid scaring the fish before the survey began. The lead diver swam 1 m off the bottom and counted fish within a 5 m wide, 3 m tall, and 20 m long area. Predatory fish species included the kelp bass (*Paralabrax clathratus*) and California sheephead (*Semicossyphus pulcher*).

Percent algae cover, invertebrate abundance and diversity, and rugosity (3D complexity) were measured twice during 2013 season and once during the 2014 season. Percent algae cover was measured by placing three 1 m quadrats placed at the 5 m, 10 m, and 15 m transect marks. At each point of a grid-lined quadrat a diver recorded the height of the algae (encrusting, 0-3 cm, 3-8 cm, >8 cm), or if the point fell on top of a sponge, rhodolith, or other encrusting invertebrate. Additionally, all visible invertebrates within each 1 m quadrat were recorded and identified to species when possible. Finally, rugosity was measured by placing a chain of known length along the transect line at 2 m, 7 m, 12 m, and 17 m. The chain was allowed to fall into the cracks and crevices of the substrate and the direct distance covered was subtracted from the length of the chain and then divided by the length of the chain.

Data analyses. The estimates of octopus abundance were analyzed separately by year with the package unmarked (Fiske and Chandler 2011) in program R (v. 3.2.2, R Development Core Team) using the binomial mixture modeling framework developed by Royle (2004). This method applies an integrated likelihood framework to temporally repeated counts of individuals to estimate the abundance of a closed population. Two processes are modeled: detection probability using a binomial distribution, and abundance using either a Poisson, negative binomial, or zero-inflated Poisson distribution. The general form of this model for site abundance is

$$N_i \sim f(\lambda) \text{ for } i = 1, 2, \ldots, M$$

and for the detection process is

$$y_{ij}|N_i \sim \text{Binomial}(Ni, p_{ij}) \text{ for } j = 1, 2, \ldots, J_i$$

where λ is the abundance per site i and p is the detection probability and *f* is a discrete distribution, such as Poisson or negative binomial, with support restricted to N*i* ≥ 0 (Royle 2004b, Royle et al. 2007, Fiske and Chandler 2011). Observation-level and site-level covariates can be incorporated into the model to investigate their effects on abundance. All covariates were converted into standard normal deviates before BMM analysis, and each transect was defined as a "site". For a complete list of detection and abundance covariates see Table 2.1.

Models were evaluated using Akaike's information criterion (AIC), and the top models were selected using the difference in AIC between the best model and all other models (ΔAIC). A systematic approach was used to identify first the top detection model and then the top abundance models. Within each year, models were first run with each detection covariate separately. From that, a second detection covariate was added to the single detection covariate that had the strongest support. This process was repeated for multiple detection covariates until the strongest detection model was identified (Table 2.2 for 2013; Table 2.4 for 2014). This top detection model was then used to fit the abundance covariates with the same sequential method. All resulting abundance models with ΔAIC ≤ 2 were tested for adequacy with a parametric bootstrapping goodness-of-fit test with 1000 simulations using the Nmix.gof.test function in the R package AICcmodavg (Mazerolle 2015). All abundance models with ΔAIC ≤ 2 that passed the goodness-of-fit test were averaged and used for all subsequent calculations. The model-averaged estimates of octopus abundance were calculated for each site, as well as the slope and intercept to plot the correlations with octopus abundance and 7 covariates of interest: predatory fish abundance, moray eel abundance, lobster abundance, gastropod abundance, rugosity, percent fleshy algae cover, and category (MPA vs. nonMPA).

RESULTS

Counts of octopuses during surveys ranged from 0 to 8 in 2013 and 0 to 4 in 2014 (Figure 2.3). All sites in both years had at least one detection indicating that occupancy at all sites was 1. After the completion of the 2014 surveys, a separate study determined that *O. bimaculatus* can travel distances that exceed the minimum distance between sites (30 m) (see this Dissertation, Chapter 3) so it is possible that the closure assumption was not met, which could have possibly contributed to an overestimation of abundance in 2013 (discussed below) (Rota et al. 2009, Dail and Madsen 2011). The best performing models for both years used a Poisson distribution. Neither year had one single best model that fit the data, but had several that had a ΔAIC ≤ 2 (Table 2.2; Table 2.3; Table 2.4; Table 2.5).

In 2013, the inclusion of Julian date and predatory fish abundance as detection covariates resulted in the strongest detection model (Table 2.2). All subsequent abundance models were fit using these covariates for detection. There was no single top abundance model (Table 2.3). Seven models met the criteria of ΔAIC ≤ 2, and all of these only included a single abundance covariate.

The null abundance model (detection covariates included but no abundance covariates included) could not be rejected indicating that there were no measured covariates that explained the data better than no abundance covariate. A total of 8 models were tested for goodness of fit (Table 2.6). All 8 selected models were adequate based on goodness of fit, and 8 models were averaged before calculating the unobserved true abundance of octopuses at each site. Perhaps due to an identifiability problem or as a result of low detection probability or high heterogeneity in count data or a failure to meet the closure assumption (Dail and Madsen 2011, Couturier et al. 2013, Dennis et al. 2015, Dr. Andrew Royle, Personal Communication), no 2013 models exhibited convergence of detection probabilities and absolute abundance values. Therefore, relative abundance estimates were used to test for correlations with environmental variables (Figure 2.4). These relative abundance values are overestimates of abundance and not ecologically realistic. However, tests varying the upper abundance limit in the model (the K parameter) revealed that relationships between octopus abundance and environmental variables did not change with different values of K. In the final model K was set at 200 as is recommended by the current literature. Cautious interpretation of the 2013 results will be made in light of this issue. These relative abundance values negatively correlated with moray eel abundance, predatory fish abundance, rugosity, lobster abundance, and fleshy algae percent cover. Gastropod abundance was positively correlated with relative octopus abundance. It should be noted that none of these relationships are particularly strong due to the high amount of variation and heterogeneity in the data (Figure 2.4). Generally, there were more octopuses in the MPA sites, and the variation in octopus abundance was wider in the nonMPA sites (Figure 2.6).

In 2014, two sites, Intake Pipes 1 and Pumpernickel 2, were identified as outliers using Grubbs test for outliers (Intake Pipes 1: $p < 0.001$; Pumpernickel 2: $p < 0.05$) and removed. The remaining 22 sites were included in the final analyses. The inclusion of rugosity and lobster abundance as the detection covariates resulted in the highest supported detection model. These covariates were used for fitting the each subsequent abundance model (Table 2.4). A total of 10 abundance models met the criteria of $\Delta AIC \leq 2$ (Table 2.5). This model set included both the overall null model (no detection or abundance covariates) and the null detection model (no abundance covariates) indicating that none of the measured covariates explained the 2014 data better than no covariates. All of the 10 selected models were adequate based on goodness of fit (Table 2.6) and all were averaged before estimating the abundance of octopuses at each site. However several models had residual variance lower than expected, which can result in more conservative estimates of error (Table 2.6). The average detection probability of octopuses in 2014 was 0.26 (lower 95% CI: 0.047, upper 95% CI: 0.69). The average estimated abundance of octopuses ranged from 7.3 (lower 95% CI: 3.2, upper 95% CI: 12.2) to 13.8 (lower 95% CI: 8.9, upper 95% CI: 19.5) (Figure 2.5). Octopus abundance was negatively related to moray eel abundance and predatory fish abundance, and was positively related to rugosity, gastropod abundance, lobster abundance, and fleshy algae percent cover. As with 2013, however, none of these relationships were strong likely due to the large amount of variation and heterogeneity in the data (Figure 2.5). As in 2013, there were more octopuses in the MPA sites, and the variation in octopus abundance was wider in the nonMPA sites (Figure 2.6).

DISCUSSION

These results demonstrate that 1) BMMs provide larger estimates of abundance than are provided by the raw count data, 2) the heterogeneity in detection could be modeled by date and

predatory fish in 2013, and by lobster abundance and rugosity in 2014, although the fit in 2014 was weak compared to 2013, 3) it is unclear whether not the sampling design met the closure assumption of the BMM model, but assumptions of presence and absence were met, and 4) though there were issues with model performance related to sample design and octopus population dynamics, the solutions to these problems can be addressed to improve estimates of octopus abundance. These results, though preliminary, are an important first step in applying BMMs to the monitoring of coastal benthic octopods. BMM model performance using the Poisson distribution showed that the selected models were robust and had a good fit to the data in both years. However, this robust fit is only reliable in the 2014 data because of the inability for the 2013 models to converge on estimates of octopus abundance. The same covariates did not contribute to the top detection and abundance models of *O. bimaculatus* between years, revealing that factors influencing octopus populations are not consistent. This is not surprising given the high level of variability in octopus populations (Boyle and Boletzky 1996, Hanlon and Messenger 1996). In 2013, detection probability was influenced strongly by date and predatory fish abundance (kelp bass and California sheephead). Looking at the raw data, there is an increase in the number of octopuses detected across visits (Figure 2.3), so it is not surprising that the "date" covariate influenced detection so strongly. With higher fish abundances, octopuses could have been more difficult to detect because they were employing more cryptic behavior. Alternatively, there could have been fewer octopuses at the site due to increased predation by predatory fishes, octopuses avoiding that site due to the high density of predators, or a combination of these possibilities. In 2013, none of the proposed hypotheses could be explicitly tested because of the non-convergence of the model. However, one can begin to examine correlations with octopuses and certain covariates that warrant further investigation. When examining the model-averaged slopes, octopus abundance was negatively correlated with predatory fish, moray eel, and lobster abundances and fleshy algae percent cover (Figure 2.4). Surprisingly, there octopus abundance was negatively correlated with octopus abundance and rugosity, suggesting that more octopuses were found in low complexity environments. This is contrary to the vast majority of other octopus field studies (Ambrose 1982, Mather 1982, Aronson 1986, Aronson 1991, Hanlon and Messenger 1996, Anderson 1997, Forsythe and Hanlon 1997, Scheel 2002, Leite et al. 2009a), and contrary to the 2014 results of this study (discussed below). Since rugosity influenced detection probability in 2014 but not 2013, it is possible that this influenced octopus correlation with rugosity. However, the overall raw octopus population size in 2013 was higher than in 2014 (Figure 2.3); it is possible that either octopus populations need to be larger in order to reveal significant trends (analogous to sample size). Alternatively, with the increase in octopus population size, there was a decrease in available dens in complex habitats and thus individual octopuses were forced to seek shelter in low-complexity environments. Finally, octopus abundance was positively related to gastropod abundance, though, like all 2014 correlations, this was weak. Given the complications with fitting models to the 2013 data, the inability to reject the null detection model, and the weak resulting relationships, these relationships cannot be accepted with confidence. Further study, including resolving the identifiability issue within the model, must be addressed before correlations with estimated octopus abundance and covariates of interest can be tested and explored.

Trends seen in 2013 were not seen in 2014. Within the BMM framework, the additive effects of rugosity and lobster abundance influenced octopus detection. However, though this detection model had more support than the null model, ΔAIC between these models was ≤ 2, indicating the inclusion of these covariates explained the patterns of octopus no better than the

absence of any detection covariate. No single abundance covariate or combined abundance covariates did a strong job explaining the data. Therefore, as with the 2014 detection models, the data were explained equally well with the absence of abundance covariate data as they were with abundance covariate data. Correlations with estimated octopus abundance and measured environmental variables were not consistent with 2013 (Figure 2.5). Octopus abundance was positively related to rugosity, lobster abundance, and fleshy algae percent cover in 2014, the opposite of what was seen in 2013. As mentioned previously, octopuses were more abundant in 2013 compared to other years surveyed (Figure 2.3), so this variation in population size could have influenced how octopuses interact within their community. Finally, these correlations were weak and likely increased samples sizes are needed to expose patterns that can be interpreted with confidence.

In both years, more octopuses were found, on average, in MPA sites than nonMPA sites, but the variation in abundance was consistently higher in nonMPA sites (Figure 2.6). The driver behind this difference is not clear from the modeling results. There were more predatory fishes in the MPA areas and more moray eels in the nonMPA areas, all of which are important octopus predators (see Chapter 4, this dissertation). If either of these biotic covariates were responsible for this pattern, there would have likely been strong relationships with these covariates and estimated octopus abundance. It is possible that the nonMPA areas experience more variation in biotic variables that contribute to higher variation in octopus abundance. Most likely, a suite of biotic and abiotic factors that exhibit different levels of intra- and inter-annual variability interact to influence patterns of octopus abundance seen in this ecosystem.

These results highlight the extreme variability and heterogeneity of octopus populations and the difficulty in identifying relationships and drivers between octopus abundance patterns and biotic variables. In addition to the challenges inherent in life history characteristics of octopuses that are likely confounding the results, there are some potential biases and limitations of the implementation of BMMs in this system. Some of these biotic variables themselves do not have a detection probability of 1, which could bias the counts of these species and impact the interpretation of the correlation with octopus abundances and these key covariates. For example, California moray eels are nocturnal and hide under rocks and in crevices during the day (Grüninger 1997), so it is highly likely that the number of moray eels detected and counted is less than the total number present at each site. The same is true for predatory fishes, lobsters, and gastropods. This adds another layer of error onto these analyses, and must be considered in the interpretation of results.

The application of BMMs to this system needs to be improved, and thus these data need to be interpreted with caution. Absolute estimates of octopus abundance for 2013 could not be made due it a lack of convergence within the models. This is likely due to heterogeneity in the data and a misinterpretation of abundance trends by the model. BMM only works if an assumption of closure can be made (Royle 2004b, Rota et al. 2009, Dail and Madsen 2011, Kendall et al. 2013). That is, that there is no immigration, emigration, birth, or mortality within the site across visits. In 2013, the number of octopus detected within each site increased as the season progressed. This increase could be interpreted as immigration of octopuses into these sites. However, based off of current knowledge of octopus population dynamics and of this specific population of *O. bimaculatus*, this increase is likely due to octopuses increasing in size and therefore becoming easier to detect. An additional factor that likely contributed to this trend is that since the same two divers completed all of the 2013 surveys, these divers' abilities to detect octopuses likely improved with subsequent surveys. Since multiple different divers completed the 2014 surveys, this effect was not seen during that season.

Finally, as mentioned previously, a more recent study conducted in this area demonstrated that *O. bimaculatus* frequently moves further distances than the minimum distance between sites (this Dissertation, Chapter 3), and therefore the closure assumption may not have been met, which could have contributed to these high estimates of abundance (Dail and Madsen 2011). Future work will apply a BMM with a relaxed closure assumption that estimates abundance across multiple seasons or years (Dail and Madsen 2011). Additional models, such as state-space models, could also be utilized as a way to account for variability in covariates and test a different modeling framework with O. bimaculatus population data (Denes et al. 2015).

Since BMMs are newly applied marine systems, the definition of "site" and "closure" furtherwithin the model still need to be parsed and optimized for continuous habitats like coastal kelp forests and rocky reefs. Some studies have solved this issue with modified sampling designs that are not applicable to the present study, such as traps and aerial surveys (Edwards et al. 2007, Hvingel et al. 2012, Wen et al. 2013, Zhou et al. 2014). Connectivity between sites and populations are generally higher in marine environments, especially for species like *O. bimaculatus* that have a planktonic paralarval phase (Kinlan and Gaines 2003, Cowen et al. 2007, Cowen and Sponaugle 2009). It is possible that it will be necessary to adjust the definition "site" in order to meet the closure assumption and make BMMs applicable to marine populations like benthic octopods. For example, a continuous coastal kelp forest may cover hundreds of square kilometers with no discernable boundaries, and a pelagic fish population has no defined area that they inhabit. Though there are several aspects about BMMs that must be addressed and tested before they can be widely applied with confidence to octopus populations, the solutions are attainable. Furthermore, optimizing models that can estimate detection-corrected abundance values is especially important for species like octopods where detection has been a constant and inescapable limitation in understanding octopus abundance dynamics.

Conclusions. Since assessment and management of populations depends on reliable estimates of abundance, there is a definite and immediate need for these types of models to be applied to the marine environment as our current understanding of marine species' distribution and abundance is biased by imperfect detection (Monk 2014). For highly variable species, like octopuses, long-term studies completed in conjunction with binomial mixture modeling are needed in order to capture the drivers of this variability and elucidate large-scale patterns that dictate community interactions and response to environmental changes.

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TABLES

Table 2.1. Detection and abundance covariates used in BMM analysis and model selection. Moray eels and lobsters abundances are number of animals per 100 m^2. Predatory fish abundance is number of animals per 300 m^3. Gastropod abundance is number of animals per 3 m^2. Predatory fishes include California sheephead and kelp bass density combined. Date was converted into Julian Date prior to analysis. Dive buddies are listed by each diver's first and last initial.

Detection Covariates	**Abundance Covariates**
Rugosity	Category (MPA or nonMPA)
Gastropod Abundance	Rugosity
Fleshy Algae Percent Cover	Gastropod Abundance
Moray Eel Abundance	Fleshy Algae Percent Cover
Predatory Fish Abundance	Moray Eel Abundance
Lobster Abundance	Predatory Fish Abundance
Date	Lobster Abundance
Time	
High Water Temperature	
Low Water Temperature	
Dive Buddy (J.B., E. G., or M. W.)	

Table 2.2. Model selection results for all detection models and the null model (no detection or abundance covariates) for 2013.

Detection Covariates				
Single Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
date	3	276.48	0.00	1.00
none	2	292.60	16.12	0.00
high temperature	3	292.74	16.27	0.00
time	3	293.13	16.66	0.00
moray abundance	3	293.14	16.67	0.00
rugosity	3	293.32	16.84	0.00
low temperature	3	293.46	16.99	0.00
predatory fish abundance	3	293.76	17.28	0.00
gastropod abundance	3	293.97	17.49	0.00
lobster abundance	3	294.54	18.07	0.00
fleshy algae % algae	3	294.57	18.09	0.00
Two Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
predatory fish abundance + date	4	273.89	0.00	0.40
date	3	276.48	2.58	0.11
moray abundance + date	4	276.92	3.03	0.09
rugosity + date	4	276.98	3.08	0.09
time + date	4	277.45	3.56	0.07
gastropod abundance + date	4	277.78	3.89	0.06
low temperature + date	4	277.93	4.03	0.05
high temperature + date	4	277.99	4.09	0.05
lobster abundance + date	4	278.46	4.56	0.04
fleshy algae % cover + date	4	278.48	4.58	0.04
none	2	292.60	18.70	0.00
More Than Two Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
predatory fish abundance + date	4	273.89	0.00	0.29
low temperature + predatory fish abundance + date	5	274.88	0.99	0.17
high temperature + predatory fish abundance + date	5	275.09	1.20	0.16
moray abundance + predatory fish abundance + date	5	275.32	1.43	0.14
low temperature + moray abundance + predatory fish abundance + date	6	276.06	2.16	0.10
date	3	276.48	2.58	0.08
moray abundance + date	4	276.92	3.03	0.06
none	2	292.60	18.70	0.00

K = number of parameters used
ΔAIC = difference between the lowest model AIC and the top model AIC
AIC Weight = model probability among all candidate models
Detection probability was modeled with observation-level and site-level covariates; abundance was modeled with site-level covariates

Table 2.3. Model selection results for all abundance models and the null model (no detection or abundance covariates) for 2013. Models with an asterisk (*) were averaged for calculating unobserved true octopus abundance.

Abundance Covariates with fish + date as the detection covariates				
Single Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
none*	4	273.89	0.00	0.22
moray abundance*	5	274.28	0.39	0.18
rugosity*	5	274.70	0.80	0.15
lobster abundance*	5	274.99	1.10	0.13
fleshy algae % cover*	5	275.76	1.87	0.09
gastropod abundance*	5	275.79	1.89	0.09
predatory fish abundance*	5	275.87	1.98	0.08
MPA vs. nonMPA*	5	275.89	2.00	0.08
none	2	292.60	18.70	0.00
Two Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
none	4	273.89	0.00	0.22
morays	5	274.28	0.39	0.18
morays + MPA vs. nonMPA	6	275.95	2.06	0.08
morays + lobster	6	276.18	2.28	0.07
morays + rugosity	6	276.18	2.29	0.07
morays + fish	6	276.25	2.36	0.07
morays + algae	6	276.26	2.36	0.07
morays + gastropods	6	276.27	2.38	0.07
lobsters + rugosity	6	276.34	2.45	0.07
lobsters + MPA vs. nonMPA	6	276.94	3.05	0.05
lobsters + algae	6	276.99	3.10	0.05
none	2	292.60	18.70	0.000

K = number of parameters used
ΔAIC = difference between the lowest model AIC and the top model AIC
AIC Weight = model probability among all candidate models
Detection probability was modeled with observation-level and site-level covariates; abundance was modeled with site-level covariates

Table 2.4. Model selection results for detection models and the null model (no detection or abundance covariates) for 2014, once the two outlier sites had been removed.

Detection Covariates Only				
Single Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
rugosity	3	185.31	0.00	0.15
none	2	185.48	0.17	0.13
low temperature	3	185.66	0.35	0.12
fleshy algae	3	185.80	0.49	0.11
high temperature	3	186.41	1.10	0.08
buddy	3	186.83	1.52	0.07
morays	3	187.10	1.79	0.06
date	3	187.10	1.79	0.06
time	3	187.15	1.84	0.06
lobsters	3	187.22	1.91	0.06
gastropods	3	187.26	1.95	0.06
fish	3	187.47	2.16	0.05
Two Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
lobsters + rugosity	4	184.76	0.00	0.17
rugosity	3	185.31	0.55	0.13
none	2	185.48	0.71	0.12
low temperature + rugosity	4	185.81	1.04	0.10
high temperature + rugosity	4	186.28	1.51	0.08
buddy + rugosity	4	186.31	1.55	0.08
date + rugosity	4	186.92	2.16	0.06
gastropods + rugosity	4	187.00	2.24	0.06
time + rugosity	4	187.06	2.30	0.05
morays + rugosity	4	187.07	2.31	0.05
algae + rugosity	4	187.07	2.31	0.05
fish + rugosity	4	187.29	2.53	0.05
More than two covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
lobsters + rugosity	4	184.76	0.00	0.19
low temperature + lobsters + rugosity	5	185.27	0.51	0.15
rugosity	3	185.31	0.55	0.14
none	2	185.48	0.71	0.13
morays + lobsters + rugosity	5	186.76	2.00	0.07
high temperature + lobsters + rugosity	6	186.97	2.21	0.06
buddy + lobsters + rugosity	6	187.04	2.28	0.06
algae + lobsters + rugosity	6	187.17	2.40	0.06
time + lobsters + rugosity	6	187.41	2.65	0.05
date + lobsters + rugosity	6	187.55	2.79	0.05
fish + lobsters + rugosity	6	187.68	2.92	0.04

K = number of parameters used
ΔAIC = difference between the lowest model AIC and the top model AIC
AIC Weight = model probability among all candidate models
Detection probability was modeled with observation-level and site-level covariates; abundance was modeled with site-level covariates

Table 2.5. Model selection results for abundance models and the null model (no detection or abundance covariates) for 2014, once the two outlier sites had been removed. Models with an asterisk (*) were averaged for calculating unobserved true octopus abundance.

Abundance covariates with lobsters + rugosity as the detection model				
Single Covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
none*	4	184.76	0.00	0.19
lobster abundance*	5	185.16	0.39	0.16
none*	2	185.48	0.71	0.13
MPA vs. nonMPA*	5	185.94	1.18	0.11
rugosity*	5	186.23	1.46	0.09
gastropod abundance*	5	186.37	1.61	0.09
fleshy algae % cover*	5	186.50	1.73	0.08
moray abundance*	5	186.55	1.79	0.08
predatory fish abundance*	5	186.60	1.83	0.08
Two covariates				
Covariates	**K**	**AIC**	**ΔAIC**	**AIC Weight**
none	4	184.76	0.00	0.22
lobster abundance	5	185.16	0.39	0.18
none	2	185.48	0.71	0.15
MPA vs. nonMPA + lobster abundance*	6	186.37	1.60	0.10
moray abundance + lobster abundance	6	186.84	2.08	0.08
gastropod abundance + lobster abundance	6	186.84	2.08	0.08
fleshy algae % cover + lobster abundance	6	186.99	2.23	0.07
rugosity + lobster abundance	6	187.00	2.24	0.07
predatory fish abundance + lobster abundance	6	187.01	2.25	0.07

K = number of parameters used
ΔAIC = difference between the lowest model AIC and the top model AIC
AIC Weight = model probability among all candidate models
Detection probability was modeled with observation-level and site-level covariates; abundance was modeled with site-level covariates

Table 2.6. Goodness of fit values for the models. Values are generated using the Pearson chi-square test. P-values < 0.95 indicate observed residual variance is lower than expected. $\hat{C}$ (c-hat) provides a value of over or underdispersion. $\hat{C}$ values > 1 indicate overdispersion, and values << 1 indicate poor model fit. All models have adequate fit, though some of the 2014 models have low residual variance.

2013			
Covariates	**X^2**	**p-value**	**$\hat{C}$**
none	58.65	0.80	0.85
morays	57.10	0.83	0.83
rugosity	57.29	0.82	0.84
lobsters	58.98	0.75	0.87
fleshy algae	58.41	0.78	0.86
gastropods	58.51	0.78	0.86
fish	58.56	0.78	0.86
MPA vs. nonMPA	58.62	0.81	0.86
2014			
Covariates	**X^2**	**p-value**	**$\hat{C}$**
none	45.47	0.95	0.73
lobsters	44.56	0.95	0.73
none	50.32	0.91	0.78
MPA vs. nonMPA	45.07	0.97	0.73
rugosity	45.80	0.93	0.75
gastropods	45.49	0.95	0.74
algae	45.84	0.94	0.76
morays	45.31	0.94	0.74
fish	45.47	0.95	0.75
MPA vs. nonMPA + lobsters	44.00	0.96	0.72

FIGURES

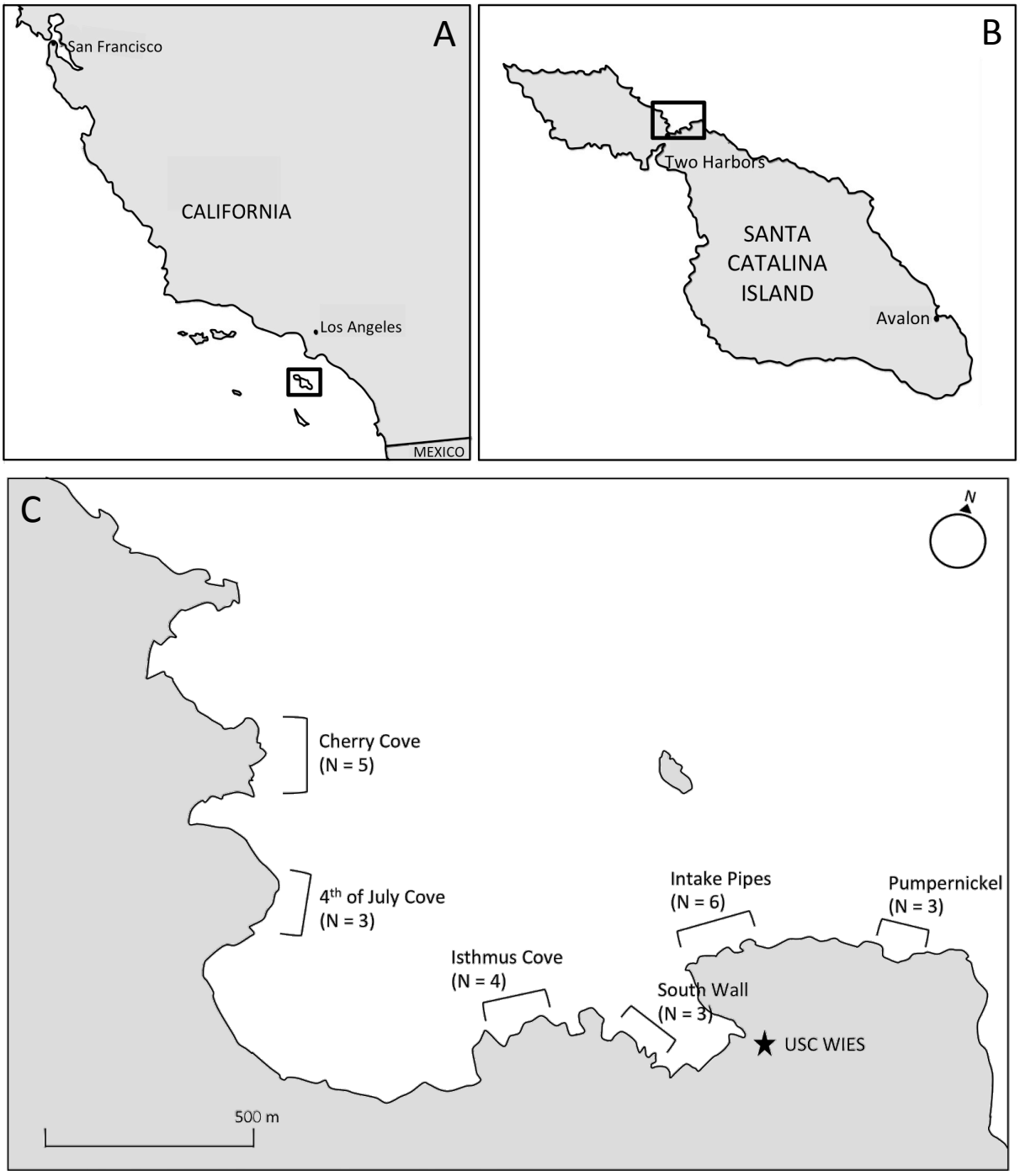

Figure 2.1. Area where the study took place on Santa Catalina Island, CA. Santa Catalina Island is located off the coast of southern California (A), and the study area was located near the town of Two Harbors (B). Numbers of transects within each area are indicated. Each transect constituted a "site" for the purpose of the binomial mixture model and were at least 30 m apart. Each site was visited 3 times, for a total of 72 surveys each year (C).

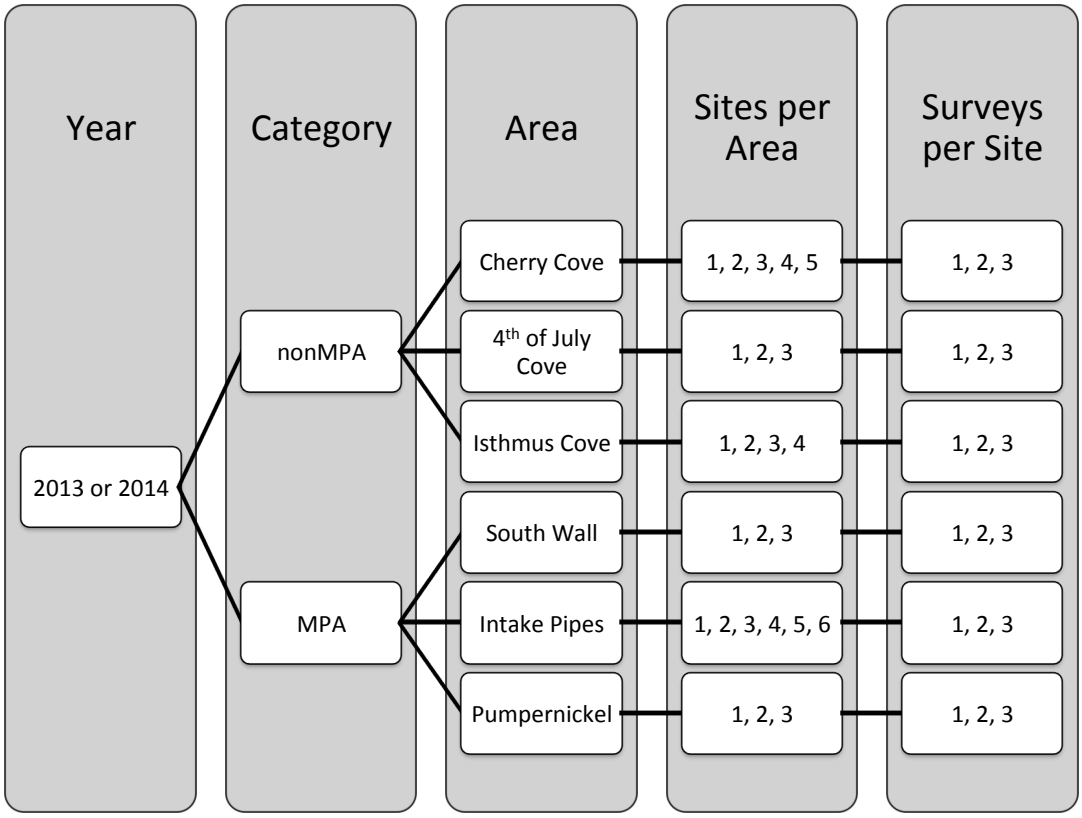

Figure 2.2. Schematic of survey method and survey replicates. The terms "site" and "transect" were synonymous in this study. Each site was surveyed three different times for a total of 72 surveys.

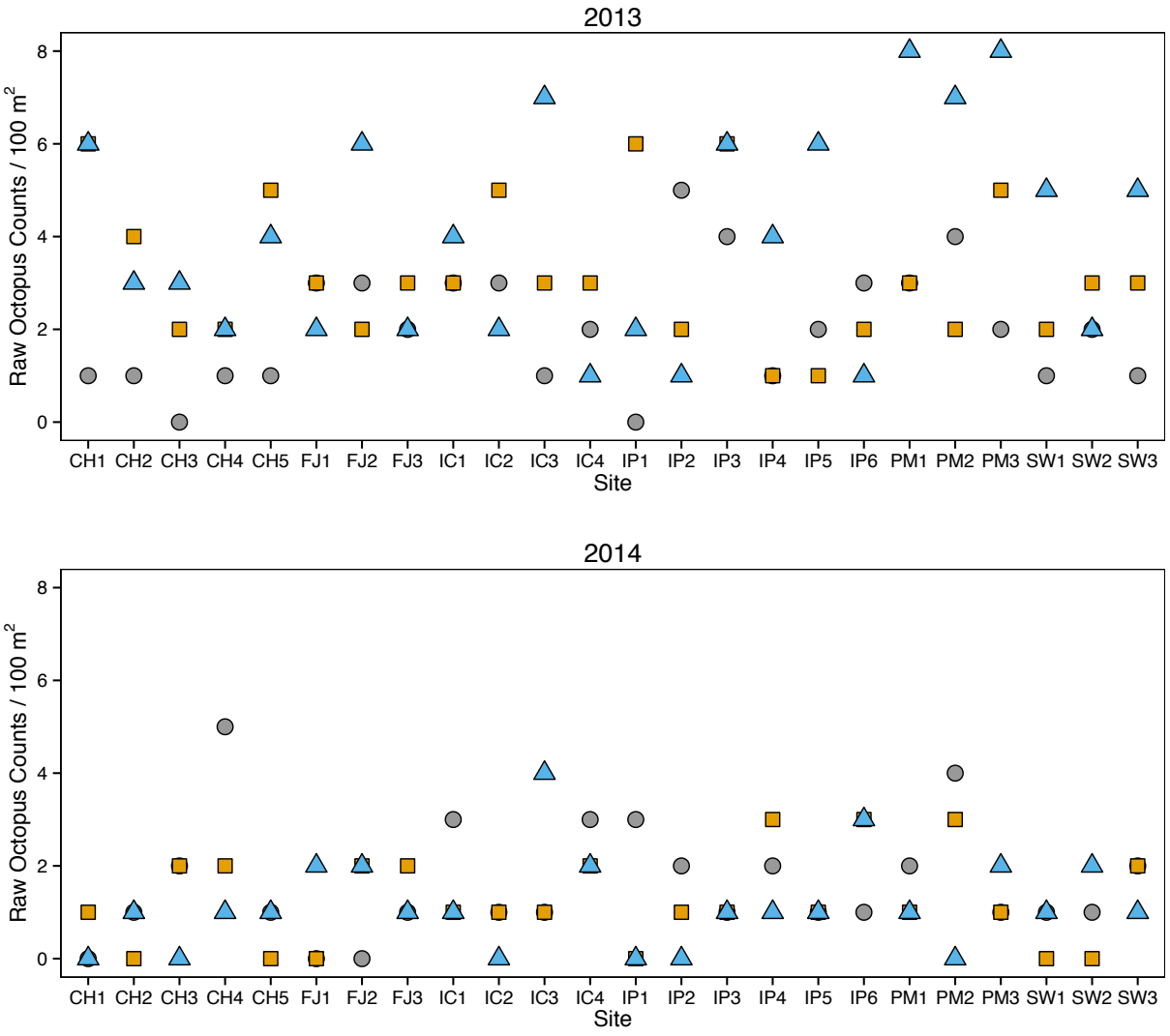

Figure 2.3. Raw octopus counts per survey by site for 2013 (upper graph) and 2014 (lower graph) Grey circles = survey 1; orange squares = survey 2; blue triangles = survey 3. Site abbreviations are: CH = Cherry Cove; FJ = 4th of July Cove; IC = Isthmus Cove; IP = Intake Pipes; PM = Pumpernickel; SW = South Wall.

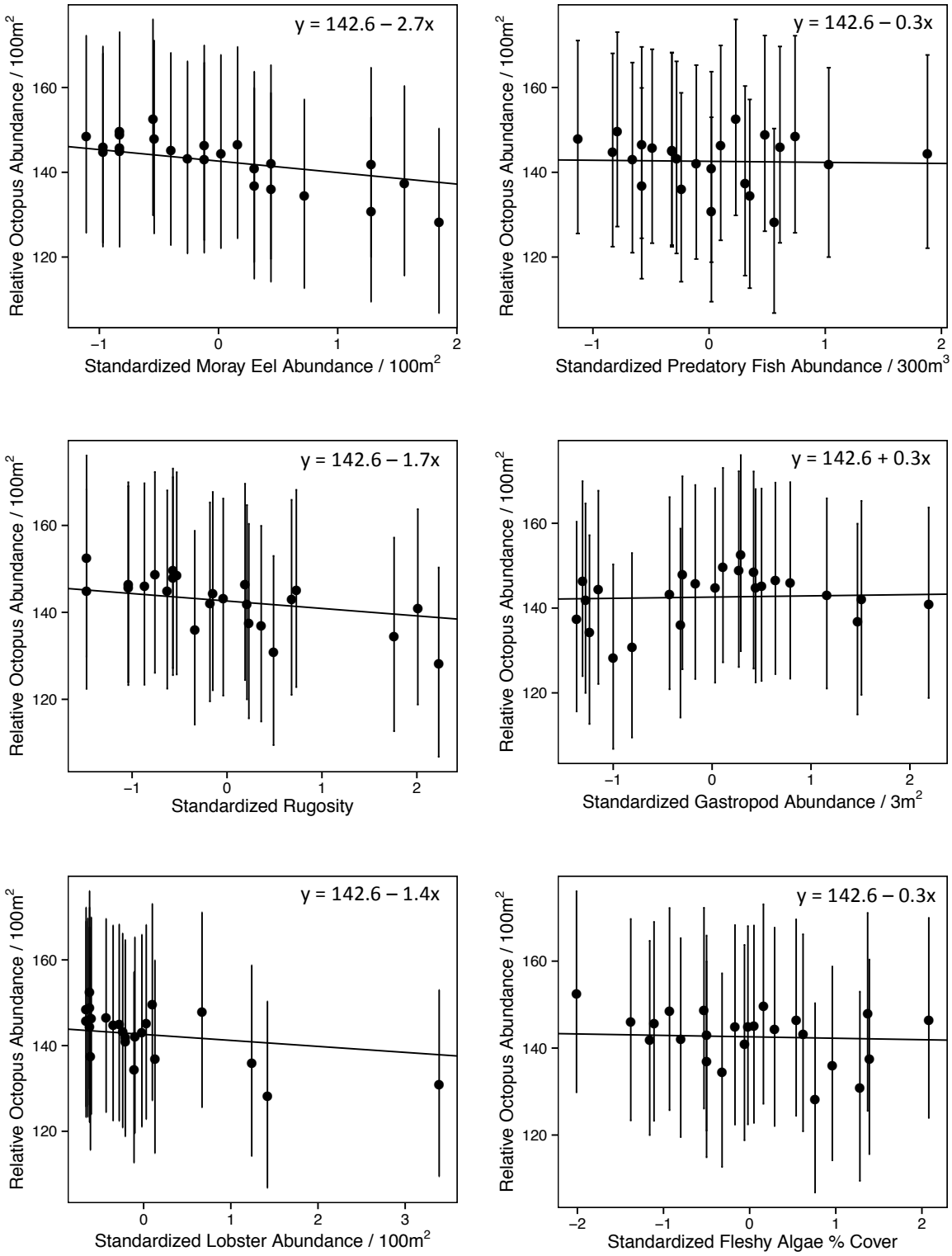

Figure 2.4. Mean relative octopus abundance (with 95% confidence intervals) against standardized (standard normal deviates) environmental covariates for 2013.

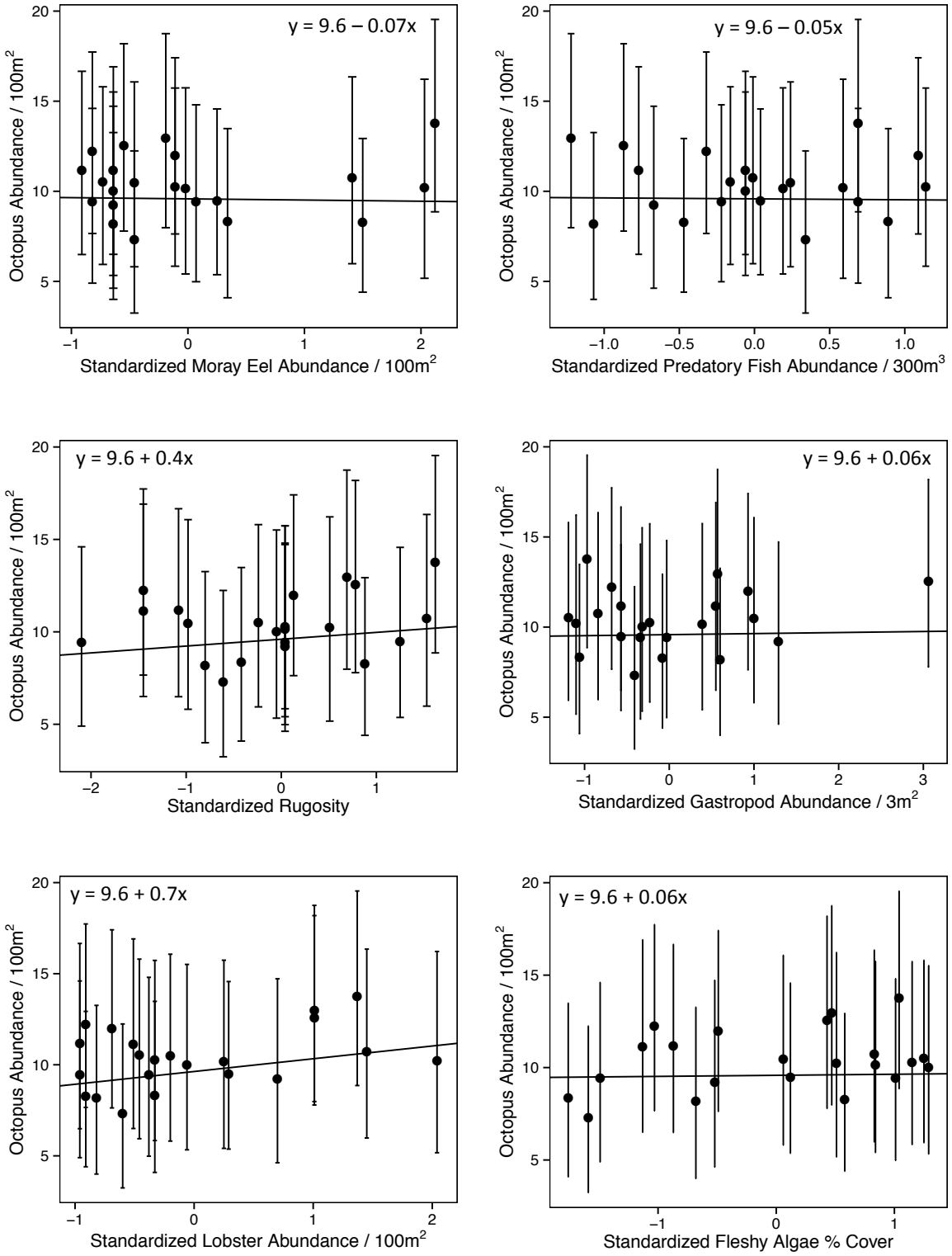

Figure 2.5. Mean octopus abundance (with 95% confidence intervals) against standardized (standard normal deviates) environmental covariates for 2014.

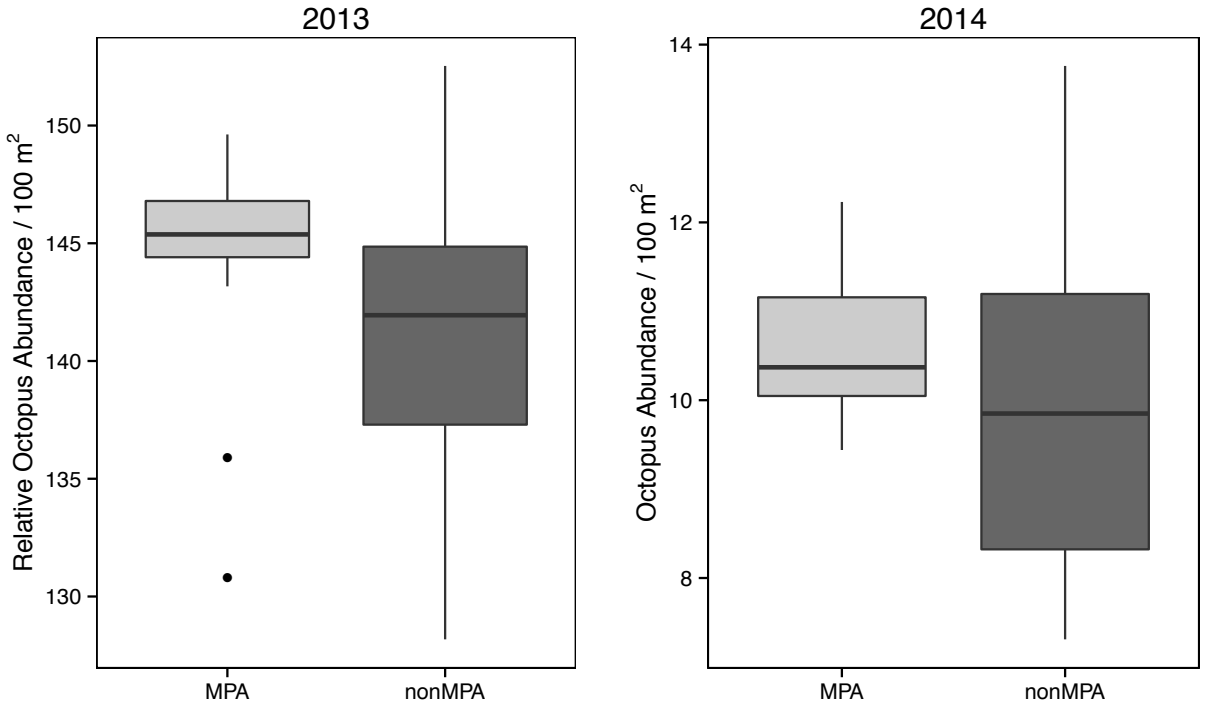

Figure 2.6. Model-averaged octopus abundance for MPA and nonMPA areas for 2013 and 2014. For 2013, relative octopus abundance values, rather than absolute octopus abundance are presented (see text for details).

CHAPTER 3

Activity space and movement patterns of *Octopus bimaculatus* around Santa Catalina Island, CA

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* 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 ± SD) and continuous movement was tracked for 20.8 ± 5.0 hours (mean ± SD) for each animal. *O. bimaculatus* occupied an activity space of approximately 6000 ± 3000 km^2 (mean ± 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 are highly variable for this species, both within and between individual octopuses. *O. bimaculatus* is 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.

INTRODUCTION

The behavior and ecology of top predators can substantially influence marine communities. Predator pressure is so high in many marine communities that the removal of predators can fundamentally change ecosystem structure and function (Duffy and Hay 2001, Barbosa and Castellanos 2005, Heithaus et al. 2008). The impacts of these predators are influenced by a number of physical, biological, ecological, and behavioral processes. The combined effect of scale, duration, and frequency of predator movement is perhaps the most important behavioral process (Swingland and Greenwood 1983). One of the main reasons why animals, and in particular predators, move is to find food. Therefore, 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 (Schmitt 1987, Rodhouse and Nigmatullin 1996, Ambrose 1986). It is thought that resource distribution strongly dictates octopus spatial movement,

but that the patterns and timing of movement are influenced by primarily by predation risk (Mather and O'Dor 1991). The cognitive abilities of octopuses in the lab have been well established, but very few researchers have explored these behaviors in a natural setting (Mather 1995, Hanlon and Messenger 1996). 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, Keiffer and Colgan 1992). Because octopuses are cryptic, rare, and often nocturnal, our understanding of octopus movement is rooted in our understanding of their patterns of shelter use. Three things are critical to our understanding of octopus movement: 1) den fidelity, 2) foraging behavior, and 3) home range or activity space.

Octopuses inhabit dens, but the duration of stay in a single den can be highly variable within a species or population, and can range from a few days to a few months (*Octopus cyanea*: Yarnall 1969, Forsythe and Hanlon 1997, Ivey 2007; *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 (Mather 1982, Iribarne 1990, Voight 1992). In habitats where dens are not limiting, other factors such as predation risk likely dictate movement to another shelter (Ambrose 1982, Hartwick et al. 1984, Forsythe and Hanlon 1997).

Octopuses leave their dens primarily to forage. Like, den fidelity, the duration of foraging bouts is also highly variable 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 (Mather 1991b, a, Mather and O'Dor 1991, Forsythe and Hanlon 1997). They are 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 (Yarnall 1969, Forsythe and Hanlon 1997, Ivey 2007, Leite et al. 2009).

Home range is difficult to measure in octopuses. They are not territorial and thus do not maintain even spacing; neither do they aggregate, unless while mating (Mather 1982, Forsythe and Hanlon 1997, Huffard 2007). 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. Current estimates methods range from 250 m^2 to 50,000 m^2 for *Enteroctopus dofleini* (Mather et al. 1985, Scheel and Bisson 2012), 100 m^2 to 2000 m^2 for *O. cyanea* (Yarnall 1969, Forsythe and Hanlon 1997, Ivey 2007), and 100 m^2 to 4000 m^2 for *O. vulgaris* (Kayes 1973, Mather and O'Dor 1991). With the exception of the few studies that used long-term acoustic tracking, these areas are likely underestimates.

Very recent improvements in tagging technology have allowed for the remote tracking of octopuses. This methodology had been 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 octopuses, 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 by members of some species (Rigby and Sakurai 2005) and the use of depth contours to navigate by members of other species (Scheel and Bisson 2012). Thus, use of acoustic tags provides a promising means for exploring further 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 small octopuses in complex habitats, and to gather preliminary data on the activity space, displacement distances, activity patterns, and demographic correlates of *O. bimaculatus*.

METHODS

Study Area. This study was conducted on Santa Catalina Island, which is located approximately 20 miles west of Los Angeles, CA . The study area was approximately 4 km^2 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. These areas were selected to take advantage of pre-existing heterogeneity in octopus predator and competitor densities.

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, 1986). Dens do not seem to limit the populations of *O. bimaculatus* (Ambrose 1982). Previous research has determined that *O. bimaculatus* individuals can occupy dens for 1 to 5 months, and dens can often be identified by a collection of prey remains, called middens, outside the den entrance (Ambrose 1982, Ambrose 1983).

Acoustic Tagging. Octopuses were caught by hand on SCUBA at various depths within the coastal rocky reef habitat around Isthmus Cove. Octopuses were found inside dens and extracted from the den by inserting fresh water from a syringe into the shelter until they because agitated enough to exit. Octopuses were then quickly grabbed by a diver and placed in a mesh collection bag. After capture, den location was marked with a buoy. Individuals were brought to the surface held in coolers filled with ambient seawater. Octopuses were transported back to the WEIS dock, weighed, measured, and sexed (Table 3.1). 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.) fixed with two sharpened nylon posts (Figure 3.1). The nylon posts were covered with sterile piercing needles, and the tag apparatus was inserted into the mantle cavity and the needles were pushed 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 bolts. 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 3.1). 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 on SCUBA into the den where they had been captured. Total time from capture to release was 76 ± 49 minutes (mean ± SD, N = 9 animals). This tagging method results in minimal changes to mobility and is not expected to significantly alter behavior of the animal (Ivey 2007).

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 receiver with a hull-mounted directional hydrophone and recorded using a hand-held GPS unit (Garmin 72H). The mean (± 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. 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 3.1). Due to weather conditions and animal location, daily locations were recorded for a 9th individual but the animal was not tracked for a 24-hour period.

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. The activity space area of each octopus was calculated in four ways. First, area was calculated using both the continuous tracking locations and the daily position locations. Second, area was calculated using only the continuous tracking locations. Animals tracked with the 12-to-12 method (N=5), area was calculated for each 12-hour tracking period separately. Area for animals tracked using the 8-to-8 method (N=3) was calculated using the full 24-hour set of location positions. Third, to allow for comparisons across individuals given that not every octopus was tracked in the same way, tracking of each octopus was divided in to 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. Third, differences in activity space were assessed for localities recorded during the day versus at night. Continuous tracks were broken up into day, night, and crepuscular (from one hour before to one hour after sunrise and sunset) time periods, after which 95% bbKUDs were calculated for each animal during each of these temporal blocks. Areas of activity were then examined for temporal differences in size with ANOVA.

The daily displacements of each animal were also calculated using only the daily position locations assess den fidelity. One 1200 and 2400 point was selected from the continuous tracks to be included in the bbKUD calculation. The overall length of the displacements was calculated and the maximum displacement was identified. Finally, to examine potential phenotypic correlates of activity space, relationships among size of the activity space and octopus weight, mantle length, sex, and habitat category (MPA vs. nonMPA) were analyzed using linear regression.

RESULTS

Tag Retention. A total of nine *O. bimaculatus* were tagged between August 5 and September 5, 2014 (Table 3.1). Of those, two tags fell off immediately, one tag remained on the animal for five days, two tags stayed on for the duration of each tag's battery life, and four tags were still active when the study ended (Table 3.2). Three of the tags that fell off of animals were recovered using a Vemco VUR 96 on SCUBA or snorkel. It is uncertain if the tags fell off or if the octopus pulled the tags out, but the nylon posts on the tag for one animal were broken, indicating this octopus likely pulled the tag out of its mantle.

Because it was not immediately apparent that tags had fallen off of two animals soon after deployment, we tracked these individuals 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 error and tracking precision for the tags. The third tag fell off after 5 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. Two animals that retained their tags throughout the study were relocated on SCUBA using a Vemco VUR96 to verify tag attachment approximately one week after deployment because the detected signal strengths were very low. One of the individuals 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 account 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 most other studies using this method (Ivey 2007, Scheel and Bisson 2012).

Position Error. Because continuous 24-hr tracks for two animals were completed prior to the determination that the tags had fallen off, these tracks were used to calculate the accuracy of the positional data. The tags were recovered less than 0.3 m from the buoy marking the initial capture and release location, implying that the octopus lost the tag 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 was 13 m, and thus any octopus displacement greater than 13 m was considered a true displacement.

Activity Space. Each of the 7 octopuses that kept their tags was tracked for up to 25 hours for a total of 125 tracking hours (Table 3.1). The mean (± SD) activity space for all octopuses using both continuous and daily locations was 6143.4 ± 3165.5 m^2 (Table 3.2, Figure 3.2). Total activity space was not correlated with hours (linear regression, $R^2 = 0.00015$, $p = 0.9817$) or days (linear regression, $R^2 = 0.0075$, $p = 0.85$) tracked, indicating that longer tracking duration did not result in larger measured areas and all octopus activity space areas are comparable regardless of tracking duration. The mean (± SD) activity space for octopuses tracked during the first non-contiguous 12-hour tracking period (12 PM to 12 AM) was 2872.4 ± 1156.2 m^2 (N = 3), and the mean (± SD) for octopus tracked for the second non-contiguous 12-hour period (12 AM to 12 PM) was 1918.8 ± 934.0 m^2 (N = 3) (Table 3.2). The mean (± SD) activity space for octopuses tracked for a continuous 24-hour period was 3250.9 ± 1631.2 m^2 (N = 3) (Table 3.2). The overall mean (± SD) activity space inhabited by octopuses for all 4-hour blocks of time was 1688.2 ± 440.8 m^2 For a breakdown of activity space sizes per 4-hour time block, see Table 3.3. 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 mean (± SD) track length for octopuses tracked during the first non-contiguous 12-hour tracking period (12 PM to 12 AM) (N = 3) was 609.0 ± 211.3 m, and the mean (± SD) for octopus tracked for the second non-contiguous 12-hour period (12 AM to 12 PM) (N = 3) was 545.6 ± 216.8 m (Table 3.4). The mean (± SD) track length for octopuses tracked for a continuous 24-hour period was 962.1 ± 548.7 m (N = 3). The overall mean (± SD) track length for each 4-hour block of time was 184.0 ± 113.0 m. For a breakdown of activity space sizes per 4-hour time block, see Table 3.4. 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, p = 0.84) or mantle length (linear regression, R^2 = 0.00025, p = 0.97), and there were no differences between sex ($t\text{-test}_{\text{two-tailed}}$, F = -0.51, *df* = 2.86, p = 0.65) or area (MPA vs. nonMPA) ($t\text{-test}_{\text{two-tailed}}$, F = -2.75, *df* = 3.57, p = 0.058) tracked. There was a significant positive relationship between mean 4-hour activity space size and octopus weight (linear regression, *df* = 5, r^2 = 0.9, p = 0.0038) and mantle length (linear regression, *df* = 5 , r^2 = 0.89, p = 0.005). There was no significant difference between mean 4-hour activity space size and octopus sex ($t\text{-test}_{\text{two-tailed}}$, F = 2.05, *df* = 20.1, p = 0.053) or MPA category ($t\text{-test}_{\text{two-tailed}}$, F = 1.46, *df* = 22.7, p = 0.16).

Activity Patterns. Mean (± SD) activity spaces for day, crepuscular, and night time periods were 1423.8 ± 778.4 m^2, 2131.4 ± 1738.4 m^2, and 1807.8 ± 1233.3 m^2, respectively. Activity space sizes within each time period were highly variable. Day activity space ranged from 256-2890 m^2, crepuscular activity space ranged from 420-3684 m^2, and night activity space ranged from 889-6268 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, F = 0.64, *df* = 2, p = 0.53).

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 m apart. 45 of 87 (51.7%) were greater than 13 m and were thus interpreted to reflect actual movement by an animal. The mean (± SD) total length of displacement calculated from the daily positions of each octopus was 232.1 ± 115.9 m (N = 45). The mean (± SD) maximum displacement was 59.5 ± 45.0 m.

DISCUSSION

O. bimaculatus is a highly 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 or environmental metrics of the octopuses, with the exception that larger animals inhabited larger activity spaces. The traits and metrics included sex, MPA vs. nonMPA area, and time of day (day, crepuscular, night). 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.

These results are presented with a few caveats. These estimations of activity space are likely an underestimate for several reasons. First, the daily positions only represent daily displacement, and not the path the octopus took to get form one location to the other. 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 (1 to 2 weeks). Since octopuses live 1 to 2 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 there are many surfaces for the sound to bounce off of, potentially providing inaccurate animal positions or weak signal strengths of transmitters, which could 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 because of deep depths and low visibility. Therefore the values presented here represent the displacement 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.

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 much 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. Data from Meisel et al. (2013) suggest that octopuses can become more nocturnal when exposed to diurnal predators. 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*). General octopus predator surveys completed in this area (see this dissertation, Chapter 4) revealed that *G. mordax* densities are much higher outside of the MPA, but these surveys were not completed in the exact locations that octopuses were tracked. There were no differences between the activity patterns of octopuses found inside vs. outside the MPA, but 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 may only be possible 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. 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 m^2. The calculated activity space or home range of *Octopus cyanea* varies from 1320 - 2016 m^2 over five days (Forsythe and Hanlon 1997) to 2151 m^2 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 m^2 over 12.9 days inhabited by *O. bimaculatus*. 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 Ivey (2007) and Mather et al. (1985) used the same methods as the present study and still found very small occupied 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, but these results demonstrate that this may not be accurate (Hochberg and Fields 1980). 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 (Yarnall 1969, Forsythe and Hanlon 1997, Ivey 2007). *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). It is possible 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. 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.

Octopuses moved to a new location 51.7% of the time, or about once every two days. This is a very large change from values previously reported for this species in this area. Ambrose (1982) found that *O. bimaculatus* on Catalina Island remained in the same den for 1 to 5 months. This apparent change in den residency is supported by several other observations. Ambrose (1984) used octopus middens primarily as a way to identify octopus dens. Midden piles are an indicator both of long-term den residency and consumption of prey items at the den rather than during a foraging bout (Ambrose 1983). However, in recent surveys (see this dissertation, Chapter 4) *O. bimaculatus* were rarely (< 5%) found with middens in front of their dens, and less than 2% of dens previously occupied by an octopus were found occupied on any subsequent visit. These data, in conjunction with the results of the present study, strongly indicate a behavioral shift in *O. bimaculatus* between the 1980s and present day. The cause of this behavioral shift remains unclear. This frequent den switching and high mobility of *O. bimaculatus* could be a result of changes in distribution and density of octopus prey, or of changes in the frequency or intensity of octopus predation. 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).

This frequent den switching could also be interpreted as an anti-predatory behavior. It is well known that predatory risk can influence prey behavior, and many animals can respond quickly and adaptively to changes in predation risk (Lima 1998). If this environment has temporal and unpredictable variation in predation risk, octopuses could increase their anti-predator behavior in certain situations. The Predation Risk Allocation Hypothesis (Lima and Bednekoff 1999) discusses the trade-off between foraging and vigilance and predicts that animals should engage in the highest amount of anti-predator behavior when predation risk is high but brief and infrequent. This hypothesis also emphasizes that anti-predator behavior is influenced by a broad temporal context rather than specific predatory encounters. If increased den switching is a response to increased predation, then this hypothesis predicts that octopuses are encountering a high number of predators but at infrequent and unpredictable times. Since the original surveys were completed in the 1980s, the Blue Cavern Marine Protected Area (BCMPA) has been established, which has resulted in an increase in certain octopus predators within the BCMPA, namely those that are recreationally fished. This could have altered the predation risk for *O. bimaculatus* and resulted in increased mobility and den switching. It is also possible that the local visual predators, like kelp bass (*Paralabrax clathratus*), California sheephead fish (*Semicossyphus pulcher*), and the Pacific harbor seal (*Phoca vitulina*) have learned to recognize and target octopus midden piles, driving octopuses to either consume prey away from a centralized den or move between dens frequently (Dr. Richard Ambrose, personal communication). While more research is needed to tease apart these hypotheses, it is clear that some change in the local environment has elicited a behavior change in *O. bimaculatus*.

In order to achieve both the long-term and continuous data gathered with active acoustic telemetry and the fine-scale movement data gathered with snorkeling, octopuses should be tracked with a combination of passive and active acoustic telemetry with a strategically placed acoustic receiver network. If acoustic receivers are placed in high enough densities *in situ*, it is possible to identify periods of rest and movement, as well as habitat use, site fidelity, and home range (Meyer et al. 2000, Lowe et al. 2003, Scheel and Bisson 2012). Applying this methodology to *O. bimaculatus* would address many of the questions about their movement and spatial behavior unable to be addressed presently.

Conclusions. The high mobility of *O. bimaculatus* could have significant implications for the kelp forest community on Santa Catalina Island, CA. *O. bimaculatus* can have a significant impact on the abundance and diversity of its prey, and increased movement could expand the predatory range of this species and thus the octopus's encounter rate of certain types of prey. This study reports the successful acoustic tagging and tracking of the smallest octopuses species to date, and opens the possibility of gathering movement data for many octopus species around the world. These types of data are crucial if we are to understand what environmental factors are influencing 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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TABLES

Table 3.1. 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 ± 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 (± SD)	**7.7 (± 4.3)**	**5 M:4 F**	**701 (± 235)**	**9.9 (± 1.4)**		**12.9 (± 5.6)**		**20.8 (± 5.0)**

Table 3.2. Activity space sizes in m^2. 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 (± SD)	**2872. 43 (± 1156.17)**	**1918.78 (± 933.95)**	**3250.85 (± 1631.24)**	**6143.36 (± 3165.53)**	**105 (± 50.64)**

Table 3.3 Activity space sizes in m^2 for each 4-hour time block for each octopus. Octo ID is the letter assigned to each tracked octopus. The mean ± standard deviation (SD) activity space size in m^2 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 (± SD)
C							**1383.09**
	1020.67	819.06	2309.53	-	-	-	**(± 808.63)**
D							**1529.40**
	1359.84	3746.41	1743.88	884.22	667.39	774.68	**(± 1159.21)**
E							**1667.78**
	-	1823.87	922.79	1149.40	2458.11	1984.71	**(± 627.13)**
F							**1266.19**
	655.37	1270.91	1417.20	968.26	2356.58	928.84	**(± 597.90)**
G							**990.24**
	-	-	1565.13	428.36	1178.15	789.34	**(± 490.54)**
I							**3003.75**
	1576.10	2282.16	2550.99	5871.08	4428.72	1313.43	**(± 1781.75)**
Mean (± SD)	**1152.99 (± 402.88)**	**1988.48 (± 1127.62)**	**1751.59 (± 597.31)**	**1860.26 (± 2257.80)**	**2217.79 (± 1453.43)**	**1158.20 (± 510.63)**	

Table 3.4. 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 ± 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 (± SD)
C							**180.24**
	113.44	149.20	278.09	-	-	-	**(± 86.60)**
D							**194.28**
	172.42	378.19	275.36	129.60	93.72	116.41	**(± 110.67)**
E							**209.14**
	-	244.58	125.87	204.94	260.51	209.79	**(± 52.07)**
F							**126.81**
	78.40	103.18	157.18	139.15	208.21	74.76	**(± 51.60)**
G							**119.32**
	-	-	164.63	79.08	177.99	55.59	**(± 61.04)**
I							**255.04**
	97.54	129.02	287.62	391.41	558.46	66.17	**(± 193.95)**
Mean (± SD)	**115.45 (± 40.59)**	**200.83 (± 112.61)**	**214.79 (± 73.10)**	**188.84 (± 121.78)**	**259.78 (± 177.58)**	**104.55 (± 63.19)**	

FIGURES

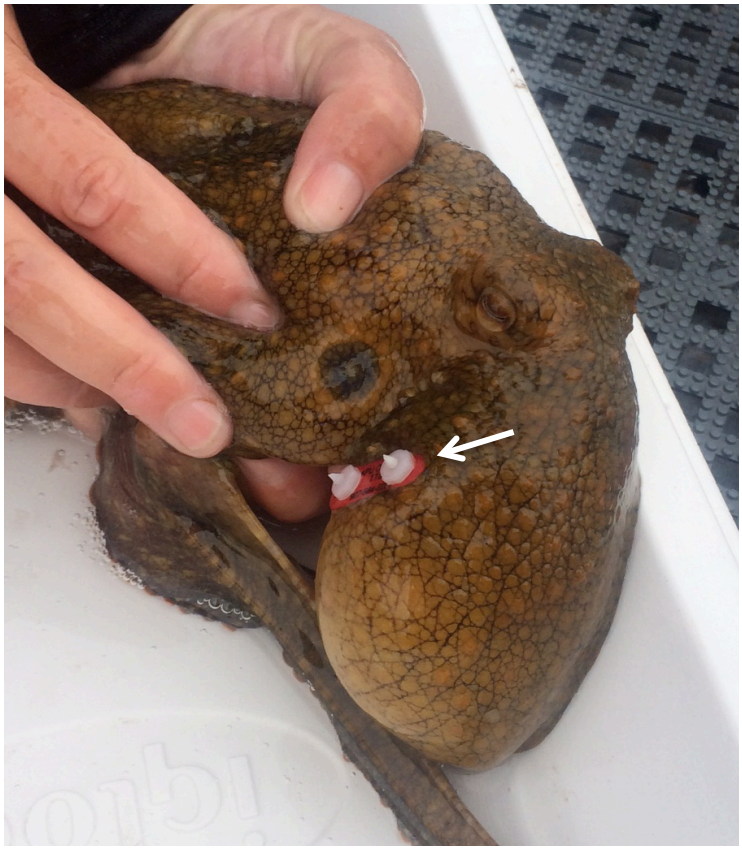

Figure 3.1. Photo of a tagged octopus. The modified Peterson disk with attached acoustic transmitter is inside the mantle of the octopus, while the Floy disk backplate and closures (indicated by the arrow) are on the outside of the animal.

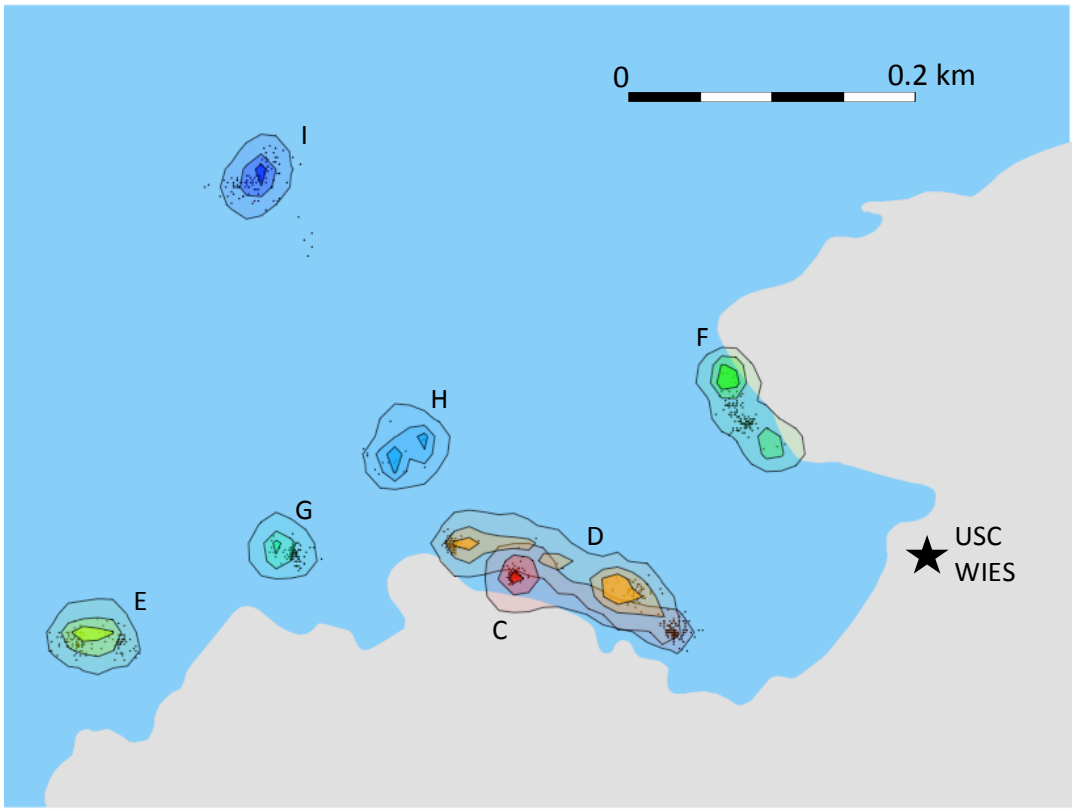

Figure 3.2. Map of the seven successfully tagged and tracked octopuses. Each color represents the estimated activity spaces of each octopus (C = red, D = orange, E = yellow, F = green, G = teal, H = light blue, I = dark blue). The outer circle of each octopus's activity space represents the 95% Kernel Utilization Distribution (KUD), 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% KUD, respectively.

CHAPTER 4

Differences in octopus diet between marine protected area and non-marine protected area sites

ABSTRACT

Anthropogenic impacts on marine environments can be far-reaching and variable, and in an effort to mitigate these impacts marine protected areas (MPAs) have been established globally. MPAs, and the heterogeneity caused by their establishment, can affect species either directly or indirectly. While direct effects are evident quickly, indirect effects are not often evident until years or decades after the disturbance. Indirect effects on marine food webs can be revealed in the diet of generalist predators. Octopuses are ubiquitous generalist predators in coastal marine ecosystems, and their diet is a reflection of both octopus preference and prey availability, therefore their diet could reflect changes in prey availability in response to MPA establishment. Octopuses (*Octopus bimaculatus*) and invertebrate prey species were collected around Santa Catalina Island, CA in the summer of 2012, 2013, and 2014 and muscle tissues were analyzed for $\delta^{13}C$ and $\delta^{15}N$. The $\delta^{13}C$ and $\delta^{15}N$ signature of octopuses caught within the MPA area and the nonMPA area were compared within diet space. Estimated contribution of prey species to octopus diet was calculated using a Bayesian mixing model. Octopuses caught in MPA areas had significantly different isotopic signatures than octopuses caught in nonMPA areas in 2012 and 2013 but not 2014. Prey contributions to diet were highly variable between areas and years. Bivalves were a consistent contributor to MPA octopus diet, and the large snail *Megastrea undosa* made up a relatively large proportion of the diet of octopuses from all areas and years. These results are contrary to previous work done on this species in this area, suggesting there has been a shift in octopus diet over the last thee decades. These results suggest octopus diet could be responding to changes in their immediate community. To fully understand the impact of anthropogenic change on marine environments we must assess changes in the entire community and the interactions that drive community function.

INTRODUCTION

Anthropogenic use of marine ecosystems is far reaching and variable, and can result in alteration and over-exploitation of the marine environment (Jackson et al. 2001). In response, marine protected areas (MPAs) have been established globally to protect and restore species, fisheries, habitats, and coastal communities (Agardy 1997, Sala et al. 2002, Day et al. 2012, Fox et al. 2012). MPAs can affect species both directly and indirectly. Species targeted either by commercial or recreational fisheries often see the most immediate and prevalent effects, including increased organism size and fecundity, and population size and density (Lester et al. 2009). Studies addressing the effectiveness and consequences of MPA establishment primarily focus on the abundance of these targeted species, with little attention paid to the indirect effects on non-targeted fish and invertebrates. Indirect effects are more varied and difficult to predict, and can take decades to reveal themselves (Micheli et al. 2004, Babcock et al. 2010). These effects can include changes in the abundances or behavior of non-targeted species. However, because of the unpredictability and lag in time before the effects can be measured, their causes and impacts on the environment are not well understood.

The majority of documented indirect effects have been trophic effects, typically resulting in a decrease in grazing invertebrates as the populations of exploited predators recovers (Pinnegar et al.

2000, Micheli et al. 2004, Babcock et al. 2010). For example, in areas where lobster fishing was restricted in New Zealand, sea urchins (a primary prey item of lobsters) significantly decreased, with a corresponding increase in kelp (Cole et al. 1990). Similar responses have been seen in Tasmania (Edgar and Barrett 1999, Barrett et al. 2009) and California (Shears and Babcock 2002, Lafferty 2004). Babcock et al. (2010) found that on average it took 13 years for indirect effects to appear, with significant lags between an increase in abundance of predators and the resulting decrease in abundance of prey (Shears and Babcock 2003, Babcock et al. 2010). Still, these tropic relationships and resulting changes become less defined because many predators consume prey on several trophic levels. Additional factors, such as habitat association and larval recruitment, may also contribute to the variability in species' responses to changes in their environment, like the establishment of marine protected areas (Alexander et al. 2014).

Changes in the size and abundance of species in a human-altered community could result in changes in the availability or distribution of prey, which could indirectly change exposure of non-targeted predators to prey items. If non-targeted predators are being affected, these changes should be apparent in their diet. Octopuses are voracious generalist predators that can have significant impacts on the prey abundance and diversity in their habitat (Ambrose 1986, Rodhouse and Nigmatullin 1996). Because they are difficult to find and to study, they are typically overlooked when assessing the effectiveness of MPAs, even though their life history strategy results in the potential large population fluctuations in response to environmental changes (Boyle and Boletzky 1996). This combination of high predatory pressure by octopuses on their prey populations with this inherent variation in octopus populations necessitate a strong understanding of octopus ecology and behavior in order to fully understand their impact on and interactions with marine communities, especially in our assessment of the effectiveness of MPAs.

Assessing the impact of MPAs and the potential indirect effects of MPA establishment on octopuses requires detailed knowledge of the diets of these animals. Since it is very rare to witness an octopus predatory event, traditional methods of assessing octopus diet have primarily consisted of examining the midden remains outside of long-term octopus dens (Ambrose 1984, Mather 1991b, Vincent et al. 1998, Scheel and Anderson 2012). Most octopus species capture prey and return to a semi-permanent den to consume their meal. The remains of these prey items, which usually include gastropod and bivalve shells and crustacean carapaces, are placed at the den opening. However, this method of assessing octopus diet is limited. Octopuses do not carry all of their prey back to their den, meaning midden piles are only a subsample of an individual octopus's diet (Mather 1991a). Additionally, many of the prey remains can be carried off by hermit crabs or shifted by water movement (Ambrose 1983). While examining midden remains highlights patterns in octopus diet, it is by no means a comprehensive analysis of all types of prey octopuses can consume. Some studies have examined stomach contents, but often prey are too digested or torn to identify (Rodhouse and Nigmatullin 1996, Grubert et al. 1999). Controlled lab studies can reveal prey preference and maximum prey consumption rates, but again can't elucidate the actual dietary composition in the wild.

One solution to these problems is the implementation of diet assessment techniques that do not require the acquisition and identification of individual prey items. One technique that has been widely used in other systems and species, but has only recently been applied to understanding octopus foraging ecology, is stable isotope analysis (Post 2002, Fry 2006). The isotopic signature of biogenic material generally reflects the isotopic composition of consumed prey items. The combined

analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes allows for the resolution of direct and indirect food web interactions within an ecosystem (Fry 2006). Primary producers differ in $\delta^{13}C$ as a result of different photosynthetic pathways coupled with local abiotic variation. These differences are reflected in consumers with a very small (~1‰) enrichment of ^{13}C, and thus carbon can be used to isolate sources of organic material (Wada et al. 1991). $\delta^{15}N$ can determine consumer trophic position since there is a 3-4‰ per trophic level enrichment as you move up the food web (Fry 1988, Wada et al. 1991). This technique can elucidate patterns in diet that other techniques cannot, especially for cryptic foragers like octopuses.

Stable isotope analyses has primarily been applied to cephalopods that live in habits that are inaccessible by humans, like the deep sea and Antarctic waters, and reconstruction of food webs has to be done by inference rather than observation. In these communities, stable isotope analysis has revealed new food web connections and trophic variability that stomach content studies had not detected (Cherel and Hobson 2005). $\delta^{15}N$ values have revealed that some larger species of cephalopod can span several trophic levels and exhibit ontogenetic and size shifts in trophic level (Cherel et al. 2009a, Cherel et al. 2009b, Chouvelon et al. 2011). The range of $\delta^{13}C$ values is variable, and difficult to interpret without also analyzing potential prey species, which is not always possible (Cherel et al. 2009b). On Santa Catalina Island in southern California there is a long-established and well-monitored MPA where octopuses are not directly fished but their predators are, providing an ideal setup to examine the indirect effects of MPA establishment on octopus diet. Additionally, the diet of the benthic octopus *Octopus bimaculatus* has been assessed in this area using midden analysis in a prior study completed before the establishment of the MPA, providing a possible baseline of octopus diet (Ambrose 1984). This study tested the hypothesis that *O. bimaculatus* in MPA areas have a different diet than *O. bimaculatus* in non-MPA areas using carbon and nitrogen stable isotope analysis.

METHODS

Study Site. This study was conducted on Santa Catalina Island, which is an island located approximately 20 miles west of Los Angeles, CA. All sites were 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). Sites were located 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. The CMSCSMR was established in the mid-1980s and currently covers 0.206 km^2. No take of any marine organism beyond approved scientific purposes is permitted. These restrictions are monitored and enforced by the California Department of Fish and Wildlife (CDFW), local lifeguards, WIES staff, and research scientists. Outside the BCSMCA, hereafter referred to as the nonMPA area, recreational and commercial fishing of finfish and shellfish are allowed. 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.

Study Species. *Octopus bimaculatus* is a common octopus species found subtidally from Point Conception, CA to Baja California, Mexico. It is distinguished from it's sister sympatic species, *Octopus bimaculoides*, by egg size (*O. bimaculatus* eggs are smaller than *O. bimaculoides*), hatchling development (*O. bimaculatus* hatchlings are planktonic and *O. bimaculoides* hatchlings are benthic), and pattern or blue color within its oscellus (Ambrose 1981). Mating occurs year round

but peaks in mid-summer (Ambrose 1988). *O. bimaculatus* consumes a wide variety of invertebrate prey items and can affect the abundance and diversity of prey in their environment (Ambrose 1984, 1986). Dens do not seem to limit the populations of *O. bimaculatus* (Ambrose 1982).

Collection. *O. bimaculatus* and prey species including common snails, bivalves, and crabs were collected. All species were collected following standards set by the California Department of Fish and Wildlife under Scientific Collection Permit #11825. Octopuses were collected on SCUBA during May-August of 2012, 2013, and 2014. Octopuses were found during they day in their dens and extracted by squirting fresh water towards the back of their dens until they emerged. They were then grabbed by hand and placed in a collection bag. They were kept at the Wrigley Institute for Environmental Studies (WIES) in 1.75 m^3 tubs with flow-through sea water. Each octopus was kept in a separate 12 inch mesh cube with a piece of PVC pipe for shelter and fed shoreline crabs (*Pachygrapsus crassipes*) daily. Some octopuses participated in a behavioral trial prior to tissue sampling, but no octopus was kept in captivity longer than 3 days before a tissue sample was taken for stable isotope analysis. Muscle tissue has one of the slowest tissue turnover rates (typically > 14 days) (Hawkins 1985, Watanabe et al. 2005, Cabanellas-Reboredo et al. 2009), so it is unlikely that this brief period of captivity and controlled feeding altered the isotopic signature of the sampled muscle tissue.

Prey items were collected on SCUBA in the same areas where octopuses were collected. Potential prey items were determined based on the choice experiments and diet determination in Ambrose (1982). Snail species were collected in MPA and non-MPA areas and included *Megastraea undosa*, *Ocenebra* sp., *Norrisia norrisii*, *Tegula aureotincta*, and *Tegula eiseni*. Some bivalve and crab species were difficult to find or limited by substrate type, and thus are not equally represented throughout the whole study area. The whole animal was frozen in a – 80 °C freezer, and then transported on dry ice back to UC Berkeley where it was stored in a – 20 °C freezer.

Tissue extraction. All octopus tissue was collected at the USC WIES. Octopuses were weighed and photographed prior to tissue extraction. Octopuses were then anesthetized in a 7% $MgCl_2$ solution mixed in a 1:1 ratio with seawater (Messenger et al. 1985, Estefanell et al. 2011). An octopus was considered fully anesthetized once its color had mostly blanched, the suckers were non-responsive, and the breathing rate had slowed down, typically within 6-8 minutes. Larger octopuses took longer to meet these criteria. During this period, sex was determined by looking for the presence of a ligula and hectocotylus on the third right arm (male sex characteristics), the mantle length was measured, and notes were made about missing arms and amount of regeneration. These data were used to ensure that no octopus was captured and sampled more than once. Once the animal was fully anesthetized, the distal third of the second left arm was removed with a clean scalpel and immediately placed in a – 80 °C freezer. If the second left arm was not available, the third left was taken. Octopuses are able to regenerate their arms and frequently lose arms in the wild, therefore the removal of arms did not introduce an uncommon injury to these individuals (Lange 1920, Alupay 2013, Fossati et al. 2013, Hofmeister, Personal Observation). Immediately following the removal of the arm, the octopus was transferred to a container with clean seawater and monitored until it resumed pre-surgery behavior, color, and breathing rate. Octopuses were transferred back to the individual mesh cubes and fed a crab, and an octopus was not released until it had eaten at least one crab. Octopuses were released on SCUBA to the general area that they were collected approximately 24 hours after surgery. Frozen arms were transported on dry ice back to UC Berkeley where they were stored in a – 20 °C freezer.

Tissue preparation and analysis. All tissue preparation was performed at UC Berkeley. An approximately 1 cm^3 piece of muscle tissue was excised from each octopus arm. All prey items were measured prior to extraction and muscle tissue was excised using a clean scalpel. For large prey items, approximately 1 cm^3 piece of muscle tissue was excised for tissue preparation and stable isotope analysis. All tissue was dried in a freeze dryer for 72 hours and then ground with a mini bead beater into a powder. All octopus tissue and subset of the prey tissue went through a lipid extraction process (Cherel and Hobson 2005, Ruiz-Cooley et al. 2011). Typically, if the C:N ratio is above 2.5, the lipid content in the tissue is high enough that it could bias the carbon signature (Post et al. 2007). Preliminary analysis (from 2012 samples) revealed that the C:N ratio of many prey specimens fluctuated around this cutoff, and thus a small study was completed to determine the difference in carbon signature between samples that did and did not have their lipids extracted. A subsample of prey tissue was chosen from the 2013 and 2014 specimens to compare $\delta^{13}C$ and $\delta^{15}N$ values between lipid-extracted and non-lipid extracted samples. Only samples that had an excess of tissue were used. Lipids were extracted from both the octopus and the selected prey tissue by soaking the ground tissue in a 2:1 chloroform:methanol solution and agitated for 1 hour (Ruiz-Cooley et al. 2011). Samples were then centrifuged to and supernatant was removed. This was repeated twice, and samples were not rinsed. Samples were then dried in a desiccator for at least 24 hours.

All samples were weighed and placed in tin capsules (5 x 9 mm, Costech Analytical Technologies, Valencia, CA, USA) and weighed to 1.47 ± 0.32 μg (mean ± 1 SD). $\delta^{13}C$ and $\delta^{15}N$ were analyzed with elemental analyzer/continuous flow isotope ratio mass spectrometry at the Center for Stable Isotope Biogeochemistry at UC Berkeley using a CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime 100 Isotope Ratio Mass Spectrometer (IsoPrime, Cheadle, UK). Isotope ratios are reported using the standard δ notation $\delta^{h}X = [(R_{sample}/R_{standard}) - 1] \times 1000$ where X is the element, h is the high mass number, R is the high mass-to-low mass isotope ratio, $R_{standard}$ and is Vienna Pee Dee belemnite (VPDB) for carbon and air for nitrogen. Units are parts per thousand (per mil, ‰). Peach leaves (Standard Reference Material [SRM] No. 1547, standard deviation [SD] of $\delta^{13}C$ = 0.1‰ and $\delta^{15}N$ = 0.2‰) and bovine liver (SRM No. 1577, SD of both $\delta^{13}C$ and $\delta^{15}N$ was 0.1‰) as a calibration standards.

Because not all samples were treated with a lipid extraction, average differences between lipid-extracted (LE) and non-lipid extracted (non-LE) samples were applied to all non-lipid extracted samples (Table 1). If a species collected from both years was included, the difference between LE and non-LE samples across all years were averaged and applied to the remaining non-LE samples. If samples of a species from only one year were included in the LE study, the difference from that year was applied to all years. The LE difference from *P. crassipes* was applied to the crab species *H. parvifrons*, *Lophopanopeus* sp., and *P. taylori*.

Invertebrate and Predatory Fish Abundance. Invertebrate and fish abundance was measured in order to establish differences in these biotic variables between MPA and nonMPA areas, and to begin to identify variables that could affect disparities in octopus diet. Surveys were completed on SCUBA during May-August of 2012, 2013, and 2014 on Catalina Island, CA near the USC Wrigley Institute for Environmental Studies. Twelve 20m transects were established in the Blue Cavern MPA and twelve outside the MPA. Invertebrate density was quantified by placing 1 m^2 quadrat at 5m, 10m, and 15m along each transect. All visible invertebrates were counted and identified to species if possible. This was completed twice per transect during 2013, and once during 2012 and 2014. Crabs and bivalves were rarely seen during invertebrate surveys, and thus were not

included in the abundance analyses. Fish abundance was quantified in two ways. Water column fishes were measured by swimming along the 20m transect and counting the species and number of fish seen within a 5m wide by 20m long by 3m high volume. Care was taken to avoid counting fish that were either attracted or deterred from the diving activity. Only the kelp bass, *Paralabrax clathratus*, and the California sheephead, *Semicossyphus pulcher* were included as they are the two primary fish predators of octopuses. California moray eels, *Gymnothorax mordax*, were counted during timed bandwidth transects. Two SCUBA divers searched a 5m by 20m band for 30 minutes and recorded the number of morays encountered. Each type of survey was completed once per transect in 2012, and three times per transect in 2013 and 2014.

Statistical Analyses. All statistical analyses were completed in R (v. 12.15.3, R Core Team 2015) or JMP v.12. To determine if the carbon and nitrogen isotopic signatures of the octopuses and prey items differed between MPA and nonMPA areas, a two-tailed t-test was applied to each species or group within each year. To determine if the isotopic space of octopuses differed between MPA and nonMPA areas, a MANOVA was applied within each year. Because of limited sample sizes, all bivalve and crab species were combined into functional groups. Bivalve species included the mussel *Mytilus californianus* and the clam *Diplodonta orbella*. No bivalve species were collected outside the MPA. Because of this, diet determination within the MPA was completed with two datasets, one including bivalves and one excluding bivalves, in order to make the diets between MPA and non-MPA sites more comparable. Crab species included *Pachygrapsis crassipes*, *Pugettia producta*, *Herbstia parvifrons*, *Lophopanopeus* sp., *Paraxanthias taylori*, and *Cancer* sp., all of which are omnivorous (Light and Carlton 2007). No crab species were collected in 2014.

To estimate *O. bimaculatus*'s diet within each habitat (MPA vs. non-MPA) and year, percent contribution of each prey item to the diet using the stable isotope mixing model siar package v. 4.2 (Parnell et al. 2010) was calculated. The package siar estimates the probable contribution of each prey item to a predator's diet using Bayesian statistical inference. This method is used when the number of prey sources is greater than the number of isotopes + 1. Standard discrimination factors were used ($\Delta^{15}N$ = 3.0 **‰** and $\Delta^{13}C$ = 1.0 **‰** per trophic level; $\Delta^{15}N$ = 1.5 **‰** and $\Delta^{13}C$ = 0.5 **‰** for omnivores) (Post 2002), because experimentally determined discrimination factors for octopuses are not available (Gannes et al. 1997). Estimates were weighted by the concentrations of elemental carbon and nitrogen of each source (Phillips and Koch 2002). Uninformative priors based on the Dirichlet distribution (a generalized Beta distribution) were used to model each prey item as equally likely to contribute to the stable isotope composition of the consumer (Parnell et al. 2010). 1,000,000 simulations were performed with Markov chain Monte Carlo and 100,000 burnins (the initial simulations that were discarded due to variability) to generate estimates of source contributions to the diet (Parnell et al. 2010). The analyses of MPA octopus diet only used prey items collected from MPA sites, and the analyses of non-MPA octopus diet only used prey items collected from non-MPA sites to account for site differences in prey and source carbon. The same division of data was applied to analyses of octopus diet between years.

RESULTS

In general, octopuses exhibited a difference between MPA and nonMPA areas in diet along the carbon axis but not the nitrogen axis. Octopuses did not have significantly different $\delta^{15}N$ values between MPA and nonMPA areas in 2012 ($t\text{-test}_{(two\text{-}tailed)}$, p-value = 0.44), 2013 ($t\text{-test}_{(two\text{-}tailed)}$, p = 0.99), or 2014 ($t\text{-test}_{(two\text{-}tailed)}$, p = 0.65). Octopuses had significantly different $\delta^{13}C$ values between

MPA and nonMPA areas in 2012 (t-test$_{(two\text{-}tailed)}$, p-value < 0.0001) and 2013 (two-tailed t-test, p < 0.0001), but not in 2014 (t-test$_{(two\text{-}tailed)}$, p = 0.25) (Table 2). None of the invertebrate species or groups had significantly different $\delta^{15}N$ values except for *T. eiseni* in 2012 (t-test$_{(two\text{-}tailed)}$, p = 0.0003) which had higher $\delta^{15}N$ values in nonMPA areas, and none of the invertebrate species or groups had significantly different $\delta^{13}C$ values (Table 4.2, Figures 4.1 and 4.2).

In all years, octopuses in nonMPA areas had more enriched $\delta^{13}C$ values than those in nonMPA areas, although this difference was only significant in 2012 and 2013 (Table 4.2, Figures 4.2 and 4.3). When comparing the isotopic space, octopuses between MPA and nonMPA areas were significantly different in 2012 (manova, $F_{2,13}$ = 9.09, *df* = 1, p = 0.0034) and 2013 (manova, $F_{2,58}$ = 17.11, *df* = 1, p < 0.0001), but not in 2014 (manova, $F_{2,13}$ = 0.38, *df* = 1, p = 0.69) (Figure 4.3).

Qualitatively, the Bayesian mixing model showed differences in estimated prey contribution (Figures 4.4 and 4.5). Bivalves, *M. undosa*, and *Ocenebra* sp. made up the largest components of MPA octopus diet across all years, and *M. undosa* and *Ocenebra* sp. made up the largest component of nonMPA octopus diet and MPA octopus diet analyzed without bivalves (Figure 4.4). In 2012, bivalves made up the largest portion of MPA octopus diets (Figure 4.5). The snail *T. eiseni* made up the largest portion of nonMPA octopus diets in 2012, but the proportions shifted to favor *M. undosa* in 2013. In 2013, bivalves made up the largest portion of MPA octopus diets, followed by *M. undosa* and *Ocenebra* sp., but when analyzed without bivalves, the model determined *M. undosa* and *Ocenebra* sp. contributed a larger proportion toward octopus dietary composition than with bivalves, though this was presented with wide 95% confidence intervals. In 2013 *M. undosa* was the majority contributor towards nonMPA octopus diet. In 2014, *M. undosa* was the largest contributor to MPA octopus diet analyzed both with, and without bivalves, although this difference was minimal relative to other prey items and most prey items made up relatively even proportions of 2014 MPA octopus diet. *M. undosa* and *Ocenebra* sp. were the largest contributing prey items toward nonMPA octopus diet, but the 95% confidence intervals were large (Figure 4.5).

The snail *T. eiseni* was the most abundant snail prey item (Figure 4.6) across all years. Within years, *Ocenebra* sp. had significantly higher abundances in MPA sites in 2012 (t-test$_{(two\text{-}tailed)}$, t = -2.32, p = 0.025) and 2013 (t-test$_{(two\text{-}tailed)}$, t = -4.02, p = 0.0004), but not 2014 (t-test$_{(two\text{-}tailed)}$, t = -1.21, p = 0.25). No other species had significantly different abundances between MPA and nonMPA sites within years [*M. undosa* (2012: t-test$_{(two\text{-}tailed)}$, t = -0.77, p = 0.44; 2013: t-test$_{(two\text{-}tailed)}$, t = 1.94, p = 0.060; 2014: t-test$_{(two\text{-}tailed)}$, t = 1.12, p = 0.28), *N. norrisii* (2012: t-test$_{(two\text{-}tailed)}$, t = 0.68, p = 0.50; 2013: t-test$_{(two\text{-}tailed)}$, t = -0.056, p = 0.96; 2014: t-test$_{(two\text{-}tailed)}$, t = 0.85, p = 0.41), *T. aureotincta* (2012: t-test$_{(two\text{-}tailed)}$, t = -1.39, p = 0.17; 2013: t-test$_{(two\text{-}tailed)}$, t = -1.47, p = 0.15; 2014: t-test$_{(two\text{-}tailed)}$, t = 0.96, p = 0.35), *T. eiseni* (2012: t-test$_{(two\text{-}tailed)}$, t = , p = ; 2013: t-test$_{(two\text{-}tailed)}$, t = , p = ; 2014: t-test$_{(two\text{-}tailed)}$, t = , p =)]. The kelp bass, *P. clathratus*, was the most abundant fish in both MPA and nonMPA areas. There were no significant differences in *P. clathratus* abundance between MPA and nonMPA areas in 2012 (t-test$_{(two\text{-}tailed)}$, t = -0.13, p = 0.90) or 2014 (t-test$_{(two\text{-}tailed)}$, t = 0, p = 1.0), but there were significantly more outside the MPA in 2013 (t-test$_{(two\text{-}tailed)}$, t = 3.38, p = 0.0012). In all years, there were significantly more California sheephead, *S. pulcher,* inside the MPA (2012: t-test$_{(two\text{-}tailed)}$, t = -3.74, p = 0.0017; 2013: t-test$_{(two\text{-}tailed)}$, t = -4.68, p < 0.0001; 2014: t-test$_{(two\text{-}tailed)}$, t = -3.92, p = 0.0003) and there were significantly more moray eels, *G. mordax*, outside the MPA (2012: t-test$_{(two\text{-}tailed)}$, t = 4.19, p = 0.0008; 2013: t-test$_{(two\text{-}tailed)}$, t = 2.99, p = 0.0045; 2014: t-test$_{(two\text{-}tailed)}$, t = 3.32, p = 0.0017) (Figure 4.7).

DISCUSSION

Octopus bimaculatus caught in MPA areas had significantly different $\delta^{13}C$ but not $\delta^{15}N$ signatures than octopuses caught in nonMPA areas in 2012 and 2013, but not 2014. This suggests that octopuses are consuming different prey items of the same trophic level, not from multiple trophic levels. Furthermore, the lack of difference between either the carbon or nitrogen signatures for any prey items between MPA and nonMPA areas (with the exception of $\delta^{15}N$ of *T. eiseni* in 2012) further supports the hypothesis that the differences in isotopic signature between these two groups of octopuses are due to differences in diet and not due to differences in the base carbon signatures of each area. Results from the mixing model determined the full range of prey *O. bimaculatus* actually consumed in the field, and revealed differences in diet between MPA and nonMPA octopuses. Bivalves are a large contributor to MPA octopus diet, with *M. undosa* and *Ocenebra* sp. making up smaller, but still relatively large, proportions. *M. undosa* is consistently consumed in large proportion by nonMPA octopuses, with *T. eiseni* and *Ocenebra* sp. consumed in smaller proportions. Invertebrate species with the highest abundances in the field were not correlated to the species that the octopuses consumed in the highest proportions. With the exception of *Ocenebra* sp. in 2012 and 2013, there were no significant differences in prey abundances between MPA and nonMPA areas, suggesting that the differences in octopus diet were not due to differences in prey availability, but another factor. Finally, there were significantly more moray eels, a nocturnal predator, outside the MPA, and significantly more California sheephead, a diurnal predator, inside the MPA. This variation in predator type and abundance could be a factor contributing to the variation in observed octopus diets.

These findings are presented with a few caveats. There are several components of this methodology that could impact these results. Lipids can affect $\delta^{13}C$ values and thus influence the interpretation of these signatures (Post et al. 2007). There are pros and cons to delipidifying tissue, but since the majority of cephalopod stable isotope studies extract lipids from tissue it was performed on octopus tissue in the present study. While it is possible that this procedure could have shifted the $\delta^{13}C$ signature of the octopuses, it does not affect the interpretation of the differences in octopus diet between MPA and nonMPA areas since relative differences between the two groups are what matters. Additionally, since lipid extraction was not performed on all prey samples, lipid corrections were estimated from some samples and applied to those not lipid-extracted. Therefore, these corrections may not be accurate. Furthermore, the lipid extraction methodology used in this study has been developed for cephalopods. A different methodology is typically used for crustaceans, and the cephalopod method may not have extracted all lipids from the crustacean tissue. However, these issues only apply to the interpretation of prey signatures, and do not affect the conclusion that octopuses found in MPA vs. nonMPA areas had different diets. Therefore, this difference stands regardless of any limitations or caveats in this study. Finally, there are limitations to the Bayesian mixing model. The model may have calculated equal likelihood probabilities for each prey item because too many sources were included in the analysis (Parnell et al. 2010). However, the mixing model estimates are more likely a result of natural variation in isotope data because high variation can also yield equal percent contributions to the diet (Parnell et al. 2010).

Differences in octopus diet between MPA and nonMPA areas could be due to several factors. Prey could vary in abundance, or the probability of octopuses encountering certain prey could be different. These differences could be caused by variability in abundance of other predators that eat the same prey items as octopuses, such as sea stars, California sheephead, lobsters, or predatory snails

(Engle 1979, Cowen 1986). Increases or decreases in these predators, either through direct or indirect effects of the MPA, could result in the decrease or increase of shared prey items. The resulting change in octopus diet from this variation in prey abundance would be evidence of an indirect effect of the establishment of the MPA on octopus predatory behavior. Alternatively, differences in octopus predators could affect the predatory behavior of octopuses. Current evidence supports that predatory pressure is one of the most significant factors influencing octopus behavior and populations (Aronson 1986, Ambrose 1988, Mather and O'Dor 1991, Leite et al. 2009a). The MPA in this study had higher abundances of the California moray eel, *Gymnothorax mordax*, a nocturnal octopus predator, whereas the nonMPA sites had higher abundances of the California sheephead fish, *Semicossyphus pulcher*, a diurnal octopus predator (Figure 4.7). It is possible that these differences in predator abundance could affect the daily activity patterns of octopuses on a localized scale. Furthermore, optimal foraging theory (OFT) predicts that patterns of foraging behavior are a result of the balance between predation risk, prey nutritional value, and prey handling time (Charnov 1976, McNamara and Houston 1985). Variability in predation risk could affect the time octopuses search for prey and could alter their prey choice (Mather and O'Dor 1991). Current evidence supports that octopuses are capable of this type of complex assessment (Mather 1995, Darmaillacq et al. 2014). Increased predation risk or variability in predation risk could influence whether octopuses consume a less-valuable prey item that took a shorter time to find, or continue searching for a rare but more valuable prey item. The nutritional values of the octopus prey items identified in this study are unknown, but other studies have determined that lipid digestibility and protein content may influence the value of prey to an octopus (Onthank and Cowles 2011). However, Onthank and Cowles (2011) found that *Octopus rubescens* prey choice was not predicted by OFT in lab, so prey choice in the field is likely influenced a complex combination of factors.

There are prey items present in *O. bimaculatus* diet that were not included in the stable isotope analyses due to difficulty collecting certain items, like clams and crabs. These unsampled species could be large contributors to the variation in octopus diet between the two areas. Ambrose (1984) found that *O. bimaculatus* on Catalina Island consumed 55 different prey items spanning 3 phyla by analyzing midden piles outside octopus dens. Furthermore, he discovered that octopus diet was not predicted by the interaction of prey abundance and octopus preference. Additionally, the invertebrate abundances presented here are limited and are likely an incomplete representation of all prey species available since octopuses are very mobile and can cover large areas in search of food. Octopuses are able to find and retrieve prey items from inside cracks and under rocks, and these types of habitats were not possible to survey without employing destructive techniques. These invertebrate surveys were completed during the day, and do not capture possible variation of nocturnal or crepuscular prey species, which could especially be a factor if octopuses are adjusting their behavior as a response to the abundance of their own diurnal or nocturnal predators. Finally, octopuses are known cannibals (Rodhouse and Nigmatullin 1996, Ibánez and Keyl 2010). It is not possible to estimate the contribution of cannibalism to an octopus's diet using stable isotope analysis. *Ocenebra* sp. have an isotopic signature similar to octopuses (Figure 4.1 and 4.2), and it is likely that the relatively high estimated contribution of *Ocenebra* sp. to octopus diets is a product of cannibalism, at least in part.

There is clear variability in octopus diet from year to year (Figure 4.5), which was expected based on the high levels of variability exhibited by octopuses in almost every facet of their behavior and population biology (Boyle and Boletzky 1996, Rodhouse and Nigmatullin 1996). Prey items

that contributed a large proportion of octopus diet in one year or one area did not necessarily contribute equally the following year, and there was no difference in octopus diet between MPA and nonMPA areas in 2014. This variation is likely due to a combination of the factors already discussed, as well as natural interannual variability in octopus populations (Ambrose 1988, Boyle and Boletzky 1996) and the variability of octopus predators and prey. 2014 may have experienced a different level of commercial fishing than in 2012 or 2013, or variations in oceanographic factors could have influenced the recruitment, growth, and/or abundance of octopuses and their prey, as invertebrate populations are highly influenced by oceanographic processes (Palmer et al. 1996, Botsford 2001). Furthermore, it is unknown if the differences in octopus diet between MPA and nonMPA areas in 2012 and 2013 are truly a response to the establishment of the MPA or if octopus diet has naturally wide variation throughout Catalina Island. Future studies should look at regional and population-level variation in *O. bimaculatus* diet to better understand the causes and consequences of this variation and its relationship to environmental change.

Some generalizations about the diet of *O. bimaculatus* can be made. The diet of *O. bimaculatus* in this area was quantified in the 1970s and 1980s prior to the establishment of the Blue Cavern MPA using midden analysis (Ambrose 1984). Ambrose found that the snail *T. aureotincta* was a primary component of octopus diets and made up a higher proportion of the diet than predicted by its abundance in the field, whereas the shells of *M. undosa* and *T. eiseni* were very rarely found in midden piles. In contrast, this study determined that *T. aureotincta* is a very small contributor to octopus diet is this area, and *M. undosa* makes up a large proportion of octopus diet in nearly every year and every site (Figure 4.5). Neither study found that either snail was very abundant in the field. However, the size of these prey items were not included in these analyses. *M. undosa* is very large relative to *T. eiseni* or *T. aureotincta*, and perhaps there is a correlation between prey biomass and diet prevalence rather than between prey abundance and diet. Finally, it has been demonstrated in many studies that octopuses show clear preference for crabs in the lab despite lower nutritional content and increased handling time, but this preference is not reflected in observed diet in the wild. It has been hypothesized that this observation may be biased because the remains of crabs are easily removed from midden piles by water movement (Ambrose 1983). However, results from the present study do not support this hypothesis; crabs do not make up a large portion of *O. bimaculatus* in these areas.

Conclusions. Octopuses are ubiquitous and voracious predators and their predatory behavior can have significant impacts on prey populations (Ambrose 1986, Rodhouse and Nigmatullin 1996). Additionally, octopuses serve as important prey items for many larger predators. Any impacts, either positive or negative, could have far reaching effects on the entire community. In areas where the establishment of an MPA directly addresses an active commercial octopus fishery, the impact on octopus populations is closely monitored (Leite et al. 2009b, Rodhouse et al. 2014). In areas where octopuses are not fished they are not monitored, even though their populations could fluctuate widely and could even be used as an indicator species if we can understand how their populations respond to biotic and abiotic changes in their environment (Boyle and Boletzky 1996, Rodhouse et al. 2014). The present study demonstrated that the establishment of an MPA could influence octopus diet and predatory behavior, but this type of analysis has not yet been commonly integrated into our evaluation of the impacts of MPAs on the immediate and surrounding marine communities. Our current assessment of both the impacts of fisheries and MPA effectiveness primarily addresses fluctuations in abundance of target species, but these types of measurements do

not paint a complete picture of ecosystem health or the functioning of ecosystem services. To fully understand the impact of anthropogenic change on marine environments and how we can best mitigate these changes, we must assess changes in the entire community and the interactions that drive community function.

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TABLES

Table 4.1. Lipid extraction (LE) differences applied to non-lipid extraction (non-LE) samples for %N, δ^{15}N, %C, and δ^{13}C. For *M. undosa*, *N. norrisii*, *T. eiseni*, *M. californianus*, and *Ocenebra* sp. differences were obtained from the average differences between individual samples subjected to both LE and non-LE treatments. "n-pair" refers to the number of samples pairs per species analyzed in this way. The mean ± standard deviation (SD) is presented. The differences obtained for *T. aureotincta*, *P. crassipes*, *Cancer* sp., and *P. producta* were generated from the average of all samples within that species given the LE treatment minus average of all samples within that species given the non LE treatment. "n-group" refers to the number of samples per species that underwent lipid extraction. Since the value presented represents the differences between the averages of two different groups, no standard deviation for this difference can be presented. The values generated from *P. crassipes* were applied to the Other Crabs group. The values generated from *M. californianus* were applied to the Other Bivalves group. The sample size for Other Crabs and Other Bivalves is listed as non-applicable as no individuals from these groups were subjected to lipid extraction.

Species	n - pair	n - group	Δ %N (± SD)	Δ δ^{15}N (± SD)	Δ %C (± SD)	Δ δ^{13}C (± SD)
M. undosa	6	-	0.88 (± 0.41)	0.36 (± 0.11)	0.44 (± 1.30)	0.93 (± 0.29)
N. norrisii	8	-	1.04 (± 0.35)	0.21 (± 0.06)	-0.33 (± 2.42)	1.66 (± 0.62)
T. aureotincta	-	20	-0.23	0.10	-4.06	-0.56
T. eiseni	2	-	0.71 (± 1.19)	0.25 (± 0.24)	1.01 (± 0.75)	0.55 (± 0.31)
Ocenebra sp.	3	-	0.62 (± 0.07)	0.13 (± 0.06)	-1.60 (± 3.54)	0.47 (± 0.10)
M. californianus	3	-	0.88 (± 0.06)	0.05 (± 0.06)	0.66 (± 0.54)	0.32 (± 0.14)
Other Bivalves	-	NA	0.88 (± 0.06)	0.05 (± 0.06)	0.66 (± 0.54)	0.32 (± 0.14)
P. crassipes	-	11	-0.03	0.09	-4.89	0.80
Cancer sp.	-	2	-1.84	1.99	-1.90	1.27
P. producta	-	9	2.47	0.76	2.84	2.53
Other Crabs	-	NA	-0.03	0.09	-4.89	0.80

Table 4.2. Mean ± standard deviation (SD) $\delta^{15}N$ and $\delta^{13}C$ of O. bimaculatus and its food sources from all years and areas. Bold indicates significant differences in $\delta^{15}N$ or $\delta^{13}C$ between areas within years. A Bonferroni corrected significance value of $p < 0.003$ was used to correct for 19 multiple comparisons of stable isotope data.

	MPA			nonMPA		
Animal	n	$\delta^{15}N$ ± SD (‰)	$\delta^{13}C$ ± SD (‰)	n	$\delta^{15}N$ ± SD (‰)	$\delta^{13}C$ ± SD (‰)
2012						
O. bimaculatus	12	14.6 ± 0.5	**-16.3 ± 0.9**	4	15.0 ± 0.4	**-14.3 ± 0.6**
Bivalves	6	10.2 ± 0.4	-19.7 ± 0.4	0	---	---
M. undosa	6	11.2 ± 0.4	-18.2 ± 1.3	6	11.4 ± 0.2	-17.1 ± 0.9
N. norrisii	7	11.3 ± 0.4	-13.7 ± 0.5	8	11.8 ± 0.4	-12.9 ± 0.6
T. aureotincta	8	11.2 ± 0.4	-14.7 ± 1.2	3	11.1 ± 0.2	-14.5 ± 0.8
T. eiseni	11	**11.6 ± 0.2**	-15.1 ± 0.3	4	**12.4 ± 0.2**	-15.2 ± 0.3
Crabs	11	13.6 ± 0.9	-14.2 ± 0.8	5	12.1 ± 1.0	-15.18 ± 1.0
Ocenebra sp.	6	14.6 ± 0.2	-15.7 ± 0.4	2	14.1 ± 1.6	-16.2 ± 0.2
2013						
O. bimaculatus	24	14.8 ± 0.3	**-16.9 ± 0.5**	37	14.8 ± 0.4	**-16.0 ± 0.5**
Bivalves	8	11.2 ± 1.1	-18.3 ± 0.2	0	---	---
M. undosa	5	11.4 ± 0.2	-17.1 ± 0.7	5	11.4 ± 0.3	-17.2 ± 0.9
N. norrisii	8	11.8 ± 0.6	-14.1 ± 0.7	7	11.8 ± 0.4	-14.5 ± 1.0
T. aureotincta	5	11.1 ± 0.3	-14.7 ± 0.8	5	11.4 ± 0.2	-13.7 ± 1.2
T. eiseni	5	12.2 ± 0.4	-14.9 ± 0.3	4	12.5 ± 0.1	-15.1 ± 0.4
Crabs	16	13.6 ± 1.0	-13.7 ± 1.1	6	13.7 ± 1.0	-14.2 ± 0.9
Ocenebra sp.	5	14.7 ± 0.2	-15.7 ± 0.3	5	14.5 ± 0.3	-15.4 ± 0.2
2014						
O. bimaculatus	5	14.6 ± 0.5	-16.9 ± 0.8	11	14.8 ± 0.6	-16.3 ± 0.7
Bivalves	2	12.1 ± 0.4	-18.3 ± 0.4	0	---	---
M. undosa	5	11.4 ± 0.6	-19.9 ± 1.4	5	11.4 ± 0.2	-17.0 ± 0.5
N. norrisii	5	12.0 ± 0.4	-14.5 ± 0.9	6	11.7 ± 0.4	-14.2 ± 0.8
T. aureotincta	5	10.8 ± 0.5	-15.7 ± 0.4	5	11.5 ± 0.4	-14.6 ± 0.7
T. eiseni	7	12.3 ± 0.5	-15.7 ± 0.6	6	12.2 ± 0.3	-15.1 ± 0.3
Crabs	0	---	---	0	---	---
Ocenebra sp.	6	14.9 ± 0.2	-15.7 ± 0.3	4	14.7 ± 0.3	-15.5 ± 0.3

n = number of individuals analyzed for $\delta^{15}N$ and $\delta^{13}C$ values

FIGURES

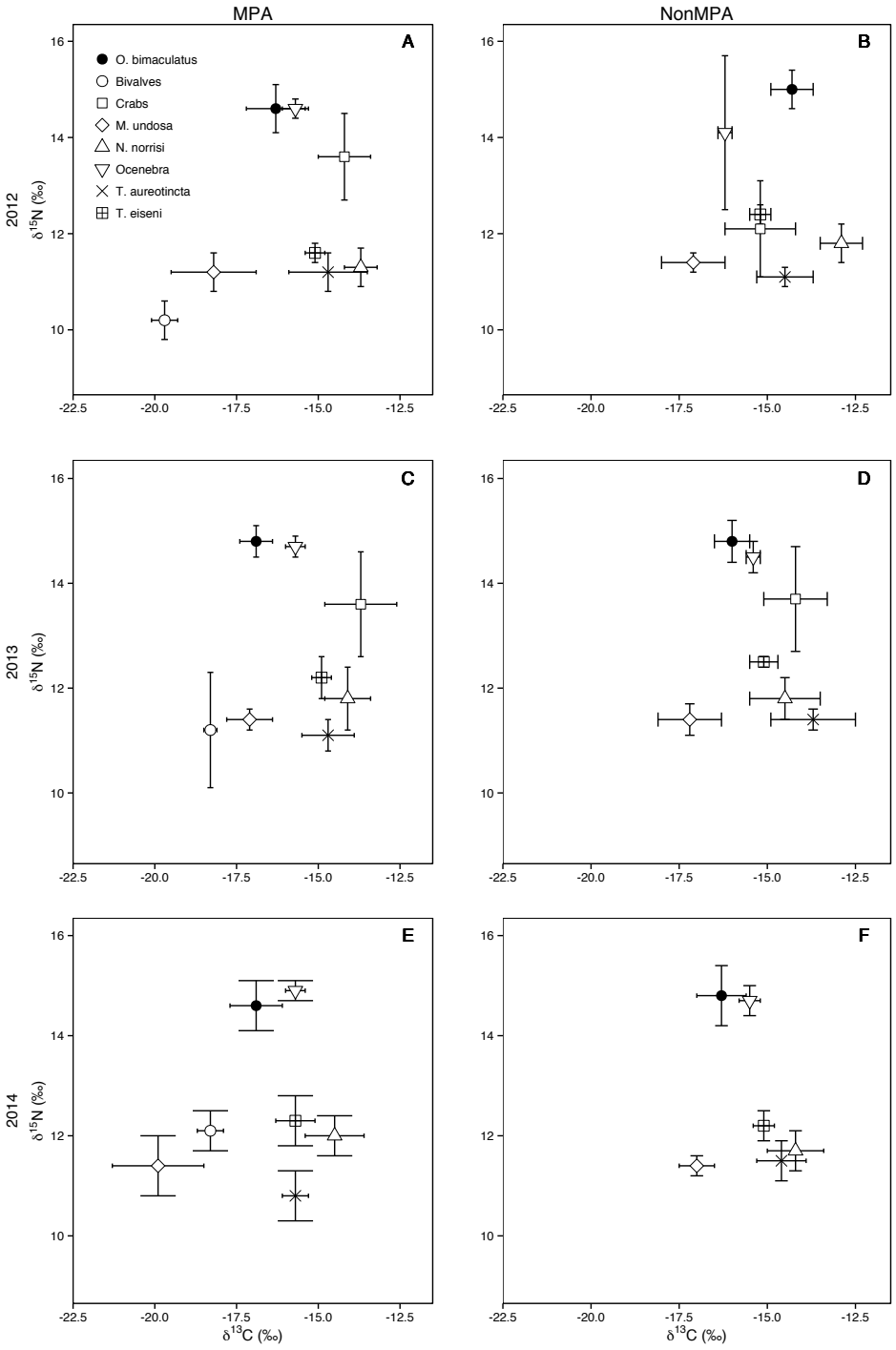

Figure 4.1. Graphic representation of mean (± SD) $\delta^{13}C$ vs. $\delta^{15}N$ values of octopuses and their potential prey items, uncorrected for trophic fractionation. MPA graphs represent the full breadth of sampled prey items. NonMPA graphs do not include bivalves. The predatory snail, *Ocenebra* sp., has a similar $\delta^{15}N$ value as the octopuses, consistent with predictions based on their carnivorous diet. Crabs have a $\delta^{15}N$ value that fall in between the carnivores (octopuses and *Ocenebra* sp.) and algae-eating snails, consistent with predictions based on their omnivorous diet.

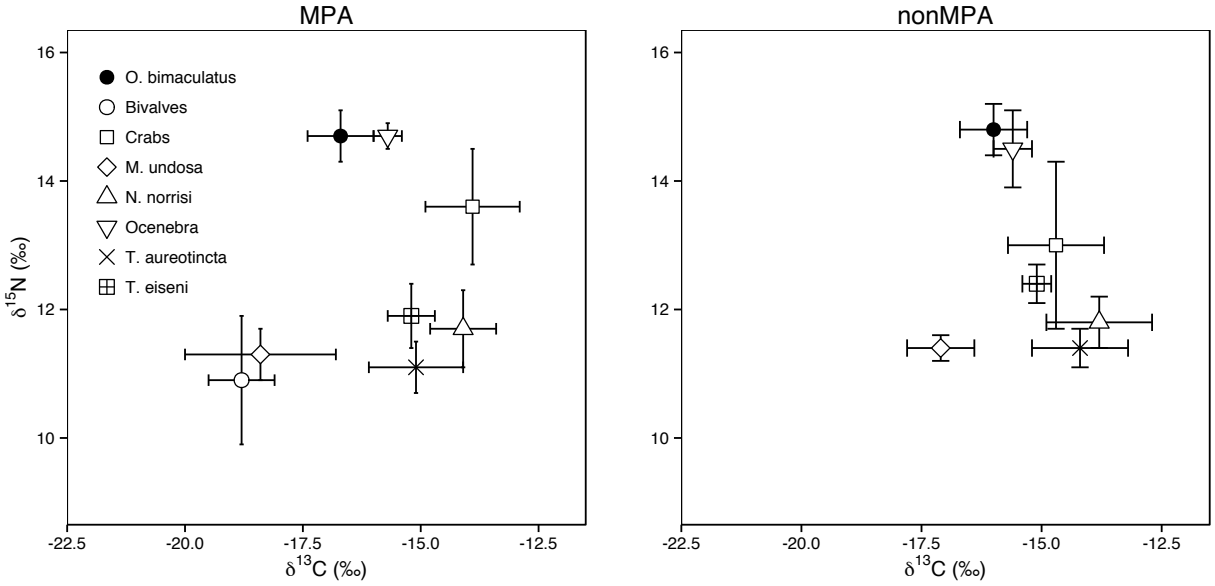

Figure 4.2. Graphic representation of mean (± SD) $\delta^{13}C$ vs. $\delta^{15}N$ values of octopuses and their potential prey items, uncorrected for trophic fractionation, for all years combined. MPA graphs represent the full breadth of sampled prey items. NonMPA graphs do not include bivalves. The predatory snail, *Ocenebra* sp., has a similar $\delta^{15}N$ value as the octopuses, consistent with predictions based on their carnivorous diet. Crabs have a $\delta^{15}N$ value that fall in between the carnivores (octopuses and *Ocenebra* sp.) and algae-eating snails, consistent with predictions based on their omnivorous diet.

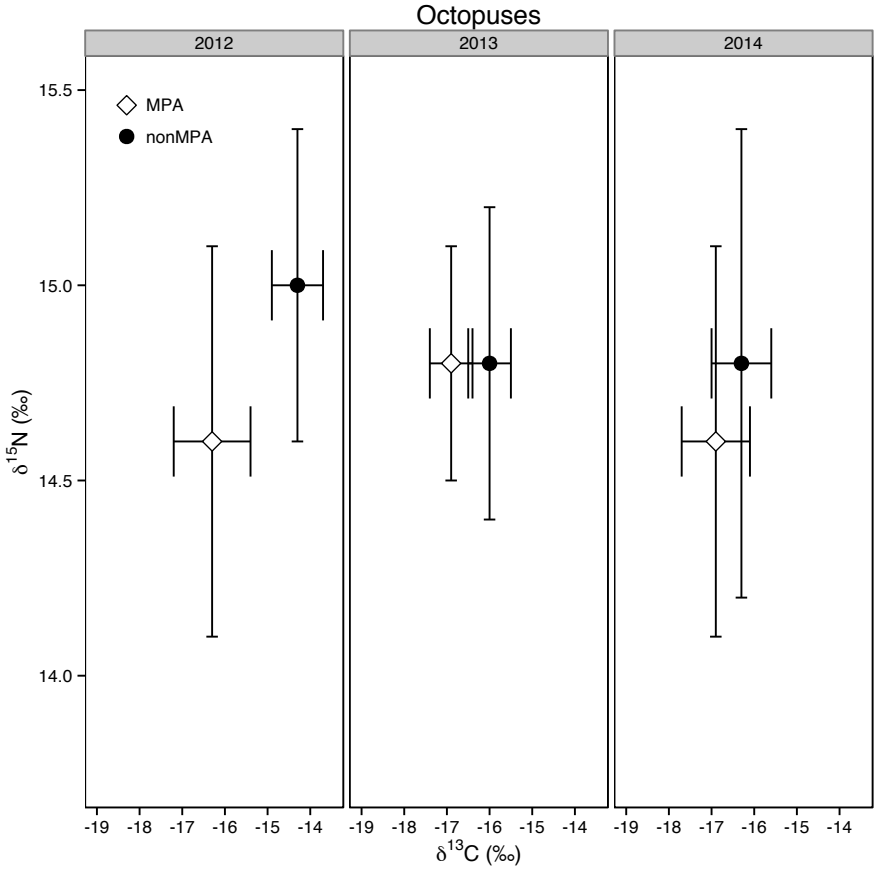

Figure 4.3. Graphic representation of mean (± SD) $\delta^{13}C$ vs. $\delta^{15}N$ values of MPA and nonMPA octopuses per year. The isotopic space inhabited by MPA and nonMPA octopuses were significantly different in 2012 and 2013, but not 2014.

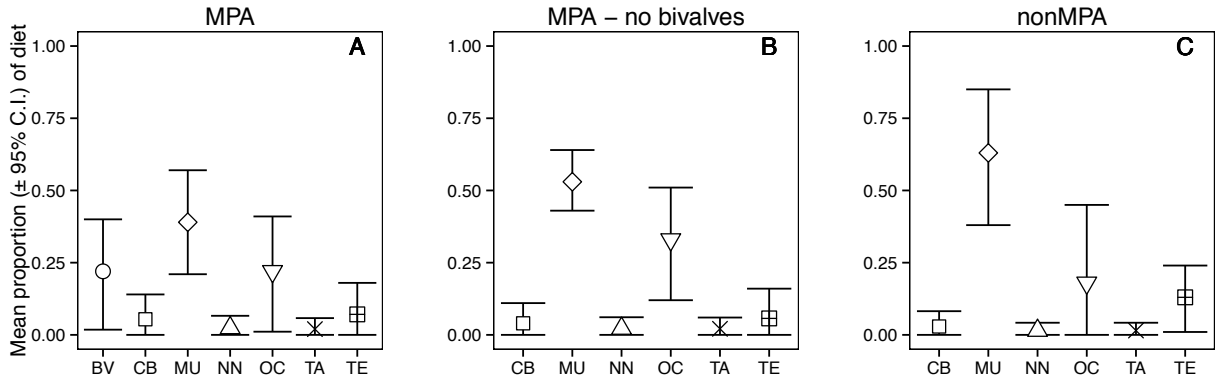

Figure 4.4. Mean proportional contributions of each prey item to *O. bimaculatus*'s diet (± Bayesian 95% C.I., n values listed in Table 2) from the Bayesian mixing model analysis. Symbols correspond to the diet items listed on the x-axes. The prey abbreviations are BV = bivalves; CB = crabs; MU = *Megastraea undosa*; NN = *Norrisia norrisii*; OC = *Ocenebra* sp.; TA = *Tegula aureotincta*; and TE = *Tegula eiseni.*

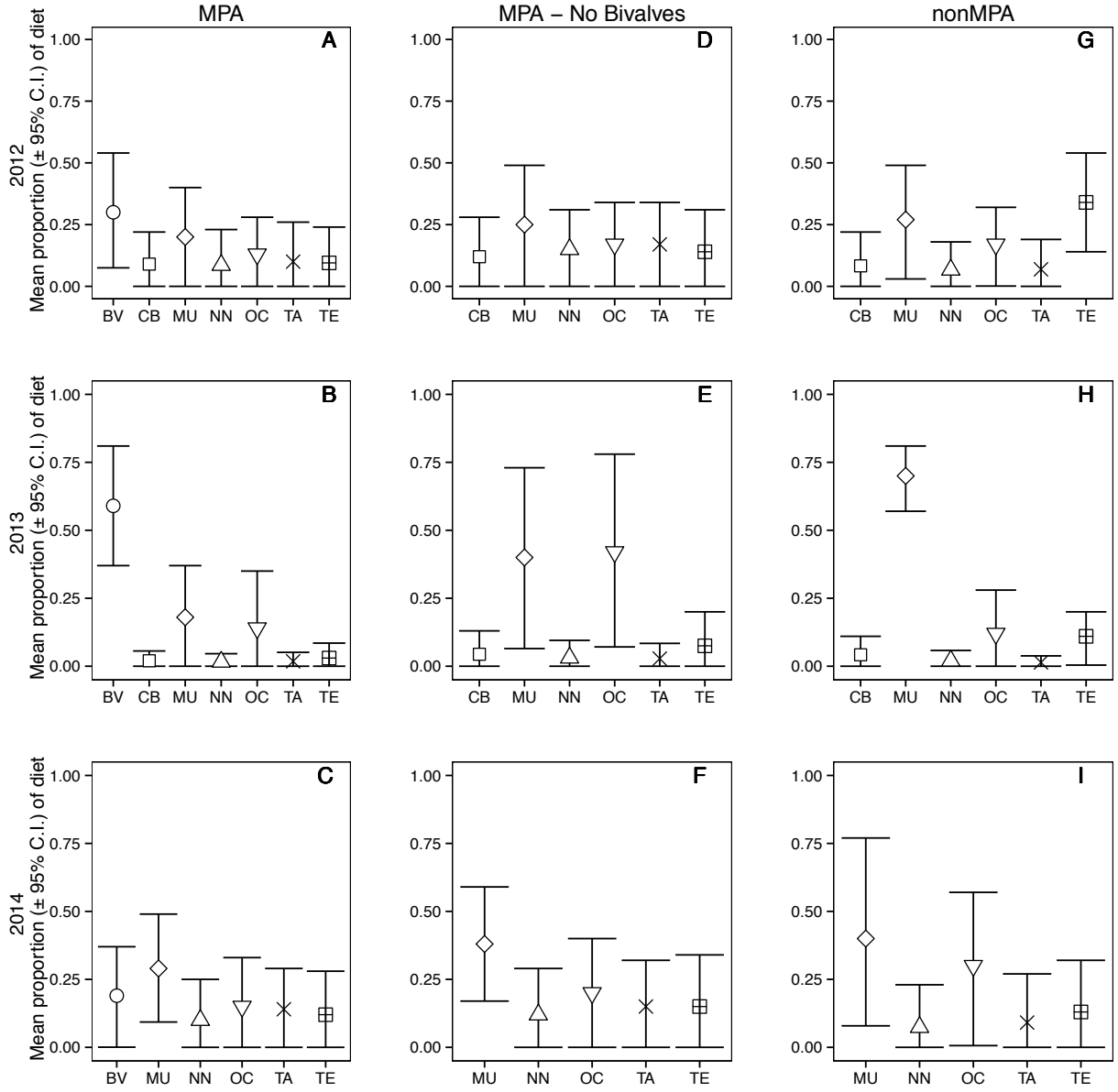

Figure 4.5. Mean proportional contributions of each prey item to *O. bimaculatus*'s diet (± Bayesian 95% C.I., n values listed in Table 2) from the Bayesian mixing model analysis. Symbols correspond to the diet items listed on the x-axes. Graphs A-C represent the diet of MPA octopuses with all prey items included. Graphs D-F represent the diet of MPA octopuses with bivalves excluded from the analysis. Graphs G-I represent the diet of nonMPA octopuses. The prey abbreviations are BV = bivalves; CB = crabs; MU = *Megastraea undosa*; NN = *Norrisia norrisii*; OC = *Ocenebra* sp.; TA = *Tegula aureotincta*; and TE = *Tegula eiseni*.

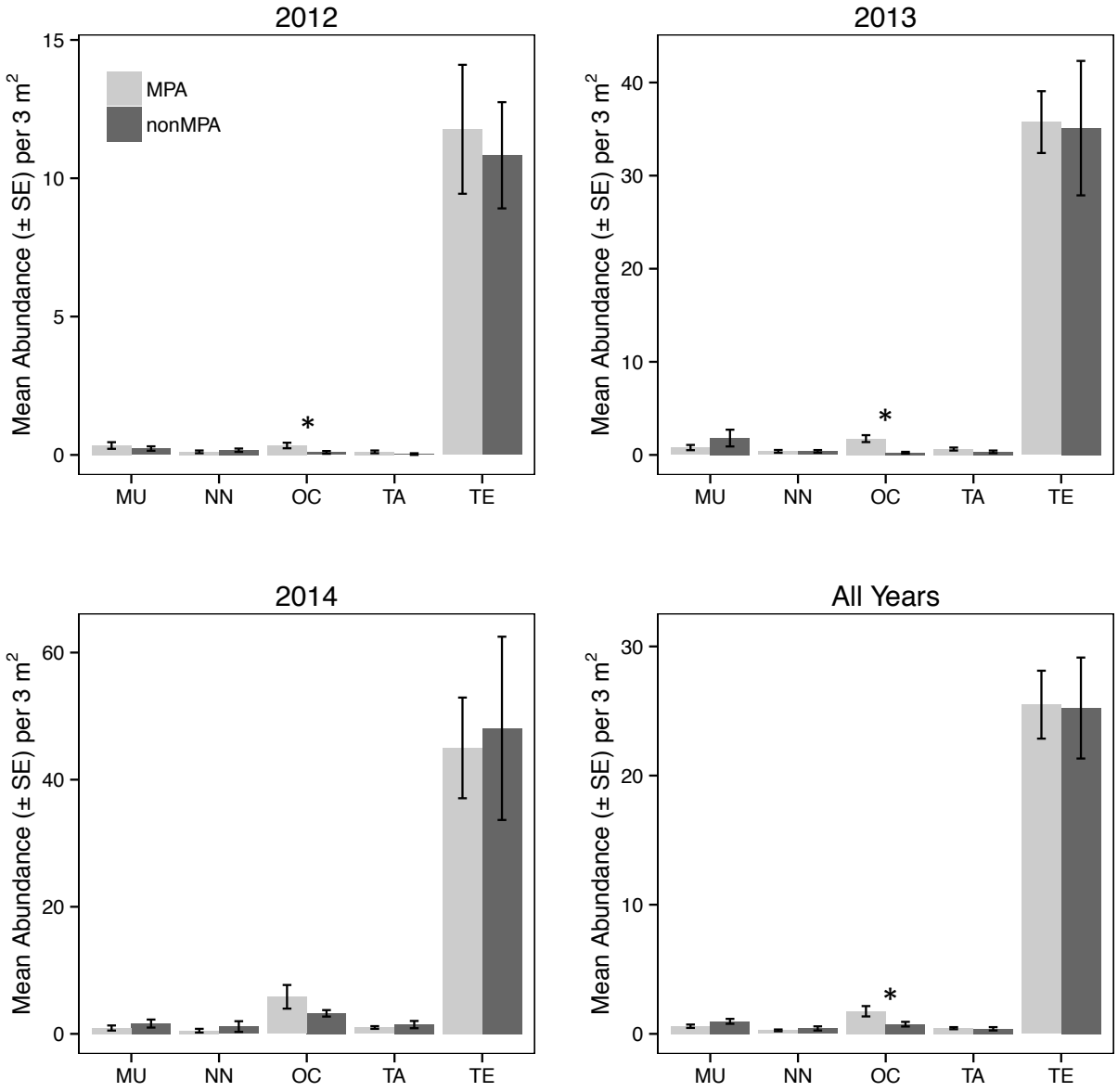

Figure 4.6. Mean (± SE) abundance of snail prey species per 3 m^2 by year and all years combined. Y-axes are not equivalent. *T. eiseni* was the most abundant species in all years and all areas. The prey abbreviations are MU = *Megastraea undosa*; NN = *Norrisia norrisii*; OC = *Ocenebra* sp.; TA = *Tegula aureotincta*; and TE = *Tegula eiseni.* Asterisks indicate significance where * < 0.05, ** < 0.001, and *** < 0.0001.

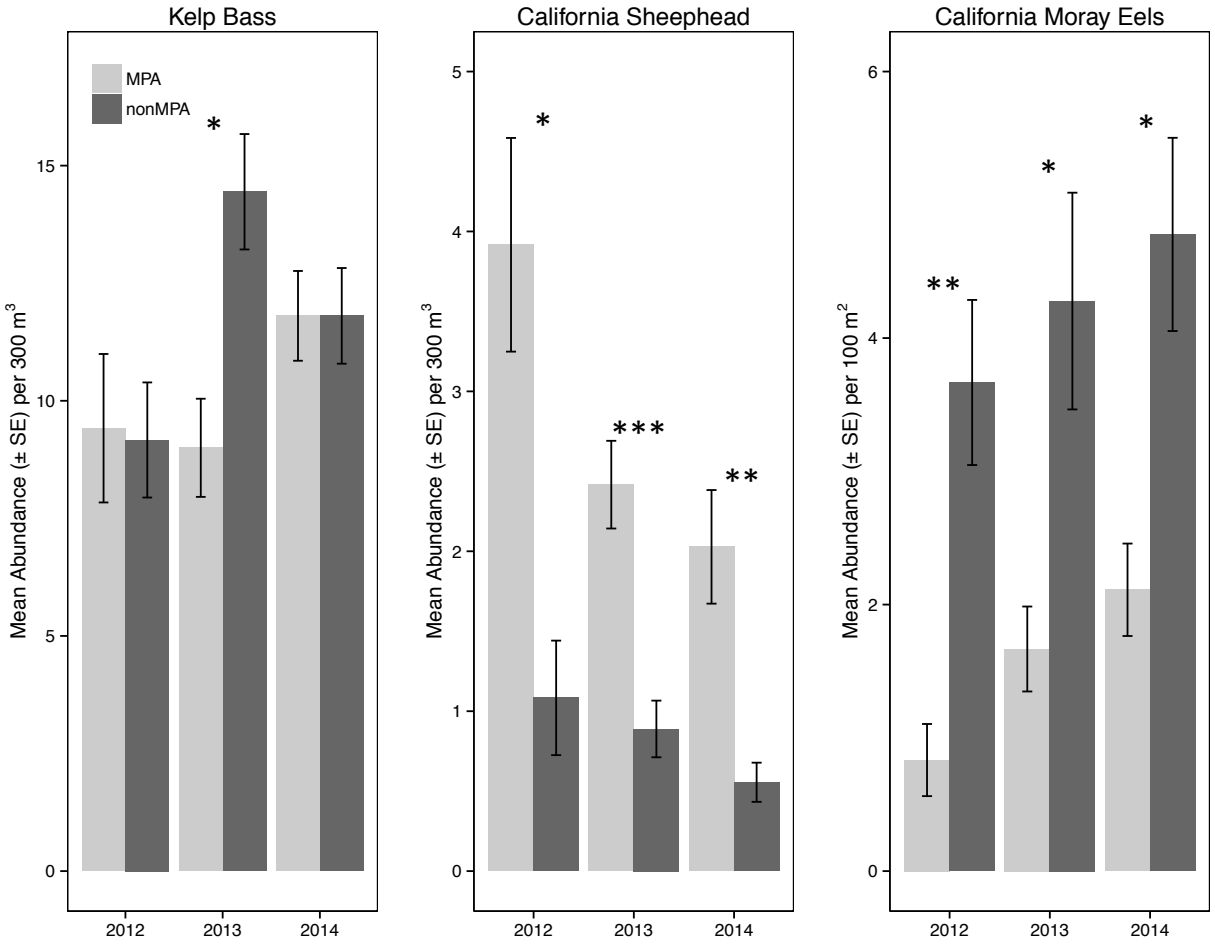

Figure 4.7. Mean (± SE) abundance of selected predatory fish species per 300 m^3 for kelp bass (*Paralabrax clathratus*) and California sheephead (*Semicossyphus pulcher*) and by 100 m^2 for California moray eels (*Gymnothorax mordax*). Asterisks indicate significance where * < 0.05, ** < 0.001, and *** < 0.0001.

CHAPTER 5

Conclusions

This dissertation investigated the abundance patterns, movement, and foraging ecology of the California two spot octopus, *Octopus bimaculatus*, around Santa Catalina Island, CA. Observed patterns of abundance could not be adequately explained by any biotic or abiotic variable measured in these studies (Chapter 2), suggesting that 1) the chosen variables are not important in driving *O. bimaculatus* abundance, 2) these variables interact in a way that cannot be explained by the data in order to produce the observed patterns, 3) there are other, unmeasured variables that explain the data, or 4) octopuses abundance and small-scale distribution is either so heterogeneous or random that it cannot be explained or predicted. *O. bimaculatus* was found to be a highly mobile octopus (Chapter 3), which contradicts earlier research on this species (Ambrose 1982). This change could indicate that either *O. bimaculatus* has exhibited a shift in behavior, possibly in response to environmental changes, or that earlier work did not adequately quantify movement. This finding has implications for our understanding of the strength and impact this species can have on prey communities; namely, this species of octopus could have a much greater predatory impact than anticipated. Finally, *O. bimaculatus* has a highly variable and diverse diet that differs interannually and between octopuses found in relatively close, but discrete, areas (Chapter 4). This population had different dietary compositions depending on whether individuals were found inside or outside of a marine protected area (MPA), which implies that there are broader, more indirect impacts that alterations to the marine environment can have on organisms (Babcock et al. 2010). This difference is likely tied to the behavioral and dietary flexibility of octopuses, which could indicate subtle, far-reaching changes in marine communities (Rodhouse and Nigmatullin 1996, Mather et al. 2014). Taken together, the results highlight the complexity of octopus behavior, community interactions, and environmental drivers that interact to produce observable patterns.

These results are consistent with what is known about the complexity and seeming unpredictability of octopus behavior and ecology (Hanlon and Messenger 1996, Grasso and Basil 2009). A primary goal of this work was to examine and identify biotic variables influencing octopus behavior in the field, with the ultimate goal of building a working model to explain and identify the important predictors of octopus behavioral choice. This research was completed on a small enough spatial scale to eliminate most abiotic and large oceanographic factors as confounding variables. We know that these larger scale processes affect octopuses on a population and regional and global scale (Boyle and Boletzky 1996, Rodhouse et al. 2014). Many of these abiotic factors, like temperature, salinity, and currents, can affect octopus prey or predator availability or density, but we don't understand which factors an individual octopus uses to make decisions given the frequency and types of interactions it has with predators, prey, and conspecifics. In addition to abiotic pressures, the life history of a generation of octopuses like *O. bimaculatus* can have effects not apparent until that cohort has reached adulthood. The drivers of octopus settlement are for the most part unknown, so a great deal of their abundance and small scale variation in distribution could be attributed to pressures on paralarval or newly settled octopuses that are difficult to measure (Robin et al. 2014).

Two octopuses in identical functional contexts will likely not behave in the exact same way. As organisms with advanced cognitive abilities, they can apply past knowledge to adapt their behavior to a particular context, and then learn from the results of this behavior to inform future decisions (Mather and Anderson 1993, Mather 1995, Sinn et al. 2010). These unique cognitive

abilities of octopuses have been thoroughly documented, but the selective pressures leading the evolution of such advanced behaviors are unclear (Packard 1972, Aronson 1991). There are many components of octopus behavior and ecology left to examine and quantify on many different scales, regarding their development during ontogeny, to their behavior as mature individuals, and their population dynamics, abundances, and distributions. Broad generalizations generally fail to provide useful information about octopuses, so understanding the importance of these individual actions and decisions requires a synthesis of all these components.

Octopuses likely play a key role in how communities and ecosystems as a whole respond to these changes, particularly as a mid-trophic predator. Many other organisms have relatively simple and predictable relationships; in fact, much of our conservation and monitoring efforts depend upon the predictably of the ecosystem and animal populations within them (Crowder and Norse 2008). The findings of this dissertation have shown that these assumptions do not uniformly apply to all octopuses. Continuing to integrate different inputs to octopus behavior, like environmental conditions and learning from past experiences, to examine like diet, movement, distribution, and abundance, will improve the way we think about the evolution of behaviorally complex animals like ourselves.

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